UV REDUCTION UNVEILS SUNBURN VULNERABILITY IN JUVENILE PLANTS OF *C. canephora* UNDER SUPRA-OPTIMAL SOLAR RADIATION

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MARCH – 2024

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“In partial fulfillment of the requirements for the degree of Master of Science in Plant Production"

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Approved on March 26th, 2024

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I dedicate this dissertation to my parents, for all the investment of work, time, and energy in my entire academic life.

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LIST OF ABBREVIATIONS

CFCs — Clorofluorocarbons

CFIS — Chlorophyll Fluorescence Imaging System

DAT — Days After Transplantation

DP — Decrease Period

F0 — Minimum Fluorescence Level of Dark-adapted Leaves

Fv — Maximum Photochemical Extinction Capacity

Fv/Fm — Maximum Quantum Yield of PSII

IP — Increase Period

IRGA — Infrared Gas Analyzer

N — Nitrogen

PAM — Pulse Amplitude Modulated

PAR — Photosynthetically Active Radiation

PI — Photosynthetic Performance

PPFD — Photosynthetic Photon Flux Density

PQ — Plastoquinone

PRI — Photochemical Reflectance Index

PSII — Photosystem II

PSRI — Plant Senescence Reflectance Index

QA — Quinone a

RH — Relative Humidity, %

ROS — Reative Oxygen Species

SD — Sunburn Day

SPAD — Soil plant analysis development

UV — Ultraviolet Radiation

UVam — Near Ambient UV Environment

UVre — Reduced UV Environment

VPD — Vapor Pressure Deficit

ABSTRACT

Santos, Anne Reis; M.Sc.; Universidade Estadual do Norte Fluminense Darcy Ribeiro; March, 2024; UV Reduction Unveils Sunburn Vulnerability in Juvenile Plants of *C. canephora* Under Supra-optimal Solar Radiation; Advisor: Prof. D.Sc. Eliemar Campostrini.

This study aimed to answer if the reduction of UV intensity implicates sunburn physiological symptoms in *Coffea canephora* plants at increasing solar radiation and air temperature. Plants were grown in two environments with different UV radiation incidences (1) near ambient UV environment (UVam), consisting of a corrugated glass compartment that maintains UV intensities similar to the external environment, excluding only 16% UV-A and 0% UV-B; (2) reduced UV environment (UVre), consisting of a transparent polycarbonate compartment, which excludes 70% UV-A and 90% UV-B, maintaining reduced UV intensities compared to the external environment. Solar radiation and temperature values had a decline period in which tagged leaves for physiological analyses were grown and had their elongation and SPAD index registered every four days. The decreased period of solar radiation and air temperature was followed by an increasing period of both parameters, reaching a peak that caused sunburn only on UVre plants. The sunburn percentage area was calculated. Physiological traits were taken on the tagged leaves to evaluate spectral reflectance, chlorophyll *a* fluorescence, single-leaf gas exchanges, specific leaf mass (SLM), and total leaf area. UVam leaves had lower elongation but attained a higher SPAD index. Photochemical Reflectance Index (PRI) and Plant Senescence Reflectance Index (PSRI) suggested an acclimation of UVam plants to high PAR, allowing plants to not suffer sunburn damage, which occurred to UVre. This acclimation was also indicated by fluorescence data, which demonstrated higher photosynthesis efficiency. Fluorescence parameters reflected on greater net CO_2 assimilation rate, stomatal conductance and transpiration on UVam, which confirms its acclimation to high PAR. Our results infer that a great reduction of UV radiation could display a sensitive status of photochemical capacity. This sensitivity allowed sunburn occurrence on UVre leaves on plants that grew up on a gradual low PAR and air temperature (decrease period of these parameters). UVam leaves had lower leaf area and higher SLM, this must be caused by UV incidence priming effect that led leaves to invest leaf growth on thickness, in detriment to expansion, to protect the mesophyll from UV radiation. This increase in SLM can be associated with anatomic, physiological, and molecular protection roles of acclimation to high PAR incidence, which protected UVam leaves from sunburn occurrence.

Key-words: ultraviolet radiation, abiotic stress, priming, coffee, leaf damage.

RESUMO

Santos, Anne Reis; M.Sc.; Universidade Estadual do Norte Fluminense Darcy Ribeiro; Março, 2024; UV Reduction Unveils Sunburn Vulnerability in Juvenile Plants of *C. canephora* Under Supra-optimal Solar Radiation; Orientador: Prof. D.Sc. Eliemar Campostrini.

Este estudo teve como objetivo responder se a redução da intensidade da radiação UV implica em sintomas fisiológicos de queimadura solar em plantas de *Coffea canephora* sob o aumento da radiação solar e da temperatura do ar. As plantas foram cultivadas em dois ambientes com diferentes incidências de radiação UV: (1) ambiente com UV próximo ao ambiente natural (UVam), consistindo em um compartimento de vidro corrugado que mantém intensidades de UV semelhantes ao ambiente externo, excluindo apenas 16% de UV-A e 0% de UV-B; (2) ambiente com UV reduzido (UVre), consistindo em um compartimento de policarbonato transparente, que exclui 70% de UV-A e 90% de UV-B, mantendo intensidades de UV reduzidas em comparação ao ambiente externo. Os valores de radiação solar e temperatura passaram por um período de declínio, durante o qual as folhas marcadas para análises fisiológicas cresceram e tiveram seu alongamento e índice SPAD registrados a cada quatro dias. O período de declínio da radiação solar e da temperatura do ar foi seguido por um período de aumento desses parâmetros, atingindo um pico que causou queimadura solar apenas nas plantas UVre. A porcentagem de área queimada foi calculada. Características fisiológicas foram avaliadas nas folhas marcadas, incluindo reflectância espectral, fluorescência da clorofila *a*, trocas gasosas foliares, massa foliar específica (SLM) e área foliar total. As folhas UVam apresentaram menor alongamento, mas atingiram um índice SPAD mais elevado. O Índice de Reflectância Fotossintética (PRI) e o Índice de Reflectância de Senescência Vegetal (PSRI) sugeriram uma aclimatação das plantas UVam à alta radiação fotossinteticamente ativa (PAR), permitindo que as plantas não sofressem danos por queimadura solar, o que ocorreu com UVre. Essa aclimatação também foi indicada pelos dados de fluorescência, que demonstraram maior eficiência fotossintética. Os parâmetros de fluorescência refletiram em maiores taxas de assimilação líquida de CO2, condutância estomática e transpiração nas plantas UVam, o que confirma sua aclimatação à alta PAR. Nossos resultados sugerem que uma grande redução da radiação UV pode resultar em um estado sensível da capacidade fotoquímica. Essa sensibilidade permitiu a ocorrência de queimadura solar nas folhas UVre de plantas que cresceram sob PAR e temperatura do ar gradualmente baixas (período de declínio desses parâmetros). As folhas UVam apresentaram menor área foliar e maior SLM, o que pode ser causado pelo efeito de “priming” da incidência de UV, que levou as folhas a investirem no crescimento em espessura, em detrimento da expansão, para proteger o mesofilo da radiação UV. Esse aumento no SLM pode estar associado a papéis de proteção anatômicos, fisiológicos e moleculares da aclimatação à alta incidência de PAR, o que protegeu as folhas UVam da ocorrência de queimadura solar.

Palavras-chave: radiação ultravioleta, estresse abiótico, priming, café, dano foliar.

INTRODUCTION

The ozone layer plays a crucial role in moderating the intensity of solar radiation incidence on the Earth's surface, thereby safeguarding ecosystems and supporting the dynamics of living organisms (Bais et al., 2019; Barnes et al., 2023). As the ozone layer regulates the intensity of solar radiation, its depletion leads to exacerbated light stress, leading to detrimental impacts on ecosystems and agricultural production (Barnes et al., 2023; Iyer et al., 2022). The increase in light incidence on plants' surface, triggers high light stress responses (Roeber et al., 2021). This depletion of the ozone layer is attributed to interactions involving ozone and chlorofluorocarbons (CFCs). Thus, the alarming increase in greenhouse gas emissions and carbon compounds in the atmosphere results in elevated solar radiation incidence on Earth's surface (di Filippo et al., 2022; Rowland, 1989).

Plants are subject to constant environmental changes; thus, their survival and development require adaptation throughout their life cycle (Lean & Rind, 2009). Among the environmental factors to which plants are exposed, solar radiation is primordial, playing a crucial role in fundamental processes such as the modulation of photomorphogenesis and the production of photoassimilates for plant growth and development (Fankhauser & Chory, 1997; Smith, 1936).

Ultraviolet Radiation (UV), which comprises approximately 8-9% of the total solar radiation, has the most potential risks to biological systems (Bornman, 1989; Frederick, 1993; Frederick et al., 1989; Hurwitz et al., 2015). In the electromagnetic spectrum of solar radiation, the shortest wavelengths (200 to 400 nm) are attributed to ultraviolet radiation (UV). This spectrum is subdivided into three regions, known as UV-A (315-400 nm), UV-B (280-315 nm), and UV-C (200-280 nm). UV-A region is the least energetic (Katariaet al., 2014), and its role is mainly in plant morphology and biomass accumulation (Krizek et al., 1997; Robson et al., 2015). UV-B region has a shorter wavelength than UV-A, which means it’s more energetic, causing changes to biological systems at the molecular level at lower doses than UV-A (Boccalandro et al., 2001). These changes triggered by UV-B radiation include an increased thickness of leaf epidermis (Kakani et al., 2003a; Ruhland et al., 2005). At higher intensity, UV-B displays very harmful effects on plants, like photooxidative stress, chlorosis, and necrotic spots, leading to sunburn symptoms (Benda, 1955; Correia et al., 1999;

Frohnmeyer & Staiger, 2003; Kakani et al., 2003a). The third region is the UV-C, which does not reach the Earth's surface as it is completely absorbed through interaction with atmospheric gases in the ozone layer (Ballaré et al., 2011; Kataria, et al., 2014; Lidon & Ramalho, 2011).

The effects displayed by UV radiation, when plants are exposed to exacerbated intensities or prolonged time, can cause severe damage, but at low intensity, UV radiation is crucial to trigger a priming effect, which means that it can induce a pre-conditioning response in plants, enhancing their tolerance to subsequent stressors (Thomas & Puthur, 2017).

A fundamental aspect of plant survival, growth, and development is based on their ability to acclimate to changing environmental conditions (Gjindali & Johnson, 2023). Environmental factors such as light and temperature, can fluctuate unpredictably, subjecting plants to various abiotic stresses (Szymańska et al., 2017). Adequate acclimation enables plants to develop adaptive mechanisms, including the accumulation of flavonoids and phenolic compounds, which have an antioxidant role, to cope with stresses, ensuring the plant’s continued growth and development (Reichel et al., 2022; Szymańska et al., 2017). However, failure to acclimate properly can cause plants to be vulnerable to adverse environmental conditions in the future. In this context, without developing robust protective mechanisms, plants may exhibit sensitivity to environmental stressors, leading to detrimental effects on their physiological processes (Walters, 2004).

Thus, the consequence of inadequate acclimation is the phenomenon of sunburn, in which overexposure to unfavorable environmental conditions results in severe damage to the photosynthetic apparatus and, consequently, the complete loss of photosynthetic tissue, displaying visible damage (Caldwell et al., 1983; Daniell et al., 1969; Krause et al., 2015; Robberecht & Caldwell, 1983). Therefore, understanding the mechanisms underlying plant acclimation and its implications for plant resilience is crucial for coping with changing environmental challenging conditions and ensuring sustainable crop production in the face of climate change and higher solar radiation incidence (Anderson et al., 1995; Athanasiou et al., 2009; Hasanuzzaman et al., 2013; Herrmann et al., 2019).

Coffee plants evolved in shaded habitats and are widely cultivated in full sun (DaMatta et al., 2018). Direct exposure to solar radiation demands adaptive mechanisms to these conditions (Glenn et al., 2010; Meyer, 1965). Regarding light environmental factors, *C. canephora* exhibits greater sensitivity to ultraviolet radiation (Bernado et al., 2021). This fact may be associated with its evolutionary origin. Indeed, the species *C. canephora* is native to the African region, corresponding to the countries Congo and Uganda, and evolved in equatorial forests, from sea level up to 1200 m, in conditions with an average annual temperature between 24 and 26°C, and average annual precipitation exceeding 2000 mm (Coste, 1992; DaMatta & Ramalho, 2006).

