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The effect of elevated air CO_2 concentration on dendrometric parameters and biomass of European beech and Norway spruce in their monocultures and intermixtures

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Abstract

An increased CO_2 concentration should have a positive effect on tree growth, but in different species mixtures, due to mutual interaction between species, this effect may be insignificant or even negative. Therefore, our research focused on the influence of elevated CO_2 concentration on the height, stem diameter and biomass production of beech and spruce planted in the following arrangements: Pure (one species), Single (an individual of one species surrounded by trees of another) and Group (groups of three trees of one species surrounded by trees of another). In autumn 2005, these saplings were planted inside two glass-domes under ambient and elevated CO_2 concentration in the Beskydy Mts. (Czech Republic). Fumigation of CO_2 took place each vegetation period from 2006 to 2013. From 2006 to 2012, the height and stem diameter of each plant were measured. In autumn 2013, the plants were harvested (together with their roots) and their biomass was determined. The beech trees were mostly statistically significant larger under elevated CO_2 concentration (the greatest difference being between trees growing in Single). Under elevated CO_2 concentration, Spruce growing in Single was larger and that growing in Pure was smaller than Spruce growing under ambient CO_2 concentration. Although trees are affected not only by increased CO_2 concentration but also by other phenomena (i.e. nutrient, water etc.), we assume that, in the future (with all current factors being maintained, except for the CO_2 concentration), it can be more suitable to grow beech almost as a monoculture or singly and spruce only singly.

Key words: above-ground biomass; below-ground biomass; tree height; stem diameter

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1. Introduction

Air concentration of CO_2 (hereinafter: CO_2 concentration) in pre-industrial time was 280 ppm (Karoly et al. 2003) and in May 2024 it reached 427 ppm (Dlugokencky & Tans 2024), which is the highest value in the past two million years (Masson-Delmotte et al. 2021). The proportion of CO_2 in the atmosphere is increasing due to human influence, such as deforestation and the burning of vegetation and fossil fuels; CO_2 absorption in the oceans and land cannot keep up with this rate (Masson-Delmotte et al. 2021; Pressburger et al. 2023). Ballantyne et al. (2012), Jones et al. (2013) and, for example, van Marle et al. (2022) claim that around 45% of this anthropogenic CO_2 remains in the atmosphere (and due to this the amount of CO_2 will increase continuously). According to older predictions, CO_2 concentration will rise up to double the then value (i.e. around 600–700 ppm) by the end of the 21st century (Schimel et al. 1995; Wigley 1997). Battisti (2011) described a "business as usual" (i.e. no change) curve where the value of concentration reaches around 850 ppm in the year 2100, but the newer NOAA model predicting CO_2 concentration shows that, with no change, the CO_2 concentration will achieve 1,100 ppm (Lindsey & Dlugokencky 2024).

More than 85% of the total carbon of terrestrial biomass is concentrated in forests (Roy 2001), whereas annual carbon sequestration into the forests through

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photosynthesis is estimated at 2–4 Gt (Qureshi et al. 2012; Issa et al. 2020). Forests mostly consist of big-sized and long-living autotrophic organisms – trees – that play a significant role in mitigation of the consequences of the Global Climate Change (Luyssaert et al. 2007), thanks to the removing of a big amount CO_2 from the atmosphere and long-term storing of carbon in their woody tissue. Elevated CO_2 concentration stimulates the growth of forests. Urban (2003) stated that visible changes in growth are a tertiary response to the effect of elevated CO_2 concentration. At first, the change is visible in photosynthesis (Yordanov et al. 2000), respiration (Thomas & Griffin 1994) and stomatal conductivity (Zhu et al. 1998). After these changes, there occur changes in photosynthate efficiency (DeLucia et al. 1985) and water balance (Granier et al. 2000), and finally in leaf area, leaf and root biomass, then, due to this, the amount of the biomass of other parts of the tree increases (Taylor et al. 1994; Pritchard et al. 1999). Moreover, there are differences in the effect of this stimulation between coniferous and broadleaved species (Wullschleger et al. 1995; Norby et al. 2005). The growth of broadleaved trees is more stimulated than that of coniferous trees, as they replace all foliage every year, unlike conifers, where a commonly occurring acclimation depression suppresses theirs photosynthetic activities (Urban 2003; Ainsworth & Rogers 2007; Hallik et al. 2009; Norby et al. 2010; Zhang et al. 2020). The response of tree species to elevated CO_2 concentration can even vary greatly in time, i.e. after short- and/or long-term stimulation by elevated CO_2 concentration (Urban 2003; Norby et al. 2010), due to a varying amount of soil nitrogen and water availability (Norby et al. 1984; Brown & Higginbotham 1986; Drake et al. 2011; Zak et al. 2011), or due to silvicultural treatments (Pokorný et al. 2012). Furthermore, forest growth can also be affected by extreme weather events (Clarke et al. 2022) and their more frequent occurrence can be presumed (Meyer et al. 2022).

Therefore, forest sustainability and stability in a landscape should be of a higher priority. The use of mixed stands, instead of monocultures, brings about beneficial effects, as they can reduce the magnitude of disturbances and the occurrence of pests, and also enhance carbon sequestration (Jandl et al. 2007; Haas et al. 2011; Huuskonen et al. 2021). Ecological attributes of various tree species are generally different, therefore forest diversity and mixtures of species in stands can influence biomass production also under elevated CO_2 concentration (Fox 2005). Intraspecific interaction in monocultures can be more detrimental than interspecific interaction within mixed stands (Loreau & Hector 2001; Zhang et al. 2012; Tobner et al. 2016). For example, due to diverse root stratification of different species, water and nutrients from different soil layers can be utilized, thus avoiding high inter-species competition (Forrester et al. 2010; Kunert et al. 2012; Huuskonen et al. 2021). The transformation of Norway spruce (*Picea abies* [L.] H. Karst) monocultures towards mixed stands has been under way in Germany for a few decades and is now also taking place in many countries in Europe include the Czech Republic (CR; MLR 1999; Kenk & Guehne 2001; Spiecker et al. 2004; Larsen 2012). European beech (*Fagus sylvatica* L.) is a suitable tree species and the most frequently used to stabilize and ameliorate Norway spruce stands.

