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Field experiments using CO_2 enrichment: a comparison of two main methods

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The dramatic increase in global atmospheric carbon dioxide over the past century is hypothesized to have significant impacts on the earth system. To understand the effects of elevated CO_2 on terrestrial ecosystems, two main methods have been used to simulate an increase of CO_2 in a semi-controlled field setting: 1) Open Top Chambers (OTC); and 2) Free Air CO_2 Enrichment (FACE). The OTC method has been applied to study the components of forest ecosystems at small scale by manipulating seedlings or isolated juvenile trees, but is not able to address ecosystem processes as a whole. For technical reasons, OTC cannot be used to consider scaling issues, interaction with the boundary layer, and competition among species. To address these issues FACE technology was developed. FACE enables longer-term studies in larger plots, and allows studies of plant processes such as leaf area and canopy development, canopy energy balance and canopy gas exchange. In this review, I synthesize results from literature, in particular from meta-analysis techniques applied either to OTC or FACE. The results are qualitatively similar: CO_2 enrichment leads to reduced stomatal conductance and leaf nitrogen, and enhanced photosynthesis and production. However, photosynthesis and crop yield were lower in FACE experiments than OTC, while starch content was higher. These results provide support for ecosystem model simulations, and help fill the gap between individual plants, forest and regional ecosystem. Neither OTC nor FACE can provide a clear indication of the regional-scale feedbacks between atmosphere and vegetation that might be expected under elevated CO_2. To address this issue, further research is needed.

Keywords: Photosynthesis, Free-Air Carbon dioxide Enrichment FACE, Open top chamber, Carbon sequestration, Forest ecosystem

Introduction

Global atmospheric CO_2 concentration has increased from a pre-industrial value of about 280 ppm in 1850 to 387 ppm in 2009 (NOAA/ESRL 2010) and it will probably exceed 700 ppm by the end of the 21st century (IPPC 2007a). A doubling of atmospheric CO_2 will most likely lead to a global warming of 3-5 °C (IPPC 2007b), whilst also inducing other non-climatic changes in the Earth system, particularly in the terrestrial biosphere which uses CO_2 for photosynthesis. It is crucial to understand the consequences of elevated CO_2 on terrestrial ecosystems, since land plants, through the process of carbon sequestration, can take up part of the atmospheric CO_2 emitted by human activities, potentially slowing the increase of CO_2 in the atmosphere and delaying climate change.

Körner (2000) estimated that the global terrestrial biosphere sequesters 1-2 Pg C/yr (Fig. 1). However, much uncertainty exists in quantifying carbon sequestration due to natural variability in carbon pools and fluxes among the different terrestrial ecosystems (Sarmiento & Wofsy 1999).

Therefore, there is a need for a better understanding of the physiological responses of plant and forest ecosystems to elevated CO_2. This information can provide support for ecosystem models and fill the gap between individual plants, forests and regional ecosystems.

To address these questions, a number of methodologies have been developed since the 1970s to simulate the effects of elevated CO_2 concentrations on plants. Most of these methods used leaf cuvettes, plant grow chambers and greenhouses (Uprety et al. 2006). However, these methods have important constraints in plot and plant size, and require active control of all environmental variables (Schulze et al. 1999). To overcome some of these limitations, other methodologies were developed that could be performed under unenclosed conditions: Open Top Chamber (OTC), Free Air CO_2 Enrichment (FACE) and Screen-aided CO_2 Control (SACC).

OTCs are made of a plastic enclosure with inclined walls and an open top while FACE is characterized by a series of vertical vent pipes, placed circularly around the plot, which release CO_2 towards the centre of the ring. SACC is a middle ground between FACE and OTC; it includes screens to break the wind minimizing its effects on the microclimate (a well-known problem in OTC). Windscreens also reduce the amount of CO_2 to be used and therefore its often-prohibitive costs (Leadley et al 1997).

OTC studies provided knowledge of mechanistic plant physiological responses such as stomatal conductance (G_s), transpiration, respiration, down-regulation of photosynthesis and yield. Those processes were further investigated under real forest conditions, by developing FACE technology (Hendrey & Miglietta 2006). Although SACC resulted to be a good compromise between FACE and OTC, especially in a grassland environment (Leadley et al. 1997, Lauber & Körner 1997, Niklaus et al. 1998, Uprety et al. 2006), it is still not able to replace FACE in a forest environment. Therefore in this mini-review paper I will only focus on FACE and OTC, which are also considered the two main methods used for CO_2 enrichment.

