Monika Vejpustková, Annika Thomalla, Tomáš Čihák,
Bohumír Lomský, Hardy Pfanz

Growth of *Populus tremula* on CO_2-enriched soil at a natural mofette site

Abstract: The main objective of the study was to evaluate inter-annual ring-width variation and cumulative growth of aspen (*Populus tremula* L.) trees growing on the spots of different soil CO_2 concentration at natural mofette site. We hypothesized that growth rate of trees is affected by CO_2 concentration within their rooting zone. The study site was situated in the flood plain of Plesná stream near Hartoušov (Western Bohemia). Trees growing in a pure aspen stand were selected according to the CO_2-gas regime within their rooting zone. Five high [CO_2] trees (10–25% CO_2 in the soil) and five low [CO_2] trees (up to 3% CO_2 in the soil) were sampled. Stem growth analysis of each trunk was carried out to study growth pattern in detail. High and low [CO_2] trees significantly differed in a growth rate. At the age of 25 years, the basal area of high [CO_2] trees exceeded low [CO_2] trees by 39 %. The positive effect of CO_2 on annual increment was pronounced particularly in the years with optimal growing conditions. Results suggest that trees can be fertilized not only by elevated atmospheric CO_2 but also when fed with CO_2 via the roots.

Addresses: M. Vejpustková, Forestry and Game Management Research Institute, Strnady 136, 252 02 Jíloviště, Czech Republic, e-mail: vejpustkova@vulhm.cz
A. Thomalla, H. Pfanz – University of Duisburg-Essen, Chair of Applied Botany and Volcano Biology, D-45117 Essen, Germany
T. Čihák, B. Lomský – Forestry and Game Management Research Institute, Strnady 136, 252 02 Jíloviště, Czech Republic

Introduction

The increase in atmospheric CO_2 from pre-industrial concentrations of 270–280 μmolmol^{-1} to the present level of 400 μmolmol^{-1} raises many questions concerning its effect on terrestrial plants and their ecosystems. Since trees play an important role in the global carbon cycle and can significantly affect atmospheric concentration of CO_2, their response to elevated levels of CO_2 needs to be known.

The effect of elevated CO_2 on trees may be manifested in variations of the growth rate or aboveground biomass accumulation (e.g. Dawes et al., 2011; Druart et al., 2006; Vodnik et al., 2005), enhanced root growth (Hättenschwiler & Körner 1998; Crookshanks et al., 1998), changes in wood-cell anatomy (Handa et al., 2006; Druart et al., 2006; Hättenschwiler et al., 1996), leaf-litter production and leaf chemistry (Asshoff & Hättenschwiler, 2006). All these changes have a background in the underlying

physiological processes (reviewed by Ainsworth & Long, 2005; Ceulemans & Mousseau, 1994; Macek et al., 2005; Pfanz et al., 2007; Raschi et al., 1997).

Different approaches were employed to study the growth reactions of trees to different atmosphere CO_2 enrichments: experiments under a controlled-environment (e.g. Druart et al., 2006; Bruhn et al., 2000; Tjoelker et al., 1998), *in situ* experiments using free-air CO_2 enrichment – FACE (Dawes et al., 2011; Eguchi et al., 2005; Pepin & Körner, 2002; Norby et al., 2001), and *in situ* studies at naturally CO_2-enriched sites (Tognetti et al., 2000; Hättenschwiler et al., 1997; Paoletti et al., 2005). Working in mofette areas enables the study of long-term tree-growth response under authentic natural conditions. Certain limitations exist, however; the historical CO_2 concentrations around degassing vents are not known, the gas flow can vary over time in relation to repeated earthquakes (Paoletti et al., 2005; Marzaioli et al., 2005), and the history of the trees studied (their origin and competitive status) and the potential effect of human activities in the area have to be considered (Saurer et al., 2003).

Tognetti et al. (2000) and Hättenschwiler et al. (1997) compared the growth of *Quercus ilex* at a CO_2-enriched site and at a control site in Tuscany (Italy) producing contradictory results. It became evident that tree selection is crucial and significant differences in growth rate occurred within the same site.

In order to further corroborate the results, we studied the growth variability of aspen trees (*Populus tremula* L.) at a naturally CO_2-degassing mofette site located in the flood plain of the Plesná stream close to Hartoušov in Western Bohemia. The main objective of this study was to evaluate the long-term inter-annual ring-width variation and cumulative growth of aspen trees growing on the spots of different soil CO_2 concentration at a natural mofette site. We hypothe-sized that the growth rate of trees is affected by CO_2 concentration within their rooting zone.

Materials and Methods

The study site was situated in the flood plain of the Plesná stream, between Milhostov and Hartoušov, in the Cheb (Eger) Basin in Western Bohemia. The basic characteristics of the site are as follows: altitude 450 m a.s.l., pseudogley soil (Kozák, 2010), a moderately warm climate (with a mean annual temperature of 7.2°C and a mean annual precipitation of 560 mm; cf Rennert et al., 2011). Many natural springs of mineral water and of CO_2 gas (mofettes) are located along the stream. A mofette line running between Hartoušov and Bublák is connected with the Počátky-Plesná Zone (Bankwitz et al., 2003). The mofette gases are composed of carbon dioxide (99 %) and helium isotopes (Bräuer et al., 2004).

In the past the area was used mainly for pasturing. Several maps of CO_2-endangered pastures are included in the local historical chronicles. The land use changed dramatically after the Second World War and once again at the end of the nineteen-eighties. Most of the land was abandoned and trees and shrubs invaded the former grasslands.

