CARLOS HENRIQUE GOULART DOS REIS

MODIFICATIONS OF GAS EXCHANGE, CHLOROPHYLL FLUORESCENCE, GROWTH, AND LEAF ANATOMY OF *Typha domingensis* PERS. UNDER ULTRAVIOLET-ENRICHED ENVIRONMENT

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Dissertação apresentada à Universidade Federal de Lavras, como parte das exigências do Programa de Pós-graduação em Botânica Aplicada, área de concentração em Botânica Aplicada, para a obtenção do título de Mestre.

Prof. Dr. Fabrício José Pereira
Orientador

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Aos meus familiares e amigos,

Por todo apoio ao longo desse caminho.

Dedico.

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RESUMO

Typha domingensis Pers. (taboa) é uma planta aquática com grande capacidade de crescimento e tolerância a uma variedade de estressores. No entanto, os efeitos da radiação ultravioleta (UV) no crescimento e desenvolvimento em *T. domingensis* ainda não foram estudados. Além disso, um aumento na radiação UV é esperado como consequência das mudanças climáticas, podendo favorecer *T. domingensis* na competição com outras espécies. O objetivo foi avaliar o efeito da radiação UV no crescimento, fotossíntese, anatomia e bioquímica de *T. domingensis* ao longo do eixo foliar. Indivíduos foram coletados e propagados para obtenção de clones viáveis ao experimento. Os clones foram submetidos às seguintes condições de radiação UV: sem sombra (US), rede sombreada (SN), estufa (GH) e estufa mais suplementação UV (GH+UV). Realizamos uma Anava bidirecional completamente randomizada para analisar os efeitos da interação entre radiação UV x posição foliar (meio e ápice). Foram avaliados crescimento, trocas gasosas foliares, fluorescência da clorofila, anatomia, conteúdos de antocianinas e de clorofila. A radiação UV compromete os estágios fotoquímicos e bioquímicos em *T. domingensis*. A maior intensidade UV (US) reduz o crescimento de *T. domingensis*, mas aumenta a produção clonal, sugerindo um mecanismo de defesa ao UV pelo aumento de crescimento populacional e autossombreamento. Além disso, o ápice foliar de *T. domingensis* apresenta maior fotossíntese em comparação ao meio, e suas folhas produzem antocianinas como um mecanismo de defesa UV devido à ausência de características anatômicas de defesa relevantes. Portanto, nossos resultados indicam que *T. domingensis* é uma espécie parcialmente tolerante ao UV.

Palavras-chave: taboa; radiação ultravioleta; tolerância; planta aquática; espécie invasiva.

ABSTRACT

Typha domingensis Pers. (cattail) is an aquatic plant presenting high growth capacity and tolerance to a variety of environmental stressors. However, effects of ultraviolet (UV) radiation on growth and development have not yet been explored for *T. domingensis*. Furthermore, an increase in UV radiation is expected as a consequence of climate change, which may favor *T. domingensis* in competition with other species. This work aimed to evaluate the effect of UV radiation on the growth, photosynthesis, anatomy, and biochemistry of *T. domingensis* depending on leaf position. Individuals were collected and propagated to obtain viable clones for the experiment. The clones were subjected to the following UV radiation conditions: unshaded (US), shaded net (SN), greenhouse (GH) and greenhouse plus UV supplementation (GH+UV). We performed a completely randomized two-way Anova to analyze the effects of the interaction between UV radiation x leaf position (leaf apex (LA) and leaf middle part (LM)). Growth, leaf gas exchange, chlorophyll fluorescence, anatomy, and anthocyanins and chlorophyll contents were evaluated. UV radiation compromises both photochemical and biochemical stages of *T. domingensis*. The highest UV intensity (US) reduces *T. domingensis* growth but increases its clone production, suggesting an UV-defense mechanism by enhancing population growth and self-shading. Moreover, the leaf apex of *T. domingensis* presents higher photosynthesis compared to the middle part, and *T. domingensis* leaves produce anthocyanins as a UV-defense mechanism due to absence of relevant anatomical defense traits. Therefore, our results indicate that *T. domingensis* is partially an UV-tolerant species.

Keywords: *Typha domingensis* Pers.; ultraviolet radiation; tolerance; aquatic plant; invasive species.

INDICADORES DE IMPACTO

Typha domingensis é uma planta aquática com alto crescimento vegetativo e rápida colonização, o que pode impactar ecossistemas aquáticos. A espécie é até certo ponto tolerante a uma variedade de estressores ambientais, como seca, alta densidade populacional, elementos potencialmente tóxicos e poluentes orgânicos. *T. domingensis* é importante para ambientes aquáticos como fonte de abrigo e alimento para animais, para ciclagem de nutrientes e em processos de fitorremediação. Além disso, para atividades humanas, tem usos medicinais, alimentícios e têxteis. No entanto, seu crescimento intensivo leva à redução da biodiversidade, interrompe a navegação fluvial e impacta reservatórios de água doce. Além disso, espera-se um aumento na radiação UV como consequência das mudanças climáticas, e isso pode beneficiar *T. domingensis* na competição com espécies sensíveis a radiação UV se for tolerante. Portanto, é importante avaliar se *T. domingensis* é tolerante à radiação UV, uma vez que pode resultar em impactos para atividades humanas e prejudicar a biodiversidade; sendo importante para o manejo da espécie.

IMPACT INDICATORS

Typha domingensis is an aquatic plant with high vegetative growth and rapid colonization, which can impact aquatic ecosystems. The species is to some degree tolerant to a variety of environmental stressors, such as drought, high population density, potentially toxic elements, and organic pollutants. *T. domingensis* is important for aquatic environments as a source of shelter and food for animals, for nutrient cycling and in phytoremediation processes. In addition, for human activities, it has medicinal, food, and textile uses. However, its intensive growth leads to a reduction in biodiversity, disrupts river navigation and impacts freshwater reservoirs. Furthermore, an increase in UV radiation is expected as a consequence of climate change, and this may benefit *T. domingensis* in competition with UV-sensitive species if it is tolerant. Therefore, it is important to evaluate whether *T. domingensis* is tolerant to UV radiation, since it can result in impacts on human activities and harm biodiversity; being important for the management of the species.

SUMÁRIO

PRIMEIRA PARTE

1 INTRODUÇÃO

Typha domingensis Pers. (taboa) é uma planta aquática com grande capacidade de crescimento e colonização. A espécie cresce enraizada em solo alagado com suas folhas eretas emergindo da superfície da água com até 3 m de altura. Além disso, *T. domingensis* é importante para os ambientes aquáticos devido seu papel na ciclagem de nutrientes, fonte de abrigo e alimento para animais, local de deposição de ovos, além de atuar na manutenção de bordas de margens de rios impedindo a erosão. Contudo, devido seu aspecto de colonização intensiva e propagação por meio de brotamentos de novos clones, *T. domingensis* pode ser caracterizada como uma planta invasiva. Dessa forma, leva a formação de grandes adensamentos que impactam na redução de biodiversidade local como também compromete as atividades humanas como no uso de recursos hídricos (navegação fluvial, pesca e comprometimento de reservatórios).

Trabalhos já demonstraram a capacidade de *T. domingensis* de tolerar diversos fatores de estresse como seca, elementos potencialmente tóxicos, eutrofização, sombreamento e adensamento populacional. Assim, entender os mecanismos de tolerância da espécie a diferentes fatores é fundamental para criar estratégias de controle e manejo eficientes.

Devido às mudanças climáticas é esperado um aumento na incidência de radiação ultravioleta (UV) nas baixas latitudes principalmente relacionado à variação na formação de nuvens e presença de aerossóis. O ultravioleta é uma região do espectro eletromagnético que, devido sua natureza energética, tem a capacidade de danificar estruturas biológicas como membranas e o material genético. As plantas desenvolveram mecanismos para lidar com essa radiação ao longo do processo evolutivo, como desenvolvimento de tricomas, espessamento de cutícula e de epiderme, além de produção de compostos do metabolismo secundário responsáveis por absorver o UV, impedindo a danificação dos demais tecidos, bem como ativação do sistema antioxidante.

Dessa forma, é importante entender se *T. domingensis* é tolerante ao UV, e se essa tolerância poderá ser mais um fator para a espécie que possa lhe conferir maior capacidade de competição com outras espécies sensíveis ao UV. O objetivo do trabalho foi avaliar os efeitos da radiação UV no crescimento, fotossíntese, anatomia e bioquímica de *T. domingensis*.

2 REFERENCIAL TEÓRICO

2.1 Macrófitas Aquáticas

As macrófitas aquáticas são plantas que desenvolveram a capacidade de crescer em ambiente aquático, variando entre grupos que apresentam hábitos de vida distintos quanto à posição na coluna de água (emersas, flutuantes, submersas) ou variações quanto estar fixada ou não ao solo, dentre outros fatores. Além disso, ocorrem em diferentes tipos de ambientes aquáticos, como lagos, rios, reservatórios, pântanos e áreas próximas de salinas ou mesmo sob cavas de minas desativadas (Pompêo, 2017).

Devido à grande ocorrência de plantas aquáticas nesses ambientes, são capazes de contribuir significativamente para acúmulo de biomassa do meio, atuando na ciclagem de nutrientes, servindo de fonte de alimento para organismos diversos, local de deposição de ovos e abrigo, bem como atuar como fitorremediadoras em áreas poluídas (Pompêo, 2017). Embora as macrófitas aquáticas não devam ser encaradas como daninhas *a priori*, seu excessivo crescimento pode acarretar prejuízos à biodiversidade local, alteração de características físico-químicas de corpos d'água e limitação do uso de recursos hídricos em atividades humanas como navegação fluvial ou abastecimento de água (Pompêo, 2017). Nesse sentido, muitas vezes são adotadas estratégias de controle e manejo, de modo a diminuir ou erradicar algumas espécies invasoras (Hussner *et al*., 2017).

2.2 *Typha domingensis* Pers.

A espécie nativa *Typha domingensis* (taboa) é representante da família Typhaceae, uma macrófita aquática emergente, que apresenta suas folhas afiladas dispostas de maneira ereta para fora da lâmina d'água e rizoma enraizado em solo submerso (Sesin *et al*., 2021). A planta pode alcançar até 3 m de altura e possui crescimento vigoroso por meio de brotações laterais e emissão de novos rizomas formando adensamentos (Sesin *et al*., 2021). É uma espécie cosmopolita presente em todos os domínios fitogeográficos brasileiros (Paiva *et al*., 2024; Pott e Pott, 2000). Sua morfologia foliar é caracterizada pela presença de grandes câmaras de aerênquima e por uma resistência mecânica conferida pelas fibras esclerenquimáticas arranjadas entre células de parênquima paliçádico e cordões não esclerenquimáticos ancorados nas trabéculas do aerênquima (Liu *et al*., 2018).

Typha domingensis apresenta tolerância a diferentes fatores ambientais, como seca (Cruz *et al*., 2019; Cruz *et al*., 2020), elementos potencialmente tóxicos (Oliveira *et al*., 2018; Oliveira *et al*., 2022; Silva 2014) e compostos tóxicos derivados de enxofre (Li *et al*., 2009). Além disso, em condições de alto adensamento populacional, a espécie promove modificações em sua morfologia foliar em resposta ao auto sombreamento, levando a maior capacidade fotossintética (Scarpa *et al*., 2021). Dadas essas características, *T. domingensis* apresenta grande capacidade de crescimento vegetativo, potencialmente levando a colonização de extensas áreas de forma descontrolada e prejudicando a estabilidade dos organismos aquáticos e atividades humanas (Bansal *et al*., 2019; Miao *et al*., 2000).

Contudo, *T. domingensis* é benéfica para o ambiente aquático, atuando na ciclagem de nutrientes (Su *et al*., 2015), fitorremediação de poluentes e elementos tóxicos (Delgado-Gonzáles *et al*., 2021; Hadad *et al*., 2006; Hegazy *et al*., 2011; López-Chávez *et al*., 2021), bem como fonte de alimento e abrigo para a biota local (Gonçalves *et al*., 2004; Maldonado e Voeks, 2021). Ademais, é incorporada na cultura humana através de seu uso medicinal (Akkol *et al*., 2011), produção de fibras têxteis e objetos (Maldonado e Voeks, 2021; Pandey *et al*., 2020), bem como alimentação não convencional (Arenas e Scarpa, 2003) e como modelo para estudos ecotoxicológicos (Sesin *et al*., 2021).

