Effect of increasing temperature and CO_2 concentration on growth of sycamore maple and European beech

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Synopsis

The effect of the possible global warming in combination with CO_2 concentration increase on dry matter production, partitioning of dry matter and growth of *Acer pseudoplatanus* L. and *Fagus sylvatica* L. saplings was investigated in ten fully climatized phytotron chambers with five different air temperature regimes. The two control chambers were based on monthly averages (day and night) from 1909–1969 in Berlin-Dahlem (52°28'N, 13°18'E): ±0 °C; the four other levels were constantly fixed to −4, −2, +2, +4 °C from this control. One chamber per temperature step was supplied with 'unchanged ambient air': 398 ±42 ('350 µmol mol^{-1} level') and the other with 690 ±55 µmol mol^{-1} CO_2 ('700 µmol mol^{-1} level').

From June to November of their 2nd year 8 saplings of *A. pseudoplatanus* in 2 dm^3-pots and 24 of *F. sylvatica* in 1 dm^3-pots grew per chamber in homogenized sandy loam without water or nutrient stress. Dry mass of all parts of *A. pseudoplatanus* was increased at elevated CO_2 (except that of coarse roots at +4 °C). Leaf masses differed most at −2 °C (35%) and least of all at +4 °C (18%). Dry masses of stems and twigs were significantly enhanced at −2, 0, +2 °C (29; 31; 23%). The difference between the mean dry masses of coarse roots was the greatest at −4 °C (43%) and gradually disappeared with increasing temperature. In total, mean dry masses of fine roots differed by 21%.

There was no significant additional dry mass accumulation of *F. sylvatica*. On the two lowest temperature levels enhancement of stem diameter and height growth of *A. pseudoplatanus* by CO_2 was greater than in the control and on the higher temperature levels. Stem height was enhanced by 20% at −2 °C and by 11% at +4 °C at the end of the vegetation period and mean number of leaves /tree was finally increased by 20 leaves/tree at the highest temperature level.

Stem diameter of *F. sylvatica* was enhanced by 14.5% at the lower temperature levels (−4, −2 °C) already in July and its number of leaves/tree by 5%.

Biomass production, growth, temperature increase, CO_2 enrichment, Acer pseudoplatanus L., Fagus sylvatica L.

* Dedicated to Prof. Dr. Reinhard Bornkamm on the occasion of his 65th birthday.

1 Introduction

Atmospheric CO_2 concentration is continuously increasing worldwide mainly caused by fossil fuel burning. From 1959–1992 the increase amounted to a rate of 1.1 µmol mol^{-1} CO_2 per year (Mauna Loa, 19°32' N, 155°35' W; KEELING & WHORF 1994). Near Osnabrück (58°18' N, 8°2'E) mean annual increase amounted to 1.3 µmol mol^{-1} CO_2 (FORSTREUTER & al. 1994).

On the other hand, mean surface temperature of the world has warmed 0.5°C since the middle of the 19th century with a considerable rise during the last decade (JONES & al. 1994). The CO_2 increase has obvious direct effects on plant metabolism and growth (POORTER 1993) since CO_2 is the carbon substrate of photosynthesis and CO_2 inhibits photorespiration (AMTHOR 1991). On leaf area basis also a small decrease of dark respiration was reported for elevated CO_2 (2–4-times ambient concentration) by POORTER & al. (1992). And it is a common assumption that an increase in temperature will directly increase plant respiration in total in the short term, although acclimation to moderate changes in temperature occurs (KÖRNER & LARCHER 1988).

Therefore, combined effects of increasing levels of temperature and CO_2 must be considered jointly (POTVIN & STRAIN 1985). One possibility could be that increasing temperatures interact with rising CO_2 to stimulate plant growth to a greater extend than one would expect from the enhancement by increases in CO_2 levels alone. IDSO & al. (1987) showed for a variety of crop species that stimulation of mean weekly plant growth by elevated CO_2 concentrations was positively correlated with mean weekly temperatures.

In contrast, HOFSTRA & HESKETH (1975) found that temperatures greater or less than the optimal growth temperature resulted in a decrease in the relative stimulation of photosynthesis by elevated CO_2. ZISKA & BUNCE (1993) detected that the relative enhancement by CO_2 declined as temperature increased. Therefore, we conducted growth experiments on sycamore maple and European beech with different temperature levels at ambient and at doubled CO_2 concentration.

2 Material and methods

Experimental design

On the base of the arithmetical means of the monthly minima of nightly air temperatures and of daily maxima from 1909–1969 in Berlin-Dahlem (Meteorological Institute of the Free University Berlin, 52° 28'N, 13° 18' E, Tab. 1) five different air temperature levels with one replication were established in ten fully climatized glass phytotron chambers of ~2.5 m^3.

