Beskydy, 2017, 10 (1, 2): 49–56
© Mendelova univerzita v Brně
ISSN: 1805-9538 (Online)
http://dx.doi.org/10.11118/beskyd201710010049

Seasonal courses of photosynthetic parameters in sun- and shade-acclimated spruce shoots

***Otmar Urban, Petr Holub, Karel Klem**

Global Change Research Institute CAS, Bělidla 4a, Brno CZ-603 00, Czech Republic,
e-mail: urban.o@czechglobe.cz

Abstract: Urban O., Holub P., Klem K. 2017: Seasonal courses of photosynthetic parameters in sun- and shade-acclimated spruce shoots – *Beskydy,* 10 (1, 2): 49–56

Exponential attenuation of light intensity passing through forest canopies leads to the formation of sun- and shade-acclimated leaves contributing to overall canopy carbon gain. Using a gas-exchange technique, seasonal changes in photosynthetic parameters were investigated *in situ* to test the hypothesis that the relative contributions of sun- and shade-acclimated Norway spruce shoots to total carbon gain vary during the growing season and that the contribution of sun-acclimated shoots to total carbon uptake may be reduced during the hot and dry summer season. In agreement with the tested hypothesis, we found reduced photosynthetic capacity as well as reduced light-use efficiency for carbon assimilation in sun-acclimated shoots during summer months while these remained almost unchanged in shade-acclimated shoots. Reduction of photosynthetic capacity was primarily associated with reduced stomatal conductance. On the other hand, seasonal courses of mitochondrial dark respiration, quantum efficiency of photosynthetic reactions, and compensation irradiance were primarily driven by changes in temperature. Accordingly, the photosynthetic characteristics of sun- and shade-acclimated shoots tended to converge in early spring and late autumn when temperature was low. Such seasonal dynamics result in an increased contribution of shade-acclimated shoots to total carbon uptake at the beginning and end of the growing season as well as during hot and dry summer periods.

Keywords: CO_2 assimilation, gas-exchange, Norway spruce, ontogeny, temperature, vapour pressure deficit, vertical canopy profile

Introduction

Solar radiation passing through a canopy is exponentially attenuated. Such attenuation is inversely proportional to, among other factors, leaf area index (LAI). Accordingly, and particularly in dense forest canopies with high LAI, light gradients within the canopy subsequently lead to the formation of sun- and shade-acclimated leaves (Boardman 1977, Lichtenthaler et al. 2007, Rajsnerová et al. 2015).

Particularly in changing climatic conditions, the seasonal course of photosynthesis and respiration of leaves from distinct parts of the crown must be known for upscaling and modelling of carbon fluxes in forest ecosystems, evaluation of active carbon sinks, and prediction of wood formation. Earlier studies of coniferous tree species have investigated mainly the effect of needle age on CO_2 exchange (Troeng and Linder 1982, Beeck et al. 2010, Urban et al. 2012a), while *in situ* investigation as to the relative contribution of sun- and shade-acclimated needles to total carbon uptake and its change during the growing season have received only limited attention.

Our earlier studies in dense spruce forest (e.g. Urban et al. 2007) revealed that 40–70 % of total leaf area may be exposed during the day to intensities of photosynthetically active radiation (PAR) below 50 µmol photons m^{-2} s^{-1} due to a mutual shading of individual shoots, branches, and trees. Such low PAR intensities together with a reduced ratio between red and far-red radiation (Navrátil et al. 2007) lead to the formation of a so-called shade-acclimated canopy. As compared to sun-acclimated leaves, shade-acclimated leaves are usually thinner but have a larger area, lower number of stomata per unit leaf area, larger chloroplasts with irregularly oriented grana, higher chlorophyll and carotenoid contents per unit mass, lower conductance to CO_2 in the mesophyll, and lower nitrogen and Rubisco contents (reviewed in Boardman 1977, Sims and Pearcy 1994, Lichtenthaler et al. 2007). Due to such morphological and biochemical acclimation, shade-acclimated leaves and plants usually have lower mitochondrial respiration, compensation irradiance, and light-saturated CO_2 assimilation rate. On the other hand, shade-acclimated leaves have higher quantum efficiency compared to sun-acclimated leaves. It has been shown, however, that shade-acclimated leaves and plants may have higher sums of assimilated CO_2 at lower amounts of daily irradiance and/or prevailing diffuse radiation (Sims and Pearcy 1994, Urban et al. 2012b) and thus play an important role in the carbon gain of the whole canopy or ecosystem. Moreover, high air temperature, irradiance, and vapour pressure deficit, typical for the upper parts of canopies, lead to an exponential increase in carbon respiratory losses (Doehlert and Walker 1981, Leakey et al. 2003) while stomata tend to close, thereby resulting in a reduced rate of photosynthesis (Farquhar and Sharkey 1982, Emberson et al. 2000, Urban et al. 2012b). Accordingly, reduced net carbon uptake by sun-acclimated leaves from the upper parts of canopies could be presumed during the summer season and particularly during hot, sunny days characterized by high temperatures and vapour pressure deficit.