2.3 Exposição ao ultravioleta (UV)

A radiação ultravioleta compreende uma região do espectro eletromagnético com comprimentos de onda inferiores à 400 nm com maior energia que o visível (Rowland, 2006). Níveis de ultravioleta seguros a vida são mantidos a partir de sua atenuação na estratosfera através da camada de ozônio (Rowland, 2006). Maior atenção aos efeitos do ultravioleta foi direcionada quando a comunidade científica relatou os efeitos nocivos de substâncias CFCs (clorofluorcarbonos) sobre a camada de ozônio (Rowland, 2006). Embora novas políticas sobre o uso de substâncias CFCs tenham sido adotadas a partir do Protocolo de Montreal e houve redução do buraco na camada de ozônio sobre a Antártica (Rowland, 2006), ainda ocorrem episódios de redução de ozônio estratosférico sobre o ártico (Neale *et al*., 2021). Esta depleção do ozônio em altas latitudes se correlaciona com maior incidência de radiação ultravioleta nestes locais (Neale *et al*., 2021); contudo, nas latitudes médias a mudança está relacionada às variações nas nuvens, aerossóis e refletividade da superfície terrestre (Neale *et al*., 2021). Além disso, modelos recentes indicam um aumento na radiação ultravioleta nos

trópicos, esperado para a segunda metade do século XXI, como resultado de mudanças climáticas (Neale *et al*., 2021).

Como consequência, algumas espécies adaptaram mecanismos de tolerância ao longo da evolução, como produção de pigmentos fotoprotetores que evitam danos no aparato fotossintético e ao material genético (Neale *et al*., 2021). Plantas heliófitas têm melhores respostas de aclimatização ao ultravioleta do que em outros espectros da radiação solar quando comparadas às espécies de sombra com menor plasticidade fenotípica (Neale *et al*., 2021). Considerando as mudanças climáticas com potencial para aumento do ultravioleta, esse cenário pode ser um fator crucial para redução de biodiversidade de espécies não tolerantes (Neale *et al*., 2021). Além disso, o ultravioleta afeta os ecossistemas de forma direta no processo de fotodegradação de matéria orgânica ou indiretamente pela foto-facilitação, resultando na liberação de CO_2 e contribuindo para as mudanças climáticas (Ballaré *et al*., 2011; Neale *et al*., 2021).

Em condições naturais, a exposição ao ultravioleta leva a uma redução na produção de biomassa devido à redução da área foliar que, de acordo com Ballaré *et al*. (2011), um aumento de 10% no UV leva a uma redução de 3 % na biomassa das plantas. Além disso, Neugart e Schreiner (2018) relatam diminuição de fotossíntese líquida em condições de elevada exposição ao ultravioleta, bem como redução de clorofila. Enquanto isso, o trabalho de Romanatti *et al*. (2019) evidencia os efeitos deletérios do ultravioleta na fotossíntese de *Solanum melongena* L., relacionados a má formação de tecidos fotossintéticos com redução na fotossíntese; essa última passou a ocorrer principalmente no parênquima esponjoso pois o parênquima paliçádico foi deformado pelo UV e atuou apenas como proteção física contra o ultravioleta.

Além disso, a exposição ao ultravioleta desencadeia cascatas de sinalização celular que levam a produção de compostos metabólicos de proteção, como compostos fotoprotetores, além de mudanças no sistema antioxidante e o estímulo de mecanismos de reparo do DNA (Ballaré *et al*., 2011; Jansen *et al*., 1998; Neugart e Schreiner, 2018; Romanatti *et al*., 2019). Dependendo das características das espécies e de outros fatores de estresse, o UV pode impor limites à sobrevivência das plantas (Ballaré *et al*., 2011).

Em *T. domingensis* não há relatos na literatura para os efeitos da sua exposição ao ultravioleta, sendo encontrado apenas o trabalho de Xu *et al*. (2014) que testou métodos construtivos de "*constructed wetland*" (zona húmida construída) e exposição ao ultravioleta em *T. angustifolia* para avaliação do sistema antioxidante e conteúdo de clorofila. Contudo, há indícios indiretos de que modificações observadas na fisiologia, morfologia e anatomia de

T. domingensis cultivadas em condições de sombreamento (Reis *et al*., 2024) possam estar relacionadas a maior intensidade de UV em condições de pleno sol. Nesse contexto, entender o crescimento de *Typha domingensis* em resposta à exposição de ultravioleta é essencial para acessar a dinâmica de sua população de forma mais holística, tendo em vista seu potencial efeito invasivo e de tolerância a fatores estressores, em um cenário com mudanças climáticas.

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SEGUNDA PARTE – ARTIGO

ARTIGO - Is Cattail Uv-Tolerant? - Response based in growth, photosynthesis, anthocyanin production, and anatomical traits along the leaf axis

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Is Cattail UV-tolerant? - Response based on growth, photosynthesis, anthocyanin production, and anatomical traits along the leaf axis

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Ecology/Ecophysiology/Environmental Biology

ABSTRACT

Typha domingensis Pers. (cattail) is an aquatic plant presenting high growth capacity and tolerance to various environmental stressors. However, the effects of ultraviolet (UV) radiation on growth and development have not yet been explored for *T. domingensis*. Furthermore, increased UV radiation is expected due to climate change, which may favor *T. domingensis* in competition with other species. This work aimed to evaluate the effect of UV radiation on the growth, photosynthesis, anatomy, and biochemistry of *T. domingensis* depending on leaf position. The clones were subjected to the following conditions: unshaded (US), shaded net (SN), greenhouse (GH), and greenhouse plus UV supplementation (GH+UV). We performed a completely randomized two-way ANOVA to analyze the interaction effects between UV radiation x leaf position (leaf apex and middle parts). Growth, leaf gas exchange, chlorophyll fluorescence, anatomy, anthocyanin, and chlorophyll were evaluated. UV radiation damaged both the photochemical and biochemical stages of *T. domingensis*. The highest UV intensity (US) reduced *T. domingensis* dry mass but increased its clone production, suggesting a UV-defense mechanism by enhancing population growth and self-shading. Moreover, the leaf apex of *T. domingensis* showed higher photosynthesis compared to its middle part. *T. domingensis* leaves synthesize anthocyanins as a UV-defense mechanism due to the absence of relevant anatomical defense traits. Therefore, our results indicate that *T. domingensis* is a UV-tolerant species although some degree of damage is found to its photosynthetic system.

Keywords: *Typha domingensis* Pers., ultraviolet radiation, stress tolerance, aquatic plants, invasive species

Introduction

Typha domingensis Pers. (cattail) is a native aquatic plant with a rhizome rooted in flooded sediment and an aerial part composed of leaves that emerge from the surface of the water (Sesin et al. 2021). *T. domingensis* is a cosmopolitan species representative of all Brazilian phytogeographic biomes (Paiva et al. 2025) being important to aquatic environments with several functions such as nutrient cycling (Su et al. 2015) and phytoremediation (Delgado-Gonzáles et al. 2021; López-Chávez et al. 2021). The species is also important for human activities being a source of natural fibers (Maldonado and Voeks 2021; Pandey et al. 2020). Nonetheless, the intensive population growth of *T. domingensis* can lead to socio-environmental problems (Bansal et al. 2019; Miao et al. 2000). *T. domingensis* shows tolerance to different stressors, such as drought (Cruz et al. 2020; Cruz et al. 2019), potentially toxic elements (Oliveira et al. 2022; Oliveira et al. 2018), shading (Reis et al. 2024), and high population density (Scarpa et al. 2021).

Ultraviolet (UV) radiation represents a bandwidth of the electromagnetic spectrum with wavelengths shorter than 400 nm (Rowland 2006) and is expected to increase as a consequence of climate change (Neale et al. 2021). UV radiation can damage the photosynthetic systems of plants if their protection mechanisms are insufficient (Neale et al. 2021; Romanatti et al. 2019). Furthermore, UV radiation can reduce photosynthesis (Neugart and Schreiner 2018), compromising plant growth and reducing their survival (Ballaré et al. 2011). Plants have evolved protective mechanisms to reduce UV-damage, including synthesis of flavonoids and anthocyanins that act as UV-absorbing pigments (Neale et al. 2021; Neugart and Schreiner 2018), anatomical modifications such as the presence of trichomes, thick cuticle and thickened epidermis (Bernado et al. 2021; Jordan et al. 2005), or by stimulating the antioxidant system (Xu et al. 2014).

There are no studies related to *T. domingensis* tolerance to UV. Even for the genus *Typha*, only one study with *T. angustifolia* is found (Xu et al. 2014). This work evaluated types of constructed wetlands where *T. angustifolia* plants were subjected to increased levels of UV radiation above ambient UV intensity causing a decrease in the chlorophyll content and increased activity of the antioxidant system (Xu et al. 2014). Reis et al. (2024) reported limitations in the growth and photosynthesis of *T. domingensis* grown in unshaded conditions

compared to 35% shading; raising the question of whether these limitations in unshaded conditions are related to UV. Moreover, it is important to investigate whether *T. domingensis* is a species tolerant to UV radiation, since it may benefit from competition with other species in a scenario of increased UV radiation increasing its invasive behavior.

To respond to these questions, we hypothesize that: *T. domingensis* is a UV-tolerant species but this radiation promotes negative effects on the growth, photosynthesis, and leaf anatomy of this aquatic plant. Thus, this study aimed to evaluate the effect of UV radiation on the growth, photosynthesis, anatomy, and biochemistry of *T. domingensis*.

Materials and methods

Plant material

Individuals of *T. domingensis* in the vegetative stage were collected from a natural population in the municipality of Alfenas, state of Minas Gerais, southeastern Brazil (21º25'15.54''S and 45º58'55.76''W). The plants were transported to the Federal University of Alfenas, washed in running water, and placed in 25 L trays containing 15 L of nutrient solution (Hoagland and Arnon, 1950) for initial propagation to obtain viable clones for the experiment. The plants were kept in a greenhouse, with daily water replenishment and the nutrient solution being replaced fortnightly. After 60 days, there were enough clones to run the study.

Experimental design

The climate data for the Alfenas region and the experimental environments are presented in Table 1. Data were obtained from a meteorological station close to the studied site (21°40'50.60''S and 45°56'39.89''W), covering the entire experimental period. According to the Köppen classification, the region's climate is humid subtropical and belongs to the Cwb climate group, with temperate summers and dry winters (Alvares et al. 2013).

The clones were standardized in the height (60 cm) and number of leaves (five), and individuals of *T. domingensis* were distributed to the following treatments: unshaded environment (US), and the shaded conditions 1) environment constructed with black polyethylene nets (SN), 2) environment inside a greenhouse (GH), and 3) environment inside

a greenhouse supplemented with ultraviolet lamps (GH+UV). The radiation spectrum of the ultraviolet lamps used comprises a region between 356 nm and 392 nm, with a peak at 370 nm (UVA). Two 8W UV lamps were installed on the open top of a wooden frame to provide supplemental UV inside the greenhouse. The wooden frame dimensions were 1.8 m in height, 1.0 m in width, and 1.2 m in length. The surface inside the wooden frame was covered with aluminum foil to reflect the radiation inside the structure. Additionally, a 46 W visible light lamp was installed to supplement the PAR radiation. The plants inside the GH+UV treatment were arranged to avoid self-shading and approximately 10 cm away from supplementary radiation lamps. The photoperiod established in the GH+UV environment was from 5:45 am to 17:45 pm.

Furthermore, additional climatic parameters were measured in the experimental environments using temperature and humidity sensors coupled to the portable modulated fluorometer model MINI-PAM-II (Walz, Germany) and radiation sensor of a spectroradiometer model SPR-4002 (Luzchem Research Inc., Ottawa, Canada) (Table 1). The radiation intensities from the studied environments were measured close to noon with a clear sky. For the analysis of radiation intensity, it was separated into photosynthetically active radiation (PAR) (400-700 nm), and ultraviolet (UV) (356-392 nm); in each case, the integrated values for each bandwidth range were shown (Table 1).

