

Photosynthesis-ecophysiological properties of beech (*Fagus sylvatica* L.) under the exclusion of ambient UV-B radiation

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ABSTRACT The effects of exclusion of UV-B radiation on leaf physiology of beech seedlings regenerating in a deforested area were studied in field. Under UV-B exclusion the chlorophyll content of leaves was higher, the chlorophyll a/b ratio and the carotenoid content was lower than in leaves under the ambient level of UV-B radiation. In leaves developed under the exclusion of UV-B a smaller degree of conversion of violaxanthin to zeaxanthin and atheraxanthin was found at noon. The results showed that the ambient level of UV-B radiation decreased the maximum photochemical efficiency (F_v/F_m) of the dark-adapted leaves, especially at noon. Beech leaves contained significantly higher quantities of UV-B absorbing compounds on the basis of leaf area at the ambient UV-B than under the UV-B exclusion. Flavonoid accumulation took place in close correlation with the increase of specific leaf weight as compared to the leaves developed under UV-B exclusion.

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KEY WORDS

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xanthophyll cycle

In natural vegetation long-life trees are potentially impressed by the global environmental changes. Due to the depletion of stratospheric ozone the enhanced level of UV-B radiation is an important stress factor for plants as it causes a number of direct and indirect effects on the photosynthetic apparatus, which may influence the whole plant development. Under natural conditions UV-B radiation is always accompanied by the visible part of the solar spectrum, which in itself can induce photoinhibition and photodamage. In this work we investigated the responses of beech seedlings regenerating in a deforested area to different UV-B/PAR ratio using UV-B exclusion in field. Our attention was focused on the alteration of photosynthetic pigment composition, including xanthophyll cycle components, furthermore, on the maximal (F_v/F_m) photochemical efficiency of PSII. We also examined the effects of reduction of UV-B on specific leaf weight (SLW) and accumulation of UV-B absorbing compounds in leaves. Ecophysiological responses to artificial exclusion of UV-B were also compared to the features of seedlings grown in the forest edge of southern exposure and the forest understory.

Materials and Methods

The experimental site is located in the Bükk Mountains (NE Hungary) at 550 m above the sea level where a nature beech forest was clear-cut in 1981. The forest has been allowed to regenerate naturally at the site. In the deforested area 5 beech seedlings of similar morphological characteristics were selected for the study. One branch of southern exposure per seedlings was covered by polyester filter to exclude the UV-B radiation before budding time in the middle of April 2000. We performed comparative measurements on the covered and uncovered branches of seedlings after the large period of leaf expansion in May in the same year and a year later. Potential

photochemical activity of leaves was measured after 20 min dark adaptation by using PAM 2000 fluorometer (Walz Co., Germany). Chlorophyll content was measured in 80% acetone extract with spectrophotometric method (Wellburn 1994), and the carotenoid composition was analysed by reversed phase HPLC method with application of zeaxanthin as standard. Accumulation of UV-B absorbing compounds was estimated on the basis of absorbances of MeOH:HCl:H₂O (90:1:1 volume) extracts at 300 nm (Day and Demchick 1996). Absorbances were expressed on leaf area basis. PAR was measured by the light sensor of AP-4 Porometer (Delta-T Devices, UK) and the UV-B by the IL 1400 A radiometer (International Light INC. USA).

Results and Discussion

There were differences in the physiological parameters between the filtered (-UV-B) and unfiltered (ambient) fully expanded leaves which already appeared in the first growing season. Under UV-B exclusion the chlorophyll content of leaves was higher, the chlorophyll a/b ratio and the carotenoid content was lower than in leaves under the ambient level of UV-B (Table 1). The main changes in the carotenoid content are resulted from the increase of the amount of the xanthophyll cycle components. High light intensity increased the activity of xanthophyll cycle, the important protective mechanism against photoinhibition and photodamage of PSII (Long et al. 1994). Under the exclusion of UV-B a smaller degree of conversion of violaxanthin to zeaxanthin and atheraxanthin was found at noon (DEEPS-index), but it was higher than in the leaves of seedlings grown in the forest edge and in the forest understory (Fig. 1). The b-carotene content changed in correlation with the increases of vaz-pool at noon in seedlings of every habitat (Fig. 1). Chlorophyll fluorescence analysis showed that the ambient level of UV-B decreased the maximum photochemical efficiency (F_v/F_m) of the dark-adapted leaves, especially at

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Table 1. Concentrations of leaf photosynthetic pigments, chlorophyll a/b ratio, maximal photochemical efficiency (Fv/Fm) in dark adapted leaves, accumulation of flavonoids estimated by absorbances of leaf methanolic extracts at 300 nm) and specific leaf weight (SLW) of seedlings under different irradiances. For pigments each value represents the average of 6 replicates \pm SE, for Fv/Fm, flavonoids and specific leaf weight each value indicates the average of 9 replicates \pm SE.