Due to the sensitivity of *C. canephora* to solar radiation, specifically to UV radiation, an increase in UV can weaken the growth of this species (Bernado et al., 2021). Therefore, mitigation strategies, which reduce UV incidence are recommended, like protected cultivation under UV-blocking materials (Katsoulas et al., 2020). Despite that, UV radiation also has an important role in plant protection mechanisms to harsh environmental conditions (Shi & Liu, 2021; Thomas & Puthur, 2017; Thomas & Puthur, 2020). Therefore, this study hypothesizes that UV reduction could affect these protection mechanisms.

OBJECTIVE

The present study aimed to answer if the reduction of UV intensity can reduce the protection mechanisms, implicating *C. canephora* cv. Conilon LB1 physiological sensibilization of leaves and allowing sunburn under increase of supra-optimal solar irradiance.

BIBLIOGRAPHIC REVIEW

Solar radiation effects on plants

Solar radiation consists of electromagnetic waves propagating at different wavelengths. Shorter wavelengths have higher frequency and energy, while longer wavelengths have lower frequency and lower energy state (Hecht et al., 1942; Langley, 1889). Solar radiation regulates photosynthesis and photomorphogenesis processes, and is crucial for plant growth and development (Goh et al., 2012). However, the optimal intensities and quality of solar radiation vary depending on the adaptations of each genotype and species. Solar radiation intensities exceeding the plant's tolerance limit affect plant growth and development (Bassett & Glenn, 2014; Danila & Lucache, 2016; Goh et al., 2012).

Within the electromagnetic spectrum of solar radiation, ultraviolet (UV) radiation has higher energy capacity and significant regulatory potential over plant photomorphogenesis (Kataria et al., 2014). The UV spectra is subdivided in UV-A (315-400 nm), UV-B (280-315 nm), and UV-C rays (200-280 nm)**,** which do not reach the Earth's surface, as UV-C are entirely absorbed by interaction with ozone layer gases (Kataria et al., 2014; Lidon & Ramalho, 2011).

The incidence of UV rays at high intensity and over a prolonged period acts as a stress factor and can negatively affect the sensitive metabolic complexes of the photosynthetic machinery, thereby reducing crop productivity (Boccalandro et al., 2001; Goh et al., 2012; Jenkins, 2009; Sullivan et al., 2003). High UV radiation results in increased synthesis of reactive oxygen species, which degrade lipids and proteins, causing damage to Photosystem II (PSII). Additionally, UV rays inhibit the resynthesis of PSII proteins, hindering the repair mechanism of PSII (Takahashi & Badger, 2011).

UV-A radiation is the least energetic within the ultraviolet range and plays a crucial role in mediating the damage caused by UV-B (Kataria et al., 2014). UV-A rays are perceived by phototropins and cryptochromes, which are photoreceptors also sensitive to the blue range of electromagnetic radiation (Casal, 2013). Increased UV-A exposure causes limitations in leaf expansion and floral diameter in Arabidopsis thaliana (Robson et al., 2015). Additionally, UV-A interferes in plant growth by reducing biomass production and can alter leaf structure in terms of size and anatomy (Krizek et al., 1997; Robson et al., 2015). In C3 plants, UV-A radiation negatively affects photosynthesis indirectly by reducing the activity and content of the enzyme Rubisco (ribulose 1,5-bisphosphate carboxylase-oxygenase) (Prado et al., 2012). Additionally, this radiation reduces electron transport rates and the maximum quantum yield of PSII, ultimately leading to a decrease in carbon assimilation in photosynthesis (Vass et al., 2002).

Compared to UV-A radiation, UV-B has the shortest wavelength and therefore has the greatest potential to cause alterations to biological systems (Ballaré et al., 2011). The UV-B spectrum affects cellular processes through molecular changes, and its action is mediated by the specific UV-B photoreceptor called "UV Resistance Locus8" (UVR8) (Jenkins, 2009). High intensities of UV radiation degrade photosynthetic pigments, and UV-B specifically inhibits the resynthesis of these pigments (Ranjbarfordoei et al., 2011; Surabhi et al., 2009; Wu et al., 2011).

The effects of increased UV-B radiation on plants include reduced height, increased branching, chlorosis, and necrotic spots, decreased biomass accumulation, and increased thickness of leaf epidermis (Bernado et al., 2021; Kakani et al., 2003a; Meijkamp et al., 2001; Reddy et al., 2013; Ruhland et al., 2005). UV-B radiation as a stress factor causes oxidative damage to proteins and lipids, as well as a reduction in membrane permeability, which can result in up to a 68% reduction in the photochemical activity of PSII (Hollósy, 2002; Swarna et al., 2012).

Studies assess the reduction of these damages through UV radiation exclusion. Reducing approximately 82% UV-A and 95% UV-B, lead to an increase in electron transport between photosystems, enhanced maximum efficiency of PSII, and efficiency in quinone reduction, augmented Rubisco enzyme activity, and higher chlorophyll content (Kataria et al., 2013). The reduction of these rays also results in increased biomass, leaf expansion, and height (Guruprasad et al., 2007; Kataria & Guruprasad, 2012a; 2012b). Despite the patterns noted in the literature, significant variation in results for different species in response to ultraviolet radiation is still observed (Krizek, 2004).

Under UV radiation exclusion, photosynthetic organisms are spared from expending energy to produce protective metabolites (which represent a high metabolic cost), which leads to a greater investment of this energy in growth and increasing productivity (Bernado et al., 2024; Kataria et al., 2013).

The Photosynthetic Active Radiation (PAR) spectrum comprises wavelengths from 400 nm to 750 nm, which, in a new approach, include the visible spectrum and part of the far-red spectrum (Zhen & Bugbee, 2020). PAR triggers the photosynthetic process and has an important role in regulating photomorphogenesis (Arnon, 1971; Engelsma, 1967; Wit & Pierik, 2016). However, excessive exposure to PAR beyond the plants' tolerance limit can cause photoinhibition, especially when the excess PAR occurs in combination with UV radiation (Aro et al., 1993; Rustioni et al., 2014).

The blue region of the spectrum, which comprises wavelengths from 400 to 500 nm, is absorbed by cryptochromes, phototropins, and chlorophylls (Björn et al., 2009; Larkum, 2006; Yang et al., 2017). Cryptochromes modulate transcription activities that regulate photomorphogenesis and physiological responses triggered by blue radiation, such as branch elongation, leaf expansion, flowering, and stomatal regulation (Yang et al., 2017). Chlorophylls, excited by blue radiation, trigger the photosynthetic process (Briggs & Huala, 1999; Cashmore et al., 1999). However, excessive blue radiation can weaken mesophyll conductance, limiting photochemical efficiency (Loreto et al., 2009).

Regarding radiation in the green region (500-600 nm), most of it is reflected as chlorophylls absorb little radiation in this wavelength range (Nishio, 2000). This radiation is only used in chloroplasts located in basal regions of the leaf lamina and in the abaxial epidermis of thick leaves, where other wavelength ranges do not penetrate. Additionally, photons from the green region reach leaves inside the canopy, allowing the usefulness of these photons in the photosynthetic process (Smith et al., 2017). When green radiation is used, responses include increased carbon assimilation, greater biomass accumulation, adaptation mechanisms to shade, and increased water use efficiency (Frechilla et al., 2000; Hogewoning et al., 2012; Murchie & Horton, 1998; Sellaro et al., 2010; Talbott et al., 2002; Vogelmann & Han, 2000).

Radiation in the red region (600–700 nm), perceived by phytochromes, is essential in photosynthesis and photomorphogenesis, particularly for growth, elongation, and germination. Like blue radiation, which is part of the chlorophyll absorption spectrum, red radiation is more efficient in energy transfer in photosynthesis (Holm-Hansen et al., 1965; Mathews, 2006; Siegelman et al., 1958).

Far-red radiation (750–850 nm) only partially comprises the PAR spectrum (400 to 750 nm) (Zhen & Bugbee, 2020). Far-red is crucial in regulating plant photomorphogenesis, especially in growth regulation under shading. This light spectrum is also perceived by phytochromes, which, upon receiving red radiation, convert to a far-red-sensitive conformation. This interconversion of phytochrome regulates the balance between these two ranges of the electromagnetic spectrum it receives, mediating physiological processes such as germination, phototropism, senescence, stem elongation, and stomatal regulation (Franklin & Quail, 2010; Takano et al., 2009). When receiving far-red, phytochrome inhibits stem elongation and promotes chloroplast and anthocyanin formation (Jiao et al., 2007). When the plant receives a sufficient amount of photons from 400 to 700 nm for saturation, photons from the far-red region are also used in photosynthesis, representing an additional use that can contribute to greater energy capture, higher photosynthetic rate, and consequently, increased carbon gain and biomass increment (Zhen & Bugbee, 2020).

Acclimation and priming effects

The increased incidence of solar radiation is a problematic issue that affects crops grown in full sunlight (Caldwell et al., 1995). This increase can cause damages that negatively impacts mainly commercially important plants on various scales, from growth and development, causing reductions in height and biomass accumulation, to molecular damage, which reduces photosynthetic capacity, increases oxidative damage, and degrades enzymes (Bader et al., 2007; Murchie & Niyogi, 2011). Such effects can lead to reduced productivity of these agronomically important plants (Bader et al., 2007; Murchie & Niyogi, 2011).

To mitigate the negative effects of increased solar incidence, techniques such as protected cultivation in greenhouses are recommended, where blocking materials used in the structure's coverings reduce the incidence of UVA and UVB radiation (anti-UV plastic coverings), as well as decrease the intensity of PAR (Alemu et al., 2017; Sabir & Singh, 2013; Silva et al., 2013; Vaast et al., 2016). These techniques are especially important to produce seedlings of agronomically important species such as coffee plants (Alemu et al., 2017; Silva et al., 2013).

However, it is important to note that these techniques (especially anti-UV covers) may alter the proportion of incident solar irradiance on plants, increasing sensitivity to high light intensity and temperature (Wittwer & Castilla, 1995). The reduction in UV incidence on plants established under UV-filtering covers may lead to increased sensitivity to high levels of PAR and alter the PAR/UV ratio, which can affect the production of photoprotective compounds, thus potentially causing damage to the photosynthetic machinery, reducing CO_2 assimilation rate, and decreasing growth and productivity (Klem et al., 2012).

In opposition to techniques that may display vulnerability to plants in adverse environmental conditions, exposure to low doses of environmental stress factors can lead plants to develop a robust protective mechanism (Walters, 2004). Regarding the potential damage of increased solar incidence on plants, acclimation and triggering of defense mechanisms is an essential tool for plant survival, growth, and productivity in challenging environments with excess excitation energy on photosystems (Ahanger et al., 2020; Gjindali & Johnson, 2023; Karpinski et al., 1999).

Priming effect means a pre-conditioning response, induced by exposure to stress factors to develop a protection mechanism, leading plants to enhance their tolerance to subsequent stressors or to respond faster to future stressors (Thomas & Puthur, 2017). However, plants exhibit defense responses not only at priming processes but also at scenarios with excessive radiation, to mitigate the damage (Jansen et al., 1998).

Exposure to light leads leaves to synthesize flavonoids and phenolic compounds as a protection mechanism. Reducing light exposure reduces these protection compounds, thus, leading to high sensitivity to solar light, mainly UV-B radiation (Li et al., 1993). Flavonols are phenolic compounds that enhance light absorption from the UV and blue regions of the spectrum and act as scavengers of Reactive Oxygen Species (ROS) molecules (Solovchenko & Merzlyak, 2008). Phenolic compounds absorb UV in the epidermal tissues, reducing the penetration of radiation into the leaf mesophyll (Chalker-Scott & Fuchigami, 2018; Duval et al., 1999; Wand, 1995).

Another leaf mechanism that mitigates the effects of high levels of UV radiation is leaf thickening, achieved through an increase in specific leaf mass, which non-photosynthetic tissues can hinder the penetration of this radiation into the lower layers of the mesophyll, attenuating the effects of excessive light (Bernado et al., 2022; Niinemets, 2001).

UV-B can activate genes that trigger photomorphogenic signaling pathways, initiating protective mechanisms against excessive UV exposure (Jenkins, 2009). In coffee plants and under current intensities of ultraviolet A and B in tropical regions, at an altitude of 10 m, protection associated with acclimation of photosynthetic rates, water use efficiency (WUE), and fluorescence variables such as the F_v/F_m ratio and photosynthetic index (PI) have been observed (Bernado et al., 2022).

Therefore, energy consumption occurs in the production pathways of protective metabolites such as phenols and flavonoids, to the detriment of energy consumption for plant productivity (Kataria & Guruprasad, 2015). For instance, exposure to UV irradiance induces the production of phenolic compounds for protection and causes decreased flowering and pollen production (Del Valle et al., 2020).