We studied a pure aspen (*Populus tremula* L.) stand (30m × 34m) with diffuse CO_2 degassing (Fig. 1). The stand was established by natural regeneration (probably through a combination of generative and vegetative propagation). Two cohorts of trees were distinguished: trees of main canopy layer (126 trees) and young trees up to 5 m high (not counted). The density of main canopy trees was 1235 trees.ha^{-1}. The mean distance between trees was about 1.6 m. Understory vegetation consists mainly of young aspen trees in shrub layer and grasses (*Agrostis sp., Carex sp., Deschampsia sp., Nardus stricta*) in herb layer.
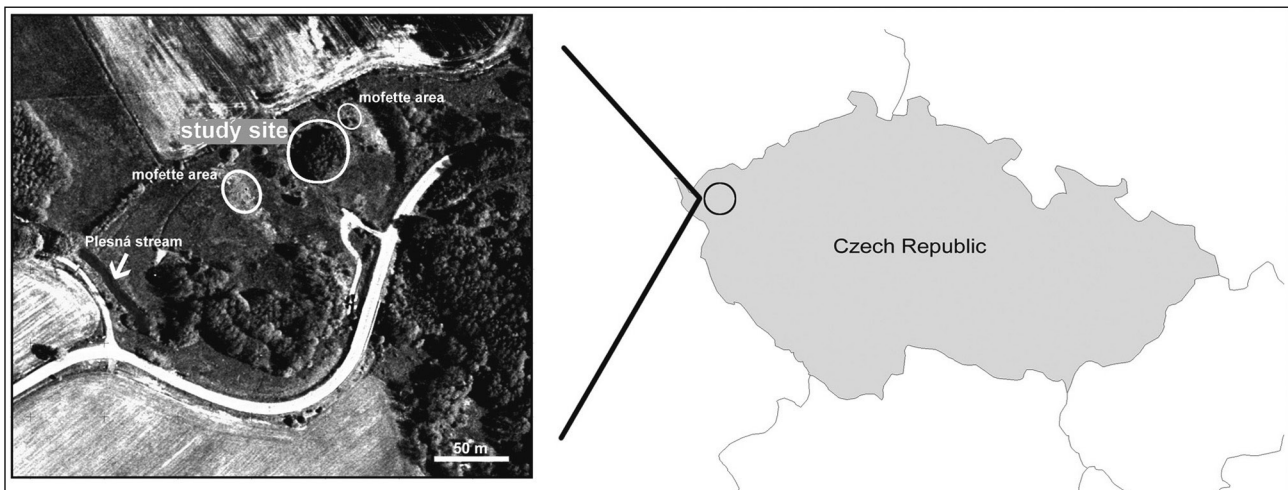

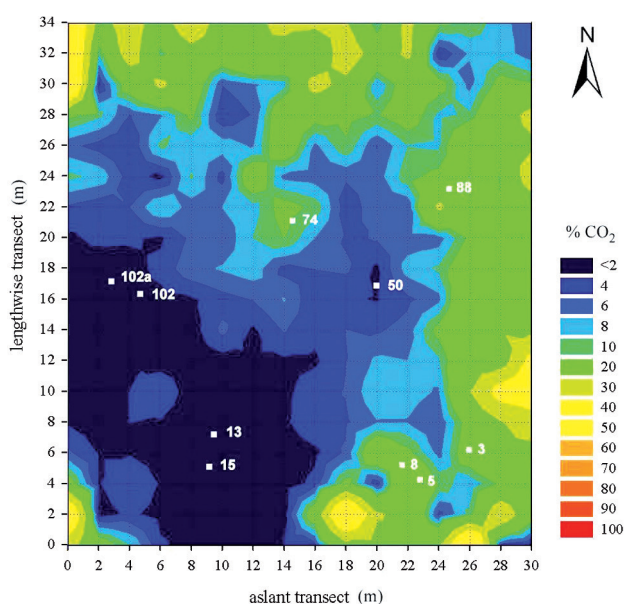Fig. 1. Study site within the Plesná Valley of the Western Czech Republic

Fig. 2. Spatial pattern of CO$_2$-soil concentration (%) within the study site in 2011. CO$_2$-soil concentration measured at a depth of 60 cm at three points around each of 126 canopy trees was used for extrapolation. White dots depict the location of sample trees

Measurements of the CO$_2$-soil concentration (at a depth of 40 cm and 60 cm) were carried out at three points around each canopy tree in the stand. Measurements were performed by drilling a hole to a required depth using an auger and measuring the CO$_2$ concentration within the hole by inserting a Teflon tubing connected to a portable infrared gas analyzer (GA 2000; Ansyco, Germany). Measurements repeated in 2008, 2010 and 2011 proved that although the CO$_2$- soil concentrations fluctuated over time, the spatial pattern of high-CO$_2$ and low-CO$_2$ spots remained the same. On the other hand measurements of atmospheric CO$_2$ concentrations were highly variable in time and space. Several measurements of atmospheric CO$_2$ concentrations were done

Table 1. Description of the sampled aspen trees growing at the Hartoušov mofette site

CO$_2$ level	Tree number	[CO$_2$] (%) in 40 cm depth	Absolute age of tree	DBH[a] (cm)	Tree height (m)
High [CO$_2$]	3	9.47	22	11.4	13.5
	5	16.37	21	13.9	12.9
	8	21.03	22	11.0	11.9
	74	9.77	29	14.5	14.1
	88	12.90	27	14.6	14.6
Low [CO$_2$]	13	0.90	31	14.2	13.6
	15	1.00	30	16.0	14.4
	50	3.00	30	11.1	13.2
	102	0.83	28	12.2	12.5
	102a	0.57	31	11.2	12.0

[a] DBH – diameter at breast height.

at different times and heights. The portable CO$_2$ analyzer as a well as a Licor gas exchange cuvette were used. Only at ground level CO$_2$ concentrations were enhanced to a certain extent. On calm days, an increase of up to 600 ppm was seen up to 50 cm above ground. At 100 cm, CO$_2$ was always around normal atmospheric values of 400 ppm. On windy days even at ground level CO$_2$ was within normal atmospheric level.

