Ultraviolet-B radiation induces physiological, biochemical, and structural changes in *Viola odorata*

Zahra Shafaghat[1] · Fatemeh Zarinkamar[1] · Mehrdad Nazari[1]

Abstract

Ultraviolet (UV) radiation is a common environmental factor that affects the growth and productivity of plants. However, many plants have evolved structural, physiological, and biochemical mechanisms to cope with UV radiation. *Viola odorata*, is exposed to extended daily sunlight and acclimatization mechanisms have been developed in response to natural UV radiations. The purpose of this study was to assess the changes in the morphology and abundance of mucilaginous structures besides the physiological and biochemical changes of *V. odorata* plants under exposure to UV-B radiation (2 h and 4 h daily). After 4 weeks of treatments, the obtained results showed that the *V. odorata* plants responded to UV-B radiation anatomically and physiologically through changes in thickening of the cuticle, production of mucilage and enzymatic and non-enzymatic antioxidants; also, the content of malondialdehyde (MDA) and hydrogen peroxide (H_2O_2) was increased. The investigation showed that the duration of exposure to UV-B radiation had a negative correlation with the content of carotenoids, chlorophyll *a*, chlorophyll *b*, and soluble carbohydrates, whereas it had a positive correlation with the content of mucilage, anthocyanins, flavonoids, MDA, H_2O_2, and activity of superoxide dismutase (SOD), catalase (CAT), and peroxidase (POX) enzymes. These findings display the different defense mechanisms in *V. od*orata plants against UV-B radiation.

Keywords Anatomical response · Antioxidant response · Mucilage · Sweet violet · Ultraviolet radiation

Introduction

Ultraviolet (UV) radiation has diverse biological effects on metabolism, development, and viability of living organisms (Verdaguer et al. 2017). In particular, plants require sunlight (UV radiation comprises approximately 3–5% of the solar energy spectrum) to sequester atmospheric carbon into structural and biochemical compounds necessary for growth and development. The UV light is composed of about 90% UV-A and 10% UV-B; whereas, UV-C does not penetrate the earth's atmosphere (Parra et al. 2019). Consequently, leaves are exposed to ultraviolet wavelengths, including UV-B and UV-A.

UV-B radiation (290–320 nm) is an important environmental factor that can affect the various physiological, morphological, biochemical, and molecular processes in plants. Accordingly, UV-B radiation may affect the morphology (Zhang et al. 2017), cellular function (Verdaguer et al. 2017), gene expression (Khudyakova et al. 2019), antioxidant defense system (Dias et al. 2020), signal transduction (Cloix and Jenkins 2008), biometric parameters (Rodríguez-Calzada et al. 2019), and phytochemicals (Nazari et al. 2018a).

Viola odorata is an aromatic and medicinal species from the Violaceae family, which is distributed worldwide with the greatest morphological and taxonomic diversity in the highlands of the northern hemisphere (Hodálová et al. 2008). *Viola odorata*, because of its habitat is exposed to extended daily sunlight, but it seems that it has developed sophisticated defense mechanisms such as structural, biochemical, and physiological adaptations against UV-B radiation.

Mucilaginous cells in the leaves of *V. odorata* produce mucilage, which performs important regulatory functions (Karioti et al. 2011). Mucilage is a mixture of polysaccharides and some lipids that is produced in solitary cells, secretory hairs as well as cells on both upper and lower epidermis (Fortuna-Perez et al. 2012; Mohammadi Shahrestani et al. 2014). The purpose of this study was to assess (1) changes

✉ Fatemeh Zarinkamar
  zarinkamar@modares.ac.ir

1   Department of Plant Biology, Faculty of Biological Biology, Tarbiat Modares University, Jalal-Al-Ahmad Highway, Nasr Bridge, Tehran, Iran

in the morphology and abundance of mucilaginous structures and (2) to determine biochemical and physiological changes of *V. odorata* exposed to extended periods of UV-B radiation.

Materials and methods

Plant material, growth conditions, and treatments

Seeds of *V. odorata* were obtained from Research Center of Jahad Keshavarzy, Esfehah, Iran. The seeds were disinfected with 2% sodium hypochlorite solution for 5 min and then washed three times with deionized water. Ten disinfected seeds were placed into a sterilized Petri dish filled with moistened sterile filter paper (Whatman No. 1) in a dark and humid chamber. The germinated seeds were planted in plastic pots: five equidistant seeds in each pot containing 500 g sterile perlite under greenhouse condition with a 16/8 h photoperiod, 65% relative humidity, and 25 ± 2 °C for 6 weeks. After this period, the experimental plants were exposed to two different UV-B treatments. To determine the effects of UV-B radiation (290–320 nm, Philips TL 12, 40 W, Eindhoven, Netherlands) (1) on the biochemical and physiological parameters, plants were exposed to two regimes of 2 or 4 h per day and (2) on plant anatomy, plants were exposed to 4 h radiation per day for 4 weeks. Because the UV-B treatment lamps emit UV-C (200–280 nm) and UV-B wavelengths, the UV radiation was filtered through 0.1-mm-thick cellulose diacetate (Cadillac Plastic Co., Baltimore, MD, USA) to remove wavelengths less than 290 nm. The dose of UV-B radiation at the level of plant leaves was measured with a spectroradiometer (SS-25, Japan Spectroscope Co., Tokyo, Japan) and was found 1.15 W m^{-2}. The biologically effective dose was 14 kJ m^{-2} as calculated using Caldwell's generalized plant action spectrum, normalized to 300 nm (Caldwell 1971). The PAR background was 500 μmol m^{-2} s^{-1} which was provided from 400 W metal halide lamps (Osram HQI-BT 400 W; Osram Ltd., St Helens, UK). The plants in the control group did not receive any UV-B exposure (using an identical lamp where UV-B radiation was attenuated by polyester). The mature leaves of control and UV-B-treated plants were selected randomly for measurements.