Here, we show seasonal changes in main photosynthetic parameters estimated *in situ* for sun- and shade-acclimated shoots of Norway spruce (*Picea abies*). The gas-exchange measurements performed at the Bílý Kříž experimental research site in the Beskydy Mts. aimed to test the hypothesis that the contribution of shade-acclimated leaves to the spruce forest's carbon gain increases during the summer season, while sun-acclimated leaves contribute to total carbon uptake particularly at the beginning and end of the growing season.

Material and Methods

The forest stand selected for this study is located at the Bílý Kříž experimental research site (Beskydy Mountains, 49°33' N, 18°32' E, north-east Czech Republic, 908 m a.s.l.) and has been described in our previous studies (e.g. Urban et al. 2007). This area has a cool (annual mean air temperature 6.7 °C) and humid (annual mean relative air humidity 80 %) climate with high annual precipitation (average for 2000–2009 is 1374 mm).

The forest stand (6.2 ha) consists of *Picea abies* (L.) Karst (99 %) and *Abies alba* Mill. (1 %) planted on a slope (11–16°) with SSW orientation. At the time of the physiological investigations, the stand density was 2044 trees ha^{-1} (leaf area index approximately 11.8 m^2 m^{-2}), spruce trees were 28 years old, and their height and stem diameter at 1.3 m were 12.2 ± 0.1 m and 13.6 ± 0.1 cm, respectively (means ± standard deviation).

Shoot-level measurements

Three representative *P. abies* trees, selected randomly among those trees of average height, stem diameter, and leaf chlorophyll content, were used for *in situ* physiological measurements. Two to three 1-year-old shoots with SSW orientation were investigated in the upper canopy (4th whorl; hereafter sun shoots) and lower canopy (10–12th whorl; hereafter shade shoots) of each tree. The average from these two or three measurements was used for statistical analyses. The shoots were marked and measured during the whole growing season from mid-April to the end of October.

The relationships between CO_2 assimilation rate and light intensity (*A-I*) were estimated during extended noon hours (10:00–14:00 LMT) on clear-sky days using a Li-6400 open gas exchange system (Li-Cor, Lincoln, NE, USA). The *A-I* response curves were measured at constant ambient CO_2 concentration (380 µmol CO_2 mol^{-1}) and a predetermined set of PAR intensities (1400, 1200, 750, 300, 160, 80, 40, 20, 10, and 0 µmol photons m^{-2} s^{-1}) while leaf temperature and vapour pressure deficit (VPD) remained unmodified. The *A* values were recorded after ca 8 min of exposure to the given irradiance during constant stomatal conductance.