I will review the design, advantages, and limitations of both methods, and discuss common and contrasting results of studies using either method. I have placed a particular emphasis on evaluating the effects of side walls in OTC, especially regarding microclimate (temperature, humidity, solar radiation and wind) and plant-atmosphere feedbacks.

List of abbreviations

- **CO_2**: carbon dioxide;
- **G_s**: stomatal conductance;
- **OTC**: Open Top Chamber;
- **FACE**: Free Air CO_2 Enrichment;
- **LAI**: Leaf Area Index;
- **A_{sat}**: light saturated carbon uptake.

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OTC and FACE design

OTCs are made of a plastic enclosure with inclined walls and an open top. Air enriched with CO_2 enters near the bottom and flows out the open top creating an enriched CO_2 environment inside the chamber (Fig. 2). FACE, by contrast, is characterized by a series of vertical vent pipes, placed circularly around the plot, which release CO_2 towards the centre of the ring. CO_2 concentration, wind velocity and wind direction are continuously measured and the information collected are used by a computer-controlled systems to maintain elevated concentration of CO_2 throughout the plot (Allen et al. 1991 - Fig. 3). Generally the CO_2 concentration-using OTC is maintained at 700 ppm while in FACE concentrations between 550 and 600 ppm are more typical.

Advantages and limitations of OTC and FACE

The main aspects of the two techniques are summarized in Tab. 1. In the OTC the presence of side walls limits CO_2 consumption but induces a significant impact on the microclimate, altering air flow, intercepting rainfall, restricting access to insect pollinators and pests, increasing air temperature and water vapour humidity and lowering transmittance on sunny days (Leadley & Drake 1993, Long et al. 2004). In OTC, the wind is removed, preventing wind effects and dispersal of pathogens and pests. In FACE experiments, microclimate is minimally affected, but large quantities of CO_2 are required to compensate the CO_2 that diffuses away from the plot, especially under windy conditions.

An additional limitation of OTC is the presence of a rooting barrier that prevents roots from exploiting soil outside the chamber and vice-versa, eventually inducing feedback inhibition on photosynthesis and production (Long et al. 2004).

While OTC is made of inexpensive materials and requires low amounts of CO_2, FACE requires a high investment in instrumentation, building material, CO_2 and transport.

The major limitations of OTC in a forest environment are: the influence of trees and stand development patterns, the lack of an ecosystem prospective, scaling issues and absence of boundary layers. Trees and forests are very well coupled to the atmosphere, but this coupling is often greatly perturbed when enclosed in chambers (Lee & Jarvis 1996). In the OTC method, ventilation disables the natural coupling between vegetation and atmosphere. The applied artificial turbulence alters the exchanging process between canopy and atmosphere, by means of periodic irruptions of air in the canopy instead of a continuous mixing as it occurs in a natural environment.

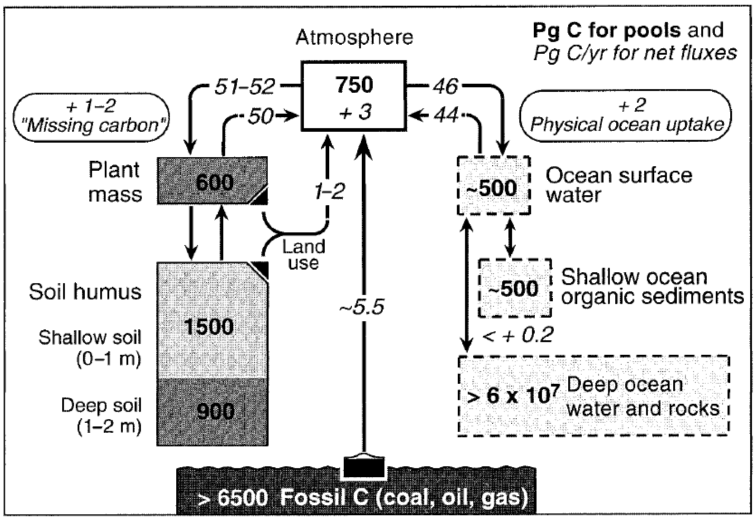

Fig. 1 - Major components involved in the global biological carbon cycle, a synthesis from many sources (from: Korner 2000).

