Effects of Rising Atmospheric Concentrations of Carbon Dioxide on Plants

Photosynthetic assimilation of CO\textsubscript{2} is central to the metabolism of plants. As atmospheric concentrations of CO\textsubscript{2} rise, how will this affect the plants we depend on?

Atmospheric concentrations of carbon dioxide have been steadily rising, from approximately 315 ppm (parts per million) in 1959 to a current atmospheric average of approximately 385 ppm (Keeling et al., 2009). Current projections are for concentrations to continue to rise to as much as 500–1000 ppm by the year 2100 (IPCC 2007).

While a great deal of media and public attention has focused on the effects that such higher concentrations of CO\textsubscript{2} are likely to have on global climate, rising CO\textsubscript{2} concentrations are also likely to have profound direct effects on the growth, physiology, and chemistry of plants, independent of any effects on climate (Ziska 2008). These effects result from the central importance of CO\textsubscript{2} to plant metabolism. As photosynthetic organisms, plants take up atmospheric CO\textsubscript{2}, chemically reducing the carbon. This represents not only an acquisition of stored chemical energy for the plant, but also provides the carbon skeletons for the organic molecules that make up a plants’ structure. Overall, the carbon, hydrogen and oxygen assimilated into organic molecules by photosynthesis make up ~96\% of the total dry mass of a typical plant (Marschner 1995). Photosynthesis is therefore at the heart of the nutritional metabolism of plants, and increasing the availability of CO\textsubscript{2} for photosynthesis can have profound effects on plant growth and many aspects of plant physiology.

Our knowledge of plant responses to future CO\textsubscript{2} concentrations rests on the results of experiments that have experimentally increased CO\textsubscript{2} and then compared the performance of the experimental plants with those grown under current ambient CO\textsubscript{2} conditions. Such experiments have been performed in a wide variety of settings, including greenhouses and chambers of a variety of sizes and designs. However plants grown in chambers may not experience the effects of increasing CO\textsubscript{2} the same way as plants growing in more natural settings. For this reason, techniques of Free-Air Carbon dioxide Enrichment (FACE) have been developed that allow natural or agricultural ecosystems to be fumigated with elevated concentrations of CO\textsubscript{2} in the field without use of chambers (Figure 1). As these experiments are the most naturalistic, they should provide the best indication of the responses of plants to increased CO\textsubscript{2} under the real-world conditions of the future. This article therefore focuses on data from FACE experiments wherever these are available. Whenever possible, to ensure the generality of conclusions, reference is made to analyses that have incorporated data from multiple experiments independently conducted at various research facilities.
One of the most consistent effects of elevated atmospheric CO$_2$ on plants is an increase in the rate of photosynthetic carbon fixation by leaves. Across a range of FACE experiments, with a variety of plant species, growth of plants at elevated CO$_2$ concentrations of 475–600 ppm increases leaf photosynthetic rates by an average of 40% (Ainsworth & Rogers 2007). Carbon dioxide concentrations are also important in regulating the openness of stomata, pores through which plants exchange gases, with the external environment. Open stomata allow CO$_2$ to diffuse into leaves for photosynthesis, but also provide a pathway for water to diffuse out of leaves. Plants therefore regulate the degree of stomatal opening (related to a measure known as stomatal conductance) as a compromise between the goals of maintaining high rates of photosynthesis and low rates of water loss. As CO$_2$ concentrations increase, plants can maintain high photosynthetic rates with relatively low stomatal conductance. Across a variety of FACE experiments, growth under elevated CO$_2$ decreases stomatal conductance of water by an average of 22% (Ainsworth & Rogers 2007). This would be expected to decrease overall plant water use, although the magnitude of the overall effect of CO$_2$ will depend on how it affects other determinants of plant water use, such as plant size, morphology, and leaf temperature. Overall, FACE experiments show decreases in whole plant water use of 5–20% under elevated CO$_2$. This in turn can have consequences for the hydrological cycle of entire ecosystems, with soil moisture levels and runoff both increasing under elevated CO$_2$ (Leakey et al. 2009).

Since photosynthesis and stomatal behavior are central to plant carbon and water metabolism, growth of plants under elevated CO$_2$ leads to a large variety of secondary effects on plant
physiology. The availability of additional photosynthate enables most plants to grow faster under elevated CO₂, with dry matter production in FACE experiments being increased on average by 17% for the aboveground, and more than 30% for the belowground, portions of plants (Ainsworth & Long 2005; de Graaff et al. 2006). This increased growth is also reflected in the harvestable yield of crops, with wheat, rice and soybean all showing increases in yield of 12–14% under elevated CO₂ in FACE experiments (Ainsworth 2008; Long et al. 2006).