Modelling of physiological responses

Instantaneous rates of CO_2 assimilation were modelled as a general nonrectangular hyperbolic function of incident *I* according to Prioul and Chartier (1977):

$$A = \frac{\alpha I + A_{\max} - \sqrt{(\alpha I + A_{\max})^2 - 4\Theta \alpha A_{\max} I}}{2\Theta} - R_D, \quad (1)$$

where α is the apparent quantum efficiency (AQE; mol CO_2 mol^{-1} photons) and represents the initial linear slope of the *A-I* relationship, Θ is a number between 0 and 1 determining the shape of the light response curve (dimensionless), A_{max} is the light-saturated value of *A* (μmol CO_2 m^{-2} s^{-1}), and R_D is the mitochondrial dark respiration rate (μmol CO_2 m^{-2} s^{-1}). Compensation irradiance (I_{comp}) was defined as *I* when processes of CO_2 assimilation and release are in equilibrium (A = 0 μmol CO_2 m^{-2} s^{-1}), while the light saturation estimate (I_{sat}) is represented by an intersection of the initial linear and light-saturated parts of the *A-I* relationship.

Results

Microclimatic conditions

Daily mean air temperature (T_{air}) during the entire year, measured at 2.0 m above the ground of an open area, ranged between −11.5 °C (February) and 25.9 °C (July). The highest temperature during the period of investigation (April 21–October 26) was observed in July and the lowest in April (0.3 °C) and October (2.6 °C; Fig. 1A). The highest values of vapour pressure deficit (daily mean VPD of approximately 0.8–1.0 kPa) were observed in June and July.

Gas-exchange characteristics

The seasonal dynamics of A_{max} in sun- and shade-acclimated shoots are shown in Fig. 2A. While A_{max} of shade-acclimated shoots was relatively constant (5.5–6.9 μmol m^{-2} s^{-1}) during summer months (June–September), a clear depression of A_{max} in sun-acclimated shoots during June and July was observed. A_{max} of sun-acclimated shoots dropped to rates of 6.5 μmol m^{-2} s^{-1} during this period followed by a substantial increase during August and September. Such changes in A_{max} are closely related to changes in light-saturated stomatal conductance to CO_2 and H_2O diffusion (G_{Smax}; Fig. 2B).

Values of AQE measured over the period of investigation in sun- and shade-acclimated shoots varied between 0.027–0.066 and 0.037–0.076 mol CO_2 mol^{-1} photons, respectively (Fig. 2C). The lowest values of AQE throughout the growing season were observed during summer, while the highest occurred in early spring and late autumn. Moreover, the AQE of sun-acclimated shoots tended to be lower as compared to shade-acclimated shoots during summer months, particularly in June and July.

Typically higher values of dark respiration rate (R_D) in sun- vs. shade-acclimated shoots were observed particularly during the summer season, with its high temperatures (Fig. 2D). Differences in R_D between sun- and shade-acclimated

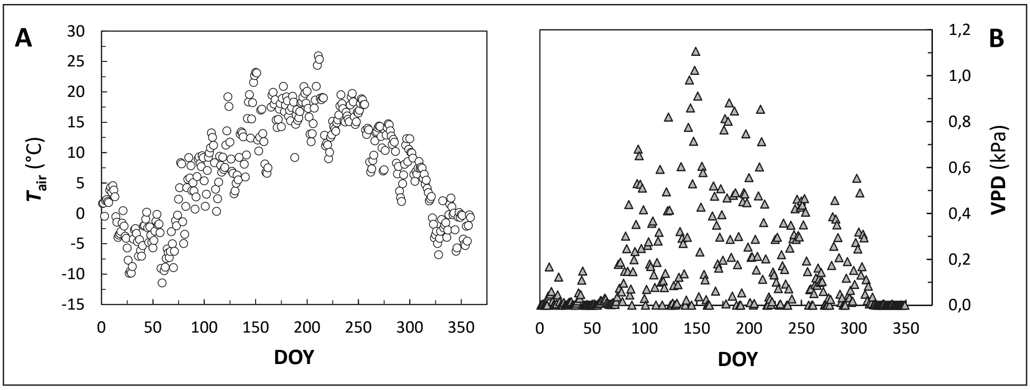

Fig. 1: Seasonal courses of daily mean air temperature (T_{air}; A) and daily mean vapour pressure deficit (VPD; B) at the Bílý Kříž experimental research site (Beskydy Mts.) during the year of investigation. DOY = day of year.

