

Collection: NFZ Summer School 2009 - Birmensdorf (Switzerland)

Long-term ecosystem research: understanding the present to shape the future

Guest Editor: Marcus Schaub (WSL, Switzerland)

Field experiments using CO₂ enrichment: a comparison of two main methods

Mauri A

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 CO₂ on terrestrial ecosystems, two main methods have been used to simulate an increase of CO₂ in a semi-controlled field setting: 1) Open Top Chambers (OTC); and 2) Free Air CO₂ 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: CO₂ 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 CO₂. 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 CO₂ 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 (IPCC 2007a). A doubling of atmospheric CO₂ will most likely lead to a global warming of 3-5 °C (IPCC 2007b), whilst also

inducing other non-climatic changes in the Earth system, particularly in the terrestrial biosphere which uses CO₂ for photosynthesis. It is crucial to understand the consequences of elevated CO₂ on terrestrial ecosystems, since land plants, through the process of carbon sequestration, can take up part of the atmospheric CO₂ emitted by human activities, potentially slowing the increase of CO₂ 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 CO₂. This information can provide support for ecosystem models and fill the gap between individual plants, forests and re-

gional ecosystems.

To address these questions, a number of methodologies have been developed since the 1970s to simulate the effects of elevated CO₂ 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 CO₂ Enrichment (FACE) and Screen-aided CO₂ 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 CO₂ 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 CO₂ 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 CO₂ 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

- CO₂: carbon dioxide;
- G_s: stomatal conductance;
- OTC: Open Top Chamber;
- FACE: Free Air CO₂ Enrichment;
- LAI: Leaf Area Index;
- A_{sat}: light saturated carbon uptake.

✉ Soil-Vegetation-Atmosphere Research Group Institute for Environmental Science and Technology, Ecole Polytechnique Fédérale de Lausanne, Station 2, CH-1015 Lausanne (Switzerland)

@ Achille Mauri (achille.mauri@epfl.ch)

Received: May 25, 2010 - Accepted: Jun 01, 2010

Citation: Mauri A, 2010. Field experiments using CO₂ enrichment: a comparison of two main methods. *iForest* 3: 109-112 [online: 2010-07-15] URL: <http://www.sisef.it/forest/show.php?id=545>

OTC and FACE design

OTCs are made of a plastic enclosure with inclined walls and an open top. Air enriched with CO₂ enters near the bottom and flows out the open top creating an enriched CO₂ 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 CO₂ towards the centre of the ring. CO₂ 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 CO₂ throughout the plot (Allen et al. 1991 - Fig. 3). Generally the CO₂ 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 CO₂ 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 CO₂ are required to compensate the CO₂ 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 CO₂, FACE requires a high investment in instrumentation, building material, CO₂ 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.

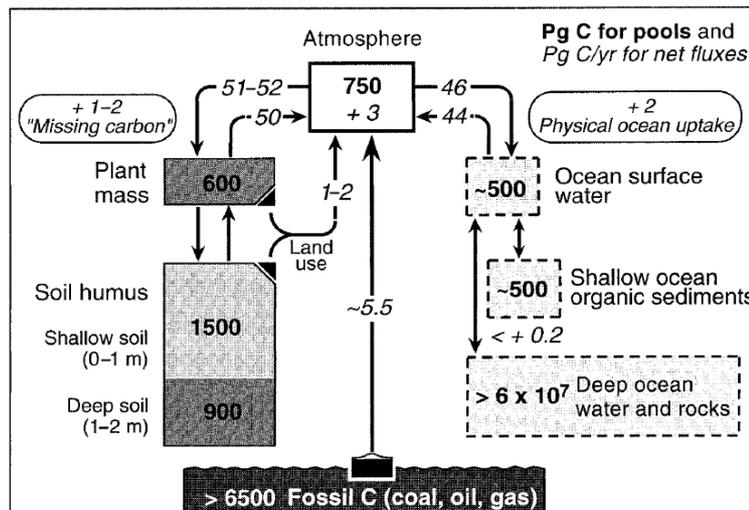


Fig. 1 - Major components involved in the global biological carbon cycle, a synthesis from many sources (from: Korner 2000).

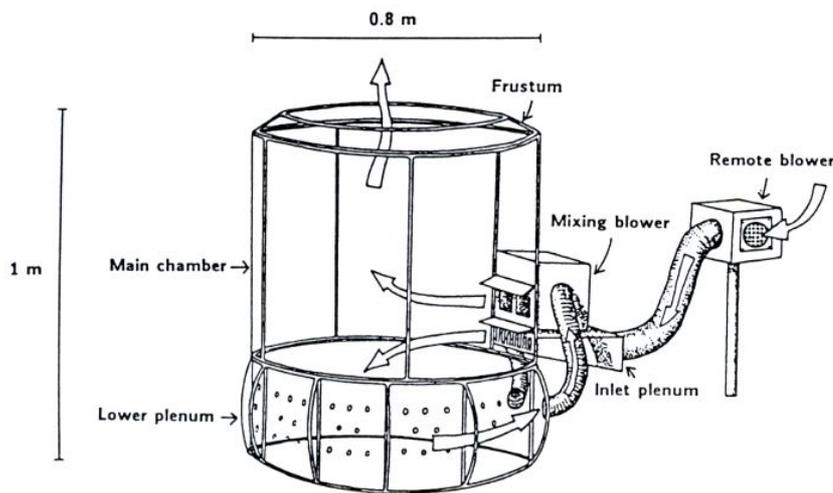


Fig. 2 - Open-top field chamber design. The diagram shows the air path through the chamber and its relative size (from: Allen et al. 1991).