Mucilage assay

To determine the mucilaginous structures, sections were stained with Alcian blue (0.1%, Sigma-Aldrich, USA) dissolved in acetic acid (3%, Sigma-Aldridge, USA) pH 3 for 30 min (Ghanem et al. 2010) and Ruthenium red (0.05%, Sigma-Aldrich, USA) for 10 min under ambient laboratory conditions (Pérez-de-Luque et al. 2006). The microscope used was the Olympus BH2 (Olympus, Tokyo, Japan) with magnifications of 10 ×, 40 ×, and 100 ×.

To determine the quantity of mucilage, plant leaves were washed and placed in 25 ml boiling ethanol 96% (Merck, Germany) inside a glass cylinder, covered tightly with foil, shaken every 10 min for 1 h, and let to soak for 3 h. Later, the plant material was dried in a 60 °C oven to constant weight and then ground to mesh size 315 μm. Two grams of powdered leaves were soaked and shaken in 200 ml of hot water (93 ± 2 °C) for 12 h. Next, the volume was adjusted to 50 ml under rotary evaporator, centrifuged (Hettich, Mikro 200, Germany) for 15 min at $4000 \times g$, allowed to stay overnight at 40 °C, and filtered through a pre-weighed filter paper (Whatman No. 1) on a Buchner funnel. The samples were dried under vacuum at 40 °C for 24 h to constant weight (Woolfe et al. 1977). The stock concentration of the leaf extract was 1900 mg L^{-1}.

Physiological and biochemical assays

The content of total soluble carbohydrates (Fales 1951), flavonoids (Chang et al. 2002), anthocyanins (Hara et al. 2004), photosynthetic pigments (carotenoids, chlorophylls *a* and *b*) (Arnon and Whatley 1949), malondialdehyde (MDA) (Choudhary et al. 2007), hydrogen peroxide (H$_2$O$_2$) (Nazari et al. 2018b) and the enzymatic activity of superoxide dismutase (SOD) (Basu et al. 2010), catalase (CAT) (Cakmak and Horst, 1991), and peroxidase (POX) (Farzadfar et al. 2017) were measured.

Statistical analyses

Statistical comparison of mean values was carried out using SPSS version 23. Assumptions of normality and homogeneity of variance of the data were tested using the Shapiro–Wilk and Levene tests, respectively, prior to ANOVA analysis. The *t* test was used when comparing two groups and Duncan's multiple range test was used when comparing multiple groups. The heat map and HCA (Hierarchical Cluster Analysis) analyses were performed using MetaboAnalyst platform (http://www.metaboanalyst.ca). Anatomical analysis was done using Ts View software.

Results and discussion

Structural changes

The anatomy of *V. odorata* leaves (Fig. 1) show mucilage cavities present in the different leaf tissues. In this study, UV-B radiation caused various anatomical changes in the leaves of *V. odorata* (Table 1). According to the obtained results, the cuticle of leaves of UV-B-treated plants was

Fig. 1 Anatomy of the *V. odorata* leaves (× 10) (**a**). Mucilage cells present in the parenchyma and mucilage cavities in the main vein (× 10, × 40, and × 100, respectively, from left to right) (**b**). *Cv* cavities, *Mc* mucilage
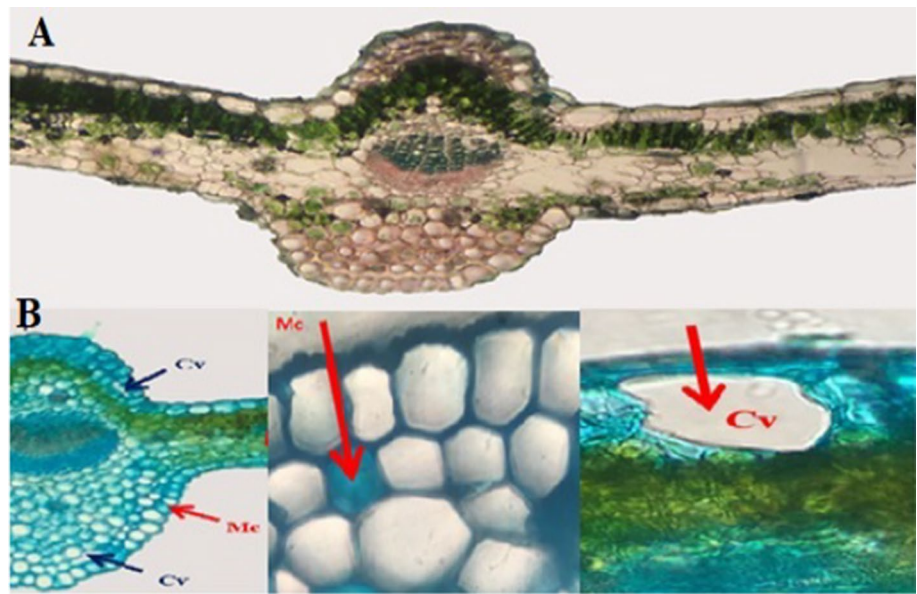