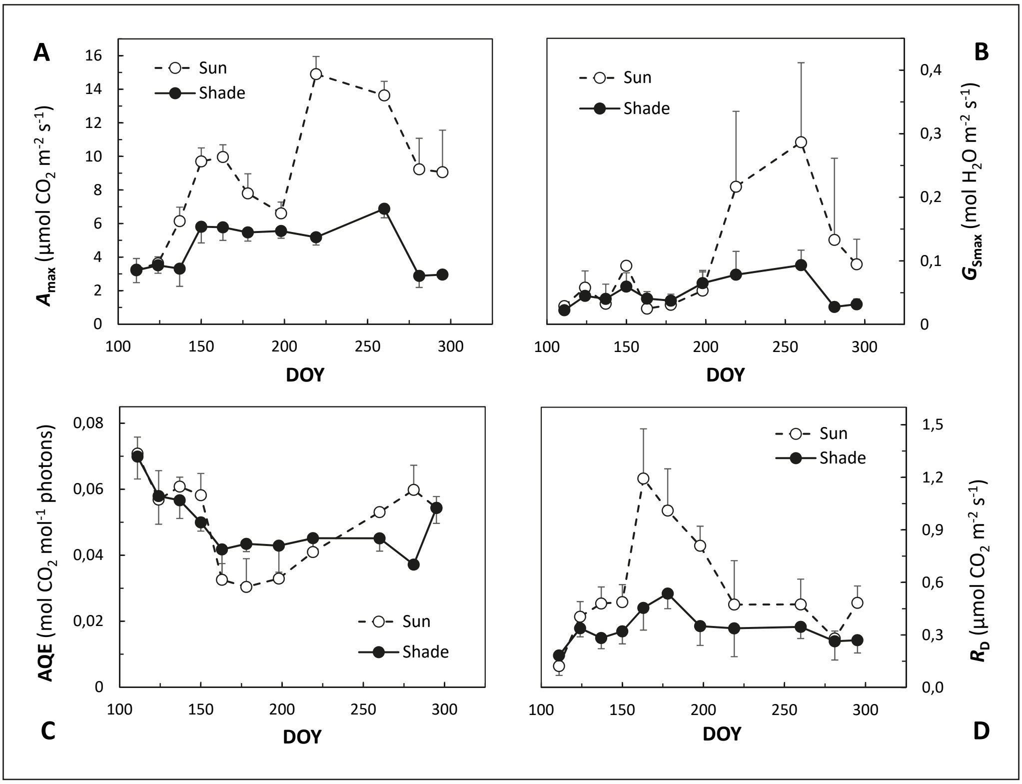

Fig. 2: Seasonal courses of light-saturated rate of CO$_2$ assimilation (A_{max}; A), light-saturated stomatal conductance (G_{Smax}; B), apparent quantum efficiency (AQE; C), and dark mitochondrial respiration (R_D; D) estimated in situ in sun- (Sun; open circles) and shade-acclimated (Shade; closed circles) Norway spruce shoots. Points represent mean values; error bars are standard deviations. N = 3, DOY = day of year.