The objective of this study was to estimate the effect of elevated CO_2 concentration on the height, stem diameter, and biomass (i.e. above-ground, below-ground and of the individual parts of above-ground biomass) of European beech and Norway spruce in each individual arrangement.

During the preparation phase of the experiment, it was hypothesized that tree growth would be dependent not only on elevated CO_2 concentration (the greater the CO_2 concentration, the higher the values of the parameters) but, also, on various arrangements of mixed types (i.e. single, group) because intraspecific interaction can have a different effect on trees than interspecific (i.e. trees in mixed types should have a greater height, thickness, amount of biomass etc. than those in pure types).

2. Materials and methods

2.1. Study site

The study took place in the Experimental Ecological Workplace (EEW) Bílý Kříž in Beskydy in CR (49°30'09.2"N; 18°32'19.3"E) at an altitude of 908 m a.s.l. According to Agyei et al. (2020), there is a cool and humid climate (mean annual air temperature of 6.8 °C, relative air humidity of 84% and precipitation of 1,318 mm). The soil is ferric podzol, developed on Mesozoic Godula sandstone (WRB 2015).

Spruce and beech trees were cultivated inside two glass domes, each 7 m tall in the centre, with 72 openable windows with adjustable panes, and built on a 9 × 9 m concrete base with inserted penetration tubes for soil "communication" between the inner and the outer space. The walls comprised a massive iron frame. The process of closing and opening of these windowpanes was automatic, in order to maintain the desired CO_2 concentration and the other environmental conditions inside the domes. The window tilting device reacted to wind speed, wind direction and air temperature, so the glass domes operated as a semi-open system (Urban et al. 2001). The air was distributed within the domes via a system of radial and auxiliary fans (models *RNH 400* and *500 W*, Janka, Czech Republic) to maintain the ambient CO_2 concentration inside the first dome with 385 $\mu mol(CO_2)mol^{-1}$ and the elevated CO_2 concentration inside the second with 700 $\mu mol(CO_2)mol^{-1}$, where additional gaseous CO_2 was transmitted 24 hours per day through the dome with elevated CO_2 concentration from a storage tank from April to November each year. A peat substrate was added inside each dome to create a soil surface layer 10 cm thick, and an artificial irrigation system maintained equal moisture inside and outside. A more detailed description of the glass dome infrastructure can be found in Urban et al. (2001).

In autumn 2005, two-year-old beech (77.1 ±14.6 cm tall) and three-year-old spruce (46 ±7.0 cm tall) saplings (96 in total) were planted inside each dome in triangular spacing, where each sapling in one dome was chosen carefully to be of the same species, size and in the same position as the corresponding one inside the other dome, so both would have the same starting growth potential and conditions, except for CO_2 concentration (Pokorný et al. 2013a). Three arrangements were established:

- Pure (Pure) – individual trees of only one species;
- Single (Single-mixed) – individual trees of one species surrounded by eight trees of another species;
- Group (Group-mixed) – groups of three trees of one species surrounded by twelve trees of another species.

The fumigation of CO_2 started in spring 2006.

2.2. Description of the measuring and harvesting processes

The measurement was conducted from the time of planting (in the autumn of 2006) to the autumn of 2012: the total height and the stem diameter 10 cm above the ground (hereinafter: H and D10, respectively), where H was measured with a folding ruler from the base of the trunk to the top of the plant late each autumn after it had stopped growing. The measuring points were marked on each stem 10 cm above the ground with permanent paint. D10 was measured with a digital calliper at this height from two sides (perpendicular to each other) and, subsequently, averaged.

The trees were harvested from mid-August to mid-September 2013. All were cut using a hand saw, as close to the ground as possible, and the remaining stump was marked (for future recognition during root system extraction). Upon the harvest of each tree, its D10 and height (i.e. its height plus the height of its stump) were measured, and the leaves, branches and stem were placed separately into marked paper bags.

Harvesting of the root system with the stump was carried out after the extraction of all the trees from both domes at the end of October 2013. The root systems were excavated from the soil using the air-spade method (Air-Spade Technology, Verona, PA, USA-Model 150/90), where the soil is removed by means of high velocity air (over 700 m s^{-1}), which causes a series of micro-explosions but solid objects such as stones or roots (except mycorrhizal roots) generally remain undamaged. More information on this method can be found in Nadehzdina & Čermák (2003) and Pokorný et al. (2013b). After the extraction, the roots and their stumps were cleaned in water and each one placed separately into a marked paper bag.

Each bag (containing a stem, branches, leaves or roots) was dried in an oven until reaching a constant weight (after approximately 48 hours). Subsequently, the bags were emptied and the content of each was weighed to estimate the amount of biomass: 1) leaf biomass (LB); 2) branch biomass (BB); 3) stem biomass (SB); 4) above-ground biomass (AGB = LB + BB + SB); 5) below-ground biomass (BGB; i.e. root biomass) and 6) total biomass (TB = AGB + BGB)

2.3. Statistical analysis

Statistical analysis of the data was performed using TIBCO Statistica™ with a confidence interval of 95%. Normality of the data distribution was examined using the Shapiro-Wilk test before the main analysis. The main effects were analysed using ANOVA, after which Fisher's LSD test was applied, in order to identify differences among the main effects and interactions.