Table 1. Climatic data obtained from the National Institute of Meteorology (INMET) for the municipality of Alfenas and from a local measurement for the experimental environments

Variable	*Mean ± Standard deviation or absolute value*
Daily mean temperature (°C) *	20.31 ± 3.20
Maximum temperature (°C) *	27.09 ± 3.47
Minimum temperature (°C) *	14.28 ± 2.92
Accumulated rainfall (mm) *	0
Mean air relative humidity (%) *	52.44 ± 13.19
Mean temperature (°C) **	
US	20.71 ± 4.39
SN	21.64 ± 5.01
GH	25.21 ± 4.11
GH+UV	25.02 ± 3.70
Mean air relative humidity (%) **	

Variable	*Mean ± Standard deviation or absolute value*
US	60.29 ± 4.61
SN	62.64 ± 7.80
GH	64.53 ± 3.01
GH+UV	63.75 ± 4.50
Peak PAR radiation intensity (Wm^{-2}) **	
US	617.88
SN	263.91
GH	181.53
GH+UV	167.29
Peak UV radiation intensity (Wm^{-2}) **	
US	14.92
SN	8.38
GH	6.36
GH+UV	9.89

US, unshaded; SN, shaded net; GH, shading in greenhouse; GH+UV, shading in greenhouse plus UV bulb; PAR, photosynthetically active radiation; UV, ultraviolet. *In the municipality of Alfenas during the entire experimental period; **punctual measurements in the environments studied

The clones were placed in plastic pots containing 3 L of soil as substrate and then tap water was added to flooding level, forming a water layer 5 cm above the soil surface. The water was replaced daily. Each pot received a single individual *T. domingensis*. In the GH+UV treatment pots were placed over an adjustable structure that was moved downward to keep plants 10 cm away from UV lamps to compensate for the leaf vertical growth. The experimental design was a two-way ANOVA completely randomized with the following factors: environments (US, SN, GH, and GH+UV) and leaf parts being the leaf apex (LA) and leaf middle part (LM). Leaves were evaluated at the apex and middle parts because the former is closer to the UV lamps since the cattail shows vertically oriented leaves. Each environment received ten replicates, and each replicate consisted of a pot containing one clone (n = 40). The experimental period lasted 65 days.

Growth analysis

Throughout the experimental period, new clones produced in each pot were counted fortnightly. At the end of the experiment, all clones were collected and separated for further growth analyses. Then, the height of clones was measured with a tape measure considering the origin of the insertion of the leaves in the rhizome up to the apical end of the longest leaf. Subsequently, the clones were separated into rhizomes, roots, and leaves. First, fresh leaves were photographed over a black background and then the leaf area was measured using ImageJ software (Rasband 2018). Plant parts were oven-dried at 60°C for one week and the dry masses from vegetative organs were measured on an AY 220 scale (Shimadzu, Japan). The total dry mass was calculated by the sum of the dry mass of each organ.

Gas exchange analyses

The gas exchange analyses were evaluated using an infrared gas analyzer (IRGA) model LI-6400XT (LI-COR, Nebraska, USA) accoupled to a 3 x 2 cm LI-6400-02B chamber. The chamber was adjusted to provide a radiation intensity of red and blue lights of 1000 µmol photons m^{-2} s^{-1} and a pump flow of 500 µmol s^{-1}, the average leaf temperature and CO_2 (carbon dioxide) concentration were 25.97 °C and 353.67 µmol mol^{-1} air, respectively. Gas exchange analysis was performed fortnightly during the experimental period, totaling four evaluations from 8 to 11 am. Analyses were made on the apex and middle regions of the first fully expanded leaf. The following variables were evaluated: net photosynthesis, intercellular CO_2 concentration, stomatal conductance, and transpiration. These parameters were used to calculate the subsequent variables as follows: the water use efficiency is equal to the net photosynthesis divided by transpiration; the carboxylation efficiency is equal to the net photosynthesis divided by intercellular CO_2 concentration; and the quantum efficiency is equal to the net photosynthesis divided by radiation intensity fixed in the cuvette (1000 µmol photons m^{-2} s^{-1}).

Photochemical analysis

A portable modulated fluorometer MINI-PAM-II (Walz, Effeltrich, Germany) was used to measure the photochemical parameters. The effective photochemical yield of the photosystem II (ϕPSII) and the electron transport rate (ETR) were automatically calculated by the fluorometer according to the following: effective photochemical yield (ϕPSII) = (Fm’ – F)

/ Fm', where Fm' is equal to the maximum chlorophyll fluorescence in light-adapted leaves and F being the momentary fluorescence level of an illuminated sample just before the applied saturation pulse; and ETR = ϕPSII * PAR * 0.42, where PAR is the photosynthetically active radiation incident on the sample and the correction factor of 0.42 is related to the fraction of incident photons absorbed by the sample multiplied by the fraction of photons that activated the photosystem II. Measurements were performed on the first fully expanded leaf in the leaf apex and leaf middle parts. The analysis was performed fortnightly between 8 to 11 am.

Biochemical analyses

The total chlorophyll content was estimated using the portable chlorophyll meter model atLEAF CHL PLUS (atLEAF, Wilmington, USA) in the first fully expanded leaf of *T. domingensis* at the apical and middle regions of the leaf. Furthermore, at the end of the experiment, an analysis of anthocyanin content was performed in leaf fragments collected from the apical and middle regions. These fragments were covered with aluminum foil, frozen in liquid nitrogen, and stored in a -20 °C freezer for further analysis. For the quantification, was used a protocol (Fuleki and Francis 1968), where the 0.5 g fragments were added to a mortar, covered with liquid nitrogen, and quickly ground using a pestle. In sequence, 5 mL of an extracting solvent (ethanol and HCl in a proportion of 8.5:1.5, pH =1) was added and mixed. The mixture was reserved in a 4 °C refrigerator for 24 hours. Then, in a dark room, the extract was filtered and 2 mL was placed in a quartz cuvette for reading in a spectrophotometer at 535 nm. The leaf anthocyanin content was calculated as follows: ACN = ABSm / E, where ACN is leaf anthocyanin content, ABSm is the absorbance from the extract, and E is the extinction coefficient equal to 98.2. The absorbance from the extract (ABSm) is calculated according to the formula: ABSm = TABS * extraction volume / total mass used, where TABS is total absorbance, extraction volume is the 5 mL used, and the total mass is equal to 0.5 g used. Finally, the total absorbance (TABS) is calculated as follows: TABS = sample absorbance * extracting volume * dilution factor, where sample absorbance is the direct reading, the extracting volume is 5 mL, and the dilution factor is 1 since there was no dilution.

Leaf anatomical analysis

197 At the end of the experiment, leaf fragments were collected in the leaf apex and
198 middle regions and fixed in 70% ethanol from the first fully expanded leaf of one clone per
199 replicate. Transversal sections were performed in the fragments using steel blades and
200 clarified with 50% sodium hypochlorite (V V^{-1}) solution for ten minutes. Next, sections were
201 washed twice with distilled water for ten minutes each and stained with safrablau solution
202 (1% safranin m V^{-1} / 0.1% astra blue m V^{-1} in a proportion of 1:9). The sections were placed
203 over slides with 50% aqueous glycerol solution (V V^{-1}) and then covered with coverslips. One
204 slide and one field per leaf were evaluated. For this, a capture system coupled to a light
205 microscope model Eclipse S*i* (Nikon, Tokyo, Japan) was used. For the paradermal analysis,
206 the two leaf sides were covered with a thin layer of ethyl cyanoacrylate adhesive. After
207 drying, the adhesive was removed and mounted in slides. One slide from the adaxial and
208 abaxial sides was prepared for each leaf and one field was captured. The same image capture
209 system described for transversal sections was used. The ImageJ software (Rasband 2018) was
210 used to measure the following variables: epidermis thickness (from abaxial and adaxial sides),
211 palisade parenchyma thickness (from abaxial and adaxial sides), stomatal density (from
212 abaxial and adaxial sides) and total epidermal cell density (from abaxial and adaxial sides).
213 The stomatal density was calculated as the number of stomata per mm^2, and the total
214 epidermal cell density as the total epidermal cells per mm^2.

215

216 **Statistical analyses**

217 The data were subjected to the normality test of Shapiro-Wilk ($P < 0.05$) and then a
218 two-way ANOVA was performed, the means were compared according to the Scott-Knott test
219 or regression analysis for $P < 0.05$. The Sisvar 5.8 software was used for statistical analysis
220 (Ferreira 2011).

221

222 **Results**

223 The summarized ANOVA results for all the parameters analyzed are indicated in
224 Table 2. There was no interaction between environment and leaf position for all variables
225 analyzed (Table 2).

226 All plants remained alive until the end of the experiment. New clones were produced
227 under all environments during the experiment; however, the US environment promoted the

228 highest vegetative growth (Fig. 1a). US environment significantly reduced the dry mass, plant
229 height, and leaf area compared with other environments (Fig. 1b, 1c and 1d, respectively).

230 Table 2. Summarized ANOVA results for all variables analyzed.

Variable	*CV%*	*Mean square value*	*F test value*	*P-value*	*n*
Dry mass per individual	21.93	0.7364	3.03	0.0418	40
Plant height	15.73	877.462	7.603	0.0022	20
Leaf area per individual	20.5	41.5417	7.372	0.0006	40
Net photosynthesis (A)	22.26	2.6994	4.596	0.0036	320
Net photosynthesis (P)	22.26	5.0567	8.61	0.0036	320
Net photosynthesis (A*P)	22.26	0.0861	0.147	0.9329	320
Intercellular CO_2 concentration(A)	7.28	266.1492	170.786	<0.0001	320
Intercellular CO_2 concentration (P)	7.28	5.2489	3.368	0.0674	320
Intercellular CO_2 concentration (A*P)	7.28	0.2835	0.182	0.9096	320
Stomatal conductance (A)	25.69	1.1247	24.606	<0.0001	320
Stomatal conductance (P)	25.69	1.3026	28.499	<0.0001	320
Stomatal conductance (A*P)	25.69	0.0424	0.929	0.4269	320
Transpiration (A)	20.88	3.2103	8.288	<0.0001	320
Transpiration (P)	20.88	8.8902	22.952	<0.0001	320
Transpiration (A*P)	20.88	0.1828	0.472	0.7017	320
Water use efficiency (A)	17.21	0.2939	7.245	0.0001	320
Water use efficiency (P)	17.21	0.2952	7.276	0.0074	320
Water use efficiency (A*P)	17.21	0.0169	0.416	0.7414	320
Carboxylation efficiency (A)	20.83	0.0435	24.325	<0.0001	320
Carboxylation efficiency (P)	20.83	0.0117	6.527	0.0111	320
Carboxylation efficiency (A*P)	20.83	0.00067	0.377	0.7694	320
Quantum efficiency (A)	31.27	0.0099	8.738	<0.0001	320
Quantum efficiency (P)	31.27	0.0033	2.915	0.0888	320
Quantum efficiency (A*P)	31.27	0.000015	0.013	1.0000	320
Effective photochemical yield (A)	7.18	0.2353	68.184	<0.0001	320
Effective photochemical yield (P)	7.18	0.0023	0.661	0.4169	320
Effective photochemical yield (A*P)	7.18	0.0005	0.14	0.937	320

Variable	*CV%*	*Mean square value*	*F test value*	*P-value*	*n*
Electron transport rate (A)	37.73	206.0616	28.953	<0.0001	320
Electron transport rate (P)	37.73	0.046	0.006	0.936	320
Electron transport rate (A*P)	37.73	3.2323	0.454	0.7142	320
Chlorophyll content (A)	6.53	3.2925	17.604	<0.0001	320
Chlorophyll content (P)	6.53	5.7334	30.654	<0.0001	320
Chlorophyll content (A*P)	6.53	0.2909	1.556	0.2002	320
Anthocyanin content (A)	17.07	0.0105	0.832	0.4863	40
Anthocyanin content (P)	17.07	0.0875	6.911	0.0131	40
Anthocyanin content (A*P)	17.07	0.0118	0.928	0.4382	40
Stomatal density (A)	19.23	16691.2225	3.868	0.0106	160
Stomatal density (P)	19.23	47336.808	10.969	0.0012	160
Stomatal density (A*P)	19.23	3343.2242	0.775	0.5097	160
Total epidermal cell density (A)	10.12	126.7816	3.447	0.0182	160
Total epidermal cell density (P)	10.12	5.1289	0.139	0.7094	160
Total epidermal cells density (A*P)	10.12	15.8616	0.431	0.7308	160
Palisade parenchyma thickness (A)	4.49	4.0955	23.816	<0.0001	160
Palisade parenchyma thickness (P)	4.49	9.4006	54.665	<0.0001	160
Palisade parenchyma thickness (A*P)	4.49	0.2655	1.544	0.2054	160
Epidermal thickness (A)	4.12	0.381	15.359	<0.0001	160
Epidermal thickness (P)	4.12	0.1686	6.797	0.01	160
Epidermal thickness (A*P)	4.12	0.0013	0.053	0.9849	160

CV% = coefficient of variation; *n* = sampling number; (A) ambient treatments (unshaded, shaded net, shading in greenhouse, or shading in greenhouse plus UV bulb), (P) leaf position (leaf apex or leaf middle part); *two-way ANOVA; neither variable showed a significant interaction at $p<0.05$.