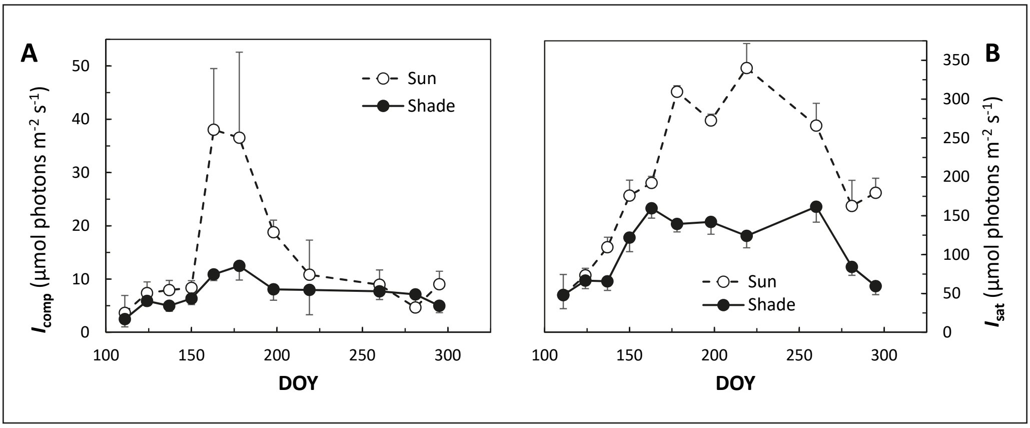

Fig. 3: Seasonal courses of light compensation irradiance (I_{comp}; A) and light saturation estimate (I_{sat}; B) calculated from the photosynthetic light response curves on the basis of Equation (1) for sun- (Sun; open circles) and shade-acclimated (Shade; closed circles) Norway spruce shoots. Points represent mean values; error bars are standard deviations. N = 3; DOY = day of year.

shoots, however, almost disappeared when temperatures decreased below 12 °C in early spring and late autumn.

Light compensation irradiance (I_{comp}) and light saturation estimate (I_{sat}) also revealed different seasonal courses in sun- and shade-acclimated shoots (Fig. 3). Sun-acclimated shoots had substantially higher values of both I_{comp} and I_{sat} as compared to shade-acclimated shoots during the summer months, while these differences almost disappeared at the beginning and end of the growing season. The substantial increase in I_{comp} of sun-acclimated shoots during the spring/summer transition is particularly associated with increased R_D (Fig. 2D) and reduced AQE (Fig. 2C) values.

Discussion

In agreement with the hypothesis tested, we found reduced photosynthetic capacity as well as reduced apparent quantum efficiency in using the sun's radiant energy for carbon assimilation in sun-acclimated shoots during summer months, while these remained almost unchanged in shade-acclimated shoots.

Reduced photosynthetic capacity was associated primarily with reduced stomatal conductance. Earlier findings had shown that G_{Smax} is particularly driven by VPD when high VPD values lead to closure of the stomatal aperture (Farquhar and Sharke 1982, Bergh et al. 1998, Urban et al. 2007). An increased resistance to CO_2 diffusion into the leaf interior is subsequently followed by reduced intercellular and chloroplastic CO_2 concentrations and by reduced carboxylation activity of the Rubisco enzyme (Farquhar et al. 1980, Caemmerer 2000, Urban et al. 2012a). In contrast, oxygenation activity of the Rubisco enzyme, leading to photorespiratory CO_2 efflux, is stimulated under such growth conditions, particularly when drought is combined with high temperatures (Doehlert and Walker 1981, Leakey et al. 2003, Urban et al. 2012b).

It has also been shown that the ratio between intercellular CO_2 and O_2 concentrations influences quantum yield efficiency (Ehleringer and Björkman 1977; Farquhar et al. 1980), that is to say how efficiently solar radiation is used for carbon assimilation. At common intercellular concentrations (around 230 µmol CO_2 mol^{-1} and 210 mmol O_2 mol^{-1}), AQE declines with temperature in C3 plants because the temperature dependence of oxygenation is greater than is that of carboxylation (Caemmerer 2000, Medlyn et al. 2002). This is in agreement with our finding that AQE of both sun- and shade-acclimated shoots is low during summer months (approximately 0.0304–0.0452 mol CO_2 mol^{-1} photons) but high in early spring and late autumn (up to 0.07 mol CO_2 mol^{-1} photons). Due to temperature gradients within canopy profiles, we hypothesize that the higher AQE values observed in shade- than sun-acclimated shoots during summer months result from temperature gradients within canopy profiles of the investigated forest stand (Urban et al. 2012b).

Similarly to other species, the rate of dark mitochondrial respiration in spruce shoots is highly sensitive to temperature (Stockfors and Linder 1998, Wallin et al. 2001) and thus exhibits a substantial seasonal course (Fig 2D). The exponential relationship between respiration rate and temperature is often described by the parameter Q_{10}, reflecting an increase in respiration rate for a 10 °C increase in temperature (Johnson and Thornley 1985, Bergh et al. 1998). Primary metabolites, saccharides and amino acids, accumulated in leaves form the initial substrate of respiratory reactions, thus coupling photosynthetic capacity with respiration rate (Whitehead et al. 2004, Atkin et al. 2005). Therefore, higher temperature sensitivity of R_D in sun-acclimated shoots characterized by higher photosynthetic capacity (Fig. 2A; Šprtová and Marek 1999, Wallin et al. 2001, Urban et al. 2012b) as compared to shade-acclimated shoots may also be assumed. Indeed, Q_{10} amounted to 1.72 in sun-acclimated shoots but was only 1.14 in shade-acclimated shoots (data not shown). At low temperatures, however, the rate of respiration is primarily limited by the biochemical activity of respiratory enzymes, while the substrate limitation becomes minor.

