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ORIGINAL PAPER

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# DYNAMICS OF PHOTOSYNTHETIC AND OXIDATIVE STRESS PARAMETERS OF TWO SPINACH SPECIES AFTER SHORT-TERM LOW UV-B RADIATION EFFECT

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**ABSTRACT**

This work aimed to underline the dynamics of photosynthetic and oxidative stress parameters of 'Matador' and 'Andromeda' spinach species after short-term 1 and 2 $kJm^{-2}$ UV-B radiation effect. When plants reached 3–4 leaves growths stage, the exposure to 1 $kJm^{-2}$ and 2 $kJm^{-2}$ UV-B radiation was done once for 68 and 136 minutes, respectively. The photosynthetic and oxidative stress parameters were determined 2, 24, 48 and 72 hours after exposure. The stimulating effect of UV-B emerged on the 3rd day after exposure. The positive effect of UV-B was more pronounced for 'Matador'. The highest DPPH radical-scavenging capacity and the highest concentration of α-tocopherols were detected 24 hours after 2 kJ UV-B exposure, but the decrease in photosynthetic rate was the highest as well. Meanwhile, on the 3rd day after 1 kJ UV-B exposure, the indicators of oxidative stress of 'Matador' decreased, and the photosynthetic rate increased. This study highlights that low UV-B radiation acts as an eustress, by awaking positive changes in photosynthetic and oxidative stress parameters of spinach.

**Key words:** antioxidants, eustress, spinach, photosynthetic parameters, UV-B

## INTRODUCTION

Exposure of plants to a stressor can cause reversible, elastic eustress (strain or bending in mechanics) and, once exposure exceeds a tolerance-limit, irreversible plastic distress (in mechanics: a strain resulting in rupturing) [Kranner et al. 2010]. Eustress is activating, stimulating stress, which is a decisive element in plant development and is also referred to as 'good stress' or 'constructive stress' [Jansen et al. 2008].

Ultraviolet-B (UV-B) radiation is an essential component of the environment acting as an eco-physiological factor with the potential to alter the plant growth and photosynthesis [Kataria et al. 2014, Zhu and Yang 2015]. The sensitivity of crop plants to UV-B radiation varies depending on a species and cultivars and also on growth conditions [Kataria et al. 2014].

UV-B radiation affects plants in many processes. The UV-B causes disruption of photosystem II reaction center [Zhu and Yang 2015], or indirectly by affecting the stomata function, leaf growth or biosynthesis of photosynthetic pigments and carotenoids

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[Wu et al. 2012]. Damage to the PS II reaction center occurs primarily in the water-oxidizing manganese (Mn) cluster, which results in the inactivation of the electron transport chain. Other targets for UV-B damage in PS II include the quinine electron acceptors, tyrosine electron donors and the reaction centers of the D1 and D2 protein [Kataria et al. 2014]. UV-B has also been shown to affect the activity of enzymes of the carbon reduction metabolism, mainly Rubisco, and therefore directly involved in the $CO_2$ assimilation and biomass production [Jansen et al. 2008].

Since UV-B induces general stress responses in plants, the synthesis of a widespread species of metabolites regarding growth, development, and defense may be affected. The accumulation of flavonoids and hydroxycinnamic acids in epidermal cells is the primary mechanism of plants to build up protection against UV [Januskaitiene 2011, Sakalauskiene et al. 2013]. Reactive oxygen species produced due to UV-B stress cause oxidative damage to membrane lipids, nucleic acids and proteins. This leads to reduction in photosynthetic pigments and proteins, which imposes limitation on the photosynthesis due to reduced photosynthetic efficiency of PS II [Gill and Tuteja 2010] and decreased activity of Rubisco under the UV-B stress [Yu et al. 2013], which ultimately results the reduced yield of crop plants [Zhu and Yang 2015]. To overcome this damage, the stressed plants invoke higher activity of antioxidant enzymes like superoxide dismutase, ascorbate peroxidase, glutathione reductase and glutathione peroxidase. Ascorbate (AsA), glutathione (GSH), carotenoids, tocopherols, and phenolics serve as potential non-enzymatic antioxidants against UV-B stress [Kumari et al. 2009]. Despite numerous reports on this issue, the actual and realistic impacts of ambient UV-B are not fully understood [Kataria et al. 2014].