Excessive PAR, defense mechanisms include the reduction of stomatal conductance and the accumulation of photoprotective compounds, including carotenoid and anthocyanin pigments. These pigments display dissipating excess energy. Additionally, exposure to stress doses of PAR activates the antioxidant system, as oxidative damage caused by high solar radiation is observed (Demmig-Adams & Adams, 1996; Demmig-Adams & Adams, 2006; Kalaji et al., 2016a).

Sunburn

As a physiological condition, sunburn results from the combined effects of excessive heat and light radiation, including both visible and ultraviolet light, and is also associated with air humidity (Munné-Bosch & Vincent, 2019; Zhao et al., 2022; Zhao et al., 2022). The sunburn effect, characterized by intense chlorosis of leaf lamina regions, occurs when these activated defense mechanisms are insufficient to repair the damage, allowing the radiation incident on the leaves to directly affect the cells, leading to DNA damage and degradation of photosynthetic pigments and other cellular compounds (D’Alessandro et al., 2020; Gambetta et al., 2021).

Excessive light stress leads to saturation of the reaction center, possibly causing an irreversible destruction of Photosystem II (PSII) as excess excitation energy accumulates (Murata et al., 2007; Ruban, 2015). This imbalance between PSII destruction and repair rates results in photoinhibition, ultimately reducing photosynthetic efficiency (Murata et al., 2007; Nishiyama et al., 2006). Furthermore, heat stress exacerbates this impairment by hindering PSII electron transport, attributable to increased thylakoid membrane fluidity, leading to detachment of the PSII light-harvesting complex (LHC) and compromising PSII integrity (Balfagón et al., 2019; Mathur et al., 2014).

Sunburn can occur a consequence from inadequate acclimation, in which over exposure to unfavorable environmental conditions without pre-conditioning results in severe damage to the photosynthetic apparatus and, consequently, the complete loss of photosynthetic tissue (Caldwell et al., 1983; Daniell et al., 1969; Krause et al., 2015; Robberecht & Caldwell, 1983). Reduction of solar light (shading) is found to be a sensitivity factor to plants, increasing severity of necrosis, due to reduced leaf transpiration (Chang & Miller, 2005).

Various types of sunburn can occur at leaves, as yellowing sunburn, photooxidative sunburn, but sunburn can manifest mainly as necrosis or browning (also called bronzing), it varies as the intensity of solar radiation and the temperature of leaf tissue (Gambetta et al., 2021; Racskó et al., 2010).

PAR intensity influences the extent of UV-B radiation damage in plants, with higher levels of PAR potentially increasing the severity of leaf symptoms like necrosis (Cen & Bornman, 1990). Light-induced photosynthetic stress may contribute to necrosis. Photoinhibition of photosynthesis, which can be induced by high photon flux density or by the interaction between light and other environmental stress factors (such as heat and air humidity), may damage the photosynthetic process and contribute to cell death (Powles, 1984).

***Coffea canephora* general aspects**

The *Coffea* genus originated in the African continent 150 to 350 thousand years ago, is part of the Rubiaceae family and Oxoroidea subfamily, and comprises 130 cataloged species (Davis & Rakotonasolo, 2021). *C. canephora* represents 40% of the coffee economy (DaMatta et al., 2018; DaMatta & Ramalho, 2006; Davis et al., 2019). Coffee cultivation is concentrated in regions of South America, Asia, Oceania, Central America, and Africa. Production takes place in more than 80 countries, with the Brazil being the main productor country, representing almost all Soth America production (ICO, 2023).

C. canephora is a diploid species (2n = 2x = 22), native to the understory of equatorial forests in the African region corresponding to the countries Congo and Uganda. The growth and development of this species occurred in lowland regions, ranging from sea level to 1200 m altitude, with average annual temperatures between 24 and 26°C and average annual precipitation exceeding 2000 mm (Coste, 1992; DaMatta & Ramalho, 2006; Ferreira et al., 2019). Due to its evolutionary origin, *C. canephora* is sensitive to environmental changes, being susceptible to damage associated with the intensity of ultraviolet radiation, infra and supra-optimal temperatures, and high air vapor pressure deficit (VPD) (Bernado et al., 2021; Kath et al., 2020; 2022; Ramalho et al., 2014).

The coffee supply chain involves over 500 million people from its management in the fields to the final product (DaMatta & Ramalho, 2006). Coffee cultivation worldwide is concentrated in regions across South America, Asia, Oceania, Central America, and Africa (ICO, 202). Except for Colombia, where shaded coffee cultivation is common, coffee-producing countries typically plant in full sun (Atallah et al., 2018). This highlights the importance of research related to light stress in *C. canephora*, particularly ultraviolet stress, considering the scenario of increasing solar radiation and the sensitivity of this specie.

MATERIAL AND METHODS

Experimental site and plant description

The experiment was conducted at the Universidade Estadual do Norte Fluminense Darcy Ribeiro, Campos dos Goytacazes, Rio de Janeiro (21º44'47" S and 41º18'24" W, at an altitude of 10 m), Southeastern Brazil, using a relevant cropped genotype, from the main commercial coffee species: *Coffea canephora* cv. Conilon LB1.

On September 11th, 2022, in tropical spring conditions, 120-day-old cuttings, with an average of five pairs of leaves and a height of 29.66 cm were transplanted. Cuttings were cultivated in 32 L pots, which were filled with a substrate and sand mixture (3:1). The transplanting day was considered the first day of the experiment. All plants were regularly watered (pot capacity). Agricultural practices of coffee plant cultivation, including fertilization and disease control were used, according to demands.

Thirty-two plants were grown in two ultraviolet (UV) conditions [Ambient UV environment (UVam) and reduced UV environment UVre]. The ambient UV environment (UVam) (1): the plants were grown under corrugated glass that maintains UV intensities similar to the local external environment, excluding only 16% UV-A and 0% UV-B. The reduced UV environment (UVre) (2): the plants were grown under a transparent polycarbonate compartment, which excludes 70% UV-A and 90% UV-B. Photosynthetic active radiation (PAR, μmol m^{-2} s^{-1}) intensities were similar between both treatments (UVam and UVre).

Micrometeorological parameters for each environment were characterized daily using temperature (°C) and relative humidity (RH, %) sensors (AK172 mini, Akso Produtos Eletrônicos Ltda, RS, BR), and dataloggers with attached sensors for monitoring PAR (PAR Photon Flux Sensor, METER Inc., Pullman, WA, USA) and UV light (UV, μmol m^{-2} s^{-1}) (Spectrum Light Scout UV Light Sensor, Spectrum Technologies, Glenside, Pennsylvania, USA). Sensors were positioned at the top of the coffee canopies and data were collected each 15 minutes for 24 hours, daily. The average, maximum, and minimum values were calculated daily.

From temperature and RH data, the air vapor pressure deficit (VPD_{air}, kPa) was calculated according to Jones (1992) using the formula $VPD_{air} = 0.61137 \cdot \exp((17.502 \cdot T{\circ}C)/(240.97 + T{\circ}C)) \cdot (1-(RH\%/100))$.

Physiological traits analysis after sunburn: contextualization

On 50 days after transplanting (50 DAT) (October 30th), light and temperature values started to decline for 33 days inside of the UVam and UVre [decline period (DP)].

From 50 DAT to 83 DAT (December 2nd) maximum PAR values declined from 1874 and 1738 µmol m^{-2} s^{-1} to 882 and 818 µmol m^{-2} s^{-1} for UVam and UVre, respectively. On this period (33 days, DP), PAR declined 53% in both environments, and increased after 83 DAT (December 2nd) to 1637 and 1518 µmol m^{-2} s^{-1} for UVam and UVre at 93 DAT (December 12th) (Figures 1A and 1B). After 83 DAT, PAR increased 46% during 10 days [increasing period (IP)] in both UV conditions.

Maximum temperature values declined on DP from 47 and 45 °C for UVam and UVre (50 DAT), to 34 and 34 °C for UVam and UVre (83 DAT), respectively. Thus, temperature declined 25% in both UV conditions. After 83 DAT, temperature increased 24% (IP), which maximum values were 46 and 45 °C for UVam and UVre, at 93 DAT (Figures 1C and 1D).

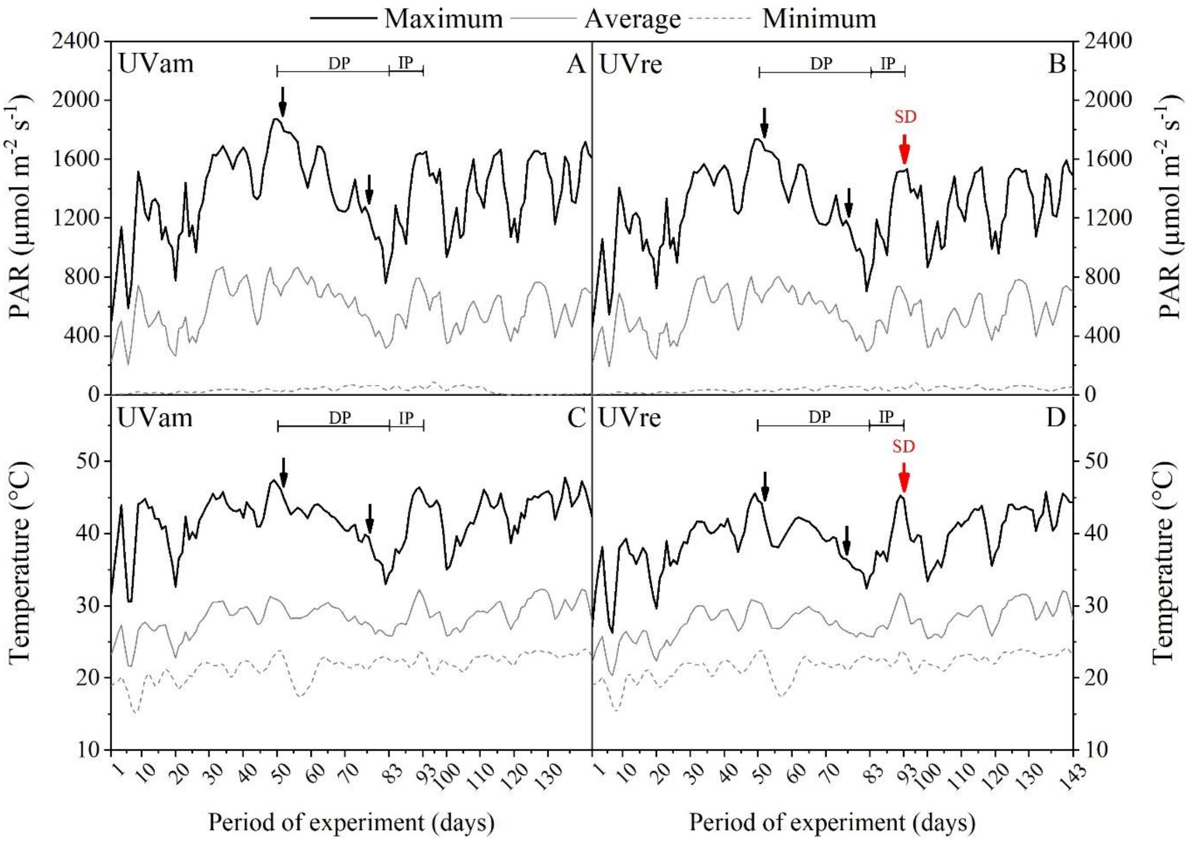

Figure 1: Diurnal maximum, average and minimum fluctuations of Photosynthetic active radiation (PAR, µmol m^{-2} s^{-1}) (A, B) and temperature (°C) (C, D), calculated daily, registered from September 11th, 2022, to January 31th, 2023, in near ambient UV environment (UVam) (A, C) and in a reduced UV environment (UVre) (B, D). Black arrows indicate the interval of monitoring individual leaf elongation on tagged leaves; red arrow indicate the day of sunburn occurrence. DP, IP and SD indicate decrease period, increasing period and sunburn day, respectively.

Sunburn analysis

Plants on UVre had sunburn on the leaves exposed to solar incidence, after the highest solar radiation intensity at 93 DAT [sunburn occurrence day (SD)].

To characterize sunburn areas, plant images on a 90° perspective from the plant apex (Figure 4A) were submitted to the photographic image processing software ImageJ. Images of plants which had sunburn were used to measure sunburned area and total leaf area. The percentage of sunburned area was calculated to demonstrate the proportion of sunburn to the 90° top-down approach area.

The same was applied to the tagged leaves which had their growth and development monitored daily (Figure 4B). Images of leaves with sunburned areas were used to demonstrate the proportion of sunburn on tagged leaves.

