POLISH JOURNAL OF ECOLOGY (Pol. J. Ecol.)	47	1	3–13	1999

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IMPACT OF ULTRAVIOLET-B RADIATION ON TWO SPECIES OF FOREST DWARF SHRUBS: BILBERRY (*VACCINIUM MYRTILLUS* L.) AND COWBERRY (*VACCINIUM VITIS-IDAEA* L.)

ABSTRACT: Impact of UV-B irradiation on chlorophyll content and chlorophyll fluorescence of two dwarf shrub species: *Vaccinium myrtillus* L. and *Vaccinium vitis-idaea* L. was investigated. The plants originating from different latitudes were used. The experiment was carried out in the greenhouse. Three variants of ultraviolet-B irradiation were applied: control = 0, lower dose = 11.32 and higher dose = 22.64 kJ m^{-2} day^{-1} $UV\text{-}B_{BE}$ (biologically effective dose of UV-B). Measurements of chlorophyll fluorescence and chlorophyll content were carried out. The response of dwarf shrubs to the increased UV-B radiation depended on UV-B dose, species traits and provenance. *Vaccinium vitis-idaea* was less sensitive to UV-B than *Vaccinium myrtillus*. The permanent discoloration was observed only on *Vaccinium myrtillus* leaves. The leaf bud break of this species was accelerated at high UV-B dose compared to the control. The UV-B radiation influenced its photosynthetic apparatus: the chlorophyll content in leaves was reduced, the maximal and the steady state fluorescence of chlorophyll were diminished.

The chlorophyll content in leaves of *Vaccinium vitis-idaea* did not change significantly but the relative vitality index and the steady state fluorescence were modified under the influence of the radiation.

KEY WORDS: UV-B radiation, dwarf shrubs, chlorophyll fluorescence, chlorophyll content, phenology

1. INTRODUCTION

The increase of ultraviolet-B irradiation (280–320 nm) has been observed on the Earth's surface. A trend of increasing biologically effective UV-B was showed by Blumthaler and Ambach (1990) in the Swiss Alps. The UV-B radiation has increased by 35% per year in the winter and 7% in the summer since 1989 to 1993 in Toronto (Kerr and McElroy 1993). This phenomenon is explained by a stratospheric ozone layer reduction called "ozone whole" (Commission of

European Community 1993). However, a variation of intensity of UV-B radiation depends mostly on natural factors: the latitude, the topographical situation, the cloud cover and the chemical composition of the atmosphere. The ultraviolet-B intensity is higher at lower latitudes (from the poles to the equator) and it is growing about 14–18% by 1000 m above sea level (Caldwell et al. 1989).

The man-made "ozone whole" observed over Antarctica (Farman et al. 1985) and over the other regions is linked to the cycle of photochemical reactions resulting from the emissions of chlorofluorocarbons and halons into the atmosphere.

The impact of UV-B radiation on human health, terrestrial and aquatic ecosystems has been intensively investigated in the last two decades. Most of researches have been carried out on annual agricultural plants, which are important for economy. Relatively few experiments have been undertaken on forest species. The reaction of plants to the UV-B exposure varies depending on species traits, provenance and even cultivars. The plants which had been growing in climate chambers or greenhouses are usually more sensitive to UV-B compared to plants growing in the field (Cen and Bornman 1990). However, most of experiments up to date has been conducted in greenhouse conditions.

The plants originating from higher latitudes are more sensitive to the enhanced UV-B radiation because their ultraviolet-B epidermal transmittance is bigger than theirs from lower latitudes. The acclimation of wildland species may have occurred in such variable UV-B climate conditions (Robberecht et al. 1980; Caldwell et al. 1982).

The purchase of this research work was to investigate a reaction of forest dwarf shrubs: bilberry (*Vaccinium myrtillus* L.) and cowberry (*Vaccinium vitis-idaea* L.) originating from different geographical regions to an enhanced UV-B irradiation. The shrubs growing under forest trees canopy are shade-tolerant and sensitive to the light of high intensity (Zarzycki 1984). It can suggest that these shrubs are also vulnerable to a high UV-B dose. However, its reaction to UV-B depends on many factors, especially on morphological traits of the species, an ultraviolet-B dose and a capacity of adaptation to the local ecological conditions.