The responses of the photosynthetic pathways to UV-B radiation depend on various experimental growth conditions and plant growth stages, flow rate and the ratio of PAR to UV-B radiation, UV-B dosage, as well as on the interaction with other environmental stresses (e.g., cold, drought, mineral availability) [Jansen 2010, Kataria et al. 2014].

Plants adapt to changing environmental conditions. High levels of UV-B can cause distress in plants. By contrast, under low UV conditions, distress is a rare event, because the specific changes in gene expression [Hectors et al. 2007, Favory et al. 2009] increased accumulation of UV-screening pigments [Agati and Tattini 2010] and altered phytochemical content [Schreiner et al. 2012] are linked to increased UV-B tolerance. These responses can be defined as eustress. However, whereas productivity may not be directly affected by UV-radiation under eustress conditions, regulatory changes in photosynthate allocation and morphology [Jansen et al. 2012] may cause subtle decreases in biomass accumulation [Ballare et al. 2011, Hideg et al. 2013]. Therefore, the main goal of our experiment was to elucidate whether short-term UV-B radiation would have a beneficial influence on spinach plants growth, biochemical metabolite accumulation and antioxidant compounds that enhance the nutritional quality of spinach.

## MATERIAL AND METHODS

Spinach (*Spinacia oleracea* L.) cv. 'Matador' and cv. 'Andromeda' was grown in the controlled environment chambers at the Institute of Horticulture, Lithuanian Research Center for Agriculture and Forestry. Three separate chambers (24 $m^2$ each) were used for the study. Seeds of spinach plants were sown in 120 ml vessels (one seed per vessel) in peat substrate (Durpeta, Lithuania). 20 vessels per one treatment variant for each spinach variety, thus 480 vessels, were sown in general. Plants were placed at 18/13°C day/night thermo-period and 12/12h day/night photoperiod. High-pressure sodium lamps (SON-T Agro, Philips) were used for illumination (150 µmol $m^{-2}$ $s^{-1}$). Plants were grown in such conditions for 21 days, i.e. until they reached 3–4 leaves growth stage. On the first day of treatment, spinach plants were exposed to 0 kJ $m^{-2}$ (reference), 1 kJ $m^{-2}$ (1 kJ) and 2 kJ $m^{-2}$ (2 kJ) UV-B once. UV-B radiation was provided by UV-B fluorescent tubes (TL 40W/12 RS UV-B Medical, Philips). The intensity of UV-B tubes (for supplementary UV-B treatment) was 0.0571 mW $cm^{-2}$. To obtain 1 kJ $m^{-2}$ UV-B dose, plants were exposed for 68 min to that lamp exposition; therefore, to obtain 2 kJ $m^{-2}$ UV-B plants were exposed for 136 minutes. UV-B radiation was filtered through 0.13 mm cellulose acetate filter paper to avoid transmission of wavelength below 290 nm. UV-B intensity was measured using radiometer VLX – 3W (Vilber Lourmat, France).

All investigated parameters were determined at 2, 24, 48 and 72 hours after UV-B exposure. The biochemical analyses were performed in tree replicates for 6 randomly selected leaves per treatment.

**Gas exchange measurements.** Plant gas exchange was measured with portable photosynthesis system LiCOR 6400 (LI-COR, Lincoln, Nebraska, USA) at 2, 24, 48 and 72 hours after the end of the UV-B treatment. Net photosynthesis (A) (µmol $CO_2$ $m^{-2}$ $s^{-1}$), intercellular $CO_2$ concentration (Ci) (µmol $CO_2$ mol $air^{-1}$), transpiration rate (E) (mmol $H_2O$ $m^{-2}$ $s^{-1}$) and water use efficiency (WUE) (µmol $CO_2$ mmol $H_2O^{-1}$) of the second fully expanded leaves were registered every 3 seconds for 3 minutes. The measurements were performed on 6 randomly selected seedlings per treatment; from these data, a daily mean of measured indices was calculated. The environmental conditions during the measurements were: air flow rate – 400 µmol $s^{-1}$; block and leaf temperature – 25°C; $CO_2$ concentration in sample cell – 300–400 µmol $CO_2$ $mol^{-1}$; relative humidity in sample cell – 50–60%; lightness in quant – 160–185 µmol $m^{-2}$ $s^{-1}$.