At 94 DAT (one day after SD), physiological assessments were conducted between 8:00 and 10:00 to understand the unexpectedly occurring physiological damage associated with sunburn. The assessments were performed on tagged leaves, which were used for calculating sunburned leaf area on ImageJ. These leaves had their growth and development monitored by central vein leaf elongation and SPAD index measurements from 53 DAT to 77 DAT, coinciding with the decrease in light and temperature values.

Leaf growth traits: Individual leaf elongation and soil plant analysis development (SPAD index)

The central vein elongation of tagged young leaves (initial length = 4.2 ± 0.5 cm), emitted at the second plagiotropic branch counting from the top of the orthotropic plant axis of each plant (n=16) was assessed to express the dynamic of individual leaf elongation (Rakocevic & Matsunaga, 2018). These length measurements were taken at the interval of 4 days, from 53 DAT until the leaf attained its final length at 77 DAT, when leaves attained the maximum elongation.

Soil plant analysis development (SPAD index) was assessed at an interval of 4 days, on the tagged leaves used for individual leaf elongation measurements from 53 DAT to the 93 DAT. The SPAD value was estimated with a portable chlorophyll meter, SPAD-502 "Soil Plant Analyzer Development" (Minolta Co. Ltd., Osaka, Japan). Assessments were conducted at three different points on the leaf lamina, avoiding the veins. At 93 DAT (SD), on leaves with sunburned areas, the SPAD index measurements were taken on green areas.

Spectral reflectance measurements

Leaf reflectance was determined using the CI-710/720 mini leaf spectrometer (CID-Bioscience, Camas, Washington, USA). Measurements were taken at tagged leaves on 94 DAT, between 8:00 and 10:00. Spectral reflectance (ρ) measurements were carried out at wavelengths from 400 nm to 1000 nm, on the same tagged leaves of individual leaf elongation and SPAD analysis. On leaves with sunburned areas, the reflectance measurements were taken on green areas. Using the software (SpectraSnap! Version 1.1.3.150) coupled to the equipment system, photochemical reflectance index (PRI) was calculated, using the equation $(R_{531} – R_{570}) / (R_{531} + R_{570})$ (Gamon et al., 1992) and Plant Senescence Reflectance Index (PSRI) was calculated by (R680 - R500) / R750 (Merzlyak et al., 1999a). R means the reflectance (ρ).

Non-modulated chlorophyll a fluorescence

Non-modulated fluorescence emission of chlorophyll *a* was evaluated at the tagged leaves with a non-modulated fluorimeter, Pocket PEA (Plant Efficiency Analyzer, Hansatech, King’s Lynn, Norfolk, UK) on 94 DAT, between 8:00 and 10:00. Before assessments, the sample area of the leaf was dark-adapted for 30 minutes using leaf clips (Hansatech, King’s Lynn, Norfolk, UK). On leaves with sunburned areas, measurements were taken on green areas. This dark adaptation allowed the PSII reaction centers to reach the "open" condition and minimized heat loss (Strasser et al., 2000).

After this adaptation, the sample was subjected to saturating irradiance (3500 $\mu mol\ m^{-2}\ s^{-1}$) to obtain rapid chlorophyll *a* fluorescence transients from PSII, used to detect stress effects on photosynthetic processes (Oukarroum et al., 2009).

Among the parameters, F_0 represents the emission of chlorophyll *a* in the PSII antenna structure, at 50 ms intensity (minimum fluorescence level of dark-adapted leaves); F_m represents the maximum fluorescence obtained for continuous light intensity (maximum fluorescence level of dark-adapted leaves); F_v corresponds to the difference between F_0 and F_m, indicating the maximum photochemical extinction capacity, occurring within 200-300 ms after dark exposure.

Maximum quantum yield of PSII (F_v/F_m) and photosynthetic performance index (PI) were calculated. PI represents the cascade processes of energy from the first absorption event to plastoquinone reduction (Strasser et al., 2004). Its calculation was carried out as $PI = (1 – (F_0/F_m))/M_0\ (F_m - F_0)/F_0\ (1 – V_j)/V_j$, where V_j corresponds to the relative variable fluorescence at 2 ms, calculated as $V_j = (F_j – F_0)/(F_m – F_0)$; where F_j is the fluorescence intensity at step j (at 2 ms). M_0 is the initial slope of the fluorescence kinetics, derived from the equation $M_0 = 4\ (F_{300}$ ms $– F_0)/(Fm – F_0)$.

Modulated chlorophyll a fluorescence

Modulated fluorescence emission was assessed on 94 DAT, between 8:00 and 10:00, on tagged leaves, which were covered with laminated paper to dark-adaptation throw 30 minutes and analyzed using a chlorophyll fluorescence imaging system (CFIS) model FluorCam 800MF (Photon System Instruments – Drásov, Czech Republic).

The CFIS was pre-configured and calibrated for a predefined quenching protocol (Figure 2) to evaluate the 'Kautsky effect' of a Pulse Amplitude Modulated (PAM) system, through a fluorescence induction curve in the light-adapted state and the relaxation dynamics after dark adaptation of the previously illuminated sample (Baker, 2008).

The protocol begins with the measurement of F_0, followed by a saturation pulse to determine F_m. Subsequently, the actinic light was turned on to induce the photochemical phase of photosynthesis. During the actinic light period, successive saturation pulses were applied, reaching the maximum pulse of 1647.6 µmol $m^{–2}\ s^{–1}$ to determine F_m', until a steady state of photosynthesis is achieved (Yao et al., 2018). This steady state reveals the dynamics of non-photochemical quenching during light adaptation. Following this, the actinic light was turned off, and sequential saturation pulses were applied, reaching the maximum pulse of 2950 µmol $m^{–2}\ s^{–1}$ to determine the relaxation of non-photochemical quenching, the reopening of the PSII reaction centers, and the relaxation of the quantum yield of PSII (Yao et al., 2018). After each saturation light pulse and dark conditions, a pulse of far-red photons was applied to determine F_0'.

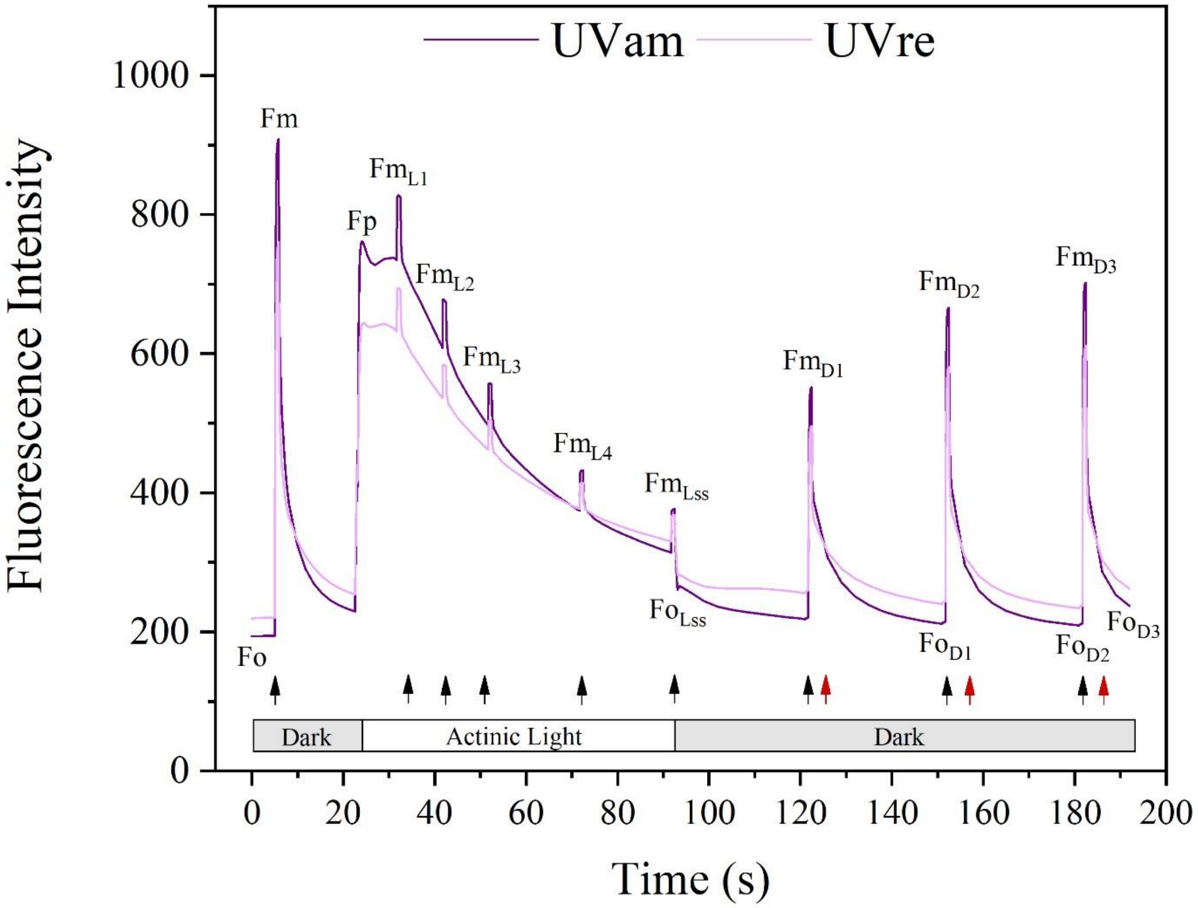

Figure 2: Quenching analysis based on modulated fluorescence in leaves of *C. canephora* grown in a near ambient UV environment (UVam) and in a reduced UV environment (UVre). Variables with the subscript 'L_n' correspond to the analysis of the sample exposed to actinic light, and variables with the subscript 'D_n' correspond to the analysis of the sample during the quenching relaxation period in the dark, where 'L' is related to light, 'D' to dark, and 'n' refers to the sequence of applied saturation pulses in the period. Unsubscripted variables refer to the sample adapted to the dark. Black arrows represent the moment of applying a saturation pulse capable of transiently oxidizing all open PSII reaction centers and saturating the electron transport chain. Dark red arrows indicate the moment of applying the far-red pulse (determination of F_0'), responsible for exciting PSI and reoxidizing the plastoquinone pool, and Q_A (quinone A) associated with PSII.

From the basic modulated parameters, calculated after the induction curve and quenching relaxation, other chlorophyll fluorescence parameters were also calculated (Table 1), assisted by FluorCam 7 software.

Table 1: Modulated chlorophyll *a* fluorescence parameters.

Parameter	Description
F_0	Minimum fluorescence in dark-adapted state
F_m	Maximum fluorescence in dark-adapted state
$QY_{Lss} = (Fm_{Lss} - F_{0\ Lss}) / Fm_{Lss}$	Steady-state PSII quantum yield
$QY_{D3} = (Fm_{D3} - F_{0\ D3}) / Fm_{D3}$	Instantaneous PSII quantum yield during dark relaxation
$qL_{Lss} = (F_m' - F_S')/(F_m' - F_0') \cdot F_0/F_S'$	Coefficient of photochemical quenching in steady state based on the lake model of PSII
$qP_{Lss} = (F_{m\ Lss} - F_{t\ Lss})/(F_{m\ Lss} - F_{0\ Lss})$	Coefficient of photochemical quenching in steady state based on the puddle model of PSII
$qP_{D3} = = (F_{m\ D3} - F_{t\ D3})/(F_{m\ D3} - F_{0\ D3})$	Coefficient of photochemical quenching during dark relaxation
$NPQ_{Lss} = (F_m - F_{m\ Lss}) / F_{m\ Lss}$	Steady-state non-photochemical quenching
$NPQ_{D3} = (F_m - F_{m\ D3}) / F_{m\ D3}$	Instantaneous non-photochemical quenching during dark relaxation
$R_{fd\ Lss} = (F_P - F_{t\ Lss}) / F_{t\ Lss}$	Fluorescence decline ratio in steady state

Leaf gas-exchange measurements

Leaf gas exchanges were assessed using the infrared gas analyzer (IRGA) (LI-6400, LI-COR, Lincoln, NB, USA) on the tagged leaves. Measurements were performed using an external CO_2 supply fixed at 415 µL L^{-1}. The photosynthetic photon flux density (PPFD) was adjusted to 1500 μmol m^{-2} s^{-1} (from a red-blue light source 6400-02B). The following measurements were conducted: net CO_2 assimilation rate (A_{net}, μmol CO_2 m^{-2} s^{-1}), transpiration (E, mmol H_2O m^{-2} s^{-1}), stomatal conductance (g_s, mol m^{-2} s^{-1}), and leaf-to-air vapor pressure deficit ($VPD_{leaf-air}$, kPa).