Table 1 Effect of UV-B radiation on the tested parameters in *V. odorata*

Parameters	Control	UV-B radiation
Cuticle thickness (μm)	2.01 ± 0.2[b]	5.43 ± 0.6[a]
lower epidermis thickness (μm)	9.76 ± 1.1[b]	21.61 ± 2.6[a]
Upper epidermis thickness (μm)	18.34 ± 2.8[b]	25.31 ± 3.2[a]
Lower mesophyll thickness (μm)	37.95 ± 3.4[b]	68.26 ± 4.6[a]
Upper mesophyll thickness (μm)	20.05 ± 2.5[b]	60.57 ± 4.3[a]
Leaf width (μm)	57.27 ± 4.6[b]	94.69 ± 5.4[a]
Epidermis cell size (μm)	15.55 ± 2.3[b]	19.79 ± 2.1[a]
Mucilage cell size (μm)	10.15 ± 1.1[b]	16.01 ± 2.5[a]
Mucilage channel area (μm)	60.64 ± 4.4[b]	362.56 ± 15.2[a]
Mucilage cavity area (μm)	553.32 ± 17.5[b]	1514.81 ± 26.9[a]
Vascular bundle diameter (μm)	3643.78 ± 37.4[b]	10,913.45 ± 80.8[a]
Mucilage cells number (%)	60 ± 3.7[b]	37 ± 3.9[a]
Upper stoma index (%)	17.79 ± 2.3[b]	24.66 ± 3.1[a]
Lower stoma index (%)	26.07 ± 2.2[b]	40.56 ± 3.7[a]
Leaf length (cm)	1.92 ± 0.3[b]	3.06 ± 0.8[a]
Leaf width (cm)	1.50 ± 0.3[b]	2.34 ± 0.7[a]

The values are averages of five independent replicates, with standard deviations. Different letters indicate significant differences ($P < 0.05$)

thicker than that in the controls. Epidermal cells showed thickened cell walls containing more mucilage, even on stomata guard cells (Fig. 2). The cortex and spongy mesophyll cells of UV-B-exposed plants were significantly greater in diameter than the controls. There were more and larger mucilaginous cells and channels in the mesophyll of UV-B-treated plants than the controls.

Increased lignification of leaf cell walls associated with increased production of mucilaginous compounds (Fig. 2 and Table 1) under UV radiation has been previously reported (Hilal et al. 2004; Sarghein et al. 2011). This is to avoid the harmful effects of UV-B radiation and increase the protection of mesophyll cells for better functioning and carbon sequestering in leaves (Hong and Ibrahim 2012). Results showed that the number of mucilaginous cells was increased significantly under exposure to 4 h UV-B radiation compared with the control condition (Table 1). In addition, UV-B radiation caused malformations and necrosis of vascular bundles, particularly of phloem (Fig. 2). Santos et al. (2004) have previously reported such findings in potato plants.

Mucilage, MDA, and H_2O_2

The results of mucilage content measurements clarified that the content of this compound was significantly increased in the leaves of *V. odorata* plants when treated with UV-B radiation compared with the controls ($P < 0.05$) (Fig. 3a). Mucilaginous cells in the control plants contained 6.46% mucilage but it reached 11.56% in the 4 h radiated plans, indicating the increase of mucilage content in the plant leaves with increasing duration of exposure to UV-B radiation. There are no published reports regarding the effect of UV-B radiation on the mucilage production in *V. odorata*. However, it has been found that mucilage provides protection to cells through maintaining a positive water equilibrium between plant and the environment (Gregory and Baas 1989) and a filtering tool against UV radiation in epidermal cells (Hong and Ibrahim 2012). Since the penetration of UV-B radiation into the cell is limited, this radiation has a strong effect on surface or near-to-surface area in plant cells.
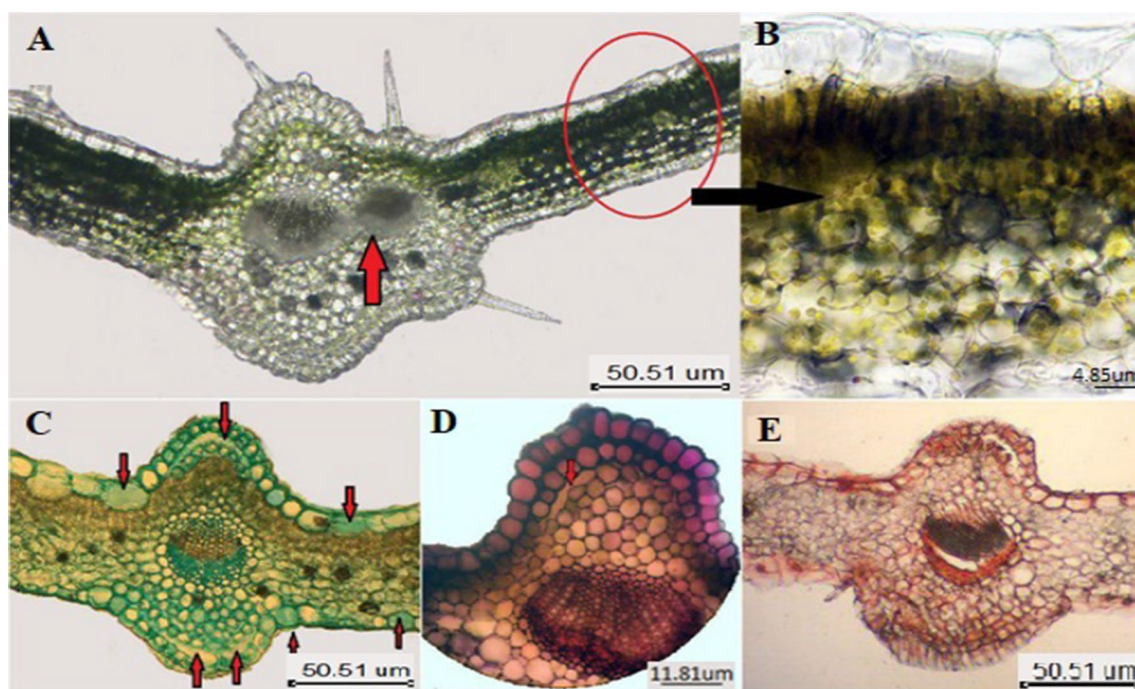
Fig. 2 Cross sections of the leaves in the UV-B-treated *V. odorata* plants. Increase of leaves thickness and pigments content under UV-B radiation (× 10 and × 40, respectively) (**a**, **b**). Staining the leaves with Alcian blue under UV-B treatment (× 10) (**c**). Arrows show an increase in the number of mucilage cells and mucilage channels. Ruthenium red staining, increased thickness of walls of epidermal and subepidermal cells as well as increased diameter of vascular bundles in the UV-B-treated plants (× 40) (**d**). Destruction of leaves structure and necrotizing of vascular bundles under the influence of UV-B radiation (× 10) (**e**)

