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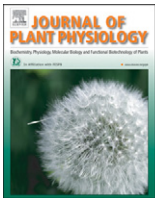

Acclimation of Norway spruce photosynthetic apparatus to the combined effect of high irradiance and temperature

Michal Štroch [a], Daniel Vrábl [b], Jana Podolinská [a], Jiří Kalina [a], Otmar Urban [c], Vladimír Špunda [a,*]

[a] *Department of Physics, Faculty of Science, Ostrava University, 30. dubna 22, CZ-701 03 Ostrava 1, Czech Republic*
[b] *Department of Plant Physiology, Faculty of Science, University of South Bohemia, Branišovská 31, CZ-370 05 České Budějovice, Czech Republic*
[c] *Laboratory of Plants Ecological Physiology, Institute of Systems Biology and Ecology, Academy of Sciences of the Czech Republic, Poříčí 3b, CZ-603 00 Brno, Czech Republic*

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ABSTRACT

Diurnal courses of photosynthetic gas exchange parameters, chlorophyll *a* fluorescence characteristics and the de-epoxidation state of the xanthophyll cycle pigments (DEPS) were measured during the gradual acclimation of 4-year-old Norway spruce seedlings to different photosynthetic photon flux density (PPFD) and air temperature (T_{air}) regimes, simulating cloudy days with moderate T_{air} (LI, maximum PPFD 300 μmol m^{-2} s^{-1}, T_{air} range 15–25 °C), sunny days with moderate T_{air} (HI, maximum PPFD 1000 μmol m^{-2} s^{-1}, T_{air} range 15–25 °C) and hot sunny days (HI-HT, maximum PPFD 1000 μmol m^{-2} s^{-1}, T_{air} range 20–35 °C). The plants were acclimated inside a growth chamber and each acclimation regime lasted for 13 d. Acclimation to HI conditions led to a strong depression of the net CO_2 assimilation rates (A_N), particularly during noon and afternoon periods. Exposure to the HI-HT regime led to a further decrease of A_N even during the morning period. Insufficient stomatal conductance was found to be the main reason for depressed A_N under HI and HI-HT conditions. Only slight changes of the maximum photosystem II (PSII) photochemical efficiency (F_V/F_M), in the range of 0.78–0.82, supported the resistance of the Norway spruce photosynthetic apparatus against PSII photoinhibition during acclimation to both HI and HI-HT conditions. The HI plants showed increased content of xanthophyll cycle pigments (VAZ) and enhanced efficiency of thermal energy dissipation within PSII (*D*) that closely correlated with the increased DEPS. In contrast, acclimation to the HI-HT regime resulted in a slight reduction of VAZ content and significantly diminished *D* and DEPS values during the entire day in comparison with HI plants. These results indicate a minor role of the xanthophyll cycle-mediated thermal dissipation in PSII photoprotection under elevated temperatures. The different contributions of the thermal dissipation and non-assimilatory electron transport pathways in PSII photoprotection during acclimation of the Norway spruce photosynthetic apparatus to excess irradiance and heat stresses are discussed.

Introduction

Under natural conditions, the assimilatory apparatus is exposed to environmental conditions (high solar irradiance, elevated air temperature, and drought) that often result in a midday depression of photosynthetic CO_2 assimilation (Faria et al., 1996; Muraoka et al., 2000; Špunda et al., 2005). The depression of net CO_2 assimilation usually ceases during the afternoon and the two distinct maxima of the CO_2 assimilation rate occur in the morning and afternoon. Under more severe stress conditions, photosynthetic activity increases with irradiance only in the morning and the depression of CO_2 assimilation persists until the late afternoon (González-Rodríguez et al., 2002; Franco et al., 2007). The main physiological processes responsible for the midday depression are stomatal closure and/or photosystem II (PSII) photoinhibition (Muraoka et al., 2000).