Specific leaf mass

Leaf discs measuring 5 cm², obtained from the tagged leaves on 94 DAT, were collected and dried at 70°C in a forced-air oven for 72 hours to obtain the specific leaf mass (SLM, g m^{-2}) (n=16).

Total leaf area

The experiment was maintained after the sunburn physiological characterization, to analyze the total leaf growth after the environmental conditions that lead to sunburn. At 143 DAT, the total leaf area of each plant was determined by removing all leaves, and each one was assessed using a leaf area meter (Li-3100, Li-Cor, Lincoln, NE, USA) (n=16).

Statistical analysis

Thirty-two plants were used (sixteen plants for each environment), in a completely randomized design.

The analyses were conducted to characterize the effects of ultraviolet radiation between the UVam and UVre environments. Central Vein Elongation and SPAD index over time was represented by linear regression models. The effect of UV was compared in both environments through analysis of variance (ANOVA), and averages were compared using the Tukey test at a 5% probability.

The remaining variables were subjected to the t-test, with a 5% probability, for comparison between the environments. The analyses were performed using computational resources from the R software (R Core Team, 2020). When conducting ANOVA and Tukey test, the "stargazer" and "ExpDes.pt" packages were used.

RESULTS

Micrometeorological variables

PAR fluctuations

During the 143 days of experiment, maximum PAR values were 1370.92 and 1271.49 µmol m^{-2} s^{-1}; average PAR values were 588.38 and 557.94 µmol m^{-2} s^{-1}; minimum values were 31.29 and 38.73 µmol m^{-2} s^{-1} (for UVam (Figure 1A) and UVre (Figure 1B), respectively).

Air temperature fluctuations

During the experiment period, maximum air temperature was 41.93 and 39.26 °C, average air temperature was 28.44 and 27.76 °C, minimum air temperature was 21.59 and 21.64 °C (for UVam (Figure 1C) and UVre (Figure 1D), respectively).

UV incidence fluctuations

Regarding all experiment period (143 days), maximum UV incidence was 107.96 and 2.40 µmol m^{-2} s^{-1}, average UV was 51.43 and 1.14 µmol m^{-2} s^{-1}, minimum UV incidence was 6.27 and 0.13 µmol m^{-2} s^{-1} (for UVam and UVre, respectively).

On DP, maximum UV incidence declined 43.55% in both environments (from 145.13 and 3.25 µmol m^{-2} s^{-1} to 81.93 and 1.84 µmol m^{-2} s^{-1} in UVam and UVre, respectively). Afterwards on IP, UV incidence increased 33.24% on both environments, attaining 122.73 and 2.75 µmol m^{-2} s^{-1} in UVam and UVre (Figures 3A and 3B).

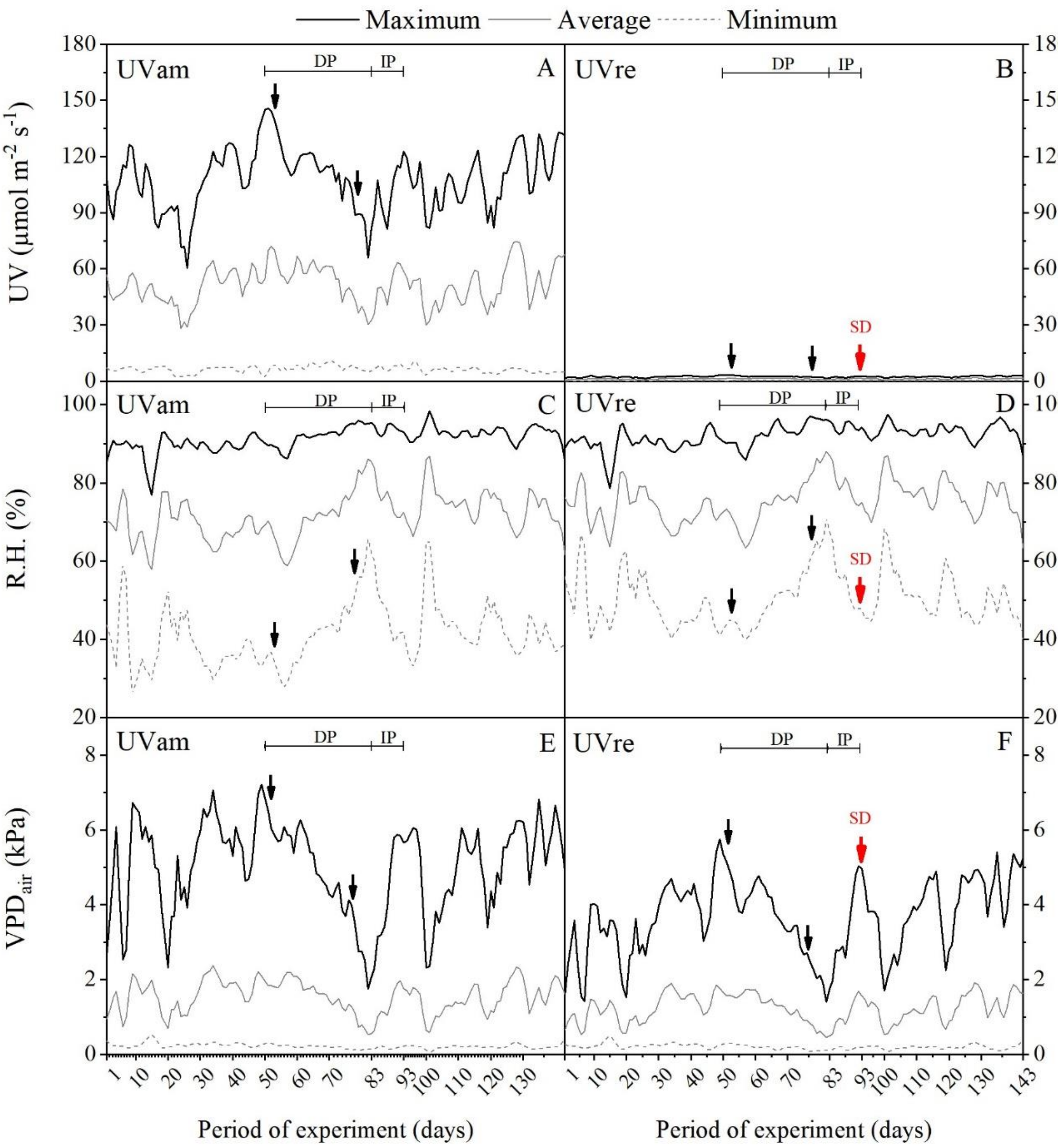

Figure 3: Diurnal maximum, average and minimum fluctuations of Ultraviolet Radiation (UV, µmol m^{-2} s^{-1}) (A, B), Relative Humidity (RH, %) (C, D), and Air Vapor Pressure Deficit (VPD_{air}, kPa) (E, F), calculated daily, registered from September 11th, 2022, to January 31th, 2023, in near ambient UV environment (UVam) (A, C, E) and in a reduced UV environment (UVre) (B, D, F). Black arrows indicate the interval of monitoring individual leaf elongation on tagged leaves; red arrow indicate the day of sunburn occurrence. DP, IP and SD indicates decrease period, increasing period and sunburn day, respectively.

Relative humidity (RH) and air vapor pressure deficit (VPD_{air})

Regarding the experiment period, RH maximum values were 91.39 and 92.10%, average values were 71.66 and 75.36%, minimum RH values were 41.33 and 50.45% (for UVam and UVre, respectively). RH maximum values maintained high and stable during the experiment, but minimum values fluctuations were inverse to light and temperature DP and IP.

During light and temperature DP, minimum RH increased from 34.80 and 42.57% to 62.20 and 67.50% (in UVam and UVre, respectively), afterwards, decreasing from these values to 41.87 and 47.67% in UVam and UVre on 93 DAT (Figures 3C and 3D). The amount of RH increase was 40.35%, followed by a 30.97% decrease.

Regarding all experiment period, maximum VPD_{air} was 5.01 and 3.67 kPa, average was 1.54 and 1.23 kPa, and minimum VPD_{air} was 0.22 and 0.21 kPa (for UVam and UVre, respectively).

On light and temperature DP, VPD_{air} maximum values also declined 68.44% in both environments (from 6.86 and 5.34 kPa to 2.08 and 1.77 kPa in UVam and UVre, respectively). Afterwards, increasing 63.80% on IP, attaining 5.67 and 4.97 kPa in UVam and UVre, respectively, on SB (Figures 3E and 3F).

Sunburned areas

UVam plants didn’t show sunburn areas. Sunburn occurred to 56.25% of UVre plants. These plants had 10.74% of its leaf area damaged by sunburn (Figure 4A).

Regarding the UVre tagged leaves used on physiological analyses, 31.25% had sunburned areas. These tagged leaves had 24.47% of their area damaged by sunburn (Figure 4B).

Figure 4: *C. canephora* grown under reduced UV environment (UVre). Images were taken at 94 DAT, showing visible leaf damage characterized by sunburn on a 90-degree perspective from the plant apex (A) and on a tagged leaf, taken for physiological analysis (B).

Dynamics of individual leaf elongation and SPAD index

UVam had lower elongation, attaining 10.03 cm length at the end of the linear elongation period, UVre attained 12.74 cm length. The central leaf vein elongation rate was ~1.19 cm and ~1.36 cm for the four-day intervals (for UVam and UVre, respectively).

SPAD values attained 61.53 and 55.58 for UVam and UVre. On sunburn day (SD), these values reduced to 59.63 (3.10%) and 46.83 (15.73%) respectively, meaning a significant lower SPAD only on UVre in SD.

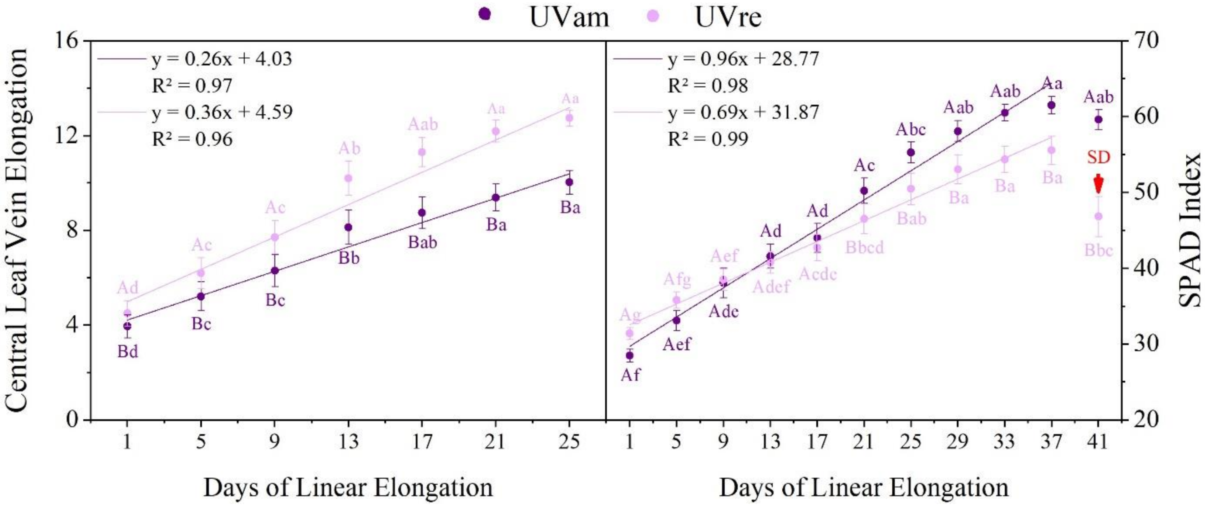

Figure 5: Central Leaf Vein Elongation (A) measured at an interval of 4 days from 53 DAT to 77 DAT and SPAD index (B) measured at an interval of 4 days from 53 DAT to 93 DAT on tagged leaves for *C. canephora* plants grown under near ambient UV environment (UVam) and reduced UV environment (UVre). Letters upwards indicate significant differences between environments, based on Tukey's test, and letters downwards indicate significant differences between days. Estimated mean values (n = 16) are shown. Leaf elongation $p_{environment} < 0.05$; $p_{days} < 0.05$ and $p_{environment*days} > 0.05$; SPAD index $p_{environment} < 0.05$; $p_{days} < 0.05$ and $p_{environment*days} < 0.05$. Red arrow and “SD” indicate the sunburn day.

Spectral reflectance

UVam plants had increased PRI in 68.77% (0.06 *vs.* 0.02 for UVam and UVre, respectively) (Figure 6A) and decreased PSRI in 49.98% (-0.05 vs. -0.02 for UVam and UVre) (Figure 6B).

