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The Effect of Air Elevated [CO_2] on Crown Architecture and Aboveground Biomass in Norway Spruce (*Picea Abies* (L.) Karst)

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Abstract

Potential influence of air elevated [CO_2] on aboveground biomass was investigated on young (17-19 year old) Norway spruce (*Picea abies* (L.) Karst.) trees cultivated inside glass domes (GD) with ambient (A, 370 μmol (CO_2) mol^{-1}) and elevated (E, 700 μmol (CO_2) mol^{-1}) atmospheric CO_2 concentrations ([CO_2]) established in 1997. GDs were working as a semi-open system (Urban et al. 2001). The trees were growing in two different stand densities (S, 5,000 tree ha^{-1} and D, 10,000 tree ha^{-1}) until 2002. Then the first analysis of harvested trees from schematic thinning was done. Two years later the second analysis was performed.

Amount of branches with secondary shoots (SS), total amount of SS on branches were higher within the crowns of E- trees comparing to A- ones, particularly in S stand. After thinning, number of branches with SS and stem SS decreased and it was found to be even lower in ES than in AS. However, leaf (LB), branch (BB), stem (SB) and total aboveground (TBA) biomass of tree were found to be unaffected by elevated [CO_2], stem dendrometric parameters and the aboveground tree organs' biomass increments were stimulated by thinning, especially in S stand. Then the number and length of whorl branches increased on average by 13 % and 8 %, and by 3 % and 10 % (insignificantly) in E- sparse and dense sub-treatments, respectively. Tree height, stem thickness, number of whorl branches, length of whorl branches and angle of their inclination were found to be unaffected by elevated [CO_2]. The percentage differences between treatments were within ±10 % interval and they showed slightly higher stimulation of initial growth for trees in D- spacing. The thinning stimulated growth of the stems and branches of primary structure.

Key words: biomass allocation, dendrometry, long-term experiment, secondary shoots, thinning

Introduction

The target tree architecture is a result of genetic predispositions and environmental factors on the site including soil and climate (Pritchard et al. 1999). Elevated atmospheric [CO_2] contributes to changes of many climatic parameters resulted in a global climate change (Houghton 1994, Miller et al. 1999, IPCC 2007). On the other hand, elevated [CO_2] modify directly and indirectly in consequence all physiological, anatomical and morphological properties of plants (Pritchard et al. 1999, Urban 2003, Körner 2006). The direct physiological actions are based on the functionality of CO_2: (i) in enzymatic activity of RuBPCO (EC 4.1.1.39; ribulose-1.5-bisphosphate carboxylase/oxygenase) and (ii) as substrate of the Calvin cycle (i.e. process of carboxylation). Thus, as CO_2 is a substrate as well as an activator for photosynthetic carbon assimilation, it affects also photorespiration, dark respiration and stomatal aperture. The secondary physiological responses, like photosynthate concentration and translocation (e.g. sucrose and starch), and plant water status, have the crucial effect on plant growth, plant tissues anatomy and plant morphology. Hypothetically, whole plant/tree architecture can change significantly as different plant organs can respond to elevated [CO_2] in various morphological traits.

Tree height and stem diameter increments respond positively in a wide range of tree species (Volanen et al. 2006, Zhang and Dang 2007), nevertheless one or both of them can be unaffected in parallel (Pushnik et al. 1995). The length of whorl branches and their frequency is usually also stimulated under elevated [CO_2] conditions (Conroy et al. 1990), even more than tree height increment as apical dominance is usually reduced (Pritchard et al. 1999). Thus, crown architecture should be changed more dramatically as branch inclination changing with branch length too.

However, under elevated atmospheric [CO_2] the low soil moisture and not-sufficient soil temperature conditions for some tree species growth could be compensated (Zhang and Dang 2007), the nitrogen content in soil modify tree growth response powerfully (Hyvönen et al. 2007, Dieleman et al. 2010). Nitrogen limitation leads to greater carbon allocation into the root system (Dyckmans et al. 2000). Extreme nitrogen deficiency in soil leads to diminish completely the positive effect of elevated [CO_2] on tree growth (Cheng and Johnson 1998), whereas sufficiency or moderate deficiency of nitrogen magnifies the positive effect of elevated [CO_2] (Urban 2003). Therefore, soil type could play even more important role in above- and below-ground biomass allocation and tree architecture modification than air elevated [CO_2] (Egli and Körner 1997, Spinnler et al. 2002).