**DPPH radical-scavenging activity.** The antioxidant activity DPPH radical-scavenging capacity was made in methanol extracts (1 g of plant tissues ground with liquid nitrogen and diluted with 10 ml of 80% methanol) and was evaluated spectrophotometrically [Ragaee et al. 2006]. The extract was homogenized using the vortex for 30 min, then centrifuged at 2012 g for 20 min. The absorbance scanned at 16 minutes at 515 nm was used for the calculation of the ability of plant leaves material to scavenge DPPH• free radicals (µmol $g^{-1}$). A Genesys 6 spectrophotometer was used for the analysis (Thermospectronic, USA).

**Determination of tocopherols contents.** The α-tocopherols content was evaluated according to Fernandez-Orozco et al. [2003] using high-performance liquid chromatography (HPLC) on Pinacle II silica column, 5 µm particle size, 150 × 4.6 mm (Restek, USA). Tocopherol was extracted using pure hexane (1 g of sample ground with liquid nitrogen / 10 ml of solvent), centrifuged (5 min, 349 g) and filtered through 0.45 µm PTFE membrane syringe filter (VWR International, USA). The HPLC 10A system, equipped with RF-10A fluorescence detector (Shimadzu, Japan) was used for analysis. Peak was detected using an excitation wavelength of 295 nm and an emission wavelength of 330 nm. The mobile phase was 0.5% isopropanol in hexane, flow rate 1 ml $min^{-1}$.

**Determination of total phenolic compounds.** The content of total phenolic compounds was determined in methanol extracts of spinach (1 g of plant tissues ground with liquid nitrogen and diluted with 10 ml of 80% methanol) using a calorimetric method [Ragaee et al. 2006]. The extract was homogenized by vortex for 30 min, then the extracts were centrifuged at 2012 g for 20 min. Then, 1 ml of extract was diluted with 1 ml Folin-Ciocalteau reagent (Folin-Ciocalteau reagent diluted with double-distilled water, 1 : 10) and with 2 ml 7.5% $Na_2CO_3$ solution. The absorbance was measured after 20 min at 765 nm with Genesys 6 spectrophotometer (Thermospectronic, USA) against water as a blank. The total phenolics were expressed through the calibration curve.

**Statistical analysis**. ANOVA was used to determine the effects of UV-B impact and plant species. For independent variables comparison, Student's t (for parametric) and U test (nonparametric) were employed. All the analyses were performed by STATISTICA, and the results were expressed as mean values and their confidence intervals ($CI_{0.05}$) ($p < 0.05$).

## RESULTS

The photosynthetic response of 'Matador' and 'Andromeda' spinach to UV-B exposure followed the same tendency (Fig. 1). On the first day, i.e. 2 hours after UV-B exposure, the photosynthetic rate of 1 kJ UV-B exposed 'Matador' plants decreased only by 8.2% ($p < 0.05$), while photosynthetic rate of 'Andromeda' decreased by 15.5% ($p < 0.05$), compared to the reference plants (Fig. 1). The lowest photosynthetic rate of 'Matador' and 'Andromeda' spinach plants was detected 24 hours after 2 kJ UV-B exposure when it decreased by 38.7% ($p < 0.05$) and 32.7% ($p < 0.05$) respectively, compared to the reference plants. After 72 hours, there was detected the increase by 7.7% ($p < 0.05$) and 2.9% ($p < 0.05$) of the photosynthetic rate of 1 kJ UV-B exposed 'Matador' and 'Andromeda' plants respectively, compared to reference treatment of that day.