	Clear-cut area ambient UV-B	Clear-cut area UV-B exclusion	Forest edge	Forest understory
Chlorophyll (mg g ⁻¹ d.w.)				
2000.05.05.	6.18 \pm 1.06	6.81 \pm 0.95	5.60 \pm 1.12	6.55 \pm 0.68
2001.05.15.	4.99 \pm 0.84	6.57 \pm 1.59	5.60 \pm 0.65	7.41 \pm 0.66
Chlorophyll a/b				
2000.05.05.	3.04 \pm 0.06	2.97 \pm 0.23	3.03 \pm 0.02	2.81 \pm 0.05
2001.05.15.	2.82 \pm 0.16	3.18 \pm 0.01	2.93 \pm 0.11	3.15 \pm 0.23
Carotenoids (mmol mol ⁻¹ chl.)				
2000.05.05.	444.07 \pm 24.61	398.81 \pm 50.72	394.10 \pm 40.28	359.10 \pm 40.75
2001.05.15.	438.34 \pm 95.25	408.92 \pm 73.04	423.32 \pm 18.42	312.58 \pm 46.81
VAZ-pool (mmol mol ⁻¹ chl.)				
2000.05.05.	134.83 \pm 19.32	97.98 \pm 18.33	97.90 \pm 15.04	51.87 \pm 5.38
2001.05.15.	112.70 \pm 30.37	104.65 \pm 31.49	114.29 \pm 11.20	47.95 \pm 10.61
Fv/Fm				
2000.05.05.	0.705 \pm 0.007	0.743 \pm 0.006	0.735 \pm 0.006	0.752 \pm 0.003
2001.05.15.	0.744 \pm 0.004	0.751 \pm 0.008	0.735 \pm 0.004	0.741 \pm 0.004
A _{300nm} cm ⁻²				
2000.05.05.	1.757 \pm 0.306	0.995 \pm 0.106	0.897 \pm 0.026	0.563 \pm 0.039
2001.05.15.	2.740 \pm 0.742	1.860 \pm 0.129	2.536 \pm 0.906	1.832 \pm 0.261
SLW (g dm ⁻²)				
2000.05.05.	0.51 \pm 0.10	0.48 \pm 0.08	0.43 \pm 0.04	0.33 \pm 0.03
2001.05.15.	0.62 \pm 0.09	0.54 \pm 0.11	0.46 \pm 0.12	0.31 \pm 0.05

noon (Table 1). Flavonoids can effectively screen the UV-B radiation thereby protect the primary metabolism, and furthermore they have antioxidant properties. Thus flavonoid accumulation can improve plant tolerance to abiotic stresses such as UV-B radiation by reducing damage to the photo-

synthetic apparatus (Estiarte et al. 1999). Beech leaves contained significantly higher quantities of UV-B absorbing compounds on the basis of leaf area at the ambient UV-B than under the UV-B exclusion (Table 1). Flavonoid accumulation took place in close correlation with the increase of SLW as compared to the leaves developed under UV-B exclusion (Table 1). Similarly to other species in the case of beech flavonoid accumulation also proved to be a useful indicator of leaf UV-B screening ability and potential plant sensitivity to increased UV-B radiation (Wand 1995). Responses of photosynthetic apparatus of seedlings under UV-B exclusion were similar to the seedlings of forest edge, where the period of high irradiance is shorter than in the clear-cut area. Results of the second year were very similar to those we could observe in the first year. The present study indicates that shortly after the budding time, the ambient level of solar UV-B radiation can have subtle effects on the maximal photochemical efficiency of beech seedlings, and cause significant changes in the photosynthetic pigment composition, the accumulation of the UV-B absorbing compounds and the morphological properties of leaves. The photosynthetic responses of seedlings in the three contrasting habitats were similar to results we observed in previous studies in the experimental site (Mészáros et al. 1995, 1998, 2002).

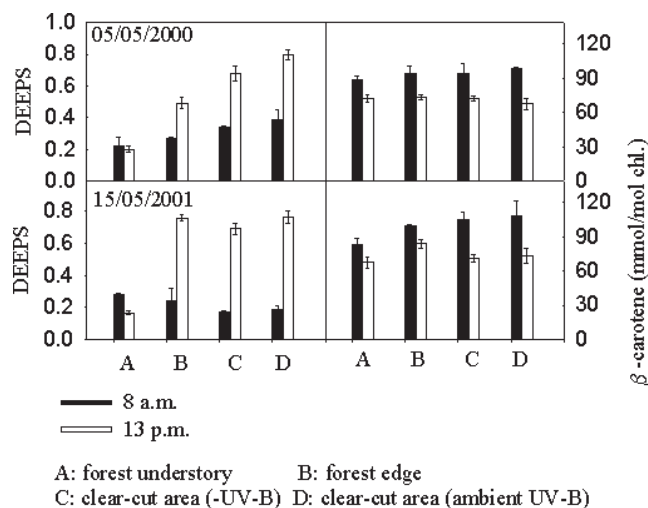


Figure 1. Changes in the de-epoxidation state of xanthophyll cycle (zeaxantin+0.5*antheraxantin/viola+anthera+zeaxantin) and the β -carotene content in leaves of beech seedlings in the morning (8 a.m.) and at noon (13 p.m.) in the three habitats. Each value represents the average of 6 replicates \pm SE.

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