Tab. 1

Mean monthly base values for a temperature (day and night) experiment with young sycamore maple and European beech in 10 fully climatized phytotron chambers.

	Min. temperature night	Max. temperature day
April	4	13,5
May	8	19
June	11	22
July	13	24
August	12,5	23
September	9	19
October	5	13
November	2	7

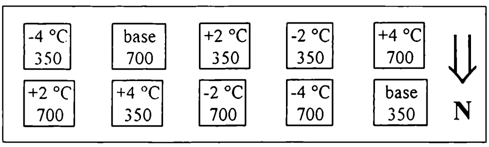

Fig. 1

Temperature regimes and CO_2 concentrations in ten fully climatized phytotron chambers for pot experiments with beech seedlings and sycamore saplings (350: 398 ±42 and 700: 690 ±55 µmol mol^{-1} CO_2).

The two control chambers were run at these monthly averages (±0 °C) and the four other levels were constantly fixed to −4, −2, +2, +4 °C from this control (Fig. 1). Temperature levels were changed from day (13 hrs) to night (11 hrs) and monthly. Air was circulated through an air conditioning system consisting of cooler and heater and a humidifier. Air temperatures and rel. air humidities were measured automatically (Pt–100 and capacitive humidity sensors, Typ 163, Testotherm, Lenzkirch, Germany), registered and controlled by an electronical device (Honeywell) combined with a computer. Temperatures of two parallel chambers deviated ±0.2 °C from each other and fluctuated ±0.2 °C around the nominal value. Vapor pressure deficits were slightly higher at higher temperature levels and differed from day to night. The mean course of air temperature and vapor pressure deficit is shown in Fig. 2 for the 2nd experimental phase.

Phytotron chambers had been constructed in two parallel rows in an open area in the field and were protected against direct sunlight by an acrylic glass roof covered with a shading coat of lime colour. Photosynthetically active photon flux density (PPFD) in the chambers amounted to 54% of outside values on the average. Deviation of PPFD between the chambers amounted to 15% max. depending on solar angle and place of chamber in the two rows.

During the 1st year all chambers were supplied with ambient air of 371 ±46 µmol mol^{-1} CO_2. During the 2nd year one chamber per temperature level was supplied with 'unchanged ambient air' of 398 ±42 µmol mol^{-1} ('350 µmol mol^{-1} level', control) and the other with 690 ±55 µmol mol^{-1} CO_2 ('700 µmol mol^{-1} level'). In order to maintain the elevated CO_2 concentration level CO_2 was injected into the air streaming back from the cooler to the chambers out of two tanks with liquid CO_2 (Air liquide, France). CO_2 concentrations were measured in the chambers by means of one absolute IRGA (Hartmann & Braun (Mannesmann), Typ: URAS 2T) connected with a multiplexer of 5 solenoid valves, and were manually adjusted to the nominal value with 5 rotation corpuscle gas flow meters (Krohne, Germany). CO_2 values were stored by a separate computer.

Plant material

a) In the 1st experiment from April 1st to July 20th eight 1.5-year-old saplings of *Acer pseudoplatanus* L. (sycamore maple) per chamber were exposed to the five temperature levels at 'ambient CO_2 concentration'. One group of eight individuals was placed into an open-sided vegetation hall. They had been grown from seeds (provenance: 80105, South Germany, 600 m above MSL) and were planted into 2 dm^3-plastic-pots filled with homogenized, humic sandy loam. Soil water supply was kept constant near field capacity by watering with tap water manually. Plants were not fertilized. At the end of the experiment all plants were harvested, separated into leaves, stems (+twigs), coarse roots (Ø >2 mm), and fine roots (Ø <2 mm), dried at 85 °C and weighed.

b) From June 29th until the end of the following vegetation period 8, in the beginning one-year-old, seedlings of *A. pseudoplatanus* L. and 24 seedlings of *Fagus sylvatica* L. (European beech) grew in the chambers at the same temperature levels as before, however at the two CO_2 concentrations described above. Seeds of *A. pseudoplatanus* were from the same population as before; provenance of *F. sylvatica* seeds was 80103, North-German Lowland, Governmental Forestry Office Ebstorf. Sycamore maple grew

