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Auswirkungen globaler Klimaänderungen auf das Wachstum und den Gaswechsel (CO<sub>2</sub>/H<sub>2</sub>O) von Rotbuchenbeständen (*Fagus sylvatica* L.)

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## **Summary**

This work studies the direct effects of increased atmospheric carbon dioxide concentration on growth and gas exchange ( $CO_2/H_2O$ ) of European beech (*Fagus sylvatica L.*) in three long term investigations. Fagus was selected as an indigenous species because of its importance and distribution in Europe. Using the microcosm technique, model ecosystems of juvenile beech stands were exposed to atmospheric  $CO_2$  concentrations of 350 and 700  $\mu$ mol mol<sup>-1</sup>. Short term and long term investigations (up to six years) were conducted at ambient and elevated  $CO_2$  under field-like conditions. Environmental factors such as temperature, PPFD, nutrients and water, as well as community factors such as intra- and inter-specific competition, both above and below ground , were included in this experimental approach. Parameter values for the key processes were derived from the experimental data on juvenile and adult beech trees at ambient and elevated  $CO_2$ . Results from leaf measurements were directly integrated and compared with the results from whole-canopy measurements.

Ecophysiological processes in beech stands were simulated by a mechanistic modelling approach using the FORSTFLUX model. The parameterised FORSTFLUX model was validated by simulating a set of gas exchange ( $CO_2/H_2O$ ) measurements obtained in 1993 at ambient and elevated  $CO_2$  with microcosms under field conditions. Model simulations of gas exchange were conducted to quantify the likely response of forests to the predicted global changes in climate.

The continuous measurements of the atmospheric  $CO_2$  concentration from 1992 to 1999 showed a significant yearly increase of 4.7  $\mu$ mol mol<sup>-1</sup>  $CO_2$  (1.3 % per year) in Berlin-Dahlem.

Growth of beech was highly enhanced between 31% and 81% by the elevated  $CO_2$ -concentration. Biomass accumulation was highest during the third year and lowest during the sixth year of exposure to elevated  $CO_2$ . Particularly at the beginning of the experiments biomass accumulation was highly enhanced and the  $CO_2$ -effect decreased slightly in the course of the experiments. Ontogeny of beech plants was speeded up so that at any moment over the sixth years growth was larger in elevated  $CO_2$  than in ambient  $CO_2$ . There was no  $CO_2$  effect on allocation of biomass within the beech trees. When trees were compared at the same size rather than at the same time, it was evident that there was no  $CO_2$  effect on the pattern of biomass allocation.

Nitrogen uptake by plants was increased at elevated  $CO_2$  in total by 40%. Fine root mass was significantly stimulated by elevated  $CO_2$ : trees grown in elevated  $CO_2$  had 84% more fine root mass than trees grown in ambient  $CO_2$ .

By the process of nutrient resorption nitrogen (up to 73% and 77%) in green leaves was relocated into the living part of the trees during leaf senescence. Nitrogen content of leaf litter was depleted in elevated  $CO_2$  by 21% (leaf mass basis) and 17% (leaf area basis). Decomposition

M. Forstreuter Summary

rate of leaf litter produced in elevated CO<sub>2</sub> was lower compared with litter produced in ambient air.

NPP (net primary production) of juvenile beech stands was  $0.81~kg~m^{-2}~a^{-1}$  in ambient  $CO_2$  and was significantly enhanced by 46% to  $1.18~kg~m^{-2}~a^{-1}$  in elevated  $CO_2$ . LAI (leaf area index) and leaf distribution in the canopy profile were affected by growth with no nutrient and water stress at elevated  $CO_2$ . LAI was increased in the juvenile beech stands at elevated  $CO_2$  in average by 48% (third year) and by 62% (fourth year). At low nutrient supply and sufficient water availability LAI was hardly affected at elevated  $CO_2$ .

Phenological observations showed no difference in dates of bud burst and leaf fall between ambient and elevated  $CO_2$  treatment. A linear effect of temperature on the timing of bud burst and leaf fall was observed. A temperature increase of  $1^{\circ}C$  advanced the date of bud burst by two days and leaf fall was observed to occur four days later in the seasons.

Net photosynthesis  $(A_n)$  was increased by 50 to 80% by elevated  $CO_2$  even after a long period of growth in elevated  $CO_2$ . Variability of  $A_n$  within a canopy was linearly related to leaf nitrogen and was affected by the different canopy structure of beech stands after growth in ambient and in elevated  $CO_2$ .

