

TREE GROWTH UNDER THE IMPACT OF ELEVATED CO₂ CONCENTRATION AND SOME PRACTICAL ASSESSMENTS

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ABSTRACT

The dynamics of forest ecosystems depend on interactions between a number of biogeochemical cycles (i.e. carbon, nutrient, and hydrological cycles) that could be modified by human actions. Conversely, these ecosystems are important components that create sources and sinks of important greenhouse gasses, e.g. carbon dioxide, methane etc. Especially, carbon is exchanged naturally through photosynthesis, respiration, decomposition, and combustion processes. Continuous increase of atmospheric carbon dioxide concentration ([CO₂]) has led to extensive research describing impacts of elevated [CO₂] on basic physiological processes and consequent changes of biomass production on the whole plant level. In this paper we present several results obtained predominantly with Norway spruce trees. Moreover, we bring a few practical recommendations for the forest management under the impact of elevated [CO₂].

Keywords: elevated CO₂, forest management, physiology

INTRODUCTION

Global carbon stock in temperate forests is estimated at 159 Gt C (59 Gt C for the vegetation, 100 Gt C for the soil) at the present time (Watson et al. 2000). Continuous emission of CO₂ into the atmosphere from fossil fuel burning, cement production, and as a result of land-use change has led to an increase of atmospheric [CO₂] from ca. 285 to 366 μmol(CO₂) mol⁻¹ during the last 150 years. An increase up to 700 μmol (CO₂) mol⁻¹ is presumed in the middle of 21st century.

The rates and trends of carbon uptake in forest ecosystems are quite uncertain, how-

ever, during the last two decades, terrestrial ecosystems may have served as a small net sink for CO₂. Nevertheless, the additional terrestrial CO₂ uptake on a global scale is likely to be maintained for a number of decades in forest ecosystems, but may gradually disappear. Moreover, forest ecosystems may even become a source of CO₂ for the following three reasons: (1) limitation of CO₂ uptake capacity by nutrients and other biophysical factors, (2) decreasing of photosynthetic rate and rise of heterotrophic respiration with increasing temperature, and (3) ecosystem degradation resulting from the climate change (Watson et al. 2000).

Carbon dioxide has two direct physiological effects on plants. It acts as: (1) the activator of RUBISCO (ribulose-1,5-bisphosphate carboxylase/ oxygenase) enzymatic activity, and (2) the substrate of the Calvin cycle in the process of carboxylation.

MATERIALS AND METHODS

In the Czech Republic the field experiments with elevated [CO₂] are carried out at the experimental research site Bílý Kríž in the Beskydy Mts. (49°30'N, 18°32'E, 908 m a.s.l.). The climate of this area is cool (annual mean temperature 5.0°C), humid with high precipitation (mean 1 300 mm). There were built two basic facilities: open-top-chambers (OTCs; Janouš et al. 1996) and semi-open glass domes (GDs) with adjustable windows (Urban et al. 2001). The both facilities were supplied with ambient or ambient plus 350 μmol (CO₂) mol⁻¹, i.e. double [CO₂], and contained individual or small populations of Norway spruce (*Picea abies* (L. (Karst.) trees (age 10-18 years).

For the evaluation of elevated [CO₂] impacts on the trees growth the both analytical and merological approaches were used. The merological approach is based on the monitoring of the selected process describing the whole system. Photosynthesis is the best suitable messenger of information about whole plant condition because it is (i) key metabolic process, (ii) cross-point of the many other metabolic pathways, (iii) it is strongly coupled to the solar radiation and microclimate, and (iv) it is related process strongly influenced by the stand energy balance. A detailed description of photosynthesis measurement was given in many previous papers, e.g. Urban et al. (2003).

RESULTS AND DISCUSSION

Effects of elevated [CO₂] on photosynthesis

Potential benefit from increasing [CO₂] is less in C₄ and CAM species (photorespiration losses are less) compared to C₃ ones. The initial assessments predicted an increase (i.e. up-regulation) of the CO₂ assimilation rate and a decrease (i.e. down-regulation) of the assimilation capacity (Percy & Björkman 1983). Experimental data confirmed the increase of assimilation rate but rejected the speculation that assimilation

capacity is always decreased (Urban 2003). It led to the formation of new alternative hypotheses to explain down-regulation of photosynthesis: (a) redistribution and/or shortage of inorganic phosphate, (b) decrease of RUBISCO amount and/or activity, (c) mechanical damage of thylakoids due to excessive starch accumulation, (d) inhibition of photosynthetic genes, (e) dilution and/or redistribution of nitrogen, (f) changes in the light harvesting, (g) differences in a new sinks-source status of the plant, and (h) modification of sink capacity due to changes in canopy space structure.

It was demonstrated that the balance between biochemical and morphological changes controls the final response to elevated $[\text{CO}_2]$, i.e. active carbon sinks may maintain enhanced assimilation rates for long time.

Effects of elevated $[\text{CO}_2]$ on respiration

A doubling of atmospheric $[\text{CO}_2]$ results in an average 15 - 20% reduction in mitochondrial respiration that varies both within and among species (some crops may show as much as a 20% increase in respiration). Maintenance respiration, that appears to be related to the nitrogen content within the tissue, is more sensitive to temperature, CO_2 concentration, protein turnover, and water stress than the growth respiration. It is unlikely that root respiration is directly affected by atmospheric $[\text{CO}_2]$, since roots already grow in air of high CO_2 concentration (ca. 3%). However, some studies have shown an increase in root activity of trees in elevated $[\text{CO}_2]$, including respiration, enhanced exudation and mycorrhizal development (reviewed by Urban 2003). Many authors point out increase of whole plant respiration, because of significant increase of biomass production in elevated $[\text{CO}_2]$.