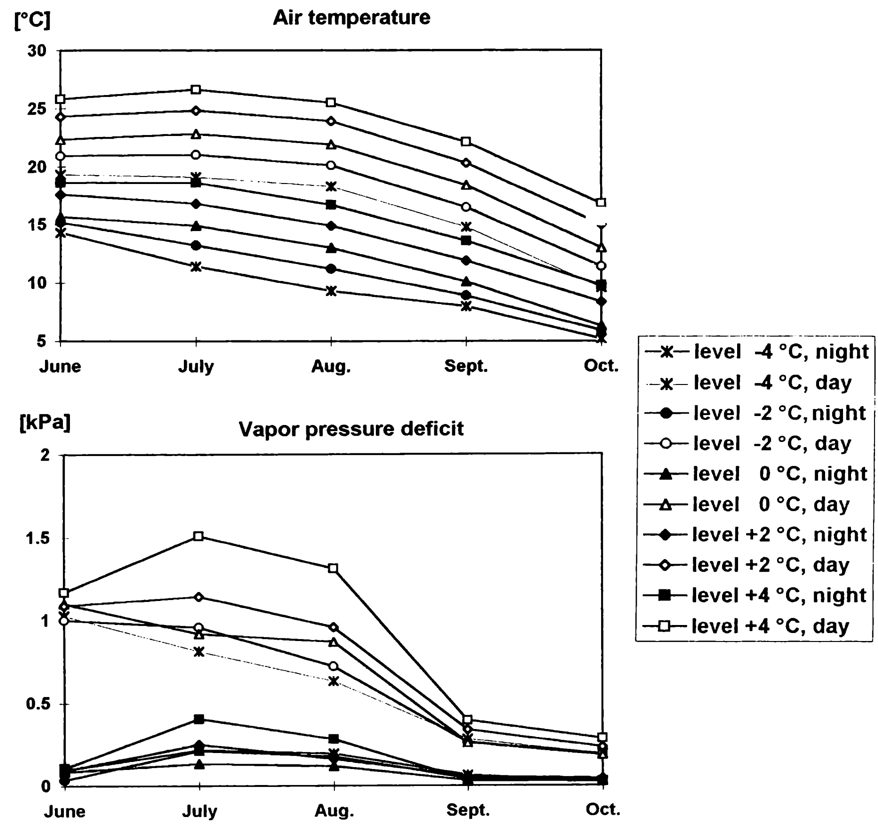

Fig. 2

Mean course of air temperature and vapor pressure deficit during a phytotron experiment with sycamore maple and European beech seedlings.

in 2 dm³-pots and beech in 1 dm³-pots. Substrate and watering procedure was not changed. Stem height and stem diameter (2 cm above soil surface) of *A. pseudoplatanus* were measured nondestructively every month from June to Sept., and from June to Nov. the same parameters were determined for *F. sylvatica*. Until Sept. leaves of both species were counted. All sycamore maple saplings were harvested before (Sept.) and the 6 smallest and the 6 tallest beech saplings after leaf fall (Nov.). Dry masses of leaves (*A. pseudoplatanus* only), stems (+twigs), coarse roots Ø >2 mm), and fine roots Ø <2 mm) were determined separately following the same procedure as in the year before.

The SAS-package was used for statistical analysis following the procedure ANOVA (multivariate F-test) for stem height and stem diameter data (SEARLE 1971).

3 Results

1st experiment

On the average, lowest dry masses were accumulated in all four plant parts of *A. pseudoplatanus* at the lower temperature levels, and there was a clear tendency of the dry mass of leaves, stems and coarse roots to increase with raised temperature levels (Fig. 3).

Optima were reached at the +2 °C level. Mean dry mass of fine roots showed a tendency to increase from +2 °C to +4 °C. Mean dry mass of leaves increased up to the +2 °C level by 44% and decreased again to the +4 °C level by 14%. Mean dry mass of stems (+twigs) increased up to the +2 level by 68% and were again 14.5% lower at the +4 °C level (relative to the optimum). Mean dry mass of coarse roots increased to the optimum by 62% and decreased to

+4 °C by 16%. Difference between dry masses of fine roots at the lowest and at the highest temperature level amounted to 62%. Dry masses of the control plants in the open vegetation hall were close to those from the lowest temperature level in the phytotron experiment (except coarse roots).

2nd experiment

Dry mass

At 'ambient CO_2 concentration' dry mass of leaves and stems (+twigs) of *A. pseudoplatanus* showed a similar relationship to temperature in the 2nd experiment as in the year before reaching optimum on the +2 °C level. Dry masses of coarse roots increased from −4 °C to 0 °C and, on the average, remained unchanged up to level +4 °C. No influence of temperature on dry mass of fine roots could be found (Fig. 4, on the left).

CO_2 effect on dry mass accumulation was evident for all parts of *A. pseudoplatanus* (except for coarse roots at +4 °C). In general, CO_2 effect was more positive at lower temperature levels. Leaf masses differed most at −2 °C (55%) and least of all at +4 °C (18%). Dry masses of stems (+twigs) were not influenced by elevated CO_2 at the lowest and at the highest temperature level. However, their dry masses were significantly enhanced at −2, 0, +2 °C (29%, 31%, 23%). At −4 °C the difference between the mean dry masses of coarse roots was the greatest and gradually disappeared with increasing temperature. At the highest temperature level mean dry mass of fine roots differed by 44.5% significantly. Averaged over all temperature levels the CO_2-induced difference of fine root masses amounted to 21%.