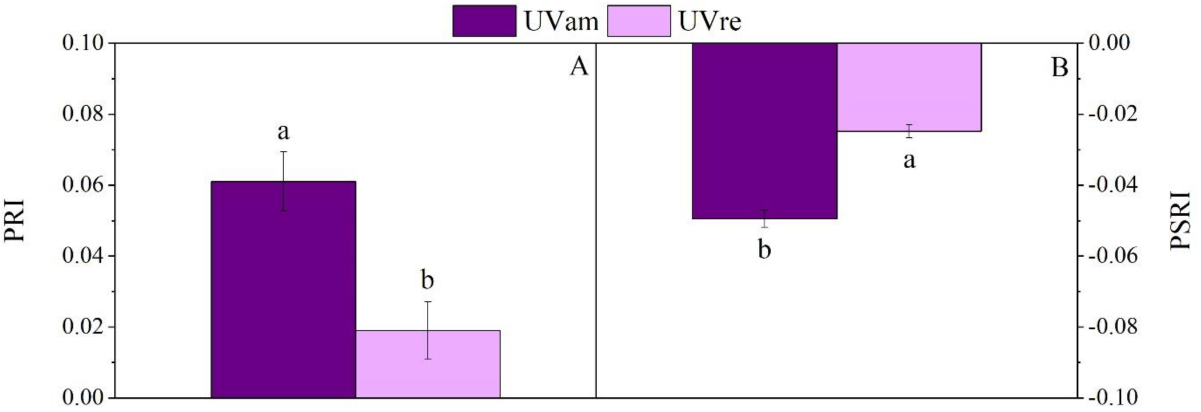

Figure 6: Photochemical Reflectance Index (PRI) (A) and Plant Senescence Reflectance Index (PSRI) (B) for *C. canephora* plants grown under near ambient UV environment (UVam) and reduced UV environment (UVre). Estimated mean values (n = 16) are shown and different letters indicate significant differences (t-test; p < 0.05).

Chlorophyll a fluorescence

UVam plants had increased F_v/F_m in 15.92% (0.73 *vs.* 0.61 for UVam and UVre, respectively) (Figure 7A) and increased PI in 48.37% (4.22 *vs.* 2.18 for UVam and UVre) (Figure 7B).

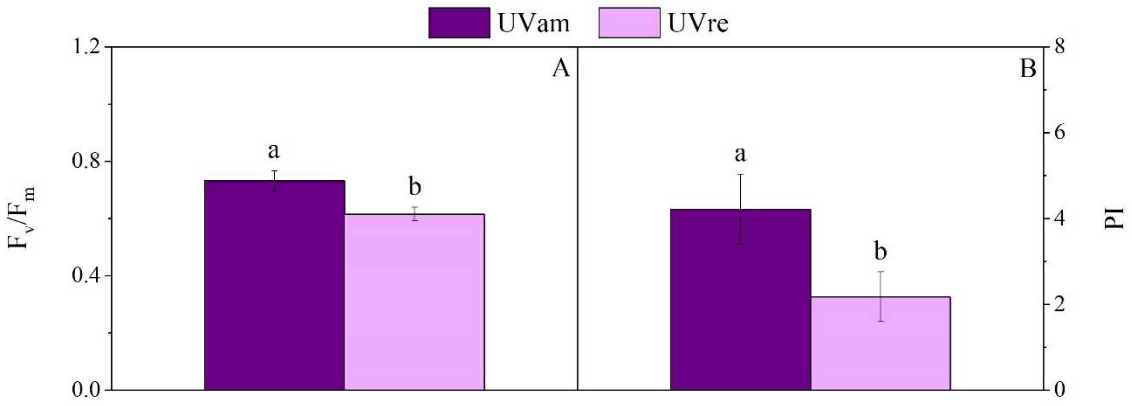

Figure 7: Maximum quantum yield of PSII (F_v/F_m) (A) and photosynthetic performance index (PI) (B) for *C. canephora* plants grown under near ambient UV environment (UVam) and reduced UV environment (UVre). Estimated mean values (n = 16) are shown and different letters indicate significant differences (t-test; $p < 0.05$).

UVam plants consistently showed higher values of on steady-state fluorescence parameters. The amount of highness was 37.61% for QY_{Lss} (0.16 *vs.* 0.10 for UVam and UVre) (Figure 8A), 25.05% for NPQ_{Lss} (1.42 *vs.* 1.07 for UVam and UVre) (Figure 8C), 35.76% for qP_{Lss} (0.57 *vs.* 0.37 for UVam and UVre) (Figure 8E), 35.76% for qL_{Lss} (0.57 *vs.* 0.37 for UVam and UVre) (Figure 9A) and 31.06% for Rfd_{Lss} (1.54 *vs.* 1.06 for UVam and UVre) (Figure 9B).

Regarding the parameters during dark relaxation, UVam was 14.57% higher at QY_{D3} (0.69 *vs.* 0.59 for UVam and UVre) (Figure 8B), 2.99% higher at qP_{D3} (0.94 vs. 0.91 for UVam and UVre) (Figure 8F). UVam and UVre environments had no differencing impact on NPQ_{D3} values (Figure 8D).

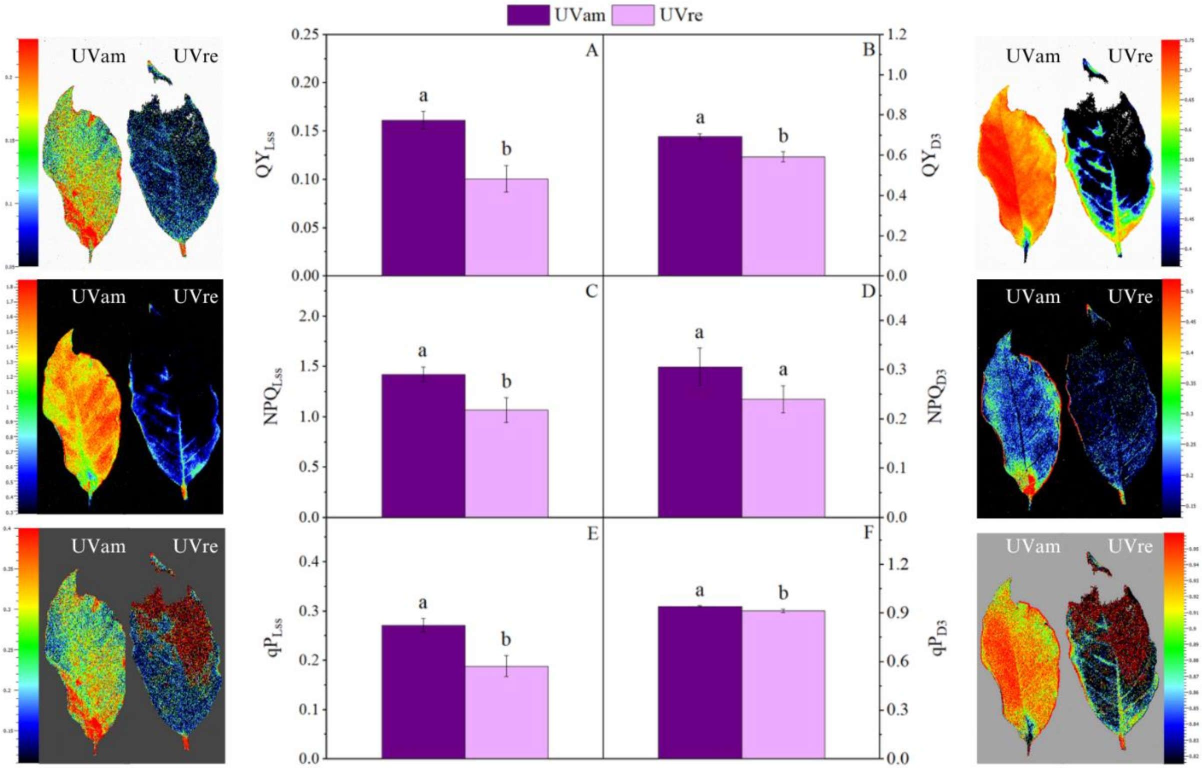

Figure 8: Steady-state PSII Quantum Yield (QY_{Lss}) (A), Instantaneous PSII Quantum Yield (QY_{D3}) (B), Steady-state Non-photochemical Quenching (NPQ_{Lss}) (C), Instantaneous Non-Photochemical Quenching (NPQ_{D3}) (D), Photochemical Quenching in Steady State based on the puddle model of PSII (qP_{Lss}) (E), Photochemical Quenching During Dark Relaxation (qP_{D3}) (F), for *C. canephora* plants grown under near ambient UV environment (UVam) and reduced UV environment (UVre). Estimated mean values (n = 16) are shown and different letters indicate significant differences (t-test; $p < 0.05$). The color scale next to each image represents the emission intensity of each parameter throughout the leaf tissue. The lack of leaf tissue on UVre leaf indicates a tissue portion of possible necrosis (from sunburn effect), with no response to fluorescence analysis.

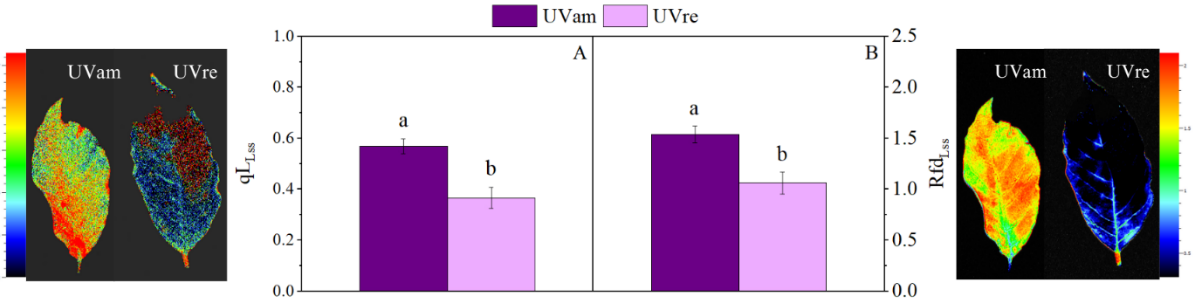

Figure 9: Photochemical Quenching in Steady State based on the lake model of PSII (qL_{Lss}) (A) and Fluorescence Decline Ratio in Steady State (Rfd_{Lss}) (A) for *C. canephora* plants grown under near ambient UV environment (UVam) and reduced UV environment (UVre). Estimated mean values (n = 16) are shown and different letters indicate significant differences (t-test; $p < 0.05$). The color scale next to each image represents the emission intensity of each parameter throughout the leaf tissue. The lack of leaf tissue on UVre leaf indicates a tissue portion of possible necrosis (from sunburn effect), with no response to fluorescence analysis.

Leaf gas exchanges

UVam plants showed higher A_{net} values on 41.43% (7.11 *vs.* 4.16 µmol CO2 m^{-2} s^{-1} for UVam and UVre). UVam showed higher g_s on 54.95% (0.11 *vs.* 0.05 mol m^{-2} s^{-1} for UVam and UVre) (Figures 10A and 10B).

UVam showed 42.17% higher *E* (2.15 *vs.* 1.24 for UVam and UVre). UVam showed 17.66% lower $VPD_{leaf-air}$ (2.09 *vs.* 2.54 for UVam and UVre) (Figures 10C and 10D).