3. Results

3.1. The effect of CO_2 enrichment on tree height

There were no statistically significant differences in H among the arrangements or CO_2 concentrations for Spruce from 2006 to 2011 and for Beech from 2006 to 2008 (Fig. 1). In 2012 and 2013, H of Single-mixed Spruce was the smallest under ambient CO_2 concentration (i.e. in 2012: 26% smaller than Group-mixed ($p = 0.0314$) and 12% smaller than Pure ($p = 0.0378$); in 2013: 30% smaller than Group-mixed ($p = 0.0248$) and 41% smaller than Pure ($p = 0.0017$)). Under ambient CO_2 concentration, Single-mixed Beech was the smallest, however there was a statistically significant difference only between Single-mixed Beech and Pure Beech in 2009 and 2010 (i.e. in 2009: 40% ($p = 0.0014$); in 2010: 48% ($p = 0.0011$)). From 2011 until end of the experiment, Single-mixed Beech was the statistically significantly smallest of all arrangements (i.e. Single-mixed vs. Group-mixed – by 17–37% (p = from 0.0179 to 0.0384); Single-mixed vs. Pure – by 27–43% (p = from 0.0041 to 0.0214)). From 2009 until the end of the experiment, under elevated CO_2 concentration, Group-mixed Beech was statistically significantly the smallest of all arrangements (i.e. Group-mixed vs. Single-mixed (by 13–54% (p = from 0.0001 to 0.0415) and Group-mixed vs. Pure (by 17–78% (p = from 0.0001 to 0.0475)).

From 2009 to the end of the experiment, there was a difference in H between Single-mixed Beech under ambient CO_2 concentration and that under elevated concentration CO_2, where Beech under elevated CO_2 concentration was taller by 31–35% ($p = 0.0001$ each year).

3.2. The effect of CO_2 enrichment on stem diameter

In 2006 and 2007, there were no statistically significant differences in D10 of Spruce or Beech among the arrangements or CO_2 concentrations (Fig. 2). From 2008, the thinnest Single-mixed Spruce differed from the Group-mixed Spruce (in the range 20–40%; p values ranged from 0.0001 to 0.0283) and Pure Spruce (in the range 38–42%; p values ranged from 0.0001 to 0.0379) under ambient CO_2 concentration. Only in 2008 and 2009 there were differences when the thickest Spruce grew in Group-mixed and the thinnest in Pure under elevated CO_2 concentration (2008: $p = 0.0386$; 2009: $p = 0.0316$). In the period from 2010 to 2013, the thinnest Single-mixed Beech differed from Group-mixed Beech (in the range 32–42%; $p = 0.0001$ each year) and Pure Beech (in the range 19–27%; p values ranged from 0.0173 to 0.0211) under ambient CO_2 concentration. In the period from 2008 to 2013, the thinnest Group-mixed Beech differed from Pure Beech (in the range 23–27%; p values ranged from 0.0001 to 0.0274) and Single-mixed Beech (in the range 20–21%; p values ranged from 0.0174 to 0.0359) under elevated CO_2 concentration.

There were differences in the D10 among Group-mixed Spruce under different CO_2 concentrations (in 2008 and 2009) and among Single-mixed Spruce under different CO_2 concentrations (2010–2012). Group-mixed Spruce was thicker under ambient CO_2 concentration than under elevated CO_2 concentration – by 24% ($p = 0.0376$) and 25% ($p = 0.0341$) in 2008 and 2009, respectively. Single-mixed Spruce was 22–24% thinner