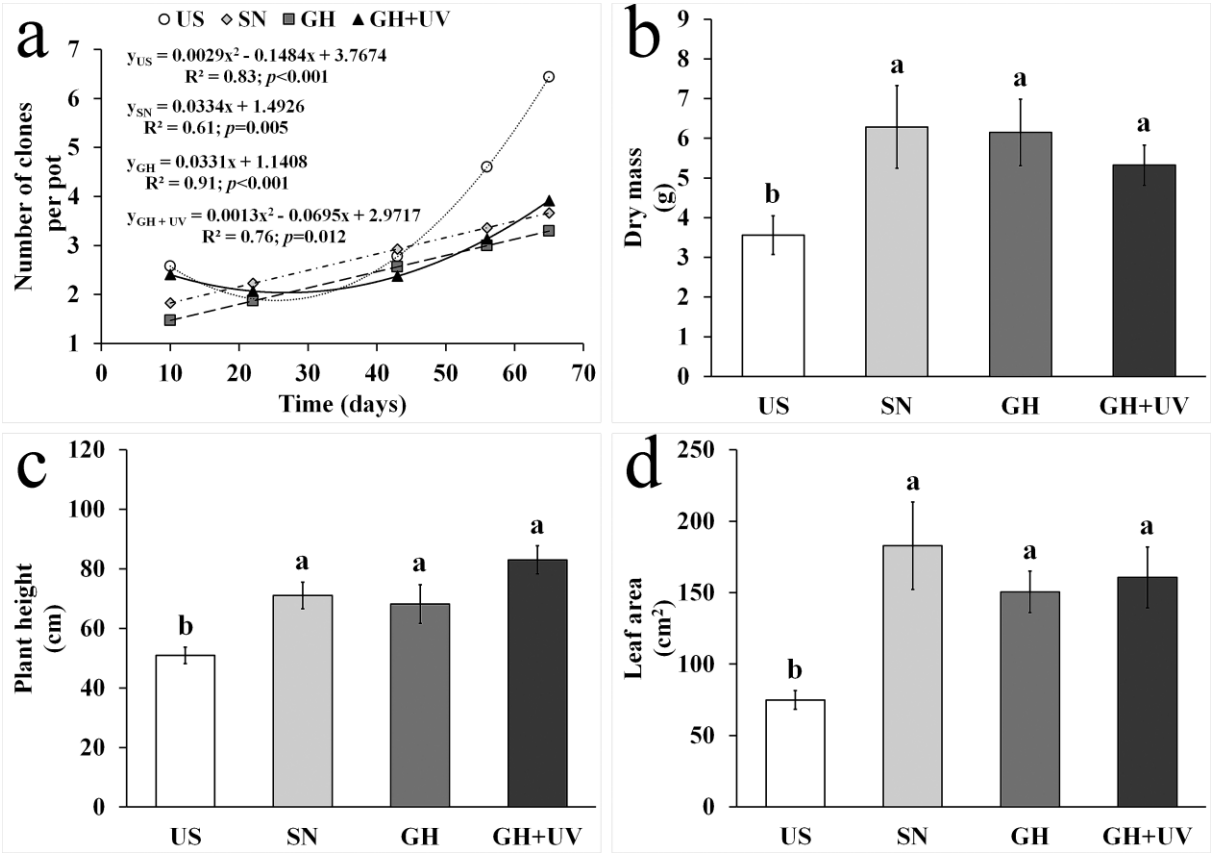


Fig. 1 Vegetative growth of *T. domingensis* under different ambiences. a, production of clones throughout the experimental period; b, c, and d, dry mass, plant height, and leaf area at the end of the experiment, respectively. *US*, unshaded; *SN*, shaded net; *GH*, shading in greenhouse; *GH+UV*, shading in greenhouse plus UV bulb. The means followed by the same letters do not differ according to the Scott-Knott test to $P<0.05$; bars = standard error.

The GH environment promoted greater net photosynthesis compared to the other environments (Fig. 2a); in addition, the leaf apex showed 14.48% higher net photosynthesis as compared to the leaf middle part (Fig. 2b). The US and SN treatments presented the lowest intercellular CO_2 concentration, followed a 40.38% higher mean in the GH treatment and the highest concentration (48.74% higher than US and SN) was observed in the GH+UV environment (Fig. 2c). There were no significant differences between leaf regions regarding the intercellular CO_2 concentration (Fig. 2d). The GH and GH+UV promoted greater stomatal conductance being 61.35% compared to US and SN environments (Fig. 2e). The stomatal conductance was 30.77% higher at the leaf apex to leaf middle part (Fig. 2f). In addition, the US and SN environments presented the lowest means of transpiration, followed by 17.33% higher values in the GH+UV environment and 31.44% in the GH, the latter being the highest

(Fig. 2g). A significant increase of 22.73% in transpiration was observed in the leaf apex as compared to the leaf middle part (Fig. 2h).

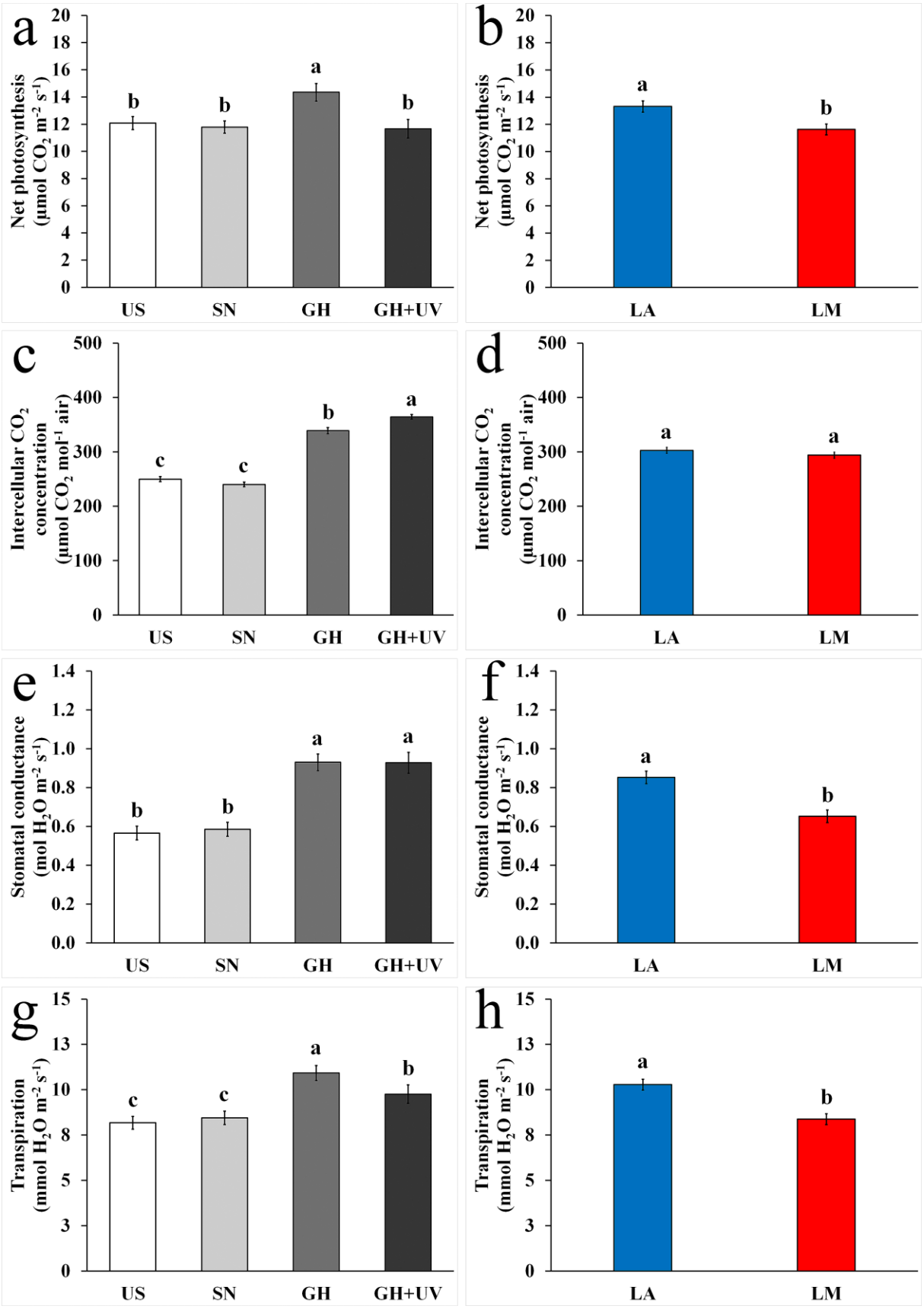


Fig. 2 Leaf gas exchange in *T. domingensis* under different environments or leaf positions. a-b, Net photosynthesis; c-d, Intercellular CO_2 concentration; e-f, Stomatal conductance; g-h, Transpiration. a, c, e and g, Ambiences treatments; b, d, f and h, Leaf positions treatments. *US*, unshaded; *SN*, shaded net; *GH*, shading in greenhouse; *GH+UV*, shading in greenhouse plus UV bulb; *LA*, leaf apex; *LM*, leaf middle part. The means followed by the same letters do not differ according to the Scott-Knott test to $P<0.05$; bars = standard error.

The GH and GH+UV environments reduced the water use efficiency by about 12.38% compared to the US and SN treatments (Fig. 3a). The leaf middle part presented higher water use efficiency compared to the leaf apex (Fig. 3b). The GH+UV environment reduced the carboxylation efficiency by 37.61% as compared to the US and SN. The GH environment also reduced the carboxylation efficiency by 16.96% compared to the US and SN treatments (Fig. 3c). The leaf apex showed higher carboxylation efficiency compared to the leaf middle part (Fig. 3d). The GH+UV environments reduced the quantum efficiency by about 15.79% compared to the US, SN and GH treatments (Fig. 3e); however, no significant differences were observed for quantum efficiency related to leaf position (Fig. 3f).