2. MATERIALS

2.1. PLANT MATERIAL

The bilberry and the cowberry originating from different latitudes were collected under forest canopy. In case of Finnish provenance of *Vaccinium vitis-idaea* it had been growing on a peat bog. The names of provenances were created from the names of the countries, where the plants were collected (Table 1).

The shrubs were planted into pots of 15 cm in diameter filled with soil from the place of the plant origin. The plants were watered every two days.

Table 1. The short characteristics of the provenance of plants used in experiments

Species	Provenance	Latitude and longitude	Altitude [m a.s.l.]	Place of plant collecting
Vaccinium myrtillus (L.)	Polish	52°N, 20°E	< 100	Under canopy
	Belgian	50°N, 5.5°E	< 100	Under canopy
	French	47°N, 5°E	< 100	Under canopy
Vaccinium vitis-idea (L.)	Polish	52°N, 18°E	< 100	Under canopy
	Finnish	65°N, 26°E	< 100	Peat bog

2.2. EXPERIMENTAL CONDITIONS

The experiment was conducted in two greenhouses. The UV-B exposure was provided by sixteen UV-B lamps (Philips UV-B TL 12 40 W). There were two groups of four lamps in each greenhouse. The spectral distribution was analysed in detail with a Spectroradiometer (Jobin Yvon HD 10) at the Institute for Spatial Aeronomy in Brussels. The biologically effective irradiance was calculated using the generalised plant response action spectrum of Caldwell in modification of Green et al. and Thimijan et al. (Young 1993) normalised to 300 nm (F. Husson – unpublished). The lamps were pre-burnt for 100 hours before being installed in the greenhouses. The radiation was filtered with a 95 m-thick cellulose diacetate filter (clarifoil – Courtaulds Ltd) to cut the transmission down to 290 nm. The filter was pre-irradiated for 100 hours to ensure uniformity of UV-B transmission.

UV-B treatments were obtained by varying the irradiation time. The plants placed in greenhouses as control were not exposed to any additional radiation and UV-B_{BE} ≈ 0 kJ m^{-2} day^{-1}. The plantlets were irradiated four hours at the treatment of low UV-B dose (UV-B_{BE} = 12.32 kJ m^{-2} day^{-1}) and eight hours at high UV-B_{BE} dose (UV-B_{BE} = 24.64 kJ m^{-2} day^{-1}). The distance between the lamps and the top of the plants was 25 cm and it was maintained throughout a period of 100 days by using the shelves with regulated height to obtain a similar UV-B dose for each exposed plant.

Climate conditions in both greenhouses were: mean temperature during irradiation was 22.1 °C (minimal temperature – 17 °C and maximal – 28 °C), mean relative humidity – 58 % and mean photosynthetic photon flux density (PPFD) – 400 μmol m^{-2} s^{-1}. The photosynthetic active radiation was strongly varied depending on the solar radiation intensity and the position of pots.

2.3. EXPERIMENTAL DESIGN

The experiment was carried out in two randomised complete blocks, with two UV-B treatments in each block (control, low UV-B and control, high UV-B) in two repetitions (two separate greenhouses). Two pots with plants from each provenance were rotated on the platforms at a rate of 10 turns an hour

under frames with four UV-B lamps in order to receive the uniformity of irradiation. The same number of plants was in the control. The position of pots was changed manually once a week apart from rotation. The supplemental pots with shrubs were placed around the platforms to avoid the border effect.

3. METHODS

3.1. PHENOLOGICAL OBSERVATIONS

The number of days from switching off the UV-B lamps to leaf bud break of plants and discoloration of leaves was noted. Observations were conducted every day.

3.2. CHLOROPHYLL CONTENT

Chlorophyll content was determined according to the procedure of Inskeep and Bloom (1985) with changes.