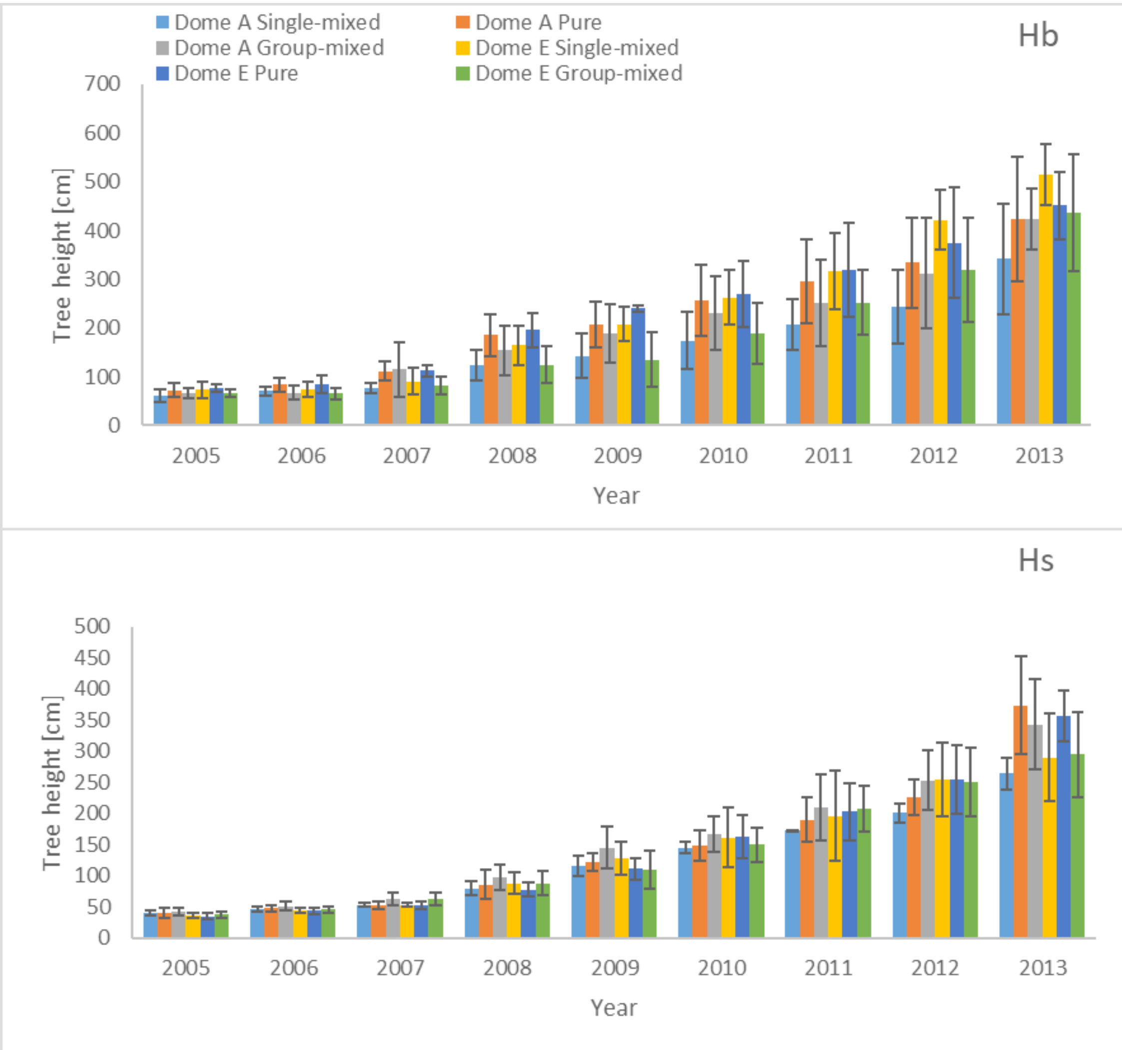

Fig. 1. Mean heights of spruce and beech growing in different arrangement types and different CO_2 concentrations. Hb – mean height of beech; Hs – mean height of spruce. Whiskers denote standard deviations. Statistically significant differences between ambient and elevated CO_2 concentration in corresponding arrangements are marked with stars. Homogenous groups in arrangements in ambient and elevated CO_2 concentration are marked with small and capital letters, respectively.

under ambient CO_2 concentration than under elevated CO_2 concentration (p values ranged from 0.0396 to 0.0438). Also, there were differences among Single-mixed Beech under the different CO_2 concentration in the period from 2011 to 2013, when Beech under elevated CO_2 concentration was thicker than under ambient CO_2 concentration (in the range 31–35%; p = 0.0001 each year).

3.3. The effect of CO_2 enrichment on biomass

After eight years of the experiment, the changes in the amount of the Beech and Spruce biomass were evident (Fig. 3 and 4). Under ambient CO_2 concentration, Single-mixed Beech had the least biomass in all parts (except BB; Table 1) and Pure Beech had the most (there was no statistically significant difference between the amounts in Group-mixed and Pure). Under elevated CO_2 concentration, there was the least Beech biomass in all parts in Group-mixed, and the most in Single-mixed Beech (there was no statistically significant difference between the amounts in Single-mixed and Pure). Moreover, we found differences in the amounts of Single-mixed Beech biomass under different CO_2 concentrations, where there was more biomass under elevated CO_2 concentration (Table 2).

Under ambient CO_2 concentration, the order of the amount of Spruce biomass in the arrangements (i.e. Single-mixed – Group-mixed – Pure, in ascending order) was the same as that of the amounts of Beech. The amounts of the biomass in all parts of Single-mixed Spruce were statistically significantly different from those of Pure Spruce and Group-mixed Spruce (Table 3), however the differences in the amounts of the biomass in all parts between Pure Spruce and Group-mixed Spruce were not statistical significance. However, under elevated CO_2

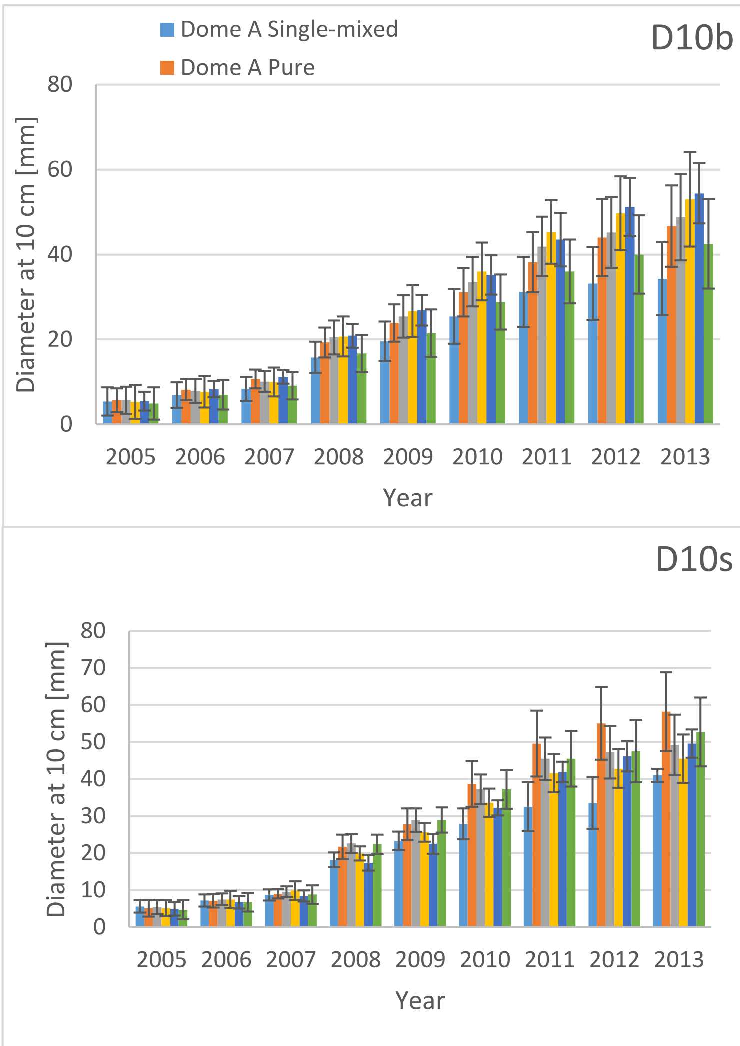

Fig. 2. Mean stem diameters of spruce and beech growing in different arrangement types and different CO_2 concentrations. D10b – mean diameter of beech; D10s – mean diameter of spruce. Whiskers denote standard deviations. Statistically significant differences between ambient and elevated CO_2 concentration in corresponding arrangements are marked with stars. Homogenous groups in arrangements in ambient and elevated CO_2 concentration are marked with small and capital letters, respectively.