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 CO₂ enrichment.

FACE (Free Air CO ₂ Enrichment)	OTC (Open Top Chamber)
<ul style="list-style-type: none"> • Diameter (8-30 m) • Side walls absent • CO₂ distributed by a ring of vertical pipes • Computer-controlled system that adjusts CO₂ flow rate • Forest canopy fully developed • Species can compete • High costs • Blower effect under still wind conditions • Steep increase in CO₂ • Undisturbed rooting 	<ul style="list-style-type: none"> • Diameter (~1 m) • Presence of side walls • CO₂ distributed by a circular tube • UV-B are not transmitted through the walls • No wind from outside • Increased temperature • No dispersion of pathogen and pests • Plant-atmosphere coupling is altered • Forest-ecosystem processes cannot be studied • 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, CO₂-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 CO₂ 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 CO₂ 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 re-

sponses to elevated CO₂. 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 CO₂ 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 as 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.

Norby et al. (1999) found an increase of fine root density between 60 and 140% in elevated CO₂. 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 CO₂ 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 elevated CO₂ on yield and photosynthesis.

Leaf Area Index (LAI) of seedlings and saplings grown in OTC has usually increased with CO₂ 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 CO₂, demonstrating that loss of a response to increased CO₂ 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 CO₂ (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

CO₂ enrichment studies using OTC are useful for research conducted at a small scale such as seedlings or juveniles, where de-

Tab. 2 - Summary of meta-analysis results from FACE and chamber techniques and literature reviews. G_s: stomatal conductance; A_{sat}: light saturated CO₂ 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% ^c	15-20% ^{b,d}

tailed 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 CO₂ 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 CO₂ leads to a decrease in G_s and therefore to a reduction in transpiration. It has been hypothesized that CO₂ enrichment acting at regional scales (> 100 km²) 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 CO₂ 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 CO₂ 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 CO₂ 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 CO₂ for decades, could help to improve our understanding.

Acknowledgements

I thank Dr. Marcus Schaub and Dr. Erwin Dreyer for beneficial discussions during the WSL Summer School that inspired me to write this review and Prof. Franco Miglietta, Prof. Jed Kaplan and Dr. Basil Davis for their valuable comments, which improved this manuscript. The Italian Ministry of Education (FIRB) through project CASTANEA (contract no. 511305) provided financial support for this work and my participation in the WSL Summer School.

