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Water relations in Norway spruce trees growing at ambient and elevated CO_2 concentrations

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Abstract

Water relations were studied in Norway spruce [*Picea abies* (L.) Karst.] trees grown at ambient (AC, 350 μmol mol^{-1}) and elevated (EC, 700 μmol mol^{-1}) CO_2 concentrations under temperate water stress. The results suggested that both crown position and variability in atmospheric CO_2 concentration are responsible for different patterns of crown water relations. Mean hourly sap flux density (F_{SA}) showed higher values in upper crown position in comparison with the whole crown in both AC and EC treatments. Mean soil-to-leaf hydraulic conductance (G_{Tsa}) was 1.4 times higher for the upper crown than that calculated across the whole crown for the trees in AC. However, G_{Tsa} did not vary significantly with crown position in EC trees, suggesting that elevated CO_2 may mitigate differences in hydraulic supply for different canopy layers. The trees in EC treatment exhibited significantly higher values of F_{SA} measured on the whole crown level and slightly higher soil water content compared to AC treatment, suggesting more economical use of soil water and therefore an advantage under water-limited conditions.

Additional key words: CO_2 enrichment, global change, *Picea abies* (L.) Karst., sap flux, shoot water potential, soil water limitation, whole-tree hydraulic conductance.

Introduction

Transpiration and photosynthesis are the two physiological processes by which plants sense directly, and respond to, the rising atmospheric partial pressure of CO_2. Understanding how these processes are affected by an increase in CO_2 concentration is therefore fundamental to any sound prediction of future response of both natural and agricultural communities to atmospheric change (Long 1999). Changes in these basic processes are responsible for shifts in both resource allocation and resource using efficiency in plants growing under elevated CO_2 concentration (Saxe *et al*. 1998, Johnson *et al*. 2002, Tognetti and Peñuelas 2003).

Various environmental factors like photosynthetic photon flux density (Bond *et al*. 1999), vapour pressure deficit (VPD) (Meinzer 2003, Sellin and Kupper 2004), and atmospheric CO_2 concentration (Jarvis *et al*. 1999) influence stomatal conductance (g_s) and therefore canopy gas exchange and water relations of trees (Whitehead 1998). Recent papers confirm that plant inner hydraulic constraints can be responsible for a decrease in g_s and net photosynthetic rate (P_N) in different woody species (Hubbard *et al*. 2001, Brodribb *et al*. 2002, Santiago *et al*. 2004). It has been documented that shaded canopy parts and/or lateral shoots of higher orders can be hydraulically more constrained than well-exposed leader shoots (Protz *et al*. 2000, Jerez *et al*. 2004, Sellin and Kupper 2005). Decline in branch growth rate leads to a decrease in the size of xylem conduits and, according to Poiseuille’s law,

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Abbreviations: C_{Soil} - soil water content; F_{SA} - xylem sap flux expressed by sapwood transverse area, g_s - stomatal conductance; G_T - soil-to-leaf hydraulic conductance; G_{Tla} - soil-to-leaf hydraulic conductance expressed by projected leaf area; G_{Tsa} - soil-to-leaf hydraulic conductance expressed by sapwood transverse area; P_N - net photosynthetic rate; RWC_W - relative water content of sapwood; VPD - vapour pressure deficit; Ψ_{Pd} - predawn shoot water potential; Ψ_S - soil water potential; Ψ_X - daily shoot water potential.

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sapwood hydraulic conductivity decreases too (Tyree and Ewers 1991, Protz *et al*. 2000). However, little information is available concerning foliage responses to changes in CO_2 concentration with respect to canopy positions (Saxe *et al*. 1998). Moreover, there is still no unequivocal conception how rise in atmospheric CO_2 concentration would influence patterns of tree's hydraulic architecture. Understanding how canopy position affects leaf water status and performance may improve mechanistic models of tree and forest growth and response to climate change.

