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Tomato plants use non-enzymatic antioxidant pathways to cope with moderate UV-A/B irradiation: A contribution to the use of UV-A/B in horticulture

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ABSTRACT

Plants developed receptors for solar UV-A/B radiation, which regulate a complex network of functions through the plant's life cycle. However, greenhouse grown crops, like tomato, are exposed to strongly reduced UV radiation, contrarily to their open-field counterparts. A new paradigm of modern horticulture is to supplement adequate levels of UV to greenhouse cultures, inducing a positive mild stress necessary to stimulate oxidative stress pathways and antioxidant mechanisms. Protected cultures of *Solanum* (cv MicroTom) were supplemented with moderate UV-A (1 h and 4 h) and UV-B (1 min and 5 min) doses during the flowering/fruiting period. After 30 days, flowering/fruit ripening synchronization were enhanced, paralleled by the upregulation of blue/UV-A and UV-B receptors' genes *cry1a* and *uvr8*. UV-B caused moreover an increase in the expression of *hy5*, of HY5 repressor *cop1* and of a repressor of COP1, *uvr8.* While all UV-A/B conditions increased SOD activity, increases of the generated H_2O_2, as well as lipid peroxidation and cell mebrane disruption, were minimal. However, the activity of antioxidant enzymes downstream from SOD (CAT, APX, GPX) was not significant. These results suggest that the major antioxidant pathways involve phenylpropanoid compounds, which also have an important role in UV screening. This hypothesis was confirmed by the increase of phenolic compounds and by the upregulation of *chs* and *fls,* coding for CHS and FLS enzymes involved in the phenylpropanoid synthesis. Overall, all doses of UV-A or UV-B were beneficial to flowering/fruiting but lower UV-A/B doses induced lower redox disorders and were more effective in the fruiting process/synchronization. Considering the benefits observed on flowering/fruiting, with minimal impacts in the vegetative part, we demonstrate that both UV-A/B could be used in protected tomato horticulture systems.

1. Introduction

Solanum lycopersicum L., tomato, is among the crops most widely produced and consumed. Nowadays, the production of this crop is diversified, ranging from open-field to protected horticulture (Martínez-Blanco et al., 2011). In protected horticultural systems (which include glass/plastic greehouses) it is possible to produce in season and off-season with or without supplemental light (Bian et al., 2014). However, crops produced off-season often have an inferior reputation regarding sensorial atributes and chemical composition, when compared to open field products (Muñoz et al., 2007).

Solar ultraviolet (UV) radiation, namely the UV-A and UV-B, is a natural environmental stressor and plants have evolved UV-photoreceptors and adaptive mechanisms to cope with UV- stress (Lin and Todo, 2005; Suchar and Robberecht, 2015; Yokawa et al., 2015). On the one hand, most plant studies in the last decades have been focused on the harmful impacts of excessive UV radiation, which include damages on cell structures and metabolism eg., photosynthesis and increased oxidative stress, that ultimately may compromise plants' productivity and lifespan (Nawkar et al., 2013). On the one other hand, protected horticulture is an example of how UV-deficiency may have detrimental impacts on crops performance and productivity (Wargent and Jordan, 2013). Crops growing in protected systems are not exposed to natural doses of UV-radiation (Kumar and Poehling, 2006) thus not benefiting from the impacts that moderate UV-radiation may have on fruit production, sensorial attributes and chemical quality (Kasim and

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Kasim, 2015; Carvalho et al., 2016). So, it is crucial to establish a compromise between the UV- intensity and duration of exposure to get a positive mild stress – "eustress" – which may increase yield and/or fruits nutritional value, and may therefore be useful in agro-industry (Hideg et al., 2013).