Dry masses of stems (+twigs), coarse roots, and fine roots of *F. sylvatica* seedlings was not affected by additional CO_2 at the lower temperature levels. A tendency to develop a certain enhancement occured at the levels +2 °C and +4 °C (statistically not significant).

Stem height and stem diameter

In the course of the experiment additional CO_2 induced differences in stem height and stem diameter of *A. pseudoplatanus* (Fig. 5).

The greatest relative difference between stem heights occured at −2 °C in Aug. (22%) and in Sept. (20%). At −4 °C differences were not significant (9% in Aug., 2% in Sept.). At the highest temperature level (+4 °C) relative difference amounted to 11% in Aug. and Sept.. Analysis of variance for the dependent variable stem height indicates the following significant influences: temperature: DF (degrees of freedom) = 4, F-value = 36.7, $p < 0.0001$; CO_2: DF = 1, F-value = 10.3, $p < 0.002$.

Stem diameter was increased by 13% at −4 °C and by 8% at −2 °C in Sept. Analysis of variance for

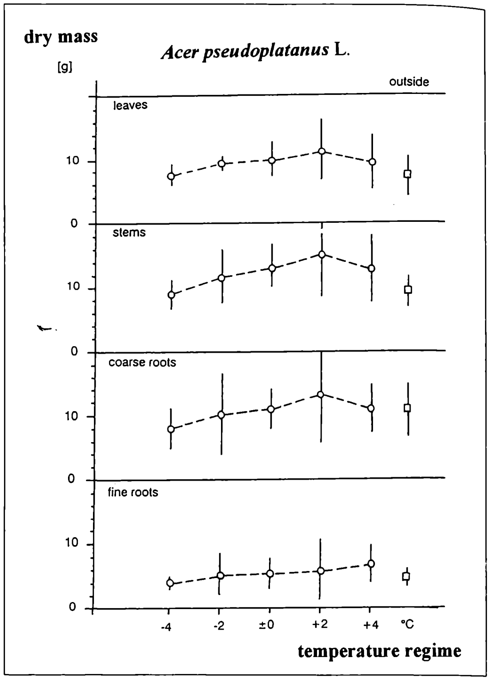

Fig. 3

Dry mass of different organs of sycamore maple saplings at the peak of the vegetation period after four months under different temperature regimes (bars indicate minimum and maximum dry mass).

the dependent variable stem diameter indicates the following significant influences: temperature: DF = 4, F-value = 5.4, $p < 0.0003$; CO_2: DF = 1, F-value = 8.07, $p < 0.005$; temperature x CO_2: DF = 4, F-value = 3.12, $p < 0.02$. DUNCAN's multiple range test and STUDENT-NEWMAN-KEUL's test point to a significant CO_2 effect, too.

Stem height of *F. sylvatica* seedlings was not significantly influenced neither by temperature nor by CO_2, whereas stem diameter was influenced by CO_2 only (Fig. 6). Difference between stem diameters were the greatest at −4 °C and at −2 °C. They occured in July already and remained approximately at the same relative value of ~14.5%. Analysis of variance for the dependent variable stem diameter indicates the following significant influences: CO_2: DF = 1, F-value = 42.6, $p < 0.0001$, temperature x CO_2: DF = 4, F-value = 19.7, $p < 0.0001$. DUNCAN's multiple range test and STUDENT-NEWMAN-KEUL's test corroberate the positive CO_2 effect on this parameter.

Mean number of leaves/tree

Temperature and CO_2 increased the number of leaves/sapling of *A. pseudoplatanus*. The higher the temperature level was the more elevated CO_2 enhanced