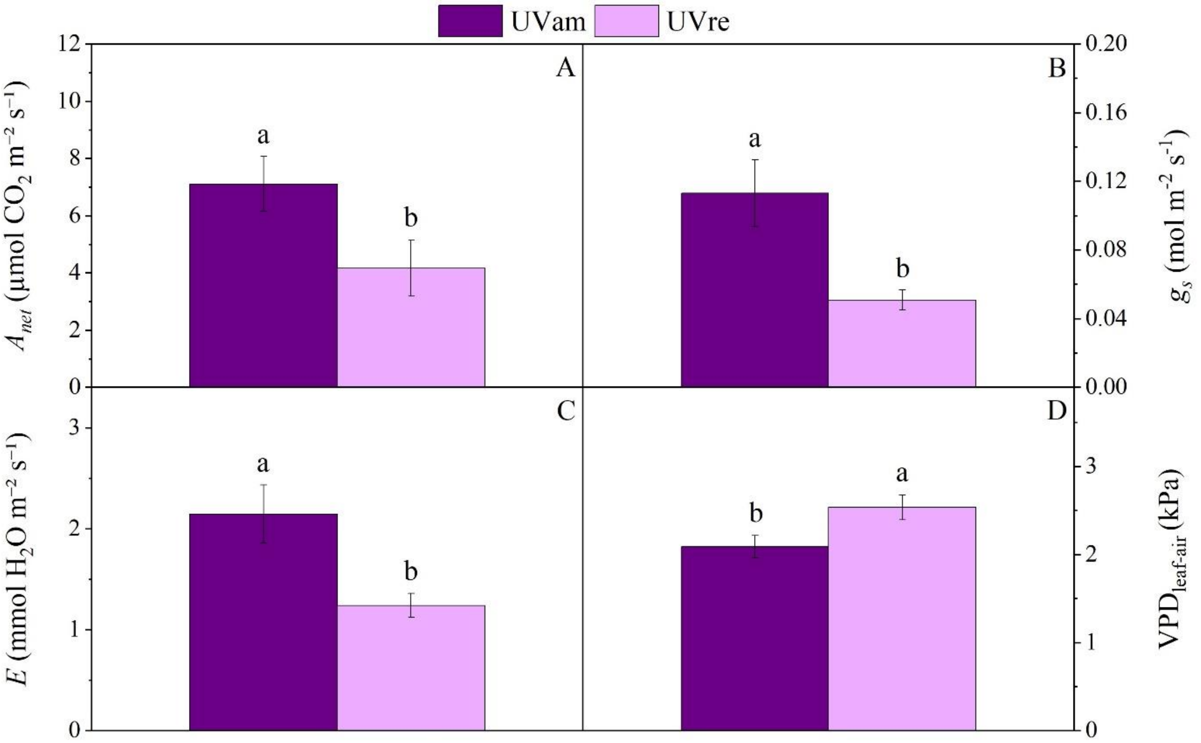

Figure 10: Net CO_2 assimilation rate (A_{net}) (A), stomatal conductance (g_s) (B), transpiration rate (C) and leaf-to-air vapor pressure deficit ($VPD_{leaf-air}$) (D) for *C. canephora* plants grown under near ambient UV environment (UVam) and reduced UV environment (UVre). Estimated mean values (n = 16) are shown and different letters indicate significant differences (t-test; $p < 0.05$).

Association between leaf area expansion and specific leaf mass (SLM)

Leaf area was 25.81% lower on UVam plants (2007.22 *vs.* 2705.60 cm² for UVam and UVre, respectively) (Figure 11A), while SLM, which is associated with leaf thickness, was 13.37% higher on UVam (82.59 *vs.* 71.55 g m^{-2} for UVam and UVre)

(Figure 11B), meaning that the relation in growth in expansion *vs.* growth in thickness was inversely proportional on both environments.

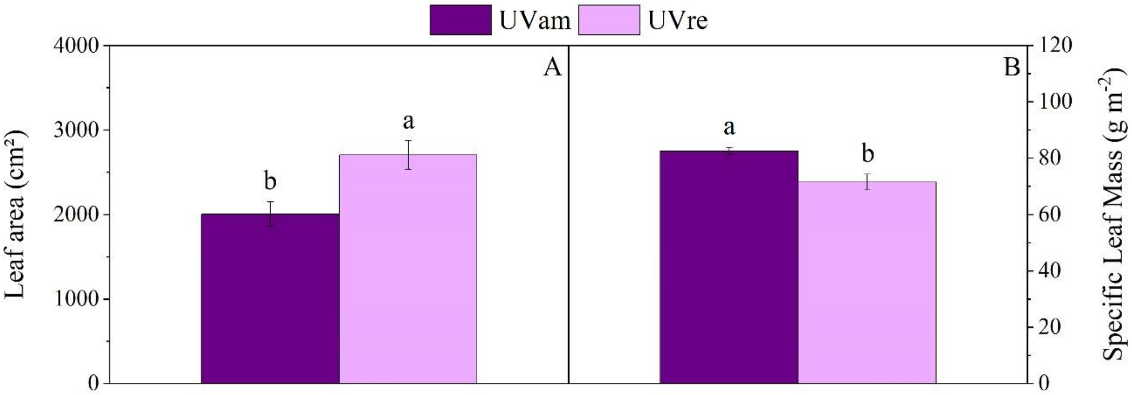

Figure 11: Leaf area (A) and Specific Leaf Mass (SLM) (B) for *C. canephora* plants grown under near ambient UV environment (UVam) and reduced UV environment (UVre). Estimated mean values (n = 16) are shown and different letters indicate significant differences (t-test; $p < 0.05$).

DISCUSSION

The findings of this research emphasize the crucial importance of UV radiation on rustification and acclimation of *Coffea canephora* leaves to supra-optimal solar irradiance.

Dynamics of individual leaf elongation and development

Morphological changes were observed in *Coffea canephora* when submitted to differently UV environment, supporting our hypothesis of UV acclimation. The UV solar radiation caused negative impacts on leaf elongation of Coffea *canephora* on UVam (Figure 5A). Morphology is one of the most sensitive parameters impacted of UV on coffea plants (Bernardo et al., 2021). Furthermore, UV radiation is crucial for plant growth regulation. However, reduced intensity is important for positive photomorphogenic induction, such as increment of cuticle tissue, based on the activation of phytochrome B and the UVR8 gene (Boccalandro et al., 2001; Jenkins, 2017; Krauss et al., 1997).

UVre environment effect on plant growth can be associated with a like-shading effect since changes in epidermal transmittance due to shading are correlated to UV reduction. UVre like-shading effects include increased leaf elongation (Figure 5A) and consequently, higher leaf area (Figure 11A) (Gregoriou et al., 2007; Liu et al., 2016; Ryel et al., 2010).

Despite lower leaf vein elongation rate, UVam increased the SPAD index when leaves attained maturity (Figure 5B). This fact suggests that at gradually low UV level (DP), UVam leaves displayed efficient acclimatation, since higher SPAD, which indicates higher chlorophyll content (Castro et al., 2014), can be associated with higher production of UV screen compounds, like flavonoids (Ferreyra et al., 2021; Kubasek et al., 1992; Pinzón-Sandoval et al., 2022). In addition, SPAD is a good tool for diagnosing the integrity of the photosynthetic system and N content in coffee leaves (Giunta et al., 2002; Netto et al., 2005; Rustioni, 2017). In this research, SPAD values in UVam condition were associated with foliar protection against photosynthetic damage on *Coffea canephora* since plants with high SPAD index showed less damage.

Impact of UV on photosynthetic capacity

The most interesting of this study centered on the photosynthetic acclimation of *C. canephora* when submitted to UV radiation. The UVam environment impacted positively in PRI values (Figure 6A). PRI is one of the most relevant reflectance indexes, which expresses the plants' responses to incident light and how it is efficiently used on photosynthesis (Alam et al., 1996; Garbulsky et al., 2011). PRI reflects the xanthophyll cycle activity, which regulates stress responses to excess light energy against oxidative stress (Demmig-Adams & Adams, 1996; Gamon et al., 1992; Kuczynska et al., 2017). In addition, PRI is correlated to carotenoid content, contributing to photoprotection from the role of carotenoids on energy dissipation (Adams III et al., 2002; Filella & Peñuelas, 1999; Gamon et al., 2023; Kohzuma et al., 2021). In this study, PRI value of UVam indicates higher acclimation for photosynthetic light-use efficiency in *C. canephora* plants, which could be a protection for plants submitted to UVam against the sunburn occurrence on sunburn day (SD) (Figure 6A). Additionally, higher PRI may not only acclimate plants to tolerate high light but also high temperatures (Sukhova et al., 2022), which had increased values on SD.

After increasing period (IP), plants submitted to UVre showed higher PSRI values (Figure 6B). PSRI is a reflectance index used to characterize changes in the physiological status of vegetation, as a sensitive parameter to changes in the ratio of carotenoids to chlorophyll (Garbulsky et al., 2011; Merzlyak et al., 1999b; Sims & Gamon, 2002). Higher UVre values of PSRI indicate senescence symptoms (Merzlyak et al., 1999b; Shaar-Moshe et al., 2017). In our study, senescence was found to be correlated with a 15.73% decline in the SPAD index in UVre green areas in SD. The lower PSRI values in plants submitted to UVam reveals the efficiency on UV acclimatation on the environmental conditions tolerance (SD).

C. canephora plants submitted to UVam environment showed a higher F_v/F_m and PI (Figure 7). The findings of this study showed vitality and acclimation to UVam leaves tolerate the SD environmental conditions since, both parameters are photosynthetic stress indicators, of which PI is most sensitive to indicate changes in PSII activity and photosynthetic performance after a stress period (Björkman &

Demmig, 1987; Genty et al., 1989; Kalaji et al., 2016b; Tsimilli-Michael & Strasser, 2008).

In contrast, the decreased PI on UVre plants indicates a low photosynthetic performance due to a decrease in chlorophyll *a* fluorescence under high light stress that occurred on SD (due to PAR and UV increase) (Brestic & Zivcak, 2013; Piccini et al., 2020). These responses are a result of either decreased absorption of a cross-section of the PSII-associated light-harvesting antenna or retarded electron flow from the PSII donor side to the PQ pool (Davey et al., 2012; Kataria et al., 2013; Piccini et al., 2020; Ranjbarfordoei et al., 2011; Xiaoqin et al., 2008).

Regarding the photosynthetic implications, SPAD index is associated to the N content, which is a component of chlorophylls molecules, thus, an essential component on photosystems I and II. Higher N concentration in leaves can lead to a greater amount of chlorophyll and higher efficiency in absorbing light for photosynthesis (Wu et al., 2019). Additionally, nitrogen is a component of electron transport proteins in the electron transport chain, contributing to the efficient transfer of electrons during photosynthesis (Danyal et al., 2011). Thus, a higher nitrogen content, indicated by the SPAD index, may be associated with a higher photochemical efficiency and this is reflected on PI values. In this context, lower PI values on UVre are associated to lower SPAD index, which displayed weaken photochemical efficiency.

In this study, all steady-state parameters on chlorophyll *a* fluorescence show acclimation of *C. canephora* on UVam while indicating the sensitivity of UVre leaves to sunburn symptoms (Figures 8A, 8C, 8E and 9).

High values of QY_{Lss} show the better integrity of the photosynthetic performance of UVam (Figure 8A). Reduction values of QY_{Lss} reveals severe damage to Q_A reduction capacity through impairment of excitation energy transfer in PSII (Marutani et al., 2012).

NPQ is a mechanism related to non-photochemical energy dissipation and is mainly controlled by changes in the xanthophyll cycle, preventing damage by oxidative effects, thus, this parameter can be correlated to PRI (Czarnocka & Karpiński, 2018; Müller et al., 2001; Yin et al., 2010; Yudina et al., 2020). In this study, higher NPQ_{Lss} on UVam (Figure 8C) indicates the role of a strong photoprotective mechanism associated with energy dissipation.

When the stress is severe, the regulated capacity of the photosynthetic electron transport system decreases, and excessive molecules of reactive oxygen species are produced, causing photooxidative stress, which can negatively affect the energy dissipation process and, consequently, damage the photosynthetic apparatus (Czarnocka & Karpiński, 2018; Foyer et al., 1994; Minkov et al., 1999).

Decrease in QY generally is accompanied by an increase in NPQ (Schreiber et al., 2019). However, in our study, high light and temperature on SD displayed severe stress, resulting in low NPQ_{Lss} in *C. canephora* sumbmited to UVre (figure 8C), indicating dysfunctional photosynthetic apparatus in the xanthophyll cycle (Müller et al., 2001; van Oort et al., 2018; Welc et al., 2021). This shows the sensitivity of UVre leaves. The NPQ_{Lss} reduction in UVre also can be associated with the use of ATP synthesized in photochemical reactions by the Calvin-Benson cycle and the decrease in the transthylakoid proton gradient to protect the PSII antenna system (Brestic et al., 2016; Joshi et al., 1995; Sharkey & Zhang, 2010).

UVam plants had less impact on the efficiency of the photochemical capacity of PSII on SD (Figure 8E), and the plants showed higher qP_{Lss}, endorsing UVam acclimation to SD environmental conditions. The reduced values of qP_{Lss} indicate a greater reduction of quinone *a* (Q_{A-}) and lower photochemical activity, due to the increase in fluorescence, which highlights the reduction of oxidized reaction centers, which refers to the process of converting open reaction centers that are ready to receive electrons (Goltsev et al., 2016; Miyake et al., 2009).

The greater electron flow through photosystems I and II on UVam diverted to protective mechanisms and N metabolism, which can be correlated with a greater SPAD index (Hunt, 2003). Consequently, higher qL_{Lss} (Figure 9A) indicates a greater efficiency of UVam plants in converting light energy into chemical energy during photosynthesis; reflecting a more efficient photochemical energy use (Daloso et al., 2014). qL_{Lss} provides an estimate of the fraction of photosystem II reaction centers that are open and involved in active photosynthesis (Kramer et al., 2004).