Most commonly elevated CO_2 reduces g_s and transpiration of plants, and as a result, their drought tolerance will be enhanced (Saxe *et al*. 1998, Schäfer *et al*. 2002, Bunce 2004). However, there is also evidence that during drought, g_s may be even higher at elevated CO_2 concentrations (Heath and Kerstiens 1997). Some studies have indicated that elevated CO_2 can lead to conditions under which trees are able to maintain higher leaf water potentials (Schulte *et al*. 1998, Tognetti *et al*. 1999, 2000). In contrast, there is data indicating that under drought conditions water potential may be even lower in plants grown at elevated atmospheric CO_2 (Centritto *et al*. 1999, De Luis *et al*. 1999). Plant resistance to drought depends upon a whole range of factors affecting the balance between evaporative demand and water supply, including g_s, total leaf area, as well as the ability of stem and root system to supply water for leaves (Saxe *et al*. 1998). As forest trees are expected to save soil water through reduced transpiration under elevated CO_2 concentration, this may permit the forest to retain greater leaf area index (Schäfer *et al*. 2002). On the other hand, there is little knowledge about the effect of elevated CO_2 concentration on plant water relations under water-limited conditions (Wullschleger *et al*. 2002), and therefore, the net effect on water use of forest ecosystems is hardly predictable.

Our objective was to assess the variation in sap flux density (F_{SA}), soil-to-leaf hydraulic conductance (G_T) and shoot water potential (Ψ_X) depending on position within the crown of Norway spruce trees growing at ambient and elevated CO_2 concentrations under conditions of soil water deficit. We hypothesised that foliage of shaded canopy parts is hydraulically more constrained at ambient than at elevated CO_2 concentration. We also presumed that the trees growing at different CO_2 concentrations show distinct patterns of crown water relations in the case of drying soil.

Materials and methods

Study area and sample trees: The experimental study was carried out on the research site at Bílý Kříž (49º33'N, 18º32'E, 908 m a.s.l.) in the Beskydy Mountains, the Czech Republic, in August 2003. The climate in this area is cool (annual mean air temperature 4.9 ºC) and humid with high precipitation (annual mean 1100 mm). The average number of days with snow cover is 160. The soil type is classified as Ferric Podzol.

Sample trees of 14-year-old Norway spruce [*Picea abies* (L.) Karst.] were grown at ambient CO_2 (AC, 350 µmol(CO_2) mol^{-1}) and at elevated CO_2 concentrations (EC, ambient + 350 µmol(CO_2) mol^{-1}) in two separate glass domes with adjustable windows; for technical details see Urban *et al*. (2001). We studied canopy water relations in five sample trees growing at different CO_2 concentrations (Table 1). The upper canopy parts of the trees received direct sunlight during most of the day, whereas lower canopy layers were partially shaded.

Gas exchange measurements: Leaf gas exchange was measured with a *CIRAS-1* infrared gas analyser (*PP Systems*, Hertfordshire, UK) in the canopy of two trees at ambient CO_2. Four shoots at the basal and top thirds of the canopy were sampled for stomatal conductance (g_s) and net photosynthetic rate (P_N) at the time of daily maximum stomatal openness (from 09:00 to 10:00) in Julian days 223 - 226 and 228. An external light source (*LEFLD*, Brno, Czech Republic) was provided to obtain a light saturated response of g_s and P_N (PPFD over 1400 and 500 µmol m^{-2} s^{-1} for the upper and lower crown positions, respectively). Projected leaf area (m^2) of sample shoots was measured with a *LI-3000* portable leaf area meter (*Li-Cor*, Lincoln, USA).

Sap flux measurements: Sap flow was measured using the heat pulse velocity technique (Köstner *et al*. 1998). Five sample trees were equipped with two pairs of sap flux gauges (*SF 300*, *Greenspan Technology*, Warwick, Australia), ten sensor pairs altogether. The first pair was installed just under the live crown in sapwood at a depth of 20 and 60 % of the stem radius. The second sensor pair was installed about 1.2 m above the first sensor pair at the same relative depth in the sapwood. Sap flux rates [dm^3 h^{-1}] were recorded and stored at 15-min intervals with a data logger (*Greenspan Technology*) on Julian days 220 to 229. The heat pulse duration was adjusted to 1.8 s.