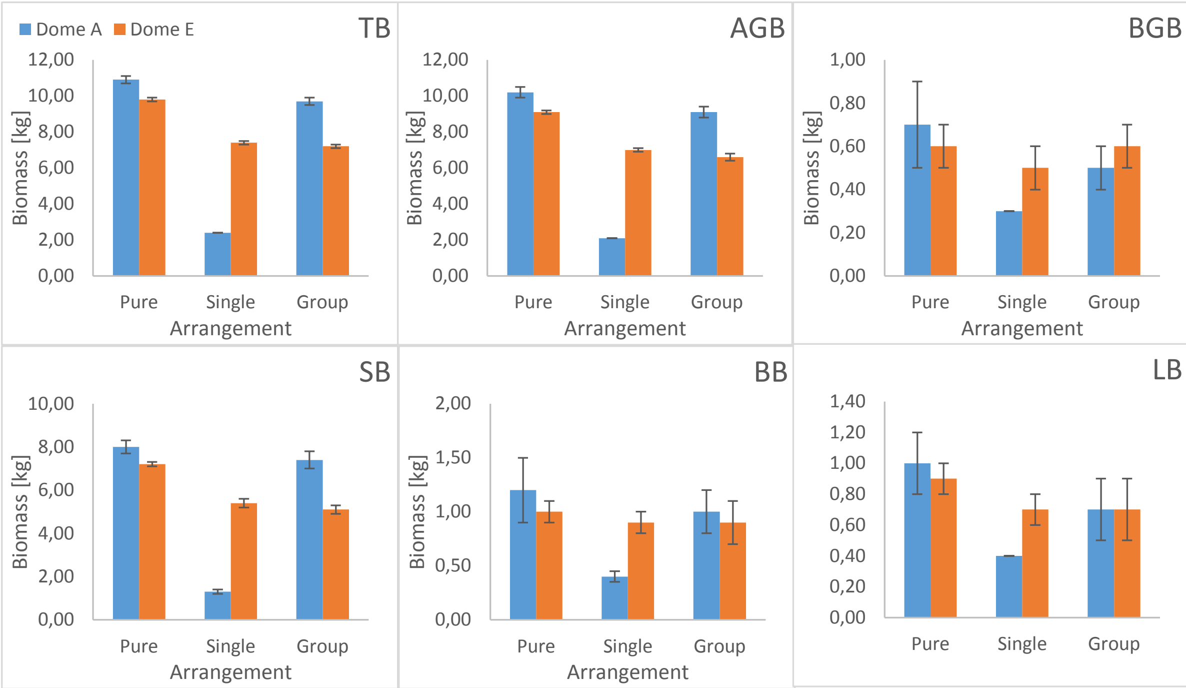

Fig. 3. The mean amount of biomass of spruce growing in different arrangement types and different CO_2 concentrations. TB – total biomass (TB = AGB + BGB); AGB – above-ground biomass (AGB = LB + BB + SB); BGB – below-ground biomass (BGB; i.e. root biomass); SB – stem biomass (SB); LB – leaf biomass (LB); BB – branch biomass (BB). Whiskers denote standard deviations.

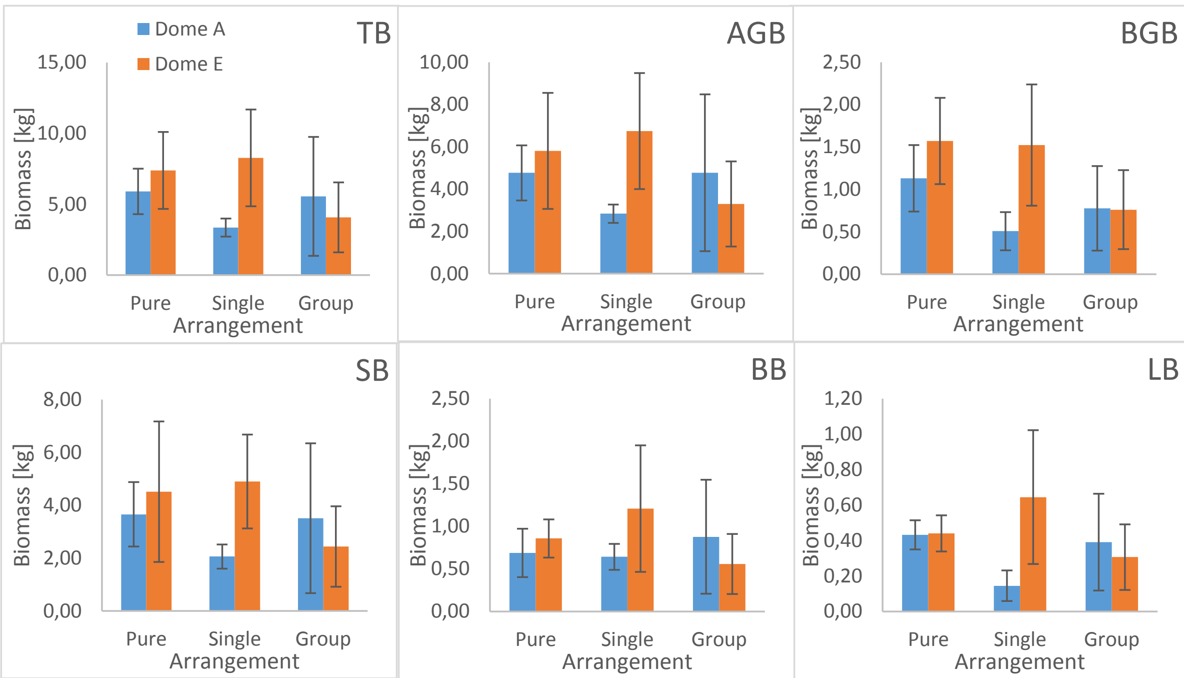

Fig. 4. The mean amount of biomass of beech growing in different arrangement types and different CO_2 concentrations. TB – total biomass (TB = AGB + BGB); AGB – above-ground biomass (AGB = LB + BB + SB); BGB – below-ground biomass (BGB; i.e. root biomass); SB – stem biomass (SB); LB – leaf biomass (LB); BB – branch biomass (BB). Whiskers denote standard deviations.