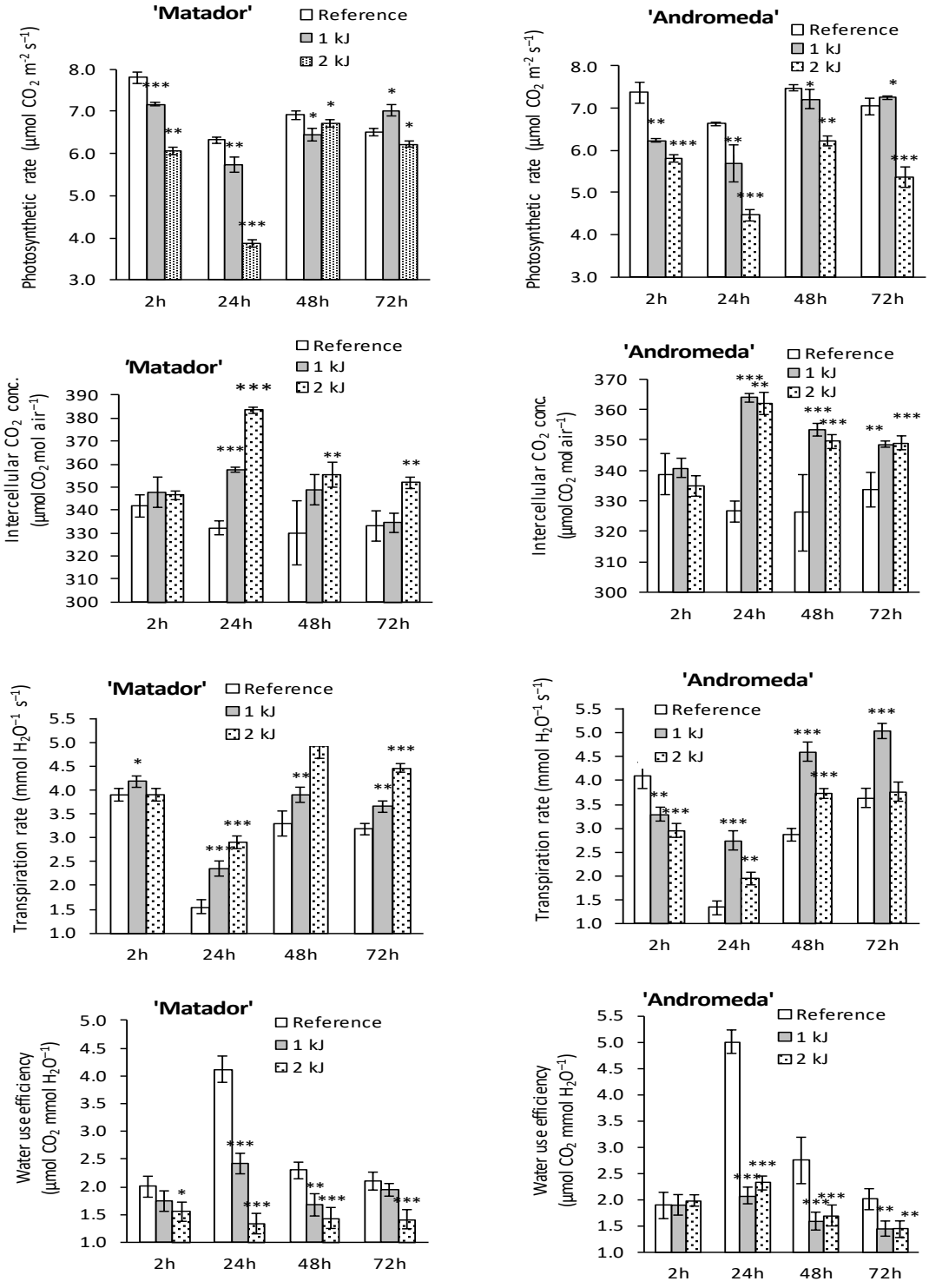


**Fig. 1.** Dynamics of gas exchange parameters of 'Matador' and 'Andromeda' spinach after short-term 1 kJ $m^{-2}$ (1 kJ) and 2 kJ $m^{-2}$ (2 kJ) UV-B radiation effect. The values are means ± $CI_{0.05}$. Significant differences from reference treatments are denoted with an asterisk; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