Nitrogen together with elevated CO_2 are the main important factors influencing the target architecture of the tree. Commonly, the secondary branching structures become more important in the crown or root system architectures when the primary structure die out after stress impact (Polak et al. 2007). Unfortunately, only a few references to secondary shoots formation under elevated [CO_2] could be found. Idso et al. (1990) found a stimulation of secondary branching under elevated [CO_2]. An occurrence of secondary shoots is often related to: i) plant species – secondary shoots are most common in angiosperms then in gymnosperms (Nicolini et al. 2001), ii) tree age - number of secondary shoots increase in older trees, which can consist of 40 to nearly 100 % of secondary shoots (Gruber 1994), and iii) exogenous stimuli such as damage and defoliation or increased nutrients availability (Zimmermann and Brown 1971). Crowns suffering permanently from abiotic or biotic stress show clustered secondary shoots called polycladies (Gruber 1994). The secondary shoots can asses as retrospective macroscopic indicator of stress in Norway spruce crowns (Polak et al. 2007). Additionally, elevated light exposure due to thinning can enhance the number of secondary shoots, behind modification of stem form and crown architecture (Roloff and Roemer 1989).

Increase in biomass under elevated [CO_2] is reported by 66 % tree growing species (Pritchard et al. 1999). Nevertheless under multi-competitive conditions the air elevated [CO_2] do not lead to stimulating effect of biomass growth as it could indicate reduction of soil N availability (Hattenschwiller and Körner 1997). From the point of view of biomass allocation, root system often shows the highest growth increment compared to other tree organs (Eamus and Jarvis 2004). Root to shoot ratio is significantly influenced by length of the growing period because of primary investment into short-term longevity tissues as fine roots and needles (Gielen et al. 2005).

The goal of this study was to estimate the effect of elevated [CO_2] on stem dendrometric and crown architecture parameters, aboveground biomass of tree organs and secondary branching of Norway spruce respect to the thinning impact. During the experimental design preparation phase, it was hypothesized that the tree morphological responses to elevated [CO_2] will be dependent on cultivation stand density.

Material and methods

Stand description: Norway spruce (*Picea abies* [L.] Karst) trees were cultivated under two different atmospheric CO_2 concentrations: i) A – ambient (A, 370 ppm, what is the mean value in the first year of harvest, i.e. 2002; since the beginning of experiment ambient [CO_2] increased about 2 ppm annually) and ii) E – elevated concentration (E, 700 ppm) within glass-domes (GD) with adjustable windows. This target value was maintained for approximately 91 % of the growing season within a range 600-800 ppm. During the remaining time, CO_2 concentration was lower due to the filling/transport, fumigation system control, or GDs repair. Glass domes with adjustable windows are located at the Experimental Ecological Study Site Bílý Kríž (Beskydy Mts., NE part of the Czech Republic). The construction of GDs and the system of air distribution was responsible for the comparable conditions in the both GD's interior. Main monitored and controlled parameters of the GD interior were: (i) means required GD atmospheric CO_2 concentration, (ii) air temperature and (iii) soil moisture. Air temperature differs between the domes negligibly (about 0.2 °C on average). The air temperature within the domes was maintained within the ambient range ±1 °C for 84 % of the time. The relative air humidity inside the domes was significantly ($p<0.05$) lower than outside (-9.6 % on average) excepting the driest periods. Then, the differences were minor. Soil moisture did not differ between the domes more than 5 % as irrigation system (AMET, CR) balanced the soil moisture values daily (Fig. 1). The adjustable-windows were automatically closed on the individual walls of GD (to exclude wind incursions into the internal GD space) according to the wind speed and wind direction to maintain stabile [CO_2] inside of dome. On the other hand they were kept fully open to minimize differences in microclimatic parameters between the domes and free-open plot.

The experimental stands enclosed in the GDs were planted in the autumn 1996 using special prepared and replanted older saplings (age of trees at the planting date: 11 years). The soil within each of GD was homogenized to the depth of 40 cm before and slightly fertilized by Silvamix-forte (17 $g.m^{-2}$) and Ureaform (21 $g.m^{-2}$) one year after the tree plantation to avoid yellowing. Each treatment consists of two stand densities with triangular spacing, i.e. ca 10.000 tree ha^{-1} (D – dense sub-treatment) and 5.000 tree ha^{-1} (S – sparse sub-treatment). The mean tree size (± SD) was 1.6 ± 0.1 m of tree height and 23.0 ± 0.2 mm of stem diameter at 0.3 m above the ground at planting time. CO_2 fumigation started in early spring 1997.

Site description: The mean annual air temperature reached to 5.4 °C in the last decade (i.e. 1995 - 2005). Annual sum of precipitation amounted to 1400 mm. The geological bedrock is formed by Mesozoic Godula sandstone (flysh type) and is overlain by ferric podzols. Soil content of mineral nitrogen and available nitrogen forms are low throughout the whole soil profile at the experimental site.