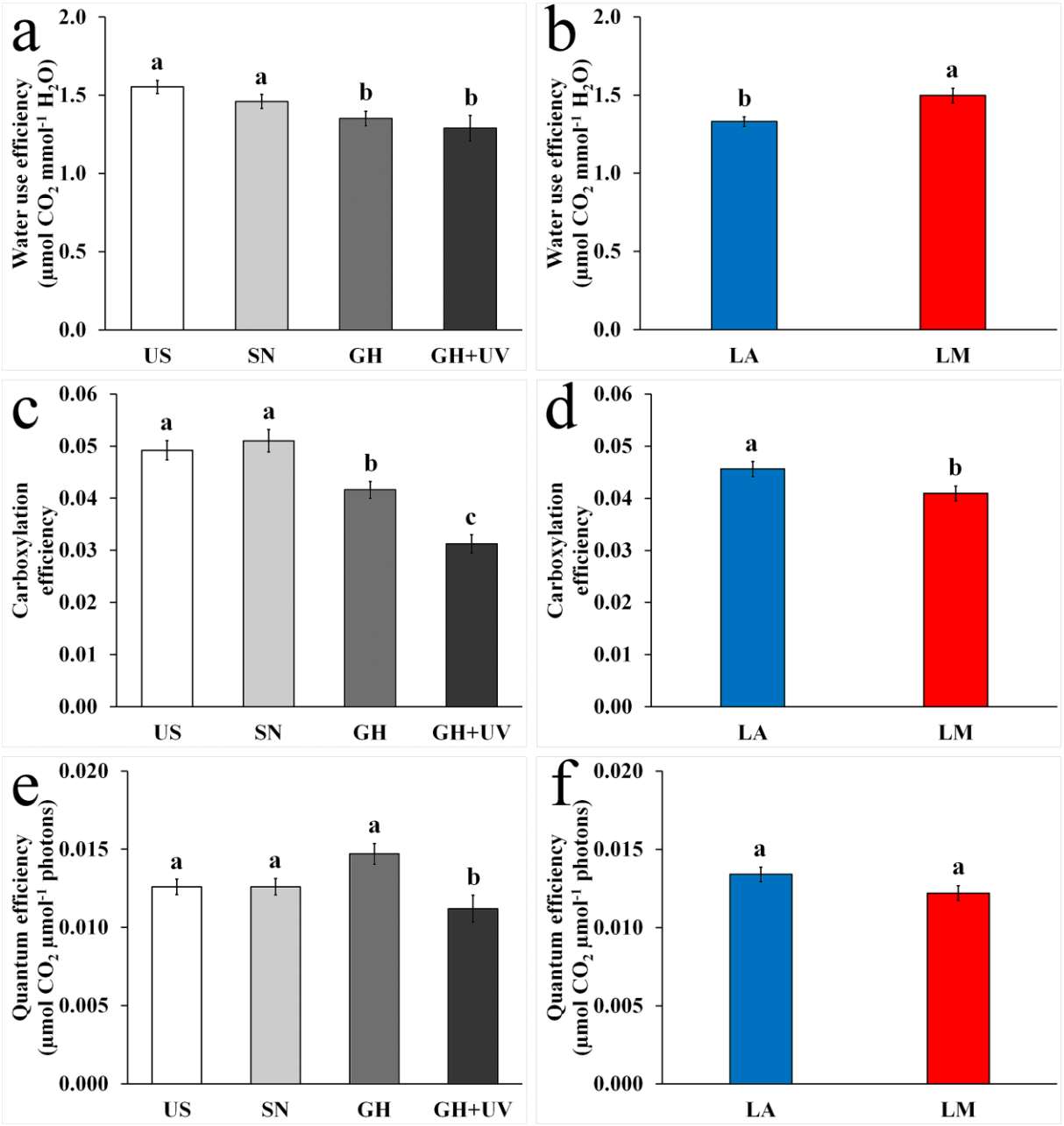


Fig. 3 Photosynthetic efficiency parameters in *T. domingensis* leaves under different environments or leaf positions. a-b, water use efficiency; c-d, carboxylation efficiency; e-f, quantum efficiency. a, c, and e, environments; b, d, and f, leaf positions treatments. *US*, unshaded; *SN*, shaded net; *GH*, shading in greenhouse; *GH+UV*, shading in greenhouse plus UV bulb; *LA*, leaf apex; *LM*, leaf middle part. The means followed by the same letters do not differ according to the Scott-Knott test to $P<0.05$; bars = standard error.

The photochemical parameters are shown in Figure 4. The US treatment reduced the effective photochemical yield by 23.18% compared to the other treatments (Fig. 4a); however,

no significant difference was observed for the leaf positions (Fig. 4b). The highest electron transport rate was observed in the US environment that is twice the means from other environments (Fig. 4c); the lowest means were observed in the SN and GH+UV environments (Fig. 4c). In addition, no significant difference was found for the electron transport rate related to the leaf position (Fig. 4d).

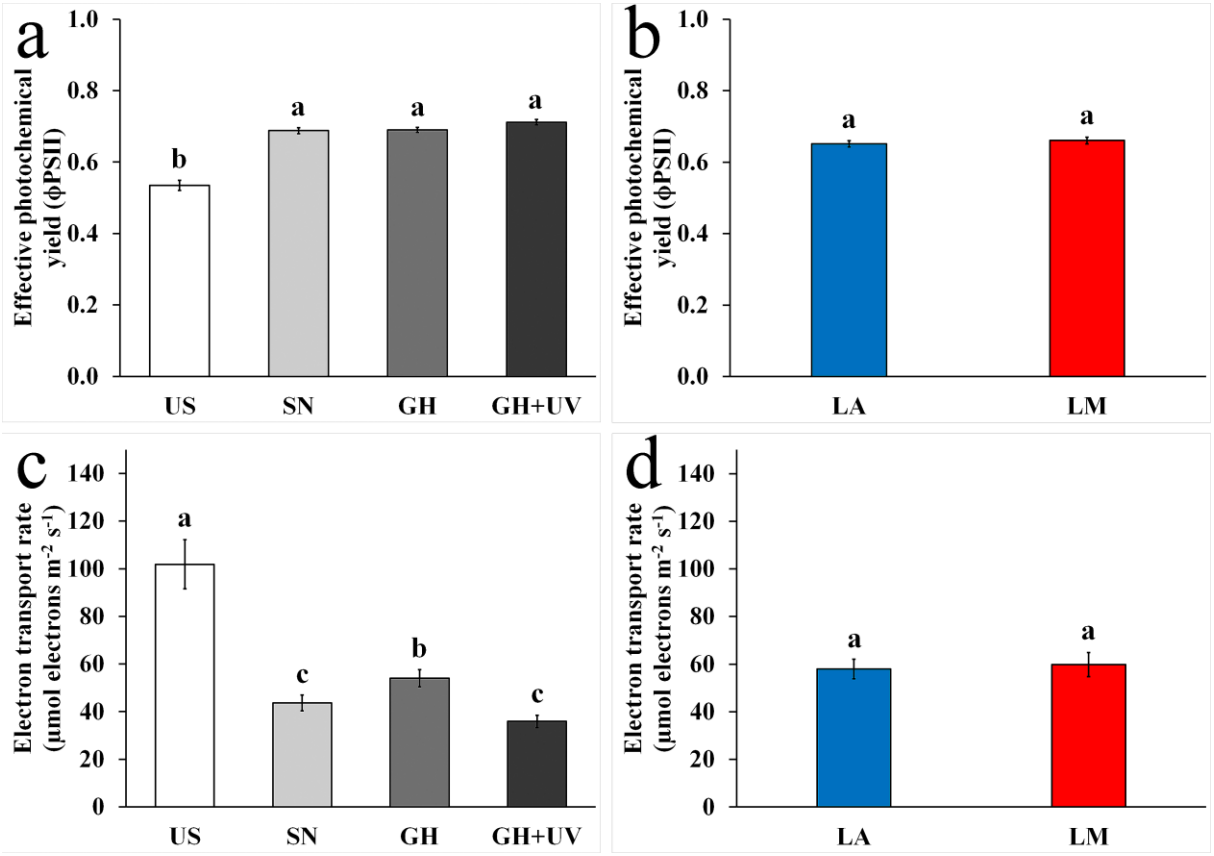


Fig. 4 Photochemical traits in *T. domingensis* under different environments or leaf positions. a-b, effective photochemical yield; c-d, electron transport rate. a and c, environments; b and d, leaf positions treatments. *US*, unshaded; *SN*, shaded net; *GH*, shading in greenhouse; *GH+UV*, shading in greenhouse plus UV bulb; *LA*, leaf apex; *LM*, leaf middle part. The means followed by the same letters do not differ according to the Scott-Knott test to $P<0.05$; bars = standard error.

The plants from the SN environment showed the highest chlorophyll content followed by the US with the second highest mean and GH with the third value, the lowest chlorophyll content was observed in the GH+UV environment (Fig. 5a). In addition, the highest chlorophyll content was observed in the leaf middle part compared to the leaf apex (Fig. 5b).

The leaf anthocyanin content showed no significant differences among the environments (Fig. 5c), although the concentration of this pigment is 27.86% higher in the leaf apex compared to the leaf middle part (Fig. 5d).

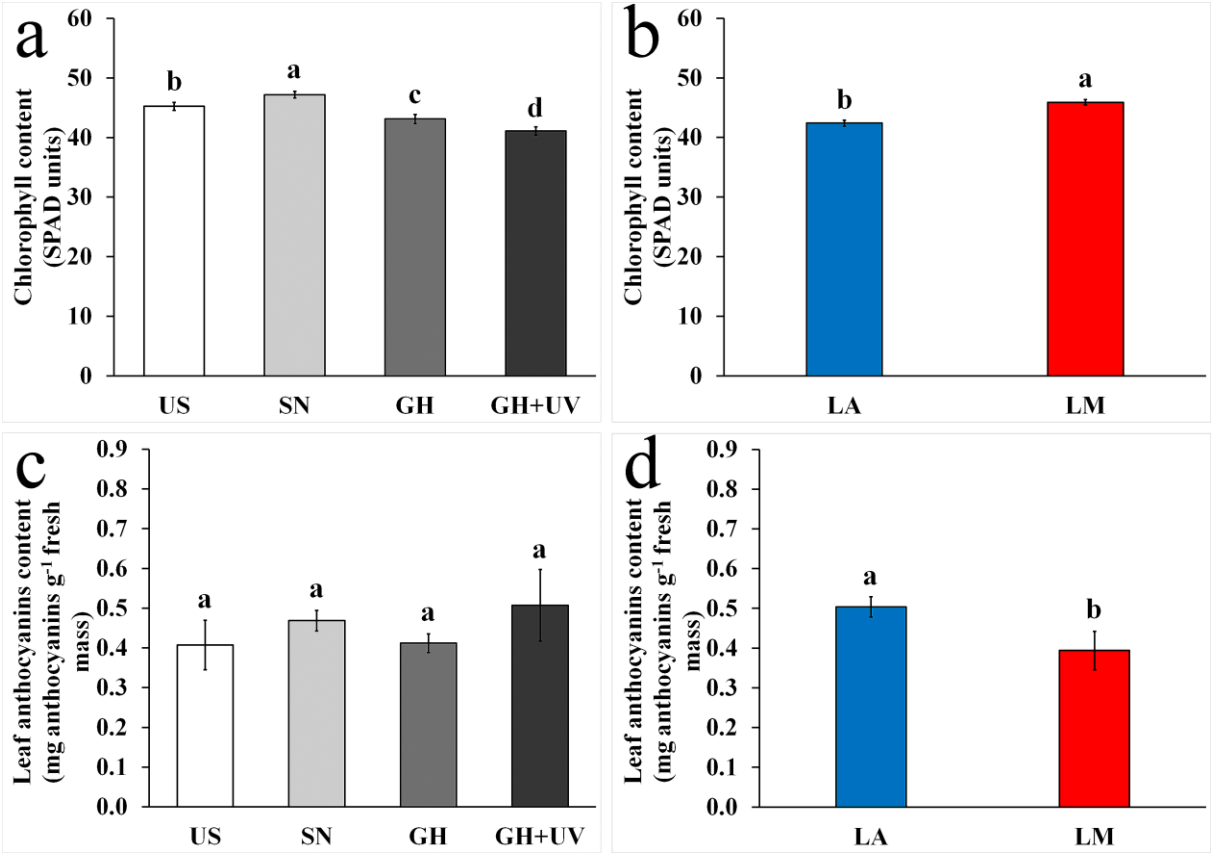
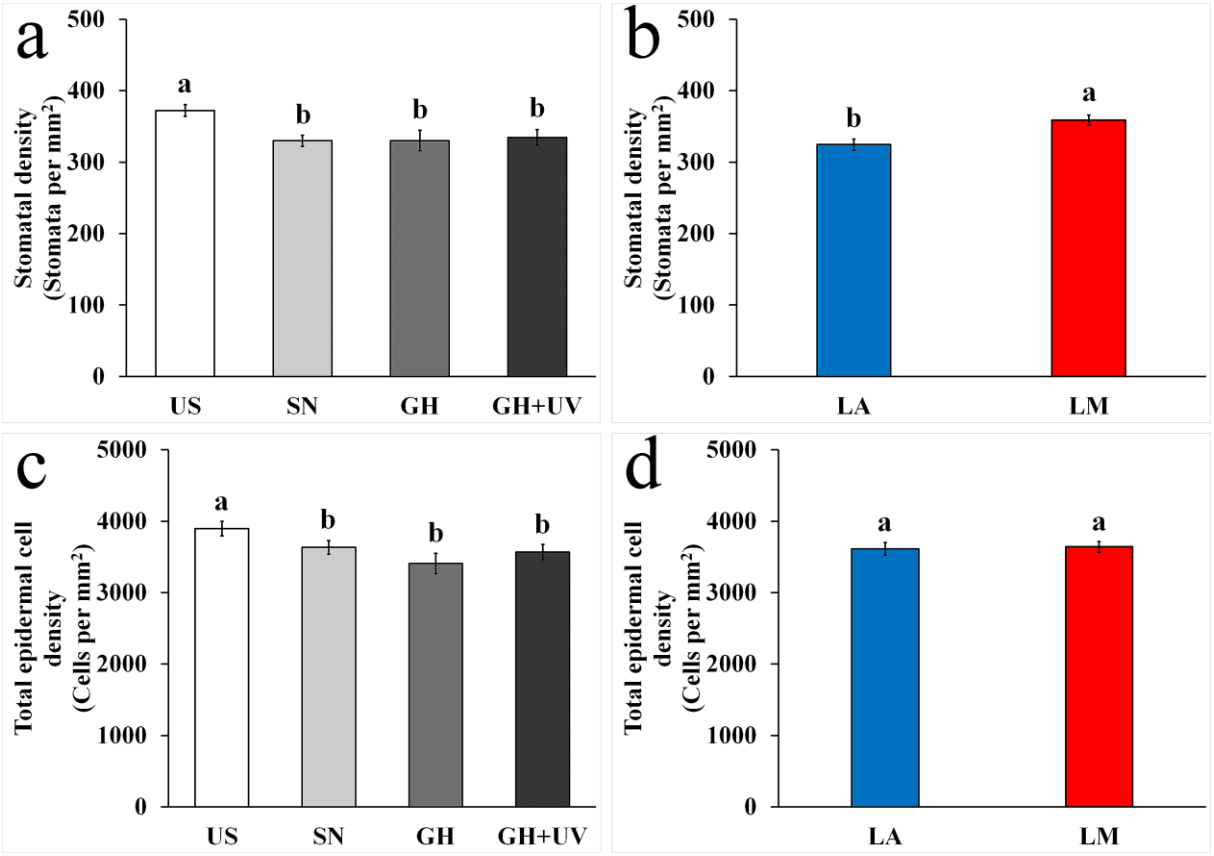