The leaves were cut into test tubes and frozen in liquid nitrogen. 100 mg of ground leaves were macerated in 10 ml of DMF (N,N-dimethylformamide) for 24 hours in the dark at 4 °C with low speed shaking. The solution was filtered with Whatman's filter No 4. The absorbance of the extract was measured using the UV/visible radiation spectrophotometer (P/N 206-14600, Shimadzu Corporation, Kyoto, Japan). The chlorophyll *a*, *b* and total chlorophyll content were calculated with the following formulae:

$$\text{Chl } a = 12.70\ A_{664.5} - 2.79\ A_{647}$$

$$\text{Chl } b = 20.70\ A_{647} - 4.62\ A_{664.5}$$

$$\text{Tot chl} = 17.90\ A_{647} - 8.08\ A_{664.5}$$

$A_{664.5}$ – absorbance at 664,5 nm

3.3. DATA ANALYSIS

The General Linear Models of Variance (one or two-way analysis with interaction) were applied. A two-way analysis with interaction tested species, provenance, UV-B treatment and interactions effect and it was followed by Tukey's and Fisher's *a posteriori* tests.

$P < 0.05$ was taken for appearing the statistically significant differences between species, provenances and treatments. Tukey's test with global $\lambda = 0.05$ and Fisher's test with $\lambda = 0.05$ for each pair of means allowed to show the statistically significant differences between treatments. Minitab 9.1 and Excel 5.0 were used for statistical calculations and graphical presentation of results.

4. RESULTS

4.1. PHENOLOGY

The analysis of the number of days from switching off the lamps to leaf bud break suggests that the increased UV-B radiation can accelerate the leaf bud break of *Vaccinium myrtillus* by 15 days and it was not affected in case of *Vaccinium vitis-idaea* (data not shown). The permanent discoloration was observed only on the leaves of the former. It was noted after 30 days of irradiation at the both UV-B treatments. The bilberry had been changing leaves several times during the experiment. Probably, it took place more often in the greenhouse than in the natural conditions.

4.2. CHLOROPHYLL CONTENT

The reduction of chlorophyll *a*, *b* and total chlorophyll content in the leaves of *Vaccinium myrtillus* irradiated with higher dose of UV-B was noted (Table 2, Figure 1). The reduction was about 20 % in comparison with the control (Table 3).

There were no statistically significant differences between treatments in case of *Vaccinium vitis-idaea* (data not shown).

4.3. CHLOROPHYLL FLUORESCENCE

The maximal fluorescence at 690 and 730 nm and steady state fluorescence at 690 nm were significantly changed by UV-B irradiation in case of *Vaccinium*