Sampling procedure: In 2002, the schematic thinning with intensity of 22 % in the inner parts of dense treatment and 27 % of sparse treatment were done. In 2004, the thinning with intensity of 25 % and 39 % were done similarly in sparse and dense treatments, respectively. During the planting process, several randomly chosen saplings were harvested to set a baseline of specific allometric relationships between stem dendrometric parameters and biomass of different tree organs (Pokorny and Regner 1998). Then, each stem thickness was measured at two perpendicular directions with a caliper (Mitutoyo, Finnland) at the 1/10 of tree height and at 0.3 m above the ground surface for a standardization of stem form factor and for ability of self-tree biomass increment rate evaluation on the base of comparison biomass values in the beginning of the experiment with these in the time of harvest. The dendrometric parameters measurement of sampled spruce trees were as following: tree height, stem diameter, number of branches per whorl, length and inclination angle of whorl branches. Whorl branch inclination angles were measured as the deflection from the vertical stem axis. The trees were cut per whorl sections and branches, and then split per green (needle biomass) and non-green parts (branch biomass and stem biomass) after drying. All components for biomass analysis were oven-dried at 80°C and weighted (model 1405 B MP8-1 Sartorius, Germany or Kern MH5K5, Haron, CR) after 48 hours.

Processing of statistical values: Each subtreatment was represented by 4–13 spruce individuals per analyzed year. There is no overlap (no repeated measurements) of biomass, structural parameters or secondary branching as different tree groups were sampled in 2002 and 2004. As all replicates of each subtreatment resided in only one dome, the study design may be characterized as a pseudo-replication (Hurlbert 1984). However, Norway spruce does not respond uniformly due to a non-clonal origin and potentially high phenotypic plasticity (Kjallgren and Kullman 2002). It is presumed that results are not biased by preliminary character despite the pseudo-replication design. Normal-like data distribution and homogenenity of the variance could be presumed. For basic dendrometric parameters, one-way and two-way ANOVA tests were used to detect the statistically significant differences and to cluster homogenous groups. Chi-square test was used for secondary shoots occurrence. Statistically significant differences were tested on the level $\alpha = 0.05$. ANOVA and Scheffe tests were performed with STATISTICA 7.0 (StatSoft Inc., Tulsa, USA).

Results

Stem dendrometric parameters - Tree height to stem thickness relationship: Firstly, the tree height to the stem thickness relations of all trees within the treatment illustrated the similarity in the basic tree size parameters between representative sampled trees chosen by random selection and/or by the schematic selection in 2002 and 2004 (Fig. 1).

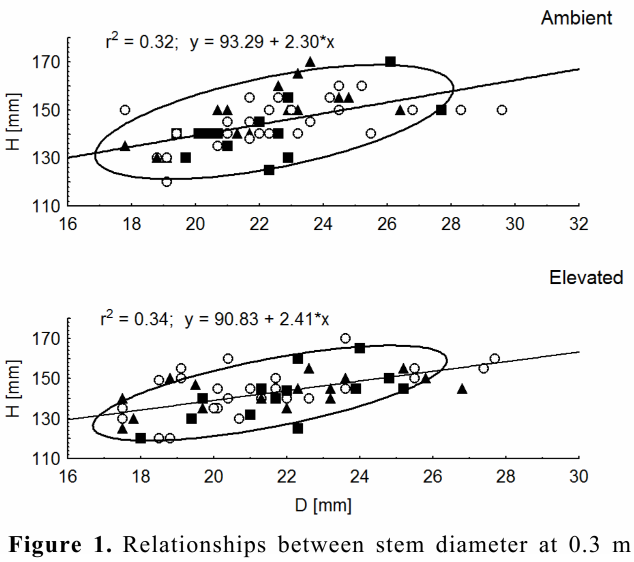

Figure 1. Relationships between stem diameter at 0.3 m above the ground ($D_{0.3}$) and tree height (H) in the beginning of the experiment (i.e. in 1997). Regressions between H and $D_{0.3}$ are described separately for ambient (a) and air elevated [CO_2] treatments (b). Ellipse demarcated the confidence interval for 95 % of all values occurrence. Full squares mark sampled trees in 2002, full triangles mark sampled trees in 2004, empty circles mark all other trees in treatment

Tree height: After the six years of tree cultivation (i.e. in 2002), no significant effect of air elevated [CO_2] on the tree height growth was detected. Trees were even higher in both sparse and dense A sub-treatments comparing to E by 8 % and 3 %, respectively. Two years after thinning (i.e. in 2004), E trees were found higher than A on average about 14 % in S and about 8 % in D sub-treatment (insignificantly; Fig.2).