Fig. 5 Biochemical traits in *T. domingensis* under different environments or leaf positions. a-b, chlorophyll content; c-d, leaf anthocyanin content. a and c, environments; b and d, leaf positions treatments. *US*, unshaded; *SN*, shaded net; *GH*, shading in greenhouse; *GH+UV*, shading in greenhouse plus Uv bulb; *LA*, leaf apex; *LM*, leaf middle part; *acn*, anthocyanin. The means followed by the same letters do not differ according to the Scott-Knott test to $P<0.05$; bars = standard error.

US environment increased the stomatal density compared to the other environments (Fig. 6a and Fig. 8) and the stomatal density was higher in the leaf middle compared to the leaf apex (Fig. 6b and Fig. 8). Furthermore, the epidermal cell density was higher in the US environment (Fig. 6c and Fig. 8), but no significant differences were observed between the leaf positions (Fig. 6d and Fig. 8).

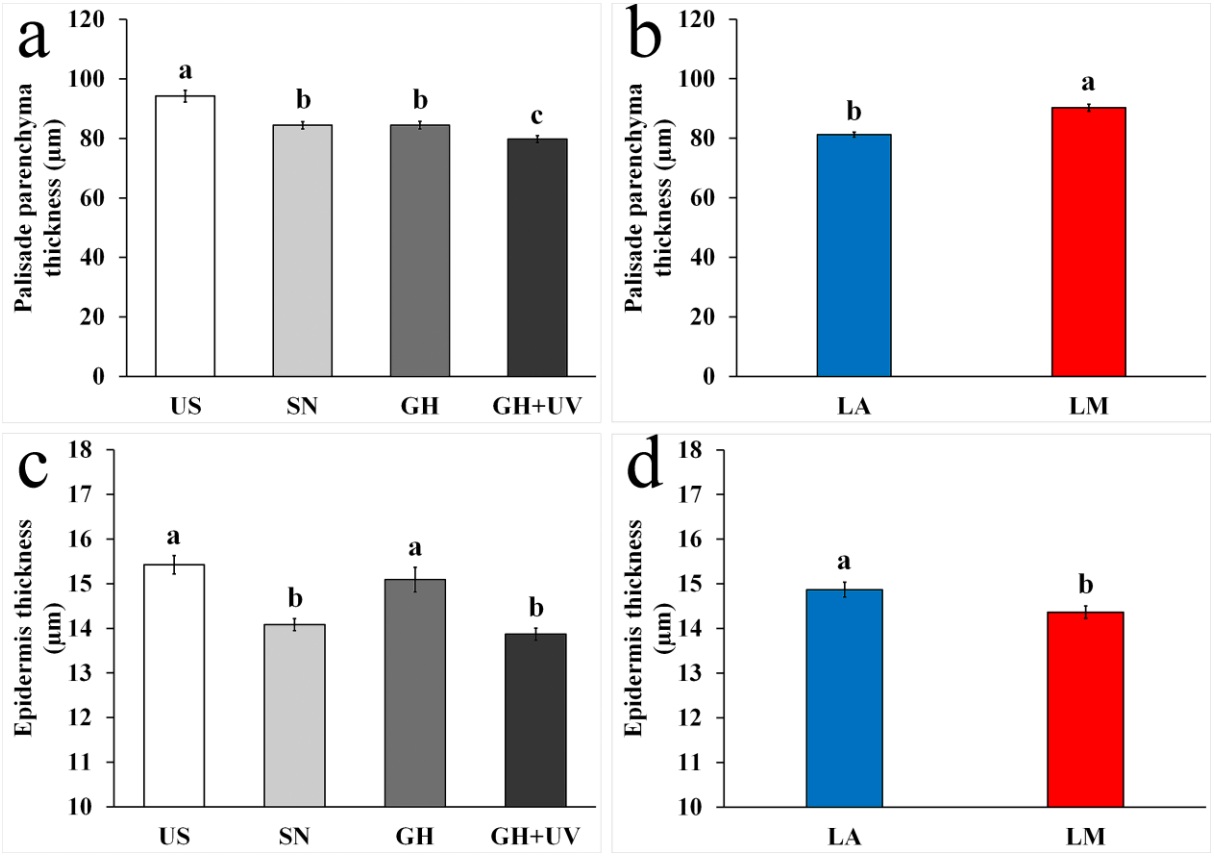


315

316 **Fig. 6** Leaf anatomical parameters of *T. domingensis*. a and b, stomatal density; c and d, total
317 epidermal cell density. a and c, environments; c and d, leaf positions treatments. *US*,
318 unshaded; *SN*, shaded net; *GH*, shading in greenhouse; *GH+UV*, shading in greenhouse plus
319 UV bulb; *LA*, leaf apex; *LM*, leaf middle part. The means followed by the same letters do not
320 differ according to the Scott-Knott test to $P<0.05$; bars = standard error.

321

322 The US environment promoted the development of the thickest palisade parenchyma,
323 followed by reductions in the SN, GH and the GH+UV that showed the thinnest tissue (Fig.
324 7a, Fig. 9, and Fig. 10). In addition, the palisade parenchyma was thicker in the leaf middle
325 part compared to its leaf apex (Fig. 7b, Fig. 9, and Fig. 10). The epidermis thickness was
326 greater in the US and GH treatments compared to SN and GH+UV treatments (Fig. 7c, Fig. 9,
327 and Fig. 10). The leaf apex presented thickest epidermis compared with the leaf middle part
328 (Fig. 7d, Fig. 9, and Fig. 10).



329

330 **Fig. 7** Leaf anatomical parameters of *T. domingensis*. a-b, palisade parenchyma thickness; c-
331 d, epidermis thickness; a and c, environments; b and d, leaf positions treatments; *US*,
332 unshaded; *SN*, shaded net; *GH*, shading in greenhouse; *GH+UV*, shading in greenhouse plus
333 UV bulb; *LA*, leaf apex; *LM*, leaf middle part. In a-d, the means followed by the same letters
334 do not differ according to the Scott-Knott test to $P<0.05$; bars = standard error.

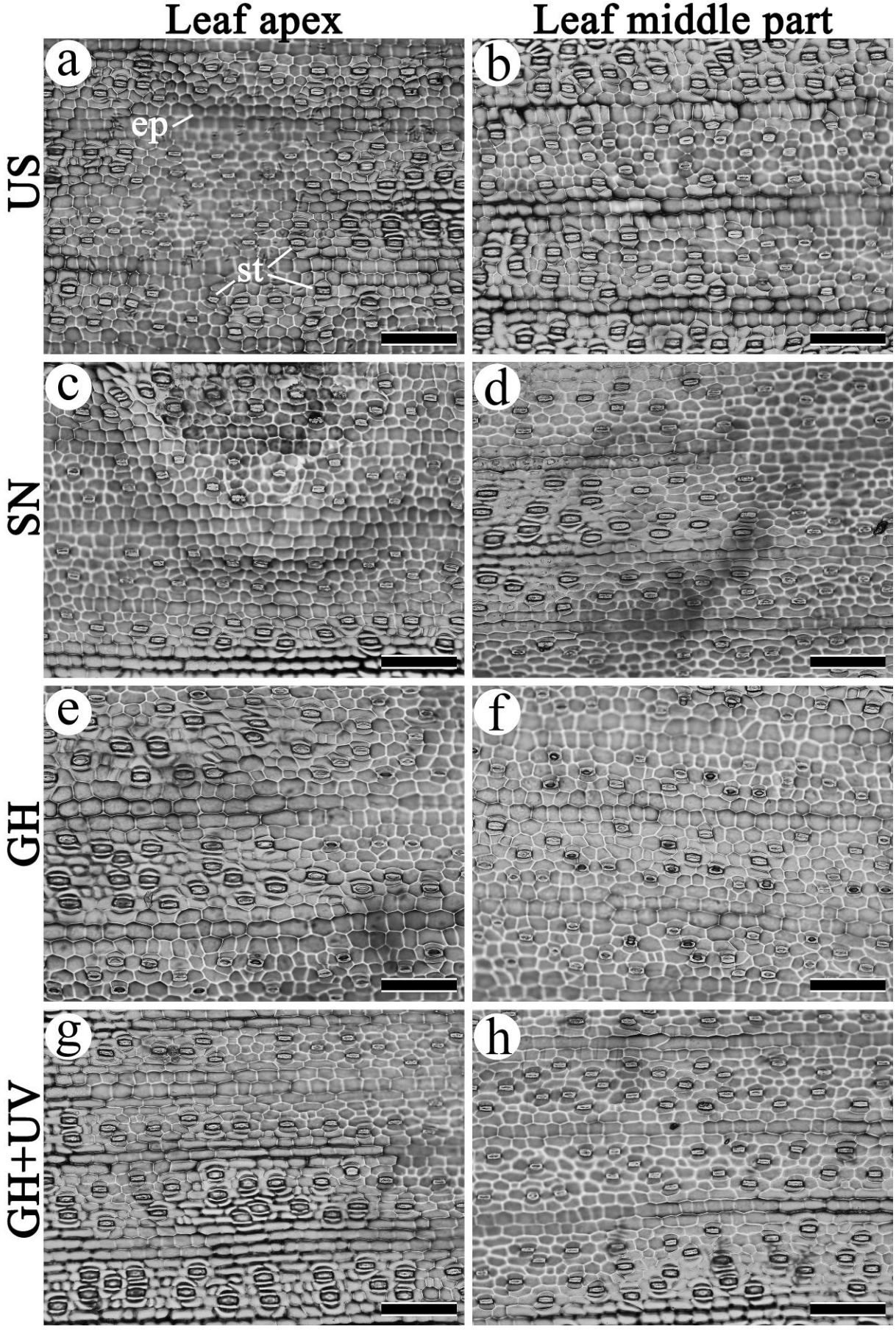

Leaf apex
Leaf middle part
US
SN
GH
GH+UV
a
b
c
d
e
f
g
h
ep
st

Fig. 8 Paradermal leaf sections of *T. domingensis* subjected to different environments and leaf positions. a-b, unshaded; c-d, shaded net; e-f, shading in greenhouse; g-h, shading in greenhouse plus UV bulb; a, c, e and g, leaf apex; b, d, f and h, leaf middle part. *ep* = regular epidermal cells; *st* = stomata. Bars = 100 µm