Rfd_{Lss} is correlated to the activity of the Calvin-Benson cycle and evaluates the vitality of plants (Lichtenthaler, 2021; Lichtenthaler et al., 2005). Greater values on UVam (Figure 9B) show adequate interactions between the photochemical and biochemical steps of photosynthesis (Goltsev et al., 2016; Lichtenthaler, 2021; Lichtenthaler et al., 2005), showing high efficiency of UV acclimatization.

We infer that the IP, especially on SD, had a direct impact on the enzymatic activity of the Calvin-Benson cycle on UVre plants, because of the high levels of light and temperature on leaves, which were not acclimated to these environmental conditions. This impact occurs mainly on the carboxylation capacity of RuBisCO (Sharkey, 2005). Reductions on Rfd_{Lss} occurred to UVre indicate an imbalance between the photochemical reactions in the thylakoids and the enzymatic reactions in the stroma reflecting both damage to the photochemical apparatus and the biochemical apparatus (Goltsev et al., 2016; Lichtenthaler et al., 2005; Rysiak et al., 2021).

Regarding the instantaneous fluorescence parameters, UVam plants had a higher efficiency of photosynthetic electron transport at the recovery phase (dark-adapted), indicating a greater efficiency of photosystem II in converting absorbed photons into usable photochemical energy during photosynthesis. This is shown in higher QY_{D3} (Figure 8B) and qP_{D3} (Figure 8F), both positively correlated to NPQ_{Lss} values of UVam plants (Dong et al., 2020; Schreiber et al., 1995; Schreiber et al., 2019).

NPQ_{D3} indicates the recovery capacity of the photosynthetic apparatus, promoted by the dynamics of the xanthophyll cycle (Dias et al., 2011). Interestingly, UV environments did not differ in values of NPQ_{D3}.

The effects of the full solar spectrum on plants involve the expression of genes involved in UV protection and hence promote plant survival due to UV-B and so, high solar incidence does not always reflect decreases in photosynthesis (Jenkins, 2009; Rozema et al., 1997), which was proved on the results of this study.

As chlorophyll fluorescence parameters elucidate the photosynthetic integrity of UVam plants, it reflects on the gas exchange parameters which shows the success in carbon uptake. Specially QY_{D3} is positively correlated with CO_2 uptake, which is shown in A_{net} values (Figure 10A) (Earl & Ennahli, 2004; Loriaux et al., 2013; Seaton & Walker, 1990).

Over the last hundred years, coffee genotypes have been selected in Brazil for monoculture (DaMatta et al., 2018) and consequently, to successfully grow under high solar irradiance, thus, including tolerance to high levels of UV. In fact, UVam plants show stimulated protective and photomorphogenetic acclimation responses on greater A_{net} (Figure 10A). This response can indicate greater electron flow through photosystems, in which the resulting energy may be invested to protective mechanisms and N metabolism, which is related to the higher SPAD index values in UVam. This reflects higher photochemical performance, since the SPAD index has been a good tool for diagnosing the integrity of the photosynthetic system and N content in coffee leaves (Bernado et al., 2022; Hunt, 2003; Netto et al., 2005).

The sunburn damage to UVre can implicate stomatal closure (Lawson & Morison, 2004; Qu et al., 2016). This is reflected in lower g_s (Figure 10B) and consequently E (Figure 10C) in UVre on SD, since UV-B strongly affects g_s (Lawson & Morison, 2004; Nogués et al., 1999; Xiaoqin et al., 2008) and its increase on IP, even on UVre environment could affect stomatal dynamics.

When stomatal effects on photosynthesis are considered, the linear association between Rdf_{Lss} and A_{net} is observed (Lichtenthaler, 2021; Rinderle and Lichtenthaler, 1988). Stomata play a crucial role in the control of leaf photosynthesis, regulating the precise balance between CO_2 assimilation and water loss to the atmosphere (Jones, 1998). *C. canephora* could have reduced stomatal density under UVre, which implicates alterations in stomatal conductance and can affect the leaf gas exchange dynamics (Bernado et al., 2021; Dow et al., 2014; Ren et al., 2019). This can be additional implications to the damage of UVre leaves that lead to lower gs and E on SD in this study.

Reduction in g_s and E in response to damage on UVre is associated with higher $VPD_{leaf\text{-}air}$ (Figure 10D), the driving force for plant transpiration (Buckley, 2019), exhibiting a linear association.

Higher $VPD_{leaf\text{-}air}$ is affected specifically due lower E, displaying a higher temperature on leaves in UVre contributing to the lower A_{net} (Broughton et al., 2021; Shirke, 2004; Zhu et al., 2022). The substantial increase of PAR on IP can be responsible for displaying the higher $VPD_{leaf\text{-}air}$ on sensitive leaves of UVre (Shirke, 2004; Zhu et al., 2022).

UVam acclimation to UV radiation

C. canephora tagged leaves, in this study, developed during DP, with gradually lower UV incidence. UV stress at low levels is important to coffee plants resilience to future light stress events since UV radiation triggers genetic expression to protect and repair mechanisms, which is necessary to survive in sunlight fluctuations (Jenkins, 2009; Thomas et al., 2022).

The reflectance indices and chlorophyll *a* fluorescence parameters, among gas exchange parameters, indicate acclimation and tolerance of *C. canephora* to SD environmental conditions of high light and temperature, reflecting a priming effect of exposure to UV incidence in UVam environment. The reduction of UV incidence (UVre), especially in DP may not be sufficient to trigger the priming effect on *C. canephora*.

UV priming activates metabolic processes related to light stress, inducing acclimatation and allowing plants to respond rapidly or with greater efficiency to future light stress conditions (Guedes et al., 2019; Thomas & Puthur, 2017), which characterizes UVam plant stress tolerance on SD after the IP, while UVre plants were subjected to sunburn, indicating sensitivity. In this study, UV priming effects displayed greater SPAD index, energy dissipation and thus, greater integrity of photosynthetic apparatus.

Sunburn sensitivity

Coffea canephora is a coffee species characterized by its sensitivity to great climatic alterations because of its evolutionary origin in lowland at regions up to 1200 m (DaMatta & Ramalho, 2006), therefore this species may not have acquired adaptation to solar radiation over time, specifically ultraviolet, as well as other coffee species like *C. arabica*, which justifies the greater sensitivity of this specie (Bernado et al., 2021; DaMatta & Ramalho, 2006). This sensitivity in addition to the non-acclimatation aspects of *C. canephora* plants in UVre environment indicated in this study, would enhance the possibility of plants under UVre being damaged due alterations in abiotic factors, i.e. temperature and light, on SD.

The vitality-related parameters (PSRI, PI, Rfd_{Lss}) indicated that green areas of UVre leaves on SD, were highly damaged, as well photosynthetic machinery was affected, as 10.74% of the plant's leaf area was sunburned.

UVre leaves that were sunburned were developed on DP, receiving gradually low PAR incidence and reduced UV incidence, which could display its sensitivity. Overall, plants grown under low PAR are indeed more sensitive to sunburn-like damage, even at low UV intensity, but this sensitivity effect can vary species dependently, which suggests sunburn sensitivity involves various physiological and anatomical mechanisms (Flint et al., 2005). In this study, *C. canephora* grown on gradually low levels of PAR on UV reduced levels (UVre), which were also gradually reduced, showed sunburn damage when PAR, temperature, and the reduced UV levels had an increased period in a short-time (IP) after a three-time longer period of decline of these parameters (DP). PAR decline seems to be the key factor in displaying the sensitivity to sunburn and likely damage (Flint et al., 2005). Despite that, even the less increment of UV radiation in UVre environment can be responsible for the photosynthetic damage. The short-period increase (IP) of UV radiation on UVre, even in low intensity could display sunburn symptoms in combination with high PAR and temperature increase on SD, since UV-B has a high potential to affect molecular systems due to its high frequency, mainly when leaves are not acclimated to this radiation (Ballaré et al., 2011; Krause et al., 1999; Rustioni et al., 2014).

The sensibilization implications to UVre were showed using chlorophyll fluorescence and gas exchange parameters, and UVre leaves were not acclimated to high light intensity, showing damage in energy dissipation.

Leaf growth dynamics: expansion *vs*. thickness

Leaf area expansion is one of the most sensitive growth parameters under ultraviolet radiation stress (Kakani et al., 2003b). UVam leaves had less leaf area and higher thickness (SLM) (Figure 11) This association of area expansion *vs.* thickness on UVam indicates that C. canephora leaves had to invest leaf growth on thickness, not expansion under UVam incidence. This is a protective mechanism that can be related to the UV priming effect, to prevent UV radiation reach basal layers of mesophyll (Rozema et al., 1997a; Wang et al., 2021). Higher thickness is also a strategy under high light intensity for efficient resource capture to maintain efficiency and survival in harsh environments (Thakur et al., 2019).

The increase in thickness is directly linked to the investment and differentiation of mesophyll cells, by changing the number of cells, dimension, and density (John et al., 2017). Also, this protection mechanism is related to increasing the investment in thickness of the epidermis and cuticle (abaxial and adaxial) as a response to exposure to UV, to which the cuticle is the primary protective barrier, while mesophyll-increased cells mainly attenuate excessive PAR light, mainly blue and red (which are available for photosynthesis use) (Krauss et al., 1997; Qi et al., 2003). Additionally, as superficial tissues, the cuticle layers in adaxial and abaxial leaf surfaces act as biophysical screening, reflecting light, scattering, and reducing light absorption by epidermal layers (Rozema et al., 1997).

Phenolic synthesis in the leaves occurs in the mesophyll tissue in response to UV and PAR (especially to high blue, green, and red wavelengths) and can have a substantial role in UV and PAR attenuation by scattering the short electromagnetic wavelengths by those molecules (Caldwell et al., 1983; McClure, 1975; Wellmann, 1974; Wellmann, 1983). In the context of protection compounds produced on mesophyll, predominantly starch is accumulated (Britz & Adamse, 1994).

Higher SPAD index can be correlated with higher thickness in UVam, since SPAD values are often positively associated with SLM and chlorophyll density is found to be almost constant to mesophyll thickness (Fijii et al., 2023; Marenco et al., 2009).

UVam acclimation could be triggered mainly due to an increase in thickness. In opposition, UVre environment effect on plants can be related to shading effects, which can reduce leaf thickness, palisade cell length, and spongy parenchyma, decreasing SLM (Gregoriou et al., 2007).

The higher leaf area and lower thickness of UVre leaves indicate that these leaves, due reduced incidence of UV, did not have the trigger factor to produce more antioxidants compounds or even invest growth on thickness, consequently not acquiring a priming effect, so the leaves invest more growth in expansion, not in thickness, leading to more photosynthetic area to the plant (Kolb & Pfündel, 2005; Rozema et al., 1997b).

Leaf area is an essential factor in capturing light, which determines crop growth and yield (Koester et al., 2014). This can be positive in a completely controlled environment, but it displayed a sensitivity role in UVre environment where plants receive natural fluctuations of light incidence. UVre *C. canephora* leaves, with the higher photosynthetic area, were affected by sunburn and had the remaining area of the young and recent mature leaves severely damaged on photosynthetic apparatus. Our results show that the investment on leaf area, to the detriment of thickness increase, is not always positive. Protecting *C. canephora* plants against UV incidence can display a sensitive role, which can implicate photosynthetic damages, considering possible future stress scenarios.

CONCLUDING REMARKS

Although UV radiation can cause damage in leaves, it also has an important role in priming effect on leaves of *C. canephora*, providing a robust protection mechanism to high light and temperature. We show that *C. canephora* grown under UVam had tolerance after a short increase period of light, temperature, and VPD_{air} that followed a three-times longer period of decrease of these environmental factors. *C. canephora* tolerance was triggered by exposure to UV, protecting leaves against damage to photosynthetic capacity and sunburn. Thus, *C. canephora* grown under UVre showed sensitiveness on the physiological traits, resulting in photosynthetic damage and sunburn after the increase of environmental parameters (light, temperature, and VPD_{air}). Our findings show that acclimation effect of UV involved investing metabolic energy in defense mechanisms like increase thickness, which implicate synthesis of UV screening compounds and synthetization of metabolic compounds to excess energy dissipation while UVre invested metabolic energy in growth (photosynthetic leaf area expansion), which was not a great investment since the leaf area was damaged (either due disfunction of photosynthetic machinery or sunburn occurrence) under stress by increase of environmental factors. Thus, using a physiological approach, this study provides valuable insights into plant defense mechanisms against environmental stresses and highlights the importance of adequate UV radiation exposure in promoting plant resilience under adverse conditions.

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