In sunny conditions, insufficient soil moisture and a high vapor potential deficit may lead to a decrease of stomatal conductance (G_S) to CO_2 diffusion (Panek and Goldstein, 2001; Urban et al., 2007) followed by decreases of CO_2 concentrations at both the intercellular (C_i) and chloroplast levels, causing the CO_2 uptake to decline. In addition, Bota et al. (2004) concluded that the impairment of Rubisco activity and ribulose-1,5-bisphosphate

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Abbreviations: A_N, net CO_2 assimilation rate; Car x+c, total carotenoids; Chl, chlorophyll; *D*, efficiency of thermal energy dissipation; DEPS, de-epoxidation state of the xanthophyll cycle pigments; ETR, photosystem II electron transport rate; F_V/F_M, maximal photochemical efficiency of photosystem II; G_S, stomatal conductance; HI, high irradiance acclimation regime; HI-HT, high irradiance and high air temperature acclimation regime; LI, low irradiance acclimation regime; P, actual photochemical efficiency of photosystem II; PPFD, photosynthetic photon flux density; PSII, photosystem II; VAZ, pool of xanthophyll cycle pigments (violaxanthin+antheraxanthin+zeaxanthin)

[*] Corresponding author. Tel.: +420 597092154; fax: +420 597092152.
E-mail address: vladimir.spunda@osu.cz (V. Špunda).

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content limit photosynthesis under severe drought stress. As a result, an assimilation optimum, given by the synergic influence of the photosynthetic photon flux density (PPFD) and other environmental factors, has been observed (Muraoka et al., 2000).

PSII photoinhibition can be of a dynamic and chronic nature (Werner et al., 2002). The first involves a rapidly reversible down-regulation of PSII photochemical efficiency observed at midday regulated by thermal dissipation of absorbed excitation energy. Chronic PSII photoinhibition is associated with slowly reversible energy dissipating mechanisms, repair processes or with permanent damage to the photosynthetic apparatus, and is reflected by a sustainable decrease in pre-dawn maximal PSII photochemical efficiency (maximal photochemical efficiency of photosystem II – F_V/F_M) (Werner et al., 2002; Williams et al., 2003).

Thus, thermal dissipation is one of the crucial photoprotective mechanisms preventing photo-oxidative damage to the photosynthetic apparatus under stressful conditions during midday (Iio et al., 2004; Franco et al., 2007). The major part of non-radiative dissipation occurs within light-harvesting complexes of PSII, thereby reducing the over-excitation of the PSII reaction centers. Under conditions of low C_i due to stomatal closure at midday, a high degree of thermal dissipation is needed to achieve a balance between the electron flow and reduction potential for carboxylation and oxygenation. The mechanism of thermal dissipation is associated with the reversible conversion of violaxanthin to antheraxanthin and zeaxanthin in the xanthophyll cycle (Štroch et al., 2004; Horton et al., 2008). The thermal dissipation efficiency and de-epoxidation state of the xanthophyll cycle pigments (DEPS) in sun-exposed leaves exhibit a similar pattern of the daily course on clear summer days. They increase gradually with the rising solar irradiance in the morning, reach their maxima around midday, and then decrease in the afternoon (Schindler and Lichtenthaler, 1996; Demmig-Adams et al., 1999). The other typical feature of the xanthophyll cycle activity in plants under environmental stress conditions is an overnight retention of de-epoxidized xanthophylls, usually associated with sustained reduction of F_V/F_M (Williams et al., 2003; García-Plazaola et al., 2008).

During midday, low C_i and elevated temperature enhance the affinity of Rubisco for O_2. As a consequence, the photorespiration rate increases. An enhanced contribution of photorespiratory CO_2 production to the total electron flow is considered another important photoprotective mechanism preventing an over-reduction of the photosynthetic electron transport chain (Valentini et al., 1995; Muraoka et al., 2000; Franco and Lüttge, 2002).