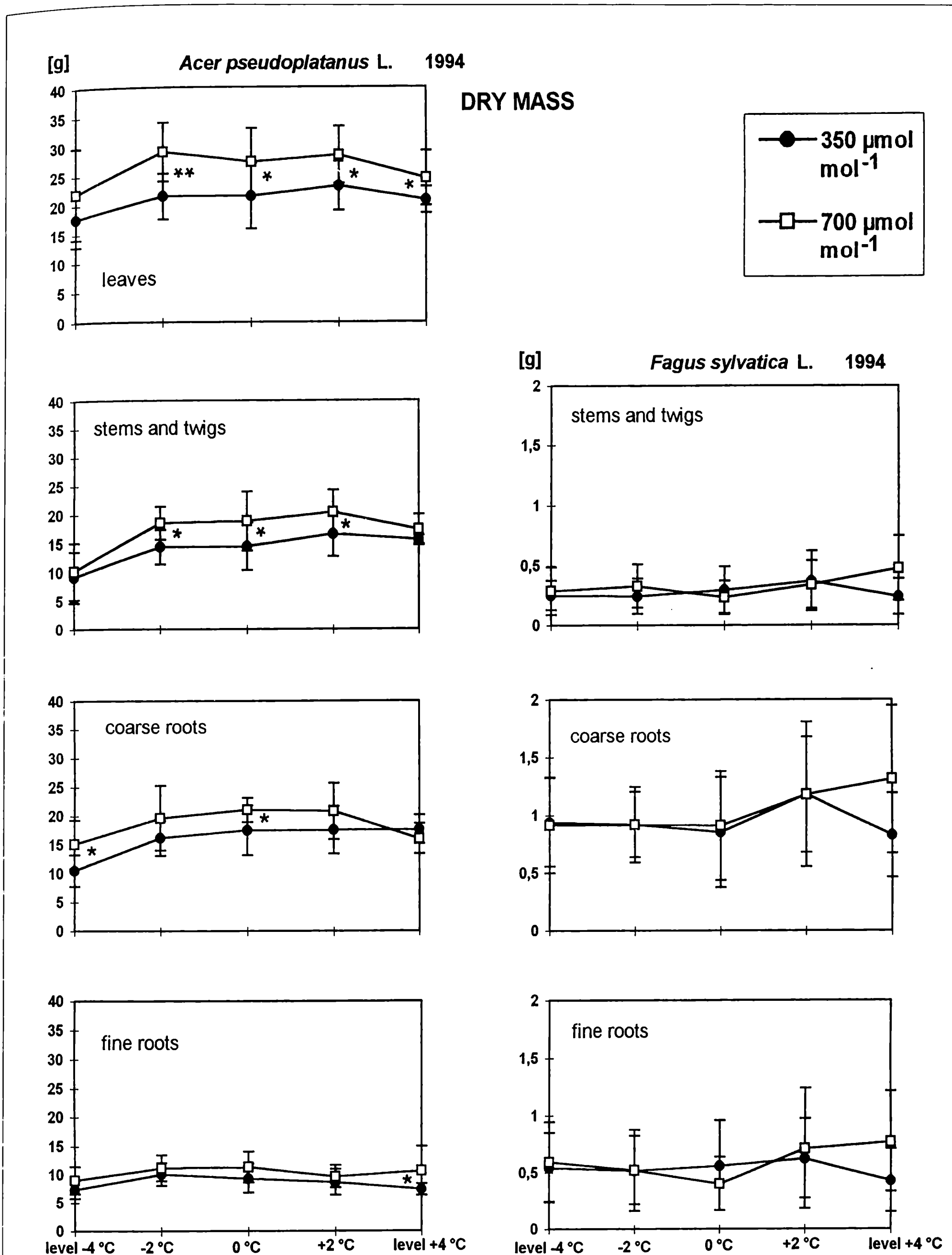

Fig. 4

Dry mass of sycamore maple saplings (on the left) and European beech seedlings after 4–5 months at five different temperature and two different CO_2 concentration levels;

'350 µmol mol^{-1}': 398 ±42 µmol mol^{-1} CO_2;
'700 µmol mol^{-1} CO_2': 690 ±55 µmol mol^{-1} CO_2;
****: significant with $p < 0.01$;**
***: significant with $p < 0.05$.**