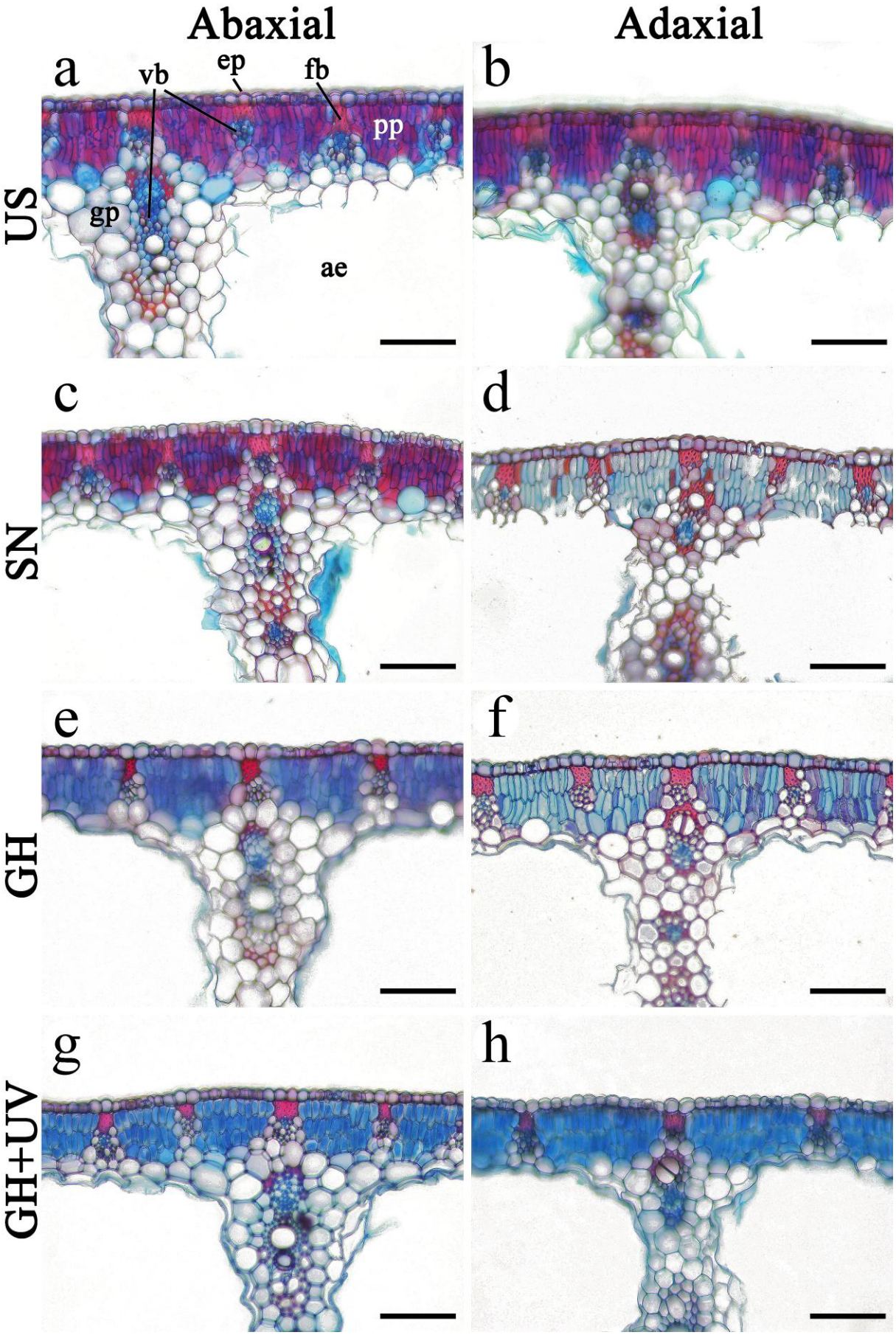

Abaxial
Adaxial
a
b
c
d
e
f
g
h
vb
ep
fb
pp
gp
ae
US
SN
GH
GH+UV

Fig. 9 Transversal sections of the leaf apex of *T. domingensis* subjected to different environments. a-b, unshaded; c-d, shaded net; e-f, shading in greenhouse; g-h, shading in greenhouse plus UV bulb. *aba* = abaxial side; *ada* = adaxial side; *vb* = vascular bundle; *ep* = epidermis; *pp* = palisade parenchyma; *fb* = sclerenchymal fibers; *gp* = ground parenchyma; *ae* = aerenchyma. Bars = 100 µm

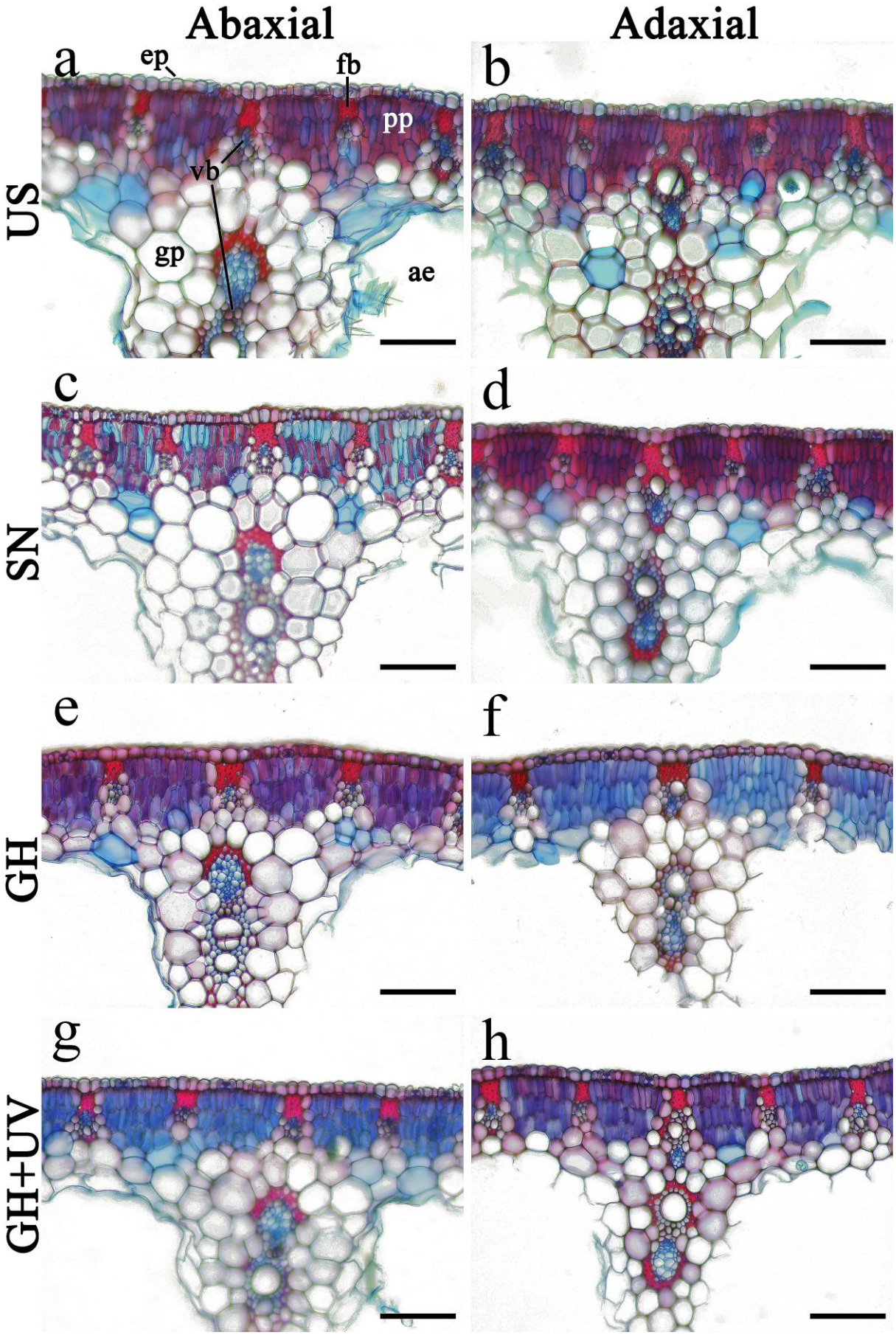

Abaxial
Adaxial
a
ep
fb
pp
vb
gp
ae
b
US
c
d
SN
e
f
GH
g
h
GH+UV

Fig. 10 Transversal sections of the leaf middle part of *T. domingensis* subjected to different environments. a-b, unshaded; c-d, shaded net; e-f, shading in greenhouse; g-h, shading in greenhouse plus UV bulb. *aba* = abaxial side; *ada* = adaxial side; *vb* = vascular bundle; *ep* = epidermis; *pp* = palisade parenchyma; *fb* = sclerenchymal fibers; *gp* = ground parenchyma; *ae* = aerenchyma. Bars = 100 µm

Additionally, all the tissues are well developed in all treatments, and it is observed that the palisade parenchyma presents cells elongated perpendicular to the leaf surface; however, there is a clear morphological difference between the palisade parenchyma of the US treatment and the GH+UV treatment, the latter presenting more compacted palisade parenchyma cells, although the three layers of the tissue are maintained in all treatments (Fig. 9 and Fig. 10).

Discussion

UV effect in carbon fixation of shaded *T. domingensis* plants

Results from this work suggest that increased ultraviolet radiation reduces the photosynthesis of *T. domingensis* by limiting carbon fixation. The stomatal conductance from *T. domingensis* leaves indicates that no impairment of CO_2 acquisition was found in plants grown in UV-enriched environment (GH+UV). The stomatal conductance from the GH+UV environment was similar to GH and even higher than US and SN (Fig. 2e), indicating that UV does not harm this parameter in *T. domingensis*. GH and GH+UV environments showed 61.3% higher stomatal conductance compared to US and SN suggesting greater diffusion capacity of CO_2 into the leaf. This resulted in higher intercellular CO_2 concentration in GH and GH+UV environments (Fig. 2c). In general, higher CO_2 concentrations tend to favor photosynthesis due to its intrinsic hole as substrate in the enzymatic fixation by Rubisco (Bowes 1993). In *Sorghum bicolor* (L.) Moench, higher photosynthesis is associated with increased intercellular CO_2 concentrations related to increased intercellular spaces in the mesophyll (Oliveira et al. 2023). Furthermore, photosynthesis is much more responsive to increased intercellular CO_2 concentrations in plants with C_3 metabolism, as expected also for *T. domingensis*, since they do not have a CO_2 concentrating mechanism (Bowes 1993; Tissue et al. 1995; Wang et al. 2020). This relationship was observed for increased photosynthesis in

the GH environment (Fig. 2a). However, the higher intercellular CO_2 concentration found in GH+UV compared to the GH did not translate into an increase in photosynthesis; on the contrary, there was a reduction in the photosynthesis of GH+UV compared to the GH environment (Fig. 2a). Romanatti et al. (2019) reported an increase in intercellular CO_2 concentration in eggplant leaves subjected to UV radiation when compared to non-irradiated ones, with reduced photosynthesis, although there was no change in stomatal conductance between treatments. Therefore, neither CO_2 uptake nor intercellular CO_2 concentration was limited by UV radiation in *T. domingensis*, suggesting that the lower photosynthesis observed in the GH+UV environment is related to specific limitations in the photosynthetic stages.

Our results indicate that ultraviolet radiation did not compromise the photochemical stage. This is because Uv enrichment (GH+UV) promoted no significant changes in the Effective photochemical yield (ϕPSII) compared to other shaded treatments and this parameter was even higher when compared to unshaded plants (Fig. 4a). Effective photochemical yield indicates the proportion of the energy absorbed by the chlorophylls released by photochemical quenching (Maxwell and Johnson 2000). Thus, a stable ϕPSII indicates adequate photochemical functioning in *T. domingensis* cultivated under the GH+UV environment. However, ultraviolet radiation reduces the ϕPSII from several plant species (González-Villagra et al. 2020; Hu et al. 2013; Joshi et al. 2013; Nayak et al. 2003; Romanatti et al. 2019; Samuoliene et al. 2020). This work is the first report of photochemical traits for *T. domingensis* being difficult to discuss comparable data of the ϕPSII; nonetheless, the absence of negative effects promoted by ultraviolet radiation in ϕPSII from *T. domingensis* leaves suggests that its photochemical stage is somewhat tolerant to UV.