Ten trees were selected for stem growth analysis according to the soil-CO$_2$ concentration: five high-CO$_2$ concentration trees (10 – 25% CO$_2$ in the soil = **HC trees**) and five low-CO$_2$ concentration trees (less than 3% CO$_2$ in the soil = **LC trees**) (Fig. 2). Dominant or co-dominant trees were chosen (Table 1). Trees growing at the edge of the stand were avoided.

Trees were felled and total length of each stem was measured. Stem was divided in the sections and discs were cut from the end of each section. The length of the first section was 1.4 m measured from the stem base, the length of other sections was 1.0 m. An extra disc was taken also from the stump to determine the exact age of the tree. After drying and sanding, the radial increments were measured on each stem disc along four radii. Ring-width measurements were done using the VIAS TimeTable measuring stage (accuracy 0.01 mm). The individual ring-width series were cross-dated and the dating was verified statistically using the COFECHA programme (Holmes, 1983).

Trees were divided according to the soil-CO$_2$ concentration (HCT, LCT). The tree-ring series of each group were aggregated into the mean ring-width chronology. Radial growth at individual cross-sections was studied separately.

The negative and positive pointer years (Schweingruber et al., 1990) were identified in the ring-width chronologies of both tree groups to examine how the growth is affected by CO$_2$ in the years of adverse conditions and vice versa in favourable years. A "pointer year" occurred when an event year was identified for at least 50 % of the trees within the tree group. An "event year" represented a year of an abrupt growth change (increase or decrease) in the ring width of at least 40% above or below the average ring width over the previous four years.

For each tree the cumulative basal area growth was expressed at the same cambial age.

Ring-width series were used to determine the height growth of the individual trees: the difference between the number of tree rings at the stump and at the given cross-section showed the number of years of growth up to the given height. Height curve of HC and LC trees was approximated by the Korf growth function (Korf, 1939) – eq. 1. Calculation was done in module for nonlinear regression of statistical software QC Expert.

$$y = ae^{-bt^{-c}} \qquad\qquad (1)$$

Where: y – tree height, t – tree age, a, b, c – regression coefficients.

The two-sided t-test was used to test differences between HC and LC trees. The growth variables to be tested included: (1) the annual ring widths in individual calendar years; (2) the mean ring widths during the entire lifespan of the trees; (3) the cumulative basal area at the same cambial age; (4) the model tree-height at the same age. Statistical analyses were carried-out using the QC Expert statistical programme.

The relationship between aspen growth and climate was examined using monthly temperature and precipitation data from 1987 to 2010 from the nearest meteorological station Cheb (10 km from Hartoušov). For dendroclimatic studies the radial growth at 1.4 m above the ground was used. The ring-width series were standardised to eliminate the age trend using the ARSTAN programme (Cook & Holmes, 1996). The trend was approximated by the Hugershoff function (Warren, 1980) which reflects well exponential decrease of annual increments in young trees. The remaining autocorrelation was removed by autoregressive modelling. The resulting index series were aggregated by calculating their mean values in terms of the HCT and LCT chronologies. The climate-growth relationship was computed for the period 1987–2010 using simple correlation analysis. The series of ring-width indices of LC and HC trees were correlated gradually with the mean monthly temperatures and precipitation from May of the previous year to September of the current year, when the specific ring was formed (i.e. 17 months in total). Pearson correlation was used.

Results

Radial growth

Annual ring widths were measured and successfully cross-dated. Some false rings were detected but no missing rings. Ring widths of HC trees measured at the cross section 1.4 m above ground exhibited greater variability and average ring width was 23 % larger than that of LC trees. Radial growth of HC trees was also more responsive to exogenous factors as indicated by the higher values of mean sensitivity (Table 2).

Table 2. Summary statistics for tree-ring series of HC and LC aspen trees from the mofette location. Cross sections were taken 1.4m above ground

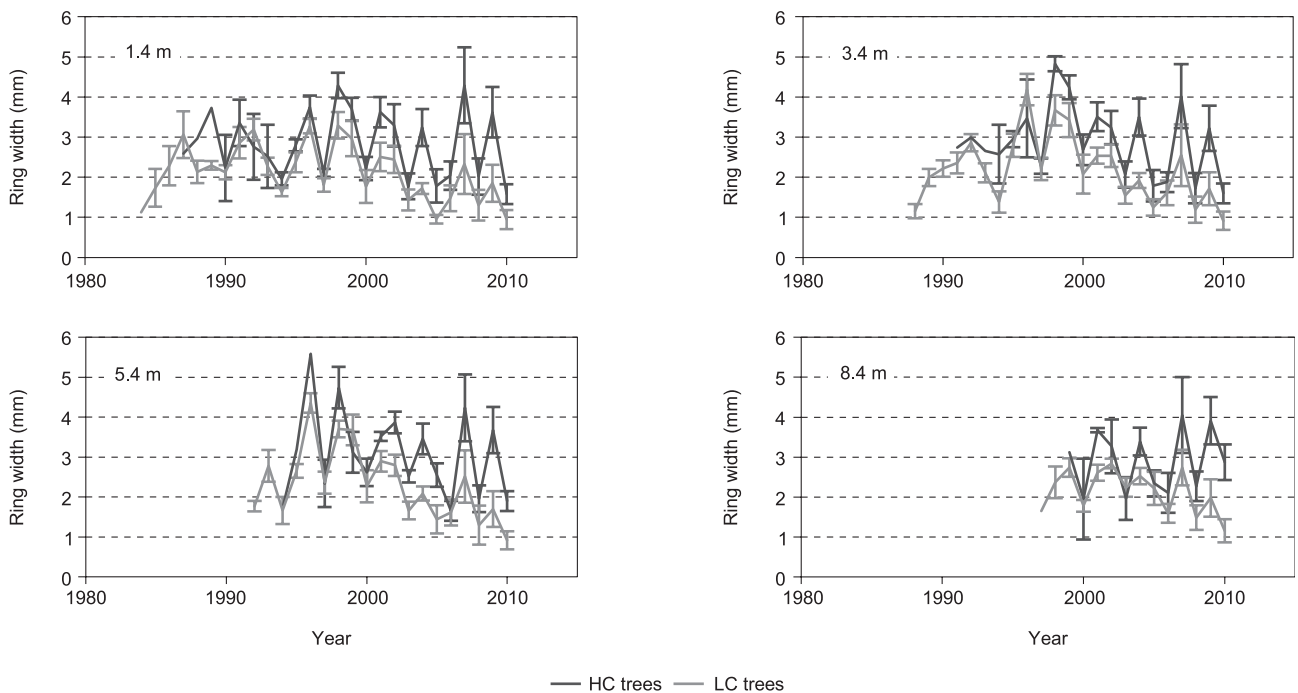| Parameter	LC trees	HC trees
Number of trees	5	5
Tree age	28–31	21–29
Number of radii	20	20
Master chronology	1983–2010	1986–2010
Proportion of missing rings (%)	0	0
Average ring width (mm)	2.13	2.79
Standard deviation	1.066	1.336
Mean sensitivity	0.425	0.521
Correlation with master chronology (r)	0.603	0.670