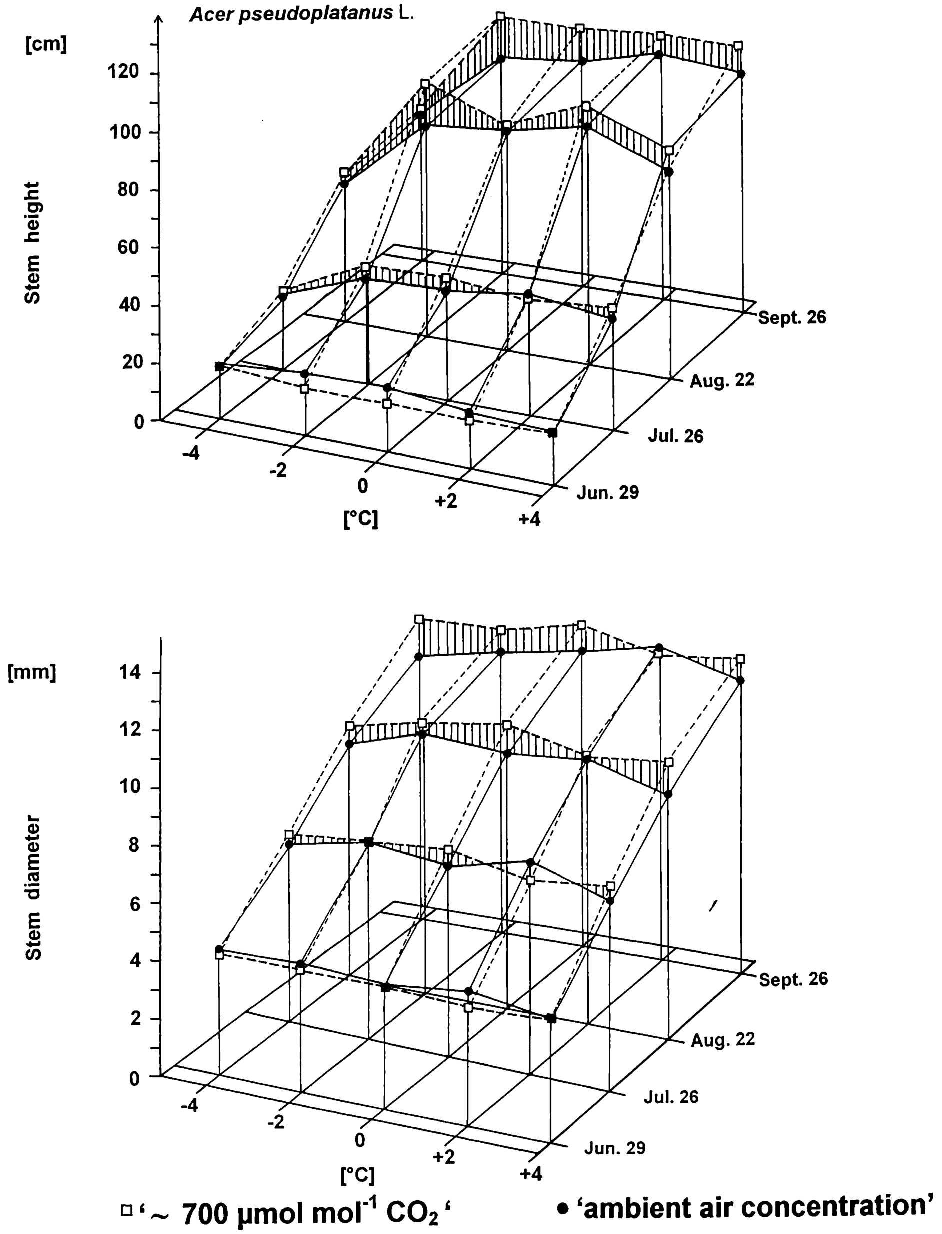

Fig. 5

Development of stem height and stem diameter of sycamore maple saplings at five different temperature and two different CO_2 concentration levels; 'ambient air concentration': 398 ±42 µmol mol^{-1} CO_2; '700 µmol mol^{-1}': 690 ±55 µmol mol^{-1} CO_2.

development of leaves (Tab. 2). Analysis of variance for the dependent variable number of leaves/tree indicates the following significant influences despite of high variability: temperature: DF = 4, F-value = 6.22, $p < 0.0001$; CO_2: DF = 1, F-value = 4.89, $p < 0.03$; temperature x CO_2: DF = 4, F-value= 2.55, $p < 0.04$). At the end of Sept. difference between the two CO_2 levels reached 36%, i.e., on the average, ~20 leaves more per tree at elevated CO_2. The two other statistical tests indicate similar significances.

Temperature effect on number of leaves/*F. sylvatica* seedling was not evident. Difference in dependence of the variable CO_2 is according to analysis of variance, DUNCAN's multiple range and STUDENT-NEWMAN-KEUL's test slightly below the critical range. 5% more leaves per tree were found, on the average, i.e ~0.5 leaf/seedling.

4. Discussion and conclusions

At least for *A. pseudoplatanus* the hypothesis that temperature and CO_2 interact on growth and dry matter accumulation can be accepted on the base of our results generally. Probability is also high that both factors together affect *F. sylvatica* not in the same way as if they were acting alone. Assumed that there is interaction for both species, it has to be described for sycamore maple and European beech differently. One reason for this different response is the fact that the shape of the response curve to temperature at contemporary CO_2 concentration already differs between the two species. In our experimentally given range of −4 °C below to +4 °C above average dry mass accumulation and growth of *A. pseudoplatanus* is following an optimum curve. However, in the case of *F. sylvatica* no clear or a slight linear relationship could be stated. So, one of many thinkable reasons for differences between these two species in their juvenile growth strategy can be their distinct ability to react upon temperature changes. If, on the one hand, response on temperature is diverse one would expect that response on temperature interacting with CO_2 is species dependent, too. In fact, three different possibilities are reported in literature: the higher the temperature the greater the CO_2 effect, no interaction between temperature and CO_2, and thirdly, CO_2 enhancement decreases with increasing temperature. DRAKE (1992) postulates that external environmental factors, such as temperature modify CO_2 response and emphazises that greatest stimulation of growth can be expected to occur at high temperature and much smaller responses at low temperature. This statement is mainly derived from studies on herbaceous perennial plants. KIRSCHBAUM's (1994) theoretical analysis of the dependence of C_3-photosynthesis on temperature and background CO_2 concentration showed that at 350 μmol mol^{-1} CO_2 and 35 °C, photosynthesis reached 51% of the rate that would have been possible with 'non-limiting CO_2', whereas at 5 °C, 77% of the CO_2 'non-limiting rate' was attained. One can conclude from this study that also photosynthesis has a greater potential to be stimulated by additional CO_2 at high temperatures. STANGHELLINI & BUNCE (1993),