After sap flow measurements, increment cores were taken from stems of the sample trees (one per each tree) using an increment borer. Thereafter, the following tree characteristics were found: *1*) bark thickness, *2*) heartwood radius, *3*) cambium thickness, *4*) sapwood to heartwood proportion, *5*) sapwood area, and *6*) relative water content of sapwood (RWC_W). Sapwood and heartwood were separated using a xylem translucence method. To compare separate treatments, values of the sap flux were recalculated and expressed per unit of sapwood area (F_{SA}, mmol cm^{-2} s^{-1}) by applying the *SAPCAL* software (*Greenspan Technology*).

Soil-to-leaf hydraulic conductance: Soil-to-leaf hydraulic conductance (G_T) was calculated as $G_T = E/(\Psi_S - \Psi_X)$, where E was crown sap flux, and ($\Psi_S - \Psi_X$) was water potential difference between soil and shoot in MPa. It was expressed on sapwood transverse area (G_{Tsa}, mmol cm^{-2} s^{-1} MPa^{-1}) or on projected leaf area (G_{Tla}, mmol m^{-2} s^{-1} MPa^{-1}). In the latter case E was shoot transpiration rate. Assuming equilibrium between soil and leaf water status prior to dawn, shoot predawn water potential (Ψ_{Pd}) was used as a proxy of the soil water potential (Ψ_S) for G_T calculation. Both, Ψ_{Pd} and Ψ_X were measured by the balancing pressure technique with a Scholander-type pressure chamber in the upper and lower canopy positions of five sample trees on Julian days 220 - 221, 223 - 226 and 228 - 230. Ψ_{Pd} was measured (one or two sample shoots per crown position) before sunrise, whereas Ψ_X was measured (two to three sample shoots per crown position) at the interval of maximum stomatal openness.

Environmental characteristics: Soil water content (C_{Soil}) was measured with a portable instrument *TRIME-FM* (*IMKO Micromodultechnik*, Ettlingen, Germany) at three depths (0 - 15, 15 - 30 and 30 - 45 cm) in both treatments on Julian days 223 - 230. Relative air humidity and temperature were monitored with a *RHA 1* sensor (*Delta-T Devices*, Cambridge, UK) installed at a height of 2 m above the ground within stands. Vapour pressure deficit of the atmosphere (VPD) was calculated as the difference between the saturation and ambient vapour pressure, using relative humidity and air temperature data. Environmental characteristics were recorded at 30-s intervals, averaged, and stored once every 30 min with a *DL2e* data logger (*Delta-T Devices*).

Data analysis: We could not detect any significant time lag between F_{SA} and VPD, and the correlation between F_{SA} and current VPD was always closer than that with any shifted VPD. There was also no time lag in F_{SA} between the upper and whole crown within 15-min periods. Therefore, we assumed that the capacitance of small trunks and branches was negligible and stored water did not play a significant role in crown water relations in our sample trees. We compared F_{SA}, G_T and Ψ_X in different crown positions (upper crown versus the whole crown and/or the lower crown) at ambient and elevated CO_2 concentrations.

We applied repeated analysis of variance (repeated *ANOVA*) with the Tukey HSD-test to estimate the differences in F_{SA} depending on canopy position between the treatments. Repeated *ANOVA* was also used to test the differences in VPD between the treatments. To avoid violation of the assumptions of normality and homogeneity of variance, we analysed data collected in the daytime from 06:00 to 18:00. To verify differences in G_T, Ψ_X and Ψ_{Pd} with crown position, we pooled the data over all treatments and used simple analysis of variance. G_T was calculated from simultaneous measurements of F_{SA} (G_{Tsa}, sap flux measurements) or E (G_{Tla}, gas exchange measurements), and Ψ_{Pd} and Ψ_X at the time of daily maximum values of g_s. To analyse variation in g_s and P_N with canopy position in the AC, we used the Student's *t*-test.

Results

The sample trees in AC treatment showed 2.7 times higher mean light-saturated g_s and 3.0 times higher light-saturated P_N ($P < 0.001$ for both cases) in the upper-canopy branches compared to the lower canopy at the time of maximum stomatal openness (Table 2). Mean hourly F_{SA} was significantly higher in the upper crown position than in the whole crown in both treatments: $P < 0.001$ for AC and $P < 0.01$ for EC (Fig. 1). The trees of the AC showed generally lower values of F_{SA} than the trees of the EC ($P < 0.001$).