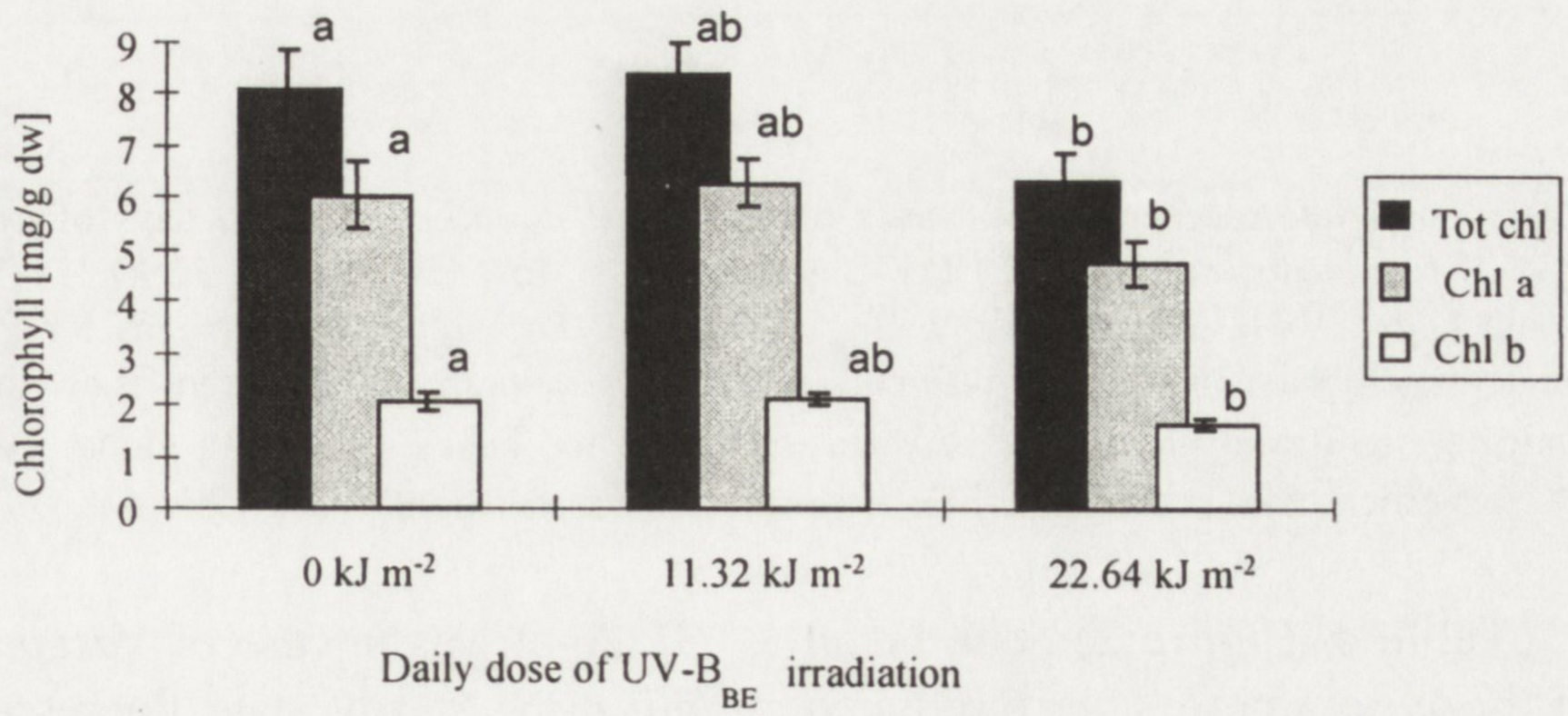

Fig. 1. Chlorophyll *a*, *b*, and total chlorophyll content in the leaves of *Vaccinium myrtillus* after 100 days of irradiation in three UV-B treatments: control (0 kJ UV-B_{BE} m^{-2} day^{-1}), low UV-B_{BE} (11.32 kJ UV-B_{BE} m^{-2} day^{-1}) and high UV-B_{BE} (22.64 kJ UV-B_{BE} m^{-2} day^{-1}). The graph shows means for Polish, Belgian and French provenances. The statistically significant reduction of chlorophyll content at high UV-B_{BE} is not dependent on provenance. The different letters above columns of histogram show that there are statistically significant differences between treatments for Fisher's test with λ = 0,05 for each pair of means. Vertical bars represent ± SD (n = 36).

Table. 2. Probability values for General Linear Model of analysis of variance. The provenance, treatment and interaction between provenance and UV-B effect on the chlorophyll content in leaves of *Vaccinium myrtillus* were examined using two-way analysis of variance with interaction after 100 days of irradiation. When $P < 0.05$, the differences between mean values of chlorophyll content are statistically different (it is marked with asterisks).

Parameter	Provenance	Treatment	P X T
Chlorophyll a	0.0001***	0.051	0.770
Chlorophyll b	0.0001***	0.033*	0.663
Total chlorophyll	0.0001***	0.041*	0.733
a/b	0.731	0.975	0.907

Table 3. Differences in chlorophyll content in leaves of *Vaccinium myrtillus* between control and high UV-B treatment after 100 days of irradiation. Control is 100 %.

Parameter	Control – High UV–B [%]
Chlorophyll a	22
Chlorophyll b	21
Total chlorophyll	22