Stem thickness: The stems of sampled trees were insignificantly thicker about 5 % in A than in E in S sub-treatment and about 4 % thicker in E than in A in D sub-treatment in 2002. However, the mean stem diameter did not differ between the related sub-treatments of A and E before and also after the thinning, a high difference (about 22 %) was found between sparse sub-treatments, to advance E two years after the first schematic thinning (Fig.2). Trees grown in D spacing exhibited lower stem thickness values (about 12-19 %) comparing to these in S spacing before as well as after the thinning (Fig. 2). The highest difference between S and D sub-treatments within one treatment was found under elevated [CO_2] conditions two years after the thinning.

Crown architecture - Branching frequency: Before the thinning, elevated [CO_2] appeared to slightly stimulate branching frequency in elevated treatment (Fig. 2). The average branching frequency was about 3 % and about 21 % (insignificantly) higher in S and D sub-treatments, respectively. After the thinning, enhancement of branching frequency about 13 % was recorded in S sub-treatment whereas it decreased in D sub-treatment (about 7 %).

Length of branches: Length of branches was similar in both sub-treatments. The differences were found up to the 5 %. The thinning had a positive effect on length of branches in D sub-treatment only, there the branches were found about 10 % longer comparing to ambient ones in 2004 (Fig. 2).

Branch inclination angle: In both treatments, D-trees had lower branch inclination angles and thus consequently slimmer crowns than S- trees probably due to the limited growing space. Values of branch inclination angle ranged commonly from 70° to 75° for all treatments and the statistically significant differences between the treatments were not found. There were no shifts in branch inclination angles after thinning.

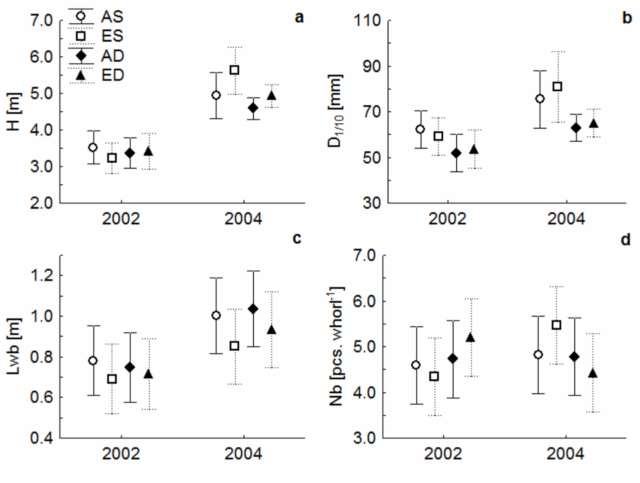

Figure 2. Stem and crown dendrometric parameters of trees growing in sparse (S) and dense (D) sub-treatments (the second letter in note) of ambient (A) and elevated [CO_2] treatment (E, the first letter in note) in 2002 and 2004. H – tree height (a), $D_{1/10}$ – stem thickness in 1/10 of tree height (counted from the ground, b), Lwb – length of whorl branches (c), Nb – number of branches within the whorl (d). Whiskers show the confidence limits of the mean

Secondary shoots on the branches: After the six years of fumigation (i.e. in 2002), the number of whorl branches with secondary shoots occurrence as well as the frequency of the secondary shoots on the branches were mostly higher in both S and D sub-treatments of E comparing to A ones (Table 1). Only the number of one-year old secondary shoots was lower in ED than in AD. Comparing to sub-treatments within E, the number of branches with secondary shoots

		Branches				Stem		
Year	Sub-treatment	Number of branches with secondary shoots	Number of secondary shoots on branches	Number of 1-year old secondary shoots on bran.	Number of 2-year old secondary shoots on branches	Number of secondary shoots on stem	Number of 1-year old secondary shoots on stem	Number of 2-year old secondary shoots on stem
		A_E	A_E	A_E	A_E	A_E	A_E	A_E
2002	Sparse	11_14	27_54	26_34	12_15	11_10	6_3	4_4
	Dense	6_6	17_9	12_9	2_6	14_13	4_5	7_6
	Whole treatment	8_10	22_31	19_21	7_10	13_12	5_4	6_5
2004	Sparse	13_4	60_20	20_7	9_6	13_11	6_4	7_5
	Dense	7_8	33_28	16_4	4_7	17_16	3_5	8_12
	Whole treatment	10_6	47_24	18_11	6_6	15_13	4_5	8_9

Table 1. The total number of the secondary shoots of two different age classes counted on whorl branches and stems of all trees in sparse and dense sub treatments of air elevated [CO_2] and ambient treatment in 2002 and 2004. (Standard deviations are not presented due to the lognormal data distribution and high variation of data)

as well as the branching frequency was higher in ED comparing to ES. Two years after the thinning (i.e. in 2004), the number of whorl branches with secondary shoots occurrence was found significantly lower in ES due to decreasing of new secondary shoots formation and discontinuing increment of early developed secondary shoots (described by 1-year old shoots; Table 1). Shoot number on whorl branches did not differ between the both comparable sub-treatments in A and E.