Mean G_{Tsa} in the AC was 1.4 times higher in the upper crown than in the whole crown ($P < 0.05$), while it did not vary significantly between the crown positions in the EC. G_{Tla} calculated from the data of transpiration rate and water potential drops in the trees of the AC showed 1.5 times higher mean G_{Tla} for the upper canopy compared to the lower-canopy foliage ($P < 0.01$). Mean G_{Tsa} of the whole crown tended to be higher in EC than in the AC, although the difference was not statistically significant (Table 2). Mean Ψ_X was significantly lower ($P < 0.001$) in the upper canopy position than in the lower canopy in AC treatments. The trees in the AC treatment showed significantly higher ($P < 0.02$; Table 2) shoot water potential than the trees at elevated CO_2 concentration.

Mean daily values of F_{SA} at the whole-crown level declined during the study period in both treatments

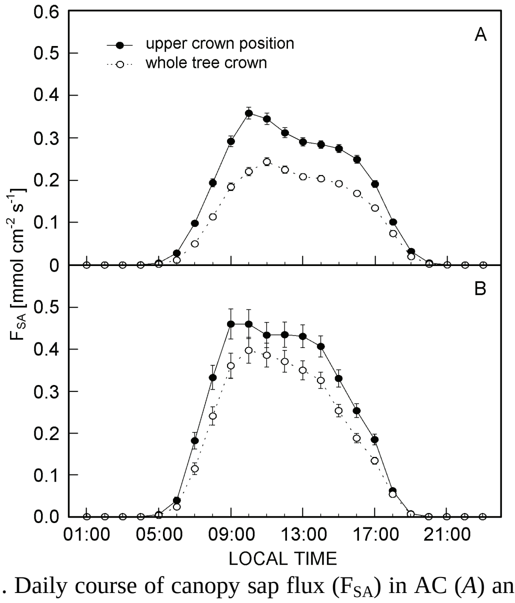

Fig. 1. Daily course of canopy sap flux (F_{SA}) in AC (*A*) and EC (*B*) treatments. The *error bars* denote ± SE.

(P < 0.001; Fig. 2), but mean G_{Tsa} did not vary significantly between days. The course of the mean daily F_{SA} followed the pattern of soil water content (C_{soil}), whereas C_{soil} was lower in the AC compared with the EC in the deepest and wettest soil layer (22.3 ± 0.3 and 26.2 ± 0.7 % in AC and EC, respectively). Mean values of Ψ_{Pd} did not vary significantly between the treatments, and when we pooled the data of both treatments, Ψ_{Pd} declined significantly in the course of the study period (P < 0.001). Although mean daily values of VPD differed slightly between AC and EC (1.56 and 1.44 kPa, respectively; P < 0.001), there were no changes in VPD during the study period.

At the end of our experiment RWC_W ranged from 28 to 46 %, while the mean of the five sample trees was 36% (Table 1), indicating a strong water deficit. Usually RWC_W of the spruce sapwood in the experimental site has been close to 60 % (Pokorný, unpublished data).

Table 1. Main parameters characterising the sample trees in AC and EC treatments measured at the end of the study period.

Characteristic	AC 1	AC 2	AC 3	EC 4	EC 5
Tree height [m]	4.8	4.1	4.5	4.2	5.0
Height of crown base [m]	0.3	0.4	0.3	0.2	0.6
Stem circumference at 1.3 m [cm]	18.0	18.0	19.5	22.5	22.0
Maximum crown radius [m]	1.3	1.1	1.2	1.1	0.9
Sapwood relative water content [%]	37.1	33.8	34.8	28.2	46.4

Table 2. Main physiological parameters characterising water relations and gas exchange in the upper and lower crown positions in AC and EC treatments [* - P < 0.05, ** - P < 0.001, n.s. - P > 0.05 (not significant), ^{1} - values for the whole crown].