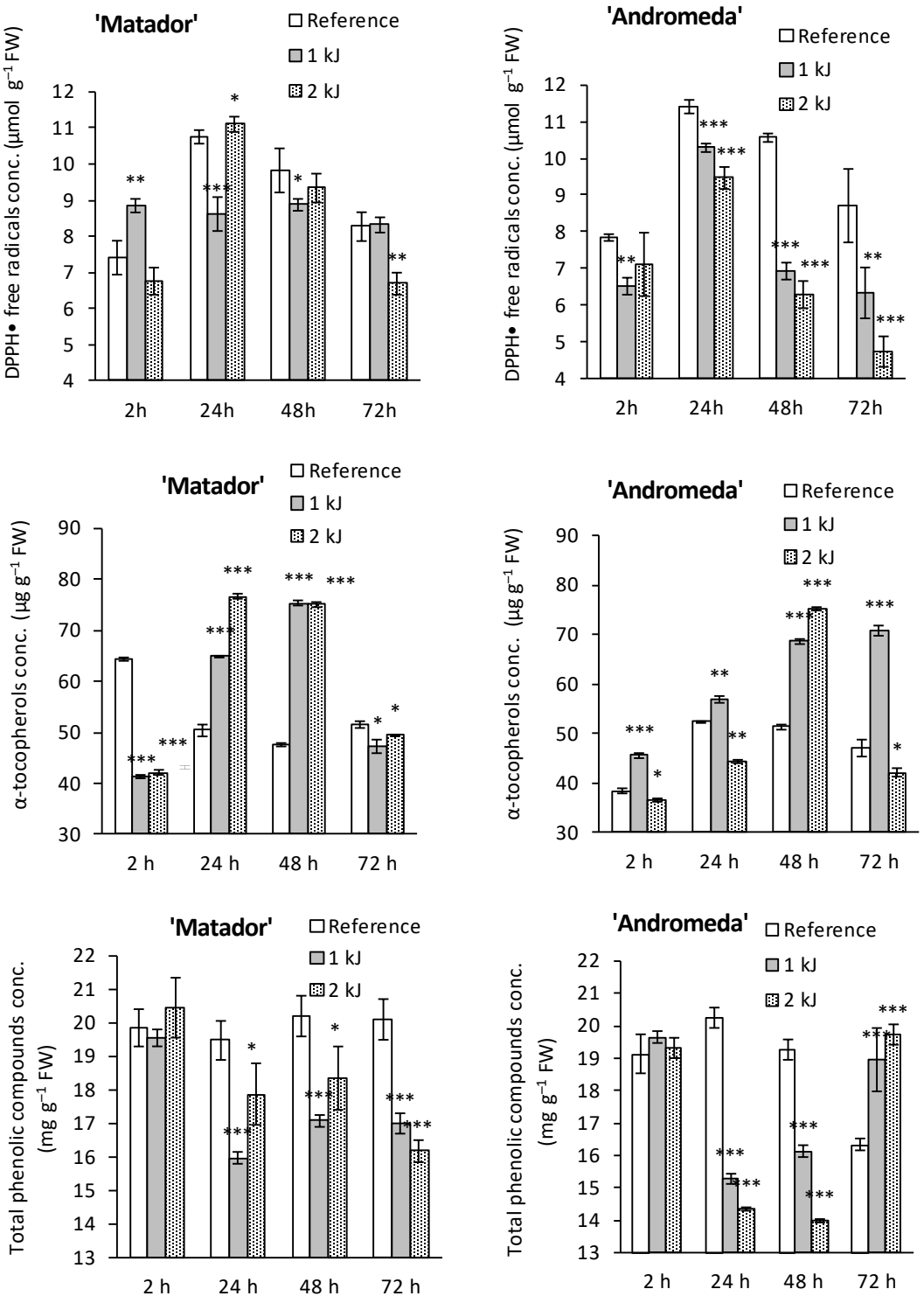


**Fig. 2.** Dynamics of biochemical parameters of 'Matador' and 'Andromeda' spinach after short-term 1 kJ $m^{-2}$ (1 kJ) and 2 kJ $m^{-2}$ (2 kJ) UV-B radiation effect. The values are means ± $CI_{0.05}$. Significant differences from reference treatments are denoted with an asterisk; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

The highest changes of intercellular $CO_2$ concentration of 2 kJ UV-B exposed 'Matador' plants were detected on the second day, i.e., 24 hours after exposure, when it increased by 15.4% ($p < 0.05$) compared to reference treatment (Fig. 1). The highest, compared to reference treatment, intercellular $CO_2$ concentration of 'Andromeda' plants was detected on the second day of experiment also, when CI increased by 11.5% ($p < 0.05$), but after 1kJ exposure. Changes in intercellular $CO_2$ concentration of investigated plants at 72 hour after UV-B exposure followed the same tendency for both species, i.e. it was increasing, but statistically significant only for 'Andromeda'.