Fig. 3. Mean ring-width chronologies of HC and LC trees derived from cross sections in different stem heights (1.4 m, 3.4 m, 5.4 m and 8.4 m above ground). Vertical bars indicate +/–SE

Table 3. Mean radial increment of HC and LC aspen trees in different stem heights

Stem height (m)		1.4	2.4	3.4	4.4	5.4	6.4	7.4	8.4	9.4	10.4
Period		1990–2010	1991–2010	1993–2010	1995–2010	1997–2010	1998–2010	1999–2010	2000–2010	2003–2010	2005–2010
Mean radial increment (mm)	HCT	2.81	2.88	2.90	3.07	3.01	3.07	3.00	2.89	2.67	2.31
	LCT	2.12	2.13	2.20	2.30	2.21	2.18	2.16	2.11	2.22	1.84
Difference (mm)		0.69*	0.75*	0.70*	0.77*	0.80*	0.88*	0.84*	0.78*	0.45	0.48*

* statistically significant difference ($\alpha=0.05$).

There was a good agreement between HC and LC trees in regard to their inter-annual ring-width variation which was confirmed by a sign test (Gleichläufigkeit): GLK>90% (i. e. the trend of year-to-year changes of ring widths which were parallel in more than 90% of the intervals). Growth pattern of the cross sections in different stem heights was very similar (Fig. 3). Mean radial increment of HC trees was significantly greater than that of LC trees in all cross-sections investigated (Table 3).

When the annual increments were examined year by year, significant differences between HC and LC trees were observed for the years 1998, 2004 and 2009. In average, the ring widths of HC trees were 1.43 mm greater than those of LC trees. These were the years with the most favourable growth conditions. They were determined as positive pointer years by single pointer year analyses. Altogether four positive pointer years were identified: 1998, 2004, 2007 and 2009. While the pointer years 1998 and 2007 were common to both tree groups, 2004 and 2009 pointers were identified for HC trees only. Negative pointer years (2000, 2003, 2005 and 2010) were common to both tree groups. In these years the differences between the HC and LC trees were insignificant.

Cumulative basal area growth

The long-term growth rate was described in terms of the cumulative stem basal area growth. Because the trees differed in their absolute age, basal area growth in the same cambial age was expressed. Until the trees had reached the age of 10 years the basal areas of trees were comparable, regardless of the soil-CO_2 concentration. Thereafter their growth started to diverge and the mean basal area of the HC trees clearly increased (Fig. 4). At the age of 15 years the difference between the tree groups became statistically significant. The accelerated growth rate of HC trees persisted for 15 years. At the age of 25 years the basal area of HC trees exceeded that of LC trees by 39%.

Height growth

All aspen trees showed an intensive height growth. For all trees it took roughly 3–4 years to grow up to the breast height. Thereafter height growth of HC trees was stimulated and the growth rates of the tree groups started to diverge (Fig. 5). During the age interval from 15 to 25 years a significant difference occurred in the cumulative height growth; sub-
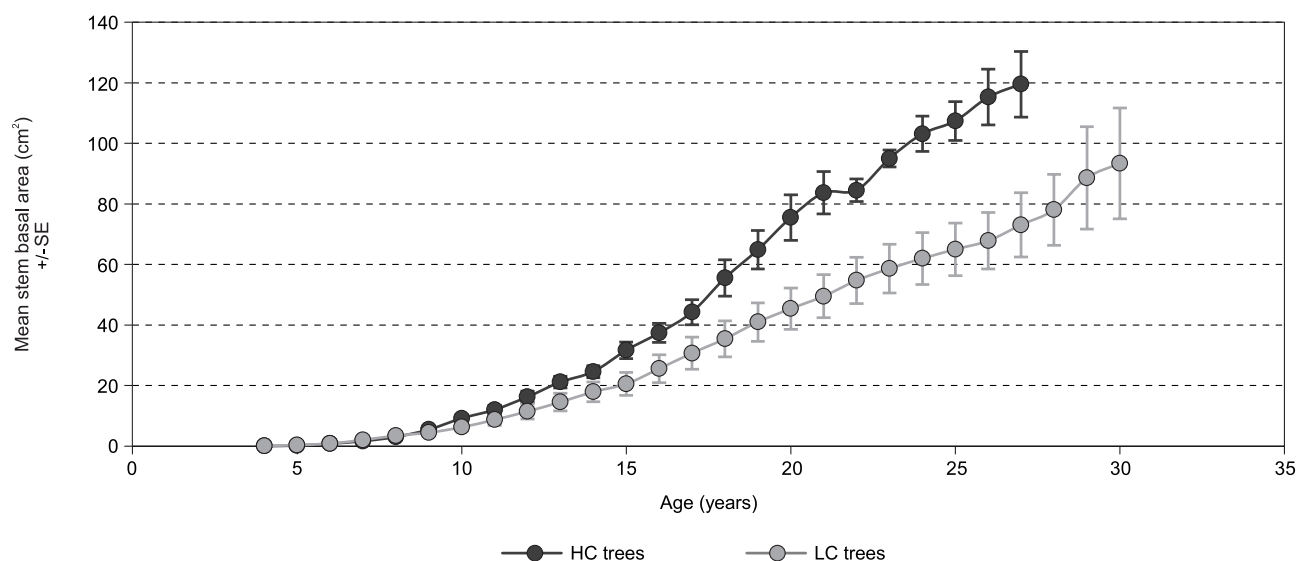