Tab. 2
***Acer pseudoplatanus* L.**

Date	−4 °C	−2 °C	−0 °C	+2 °C	+4 °C	μmol^{-1} CO_2
June 29	17.6 ±3.1	15.5 ±2.5	16.5 ±2.5	15.8 ±1.7	18.3 ±4.3	'700'
	17.5 ±3.7	19.9 ±3.6	17.4 ±3.3	16.6 ±3.9	17.0 −1.6	'350'
July 26	28.9 ±10.1	35.6 ±5.8	35.1 ±7.7	31.3 ±5.4	37.3 ±8.9	'700'
	31.0 ±7.4	35.1 ±6.2	33.6 ±10.5	33.1 ±6.1	34.5 ±8.9	'350'
Aug. 22	47.8 ±21.9	63.0 ±12.0	61.4 ±17.1	55.6 ±13.3	71.5 ±14.6	'700'
	51.1 ±17.2	59.5 ±11.2	54.4 ±20.9	47.9 ±10.4	53.3 ±18.7	'350'
Sept. 26	49.8 ±23.0	63.5 ±9.2	62.1 ±16.3	54.6 ±10.9	75.4 ±16.7	'700'
	52.8 ±14.3	63.1 ±11.4	55.5 ±22.7	48.3 ±8.7	55.5 ±14.9	'350'

***Fagus sylvatica* L.**

	700	350
June 28	8.3 ±0.6	7.7 ±0.7
July 26	9.1 ±0.7	8.7 ±0.5
Aug. 22	9.5 ±0.6	9.0 ±0.3
Sept. 21	9.0 ±0.2	9.1 ±0.2