Conclusions

We have confirmed our initial hypothesis that the contribution of sun- and shade-acclimated shoots to total carbon gain changes during the growing season. We have found that the photosynthetic capacity as well as quantum efficiency of sun-acclimated shoots may be reduced during summer months, while these remain almost unchanged in shade-acclimated shoots.

Reduced photosynthetic capacity was primarily associated with reduced stomatal conductance to diffusion of gasses, while seasonal courses of mitochondrial dark respiration, quantum efficiency of photosynthetic reactions, and compensation irradiance are primarily driven by temperature. Accordingly, the differences in photosynthetic characteristics between sun- and shade-acclimated shoots disappear in early spring and late autumn when temperatures decrease below 12 °C.

Acknowledgements

Thanks are due to Martina Zitová for her help with field measurements. This work was supported by the Ministry of Education, Youth and Sports of the Czech Republic within the National Sustainability Program I (NPU I), grant number LO1415.

References

Atkin, O.K., Bruhn, D., Hurry, V.M., Tjoelker, M.G. 2005: The hot and the cold: unravelling the variable response of plant respiration to temperature. *Functional Plant Biology*, 32: 87–105.

Beeck, M., Gielen, B., Jonckheere, I., Samson, R., Janssens, I.A., Ceulemans, R. 2010: Needle age-related and seasonal photosynthetic capacity variation is negligible for modelling yearly gas exchange of a sparse temperate Scots pine forest. *Biogeosciences*, 7: 199–215.

Bergh, J., McMurtrie, R.E., Linder, S. 1998: Climatic factors controlling the productivity of Norway spruce: a model-based analysis. *Forest Ecology and Management*, 110: 127–139.

Boardman, N.K. 1977: Comparative photosynthesis of sun and shade plants. *Annual Review of Plant Physiology*, 28: 355–377.

Caemmerer Von, S. 2000: Biochemical models of leaf photosynthesis. Csiro publishing.

Doehlert, D.C., Walker, R.B. 1981: Photosynthesis and photorespiration in Douglas-fir as influenced by irradiance, CO_2 concentration, and temperature. *Forest Science*, 27: 641–650.

Ehleringer, J., Björkman, O. 1977: Quantum yields for CO_2 uptake in C_3 and C_4 plants. *Plant Physiology*, 59: 86–90.

Emberson, L.D., Wieser, G., Ashmore, M.R. 2000: Modelling of stomatal conductance and ozone flux of Norway spruce: comparison with field data. *Environmental Pollution*, 109: 393–402.

Farquhar, G.D., Caemmerer, S. von, Berry, J.A. 1980: A biochemical model of photosynthetic CO_2 assimilation in leaves of C_3 species. *Planta*, 149: 78–90.

Farquhar, G.D., Sharkey, T.D. 1982: Stomatal conductance and photosynthesis. *Annual Review of Plant Physiology*, 33: 317–345.

Johnson, I.R., Thornley, J.H.M. 1985: Temperature dependence of plant and crop process. *Annals of Botany*, 55: 1–24.

Leakey, A.D.B., Press, M.C., Scholes, J.D. 2003: High-temperature inhibition of photosynthesis is greater under sunflecks than uniform irradiance in a tropical rain forest tree seedling. *Plant, Cell & Environment*, 26: 1681–1690.

Lichtenthaler, H.K., Ač, A., Marek, M.V., Kalina, J., Urban, O. 2007: Differences in pigment composition, photosynthetic rates and chlorophyll fluorescence images of sun and shade leaves of four tree species. *Plant Physiology and Biochemistry,* 45: 577–588.

