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Comparison of susceptibility of leaves on short-term UV-B irradiation

E. Skórska and A. Murkowski*

Department of Physics and Agrophysics, West Pomeranian University of Technology, Papieża Pawła VI 3, 71-459 Szczecin, Poland

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A b s t r a c t. The effects of short-time ultraviolet-B irradiation (0.74 kJ m^{-2} d^{-1}) at light on cucumber and peppermint leaves were studied. A considerable decrease of the most important chlorophyll fluorescence parameters values mainly in the cucumber leaves, compared to the control, was observed. It indicates damages as well as at a donor and acceptor side of photosystem II, specially in the oxygen evolving complex, electron transport and connected with the dark reactions. In the peppermint leaves these values were unchanged or slight decreased. After 24 h from disappearing of the applied UV-B stress, adverse changes became established, especially in the cucumber leaves show irreversible damages of photosystem II. Coefficient of nonphotochemical quenching increased by 50% in the peppermint leaves, while in cucumber remained unchanged. Chlorophyll delayed luminescence coefficient was decreased by 36% in the UV-B irradiated cucumber leaves and by 25% in the peppermint leaves. Content of ultraviolet-absorbing compounds was higher in peppermint leaves by 78% than in the cucumber. Generally, peppermint seemed to be more tolerant to the applied UV-B radiation compared to cucumber.

K e y w o r d s: ultraviolet-B, leaves, cucumber, peppermint, photosynthesis reactions

INTRODUCTION

UV-B radiation (280-315 nm) affects plants by modifying both their biological and chemical environment (Hollosy, 2002; Jansen *et al*., 2008; Kakani *et al*., 2003; Vu *et al*., 2009). Damage may occur in many places, including the direct destruction of the DNA, deactivation of protein and enzymes, disruption of membranes and other cell structures and the generation of highly reactive chemical agents known as 'free radicals' (Björn *et al*., 2002; Caldwell, 1971; Rozema *et al*., 1997). UV-B can cause damage of cell membranes by photoabsorption and peroxidation of unsaturated fatty acids and changes in the membrane lipid composition. The direct effect of enhanced UV-B radiation in sensitive plants are the following: impairment of photosystem II (PS II), decrease in Rubisco activity, carbon dioxide fixation and oxygen evolution; reduction in dry weight, starch and chlorophyll content (Bormann, 1989; Jansen *et al*., 2008). The water-oxidizing complex of PS II is an important target of ultraviolet-B radiation (Björn, 2002; Szilárd *et al*., 2007). Large differentiation in the susceptibility to UV-B radiation is observed among known species of crop plants, about 50% have been considered sensitive, 20-30% moderately sensitive, and the rest insensitive to UV-B radiation (Caldwell e*t al*., 1994; Hollosy 2002). In many sensitive plant species *eg* wheat, rice, maize, rye, sunflower, cucumber reduced leaf area and/or stem growth has been found, and visual symptoms consisting of chlorosis or necrosis on leaves exposed to UV-B were not unique (Hollosy, 2002; Kakani *et al*., 2003; Vu *et al*., 2009). Decrease in photosynthesis (3-90%), particularly at higher UV-B doses, was due to both direct (effect on photosystem) and indirect (decrease in pigments and leaf area) effects. Genotypes of crop species exhibited variability in leaf wax layer thickness, loss of chlorophyll, and increase in phenolic compounds as mechanisms of tolerance to enhanced UV-B radiation resulting in changes in biomass or yield (Caldwell *et al*., 2007; Holosy, 2002; Kakani *et al*., 2003; Rozema *et al*., 1997). Generally cereals plant seems to be more tolerant to UV-B than dicotyledon plants due to vertical position of leaves, which are less exposed to harmful radiation (Caldwell *et al*., 1994; Kakani *et al*., 2003; Lizana *et al*., 2009; Skórska, 2000). Physically avoiding UV-B radiation through scattering and reflection is main strategy of plants, it can be done by manipulating epidermal and cuticular layers of the leaf. Skórska and Szwarc (2007) showed that special line of triticale with devoiding wax cover was