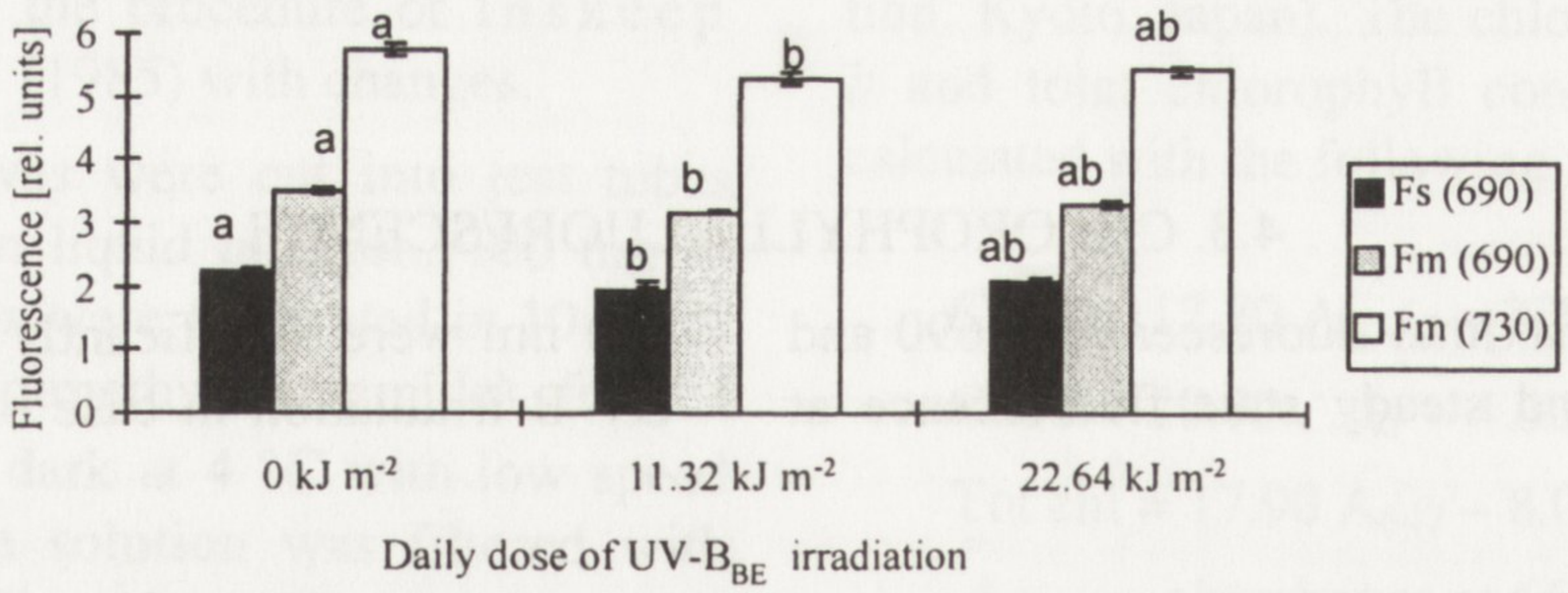

Fig. 2. Chlorophyll fluorescence of the leaves of *Vaccinium myrtillus* after 100 days of irradiation in three UV-B treatments: control (0 kJ UV-B_{BE} m^{-2} day^{-1}), low UV-B_{BE} (11.32 kJ UV-B_{BE} m^{-2} day^{-1}) and high UV-B_{BE} (22.64 kJ UV–B_{BE} m^{-2} day^{-1}). The graph shows means for Polish, Belgian and French provenance. The different letters above columns of histogram show that there are statistically significant differences between treatments for Tukey's test with global $\lambda = 0{,}05$. Vertical bars represent ± SD ($n = 48$). For abbreviations – see table 4.

myrtillus (Table 4, Figure 2). The mean values of these parameters were reduced about 9% at low UV-B treatment and 6% at high UV-B treatment (Table 5).

The relative vitality index and the steady state fluorescence at both wavelengths were statistically significant for *Vaccinium vitis-idaea* (Table 6, Figure 3). As it was in case of *Vaccinium myrtillus*, the steady state fluorescence was reduced at low and high UV-B irradiation compared to the control. The relative vitality index was higher by about 43 % at low UV-B treatment and by 15 % at high UV-B treatment than at the control (Table 7).

Table 4. Probability values for General Linear Model of analysis of variance. The provenance, treatment and interaction between provenance and UV-B effect on the chlorophyll fluorescence parameters of leaves of *Vaccinium myrtillus* after 50 and 100 days of irradiation were examined using two-way analysis of variance with interaction. When $P < 0.05$, the differences between mean values of chlorophyll content are statistically significant (it is marked with asterisks).

	After 50 days of irradiation			After 100 days of irradiation		
Parameter	Provenance	Treatment	P x T	Provenance	Treatment	P x T
Fm (690)	0.739	0.442	0.254	0.079	0.001**	0.177
Fs (690)	0.641	0.470	0.463	0.107	0.009**	0.136
Rfd (690)	0.225	0.450	0.113	0.989	0.716	0.886
Fm (730)	0.025*	0.936	0.612	0.044*	0.008**	0.240
Fs (730)	0.049*	0.870	0.566	0.140	0.064	0.259
Rfd (730)	0.902	0.546	0.218	0.996	0.787	0.780
Fm(690)/Fm(730)	0.003**	0.515	0.852	0.989	0.716	0.778

List of abbreviations: Fm – maximal fluorescence, Fs – steady state fluorescence, Rfd – relative vitality index, Tot chl – total chlorophyll content, P – probability, λ – significance level.