Parameter	AC upper	AC lower	EC upper	EC lower
g_s [mmol m^{-2} s^{-1}]	80.60	30.30**	-	-
P_N [μmol m^{-2} s^{-1}]	6.70	2.20**	-	-
G_{Tsa} [mmol cm^{-2} s^{-1} MPa^{-1}]	0.37	0.27*^{1}	0.35	0.33n.s.^{1}
G_{Tla} [mmol m^{-2} s^{-1} MPa^{-1}]	1.16	0.78*	-	-
Ψ_X [-MPa]	1.14	0.91*	1.46	1.33n.s.

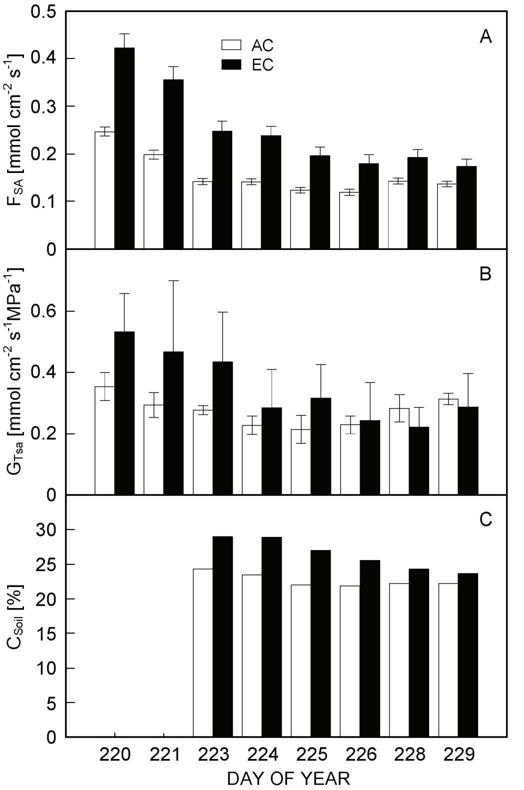

Fig. 2. *A* - mean daily sap flux (F_{SA}) of the whole crown; *B* - mean soil-to-leaf hydraulic conductance (G_{Tsa}) of the whole crown; *C* - soil water content (C_{Soil}) of the wettest soil layer in early morning. The *error bars* denote ± SE.

Discussion

Our experiments revealed significantly higher values of mean F_{SA} and G_{Tsa} for the upper crown position compared to the whole crown in the trees of the AC (Fig. 1, Table 2). Because the values calculated for the whole crown are based on fluxes including both the upper and lower canopy parts, we would expect the differences between the upper and lower crown position to be even higher. Recent studies in Norway spruce (Mayr *et al.* 2003, Sellin and Kupper 2004) have consistently shown that branches located at the crown base are hydraulically more constrained than upper-canopy branches. Moreover, it has been confirmed that g_s can be limited by the tree hydraulic conductance, being responsible for reduced P_N in canopies of tall trees (Hubbard *et al.* 2001, Brodribb *et al.* 2002). So, we suppose that the 1.5 times smaller G_{Tla} (P < 0.01) observed in lower-canopy branches in the trees of the AC might contribute to the decreased light saturated g_s and P_N (P < 0.001) at the bottom of the Norway spruce canopy. However, biochemical and anatomical changes in response to shade conditions are also known to decrease photosynthesis in connection with canopy position (Niinemets *et al.* 1998, Bond *et al.* 1999).

Trees growing at an elevated CO_2 concentration also showed some variability in F_{SA}, but there was no significant difference in G_{Tsa} within the canopy (Fig. 1, Table 2). Marek *et al.* (2001, 2002) have indicated that elevated atmospheric CO_2 enables the light limitation of photosynthesis to be mitigated in shade foliage of Norway spruce. It is likely that a compensatory effect could result from improved canopy water relations as well, because of the existing linkage between photosynthesis, growth and hydraulics (Meinzer 2003). We suppose that water status of shaded canopy layers could be improved at elevated CO_2 concentration through increased tracheid size or sapwood area of the branches. Although several authors (Ceulemans *et al.* 2002, Atwell *et al.* 2003) have studied xylem conduit diameters and hydraulic efficiency in different tree species at elevated CO_2, there is no explicit conception of how these parameters change with canopy position. Improved hydraulic efficiency in shaded canopy layers at elevated CO_2 concentration could cause changes in crown architecture of trees (Pritchard *et al.* 1999) and therefore influence functioning of the whole forest stand.