Fig. 4. Mean cumulative stem basal area of aspen HC and LC trees from the Hartoušov mofette location. Vertical bars indicate +/–SE
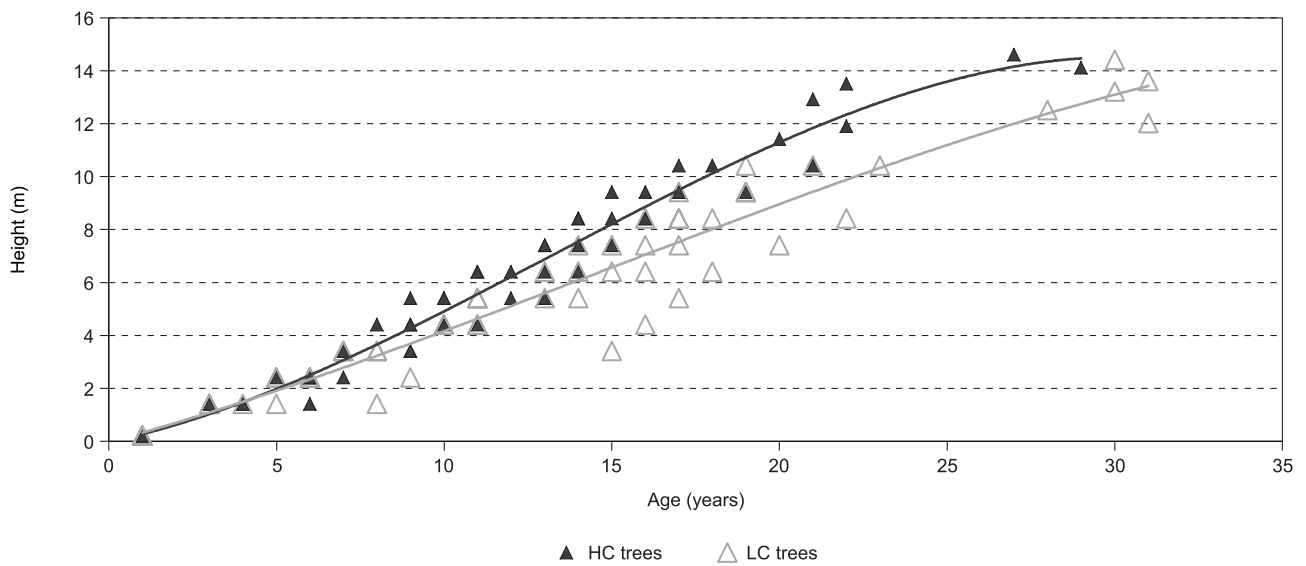
Fig. 5. Cumulative height growth of HC and LC aspen trees from the Hartoušov mofette location. The triangles represent measured values; the lines indicate height growth approximated by Korf's growth function

sequently the curves narrowed again. The average height increment during the entire lifespan was 56 cm per year for HC trees and 44 cm per year for LC trees.

Climate-growth relationship

Correlation analysis revealed that there are no significant differences between the HC and LC trees in regard to their relationship to climatic factors. Therefore we built a common chronology that has been correlated with climatic variables. The main drivers of aspen growth in Hartoušov are winter precipitation and summer temperatures. Both factors affect growth negatively. On the contrary, growth of aspen is stimulated by warm April and wet June of current year (Fig. 6). Correlation coefficients between tree growth and monthly variables were not statistically significant. However, significant values ($\alpha = 0.05$) was reached for the sum of winter precipitation (November – January; R= –0.51).

Discussion

As the results presented in this paper originate from a geologically active mofette site, certain limitations exist in regard to the interpretation. Historical CO_2 concentrations around degassing vents are mostly unknown and CO_2 gas flow can vary over time (Vodnik et al., 2006). However, 15 years of measuring at the nearby Bublák mofette (at a distance of 1 km from the study site) revealed a steady increase in the geogenic CO_2-emission (Koch et al., 2008).
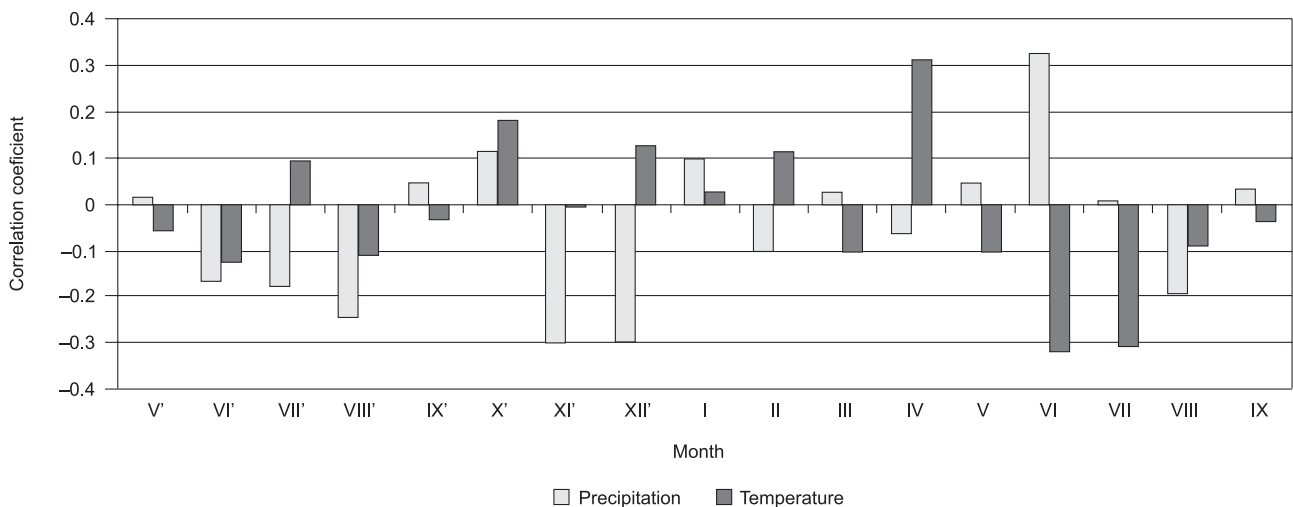