Table 5. Differences between chlorophyll fluorescence parameters of leaves of *Vaccinium myrtillus*. Control is 100 %. For abbreviations – see table 4.

Parameter of fluorescence	Control – Low UV-B [%]	Control – High UV-B [%]
Fm (690)	9.26	5.57
Fs (690)	8.34	6.82
Fm (730)	7.77	5.70

Table 6. Probability values for General Linear Model of analysis of variance. The provenance, treatment and interaction between provenance and UV-B effect on the chlorophyll fluorescence parameters of leaves of *Vaccinium vitis-idaea* after 100 days of irradiation were examined using two-way analysis of variance with interaction. When $P < 0.05$, the differences between mean values of chlorophyll content are statistically significant (it is marked with asterisks).
For abbreviations – see table 4.

Parameter	Provenance	Treatment	P x T
Fm (690)	0.786	0.506	0.234
Fs (690)	0.260	0.014*	0.360
Rfd (690)	0.187	0.034*	0.667
Fm (730)	0.555	0.242	0.215
Fs (730)	0.455	0.029*	0.373
Rfd (730)	0.124	0.041*	0.884
Fm(690)/Fm(730)	0.607	0.428	0.423

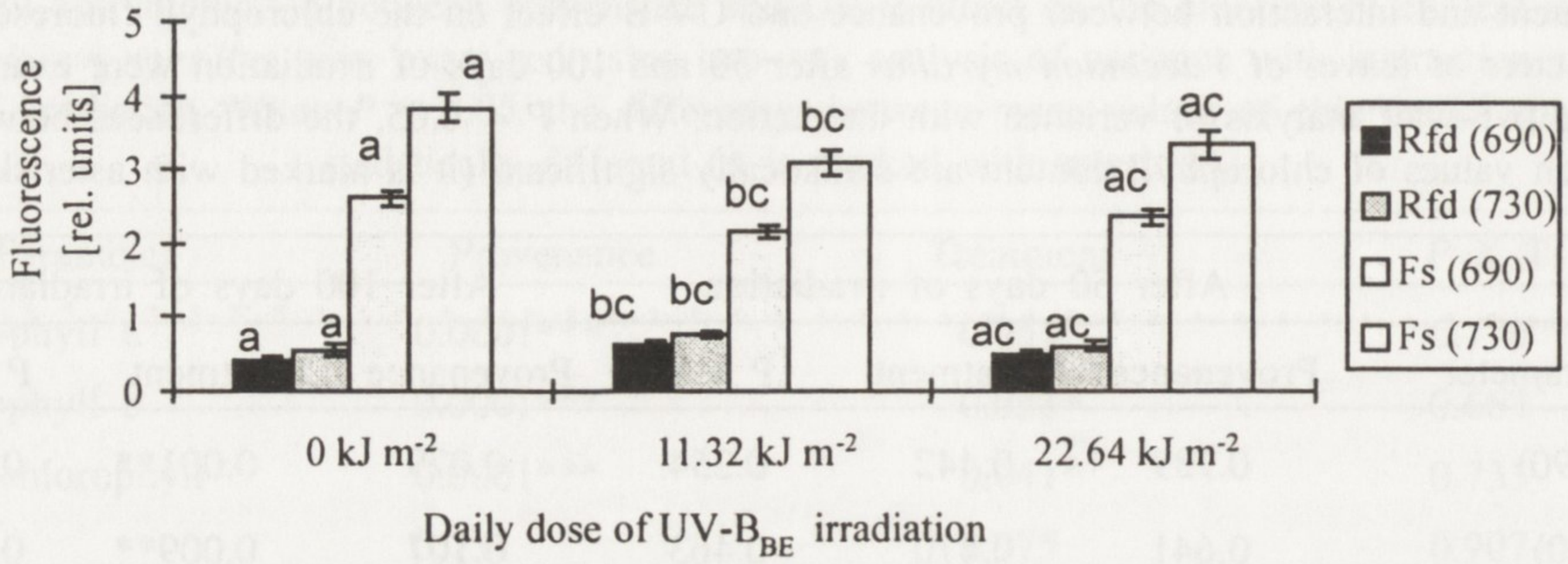

Fig. 3. Chlorophyll fluorescence of the leaves of *Vaccinium vitis-idaea* after 100 days of irradiation in three UV-B treatments: control (0 kJ UV-B_{BE} m^{-2} day^{-1}), low UV-B_{BE} (11.32 kJ UV-B_{BE} m^{-2} day^{-1}) and high UV-B_{BE} (22.64 kJ UV-B_{BE} m^{-2} day^{-1}). The graph shows means for Polish and Finnish provenances. The different letters above columns of histogram show that there are statistically significant differences between treatments for Tukey's test (Rfd (690), Fs (690), Fs (730)) with global $\lambda = 0{,}05$ and for Fisher's test (Rfd 730) with $\lambda = 0{,}05$ for each pair of means. Vertical bars represent ± SD ($n = 32$). For abbreviations – see table 4.

Table 7. Differences between chlorophyll fluorescence parameters of leaves of *Vaccinium vitis-idaea*. Control is 100 %. For abbreviations see table 4.

Parameter of fluorescence	Control – Low UV-B [%]	Control – High UV-B [%]
Fs (690)	17	9.7
Fs (730)	20	13
Rfd (690)	–47	–19
Rfd (730)	–42	–12

5. DISCUSSION

The reaction of the forest dwarf shrubs: *Vaccinium myrtillus* and *Vaccinium vitis-idaea* to an increased UV-B irradiation was dependent on the ultraviolet-B dose. The difference in the response to the enhanced UV-B irradiation between the investigated species was noted. It seems that the cowberry is less sensitive to the radiation than the bilberry. It suggests that the high dose of UV-B radiation can affect a quantity and a quality of plant species