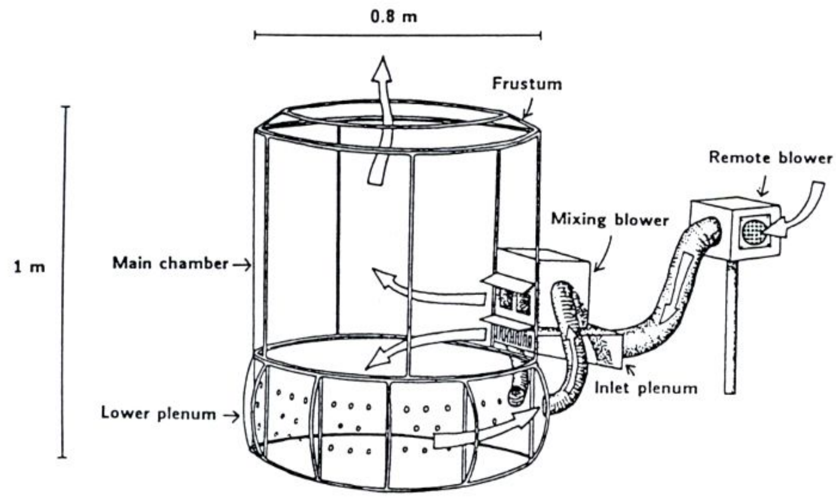

Fig. 2 - Open-top field chamber design. The diagram shows the air path through the chamber and its relative size (from: Allen et al. 1991).

Fig. 3 - FACE plots at the Aspen FACE experiment. [online] URL: http://aspenface.mtu.edu/

Tab. 1 - Main aspects of the two major techniques used for CO_2 enrichment.

FACE (Free Air CO_2 Enrichment)	OTC (Open Top Chamber)
• Diameter (8-30 m)	• Diameter (~1 m)
• Side walls absent	• Presence of side walls
• CO_2 distributed by a ring of vertical pipes	• CO_2 distributed by a circular tube
• Computer-controlled system that adjusts CO_2 flow rate	• UV-B are not transmitted trough the walls
• Forest canopy fully developed	• No wind from outside
• Species can compete	• Increased temperature
• High costs	• No dispersion of pathogen and pests
• Blower effect under still wind conditions	• Plant-atmosphere coupling is altered
• Steep increase in CO_2	• Forest-ecosystem processes cannot be studied
• Undisturbed rooting	• Rooting barrier

In FACE experiments, the components of the plant-soil nutrient cycle can be integrated, species can compete for resources, and a forest canopy may fully develop (Norby et al. 1999).

However, FACE also has several important limitations. For example, CO_2-enriched through vent-pipes has the potential to cause microclimate perturbations ("blower effect") under very stable and calm atmospheric conditions as during still nights (Hendrey & Miglietta 2006).

FACE experiments typically impose a steep increase in CO_2 concentrations at the beginning of the experiment. This abrupt change in environmental conditions may induce different responses of plants and ecosystem processes that have grown under normal CO_2 for decades. In particular, enhanced photosynthesis induces an elevation in nitrogen-demand, which often leads to nutrient stress and consequent down-regulation of photosynthesis (Hendrey & Miglietta 2006).

Finally, even though FACE experiments are sufficiently large to capture most critical ecosystem processes, they are still like an island within the surrounding ecosystem (Hendrey & Miglietta 2006).

Results and discussion

A considerable number of papers have been published that investigated plant responses to elevated CO_2. Here we focus on reviews, where meta-analytic techniques have been adopted for quantitatively analysing the results obtained by independent experiments made using chambers and FACE methodology. A synthesis of the results obtained with these studies is presented (Tab. 2).

Conclusions mainly drawn from chamber studies suggest that an increase in CO_2 induced a reduction in G_s and transpiration while improved water-use efficiency, photosynthesis and light use efficiency (Drake et al. 1997). Drake et al. (1997) also found that due to increased soil water content, water use efficiency and growth would be enhanced an that photosynthesis and growth increased even when N is limited, because of higher nitrogen use efficiency. In contrast, Norby et al. (1999) reported from a meta-analysis of OTC experiments little evidence of G_s reduction, furthermore photosynthesis and growth did not increase where N is limiting. Results from Ainsworth & Long (2004) and Curtis & Wang (1998) confirm the findings of Drake et al. (1997), reporting a 20% decrease in G_s.

Ainsworth & Long (2004), found an increase in light-saturated carbon uptake (A_{sat}) for trees, grass and crop of 47%, 37% and 17% respectively. Different functional group responses are also found by Norby et al. (1999) regarding above-ground growth.

Tab. 2 - Summary of meta-analysis results from FACE and chamber techniques and literature reviews. G_s: stomatal conductance; A_{sat}: light saturated CO_2 uptake. Sources: (a): Ainsworth & Long 2004; (b): Curtis & Wang 1998; (c): Long et al. 2004; (d): Drake et al. 1997; (e): Leakey et al. 2009.