Fig. 6. Results of climate-growth relationship for common chronology of HC and LC trees from Hartoušov. Rsig=0.4

For the whole tree sampling strategy, number of sampled trees was limited to 10 due to the small size of the stand and to parallel research activities. Disc sampling and the detailed measurements of at least four radii per disc ensured the reliable identification of the tree rings within the cross-sections taken at different stem heights. The sampling of stump discs enabled the precise determination of tree age, a feature that is crucial when the cumulative growth of trees needs to be compared. Stem analysis also enabled the assessment of the absolute height growth of trees, one of the best indicators of site quality. The height growth of dominant and co-dominant trees is less influenced by competition within the stand in comparison to the radial growth (Spiecker, 1999).

High [CO$_2$] trees and low [CO$_2$] trees were located within the same stand at a distance between 5 and 20 m. Therefore the abiotic parameters within the stand (microclimate, soil type) were considered to be quite similar. The differences observed in growth rate can be therefore attributed to the different soil CO$_2$ regime in the rooting horizon of trees.

The inter-annual ring-width variation was independent of the CO$_2$ concentration, which is consistent with the findings of Hättenschwiler et al. (1997) and Tognetti et al. (2000). Analysis of the climate-growth relationship revealed, that growth of both the HC and the LC trees in Hartoušov is driven by the same climatic factors. Strong negative relationship to the winter precipitation was found. We assume an indirect effect on aspen growth through fluctuation of groundwater level. The shallow groundwater is typical for the flood plain of the Plesná stream and water table further elevates during the spring time after thawing snow. A persistent high water table in the beginning of growing season may restrict tree growth as for aspen the optimum groundwater level is around 1 m (Čížek, 2007).

Ring widths of HC trees were larger in all the cross sections than those of LC trees. Interestingly, growth stimulation of the HC trees was much more pronounced during the years with favourable climatic conditions (positive pointer years). According to the theory of Sprengel and Liebig, the reaction of plants clearly follows the law of the minimum factor; therefore a surplus of CO$_2$ will feed photosynthesis and growth to a much greater extent if all the other factors are optimal (Mitscherlich, 1909). In contrast, in years with adverse climatic conditions, additional fertilisation with CO$_2$ will not largely enhance photosynthesis. Evidently, there was no significant difference between HC and LC trees from Hartoušov during the years of low radial increment. Also Tognetti et al. (2000) found for several tree species in coppiced forest stands, that negative pointer years (triggered by drought) rarely differed between the CO$_2$-enriched site and the control. Dawes et al.

(2011) came to a similar conclusion when investigating the growth of larch at a CO$_2$-enriched site established within the framework of FACE.

In contrast to the FACE experiments or to other high-level CO$_2$ treatments, the additional CO$_2$ in mofettes is not supplied via the atmosphere but via soil emissions (Pfanz, 2008). Geogenic CO$_2$ diffuses through the soil and mostly degasses into the adjacent atmosphere where it is largely diluted. Therefore CO$_2$ concentrations within the canopy were not enhanced and so a positive fertilisation effect cannot be expected. On the other hand, CO$_2$ diffuses from the high CO$_2$ soil into the intercellular system of the living tree roots. Here there are two potential transport pathways: (i) the surplus CO$_2$ may diffuse as a dry gas throughout the entire intercellular system of the tree, following the concentration gradients and finally reaching the leaves; diffusive transport will follow Fick's law of diffusion and this will be extremely slow; (ii) the second possibility is the physico-chemical dilution of the geogenic CO$_2$ within the xylem water and the CO$_2$-enriched xylem water then feeding leaf photosynthesis by apoplastic transport (Pfanz et al., 2002, Pfanz, 2008; Teskey et al., 2008). Yet, the ratio between the photosynthetical usage of geogenic and atmospheric CO$_2$ is completely unknown. CO$_2$ from soil, root or stem respiration may diffuse out through the bark, but it is also transported within the xylem and to some extent consumed by photosynthesis in the leaves (Levy et al., 1999; Teskey & McGuire, 2002; Bloemen et al., 2013).

Interestingly, up to the age of 10 years the growth rate of both tree groups was similar. Growth acceleration of HC trees from Hartoušov started at the age of 15 years. While the acceleration of the basal area growth persisted, modelled height growth slightly declined at the age of 25 years. Our findings cannot easily be compared with the results of experiments in controlled-environment chambers which commonly, from the very beginning, show large positive effect of CO$_2$ on tree growth (e.g. Druart et al., 2006; Bruhn et al., 2000; Tjoelker et al., 1998). In these experiments the potted tree seedlings grew under optimal fertilized condition and were furthermore not affected by competition. The aspen stand at Hartoušov was established by natural regeneration (probably through a combination of generative and vegetative propagation). The diameter at breast height of ten years old aspen trees was ca. 3 cm and their total height was about 4.5 m regardless of the soil CO$_2$ concentration. We therefore assume a rather high-density stand during this first stage of forest formation. Strong interspecies competition could be the probable reason for the observed lack of growth response of high [CO$_2$] trees at this very young age. McDonald et al. (2002) were able to demonstrate, studying trembling aspen (*Populus tremuloides*

Michx.) at the FACE facility, strong influence of the competitive status on growth response to elevated [CO_2].