Secondary shoots on the stem: Higher secondary shoots frequency were recorded in E comparing to A. Higher number of the secondary shoots was counted in ES than in ED, particularly of one-year old secondary shoots (Table 1). After the thinning, higher number of secondary shoots was counted on stems in A comparing to E in both sub-treatments. Similarly to secondary shoots on branches, the secondary shoots on the stem showed discontinuous increment of older secondary shoots, especially in ES. The secondary shoots were developed on whorl branches and stem one year after fumigation – indicated by 2-year-old shoots and older. Then the occurrence of SS was remarkably reduced more on stem than on branch. Shoots number on stem similarly to the number of branches with secondary shoots were reduced by thinning in E treatment.

Biomass allocation: After the six years of experiment duration, elevated [CO_2] showed slight stimulation of the aboveground biomass increment in dense tree spacing sub-treatment, whereas no stimulation effect on aboveground biomass increment was found in the sparse one (Fig. 3). Total aboveground biomass (TBA) was even higher about 9 % in AS comparing to ES. To follow the trajectory of biomass allocation into aboveground tree organs, biomass was allocated more into the branch biomass than into the stem. The lowest biomass allocation was observed into the leaf biomass, especially in S tree spacing treatment. Any statistically significant differences were found between subtreatments within the A and E treatment, except significantly lower LB values in AD comparing to AS ($p=0.046$). Two years after the schematic thinning with intensity of ca 25 %, the TBA highly increased in both E sub-treatments, especially in S. Then, trees from the both E sub-treatments invested more biomass into the stems (up to 39 % in sparse sub-treatment) and branches (up to 29 %, insignificantly) than into the leaves comparing to A treatment (Fig. 3). Highly stimulated stem and branch biomass increment by thinning under air elevated [CO_2] resulted in higher TBA in both investigated spacing densities (about 22 %). Similarly as in 2002, no significant differences among investigated parameters were found in 2004. Overview of a temporal development of stand density, stand basal area, and leaf area index per subtreatments is presented in Table 2.