*Corresponding author's e-mail: elzbieta.skorska@zut.edu.pl

more susceptible to UV-B radiation than the traditional variety. Other way of plant defense against UV-B radiation involves increasing UV-B absorbing pigments such as flavonoids and anthocyanins after the actual entry of UV-B into the outer layer of leaf surface (Jansen *et al*., 2008; Rozema *et al*., 1997). Relatively little data concerns herbal plants, while some of them *eg* peppermint plants are cultivated on plantations. Until now, a few data on sensitivity of peppermint exposed to UV radiation has been published and concerning mainly on photomorphogenesis and essential oil composition (Maffei and Scannerini, 2000).

The aim of this work was to study photosynthetic primary reactions of peppermint leaves exposed to UV-B radiation applied in a short period time in comparison with cucumber leaves known rather as a susceptible species and recovery capacity of both species after the applied stress condition.

MATERIAL AND METHODS

Seeds of cucumber (*Cucumis sativus* L. cv. Dar) and peppermint (*Mentha piperita* L. cv. Asia) were sowed in moist sand and cultivated in the controlled conditions (PPFD 200 μmol m^{-2} s^{-1}, photoperiod 12 h, 22/18°C, day/night). They were watered daily and fertilised twice a week with Hoagland nutrient solution. In the phase of well developed leaves, the second of cucumber and on the second level of peppermint, discs (Ø 13 mm) were cut out, put into Petri dishes with water and placed for 4 h into a chamber with PPFD 170 μmol m^{-2} s^{-1} (control) or into the second chamber with the same light and additional UV-B radiation. Intensity of UV-B irradiation, equal 1.0 W m^{-2}, was measured using a radiometer IL 1403 with a calibrated detector SEL 240-UVB1 (International Light Inc., USA). The source of UV-B was a lamp type VL-115 M (Vilber Lourmat, France) emitting in the range of 280 to 320 nm with the maximum emission at wavelength of 313 nm (Fig. 1). Emission spectrum of the applied UV-B lamp was recorded using a spectroradiometer H 2000 (Ocean Optics, USA). Daily biologically effective dose of ultraviolet-B radiation, $UV\text{-}B_{BE}$, equal 0.74 kJ m^{-2} d^{-1} was calculated according to plant generalised model of Caldwell (1971). After irradiation the samples were moved to dark room and measurements of photochemical efficiency of photosystem II were done. Chlorophyll fluorescence was measured by means of PAM-210 fluorometer (Heinz Walz GmbH, Germany). Before measurements the plants were dark adapted 20 min. The leaf disc was placed on the head (on the adaxial surface down, towards the head) and covered by magnetic clip. Weak measuring beam (0.04 μmol m^{-2} s^{-1}, 650 nm), pulse saturating light (3200 μmol m^{-2} s^{-1}, 665 nm) and actinic light (120 μmol m^{-2} s^{-1}, 665 nm) were used for measurements. The fluorescence signal was recorded for 4 min. Following parameters were estimated: F_o, F_m, F_v/F_m, F_v/F_o, Yield, vitality index $Rfd = (F_m - F_s)/F_s$, where F_o, F_m, F_s, F_v denote respectively intensity of the initial, maximum, stationary, variable fluorescence ($F_v = F_m - F_o$), qP and qN – coefficients of photochemical and nonphotochemical quenching, according to generally accepted denotations (Lichtenthaler *et al*., 1986, 2005; Van Kooten and Snell, 1990). Analysis of chlorophyll fluorescence induction of the leaves was performed using a fluorometer with a photomultiplier M12FC51 with S20 photocathode (Carl Zeiss, Jena, Germany) through a cut-off filter 685 nm, steered by microcomputer (Murkowski, 2002). Chlorophyll delayed luminescence (L_D) was measured, in the range of 0.5 s to 16.5 s after switching off the actinic light (PPFD 120 μmol m^{-2} s^{-1}) by means of a high-sensitive luminometer working in the system of one electron pulse counting (Murkowski, 2002). It includes one 100 W Tungsten lamp for photo-excitation (PPFD 120 μmol m^{-2} s^{-1}), and a red-light-sensitive photomultiplier tube (EMI 9558B, Thorn, UK) as a detector of emitted light. It was calculated L_D parameter determining a ratio of decasecond and second components of delayed luminescence (Murkowski and Skórska, 2010). All luminescence measurements were also done after 24 h after irradiation. Content of UV-absorbing compounds was determined as a value of absorbance at 305 nm dm^{-2} of leaf area, according to procedure of Caldwell *et al*. (1994). Absorption spectra of the extract were measured by means of spectrophotometer M-42 (Carl Zeiss, Jena, Germany). The results are presented as means from 6-8 replications (independent leaves).