Photoreceptors modulate the expression of hundreds of light-regulated genes, which leads to adaptive changes at the cellular and systemic levels (Major et al., 2017). Blue light (400–500 nm) and UV-A radiation (315–400 nm) are perceived by phototropins (PHOT), cryptochromes (CRY) and LOV/F-box/Kelch-domain proteins (Yu et al., 2010). Besides CRY, UV resistant locus 8 (UVR8) is also an important receptor to lower wavelength UV-A and to UV-B (280–315 nm) (Rizzini et al., 2011). Four *CRY* genes expressed in response to UV-A and blue light were identified in tomato cultivars such as "Moneymaker" (Facella et al., 2016). These genes unleash multiple responses during the different plant developmental stages (Liu et al., 2011). There are two types of *CRY1* genes (*CRY1a* and *CRY1b*), one *CRY2* gene and one *CRY3* gene. *CRY1* mostly controls photomorphogenesis in young plants, anthocyanins pathways and plant development (Facella et al., 2016). *CRY2* is involved in flowering and fruit quality (Kharshiing and Sinha, 2015). Giliberto et al. (2005) showed that *CRY2* overexpression increases pigment contents, stimulating an overproduction of anthocyanins and chlorophylls in leaves and of flavonoids and lycopene in fruits. *CRY3* has a DNA repair and protective role, occurring mostly in mitochondria and chloroplasts (Facella et al., 2016).

PHY and CRY control the Constitutive Photomorphogenic 1 (COP1) repressor, which promotes the degradation of the transcription factor (TF) elongated hypocotyl 5 (HY5) (Heijde and Ulm 2012). Most data refer to blue or UV-B effects and little is known about UV-A modulation, being assumed it is similar to the blue one. UV-B radiation promotes the separation of the UVR8 dimer and the resulting UVR8 monomers interact with COP1 blocking HY5 proteasomal degradation, and allowing this TF to promote the transcription of several genes involved in protection against UV. Some of the proteins coded by these genes include Chalcone Synthase (*CHS*), Chalcone Isomerase (*CHI*) and Flavonol Synthase (*FLS*) that are involved in phenylpropanoid biosynthesis (Heijde and Ulm, 2012).

Phenols resulting from the phenylpropanoid pathway are important antioxidants, pointed out as contributing to the efficient control of reactive oxygen species (ROS) (Agati et al., 2012; Martinez et al., 2016). ROS are free radicals, a typical by-product of the photo- excitation in thylakoidal photosystems I and II compounds (Anjum et al., 2014). ROS levels are commonly increased by biotic and abiotic factors (including UV radiation), changing the redox-homeostasis necessary for the regulation of cellular bioactivity (Yokawa et al., 2015). As reported above, blue/UV-A radiation leads to an overexpression of CRY and PHOT proteins. This increase affects gene transcription and triggers molecular responses that include changes in the biosynthesis of secondary metabolites, including polyphenols (Müller-Xing et al., 2014). Several polyphenols, of which flavonoids (eg, anthocyanins, flavonols) represent a major family, result from the phenylpropanoid pathway, and not only may scavenge and/or inhibit the generation of ROS (Brunetti et al., 2013; Zoratti et al., 2014) but also may selectively absorb UV-A and UV-B wavelengths (Agati and Tattini, 2010).

UV radiation also enhanced the transcription, translation and activity of antioxidant enzymes (Kumari et al., 2010). These enzymes are responsible for scavenging the excess of ROS molecules, such as $O2^{\cdot-}$, H_2O_2, $^1O_2$, $HO_2^{\cdot-}$, $OH^{\cdot}$, $ROOH$, $ROO^{\cdot}$, and $RO^{\cdot}$. Superoxide Dismutase (SOD) family acts in the first step of ROS scavenging by catalyzing the $O_2^{\cdot-}$ dismutation to H_2O_2 and O_2. The following step involves de decomposition of H_2O_2 catalyzed by various enzymes, e.g. catalase or peroxidases such as Catalase (CAT), Ascorbate Peroxidase (APx) and Peroxidases that use guaiacol as substrate (GPx) (Choudhury et al., 2013; Das and Roychoudhury, 2016). While it is well described that UV-rays are perceived by photoreceptors and also increase oxidative stress, several aspects remain to unveil related with the distinctive modulation of UV-A vs UV-B, and the pathways involved in the stimulation of antioxidant enzymes as well as their contribution through exposure time. For example, it was demonstrated that nitric oxide is involved in the signaling pathway that up-regulates specific isoforms of antioxidant enzymes protecting against UV-B-induced oxidative stress (Santa-Cruz et al., 2014). Also, Kumari et al. (2010) demonstrated in *Acorus calamus*, that UV-B stimulation of antioxidant enzymes activities (SOD, CAT, APX, GR) was observed at initial growth period but CAT and SOD activities decreased at later age of sampling.