Effects of elevated $[\text{CO}_2]$ on water use efficiency

Numerous field experiments have shown typical reduction of stomatal conductance by 20 - 60% when exposed to elevated atmospheric $[\text{CO}_2]$. The response is significantly stronger in (i) young trees compared to old ones, (ii) in deciduous compared to coniferous trees, and (iii) in water stressed compared to nutrient stressed trees (Medlyn et al. 2001). Growth in elevated $[\text{CO}_2]$ reduced sensitivity of stomata to vapour pressure deficit, reduced sensitivity to drought, and reduced sensitivity to atmospheric $[\text{CO}_2]$.

Moreover, together with increased epicuticular wax deposition under elevated $[\text{CO}_2]$ it led to a decrease of the transpiration rate per unit leaf area. However, enlarged leaf area under elevated $[\text{CO}_2]$ may be the reason of increased transpiration rate per plant or even whole ecosystem evapotranspiration.

An increase (up to 170%) of water use efficiency is the most common positive effect (reported in ca. 90% studies). On the base of direct measurements, reduced sap flow was found for *Quercus ilex*, *Pinus sylvestris* or *Picea abies* (e.g. Pokorný et al. 2001). All these processes under elevated $[\text{CO}_2]$ enable plants to maintain a higher leaf water

potential and ameliorate the negative effects of drought stress (e.g. Tolley & Strain 1985). Because leaf growth by cell enlargement is extremely sensitive to the water stress, it is presumable that plants grown in elevated $[\text{CO}_2]$ will survive higher drought stress that can lead to the extensions of current biotope and changes in biodiversity (e.g. Amthor 1999).

Effects of elevated $[\text{CO}_2]$ on growth processes

Generally, elevated CO_2 concentration stimulates production of the most tree species. Increase of total biomass production (mean ca. 33%) is primarily given by the stimulating cell division within shoot apices. Because of increases of the quantum yield efficiency under the elevated $[\text{CO}_2]$ treatment (Marek et al. 1997), relative higher growth enhancements were observed under low light conditions (up to $400 \mu\text{mol m}^{-2} \text{s}^{-1}$). These irradiances are the most frequent in the nature environment, and thus shaded leaves may produce relatively higher amount of assimilates. Furthermore, increased tissue water availability and increasing root proliferation could contribute to increased cell expansion due to increased cell turgor pressure.

However, cell proliferation may be stimulated to different extents throughout different meristematic regions that perhaps accounts for observed increases in nodal elongation relative to branch initiation, and other shifts in whole plant architecture (Pritchard et al. 1999). It was usually observed that the growth and development of cells and tissues below the site of lateral organ formation are stimulated to a greater extent than is the formation of organ primordia at the shoot tip. Although node number appears rather insensitive to elevated $[\text{CO}_2]$, several studies have been reported that branch initiation and number have been stimulated.

Initial stimulation of growth in response to elevated $[\text{CO}_2]$ may diminish over time, possibly because of down-regulation of photosynthesis, modifications in biomass allocation, and/or phenology. For example, Jach & Ceulemans (1999) observed an enhancement of the relative growth rates during the first season of exposure three-year-old *Pinus sylvestris* to elevated $[\text{CO}_2]$, but reported similar growth rates to control plants during the second season.

Plants are generally predicted to allocate biomass to structures that are involved in the limiting resources uptake. Therefore, relative limitations in nitrogen and other soil nutrients at elevated $[\text{CO}_2]$ were initially predicted to increase the allocation of biomass to the roots, i.e. an increase of root/shoot biomass ratio up to 75%. Also the number of roots, root length and root growth and fine root mass were substantially higher under elevated $[\text{CO}_2]$. The flow of carbon through the roots into the soil is one of the key processes for the formation of final photosynthetic acclimation and understanding the functioning of forest ecosystem under elevated $[\text{CO}_2]$.

Elevated $[\text{CO}_2]$ can alter plant phenology (i.e. development rate) and time to senescence at both the leaf and whole-plant levels. Jach & Ceulemans (1999) observed that in *Pinus sylvestris* needle fall occurred earlier at elevated $[\text{CO}_2]$ than at current ambient

[CO₂], which the authors attributed to possible changes in transpiration rate or earlier translocation of nutrients away from the leaves.

PRACTICAL ASSESSMENTS

Many experiments manifested higher stimulation of growth for broadleaf species by elevated [CO₂] comparing to coniferous ones. Biomass increments will tightly correlate to nitrogen availability, i.e. its insufficiency may be a strong limiting factor controlling the carbon allocation between above- and below-ground biomass. Consequently, revaluation of site index for individual tree species will be necessary.

Furthermore, existence of active carbon sinks and formation of new alternative ones, e.g. formation of secondary branches, are also important factors accelerating tree growth. Sink quality is given by the mutual interactions among trees and it could be stimulated by frequent thinning operations of low intensity. It applies mainly for coniferous forests.

Significant increase of root system leads to higher mechanical anchoring of trees and decrease the risk of windfalls in this way. The enlarged root system together with higher water use efficiency under the influence of elevated [CO₂] will improve the biomass production in the drought periods via decreased water stress impact.

It is highly presumable that the formation of new stands will be accompanied with urgent protection against weeds and *Homoptera insects* such as *Aphidoidea*, *Adelgidae*, *Tetranychidae*, and *Lecaniidae families*.

From the point of long-term carbon storage in forest ecosystems it seems as better to plant long-aged shade adapted tree species in multi-storey forests. Clear cutting management should be left out and it should be accented by individual sampling silvicultural system.

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