All data were analysed using Statistica 8.0 software (Statsoft, USA-PL) by means of two-way ANOVA. Multiple range Newman-Keul test at a significance level of $p < 0.05$ was used to separate homogenous groups of the means (for each species independently), which were marked by different letters.

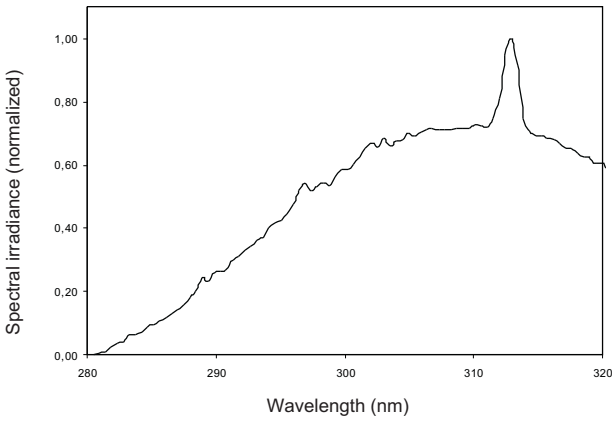

Fig. 1. Emission spectrum of the applied source of UV-B radiation, VL-115 M (Vilber Lourmat, France), normalized to maximum at 313 nm.

RESULTS AND DISCUSSION

Values of chlorophyll fluorescence parameters of cucumber and peppermint leaves subjected to UV-B irradiations are clearly varied (Table 1). It is particularly noticeably in the value of maximal fluorescence, F_m, which is lower by 40% in the irradiated leaves of cucumber compared to the control ones, and only by 15% in the irradiated peppermint leaves. Given the constant initial fluorescence, F_o, in both species, such, F_m, decrease influenced on the values of F_v/F_o parameter, which was decreased by 40% in the cucumber leaves, while in a case of peppermint did not change. Value of stationary fluorescence, F_s, was unchanged in the cucumber leaves, and was decreased in the UV-B irradiated peppermint. It is notable decrease of Yield value in cucumber leaves by 23%, while in the peppermint only insignificant. Similar changes were observed in Rfd index, which was reduced in the UV-B irradiated cucumber leaves by 40% compared to the control, while in the peppermint leaves it remained unchanged. qP parameter determined photochemical quenching did not changed in both species. However, nonphotochemical quenching coefficient qN increased only in peppermint leaves by 50%, and after 24 h of recovery value of this coefficient increased by 75% compared to the control, while in cucumber leaves it remained unchanged. Most values of other measured parameters of chlorophyll

T a b l e 1. Values of parameters of chlorophyll fluorescence of cucumber and peppermint leaf discs subjected to UV-B irradiation ($UV\text{-}B_{BE}$ = 0.74 kJ m^{-2} d^{-1}) in the light (PPFD 170 μmol m^{-2} s^{-1}) and after 24 h of recovery