composition. It is of importance that an enhanced UV-B irradiation influences shrubs phenology, especially leaf bud break, flowering, ripening of fruits and onset of senescence (Johanson et al. 1995b). The leaf bud break of bilberry exposed to the high dose of UV-B radiation was noted 15 days sooner than at the control. However, Johanson et al. (1995b) did not observe significant differences between treatments. They carried out the experiment in the field (without forest trees canopy) and they

applied relatively low UV-B dose, as compared to the high UV-B dose of 22.4 kJ m^{-2} day^{-1} used in the greenhouse.

The permanent discoloration was observed on the leaves of *Vaccinium myrtillus*. The visual symptoms of UV-B effects have been noted only on the leaves of the sensitive plants, mostly in greenhouse experiments, and it was linked to important changes in leaf chemistry. The balance of photosynthetic pigments was changed – chlorophyll content was reduced and a concentration of phenol compounds, especially flavonoids, was increasing (Caldwell et al. 1995). Gherke et al. (1995) noted that the enhanced UV-B radiation changed the litter quality (decrease in cellulose, increase in tannins) during growth. Total microbial respiration was decreased, indicating the micro-organisms' sensitivity to ultraviolet-B. It may have unpredictable implications for forest ecosystem functioning.

The photosynthetic apparatus of *Vaccinium myrtillus* was strongly affected by the high UV-B dose. It is of evidence that the photosynthetic pigments content was changed: the phenol compounds concentration increased (permanent discolorations of leaves) and the reduction of chlorophyll content by 20 % was detected.

The enhanced UV-B irradiation can damage the photosystem PS II. The reduction of variable fluorescence, relative vitality index, maximal and steady state fluorescence of chlorophyll were noted for many crops exposed to UV-B (Ivanzik et al. 1983; Renger et al. 1989; Nogues and Baker 1995; Łukaszek and Poskuta 1996). The maximal and the steady state fluorescence of the investigated shrubs were also reduced. The physiological changes in the leaves of *Vaccinium myrtillus* suggest that the photosynthetic activity should be reduced. The reduction of stem growth and leaves thickness of bilberry observed by Johanson et al. (1995a) may be explained by the reduction of chlorophyll content and a disruption of photosystem II functionning, which lead to an alteration of photosynthesis and biomass production.