For all  $CO_2$  treatments and all periods of the investigated beech stands generic relationships were obtained from the experiments between the photosynthetic parameters  $J_{max}$  (electron transport capacity) and leaf nitrogen concentration ( $N_a$ ), and between  $V_{cmax}$  (carboxylation capacity) and  $N_a$  were obtained from the experiments.  $J_{max}$  values were 52.2  $\mu$ mol m<sup>-2</sup> s<sup>-1</sup> and 51.2  $\mu$ mol m<sup>-2</sup> s<sup>-1</sup> and  $V_{cmax}$  showed values of 33.5  $\mu$ mol m<sup>-2</sup> s<sup>-1</sup> and of 31.7  $\mu$ mol m<sup>-2</sup> s<sup>-1</sup> in ambient and elevated  $CO_2$  treatments.  $V_{cmax}$  /  $J_{max}$  ratio was in the range of 0.62 and 0.64 . It was not affected by environmental changes. No down-regulation of the parameters  $J_{max}$  and  $V_{cmax}$  was observed in the investigations when nutrients were in sufficient supply. Nitrogen use efficiency was at the same level in both  $CO_2$  treatments. Net photosynthesis ( $A_n$ ) was not affected by increased TNC concentrations in beech leaves of 30% to 35% at elevated  $CO_2$ .

Increase of net photosynthesis at elevated  $CO_2$  was higher at elevated temperature. At ambient  $CO_2$  concentration the optimal temperature for  $A_n$  ranged between 27.7 and 29.1°C. At elevated  $CO_2$  temperature optimum was changed by 1-2°C to higher temperature values.

Temperature optima of photosynthetic parameters ranged between  $31.0^{\circ}$ C and  $31.1^{\circ}$ C for  $J_{max}$  and between 33.2 and  $34.4^{\circ}$ C for  $V_{cmax}$ . No differences between the  $CO_2$  treatment were observed.

Dark respiration of leaves, stems and fine roots was not affected by elevated  $CO_2$ .  $Q_{10}$  values in the temperature range between 10 and 20°C of 2.3 for leaf respiration and 1.75 for stem respiration were observed.

The study also showed that below-ground respiration rates of the model ecosystems were greater under elevated  $CO_2$  treatments. The increase (34%) of below-ground respiration rates was related to the higher amount of fine root mass in model ecosystems, which were grown under high  $CO_2$  treatment, in comparison to model ecosystems grown under ambient  $CO_2$  treatment ( $R_{dsoil}$  [ $\mu$ mol m<sup>-2</sup> s<sup>-1</sup>]= 0.0027 \* FWM [g] + 2.02).

Total non structural carbohydrate (TNC) content was higher in source organs (leaves) at elevated  $CO_2$  and no differences in the content were observed in sink organs (stem and roots) between the  $CO_2$  treatments. Therefore TNC content in beech, in average 7.4 % of dry mass, was

Summary M. Forstreuter

proportional to the amount of total biomass.

Lignin contents in leaves and roots were not affected by growth under elevated atmospheric  $CO_2$ , but stems showed a significant reduction in lignin content at elevated  $CO_2$ .

Stomatal conductance showed a significant decrease (27%) in response to growth in elevated  $CO_2$ . The response in stomatal conductance to elevated  $CO_2$  did not differ between juvenile and adult beech trees. No acclimation of stomatal conductance to growth in elevated  $CO_2$  was observed in the investigation.

Water use efficiency (WUE) was significantly increased at higher CO<sub>2</sub> concentrations. Leaf area index (LAI) of the model ecosystems was also higher at elevated CO<sub>2</sub> concentration. Therefore the CO<sub>2</sub> effect on stomatal conductance was compensated by the higher LAI, the water budgets of the model ecosystems showed no difference between the CO<sub>2</sub> treatments.

The simulated net ecosystem  $CO_2$  exchange (NEF) of the FORSTFLUX model, which took a change in canopy structure at elevated  $CO_2$  into account, was increased between ambient and elevated  $CO_2$  by 17% from 20.0 mol m<sup>-2</sup> a<sup>-1</sup> to 23.4 mol m<sup>-2</sup> a<sup>-1</sup>. Simulated Evapotranspiration (ET) of the model ecosystems war hardly affected by elevated  $CO_2$ . Net photosynthesis simulated by FORSTFLUX for the beech stands showed an increase between ambient and elevated  $CO_2$  by 35% from 87.1 mol m<sup>-2</sup> a<sup>-1</sup> to 118.8 mol m<sup>-2</sup> s<sup>-1</sup>. The increase in net  $CO_2$  gain at elevated  $CO_2$  was nearly compensated by enhanced system respiration rates. Below-ground respiration ( $R_{dsoil}$ ) was the largest component of  $CO_2$  efflux and increased between ambient and elevated  $CO_2$  treatment by 34% from 58.4 mol m<sup>-2</sup> a<sup>-1</sup> to 78.5 mol m<sup>-2</sup> a<sup>-1</sup>.

The effect of increased temperature (+2 and  $+4^{\circ}$ C) on the simulated fluxes resulted in a strong reduction of NEF and an enhancement of ET (increase of 11% and 23%). Increased nitrogen supply (+25% and +50%) in the canopy was generally predicted to have a large positive effect on NEF (45% and 102%) and on ET (of 15% and 30%).

Model simulations of the synergistic effects of all three environmental factors (CO<sub>2</sub>, temperature and nitrogen) showed that a negative response on NEF by increased temperature was overcompensated by a positive response on NEF by increased nitrogen supply. The model results indicated a potentially higher NEF. In addition the values of ET were increased by 5% to 49%.