Parameter	Cucumber cv. Dar			Peppermint cv. Asia		
	Control	UV-B	UV-B-24 h	Control	UV-B	UV-B-24 h
F_o	264 a± 37	234 a± 49	287 a± 29	182 A± 25	164 A± 14	175 A± 29
F_m	1130 a± 138	688 c± 125	933 b± 151	985 A± 120	834 B± 64	801 B± 68
F_s	323 a± 49	281 a± 72	324 a± 36	262 A± 28	210 B± 22	200 B± 17
F_v/F_o	3.29 a± 0.11	1.97 b± 0.35	2.25 b± 0.46	4.42 A± 0.28	4.11 A± 0.36	3.62 B± 0.44
Yield	0.62 a± 0.02	0.48 b±0.07	0.55 b±0.07	0.65 A± 0.03	0.61 B± 0.03	0.58 B± 0.03
qP	0.90 a± 0.01	0.84 a± 0.11	0.92 a± 0.03	0.86 B± 0.02	0.88 B± 0.02	0.92 A± 0.05
qN	0.32 a± 0.08	0.32 a± 0.06	0.30 a± 0.18	0.30 B± 0.07	0.45 A± 0.09	0.51 A± 0.10
Rfd	2.51 a± 0.19	1.51 b± 0.42	1.88 b± 0.35	2.76 A± 0.15	2.99 A± 0.35	3.02 A± 0.39

abc – means marked the same letters belong to the same homogenous group, independently for cucumber (abc) and peppermint (AB) at significance level of $p < 0.05$ (Newman-Keul test).

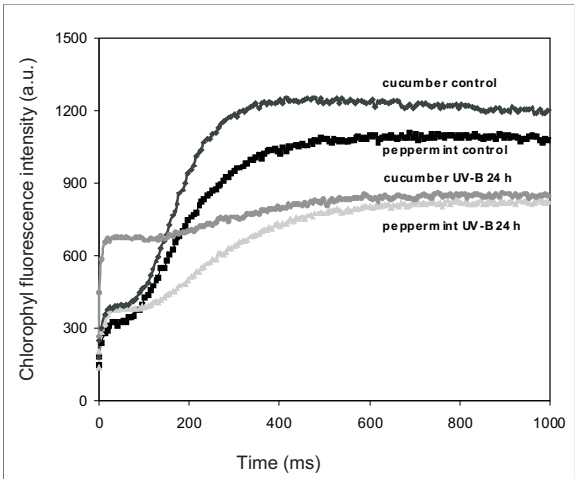

Fig. 2. Curves of fast chlorophyll fluorescence induction of the cucumber and peppermint leaves: control (PAR, without UV-B), UV-B 24 h – after 24 h of recovery after PAR + UV-B irradiation. Each curve is the average of four measurements.

fluorescence after 24 h of recovery increased compared to the values measured directly after irradiation. However, they were not differ significantly from them, except for F_v/F_o in a case of peppermint leaves which was lower than directly after irradiation. On the contrary, both quenching coefficients qP and qN increased by 7 and 70%, respectively. Presented curves of fast chlorophyll fluorescence induction of both species are different in the studied range, specially in first 100 ms (Fig. 2) confirming their varied susceptibility on the applied UV-B radiation. The UV-B irradiated cucumber leaves even after 24 h of recovery showed clearly higher intensity directly after illumination compared with other samples. An area above the fluorescence induction curves in the range from the start to the reaching time of maximal fluorescence is visible lower in a case of UV-B irradiated leaves of cucumber.

Chlorophyll delayed luminescence coefficient L_D was decreased by 36% in the UV-B irradiated cucumber leaves and by 25% in the peppermint leaves (Fig. 3). However, it should be noticed that value of this parameter in peppermint