It is possible that mucilage mitigate the adverse effects of UV-B radiation on plant cells because it is chemically complex and contains UV-absorbing compounds (de Menezes et al. 2015). In addition, it has been suggested that polysaccharides can act as free radical scavengers and inhibit DNA damage (Cui et al. 2019). The molecular mechanism of UV-B induced mucilage accumulation in plant tissues is not fully understood; however, it is known that many plant genes that respond to environmental changes are modulated by UV-B radiation. In addition to these genes, some other genes encode transcription factors, enzymes/proteins, and signaling proteins are affected by this radiation (Gupta et al. 2018).

According to obtained results, UV-B radiation caused a significant increase in the content of MDA and H_2O_2 in plants exposed to 2 and 4 h radiation compared with the controls ($P < 0.05$) (Fig. 3b, c). However, as the radiation exposure period increased, the MDA content was increased. MDA is a secondary product of lipid peroxidation and is widely used as a biomarker of oxidative stress in plants. The increased level of MDA indicates a distinct deterioration of permeability (Kakani et al. 2003), functioning (Berli et al. 2010) and structure of cell membrane (Murphy and Vu 1996). It has been reported that the level of H_2O_2 increased during the exposure of Mono Maple seedlings to UV radiation (Yao and Liu 2006), which is in agreement with our findings. In plants, H_2O_2 is naturally produced in cells and regulates several biological processes. The increased production of reactive oxygen species (ROS) may trigger a cascade of events to enhance the cellular defense against oxidative stress.