The results of FACE experiments using free-air CO_2 enrichment are not unambiguous. Mature trees did not respond at all to elevated CO_2 (Körner et al., 2005; Rasmussen et al., 2002) or trees exhibited an increased growth only during the first year of the study which indicates that large trees that are no longer in an exponential growth phase retain the capacity to respond to elevated CO_2 (Norby et al., 2001). At the mofette site in Hartoušov, the age of aspen trees ranged from 21 to 31 years. As a fast-growing tree species, aspen reaches its maturity approximately at the age of 60 years. This means that studied trees were within their most intensive growth phase and they had potential to profit from an elevated CO_2 concentration.

Conclusion

The presented study brings new findings about long-term growth response of trees to increased soil CO_2 concentration. After a 10–15 years lag phase, where no clear response to the enhanced soil [CO_2] could be observed, growth was stimulated. At the age of 25 years the basal area of HC trees exceeded that of LC trees by 39%. Yet, inter-annual ring-width variation was independent on the CO_2 concentration. Climate-growth analysis revealed that growth of both HC and LC trees is driven by the same climatic factors. In years with sub-optimal conditions, a surplus of CO_2 didn't cause any significant effect, while in favourable years there was a substantial growth stimulation of HC trees. These data suggest that growth rate of trees can be enhanced by elevated CO_2 concentration within their rooting zone.

Acknowledgement

References

Ainsworth EA & Long SP (2005) What have we learned from 15 years of free-air CO_2 enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy properties and plant production to rising CO_2. New Phytologist 165: 351–372.

Asshoff R & Hättenschwiler S (2006) Changes in needle quality and larch bud moth performance in response to CO_2 enrichment and defoliation of treeline larches. Ecological Entomology 31: 84–90.

Bankwitz P, Schneider G, Kämpf H & Bankwitz E (2003) Structural characteristics of epicentral areas in Central Europe: study case Cheb Basin (Czech Republic). Journal of Geodynamics 35: 5–32.

Bloemen J, McGuire MA, Aubrey DP, Teskey RO & Steppe K (2013) Transport of root-respired CO_2 via the transpiration stream affects aboveground carbon assimilation and CO_2 efflux in trees. New Phytologist 197: 555–565.

Bräuer K, Kämpf H, Niedermann S, Strauch G & Weise SM (2004) Evidence for a nitrogen flux directly derived from the European subcontinental mantle in the Western Eger Rift, central Europe. Geochimica et Cosmochimica Acta 68: 4935–4947.

Bruhn D, Leverenz JW & Saxe H (2000) Effects of tree size and temperature on relative growth rate and its components of *Fagus sylvatica* seedlings exposed to two partial pressures of atmospheric [CO_2]. New Phytologist 146: 415–425.

Ceulemans R & Mousseau M (1994) Tansley Review No. 71 Effects of elevated atmospheric CO_2 on woody plants. New Phytologist 127: 425–446.

Cook ER & Holmes RL (1996) Users Manual for Program ARSTAN. Laboratory of Tree-Ring Research. University of Arizona, Tucson, USA.

Crookshanks M, Taylor G & Broadmeadow M (1998) Elevated CO_2 and tree root growth: contrasting responses in *Fraxinus excelsior, Quercus petraea* and *Pinus sylvestris*. New Phytologist 138: 241–250.

Čížek V (2007) Jaké u nás můžeme pěstovat topoly? [What poplars can be cultivated in the Czech Republic]. Lesnická práce 86: 27–29.

Dawes MA, Hättenschwiler S, Bebi P, Hagedorn F, Handa IT, Körner C & Rixen C (2011) Species-specific tree growth responses to 9 years of CO_2 enrichment at the alpine treeline. Journal of Ecology 99: 383–394.

Druart N, Rodriguez-Buey M, Barron-Gafford G, Sjodin A, Bhalerao R & Hurry V (2006) Molecular targets of elevated [CO_2] in leaves and stems of *Populus deltoides*: implications for future tree growth and carbon sequestration. Functional Plant Biology 33: 121–131.

Eguchi N, Funada R, Ueda T, Takagi K, Hiura T, Sasa K & Koike T (2005) Soil moisture condition and growth of deciduous tree seedlings native to northern Japan grown under elevated CO_2 with a FACE system. Phyton-Annales Rei Botanicae 45: 133–138.

Handa IT, Körner Ch & Hättenschwiler S (2006) Conifer stem growth at the altitudinal treeline in response to four years of CO_2 enrichment. Global Change Biology 12: 2417–2430.

Hättenschwiler S, Schweingruber FH & Körner Ch (1996) Tree-ring responses to elevated CO_2 and increased N-deposition in *Picea abies*. Plant, Cell and Environment 19: 1369–1378.

Hättenschwiler S, Miglietta F, Raschi A & Körner Ch (1997) Thirty years of in situ tree growth under elevated CO_2: a model for future forest responses? Global Change Biology 3: 463–471.

Hättenschwiler S & Körner Ch (1998) Biomass allocation and canopy development in spruce model ecosystems under elevated CO_2 and increased N deposition. Oecologia 113: 104–114.

Holmes RL (1983) Computer-assisted quality control in tree–ring dating and measurement. Tree-Ring Bulletin 43: 69–78.