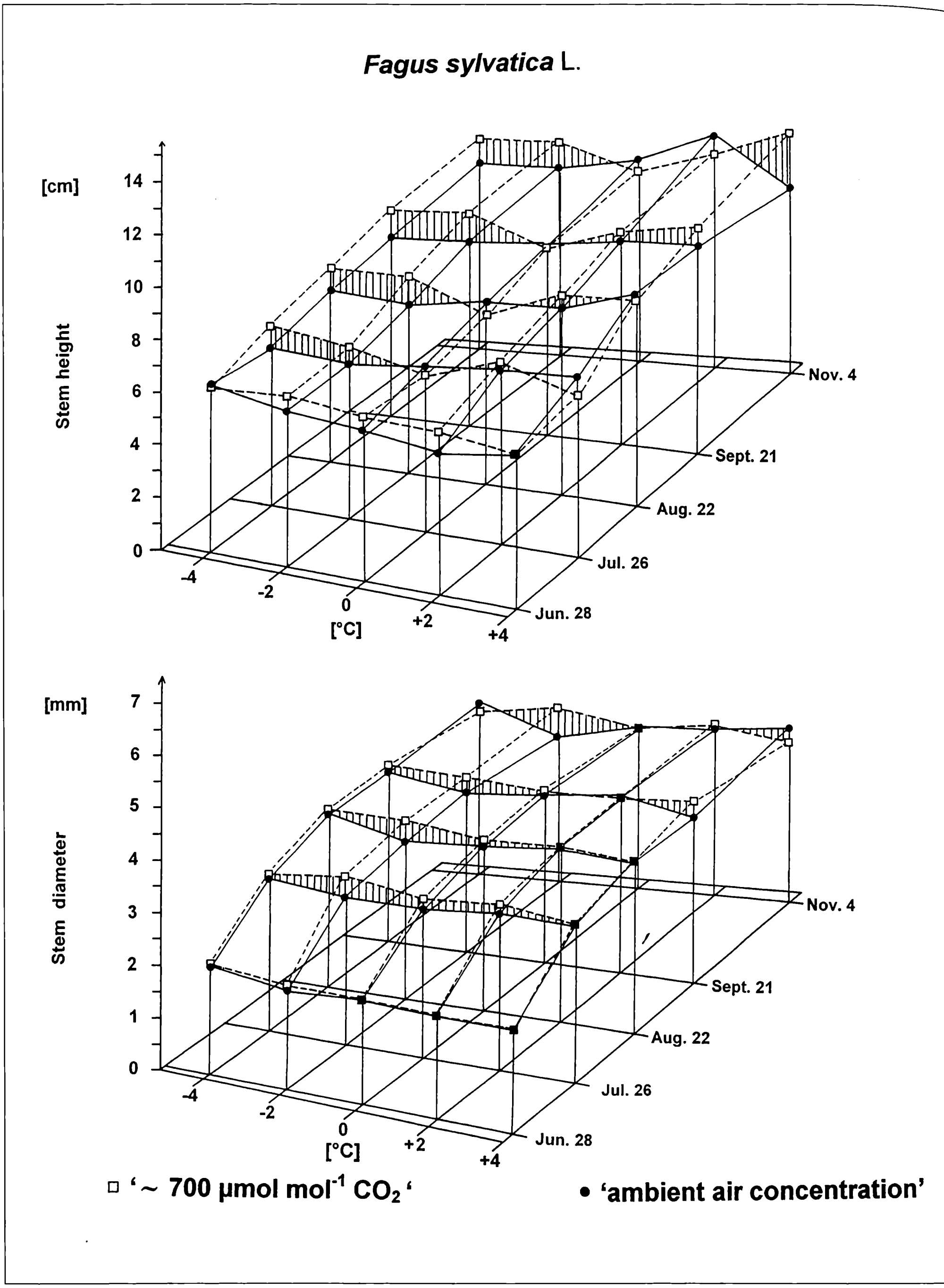

Fig. 6

Development of stem height and stem diameter of European beech seedlings at five different temperature and two different CO_2 concentration levels; 'ambient air concentration': 398 ±42 µmol mol^{-1} CO_2; '700 µmol mol^{-1}': 690 ±55 µmol mol^{-1} CO_2.

however, found that net CO_2 assimilation rates of tomato (*Lycopericon esculentum*) are not affected by temperature over the range 18 to 32 °C co-occuring with a clear enhancement by 700 μmol mol^{-1} CO_2. COLEMAN & BAZZAZ (1992) point at the difference between C_3- and C_4-plants: increase from 28 °C to 38 °C had no effect on biomass of *Abutilon theophrasti* (C3) whereas dry mass of *Amaranthus retroflexus* (C4) was enhanced by elevated CO_2 at 28° but was depressed at 38 °C. ZISKA & BUNCE (1994) determined dry mass of the herbaceous perennials *Medicago sativa* and *Dactylis glomerata* exposed to 362 and 717 μmol mol^{-1} CO_2. Their data show that stimulatory effects of increasing atmospheric CO_2 on growth may decline with increase in temperature. And it can be argued that synergistic effects between temperature and CO_2 cannot be expected because these factors can drive growth of plants into different directions: elevated CO_2 reduces the amount of carbon lost via photorespiration and, on the other hand, photorespiration increases with temperature. CAPORN & al. (1994) found in a study on canopy photosynthesis of CO_2-enriched *Lactuca sativa* that reduction in air temperature from 16 to 6 °C at 1000 μmol mol^{-1} CO_2 halved the rate of dark respiration, and if it is also true that additional CO_2 directly reduces dark respiration slightly (POORTER & al. 1992, BUNCE 1994), it follows from these studies that CO_2 effects have to be greater at low than at high temperatures. No literature was available about combinational effects of CO_2 and temperature on trees. However, similar differences in response to CO_2 alone as between *F. sylvatica* and *A. pseudoplatanus* were found between *Fagus grandifolia* and *Acer saccharum* by REID & STRAIN (1994).

Generalized, our results support the hypothesis that tree growth and productivity is less enhanced by elevated CO_2 at slightly increasing temperatures. Mainly the worse growth of coarse roots and stems (+twigs) of *A. pseudoplatanus* is plausible because of probably increased C-losses via respiration at increasing temperature. On the base of the results for fine roots of *A. pseudoplatanus* it can be hypothezised that trees use the additional C at elevated CO_2 combined with increasing temperature to strengthen their below-ground system for nutrient and water uptake in a considerably wide temperature range; also more root dissipation and exudation may become possible. In contrast, the combinational effect of increasing temperature and CO_2 concentration leads to decreasing amounts of additional dry mass but much more leaves/sapling of *A. pseudoplatanus*. So it can be assumed that this species, which is earlier in succession than European beech, will mainly take advantage from the greater C-source and increasing temperature by spreading its photosynthetically active surface as early as possible without much additional dry matter accumulation in this compartment.

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