Photosynthetic pigments, soluble carbohydrates, anthocyanins, and flavonoids

In this study, physiological and biochemical changes in the *V. odorata* leaves exposed to the UV-B radiation were observed. Results showed a significant reduction in the content of Chl *a* and Chl *b* in the leaves of UV-B-treated plants compared with the control plants. However, the content of carotenoids in the leaves of 2 h radiated plants initially increased but reduced as exposure period prolonged (Fig. 4a). This in agreement with Mishra et al. (2008) who indicated a reduction in the level of photosynthetic pigments correlated with duration and intensity of UV-B exposure (Mishra et al. 2008). In plants, carotenoids are more resistant to radiation degradation than chlorophylls and play a more protective role in response to UV-B radiation (Yao et al. 2006). Initial increase in the carotenoids content may be because of their resistance to break down to a threshold of
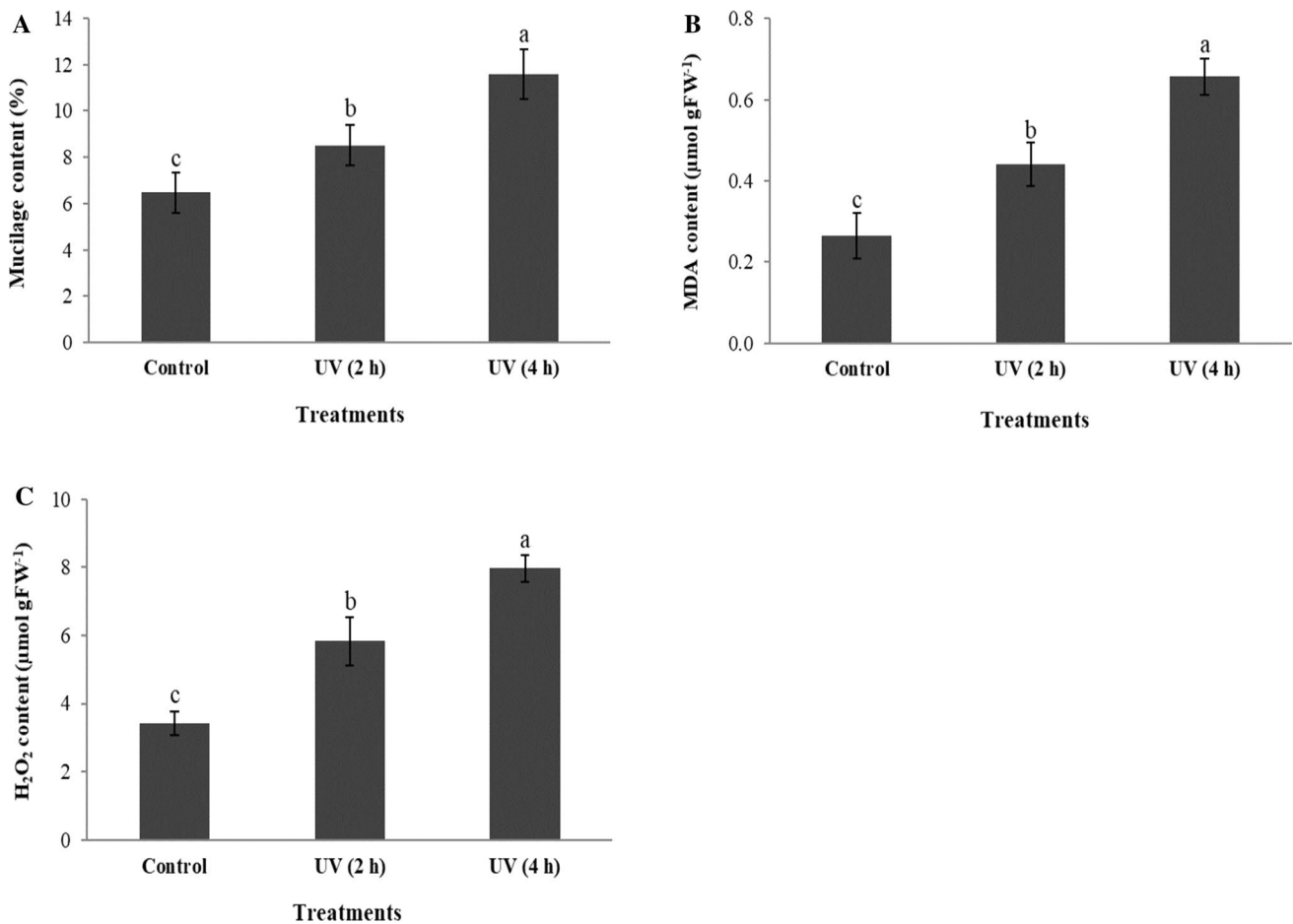
Fig. 3 Effect of UV-B radiation on the content of mucilage (**a**), MDA (**b**), and H_2O_2 **c** in the leaves of *V. odorata*. The bars represent averages of five independent replicates, with standard deviations. Different letters indicate significant differences ($P < 0.05$)

radiation as their quantity was reduced with increasing duration of exposure or reduction in the content of chlorophylls which can reflect the relative abundance of carotenoids at the early stages of radiation exposure. Carotenoids are antioxidant compounds that play an important role in the light-harvesting complex as photosynthetic pigments, and protect the photosystems. They quench triplet state chlorophyll molecules and scavenge singlet oxygen and other toxic ROS that are formed within the chloroplast, thus dissipating the excess of excitation energy under stress conditions. On the other hand, it has been known that carotenoids are degraded and transformed to abscisic acid (a plant growth regulator) as a result of environmental stresses such as UV-B radiation (Allen et al. 1998).

Several studies have reported the reduction of photosynthetic pigments content under UV-B radiation (Bischof et al. 2002; Mishra et al. 2008). This can result in a lower production of primary metabolites, such as carbohydrates (Gill et al. 2001; Liu et al. 2005), as evident in the reduction in the content of soluble carbohydrates, particularly in the

plants exposed to 4 h of UV-B radiation compared with the controls. The soluble carbohydrates content in the plants leaves was different, depending on the duration of UV-B treatment (Fig. 4b). Accordingly, the soluble carbohydrates content increased first, and then decreased as the period of UV-B radiation increased. This finding supports the fact that *V. odorata* spends much of its carbon resources towards the biosynthesis of protective metabolites, both structural such as lignification of cell walls, and physiological and biochemical, including the production of protective enzymatic and non-enzymatic antioxidants.