Table 1. Percentage differences and statistically significant values in Beech biomass among the arrangements inside the domes. The percentages represent the increase in Beech biomass listed in the column compared to that in the row. For example, there was 66% more biomass in the Group-mixed under ambient CO_2 concentration than in the Single-mixed under ambient CO_2 concentration. TB – total biomass (TB = AGB + BGB); AGB – above-ground biomass (AGB = LB + BB + SB); BGB – below-ground biomass (BGB; i.e. root biomass); SB – stem biomass (SB); LB – leaf biomass (LB); BB – branch biomass (BB).

Domes		Dome A			Dome E		
	Arrangement	Single	Group	Pure	Single	Group	Pure
					TB		
Dome A	Single		66% p = 0.0001	76% p = 0.0001			
Dome E	Group				103% p = 0.0001		81% p = 0.0001
					BGB		
Dome A	Single		53% p = 0.0167	123% p = 0.0001			
Dome E	Group				100% p = 0.0001		107% p = 0.0001
					AGB		
Dome A	Single		68% p = 0.0227	68% p = 0.0067			
Dome E	Group				101% p = 0.0004		85% p = 0.0003
					SB		
Dome A	Single		70% p = 0.041	77% p = 0.0238			
Dome E	Group				101% p = 0.0004		85% p = 0.0003
					BB		
Dome E	Group				117% p = 0.0169		54% p = 0.0326
					LB		
Dome A	Single		170% p = 0.0024	197% p = 0.0001			
Dome E	Group				110% p = 0.0098		44% p = 0.0184

Table 2. Percentage differences and statistically significant values between the same arrangements inside the domes. The percentages represent the increase in biomass listed in the column compared to that in the row. For example, there was 146% more biomass in the Single-mixed under elevated CO_2 concentration than in the Single-mixed under ambient CO_2 concentration. TB – total biomass (TB = AGB + BGB); AGB – above-ground biomass (AGB = LB + BB + SB); BGB – below-ground biomass (BGB; i.e. root biomass); SB – stem biomass (SB); LB – leaf biomass (LB); BB – branch biomass (BB).

Part of biomass	Dome and arrangement	Dome E Single	Dome E, Group	Dome E, Pure
		Beech		
TB	Dome A, Single	146% p = 0.0001		
BGB	Dome A, Single	201% p = 0.0001		
AGB	Dome A, Single	137% p = 0.0001		
SB	Dome A, Single	138% p = 0.0001		
BB	Dome A, Single	88% p = 0.0001		
LB	Dome A, Single	345% p = 0.0001		
		Spruce		
TB	Dome A, Single	209% p = 0.0001		
	Dome A, Group		33% p = 0.0001	
	Dome A, Pure			11% p = 0.0001
BGB	Dome A, Single	33% p = 0.0412		
AGB	Dome A, Single	238% p = 0.0001		
	Dome A, Group		37% p = 0.0001	
	Dome A, Pure			12% p = 0.0001
SB	Dome A, Single	325% p = 0.0001		
	Dome A, Group		47% p = 0.0001	
	Dome A, Pure			11% p = 0.0001
BB	Dome A, Single	98% p = 0.0001		
LB	Dome A, Single	103% p = 0.0001		

Table 3. Percentage differences and statistically significant values in Spruce biomass among the arrangements inside the domes. The percentages represent the increase in Spruce biomass listed in the column compared to that in the row. For example, there was 301% more biomass in the Group-mixed under ambient CO_2 concentration than in the Single-mixed under ambient CO_2 concentration. TB – total biomass (TB = AGB + BGB); AGB – above-ground biomass (AGB = LB + BB + SB); BGB – below-ground biomass (BGB; i.e. root biomass); SB – stem biomass (SB); LB – leaf biomass (LB); BB – branch biomass (BB).

Domes		Dome A			Dome E		
	Arrangement	Single	Group	Pure	Single	Group	Pure
					TB		
Dome A	Single		301% p = 0.0001	353% p = 0.0001			
Dome E	Group						35% p = 0.0001
	Single						31% p = 0.0001
					BGB		
Dome A	Single		61% p = 0.0059	107% p = 0.0009			
					AGB		
Dome A	Single		340% p = 0.0001	393% p = 0.0001			
Dome E	Group						38% p = 0.0001
	Single						31% p = 0.0001
					SB		
Dome A	Single		487% p = 0.0001	535% p = 0.0001			
Dome E	Group						43% p = 0.0001
	Single						35% p = 0.0001
					BB		
Dome A	Single		132% p = 0.0001	167% p = 0.0001			
					LB		
Dome A	Single		82% p = 0.0001	175% p = 0.0001			

concentration, the order of the amounts of the Spruce biomass (i.e. Group-mixed – Pure – Single-mixed, in ascending order) was different from that of the Beech. Generally, there was most Spruce biomass in Pure and least in Single-mixed and Group-mixed. However, there were statistically significant differences only in TB, AGB and SB, with more Spruce biomass in Pure than elsewhere. The differences among the amounts of the Spruce biomass in Single-mixed and Group-mixed were very small (and without statistical significance). Moreover, we found differences in the amounts of Spruce biomass in the same arrangement, but in different CO_2 concentration (Table 2). Single-mixed Spruce had more biomass in all parts under elevated CO_2 concentration, and Group-mixed and Pure Spruce had more biomass in AGB, TB and SB under ambient CO_2 concentration.

The root:shoot ratio achieved relatively low values of Pure Beech (0.23 ±0.02). It was statistically significantly greater than those of Group-mixed Beech and Single-Beech (0.16 ±0.01 and 0.18 ±0.01, respectively; p = 0.0001 in both cases). The greatest ratio of spruce trees achieved only 0.14 (±0.01) in Single-mixed Spruce. The values of the ratios of Group-mixed and Pure Spruce were statistically significantly smaller – 0.05 (±0.01) and 0.07 (±0.01), respectively (p = 0.0001 in both cases).