Medlyn, B.E., Dreyer, E., Ellsworth, D., Forstreuter, M., Harley, P.C., Kirschbaum, M.U.F., Le Roux, X., Montpied, P., Strassemeyer, J., Walcroft, A., Wang, K. 2002: Temperature response of parameters of a biochemically based model of photosynthesis. II. A review of experimental data. *Plant, Cell & Environment*, 25: 1167–1179.

Navrátil, M., Špunda, V., Marková, I., Janouš, D. 2007: Spectral composition of photosynthetically active radiation penetrating into a Norway spruce canopy: the opposite dynamics of the blue/red spectral ratio during clear and overcast days. *Trees-Structure and Function*, 21: 311–320.

Prioul, J.L., Chartier, P. 1977: Partitioning of transfer and carboxylation components of intracellular resistance to photosynthetic CO_2 fixation: a critical analysis of the methods used. *Annals of Botany*, 41: 789–800.

Rajsnerová, P., Klem, K., Holub, P., Novotná, K., Večeřová, K., Kozáčiková, M., Rivas-Ubach, A., Sardans, J., Marek, M.V., Peñuelas, J., Urban, O. 2015: Morphological, biochemical and physiological traits of upper and lower canopy leaves of European beech tend to converge with increasing altitude. *Tree Physiology*, 35: 47–60.

Sims, D.A., Pearcy, R.W. 1994: Scaling sun and shade photosynthetic acclimation of *Alocasia macrorrhiza* to whole-plant performance. I. Carbon balance and allocation at different daily photon flux densities. *Plant, Cell & Environment*, 17: 881–887.

Šprtová, M., Marek, M.V. 1999: Response of photosynthesis to radiation and intercellular CO_2 concentration in sun and shade shoots of Norway spruce. *Photosynthetica*, 37: 433–445.

Stockfors, J., Linder, S. 1998: The effect of nutrition on the seasonal course of needle respiration in Norway spruce stands. *Trees-Structure and Function*, 12: 130–138.

Troeng, E., Linder, S. 1982: Gas exchange in a 20-year-old stand of Scots pine. *Physiologia Plantarum*, 54(1): 7–14.

Urban, O., Janouš, D., Acosta, M., Czerný, R., Marková, I., Navrátil, M., Pavelka, M., Pokorný, R., Šprtová, M., Zhang, R., Špunda, V., Grace, J., Marek, M.V. 2007: Ecophysiological controls over the net ecosystem exchange of mountain spruce stand. Comparison of the response in direct vs. diffuse solar radiation. *Global Change Biology*, 13: 157–168.

Urban, O., Hrstka, M., Zitová, M., Holišová, P., Šprtová, M., Klem, K., Calfapietra, C., De Angelis, P., Marek, M.V. 2012a: Effect of season, needle age and elevated CO_2 concentration on photosynthesis and Rubisco acclimation in *Picea abies*. *Plant Physiology and Biochemistry*, 58: 135–141.

Urban, O., Klem, K., Ač, A., Havránková, K., Holišová, P., Navrátil, M., Zitová, M., Kozlová, K., Pokorný, R., Šprtová, M., Tomášková, I., Špunda, V., Grace, J. 2012 b: Impact of clear and cloudy sky conditions on the vertical distribution of photosynthetic CO_2 uptake within a spruce canopy. *Functional Ecology*, 26: 46–55.

Wallin, G., Linder, S., Lindroth, A., Räntfors, M., Flemberg, S., Grelle, A. 2001: Carbon dioxide exchange in Norway spruce at the shoot, tree and ecosystem scale. *Tree Physiology*, 21: 969–976.

Whitehead, D., Griffin, K.L., Turnbull, M.H., Tissue, D.T., Engel, V.C., Brown, K.J., Schuster W.S.F., Walcroft, A.S. 2004: Response of total night-time respiration to differences in total daily photosynthesis for leaves in a *Quercus rubra* L. canopy: implications for modelling canopy CO_2 exchange. *Global Change Biology*, 10: 925–938.