In plants, further protection against UV-B radiation is achieved through the production of antioxidants such as anthocyanins (Tsurunaga et al. 2013). Many plants growing in alpine ecosystems produce anthocyanins as an adaptive strategy to face UV radiation. UV radiation enhances the anthocyanins biosynthesis as a result of gene activation for the production of phenolic secondary metabolites and other antioxidants pathways (Jiao et al. 2018). Results of this work concerning the production of
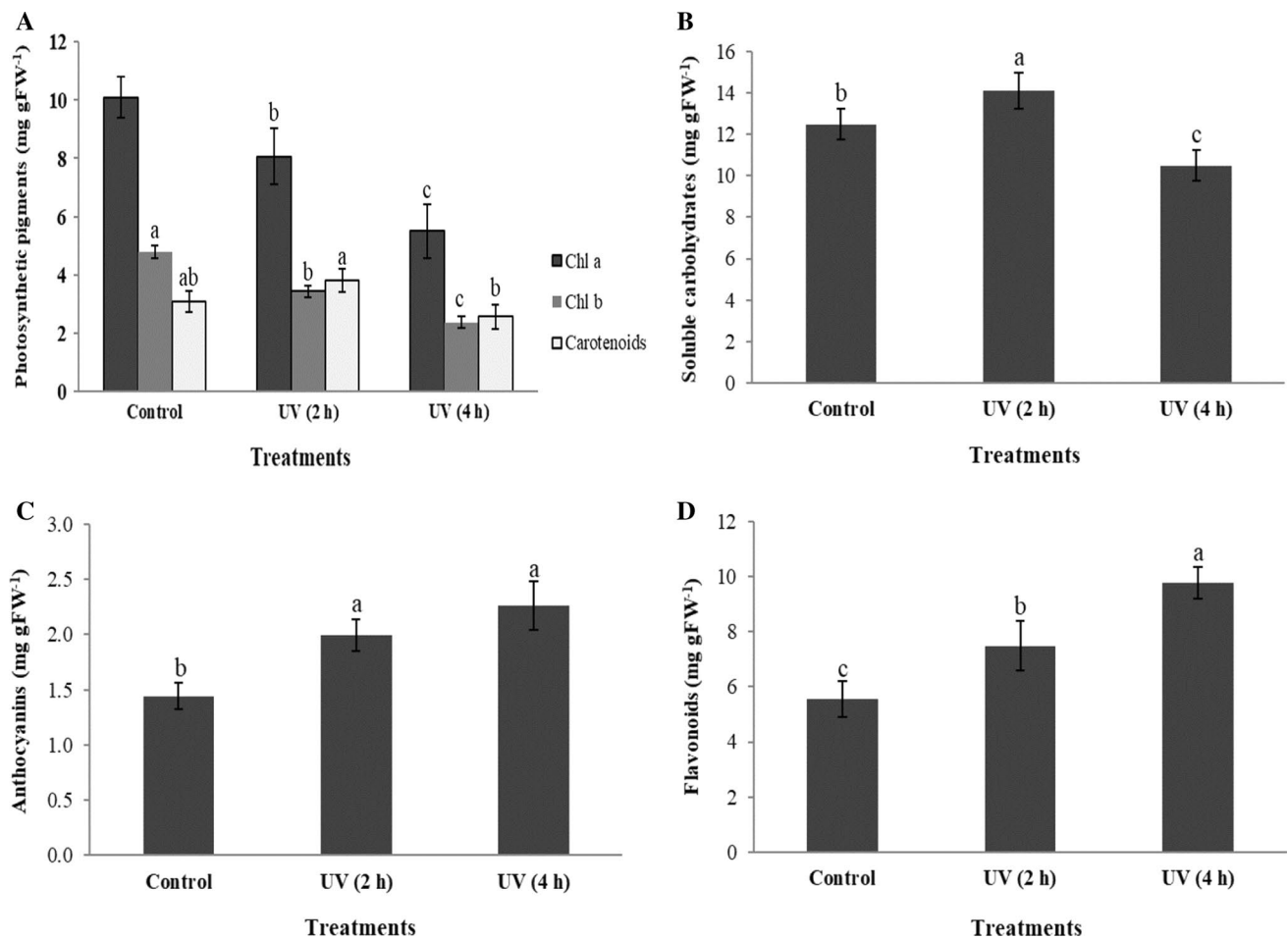
Fig. 4 Effect of UV-B radiation on the content of photosynthetic pigments (**a**), soluble carbohydrates (**b**) anthocyanins (**c**), and flavonoids **d** in the leaves of *V. odorata*. The bars represent averages of five independent replicates, with standard deviations. Different letters indicate significant differences ($P < 0.05$)

anthocyanins under UV-B radiation (Fig. 4c) supported previous findings on tomatoes (Luthria et al. 2006) and strawberry plants (Erkan et al. 2008). Additional evidence for an active protective strategy of *V. odorata* was provided by the enhanced production of flavonoids as the duration of exposure increased (Fig. 4d). Such findings have been reported previously for spinach (Smirnoff et al. 2001) and petunia (Ryan et al. 2002). Flavonoids are non-enzymatic antioxidants that are produced in response to stress via the phenylalanine ammonia-lyase (PAL) enzyme pathway, combat free radicals and offer further physiological protection to cellular integrity (Guo and Wang 2009). These compounds are well documented for their ability to absorb the UV-B radiation, inhibit the generation of ROS, and quench ROS once they are formed (Kumar and Pandey 2013a). The antioxidant activity of phenolic compounds is mainly due to their reducing power and lipid peroxidation inhibitory activity (Kumar and Pandey 2013b; Sharma et al. 2017).

