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High blue light improves acclimation and photosynthetic recovery of pepper plants exposed to UV stress

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ABSTRACT

Intensity of photosynthetic active radiation (PAR) plays an important role in the acclimation of plants to UV radiation. Thereby, specific morphological and physiological characteristics influenced by high irradiance are also affected by blue light. With this background we conducted two experiments to evaluate the impact of light intensity and the relevance of blue light for the acclimation of pepper plants to UV. In this context we hypothesized that higher amount of blue light in the PAR spectrum significantly improves the plant acclimation and recovery to UV radiation. Our results demonstrate that UV stressed plants cultivated either under the higher light intensity (PAR 300 $\mu mol\ m^{-2}\ s^{-1}$) or under higher amount of blue light (62%) show better photosynthetic performance (i.e., higher photosynthetic rate (Pn), higher maximal photochemical efficiency of PSII (*Fv*/*Fm*) and lower non-photochemical quenching (NPQ)) than UV stressed plants grown under lower light intensity (PAR 100 $\mu mol\ m^{-2}\ s^{-1}$) or lower amount of blue light (30%). Contents of chlorophyll *a* and *b*, as well as carotenoids, had a stronger decrease due to UV in those plants cultivated either under the lower light intensity or under the lower amount of blue light. In contrast, plants grown either under 300 $\mu mol\ m^{-2}\ s^{-1}$ or 62% blue light accumulated more epidermal flavonols. Analogous to the well described effects of high PAR intensity, we demonstrate here that high amount of blue light triggers specific biochemical and physiological processes resulting in better acclimation and recovery of plants to UV stress.

1. Introduction

The effects of UV on plant development, morphology and physiology have been intensively studied and summarized in several reviews (e.g., Teramura, 1983; Stapleton, 1992; Jordan, 1996; Mackerness, 2000; Frohnmeyer and Staiger, 2003; Kakani et al., 2003; Vass et al., 2005; Jenkins, 2009; Schreiner et al., 2012; Hideg et al., 2013). In general, energy-rich UV radiation leads to the generation of free radicals which damage DNA, proteins, membrane lipids and the photosynthetic machinery including chloroplasts and the degradation of photosynthetic pigments (a detailed review is presented by Hideg et al., 2013). In the sum, photosynthesis is impaired leading to a decrease in biomass accumulation (Smith et al., 2000; Kakani et al., 2003).

The damaging potential of UV irradiation forces plants to adapt to high energy fluxes. Typical morphological adaptations comprise the lower leaf area (Teramura, 1983) and higher leaf mass per area (LMA) resulting in lower penetration of UV light in the deeper layers of the tissue (see reviews of Teramura, 1983 and Kakani et al., 2003). Acclimation processes include also the accumulation of secondary metabolites in the tissues, particularly in the epidermal layer (Müller et al., 2013). Of particular note are flavonoids and hydroxycinnamic acids that screen UV radiation and shield the underlying tissues (Olsson et al., 1998; Cerovic et al., 2002; Falcone Ferreyra et al., 2012). Finally, the susceptibility of plants to UV strongly depends on their acclimation- and recovery-capacity which are also strongly influenced by the growth conditions (Ziska et al., 1992).

In general, plants cultivated under elevated intensities of PAR are better adapted to UV than plants cultivated under lower intensities of PAR (Walters, 2005). This phenomenon was elucidated very early, more than 30 years ago. For example Teramura (1980) found that soybeans cultivated under low PAR regimes were more affected by UV-B light, as shown by a stronger reduction in

Abbreviations: Abs., absorbance; Anth, anthocyanins; AOIs, areas of interest; BE, biologically effective; Car, carotenoids; CHS, chalcone synthase; Chl, chlorophyll; Chl-index, chlorophyll index; das, days after sowing; DW, dry weight; Flav, flavonoids; FLAV-index, flavonol-index; Fm, maximum chlorophyll fluorescence; Fo, ground chlorophyll fluorescence; *Fv*/*Fm*, maximum photochemical efficiency of the photosystem II; FW, fresh weight; LED, light emitting diodes; LMA, leaf mass per area; NPQ, non-photochemical quenching; n.s., non significant; PAR, photosynthetic active radiation; Pn, net photosynthetic rate; UV, ultraviolet.