Parameters	FACE	Chambers
A_{sat}	47% [a]	31% [b]
Above-ground dry-matter	28% [a]	28.8% [b]
Yield	17% [a]	28-35% [b]
G_s	-20% [a]	-20% [b]
Starch content	83% [c]	67.6% [b]
Leaf Nitrogen	-4% [a]	-15 % [b]
Rubisco	-20% [c]	-20% [b, d]
Photosynthesis	30% [c]	53% [b]
Dark respiration	0% [e]	15-20% [b, d]

Norby et al. (1999) found an increase of fine root density between 60 and 140% in elevated CO_2. This induces an increase of carbon in the soil profile suggesting that forests may have more potential for C sequestration that may be apparent from aboveground analysis (Norby et al. 2006).

The lower increase in crop yield and the 20% increase in photosynthesis reported in FACE compared with chamber studies could be explained by the lower CO_2 concentration of FACE (600 ppm) compared with chambers (700 ppm). However, as yield and photosynthesis responses are not linear, the alteration of microclimate in OTC could underestimate the effect of elevate CO_2 on yield and photosynthesis.

Leaf Area Index (LAI) of seedlings and saplings grown in OTC has usually increased with CO_2 enrichment (Norby et al. 1999), while no increases in LAI are reported in most of the FACE experiments (Ainsworth & Long 2004, Drake et al. 1997). This is in contrast with results from global vegetation models, which report an increase in LAI; consequently they may overestimate future evapotranspiration and photosynthesis carbon uptake (Long et al. 2004).

Plant starch content observed by Long et al. (2004) in a FACE study was 15.4% higher than the one observed by Curtis & Wang (1998) using OTC. Plants grown in chambers receive less light than in FACE because of the effect of the side walls; this effect may be the cause of these contrasting results.

Chamber studies showed that the initial stimulation of photosynthesis and growth diminishes or disappears in the long term, while FACE studies show that there is little or no evidence of loss of stimulation of photosynthesis on the long-term (Long et al. 2004). Reduction in stimulation could be the result of either down-regulation by carbohydrate accumulation or acclimation (Norby et al. 1999).

Arp (1991) reported that rooting volume suppressed the response of plants to elevated CO_2, demonstrating that loss of a response to increased CO_2 through acclimation was an artifact of pot size (the "pot effect"). Experiments at the Oak Ridge FACE site confirm that there has been no evidence for acclimation of photosynthesis to elevated CO_2 (Norby et al. 2006). However, a mechanism that fully explains this response is not yet known.

Dark respiration is usually inhibited by 15-20% in chamber studies while FACE experiments on average did not observe increased dark respiration (Leakey et al. 2009).

Conclusions

CO_2 enrichment studies using OTC are useful for research conducted at a small scale such as seedlings or juveniles, where detailed measurements are conducted to provide a fundamental and mechanistic understanding of component plant-processes. For investigations at ecosystem scale, FACE experiments are the only currently available method of providing realistic CO_2 enrichment. Direct scaling from OTC to FACE is difficult because seedlings or saplings respond differently as compared with mature trees: competition is altered, plant architecture and species composition is different, leaf area and tree density may change.

FACE experiment provides support for the inclusion of a carbon sequestration effect into models of the future trajectory of the global carbon cycle (Norby et al. 2006).

Elevated CO_2 leads to a decrease in G_s and therefore to a reduction in transpiration. It has been hypothesized that CO_2 enrichment acting at regional scales (> 100 km^2) may result in the drying of the lower troposphere. This in turn could increase evaporative demand on plants. But quantifying this feedback is difficult. Neither OTC nor FACE can provide an answer to this question that implies a direct action of the vegetation on the atmosphere.

Predicting the future responses of ecosystems to elevate CO_2 remains difficult. This is because species respond differently and the complex interaction between plants, soils, pests and pollutants are difficult to detect. A description of the different species responses to CO_2 enrichment, especially in form of functional groups, could be important for ecosystem models.

FACE is the best methodology available even though the study site remains an island in the host ecosystem and large-scale feedbacks cannot be detected (Hendrey & Miglietta 2006). There is a need for studies under realistic conditions where trees are exposed to elevated CO_2 for their entire life span of the stand, with natural stresses and where species can compete with each other (Karnosky 2003). Further studies conducted in natural springs, where the local vegetation has been exposed to elevated CO_2 for decades, could help to improve our understanding.

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