Changes in transpiration rate of investigated plants were different, as well. At 2 hour after UV-B exposure, transpiration rate of 'Matador' plants increased by 7.2% ($p < 0.05$) and 0.1% ($p > 0.05$) after 1 and 2 kJ exposure respectively, while transpiration rate of 'Andromeda' decreased by 19.9% ($p < 0.05$) and 28.3% ($p < 0.05$) respectively, compared to plants of reference treatment (Fig. 1). The highest increase in transpiration rate of 'Andromeda' plants was detected on the 2$^{nd}$ day of the experiment, when it increased by 105.4% ($p < 0.05$) 24 hours after 1 kJ exposure, compared to the reference. Transpiration rate of 1 and 2 kJ UV-B exposed 'Matador' plants were also higher on the second day, but only 52.7% ($p < 0.05$) and 87.5% ($p < 0.05$) respectively, compared to reference treatment. Transpiration rate of 2 kJ UV-B exposed plants after 72 hours increased by 40.2% ($p < 0.05$) and 3.8% ($p > 0.05$) for 'Matador' and 'Andromeda', respectively compared to the reference treatment. While higher increase of transpiration rate was detected for 1 kJ UV-B exposed 'Andromeda' plants, when it was 38.8% ($p < 0.05$) higher, compared to the reference treatment. The changes of stomatal conductance followed the same tendency as transpiration rate.

Water use efficiency of UV-B exposed plants was lower on every day, compared to reference plants, except from 'Andromeda' plants 2 hours after exposure, when it increased but was statistically insignificant (Fig. 1). The highest decrease was detected on the second day after UV-B exposure, when WUE of 1 and 2 kJ exposed plants decreased by 41.2 and 67.6% ($p < 0.05$) for 'Matador' and by 58.6 and 53.6% ($p < 0.05$) for 'Andromeda' respectively, compared to reference treatment. On the last day of experiment, decrease of water use efficiency of UV-B exposed plants was similar for both species: it ranged from 28 to 33% ($p < 0.05$), except for 1 kJ UV-B exposed 'Matador' plants, when it decreased only by 7.7% ($p < 0.05$), compared to reference treatment.

Changes in the antioxidant activity (DPPH radical-scavenging capacity) were slightly different for investigated species after 2 hours of UV-B exposure (Fig. 2). Mostly by increasing UV-B radiation, it was decreasing, and this tendency was more pronounced for 'Andromeda'. On the last day of experiment, DPPH radical-scavenging capacity of 1 kJ UV-B exposed plants increased by 0.5% ($p < 0.05$) and decreased by 27.4% ($p < 0.05$) for 'Matador' and 'Andromeda', respectively compared to the reference treatment. While higher 19.0% ($p < 0.05$) and 45.8% ($p < 0.05$) decrease of DPPH was detected for 2 kJ UV-B exposed 'Matador' and 'Andromeda' plants respectively, compared to the reference treatment.

The content of α-tocopherols of UV-B exposed 'Matador' plants decreased on the first day, while the changes of tocopherols of UV-B exposed 'Andromeda' plants were slightly different, i.e. after 1 kJ UV-B exposure, it increased by 18.8% ($p < 0.05$) and after 2 kJ – decreased by 4.7% ($p < 0.05$) (Fig. 2). After UV-B exposure, the content of tocopherols increased in both cultivars on the third day, and on the last one, it was different again, i.e. the content of tocopherols decreased in both species, except from 1kJ UV-B exposed 'Andromeda' plants, when it increased by 50.1% ($p < 0.05$), compared to reference treatment.

The concentration of total phenolic compounds two hours after UV-B exposure did not change for both species, but 2 and 3 days after exposure, it decreased for 'Matador' and increased for 'Andromeda', and higher changes were detected for 'Andromeda' (Fig. 2). Changes in phenolic compounds concentration on the last day of experiment showed different tendency: for 1 and 2 kJ UV-B exposed 'Matador' plants, it decreased by 15.5 and 19.6% ($p < 0.05$), and for 'Andromeda', it increased by 16.0 and 20.8% ($p < 0.05$) respectively, compared to reference treatment.

The analysis of variance (ANOVA) showed that the highest effect was detected for the period of hours after UV-B exposure ($F = 3547$; $p < 0.05$) then the impact of UV-B ($F = 2032$; $p < 0.05$) and the lowest impact of species ($F = 352$; $p < 0.05$).