The mean values of the vitality index of the cowberry's leaves suggest that the irradiation could increase the potential efficiency of photosystem II of this species. Johanson et al. (1995a) noted that after one treatment season the absolute annual growth of *Vaccinium vitis-idaea* was significantly increased by 23 % and the thickness of leaves was also increased under enhanced UV-B but after two treatment seasons the growth had decreased by 20 %. The higher values of relative vitality index and a lack of decrease in chlorophyll content in irradiated leaves compared to the control may indicate an increase in the potential efficiency of photosynthesis and in biomass production, which seem to confirm that a short period of the UV-B irradiation can intensify growth of cowberry's stems and leaves' thickness.

It is evident that the cowberry is better acclimated to the high UV-B irradiation than the bilberry. It can be a result of the differences in leaf morphology. The leaves of *Vaccinium vitis-idaea* are thicker and covered with a lucent wax layer, which can reflect light and protect against enhanced UV-B radiation. The leaves of *Vaccinium myrtillus* are thin and "delicate" if we compare with those of the cowberry.

The results of the analysis of the screening pigments content in leaves of

wild plants show that the plants originating from equatorial zone are better acclimated to UV-B irradiation than the plants from mid latitudes (Robberecht et al. 1980). The reaction of the shrubs from the different geographical provenances did not reveal any significant trend dependent on latitude. The impact of the stress caused by the UV-B radiation could probably mask an effect of provenance or the latitudinal step was not sufficient to show clear differences between geographical provenances in the described experiment.

The physiological perturbations observed in photosynthetic apparatus of two investigated shrub species in the greenhouse are in accordance with the results of biometric measurements conducted on the same species in the other experiments. Nevertheless there are many important differences in experimental conditions, the general conclusions of all the experiments concerning the impact of UV-B radiation on plants are very similar. If the trend of increasing in UV-B radiation reaching Earth's surface was stable, it would affect the plant physiology and it would lead to significant changes at the plant communities and the whole forest ecosystem.

ACKNOWLEDGEMENTS – The author's research works were supported by the European Union with the Individual Mobility Grant from the programme "Tempus". The experiment was carried out at the Faculty of Agronomy in Gembloux, Belgium. I wish to thank dr Eric Laitat for the invitation to his large research project and valuable discussions. I thank the staff at the Faculty of Agronomy in Gembloux for technical assistance to run the experiment in the greenhouse and for chlorophyll analyses.

6. SUMMARY

Reduction of stratospheric ozone layer caused by emission of chlorofluorocarbons and halons into the atmosphere is a reason of enhanced UV-B radiation (280 – 320 nm) reaching the Earth's surface.

Impact of UV-B irradiation on photosynthetic apparatus of two shrub species: *Vaccinium myrtillus* L. and *Vaccinium vitis-idaea* L. was investigated. The plants originating from different latitudes were used (Table 1). The experiment was carried out in the greenhouse. Three variants of ultraviolet-B irradiation were applied: control = 0, lower dose = 11.32 and higher dose = 22.64 kJ m^{-2} day^{-1} $UV\text{-}B_{BE}$ (biologically effective dose of UV-B).

The response of shrubs to the increased UV-B radiation depended on UV-B dose, species traits and provenance. The cowberry was less sensitive to UV-B than the bilberry. The permanent discolorations observed on the leaves of *Vaccinium myrtillus* prove its sensitivity to the high UV-B radiation. The leaf bud break of the bilberry was accelerated at high UV-B dose compared to the control. The UV-B radiation influenced the photosynthetic apparatus of *Vaccinium myrtillus*: the chlorophyll content in leaves was reduced, the maximal and the steady state fluorescence of chlorophyll were diminished (Table 2, 3, 4, 5; Figure 1, 2).

The chlorophyll content in leaves of *Vaccinium vitis-idaea* did not change significantly. The relative vitality index was higher and the steady state fluorescence of irradiated leaves was reduced compared to the control (Table 6, 7; Figure 3).

The UV-B radiation can affect the pigments' content in leaves and the efficiency of the shrubs' photosynthesis. The variety of its reaction to the increased UV-B radiation may have important consequences to the forest ecosystem altering the species competition and micro-organisms' activity.

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(Received after revising September 1998)