Antioxidant enzymes

The experimental data showed that UV-B radiation caused a rise in the activity of antioxidant enzymes, including SOD (Fig. 5a), POX (Fig. 5b), and CAT (Fig. 5c). Accordingly, the activity of these enzymes was significantly increased in the leaves cells of radiation-exposed plants compared with the control plants. The highest period of UV-B treatment (4 h) resulted in the highest activity of these enzymes in the leaves of *V. odorata* plants. The observed increase in the antioxidant capacity of these enzymes in the leaves of UV-B-treated plants can be due to the increased levels of superoxide radicals in these plants. The relationship between enzyme activity and UV-B radiation duration indicated that antioxidant enzymes play an important role in the detoxification of ROS produced by this radiation. These findings suggest that UV-B radiation induced the antioxidant defense system in the leaf tissues, allowing plant survival in spite of the oxidative stress generation. It has been reported that
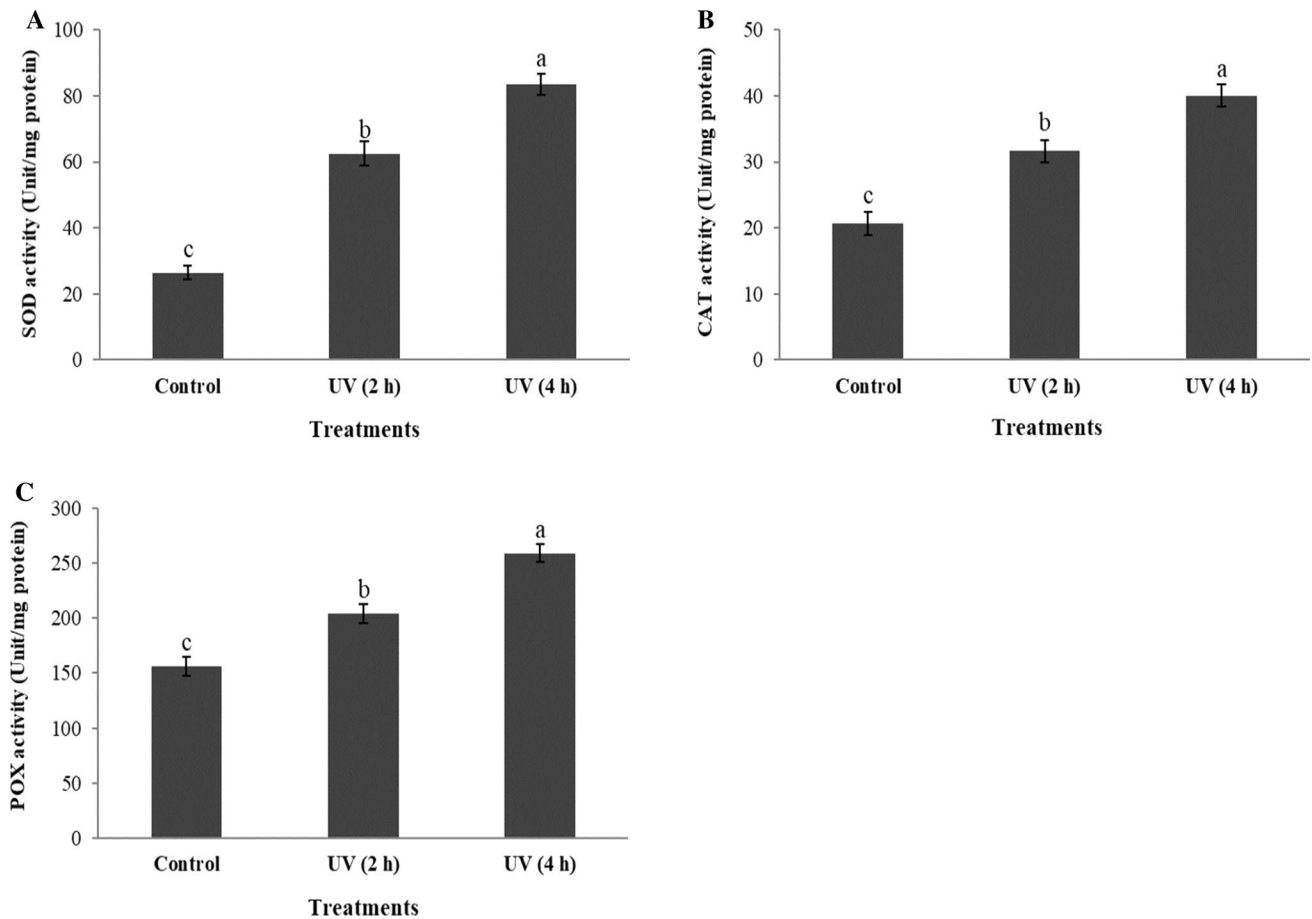
Fig. 5 Effect of UV-B radiation on the enzymatic activity of superoxide dismutase (SOD) (**a**), catalase (CAT) (**b**), and peroxidase (POX) **c** in the leaves of *V. odorata*. The bars represent averages of five independent replicates, with standard deviations. Different letters indicate significant differences ($P < 0.05$)

UV-B radiation increased the expression of genes coding for antioxidant enzymes (Cantarello et al. 2005). Consistent with our findings, the increase of antioxidant enzymes activity under UV-B radiation has been indicated as a protective adaptation strategy by other studies (Santos et al. 2004; Yannarelli et al. 2006).