An elevated temperature during the midday period can also exert direct negative effects on photosynthetic CO_2 assimilation of high-temperature-sensitive species. In particular, the thermal lability of Rubisco activase can lead to a Rubisco activity reduction at temperatures normally considered as optimal (Salvucci and Crafts-Brandner, 2004; Sharkey, 2005). The temperature optimum of the electron transport rate is usually higher than that of CO_2 assimilation (Yamori et al., 2008). However, at super-optimum temperatures, the inhibition of linear electron transport occurs at the expense of cyclic electron transport pathways that lead to stimulation of ΔpH-dependent thermal dissipation (Kramer et al., 2004; Sage and Kubien, 2007). Thus, usually both enhanced photorespiration and thermal dissipation contribute to PSII photoprotection under combined exposure to high irradiance and temperature (Franco et al., 2007).

Thermal acclimation abilities differ considerably among species (Sage and Kubien, 2007) and even among congeneric plants originating in different latitudes and/or altitudes (Atkin et al., 2006; Weston and Bauerle, 2007). Systematic studies on acclimation to increased temperature (particularly to the periods of extremely high temperatures) in coniferous species, representing dominant tree species of boreal and temperate forests, are relatively scarce. Recently, Way and Sage (2008a, b) documented that the development of black spruces at a constantly elevated growth temperature (30/22 °C day/night temperature) led to a reduction of net photosynthetic rates at their growth temperature in comparison with plants acclimated to a 22/16 °C temperature regime. To the best of our knowledge, there has been no comprehensive study on the adaptability of the Norway spruce assimilatory apparatus to combined high irradiance and high temperature conditions.

In the present study Norway spruce seedlings were exposed to defined conditions simulating daily courses of microclimatic parameters during cloudy and sunny days with moderate temperatures and during hot sunny days. With regard to sensitivity of the spruce photosynthetic apparatus to high growth temperature (Way and Sage, 2008a), we expected that high temperature would be a synergic stress factor resulting in a persistent depression of photosynthetic CO_2 assimilation during the prevailing part of the photoperiod. The aims of this study were (1) to analyze the acclimation ability of the assimilatory apparatus of Norway spruce to elevated irradiance and temperature during simulated hot sunny days, and (2) to test the hypothesis that combined exposure of spruce seedlings to elevated irradiance and temperature would result in an increased demand on photoprotective processes, such as a xanthophyll cycle-dependent thermal energy dissipation and photorespiration.

Materials and methods

Plant material and experimental design

Four-year-old seedlings of Norway spruce (*Picea abies* [L.] Karst.) were gradually acclimated to three consecutive environmental conditions inside a growth chamber (HB 1014, Bioline-Heraeus, Germany). The duration of each acclimation regime was 13 d. The daily courses of microclimatic parameters for the individual acclimation regimes were adjusted as shown in Fig. 1. The seedlings were initially acclimated to low photosynthetic photon flux density (PPFD) together with moderate air temperature (T_{air}) (low irradiance acclimation regime (LI regime); maximum PPFD at "midday" 300 μmol m^{-2} s^{-1}, T_{air} in the range 15–25 °C). Then, PPFD was increased (maximum PPFD 1000 μmol m^{-2} s^{-1}), whereas the daily course of T_{air} remained unchanged (high irradiance acclimation regime – HI regime). Finally, only T_{air} over the entire day was increased (high irradiance and high air temperature acclimation regime (HI-HT regime); T_{air} range 20–35 °C). The plants were sufficiently watered and the daily course of relative air humidity was adjusted in the range of 50–65% for all regimes to avoid drought stress. Due to horizontal heterogeneity of illumination inside the growth chamber, the incident PPFDs on the measured shoots varied up to 10% in comparison with the estimated average PPFDs, which were 10, 100, 160, 230 and 300 μmol m^{-2} s^{-1} for LI plants and 25, 310, 590, 850 and 1000 μmol m^{-2} s^{-1} for HI plants (Fig. 1). All measurements were carried out on current needles and shoots from the two uppermost whorls of the crown, where the incident PPFD was at the required level (see Fig. 1).

Gas-exchange measurements

Measurements of the steady-state net CO_2 assimilation rate (A_N) and stomatal conductance (G_S) were carried out on attached shoots under the given acclimation conditions (PPFD, T_{air} and CO_2