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Physiological plasticity of beech (*Fagus sylvatica* L.) under contrasting light conditions

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ABSTRACT In this work pigment composition and chlorophyll fluorescence characteristics were studied in seedlings of *Fagus sylvatica* regenerating in contrasting light environments of forest understory, forest edge and deforested area. The results have shown that the survival of beech seedlings under high light conditions in the forest edge and deforested area, as well as their acclimation to excess light require effective functional plasticity of the photosynthetic apparatus and protective mechanisms. Physiological acclimation of beech seedlings to high light involves significantly the carotenoids both in the short-term through the reversible conversion of violaxanthin to zeaxanthin and in the long-term through the increase of total carotenoid content and the size of xanthophyll cycle pool.
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European beech (*Fagus sylvatica*) is an important late successional and climax species of the temperate regions in Europe. Beech covers a significant part of mountainous areas where it can be found in clear or mixed forests. In closed forests, beech regenerates properly in the understory, and shows a typical shade tolerant character (Kozlowski et al. 1991). Canopy openings by thinning or clear-cutting of mature beech forests induce severe abiotic stress conditions for the previous understory vegetation and the regeneration process of beech seedlings. For the survival in the stressful environment, light tolerance of beech seedlings is an important element of post-harvest succession, and determines the rate of forest regeneration (Küppers and Schneiders 1993; Mészáros 1990).

In this study the physiological plasticity and behaviour of seedlings of beech regenerating under contrasting light conditions. The investigations were performed along a forest understory/forest edge/clear-cut area transect.

Materials and Methods

The study site is located in Bükk Mountains (Rejtek Research Site, NE Hungary) at 550 m above the sea level. Until 1981 the site was covered by an 80-year-old mature beech forest stand. In 1981 a part of the forest was clear-cut. To study the effects of contrasting light conditions on the leaf physiology of regenerating beech seedlings, three experimental plots were established along a transect perpendicular to the margin of the remaining forest: in the forest interior, in the clear-cut area and in the transitional forest edge (Mészáros 1990). The forest edge has a southern exposure, which restricts the penetration period of photosynthetically active radiation into the foliage of seedlings in the understory to 5–6 hours around noon. The closure of tree canopy of the forest is 80%, which allows sunflecks in the understory. In each plots 5 seedlings were selected for the study. Physiological measurements were performed in the following periods: 10–13 July 1996 and 06–10 July 1997. Chlorophyll fluorescence parameters were measured in the attached leaves using a PAM 2000 fluorometer (WALZ, Germany). The fluorescence parameters (Fv/Fm, ΔF/Fm', qP, NPQ) were calculated by Scheiber's (1994) and Genty et al.'s (1989) formulae. The photosynthetic pigment composition of leaves was measured in 80% acetone extract of leaves frozen in liquid N_2 in field immediately after the sampling. Chlorophylls and total carotenoid content were determined by spectrophotometric method (Shimadzu UV/VIS spectrophotometer) using the Wellburn's (1994) equations. The carotenoid composition was studied by the reverse-phased HPLC method, (UV/VIS HPLC, Jasco, Japan) with the application of zeaxanthin as the standard. Chloroplasts, thylakoids and chlorophyll protein complexes were isolated as in Sárvári and Nyitrai (1994). Chlorophyll-protein bands were separated by Deriphat PAGE after solubilization with mainly glucosidic detergents (dodecyl sucrose:nonyl-glucoside:lithium dodecyl sulfate = 4.5:4.5:1). Polypeptide patterns for identification of green bands were obtained on 10–18% gradient gels according to Laemmli (1970). Fluorescence emission spectra (excited at 440 nm) of chloroplasts suspended in isolation buffer and glycerine 1:1 (v/v) were measured at 77K with a Jobin Yvon FluoroMax-2 spectrofluorimeter. The Chl concentration of samples was 5 μg ml^{-1}.

Results and Discussion

Seedlings showed highest chlorophyll content (7.64 mg g^{-1} d.w.), and smallest carotenoid pool (258 mmol mol^{-1} chl) in the forest understory. Chlorophyll content progressively decreased to 5.32 and 2.21 mg g^{-1} and total carotenoid content increased to 258 and 334 mmol mol^{-1} chl in the forest edge and clear-cut area, respectively. Chl a/b and β-carotene/neoxanthin ratio increased with increasing growth irradiance

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corresponding to the decrease of relative amount of LHCII and reduction at the long wavelengths of fluorescence emmision spectra of isolated chloroplasts. VAZ was 46 mmol mol^{-1} chl in the forest understory and doubled to 107 mmol mol^{-1} chl in the clear-cut area. Change of total carotenoid pool was due to accelerated accumulation of xanthophyll cycle pigments. VAZ was 17%, 27% and 32% of total carotenoids in forest understory, forest edge and clear-cut area.

There occurred a midday depression of Fv/Fm (10%) in the clear-cut area and forest edge which took place in correlation with high rate of violaxanthin conversion to zeaxanthin and antheraxanthin (70-80%). Midday decline of Fv/Fm was more rapidly reversible by evening in the forest edge than in the forest area. ΔF/Fm' was the highest and did not change in the forest understory during the day, but it showed high extent of fluctuation in an inverse correlation with PFD in the forest edge and clear-cut area, its minimum value was around 0.2 at midday when accumulation of de-epoxi xanthophylls reached the maximal extent. Indexes of V (1-qP) and (1-qP)/NPQ derived the Kautsky kinetics recorded for 5 min indicated that seedlings in the clear-cut area were less susceptible to photoinhibition.

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