4. Discussion

All saplings had a similar stem diameter and height at the start of the experiment. In the first two years after planting, their stem diameters and heights stagnated. There are two reasons: 1) planting shock and 2) the time needed for a physiological response to an elevated CO_2 concentration. The planting shock is a phenomenon where transpiration slows down and photosynthesis and growth of a plant is severely limited, or even ceases (Hallman et al. 1978; Coutts 1980; Mora et al. 2023). Lamhamedi et al. (1998) showed that the planting shock camouflages physiological and/or growth changes. Also, Spinnler et al. (2002), Hasstedt & Annighöfer (2020) and Kouassi et al. (2023) mentioned attenuation of growth of transplanted plants. The plants in our experiment stopped growing for a period of two years, as is stated in the cases of the above-mentioned authors. Goisser et al. (2013) suggested that the first years after planting should not be included in the results because throughout this period the plants are recovering from planting shock and the data is therefore misleading. Moreover, faster growth of the trees was not evident in the dome with elevated CO_2 concentration during the first few years, due to the longer interval of physiological response to elevated CO_2 concentration. At first, the change is visible in the physiological reactions, and only after a longer period in the biomass (DeLucia et al. 1985; Taylor et al. 1994; Thomas & Griffin 1994; Pritchard et al. 1999; Granier et al. 2000; Yordanov et al. 2000; Walken et al. 2021).

After overcoming the initial stagnation, the development of both species began to differ, which was probably caused by different inter- and intra-actions between spruce and beech under different CO_2 concentrations. Biber (1996) showed that a neighbouring spruce crown restricts spruce and beech growth more than a neighbouring beech crown of the same size. Similar results were obtained by Grundmann (2009). We noted agreement between Biber (1996) and Grundman (2009) regarding beech where, in Single-mixed under ambient CO_2 concentration, the height and thickness were the lowest of all variants. However, in our case, even the spruce surrounded by beeches was the lowest and thinnest of all variants under ambient CO_2 concentration. In both cases (for Single-mixed Beech and Spruce), the canopy probably had the greatest influence. According to Sprauer & Nagel (2014), the canopy areas of both tree species generate different competitive pressures on both spruce and beech. Trees of the same species surrounding one tree of the other species compete more and, as a result, grow taller and the crowns of the trees try to expand more to the detriment of the individual tree, which, as a result, reaches smaller dimensions. Similar results were also achieved by Sterba et al. (2002).

On the other hand, under elevated CO_2 concentration, Single-mixed Beech that was surrounded by spruce competitors had better growth (and at the same time the growth of the spruce in the group mixture was similarly small, as in Single-mixed). This may be due to the growth curve of young beech, which is steeper than that of spruce (Vyskot 1978), enhanced by increased CO_2 concentration. Subsequently, the Pure beech was able to spread its crown more and expose itself more to the sun, which is also evident from the increase in the amount of the biomass of its foliage. On the other hand, the same trend as under ambient CO_2 concentration was shown by Single-mixed Spruce in competition with beech under elevated CO_2 concentration. It can be concluded that the elevated CO_2 concentration has no effect on the height and thickness of Single-mixed Spruce.

According to Asshoff et al. (2006), Dieleman et al. (2010), Sigurdsson et al. (2013) and Lotfiomran et al. (2016), the values of the dendrometric parameters increase under elevated CO_2 concentration only when there are sufficient nutrients in the soil. Kubiske et al. (1998), Oren et al. (2001) and Norby & Zak (2011) described that above-ground growth under elevated CO_2 concentration can even slightly decrease in poor soil in boreal forests or temperate zones. In our case, the soil in which the trees were planted was nutritionally poor. However, our results brought different values for Spruce and Beech. Pure Spruce, and even Group-mixed Spruce, reacted negatively to elevated CO_2 concentration and had a smaller stem diameter and height than under ambient CO_2 concentration (differences were visible but without statistical significance); Pure Beech had the opposite trend – it was taller and thicker under elevated CO_2 concentration (all differences were visible but some without statistical significance).

Many authors generally described an increase in the amount of biomass with elevated CO_2 concentration, especially in the case of broad-leaved tree species (e.g., the fast-growing, such as *Populus* and *Salix* spp.), and, on the other hand, an acclimation depression of photosynthetic activities limiting growth of conifers (Luo et al. 1999; Pritchard et al. 1999; Urban 2003; Büntgen et al. 2019; Terrer et al. 2019; Maschler 2023). Other factors, in general, that significantly affect tree growth (Eamus & Jarvis 1989; Bazzaz 1990; Johnson 1992; Egli & Körner 1997; Dyckmans et al. 2000; Reich et al. 2001; Spinnler et al. 2002; Reich et al. 2004; Körner 2006; Franklin 2007; Hyvönen et al. 2007; Wang 2007; Dieleman et al. 2010; Maschler 2023) are:

- soil properties (nitrogen/nutrient content, acidity, type etc.);
- the experimental facility used (i.e. closed, semi-open and open systems);
- the duration of the experiment (i.e. days, months, years, even decades);
- the CO_2 concentration;
- the structure of the stand/community being tested (i.e. tree/plant species composition, the age of the plants;
- the spatial structure of the stand/community and its “functionality” i.e. coupling with natural processes) and;
- simulation of additional stresses (i.e. elevated temperature, drought, ozone concentration).