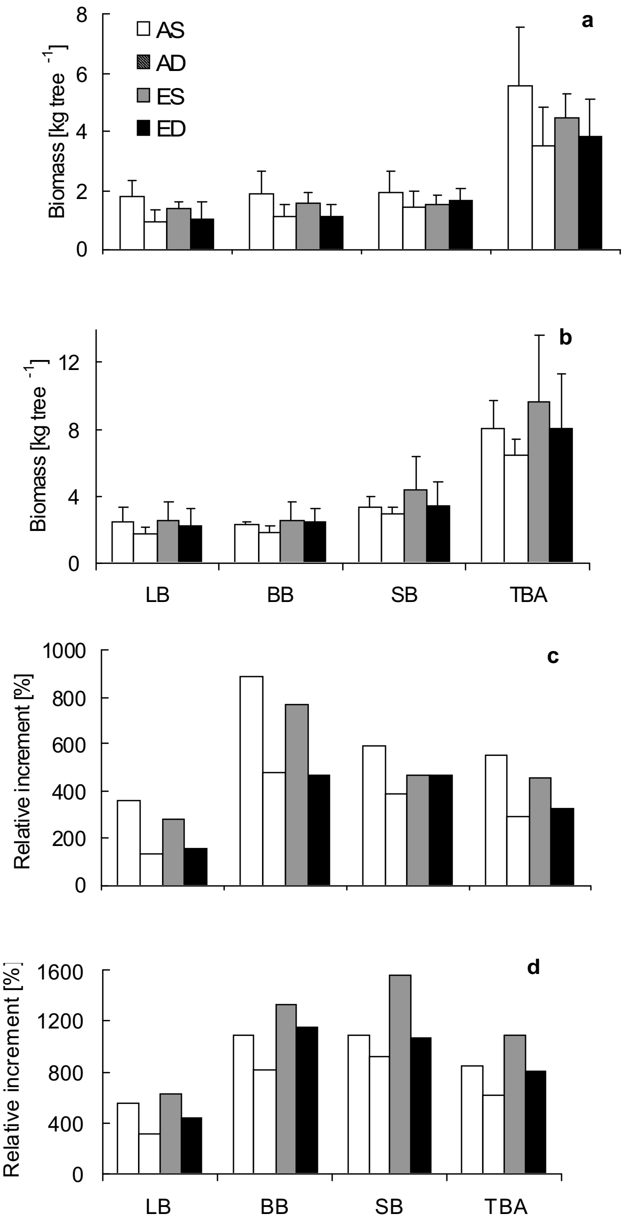

Figure 3. Mean tree biomass of the sampled tree aboveground organs in 2002 (a) and 2004 (b), and relative sampled tree aboveground organ biomass increment in 2002 (c) and 2004 (d) comparing to its own values derived allometricaly from the dendrometric parameters in the beginning of the experiment (i.e. in 1997, baseline = 100 %). AS – ambient sparse sub-treatment, AD – ambient dense sub-treatment, ES – elevated [CO_2] sparse sub-treatment, ED – elevated [CO_2] dense sub-treatment, LB – leaf biomass, BB – branch biomass, SB – stem biomass, TBA – total above-ground biomass. Whiskers mark standard deviations

Table 2. Stand basal area (BA, cm^2 m^{-2}) at 0.3 m above the ground, seasonal maximum of hemi-surface leaf area index (LAI, m^2 m^{-2}) and stand density (DEN, trees per hectare) in the end of choosing years of investigated period from 1997-2004. Values and standard error of estimation (SE) of the means are presented for sparse and dense sub-treatments of air elevated [CO_2] treatment and ambient one

	1997					2000					2002 after (before) thinning					2004 after (before) thinning				
	BA	SE	LAI	SE	DEN	BA	SE	LAI	SE	DEN	BA	SE	LAI	SE	DEN	BA	SE	LAI	SE	DEN
Ambient sparse	4.6	0.9	0.9	0.2	4,900	16.2	5.8	2.0	0.3	4,900	31.9	12.9	3.1 (4.3)	0.3 (0.3)	3,600	44.9	7.3	4.3 (5.3)	0.3 (0.3)	2,700
Ambient dense	4.8	1.3	1.9	0.3	9,300	15.4	3.1	3.7	0.3	9,300	21.5	5.8	4.9 (6.2)	0.3 (0.3)	7,400	31.3	5.1	5.3 (10.2)	0.3 (0.3)	5,500
Elevated sparse	4.3	1.3	0.8	0.3	4,900	18.9	7.0	2.2	0.3	4,900	29.0	11.7	5.7 (7.9)	0.5 (0.7)	3,600	68.6	24.6	5.9 (7.9)	0.5 (0.7)	2,700
Elevated dense	4.7	1.7	1.8	0.3	9,300	15.7	4.9	3.7	0.3	9,300	23.0	5.9	7.1 (9.0)	0.9 (1.2)	7,400	34.4	13.6	7.0 (13.5)	0.9 (1.2)	5,500

Discussion

Increased tree height has been frequently recorded under elevated [CO_2] conditions when growth resources – such as nutrients and water – are not limiting (Curtis and Wang 1998). Soil type and soil nitrogen availability seem to be the most important factors modifying growth response of Norway spruce to elevated [CO_2] (Egli and Körner 1997). Presented results showed no effect of air elevated [CO_2] on the Norway spruce tree height and stem thickness increments probably as soil nutrients are close to limiting conditions in the experimental site in the Beskydy Mts. Similarly, in open top chamber (OTC- for individual tree cultivation) experiment in the Beskydy Mts., the 15-year old Norway spruce trees did not show significant differences in the dendrometrical parameters of stem, length of whorl branches and branch base diameter as well (Oplustilova and Dvorak 1997). Compared to other experimental sites from Switzerland, Sweden and Oregon (USA), Norway spruce showed no significant growth response to air elevated [CO_2] except when nutrient were added (Körner 2006).

The planting density had no impact on the total tree height as well as on stem thickness until the thinning impact application. Afterwards, thinning forced tree height and stem thickness increments more in E than in A. Tree height increment as well as stem diameter increment can be stimulated after thinning by increasing growing space, nutrient availability and/or irradiation (Spinnler et al. 2003, Körner 2006). Both discussed stem dendrometric parameters can change in a disproportional way, e.g. stem diameter increment can respond positively to elevated [CO_2], but tree height should not be affected in parallel and vice versa (Pushnik et al. 1995, for *Pinus ponderosa*). Trees grown in dense spacing exhibited lower stem thickness dimensions comparing to these in sparse spacing. Therefore, as stem diameter of tree was strongly dependent on stand density, it was presumed that changes in this parameter arising to be obvious after thinning.