The presence of anthocyanins in the *T. domingensis* leaves suggests that these pigments contribute to their UV protection and tolerance. Anthocyanins are a class of phenols that protect plants by absorbing UV radiation and avoiding its harmful effects on leaf tissues (Liu et al. 2022; Neugart and Schreiner 2018). The presence of anthocyanins in *T. domingensis* leaves is important because, as an aquatic plant that does not show defense mechanisms commonly found in UV-tolerant species, such as thick cuticles (Bernado et al. 2021; Cruz et al. 2023; Jordan et al. 2005; Liu et al. 2022; Reis et al. 2024), the thick epidermis (Cruz et al. 2023; Jordan et al. 2005; Reis et al. 2024), and trichomes (Cruz et al. 2023; Jordan et al. 2005; Reis et al. 2024). *T. domingensis* leaves show a thin epidermis which was even reduced by the UV-enriched environment (Fig. 7). This is the first report of anthocyanins being quantified in *T. domingensis* leaves. Therefore, there is no comparable

data to discuss it; however, its presence in the UV-enriched environment suggests that it was sufficient to protect the photosynthetic system. Samuoliene et al. (2020) reported differences in anthocyanin levels of lettuce exposed to UV radiation avoiding impairment to photochemical traits. Thus, our results indicate that the amount of anthocyanins produced by *T. domingensis* leaves is sufficient to protect ϕPSII; however, further studies should be conducted to better understand the processes of synthesis and degradation of anthocyanins in *T. domingensis* exposed to UV radiation.

All shaded treatments (SN, GH, and GH+UV) showed lower ETR values compared with the US environment (Fig. 4c). Because the lowest ETR values were found in SN and GH+UV environments that also show the lowest PAR radiation, this indicates that ETR values are related to lower PAR instead of higher UV. To understand this, it is important to examine the equation for ETR calculation (Maxwell and Johnson 2000): ETR = ϕPSII * PAR * ETR factor, where the ETR factor is a correction related to photon absorption in photosystem II, the PAR is the photosynthetically active radiation, and the is the effective photochemical yield. Therefore, higher PAR also increases the ETR given the highest ETR means for the US environment and the lowest for SN and GH+UV environments. Thus, our results indicate that UV-limited photosynthesis in *T. domingensis* is not related to the photochemical stage.

Results for carboxylation efficiency and quantum efficiency suggest that UV-limited photosynthesis in *T. domingensis* leaves is related to the biochemical stage, particularly to the carboxylation reaction. The UV-enriched environment presented the lowest values of carboxylation efficiency and quantum efficiency (Fig. 3), and this is related to the increased intercellular CO_2 concentration and lower photosynthesis (Fig. 2). Carboxylation is the first step from the Calvin-Benson cycle, where carbon is fixed by the enzyme Rubisco, which dependents on CO_2 and ribulose-1,5-biphosphate (RuBP) (Sharkey 2024). Carboxylation depends on substrate concentration (CO_2 and RuBP) and the amount of Rubisco molecules (Bowes 1993). The UV-enriched environment (GH+UV) did not limit CO_2 acquisition in *T. domingensis*, as shown by the higher stomatal conductance and intercellular CO_2 concentration variables. In addition, the GH+UV environment promoted no significant changes in stomatal density in *T. domingensis* leaves (Fig 6), indicating no limitation to CO_2 uptake.

According to Shipley et al. (2005), the thickness of photosynthetic tissues is related to photosynthetic activity. Reduced palisade parenchyma thickness is often associated with

lower photosynthesis as was shown in *T. domingensis* grown under excessive phosphorus levels (Santos et al. 2015) and for *Solanum melongena* L. grown in a UV-enriched environment (Romanatti et al. 2019). Thus, the lower photosynthesis from *T. domingensis* grown in a GH+UV environment may be related to thinner palisade parenchyma observed in its leaves developed in this condition (Fig. 7). Nonetheless, we could not evaluate Rubisco activity or RuBP concentration in *T. domingensis* leaves, and these aspects must be further investigated to better understand the UV effects in the carboxylation stage of the species.

UV-tolerance in *T. domingensis*

Despite the impairment in carboxylation shown in the UV-enriched environment, our results indicate that *T. domingensis* is partially UV-tolerant. This is corroborated by greater biomass, plant height, and leaf area produced under the shaded environments which were not reduced in the GH+UV (Fig. 1). However, it is worth noting that the US environment presents the highest values of PAR and UV radiation (Tab. 1) and lower growth parameters (Fig. 1). Reis et al. (2024) built light response curves for *T. domingensis* leaves which showed saturation points of 2800 μmol m^{-2} s^{-1}. This PAR radiation intensity is equivalent to 609 W m^{-2} which is close to the PAR intensity measured in the unshaded environment (Tab. 1). This suggests that photoinhibition is not limiting photosynthesis in this US environment and lower growth parameters of *T. domingensis* in unshaded conditions is caused by excessive UV intensity. The UV intensity in the US environment is about 50.8% higher than the GH+UV environment and exceeds the defensive capacity of *T. domingensis*. Plants that do not have adequate protection mechanisms against UV radiation will suffer from limited photosynthesis (Romanatti et al. 2019). Because *T. domingensis* leaves do not show anatomical traits that give UV tolerance and only anthocyanins provide some degree of protection, its UV tolerance is limited, and this species is partially UV-tolerant.

In this work, plants in unshaded conditions present higher carboxylation efficiency (Fig 3c); however, this results from a lower CO_2 acquisition as shown by the reduced stomatal conductance and intercellular CO_2 concentration in *T. domingensis* leaves grown in the US environment (Fig. 2). The carboxylation efficiency equation is calculated by dividing the net photosynthesis by the intercellular CO_2 concentration. Therefore, the carboxylation efficiency found in *T. domingensis* from the US environment is high due to the lower intercellular CO_2 concentration in their leaves. The reduction in intercellular CO_2 concentration can be related

to decreased stomatal conductance (Oliveira et al. 2023). *T. domingensis* grown in the US environment showed increased stomatal density, thus the stomatal conductance was not limited by the number of stomata suggesting that its lower stomatal conductance is related to stomatal closure (Figs. 2g and 3a). This is a common response from leaves exposed to different shading levels (Reis et al. 2024) and water availabilities (Oliveira et al. 2023). Thus, results suggest that *T. domingensis* suffered some limitations for CO_2 acquisition in unshaded conditions with the highest UV level tested and detailed aspects of this response must be further investigated.

T. domingensis grown in the US environment reduced the ϕPSII indicating some photochemical limitation. Both PAR and UV radiation at excessive levels may limit the photochemical stage (Bassi and Dall'Osto 2021; Li et al. 2018; Nayak et al. 2003; Romanatti et al. 2019); however, in this work, the reduced ϕPSII in *T. domingensis* grown in US environment may be related to excessive UV radiation. The PAR level of the US environment is close to the saturation point of *T. domingensis* photosynthesis (Reis et al. 2024) suggesting that the photochemical limitation is related to excessive UV. This indicates that excessive UV radiation limits both photochemical and biochemical photosynthetic stages in *T. domingensis* leaves, surpassing the defensive capacity of its anthocyanin defense.

Although *T. domingensis* grown in the US environment (highest UV intensity) showed lower biomass, height, and leaf area, no anatomical deformities or mortality were found. Shading levels of 73% or higher limit the development of photosynthetic tissues in *T. domingensis* leaves (Reis et al. 2024), although there is no information about UV-limited tissue development in *T. domingensis*, this work showed no evidence of such effects. Another interesting result was the greater clone production shown in the US environment at the end of the experiment (Fig. 1a). This indicates a self-shading mechanism that may help avoid excessive UV radiation at a population level. High population density may cause competition in the *T. angustifolia* L. (Correa et al. 2017); nonetheless, the high population density of *T. domingensis* promotes a self-shading effect benefiting the photosynthesis and growth of this species (Scarpa et al. 2021). Furthermore, Reis et al. (2024) demonstrated that *T. domingensis* benefits from mild shading through an increase in total leaf area, which increases the whole plant's photosynthesis. Therefore, increasing clone production found in the US environment may increase the population density, promoting some degree of protection from UV radiation being an interesting tolerance mechanism.

Anatomical and photosynthetic variation along the leaf axis

Some photosynthetic and anatomical traits vary with leaf position in *T. domingensis*. In the leaf apex of *T. domingensis* the higher stomatal conductance may have increased the photosynthesis by improving CO_2 acquisition that was readily fixed keeping the intercellular CO_2 concentration levels similar to the leaf middle part (Fig. 2). According to Terashima et al. (2006) higher stomatal conductance and CO_2 acquisition enhance photosynthetic activity. In addition, CO_2 is the substrate for Rubisco activity (Bowes 1993), and improving its uptake favors carboxylation. Interestingly, thinner palisade parenchyma and lower chlorophyll content were found at the leaf apex (Figs. 5 and 7) and no significant photochemical differences between the leaf apex and leaf middle part were observed. Thus, the increased photosynthesis in leaf apex cannot be explained by anatomical or photochemical traits, suggesting that the biochemical stage of photosynthesis is more relevant to such photosynthetic variation. Thus, the higher photosynthesis in the leaf apex of *T. domingensis* may be due to increased carboxylation efficiency (Fig. 3) which quickly fixes the intercellular CO_2 leading to similar intercellular CO_2 concentrations compared with the leaf middle part (Fig. 2).

The increased carboxylation in the leaf apex of *T. domingensis* must be further investigated in studies regarding Rubisco activity. In addition, the higher anthocyanin content in the leaf apex of *T. domingensis* (Fig. 5) indicates a higher protection to the photosynthetic system. Nonetheless, this is the first report on photosynthetic, anatomical, and biochemical traits along the leaf axis of *T. domingensis* and this subject deserves further investigation.

Conclusion

Our work indicates that *T. domingensis* is partially a UV-tolerant species. The ultraviolet radiation compromises both the photochemical and biochemical stages of *T. domingensis* depending on UV intensity. The UV-enriched environment causes impairment in carbon fixation and the US environment (highest in UV intensity) damages the photochemical and biochemical stages of *T. domingensis* leaves. The unshaded condition reduces *T. domingensis* growth but increases its clone production, suggesting a UV-defense mechanism by enhancing population growth and self-shading. The leaf apex of *T. domingensis* presents higher photosynthesis compared to the middle part suggesting a more efficient biochemical stage because no photochemical traits significantly change. *T. domingensis* leaves produce

anthocyanins as a defense mechanism against UV due to the absence of relevant anatomical defense traits.

Conflict of interest declaration

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

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3 CONSIDERAÇÕES FINAIS

Esse trabalho indica que *T. domingensis* é parcialmente tolerante à radiação ultravioleta e, embora esse fator ainda deva ser explorado de outras formas em futuras pesquisas, já sinaliza a resiliência da espécie frente a mais um fator de estresse. Foi demonstrado que a radiação ultravioleta afeta o tanto a etapa fotoquímica quanto a etapa bioquímica das folhas de *T. domingensis*, sendo que a maior intensidade de UV resulta em maior produção de clones. Essa maior produção clonal é uma forma da espécie contornar os problemas da exposição à radiação ultravioleta a nível populacional, uma vez que leva ao autossombreamento e permite reduzir a exposição de UV ao longo do processo de colonização de uma área. Além disso, maior quantidade de antocianinas no ápice foliar permite maior proteção dessa parte aérea mais exposta à radiação ultravioleta. Dessa forma, *T. domingensis* pode se beneficiar em um cenário de aumento de radiação ultravioleta quando em competição com outras espécies sensíveis, podendo levar a redução de biodiversidade local. Além disso, trabalhos futuros poderão esclarecer melhor de que forma a etapa bioquímica é afetada pela radiação UV e como ocorre estímulo para produção clonal. Caso seja possível identificar quais mecanismos que regem esses processos, talvez as descobertas possam ser úteis para aplicação no manejo da espécie.