Egli & Körner (1997) and Spinnler et al. (2002) described an experiment with a mixed beech-spruce stand under elevated CO_2 concentration. After the first year, the effect of elevated CO_2 concentration on biomass production was insignificant, as in our results, however, after four years, data analysis showed a significant difference in biomass production, comparing ambient and elevated CO_2 concentration. There was more beech biomass (only in calcareous soil) and spruce biomass (in calcareous and acidic soil) under elevated CO_2 concentration, and there was less beech biomass in acidic soil under elevated CO_2

concentration than under ambient CO_2 concentration. Also, Spinnler et al. (2003) described that an increase or decrease in the amount of beech biomass depends on the type of soil, whereas the amount of spruce biomass increases always. Kozovits et al. (2005), after two years of experimentation with juvenile spruce and beech in a phytotron, concluded that, compared to monoculture, spruce was a stronger competitor than beech, as displayed by a higher increment of the spruce above-ground biomass and a decrease in the beech biomass increment in a mixed stand. Even Smith et al. (2013) described a four-year experiment under elevated CO_2 concentration (ca 580 µmol mol^{-1}) in a monoculture and a mixed stand of *Betula pendula* Roth, *Alnus glutinosa* [L.] Gaertn. and *Fagus sylvatic*a L., in order to compare wood biomass production. The amount of biomass of *Fagus sylvatica* L. increased by about 22% in the monoculture, but not at all in the mixed stand.

In all presented experiments, only Group-mixed and Pure were applied. Our results are comparable with those of the above beech-spruce experiments and the birch-alder-beech experiment, where the biomass production of the beech was stimulated in Pure but not in Group-mixed. Unfortunately, we found no estimation of Beech biomass in Single-mixed in available literature. The type of arrangement can play a crucial role in tree biomass production in the future. Our results showed that there are differences between Single-mixed Beech and Group-mixed Beech. While the amount of the total biomass and of the individual biomass parts of Beech was significantly greater in Single-mixed Beech (which was surrounded by spruce), and only slightly greater in Pure Beech, there was less biomass of Group-mixed Beech inside Dome E than Dome A.

Egli & Körner (1997), Spinnler et al. (2002, 2003) wrote that the amount of biomass of Spruce increases within both a monoculture and a mixed stand. Sigurdsson et al. (2013) showed that there is more above-ground biomass under elevated CO_2 concentration in a monoculture. Our results showed a very slight decrease in the total amount of biomass (i.e. above-ground and below-ground biomass) in Group-mixed and Pure, which corresponds to the results of the following authors: Hättenschwiler & Körner (1997) stated that the biomass components (except root biomass) of spruce were affected only by N deposition (not CO_2 concentration); Kostiainen et al. (2004) demonstrated the insignificant effects of CO_2 concentration on the growth of Spruce in a monoculture, and Terrer et al. (2021) and Maschler (2023) report a negative relationship between increased concentration and biomass growth (in general) if there is a lack of N in the soil. In Pure Spruce, not only was there no increase in the amount of biomass in all components inside Dome E there was less biomass than inside Dome A. There was more biomass only from the roots (i.e. below-ground biomass) and needles in Group-mixed inside Dome E than inside Dome A. These results corresponded to those of Klein et al. (2016), where fine roots did not respond to elevated CO_2 concentration in Pure Spruce but did not correspond to those of Hättenschwiler & Körner (1997) who state that the more elevated the CO_2 concentration the more root biomass there is in Pure Spruce.

We found a greater increase in the amount of the biomass in Single-mixed Beech and Single-mixed Spruce inside Dome E than inside Dome A. It seems that growth stimulation with elevated CO_2 concentration can increase the amount of the biomass of the trees in Single-mixed, due to less inter-specific competition. A greater amount of biomass was found in all parts of beech and spruce. According to Taylor et al. (1994) and Pritchard et al. (1999), first the amounts of leaf and root biomass increase, and then of the other parts of the tree. However, the amount of biomass of each part of our Single-mixed Beech and Single-mixed Spruce trees was greater. Therefore, we suppose that these trees completely adapted to the elevated CO_2 concentration in under eight years (which was the duration of the experiment) and the increase in the amount of biomass under elevated CO_2 concentration, compared to that under ambient CO_2 concentration, will most probably continue. Spruce trees develop a root system just beneath the ground surface, or in a shallow soil layer, whereas the beech root system occupies deeper layers (Schmid 2002; Bolte & Villanueva 2006; Zwetsloot et al. 2019). Therefore, there is practically no competition between the root systems of beech and spruce in below-ground space, mainly for water. According to Pretzsch et al. (2020), Bošeľa et al. (2021) and Rohner et al. (2021), spruce growing in an inter-specific environment with beech was less affected by natural episodic drought than that in an intra-specific environment. Spruce as a coniferous tree species can suffer by acclimation depression under elevated CO_2 concentration, thus exhibiting slower initial growth, compared to beech (Urban & Pokorný 2003; Špunda et al. 2005; Pokorný et al. 2012; Urban et al. 2012; Pokorný et al. 2013a). Due to this, Single-mixed Beech can grow faster (to a greater height, stem diameter and amount of biomass) than the surrounding spruce trees. Moreover, Beech trees were taller (about 20 cm) than Spruce at the beginning of the experiment. On the other hand, Single-mixed Spruce growing among only Beech trees can have enough nutrients and water (since it alone occupies the shallow soil) and is forced by the surrounding Beech trees to grow rapidly. However, its height and thickness growth are slower than those of the surrounding beech trees (Vyskot 1978), therefore it achieves more biomass in the form of larger branches, more needles and more voluminous roots, thereby occupying more space and gaining more water and nutrients for the future, but it is smaller than the surrounding beech trees.

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5. Conclusions

During the first two years of the experiment, there were no changes in the height and stem diameter, as a result of planting shock and the time response to the elevated CO_2 concentration. After this period, the stem diameters and heights of the trees began to differ from those in the other arrangements. At the end of the experiment, beech and spruce trees growing in different arrangements and CO_2 concentrations differed in their heights and thicknesses, and also in the amounts of their biomass.

Beech is an important species and its cultivation in larger quantities will be desirable in the future. According to our results, it will be more suitable to grow beech as a monoculture or singly. Spruce, from the viewpoint of economic utilization, is very important and, therefore, it will be necessary to maintain its presence in general (in an economically and ecologically appropriate ratio) growing singly.

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