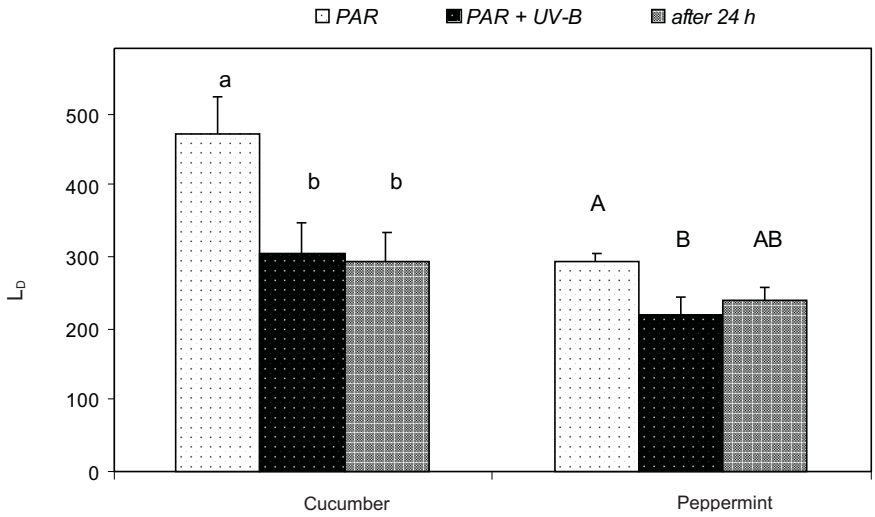

Fig. 3. Values of chlorophyll delayed luminescence parameter (L_D) of cucumber and peppermint leaves: control (PAR, without UV-B), UV-B – after 4 h of PAR + UV-B irradiation and after 24 h of recovery. Vertical segments present standard deviations (n = 8). Other explanations as in Table 1.

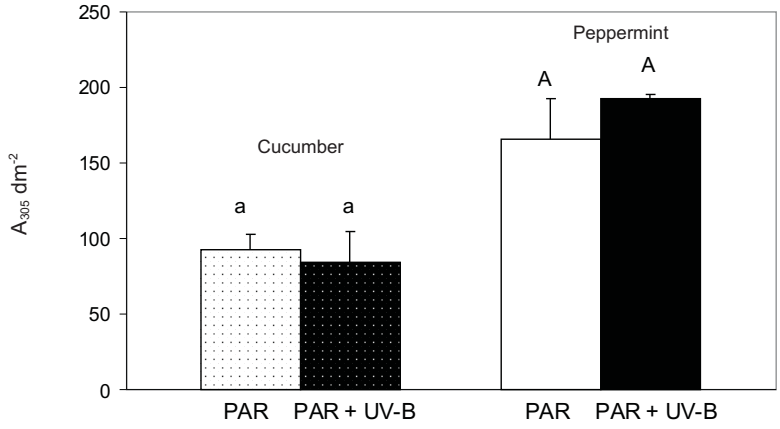

Fig. 4. Content of ultraviolet absorbing compounds in *Cucumis sativus* L. and *Metha peperita* L. leaves: PAR – control (PAR without UV-B), PAR + UV-B – after 4 h of UV-B irradiation at PAR. Vertical segments present standard deviations(n = 5). Other explanations as in Table 1.

control leaves was lower by 37% than in the cucumber ones. After 24 h of recovery decrease remained the same in the cucumber while in the peppermint was decreased only by 18% in comparison with the control.

Absorption spectra of ethanol extracts of both species are similar and do not include specific points and absorbance in the range of 280 to 320 nm was almost twice higher in the peppermint than in the cucumber (data not presented). Content of ultraviolet-absorbing compounds was higher in peppermint leaves by 78% than in the cucumber leaves, and increased after UV-B irradiation however the change was not statistically significant (Fig. 4). In a case of the cucumber leaves amount if this protective compounds did not change after irradiation.

Measured chlorophyll fluorescence parameters, specially F_v/F_o just attributed to inhibition of photosynthetic electron transport at the donor side of the photosystem II, was observed only in the cucumber leaves subjected to UV-B. Unchanged value of this parameter in the peppermint leaves directly after UV-B irradiation can be attributed to higher tolerance of this species to UV-B. It is worth pointing out that after 24 h from disappearing of the applied stress factor, lowering of the F_v/F_o was observed. It indicates that damages of the acceptor side of photosystem II caused by UV-B were irreversible character. Damages of the donor side, presented by the overall quantum yield Yield and the vitality index Rfd also seemed to be irreversible, specially in a case of cucumber leaves. Decrease in Yield is associated