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biomass. Also, classical works demonstrating the structural and functional adaptations of sun and shade leaves to UV-radiation (e.g., Lichtenthaler et al., 1980) contribute for a better understanding of the role of light intensity.

Apart from the impact of light intensity recent studies indicate that the light quality also regulates a variety of pathways as related to plant development, and might also influence certain acclimation processes. Photoreceptors such as the UV-A/blue light receptors cryptochrome and phototropin or the red/far red light receptor phytochrome perceive specific wavelengths and trigger morphological and functional adaptations at chloroplast and plant level (Banerjee and Batschauer, 2005; Taulavuori et al., 2005; Nagatani, 2010). As indicated, blue light (400–500 nm) can initiate plant responses and induce leaf characteristics that also develop under high irradiance (Hogewoning et al., 2010). Amongst others, chloroplast movement was induced by enhanced light intensities as well as by increased percentage of blue light, a process mediated by the phototropin (UV-A/blue light receptor) related NPL1 gene that controls the chloroplast relocation (Jarillo et al., 2001; Kagawa et al., 2001; Banás et al., 2012; Wada, 2013). In addition, experiments with barley and radish seedlings have shown that formation of sun type chloroplasts, which typically happens under high light conditions, can also be initiated at low intensities of blue light (Buschmann et al., 1978; Lichtenthaler and Buschmann, 1978). Similarly, the biosynthesis of phenolic compounds such as UV-screening flavonoids depends on both light intensity and light quality (Taulavuori et al., 2013). Cryptochrome and phytochrome photoreceptors are involved in the induction of CHS gene expression that leads to the formation of chalcone synthase (CHS) which is the first step in flavonoid biosynthesis (Feinbaum et al., 1991; Wade et al., 2001).

Up to now, the impact of light quality on the acclimation of plants to abiotic stress factors has hardly been taken into account. Nowadays LEDs providing 'consumer-tailored' light can be used as light sources for the commercial cultivation of horticultural crops in controlled and semi-controlled environments (Morrow, 2008). In parallel, basic and applied research evaluate the impact of light quality on plant development and physiology, more recently using LEDs as light sources. Thereby, most studies focus on the impact of light composition on biomass production and photomorphogenesis (e.g. germination, growth habit, flower production) (Brown et al., 1995; Carvalho et al., 2011; Abidi et al., 2013). Already about 20 years ago Adamse et al. (1994) demonstrated that supplemental blue light alleviates UV-B induced growth inhibition in cucumber. In a more recent study it is suggested that in diatoms the perception of blue light might be of central importance for high light acclimation. (Schellenberger Costa et al., 2013). However, besides the relevance of this topic, this research field remains widely underexplored.

In the present study we investigate the relevance of blue light for the UV acclimation of pepper plants (*Capsicum annuum* L.). Our studies base on the hypothesis that higher amount of blue light in the light spectrum induces similar structural and functional adaptations at chloroplast, leaf and plant level as observed for high light, resulting in lower susceptibility to UV. Non-destructive methods (fluorescence and gas exchange measurements) as well as biochemical indicators and biometric parameters were adopted to evaluate the effects of light intensity, light quality and UV.