Time duration of elevated [CO_2] exposure seems to be another crucial factor for evaluation of changes in dendrometric (and/or morphological) parameters, as an insignificant effect of elevated [CO_2] on stem diameter or tree height is presented mostly for a short time studies (Olszyk et al. 1998). Many authors confirmed time dependent response to elevated [CO_2] with higher initial growth stimulation, but with diminishing effect over time (Jach and Ceulemans 1997), probably as there appear various limitations on other hierarchical levels. For Norway spruce these are: i) decreasing amount and/or activity of RuBPCO (Hrstka et al. 2005), ii) increasing accumulation of carbohydrates in needles, iii) decreasing nitrogen concentration in plant (Urban and Marek 1999, Kosvancova et al. 2009), and iv) decreasing carbon sink capacity (Urban et al. 2003). Actually, the plants respond in time primarily on physiological processes level (i.e. in scale of seconds; e.g. stomatal aperture, photosynthesis, photorespiration, respiration etc.), secondarily on photosynthate concentration and reallocation level and thirdly on anatomical and morphological level (i.e. in scale of growing seasons). Therefore, rapidly changed "growth strategy" and/or highly increased differences between A and E sub-treatments in stem dendrometric and crown morphological parameters during two growing seasons (comparing data from 2002 with 2004) should be taken into consequence with the thinning. In short-time studies, the effect of tree/ plant spacing or different competitive conditions could not be displayed significantly on some morphological parameter level due to enough of growing space and just starting limitation of growth resources (Körner 2006). For example, Qiao et al. (2008) confirmed suppressed tree height increment of fir grown in high planting density under elevated [CO_2]. With respect to this findings, information about reduced or increased tree height are less evident or uncompleted without stand density description. Similarly, elevated [CO_2] investigation applied on isolated trees seems to be not relevant information from this point of view.

Numerous studies have shown an increasing branch elongation in plants grown under elevated [CO_2], e.g. for *Pinus taeda* and *Pinus radiata* (Conroy et al. 1990), but studies for Norway spruce (*Picea abies*) or Sitka spruce (*Picea sitchensis*) show no effect of elevated [CO_2] on growth of branches (Oplustilova and Dvorak 1997, Barton 1997, Roberntz and Linder 1999). No effect of elevated [CO_2] on branch length was confirmed also by presented results for Norway spruce. The first reason should be that elongation of lateral branches is not completely controlled by auxin produced and transported from apical meristem (Stafstrom 1995). The second reason should be simply that larger amount of assimilates fixed by branches growing in elevated [CO_2] do not lead to stimulation of growth (Barton and Jarvis 1999). The number of branches was stimulated rather in ED sub-treatment; however the results were not consistent throughout the whole crown vertical profile as the I. and the V. whorl in ED sub-treatment had even less branches (data not shown). Elongation growth of whorl branches and branch biomass independently on tree spacing density treatment, and number of whorl branches of trees grown in sparse spacing were stimulated by the thinning impact under elevated [CO_2]. Thinning had a positive effect on the formation of new branches in ES. Branch inclination angle was found completely unaffected by the elevated [CO_2] as well as by the thinning impact.

Since the beginning of fumigation, air elevated [CO_2] can operate as a stress activator (Polak et al. 2007) or as an exogenous stimuli (Zimmermann and Brown 1971) for the secondary shoots formation. Thus, amount of branches with secondary shoots (SS), total amount of SS on branches and on stems were found higher within the crowns of E- trees comparing to A-ones, particularly in sparse sub-treatment. After the thinning, number of branches with SS and stem SS decreased more rapidly in E compared to A. Contrariwise, growth of primary branch structure was stimulated in ES. Nevertheless, high secondary shoot formation as a possible alternative carbon sink helps to slow down reduction of photosynthesis and growth in the D- tree spacing compared to S. In our previous study, shoot elongation growth dynamic was found stimulating during the first one-three weeks after budburst, but the total shoot length of primary branching structure did not differ between the A and E treatments in the end of shoot size growth (Pokorny et al. 2010). Formation of secondary shoot structures serve as an alternative sink, which is one from essential components of the positive growth response of Norway spruce to CO_2 (Eamus 1996). Norway spruce, as fixed-growth species, produce foliage and branches early in the growing season comparing to free-growth deciduous species producing leaves and branches continuously during the growing season (Keller 1988). Thus, the growth of branch primary structure, what is an essential C sink, can be positively affected by elevated [CO_2] only during the first months of growing season (May – June).