with increases in excitation energy quenching in the photosystem II antennae and is generally considered indicative of 'down-regulation' of electron transport. Consequently, the decreases of yield after 24 h from disappearing of UV-B in both species can be taken as indicative of a physiological regulation of electron transport by increasing excitation energy quenching process in the photosystem II antennae. That is mainly due to the non-photochemical conversion of absorbed light energy for thylakoid membrane energization as qN coefficient. At this light conditions nearly all reaction centres of photosystem II in control and UV-B-treated leaves remain oxidized (opened), as indicated by qP values (Schreiber *et al.*, 1994; Van Kooten and Snel, 1990). Results of the experiment presented in this paper show that only the peppermint leaves as well directly as after 24 h from disappearing UV-B irradiation had increased qN value indicating a way of loss of energy excess. It can explain less susceptibility of peppermint to UV-B radiation.

It is known that dicotyledonous species would be more sensitive to UV-B radiation than monocotyledonous species (Caldwell et al., 2007; Skórska, 2000). Yao *et al*. (2006) was shown decrease of the Yield of cucumber affected by UV-B of similar dose as our experiment. Similar changes of the measured parameters were also observed in our earlier experiment with other variety of cucumber subjected as well UV-B as chilling of leaves (Skórska, 1999). Decrease of the F_v/F_o parameter can resulted from as well increase of F_o as decrease of F_m. In our experiment decrease of the F_v/F_o in the UV-B irradiated leaves resulted only from decrease of F_m, while F_o remained unchanged. It is typical for this type of abiotic stress, unlike other stress factors *eg* chill in a case of cucumber when F_o increased (Skórska, 1999). Van Rensen *et al*. (2007) studied the effects of ultraviolet-B radiation on leaves of *Chenopodium album* using similar chlorophyll fluorescence technique. The efficiency of photosystem II decreased both with increasing time of UV-B radiation and with increasing intensity of the UV-B. Fluorescence induction rise curves analyzed using a mechanistic model of energy trapping appeared that the damage by UV-B radiation occurs first at the acceptor side of photosystem II, and later at the donor side (van Rensen *et al*., 2007).

The Rfd-values being measured at the saturation irradiance of photosynthesis exhibit a highly significant linear correlation to net photosynthesis intensity (Lichtenthaler *et al*., 2005). The Rfd is higher in sun leaves of trees (values of 3-5) than in shade leaves (values of 1.0-2.5) reflecting their higher photosynthetic capacity and CO_2 fixation rates. Decreased Rfd value in the UV-B irradiated cucumber leaves indicates more susceptibility of its photosyntehtic apparatus compared to the peppermint, in the phase of cooperation between the light reactions with the dark ones. Higher susceptibility of cucumber to UV-B radiation can be observed also on basis of fast phase of chlorophyll fluorescence induction as decrease of area above the curve between F_o and F_m indicating reduction of non-reduced electron transfers between photosystem II and I. Such reduction of area is usually observed as the effect of herbicides – inhibitors of photosysytem II (Murkowski, 2002; Schreiber *et al*., 1994).

Shinkle *et al*. (2004) examined the influence of short-term exposure of different UV wavebands on the fine-scale kinetics of hypocotyl growth of dim red light-grown cucumbers. The response to short wavelength UV-B was persistent for at least 24 h, while the response to long wavelength UV-B lasted only 3 h. They concluded that different photosensory processes involved in mediating growth and morphological responses to short wavelength UV-B, 280-300 nm, long wavelength UV-B, essentially 300-320 nm. Results presented here, in the experiment using the source of broadband UV-B did not confirmed this conclusion. They could be interpreted differently, particularly in relation to conclusions of Van Rensen *et al*. (2007) that damages caused by UV-B radiation occurred first at the acceptor side of photosystem II, and only later at the donor side.

Chlorophyll delayed luminescence emission in the range of the second and decasecond range is a result of radiation recombination of electrons localized on the acceptors in electron transport chain in photosystem II (Hideg and Demeter, 1986; Rutherford and Inoue, 1984). The L_D parameter value is a sensitive indicator of electron transfer effectiveness from a primary stable acceptor Q_A (on the D2 protein) to electron transfer effectiveness from a second stable acceptor Q_B which is localised on the D1 protein, the acceptor Q_B, which is localised on the D1 protein (Murkowski, 2002). Characteristic modifications in the kinetics of delayed luminescence decay indicates possible mutations in the structure of photosynthetic apparatus (Li *et al*., 2007).