Classification of physiological and biochemical parameters

Correlation analysis between pairs of the examined parameters (mucilage, photosynthetic pigments, soluble carbohydrates, flavonoids, anthocyanins, MDA, H_2O_2, and activity of antioxidant enzymes) in response to UV-B radiation is presented in Fig. 6. The obtained results were visualized using a color-coded heat map according to the Pearson correlation coefficient of each parameter with others and resulted in several clusters. Altogether, these data clearly show that the content of MDA, H_2O_2, flavonoids, anthocyanins, mucilage, and the activity of antioxidant enzymes (SOD, CAT, POX) were correlated positively with increasing UV-B exposure period. On the other hand, other parameters including Chl *a*, Chl *b*, carotenoids, and soluble carbohydrates had lower correlations with the UV-B exposure period and therefore were classified in another cluster.
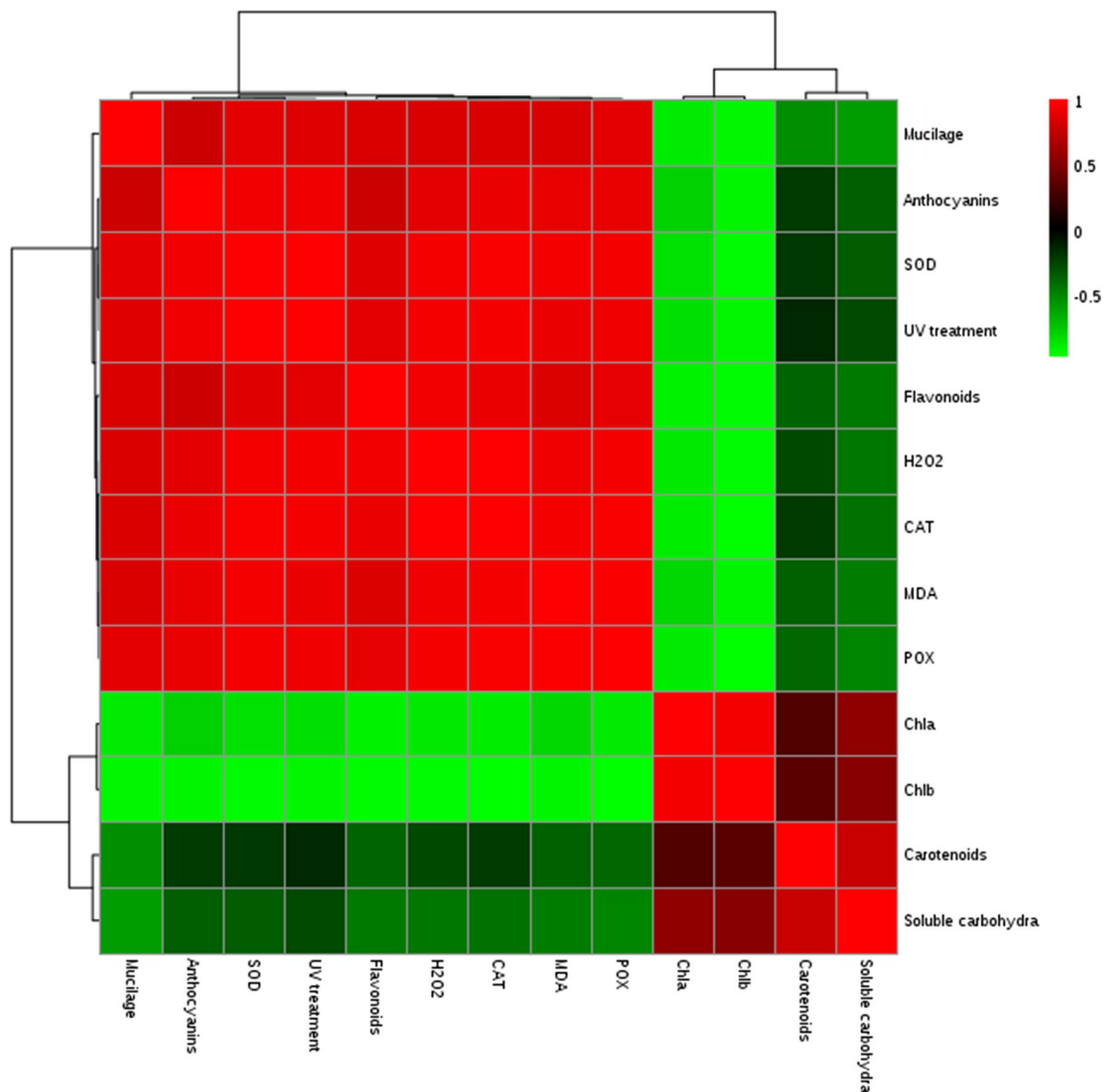
Fig. 6 Correlations (Pearson coefficient) between pairs of the physiological and biochemical parameters [mucilage, carotenoids, chlorophyll *a*, chlorophyll *b*, soluble carbohydrates, anthocyanins, flavonoids, malondialdehyde (MDA), hydrogen peroxide (H_2O_2), superoxide dismutase (SOD), catalase (CAT), and peroxidase (POX)] in the leaves of *V. odorata* plants that were treated with UV-B radiation. Colors in the matrix boxes display the magnitude and direction of the correlations: intense green and red indicate strong negative and positive correlations, respectively

Conclusion

The exposure of *V. odorata* plants to the elevated UV-B radiation affected the metabolism of photosynthetic pigments, soluble carbohydrates, phenolic compounds, mucilage, oxidants, antioxidants, and structure of leaves. The changes were more pronounced in the plants exposed to the 4 h UV-B radiation compared with those exposed to 2 h UV-B radiation. The findings confirm the adaptive ability of *V. odorata* to moderate levels of UV-B radiation

and physiological adjustment to longer duration of UV-B radiation. It appears that the acclimation of *V. odorata* under UV-B radiation operated through changes in its morphology (thickening of the cuticle), biochemistry, and physiology (production of mucilage and enzymatic and non-enzymatic antioxidants). The results suggest that photosynthetic carbon assimilation in the UV-B-exposed plants lead to the production of phytochemicals. Positive and negative correlations were found among the physiological and biochemical processes under the UV-B radiation. However, further comprehensive investigations are

required to identify the underlying physiological, biochemical, and molecular mechanisms associated with the plant response to UV-B radiation.

Compliance with ethical standards

Conflict of interest The authors declare no conflict of interest.

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