Koch U, Bräuer K, Heinicke J & Kämpf H (2008) The gas flow at mineral springs and mofettes in the Vogtland/NW Bohemia: an enduring long-term increase. Geofluids 8: 274–285.

Korf V (1939) Příspěvek k matematické definici vzrůstového zákona lesních porostů [Contribution to the mathematical definition of growth principle of forest stands] (in Czech). Lesnická práce: 339–356.

Körner C, Asshoff R, Bignucolo O, Hättenschwiler S, Keel SG, Pelaez-Riedl S, Pepin S, Siegwolf RTW & Zotz G (2005) Carbon flux and growth in mature deciduous forest trees exposed to elevated CO_2. Science 309: 1360–1362.

Kozák J (2010) Soil Atlas of the Czech Republic. Prague, Czech University of Life Sciences Prague.

Levy PE, Meir P, Allen SJ & Jarvis PG (1999) The effect of aqueous transport of CO_2 in xylem sap on gas exchange in woody plants. Tree Physiology 19: 53–58.

Maček I, Pfanz H, Francetič V, Batič F & Vodnik D (2005) Root respiration response to elevated CO_2 – the effect of extremely high CO_2 concentrations at natural CO_2 springs. Environmental and Experimental Botany 54: 90–99.

Marzaioli F, Lubritto C, Battipaglia G, Passariello I, Rubino M, Rogalla D, Strumia S, Miglietta F, D'Onofrio A, Cotrufo MF & Terrasi F (2005) Reconstruction of past CO_2 concentration at a natural CO_2 vent site using radiocarbon dating of tree rings. Radiocarbon 47: 257–263.

McDonald EP, Kruger EL, Riemenschneider DE & Isebrands JG (2002) Competitive status influences tree-growth responses to elevated CO_2 and O_3 in aggrading aspen stands. Functional Ecology 16: 792–801.

Mitscherlich EA (1909) Das Gesetz des Minimums und das Gesetz des abnehmenden Bodenertrages. Landwirtschaftliche Jahrbücher 38: 537–552.

Norby RJ, Todd DE, Fults J & Johnson DW (2001) Allometric determination of tree growth in a CO_2-enriched sweetgum stand. New Phytologist 150: 477–487.

Paoletti E, Pfanz H & Raschi A (2005) Pros and cons of natural CO_2 springs as experimental sites: Plant Responses to Air Pollution and Global Change (ed. by K Omasa, I Nouchi & LJ De Kok). Springer-Verlag, Tokyo, pp. 195–202.

Pepin S & Körner Ch (2002) Web-FACE: a new canopy free-air CO_2 enrichment system for tall trees in mature forests. Oecologia 133: 1–9.

Pfanz H, Aschan G, Langenfeld-Heyser R, Wittmann C & Loose M (2002) Ecology and ecophysiology of tree stems: corticular and wood photosynthesis. Naturwissenschaften 89: 147–162.

Pfanz H, Wittmann C, Vodnik D, Aschan G, Batič F, Turk B & Maček I (2007) Photosynthetic performance (CO_2-compensation point, carboxylation efficiency, and net photosynthesis) of timothy grass (*Phleum pratense* L.) is affected by elevated carbon dioxide in post-volcanic mofette areas. Environmental and Experimental Botany 61: 41–48.

Pfanz H (2008) Bark photosynthesis. Trees 22: 137–138.

Raschi A, Miglietta F, Tognetti R & van Gardingen PR (1997) Plant responses to elevated CO_2 – evidence from natural springs. Cambridge Univ Press.

Rasmussen L, Beier C & Bergstedt A (2002) Experimental manipulations of old pine forest ecosystems to predict the potential tree growth effects of increased CO_2 and temperature in a future climate. Forest Ecology and Management 158: 179–188.

Rennert T, Eusterhues K, Pfanz H & Totsche KU (2011) Influence of geogenic CO_2 on mineral and organic soil constituents on a mofette site in the NW Czech Republic. European Journal of Soil Science 62: 572–580.

Saurer M, Cherubini P, Bonani G & Siegwolf R (2003) Tracing carbon uptake from a natural CO_2 spring into tree rings: an isotope approach. Tree Physiology 23: 997–1004.

Schweingruber FH, Eckstein D, Serre-Bachet F & Bräker OU (1990) Identification, presentation and interpretation of event years and pointer years in dendrochronology. Dendrochronologia 8: 9–38.

Spiecker H (1999) Growth trends in European forests – do we have sufficient knowledge?: Causes and consequences of accelerating tree growth in Europe (ed. by T Karjalainen, H Spiecker & O Laroussinie) EFI Proceedings No. 27.

Teskey RO & McGuire MA (2002) Carbon dioxide transport in xylem causes errors in estimation of rates of respiration in stems and branches of trees. Plant, Cell and Environment 25: 1571–1577.

Teskey RO, Saveyn A, Steppe K & McGuire MA (2008) Origin, fate and significance of CO_2 in tree stems. New Phytologist 177: 17–32.

Tjoelker MG, Oleksyn J & Reich PB (1998) Temperature and ontogeny mediate growth response to elevated CO_2 in seedlings of five boreal tree species. New Phytologist 140: 197–210.

Tognetti R, Cherubini P & Innes JL (2000) Comparative stem-growth rates of Mediterranean trees under backround and naturally enhanced ambient CO_2 concentrations. New Phytologist 146: 59–74.

Vodnik D, Sirčelj H, Kastelec H, Maček I, Pfanz H & Batič F (2005) The effects of natural CO_2 en-

richment on the growth of maize. Journal of Crop Improvement 13: 193–212.

Vodnik D, Kastelec D, Pfanz H, Maček I & Turk B (2006) Small-scale spatial variation in soil CO_2 concentration in a natural carbon dioxide spring and related properties at the plant level. Geoderma 133: 309–319.

Warren WG (1980) On removing the growth trend from dendrochronological data. Tree-Ring Bulletin 40: 35–44.