References

- Ainsworth EA, Long SP (2004). What have we learned from 15 years of free air CO₂ enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy properties and plant production to rising CO₂. *New Phytologist* 165: 351-372. - doi: [10.1111/j.1469-8137.2004.01224.x](https://doi.org/10.1111/j.1469-8137.2004.01224.x)
- Allen LH, Baldocchi DJr, Bazzaz F, Burke K, Dahlman R, Denmead T, Hendrey G, McLeod A, Melillo J, Oechel W, Risser P, Rogers H, Rozema J, Wright R (1991). Available technologies for field experimentation with elevated CO₂ in global change research. In: "SCOPE 45 Ecosystem Experiments", Chapter 15 (Mooney HA, Medina E, Schindler D, Schulze ED, Walker BH eds). Wiley, UK, pp. 296.
- Arp WJ (1991). Effects of source-sink relations on photosynthetic acclimation to CO₂. *Plant, Cell and Environment* 14: 869-875. - doi: [10.1111/j.1365-3040.1991.tb01450.x](https://doi.org/10.1111/j.1365-3040.1991.tb01450.x)
- Curtis PS, Wang X (1998). A meta-analysis of elevated CO₂ effects on woody plant mass, form, and physiology. *Oecologia* 113: 299-313. - doi: [10.1007/s004420050381](https://doi.org/10.1007/s004420050381)
- Drake BG, Gonzà lez-Meler MA, Long SP (1997). More efficient plants: a consequence of increased atmospheric CO₂? *Annual Review of Plant Physiology and Plant Molecular Biology* 48: 609-639. - doi: [10.1146/annurev.arplant.48.1.609](https://doi.org/10.1146/annurev.arplant.48.1.609)
- Hendrey GR, Miglietta F (2006). FACE technology: Past, Present, and Future. In: "Managed Ecosystems and CO₂" (Nösberger J, Long SP, Norby RJ, Stitt M, Hendrey GR, Blum M eds). Springer, Berlin, Heidelberg, New York, pp 15-43.
- IPPC (2007a). Fourth Assessment Report. Chapter 10. Global climate projections. 10.7 Long Term Climate Change and Commitment 10.7.1, Climate Change Commitment to Year 2300. Based on AOGCM, pp. 822.
- IPPC (2007b). Fourth Assessment Report. Summary for Policymakers. [online] URL: <http://www.ipcc.ch/pdf/assessment-report/ar4/wg1/ar4-wg1-chapter4.pdf>
- Karnosky DF (2003). Impacts of elevated atmospheric CO₂ on forest trees and forest ecosystems: knowledge gaps. *Environmental International*. 29: 161-169. - doi: [10.1016/S0160-4120\(02\)00159-9](https://doi.org/10.1016/S0160-4120(02)00159-9)
- Körner C (2000). Biosphere responses to CO₂ enrichment. *Ecological Applications* 10 (6): 1590-1619. - doi: [10.1890/1051-0761\(2000\)010\[1590:BRTEC\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2000)010[1590:BRTEC]2.0.CO;2)
- Lauber W, Körner C (1997). *In situ* stomatal responses to long term CO₂ enrichment in calcareous grassland plants. *Acta Oecologica* 18: 221-229 - doi: [10.1016/S1146-609X\(97\)80008-2](https://doi.org/10.1016/S1146-609X(97)80008-2)
- Leadley PW, Drake BG (1993). Open top chambers for exposing plant canopies to elevated CO₂, concentration and for measuring net gas exchange. *Vegetatio* 104/105: 3-15. - doi: [10.1007/BF00048141](https://doi.org/10.1007/BF00048141)
- Leadley PW, Niklaus P, Stocker R, Körner C (1997). Screen-aided CO₂ control (SACC): middle ground between FACE and open-top chambers. *Acta Oecologica* 18 (3): 207-219. - doi: [10.1016/S1146-609X\(97\)80007-0](https://doi.org/10.1016/S1146-609X(97)80007-0)
- Leakey ADB, Ainsworth EA, Bernacchi CJ, Rogers A, Long SP, Ort DR (2009). Elevated CO₂ effects on plant carbon, nitrogen, and water relations: six important lessons from FACE. *Journal of Experimental Botany* 60: 2859-2876. - doi: [10.1093/jxb/erp096](https://doi.org/10.1093/jxb/erp096)
- Ledford H (2008). Forestry carbon dioxide projects to close down. *Nature* 456 (7220): 289.
- Lee HSI, Jarvis PG (1996). The effects of tree maturity on some responses to elevated CO₂ in Sitka Spruce (*Picea sitchensis* Bong. Carr.). In: "Carbon Dioxide and Terrestrial Ecosystems" (Koch GW, Mooney HA eds). Academic Press Inc., S. Diego, CA, USA, pp 53-70.
- Long SP, Ainsworth EA, Rogers A, Ort DR (2004). Rising atmospheric carbon dioxide: plants FACE the future. *Annual Review Plant Biology* 55:591-628. - doi: [10.1146/annurev.arplant.55.031903.141610](https://doi.org/10.1146/annurev.arplant.55.031903.141610)
- Niklaus PA, Spinnler D, Körner C (1998). Soil moisture dynamics of calcareous grassland under elevated CO₂. *Oecologia* 117: 177-186. - doi: [10.1007/s004420050649](https://doi.org/10.1007/s004420050649)
- NOAA/ESRL (2010). Use of NOAA/ESRL data (Conway T ed). Earth System Research Laboratory, National Oceanic and Atmospheric Administration, US. Department of Commerce, Boulder, Colorado, USA. [online] URL: ftp://ftp.cmdl.noaa.gov/ccg/co2/trends/co2_mm_gl.txt
- Norby RJ, Wullschlegler SD, Gundersen CA, Johnson DW, Ceulemans R (1999). Tree responses to rising CO₂ in field experiments: implications for the future forest. *Plant, Cell and Environment* 22: 683-714. - doi: [10.1046/j.1365-3040.1999.00391.x](https://doi.org/10.1046/j.1365-3040.1999.00391.x)
- Norby RJ, Wullschlegler SD, Hanson PJ, Gundersen CA, Tschaplinski TJ, Jastrow JD (2006). CO₂ enrichment of a deciduous forest: the Oak Ridge FACE experiment. In: "Managed ecosystems and CO₂: case studies, processes, and perspectives" (Nösberger J, Long SP, Norby RJ, Stitt M, Hendrey GR, Blum H eds). *Ecological Studies*, Springer, Berlin, vol. 187, pp. 231-251.
- Sarmiento JL, Wofsy SC (1999). A U.S. carbon cycle science plan: a report of the carbon and climate working group. U.S. Global Change Research Program, Washington, DC, USA, pp. 69.
- Schulze ED, Scholes RJ, Ehleringer JR, Hunt LA, Canadell J, Chaprin FS, Steffen WL (1999). The study of ecosystems in the context of global change. The terrestrial biosphere and global change. *International geosphere-biosphere programme book series* 4, pp 27.
- Upreti DC, Garg SC, Bisht BS, Maini HK, Dwivedi N, Paswan G, Raj A, Saxena DC (2006). Carbon dioxide enrichment technologies for crop response studies. *Journal of Scientific and Industrial Research* 65 (11): 859-866.