2. Material and methods

2.1. Plant material, growth conditions and experimental setup

Two experiments were conducted in order to evaluate the photosynthetic acclimation of pepper plants as affected by different light intensities and light qualities. The experiments were performed in a custom-built climate chamber that can be divided in up to six light compartments. During pre-cultivation, plants were illuminated with white fluorescence lamps (Master PL-L 4P, Philips, The Netherlands). As the different light treatments were initiated light emitting diodes (LEDs) from a prototype optimized for our research purposes (Ushio Lighting Inc., Japan) were used for illumination. The LED-modules are characterized by a 2:1 combination of red and blue LEDs with single peaks, respectively, at 665 nm and 445 nm. The LED settings (intensity and spectral composition) are controlled by the equipment-specific software. Interspacing the LED-modules we installed UV tubes (UV-XEFL 290BB, Ushio Lighting Inc., Japan). The tubes emit mostly (60%) in the UV-B region (280–320 nm) with a dominant peak at 290 nm; 30% is emitted in the UV-A spectrum (320–400 nm), 4% in the UV-C region (200–280 nm) and 6% in the visible spectrum (400–700 nm) (Fig. 1). Plants were grown under a photoperiod of 12 h, with day/night temperature of 21 °C/20 °C and relative humidity of 82%. During the experiments plants were irrigated with a standard Hoagland nutrient solution (pH 6.2).

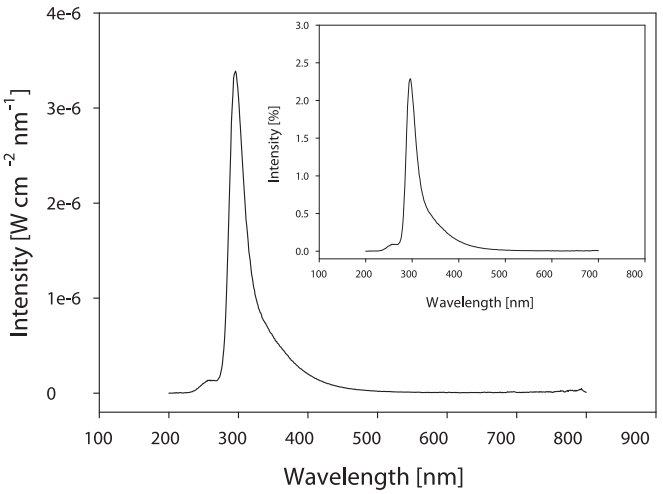

Fig. 1. Light spectrum of the UV-tube (UV-XEFL 290BB, Ushio Lighting Inc., Japan); inset indicates the normalized spectrum (200–700 nm) in percent. The measurement was done under standardized conditions (distance = 0.35 m; T = 22 °C) with the spectroradiometer OL 756 (Gooch and Housego's, Ilminster, UK).

Before running light treatments, seeds of the pepper (*C. annuum* L.) genotype Ziegenhorn Bello (Austrosaat AG, Austria) were sown in trays filled with a mixture of peat, sand and perlite and allocated under 100 μmol m^{-2} s^{-1} white fluorescence lamps (Philips, MASTER PL-L 4P). Four weeks after sowing in the 1st experiment and five weeks after sowing in the 2nd experiment, plantlets were transferred into standard pots (7 × 7 × 8 cm) and cultivated under same environmental conditions for four more weeks.

2.1.1. Impact of light intensity

In the first experiment we analysed the relevance of light intensity without any changes in the spectral quality. For this purpose, eight-week old plants were placed under LED lamps (45% blue light, 55% red light) either under 100 ± 5 μmol m^{-2} s^{-1} or 300 ± 5 μmol m^{-2} s^{-1}. Light intensities were measured and monitored with a radiometer (RM21, Dr. Gröbel UV Elektronik, Germany). One week after acclimation (58–64 das) to the new light intensities half of the plants of each light intensity were exposed to UV light of 4.98 kJ m^{-2} per hour per day which is equivalent to a biologically effective UV radiation of 5.53 kJ m^{-2} per hour per day ($UV\text{-}B_{BE}$ = 4.5, $UV\text{-}C_{BE}$ = 1.0, $UV\text{-}A_{BE}$ = 0.03 per hour per day). The biologically effective UV was calculated using the action spectrum of Flint and Caldwell (2003). UV radiation was supplied during