Tree height, stem thickness, number of whorl branches, length of whorl branches, angle of their inclination and biomass of above-ground tree organs were found to be unaffected by elevated [CO_2] after the six years of experiment duration. The percentage differences between the treatments were mostly within ±10 % interval and there slightly higher stimulation of initial growth was registered for trees in D- spacing. Oplustilova and Dvorak (1997) presented also slightly stimulated branching ratio by elevated [CO_2]. It can be supported by the results of high relative effect of [CO_2] enrichment under low light, most likely because of a reduction of the light-compensation point (Körner et al. 2003). In opposite, irradiances above 250 mmol m^{-2} s^{-1} significantly enhanced daily courses of net CO_2 assimilation for E-trees in comparison with A ones (Špunda et al. 2005). Therefore, thinning impact can have a high stimulation effect on growth under elevated [CO_2] environment. It was supported by the presented results when thinning highly stimulated growth of the primary branch structure and biomass increment of branches and stems.

Conclusion

As our experimental design may be considered as a pseudoreplication, we suggest, the most of stem dendrometric and crown morphological parameters of Norway spruce trees grown in different tree spacing treatments are not significantly affected by the air elevated [CO_2]. Nevertheless, based on the presented data, the growth stimuli or forcing preferences of biomass allocation into different tree aboveground organs changed rapidly as young trees develop with temporal onset and especially after the thinning impact. Thinning forced growth of stem dendrometric parameters, stem biomass and primary branch structure as described by enhancing branching frequency of whorl branches and biomass increment of all branches. Stimulation of the secondary shoots development before the thinning was identified as the first "alternative sink" for enhancing assimilates production under air elevated [CO_2]. Thus, tree spacing respective the thinning modified this "sink strategy" as the amount of secondary shoots decreased, and growth of primary branching structure, stem size and biomass increment showed high positive consecutive stimulation under elevated [CO_2].

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ЭФФЕКТ ВЛИЯНИЯ ПОВЫШЕНОГО СОДЕРЖАНИЯ [CO_2] НА НАДЗЕМНУЮ БИОМАССУ И АРХИТЕКТУРУ КРОНЫ ЕЛИ ОБЫКНОВЕННОЙ (*PICEA ABIES* (L.) KARST)

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Резюме

Изучение дендрометрических параметров стволов, архитектуры кроны и биомассы проводилось на молодых (17-19 лет) деревьях ели обыкновенной (*Picea abies* [L.] Karst.), произраставших внутри стеклянных куполов (GDs) со средней (A, 370 μmol (CO_2) mol^{-1}) и повышенной (E, 700 μmol (CO_2) mol^{-1}) атмосферной концентрацией CO_2 ([CO_2]) с начала 1997. Крупноразмерные купола действовали как полуоткрытая система. Деревья росли в двух насаждениях с различными плотностями (S – редкая посадка, 5.000 деревьев/га и D – плотная посадка, 10.000 деревьев/га) до 2002. Затем было проведено схематическое разреживание (интенсивность 25%) и анализ вырубленных деревьев. Второй анализ проведен два года спустя.

Увеличенное содержание CO_2 не влияло на высоту дерева, толщину ствола, количество основных ветвей и их длину, а также угол отклонения от вертикали. Процентные различия между опытными посадками находились в пределах ±10 %, однако большая стимуляции начального роста оказалась у деревьев с плотной посадкой типа D. Только величина плотности ветвей (количестве ветвей на дереве) превзошла этот показатель. Она была на 21% выше для E-деревьев в сравнении с A-деревьями в посадке типа D. Количество вторичных ветвей (SS), общее количество SS на ветвях и стволах было выше на кронах E-деревьев, по сравнению с A-деревьями, особенно в плотной посадке. После прореживания, количество ветвей с SS и стволовых SS снизилось и выяснилось, что оно даже меньше у E-деревьев, чем у A-деревьев. Тем не менее, относительно параметров дендромертии ствола и архитектуры кроны, листа (LB), ветви (BB), ствола (SB) и вообще биомассы всей наземной части дерева (TBA), изменения в зависимости от повышенного количества CO_2 не наблюдались, все эти параметры и биомасса надземной части дерева стимулировались с помощью прореживания, особенно в редкой посадке. При этом незначительно увеличились количество (на 13 % и 8 %) и длина (на 3 % и 10 %) основных ветвей в посадке типа S и D. Было обнаружено, что ель обыкновенная, также как и другие хвойные деревья, в начале увеличивает свою фотосинтетическую активность в условиях повышенного уровня CO_2, а затем уменьшает способность ассимиляции (модифицированной доступностью азота). Высокая способность к формированию вторичных ветвей, выступает альтернативой снижению производства углерода, уменьшения фотосинтеза и роста в насаждениях типа D, по сравнению с насаждениями S. И наоборот, прореживание сильно стимулирует рост первичной структуры и биомассы надземной части дерева, особенно ветвей и ствола, в насаждениях обоих плотностей.

Ключевые слова: распределение биомассы, стеклянный купол, дендрометрия, длительный эксперимент, вторичные ветви