Shinkle *et al*. (2010) showed that brief (1-100 min) irradiations of 5 kJ m^{-2} ultraviolet-B induced increases the UV-absorbing pigments extracted from cucumber. Spectra showed a single defined peak at 317 nm. When seedlings were irradiated with UV-B containing proportionally greater short wavelength UV-B (37% of UV-B between 280 and 300 nm), tissue extracts showed an overall increase in absorption (91% increase at 317 nm). In contrast, seedlings irradiated with 5 kJ m^{-2} UV-B including only wavelengths longer than 290 nm resulted only in a general increase in absorption (80% at 317 nm).

CONCLUSIONS

1. The applied dose of UV-B radiation caused damages as well as at a donor and acceptor side of photosystem II, specially in the oxygen evolving complex (F_v/F_o), electron transport (Y, L_D) and connected with the dark reactions (Rfd), but in the peppermint leaves these values were unchanged or slight decreased compared to the control samples (not exposed to UV-B).

2. Coefficient of nonphotochemical quenching (qN), indicating a way of loss of energy excess, increased by 50% in the peppermint leaves, while in cucumber remained unchanged, what could explain less susceptibility of peppermint to UV-B radiation.

3. After 24 h from disappearing of the applied UV-B stress, adverse changes became established especially in the cucumber leaves show irreversible damages of photosystem II.

4. Content of ultraviolet-absorbing compounds was higher in peppermint leaves by 78% than in the cucumber, but UV-B did not cause significance changes.

5. Generally, the photosystem II of peppermint leaves seemed to be more tolerant to the applied UV-B radiation compared to the cucumber ones.

REFERENCES

Björn L.O., Widell .S., and Wang P., 2002. Evolution of UV-B regulation and protection in plants. Adv. Space Res., 30, 1557-1562.

Caldwell M.M., 1971. Solar UV irradiation and growth and development of higher plants. In: Photophysiology (Ed. A.C. Giese), Academic Press, New York, USA.

Caldwell M.M., Bornman J.F., Ballar'e C.L., Flint S.D., and Kulandaivelue G., 2007. Terrestrial ecosystems, increased solar ultraviolet radiation, and interactions with other climate change factors. Photochem. Photobiol. Sci., 6, 252-66.

Caldwell M.M., Flint S.D., and Searles P.S., 1994. Spectral balance and UV-B sensitivity of soybean: a field experiment. Plant, Cell Environm., 17, 267-276.

Hideg E. and Demeter S., 1986. Comparison of the decay of slow delayed luminescence in triazine-susceptible and -resistant biotypes of *Erigeron canadensis* L. FEBS Lett., 200, 139-143.

Hollosy F., 2002. Effects of ultraviolet radiation on plant cells. Micron, 33, 179-197.

Jansen M.A.K., Hectors K., O'Brien N.M., Guisez Y., and Potters G., 2008. Plant stress and human health: Do human consumers benefit from UV-B acclimated crops? Plant Sci., 175, 449-458.

Kakani V.G., Reddy K.R., Zhao D., and Sailaja K., 2003. Field crop responses to ultraviolet-B radiation: a review. Agric. Forest Meteorol., 120, 191-218.

Li Q., Da X., Li J., and Wang J., 2007. Mechanism study on the origin of delayed fuorescence by an analytic modeling of the electronic reflux for photosynthetic electron transport chain. J. Photochem. Photobiol. B: Biol., 87, 183-190.

Lichtenthaler H.K., Buschmann C., and Knapp M., 2005. How to correctly determine the different chlorophyll fluorescence parameters and the chlorophyll fluorescence decrease ratio Rfd of leaves with the PAM fluorometer. Photosynthetica, 43, 379-393.

Lichtenthaler H.K., Buschmann C., Rinderle U., and Schmuck G., 1986. Application of chlorophyll fluorescence in ecophysiology. Rad. Environm. Biophys., 25, 297-308.