## DISCUSSION

UV-B radiation has been amply demonstrated to induce specific changes in gene expression [Favory et al. 2009], increased accumulation of UV-screening pigments [Agati and Tattini 2010] and altered phytochemical content [Schreiner et al. 2012]. Many of these responses have been linked to increased UV-B tolerance and can be induced by below ambient, chronic UV-doses, which do not cause any substantial damage [Ballare et al. 2011]. These responses can, therefore, be defined as eustress. However, whereas productivity may not be directly affected by UV radiation under eustress conditions, regulatory changes in photosynthate allocation and morphology [Jansen et al. 2012], may still cause subtle decreases in biomass accumulation [Hideg et al. 2013]. UV-B radiation effect in this research acted as eustress, but only at 1 kJ impact for both species, while 2 kJ effect was somewhat negative. The stimulating effect of UV-B emerged only 4 days after exposure when the 1 kJ UV-B exposed spinach photosynthesis was 7.7% higher compared to the control plants. The positive effect of UV-B is more pronounced for 'Matador' when the photosynthetic rate of both UV-B doses exposed spinach was higher compared to the control plants on the last day of the experiment. The increase in the photosynthetic rate of 'Matador' could be determined by more opened stomata, through which the plant got more $CO_2$, which is reflected in an increased CI. Therefore, the highest quantity of $CO_2$ was got in for the enzymatic carbon fixation reactions. The increase in the photosynthetic rate of 'Andromeda' after 1 kJ UV-B exposure can also be explained by the same regularity as the 'Matador'. Meanwhile, after 2 kJ UV-B exposure, the photosynthetic rate decreased and thus did not rise above reference plants until the end of the experiment. The effect of UV-B can explain this decrease of photosynthesis on enzymatic reactions of photosynthesis, or on the regeneration of Rubisco [Lu et al. 2009].

Thus, the positive effect of UV-B on photosynthetic rate of spinach could be associated with the stomata response to the stressor. When the stressor affected wider opening of the stomata, and with a sufficient amount of water, due to the higher transpiration rate, the photosynthetic rate became more intensive due to increased $CO_2$ income (Fig. 1). When the stressor affected the closure of stomata, the photosynthetic rate decreased. Several studies have also shown that reduction in $CO_2$ assimilation is caused by UV-B induced reduction in stomatal conductance [Reddy et al. 2013] or may be further mediated through a decrease in light-harvesting complexes, disruption of thylakoid membrane integrity, and degradation and inactivation of Rubisco [Kataria et al. 2014].

Both low and high levels of UV-B radiation can change antioxidant metabolism: altering the size and oxidation–reduction state of the ascorbate, glutathione, and tocopherol pools, inducing accumulation of flavonoids and related phenolics [Bornman et al. 2015, Thomas and Puthur 2017]. Such changes in the metabolism are an intrinsic part of both eustress and distress [Hideg et al. 2013, Bornman et al. 2015]. In this research by increasing UV-B radiation, DPPH radical-scavenging capacity was decreasing, and this tendency was more pronounced for 'Andromeda' (Fig. 2). The highest DPPH radical-scavenging capacity and the highest concentration of α-tocopherols were detected 24 hours after 2 kJ UV-B exposure when the decrease of photosynthetic rate was the highest that day as well (Figs. 1 and 2). Till the last day of experiment, DPPH radical-scavenging capacity and concentrations of α-tocopherols and phenols were decreasing and the photosynthetic rate turned back to the level of 'Matador' reference plants. UV-B-specific perception and signaling pathways comprise the main regulatory pathway under low UV conditions [Jenkins 2009] activating antioxidant defenses before potential oxidative pressure [Bornman et al. 2015, Thomas and Puthur 2017]. While for 'Andromeda', the changes were a little bit different: photosynthetic rate decreased more, and it might be because of the adverse effect of UV-B radiation on enzymatic reactions of photosynthesis mentioned above and higher impact of oxidative stress or by lower efficiency of the antioxidant system [Hideg et al. 2013].

## CONCLUSIONS

The results obtained in our study show that there is a window to improve the nutritional quality of spinach by applying the short-term UV-B exposition. What's important, we have detected that the highest

concentration of α-tocopherols was detected 24 hours after 2 kJ UV-B exposure when the decrease in photosynthetic rate was the highest that day as well. However, our results clearly showed that there are genotypic differences precluding a generalization of the use of such eustress to the whole spinach species.

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