The aim of this work is to functionally understand how moderate supplementation of UV-A or UV-B on protected tomato cultures increases oxidative eustress, which defense mechanisms are activated, and if this supplementation may improve protected cultured tomato yield, and favour agronomic traits. With this work, we will also be able to distinguish UV-A and UV-B specific mechanisms of oxidative stress and defense strategies.

2. Material and methods

2.1. Plant growth conditions and UV treatments

Seeds of *Solanum lycopersicum* L. cv. MicroTom (Just Seed, UK) were soaked in distilled water and germinated on 0.3 L plastic pots with Peat:Perlite (2:1) substrate. Germinated plants were grown in a growth chamber with a photosynthetic photon flux density (PPFD) of 200 $\mu mol{\cdot}m^{-2}$

 83;s^{-1} provided by fluorescent light lamps (OSRAM L 30W/77 FLUORA) and a photoperiod of 16 h:8 h light:dark. Relative humidity (RH) and temperature were maintained at 45 ± 5% and 23 ± 2 °C, respectively. Pots were irrigated twice a week with Hoagland medium (Sigma, USA), with pH adjusted to 5.70 ± 0.05. At the 90th day, the first flower buds emerged and after 10 days (100-day-old plants) a high synchronization in flowering was observed. Between days 100 and 130 (i.e., during fruiting and fruit ripening), plants were randomly divided in five groups, and each group exposed to a different UV condition: *Control Group* (C): plants were maintained under the same irradiation conditions, with no UV supplementation; *UV-A 1 h Group*: plants were exposed for 1 h per day to 0.8 J/m^2 UV-A supplied by black light lamps (F20T12/BLB – 20W T12 (T10)) Fluorescent Blacklight Blue (Supra Life®, Italy), with a peak wavelength at 368 nm (the intensity of light at wavelengths below 368 nm was close to 0 W/m^2); *UV-A 4 h Group*: plants were exposed for 4 h per day to 0.8 J/m^2 UV-A, supplied by the same blacklight lamps; *UV-B 2 min Group*: plants were exposed for 2 min per day to 2.94 J/m^2 UV-B, supplied by six 312 nm TFP-M/WL 8W lamps (Vilber, Germany), which have an irradiation of wavelengths below 312 nm close to 0 W/m^2); *UV-B 5 min Group*: plants were exposed for 5 min per day to 2.94 kJ/m^2 UV-B, supplied by the same UV-B lamps. UV-A and UV-B irradiance was measured by Sensor Meters Philip Harris (serial number: 4375 model SEL240) and International Light INC (Newbryport, Massachusetts, model: 01950, IL1400A), respectively. Irradiation values are the mean of the irradiance measured at the top mature-leaves in the first and last days of exposure. These leaves receiving the measured irradiance (and with similar age and size) were sampled for the biochemical and transcriptional analyses.

2.2. Plant morphology and productivity evaluation

Thirty days after UV exposure, plant morphological characteristics, including shoot length, leaf chlorosis, and necrosis were evaluated. Plant productivity and nitrogen metabolism were evaluated using the glutamine synthase (GS) activity (Thomsen et al. (2014). GS activity was evaluated according to Pinto et al. (2014) with some modifications. Leaf samples (0.1 g) were homogenized in 1.5 mL extraction buffer containing 0.1 M phosphate buffer (pH 7.0), 0.5 M ethylenediaminatetracetic acid disodium salt (Na_2EDTA), 1% polyvinylpyrrolidone (PVP), 1 mM phenylmethylsulphonyl fluoride (PMSF), 0.2% triton X-

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