Lizana X.C., Hess S., and Calderini D.F., 2009. Crop phenology modifies wheat responses to increased UV-B radiation. Agric. Forest Meteorol., 149, 1964-1974.

Maffei M. and Scannerini S., 2000. UV-B effect on photomorphogenesis and essential oil composition in peppermint (*Mentha piperita* L.). J. Essential Oil Res., 12, 523-529.

Murkowski A., 2002. Application of luminescence methods in research on responses of crop plants to some stress factors (in Polish). Acta Agrophysica, 61, 3-158.

Murkowski A. and Skórska E., 2010. Effect of $(C_6H_5)_3PbCl$ and $(C_6H_5)_3SnCl$ on delayed luminescence intensity, evolving oxygen and electron transport rate in photosystem II of *Chlorella vulgaris.* Bull. Environm. Contam. Toxicol., 84, 157-160.

Rozema J., Lenssen G.M., van de Staaij J.W.M., Tosserams M., Visser A.J., and Broekman R.A., 1997. Effects of UV-B radiation on terrestrial plants and ecosystems: interaction with CO_2 enrichment. Plant Ecol., 128, 183-191.

Rutherford A.W. and Inoue Y., 1984. Oscillation of the light luminescence from PSII: recombination of $S_2Q_B^-$ and $S_3Q_B^-$. FEBS Lett., 165, 165-170.

Schreiber U., Bilger W., and Neubauer C., 1994. Chlorophyll fluorescence as a nonintrusive indicator for rapid assessment of *in vivo* photosynthesis. In: Ecophysiology of Photosynthesis, Ecological Studies (Eds E.D. Schulze, M.M. Caldwell). Springer Press, Berlin, Germany.

Shinkle J.R., Atkins A.K., Humphrey E.E., Rodgers C.W., Wheeler S.L., and Barnes P.W., 2004. Growth and morphological responses to different UV wavebands in cucumber (*Cucumis sativum*) and other dicotyledonous seedlings. Physiol. Plant., 120, 240-248.

Shinkle J.R., Edwards M.C., Koenig, A., Shaltz A., and Barnes P.W., 2010. Photomorphogenic regulation of increases in UV-absorbing pigments in cucumber (*Cucumis sativus*) and *Arabidopsis thaliana* seedlings induced by different UV-B and UV-C wavebands. Physiol. Plant., 138, 113-121.

Skórska E., 1999. Effect of chill on chlorophyll a fluorescence of cucumber leaves in plants subjected to UV-B irradiation. Adv. Agric. Sci. Problem Iss., 469, 137-144.

Skórska E., 2000. Responses of some crop plants on UV-B radiation (in Polish). Rozprawy, 192. Agricultural University Press, Szczecin, Poland.

Skórska E. and Szwarc W., 2007. The effect of UV-B radiation on young triticale plants belonging to two forms differing of wax presence. Biol. Plant., 51, 189-192.

Szilárd A., Sass L., Deák Z., and Vass I., 2007. The sensitivity of Photosystem II to damage by UV-B radiation depends on the oxidation state of the water-splitting complex. Biochim. Biophys. Acta, 1767, 876-882.

Van Kooten O. and Snel J.F.H., 1990. The use of chlorophyll fluorescence nomenclature in plant stress physiology. Photosynth. Res., 25, 147-150.

Van Rensen J.J.S., Vredenberg W.J., and Rodrigues G.C., 2007. Time sequence of the damage to the acceptor and donor sides of photosystem II by UV-B radiation as evaluated by chlorophyll a fluorescence. Photosynth. Res., 94, 291-29.

Vu J., Guand D., Yuan F., and Zhang X., 2009. Research advances on the biological effects of elevated ultraviolet-B radiation on terrestrial plants. J. Forestry Res., 20, 383-390.

Yao Y., Yang Y., Ren J., and Li C., 2006. UV-spectra dependence of seedling injury and photosynthetic pigment change in *Cucumis sativus* and *Glycine max*. Environm. Exp. Botany, 57, 160-167.