In the present study, trees growing at elevated CO_2 concentration exhibited significantly higher F_{SA} compared with the trees at ambient CO_2 concentration. In contrast, some studies have indicated that both leaf conductance and xylem sap flux declined at elevated CO_2 concentration (Tognetti *et al.* 1999, Wullschleger and Norby 2001, Herrick *et al.* 2004). Tognetti *et al.* (1998) showed that leaf conductance in *Quercus ilex* was higher in control trees compared to the trees growing near a natural CO_2 source at low VPD, but the difference was small at the peak of mid-summer water stress. Centritto *et al.* (1999) observed that also seedlings of *Prunus avium* showed little or no reduction in g_s in response to elevated CO_2 under drought conditions. Moreover, there is evidence that during drought stomatal conductance in some species may be even higher at elevated CO_2 (Heath and Kerstiens 1997), and therefore, transpiration or sap flux is expected to increase as well. We suppose that higher F_{SA} in the trees growing at elevated CO_2 compared with trees in the AC was related to higher soil water content in deeper soil layers in the EC (Fig. 2). The higher C_{Soil} in the dome with an elevated CO_2 concentration already formed before we started our measurements. This could have resulted from the lower transpiration rate of the trees growing at elevated CO_2, which is very common for plants under normal conditions without water limitation (Medlyn *et al.* 2001, Bunce 2004). As stomatal conductance is highly correlated with soil water status under drought conditions (Centritto *et al.* 1999) and VPD did not vary significantly during our study period, we suppose that C_{Soil} was primarily responsible for the changes in whole-canopy water relations. Also in *Populus deltoides*, changes in VPD had less effect on transpiration than changes in C_{Soil} for trees grown at both ambient and elevated CO_2 concentrations under soil water limitation (Engel *et al.* 2004). In our study, the trees of the EC probably did not deplete soil water storage as fast as the trees in the AC. Therefore, trees growing at elevated CO_2 conditions would have an advantage over the trees at ambient CO_2 because of their more economical water use under water-limited conditions. However, this seems not to be a general rule, because different species do not respond similarly to water stress under elevated atmospheric CO_2. For example, Johnson *et al.* (2002) indicated that elevated CO_2 concentration did mitigate the effect of water stress in willow, but not in poplar trees. Schäfer *et al.* (2002) studied the effect of free air CO_2 enrichment on sap flux and soil water saving in *Pinus taeda* L. stand. They found that *P. taeda* trees transpired less per unit leaf area only when soil drought was severe and therefore water saving in the stand was undetectable.

The whole-crown G_{Tsa} tended to be higher for the trees in the EC than in the AC, although statistical difference was not found. However, there was an unequivocal difference in Ψ_X between the two treatments: Ψ_X at elevated CO_2 concentration was significantly lower for both crown positions. In contrast to our results, some studies (Schulte *et al.* 1998, Tognetti *et al.* 1999) have indicated that elevated CO_2 concentration leads to an increase in leaf water potential in different species due to decreased transpiration rate. In the present study, the mean F_{SA} was higher for trees growing at an elevated CO_2 concentration, which seems to be a reason for the decreased Ψ_X as well.

To summarise, our results suggest that changes in atmospheric CO_2 concentration are responsible for different patterns of crown water relations and, on the other hand, plant responses to elevated CO_2 depend on soil water availability. Soil water content was a primary factor determining the variation in xylem sap flux and shoot water potential between the Norway spruce trees growing at ambient versus elevated CO_2 concentration. Trees grown at elevated CO_2 concentration showed higher G_{Tsa} at the whole-crown level than trees at ambient CO_2 concentration, suggesting that elevated CO_2 could improve water supply for foliage located in lower canopy layers under shade conditions. Trees growing at elevated CO_2 concentration would have an advantage compared to the trees at ambient CO_2 concentration under water-limited conditions because of their more economical water use. This advantage, however, will probably be balanced by the effect of increasing leaf area index on the stand scale at rising atmospheric CO_2 concentration in the future.

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