Elevated CO₂ also leads to changes in the chemical composition of plant tissues. Due to increased photosynthetic activity, leaf nonstructural carbohydrates (sugars and starches) per unit leaf area increase on average by 30–40% under FACE elevated CO₂ (Ainsworth 2008; Ainsworth & Long 2005). Leaf nitrogen concentrations in plant tissues typically decrease in FACE under elevated CO₂, with nitrogen per unit leaf mass decreasing on average by 13% (Ainsworth & Long 2005). This decrease in tissue nitrogen is likely due to several factors: dilution of nitrogen from increased carbohydrate concentrations; decreased uptake of minerals from the soil, as stomatal conductance decreases and plants take up less water (Taub & Wang 2008); and decreases in the rate of assimilation of nitrate into organic compounds (Bloom et al. 2010).

Protein concentrations in plant tissues are closely tied to plant nitrogen status. Changes in plant tissue nitrogen are therefore likely to have important effects on species at higher trophic levels. Performance is typically diminished for insect herbivores feeding on plants grown in elevated CO₂ (Zvereva & Kozlov 2006). This can lead to increased consumption of plant tissues as herbivores compensate for decreased food quality (Stiling and Cornelissen 2007). Effects on human nutrition are likely as well. In FACE experiments, protein concentrations in grains of wheat, rice and barley, and in potato tubers, are decreased by 5–14% under elevated CO₂ (Taub et al. 2008). Crop concentrations of nutritionally important minerals including calcium, magnesium and phosphorus may also be decreased under elevated CO₂ (Loladze 2002; Taub & Wang 2008).

**Effects of Other Environmental Factors on Plant Response to Elevated CO₂**

The effects of elevated CO₂ on plants can vary depending on other environmental factors. While elevated CO₂ makes carbon more available, plants also require other resources including minerals obtained from the soil. Elevated CO₂ does not directly make these mineral elements more available and, as noted above, may even decrease the uptake of some elements. The ability of plants to respond to elevated CO₂ with increased photosynthesis and growth may therefore be limited under conditions of low mineral availability. This effect has been best documented for nitrogen. In FACE experiments, there is less enhancement of photosynthesis by elevated CO₂ under low than high soil N conditions (Ainsworth & Long 2005; Ainsworth & Rogers 2007). Crop yield in FACE also appears to be enhanced by elevated CO₂ to a lesser extent under low-N than under high-N (Ainsworth & Long 2005; Ainsworth 2008; Long et al. 2006). Across studies using all types of CO₂ fumigation technologies, there is a lower enhancement of biomass production by elevated CO₂ under low-nutrient conditions (Poorter & Navas 2003). Crops grown with low amounts of N fertilization also show a greater decrease in protein concentrations under elevated CO₂ than crops grown with higher N fertilization (Taub et al. 2008).

Another environmental factor that interacts with elevated CO₂ is atmospheric ozone (O₃), a gaseous toxin. Ground-level O₃ concentrations have been increasing worldwide (and are expected to continue to increase) due to increased emissions of pollutants that react to produce O₃ (Vingarzan 2004). High atmospheric concentrations of ozone can cause damage to leaves and decreased plant growth and photosynthesis (Feng et al. 2008; Morgan et al. 2003). The
primary location of \( \text{O}_2 \) injury to plants is the internal tissues of leaves. Decreased openness of stomata under elevated \( \text{CO}_2 \) can therefore decrease exposure of sensitive tissues to ozone. Elevated \( \text{CO}_2 \) substantially decreases the negative effects of high ozone on photosynthesis, growth, and seed yield in both soybeans and rice (Feng et al. 2008; Morgan et al. 2003). Across experiments with all plant species, the enhancement of growth by elevated \( \text{CO}_2 \) is much greater under conditions of ozone stress than otherwise (Poorter & Navas 2003).

**Differences among Plant Functional Types in Response to Elevated \( \text{CO}_2 \)**

The preceding discussion has presented the average effects of elevated \( \text{CO}_2 \), but obscures important patterns of difference in response among plant species. One of the most important determinants of species differences in response to elevated \( \text{CO}_2 \) is photosynthetic type. Most plant species (~90%) utilize a photosynthetic process known as \( \text{C}_3 \) photosynthesis. Other species use either of two physiologically distinct processes known as \( \text{C}_4 \) and CAM photosynthesis (Figure 2). \( \text{C}_4 \) plants include most tropical and sub-tropical grasses and several important crops, including maize (corn), sugar cane, sorghum, and the millets. There has therefore been considerably more research on the responses to elevated \( \text{CO}_2 \) in \( \text{C}_4 \) than in CAM plants.

**Figure 2: Each plant species utilizes one of several distinct physiological variants of photosynthesis mechanisms, including the variants known as \( \text{C}_3 \) and \( \text{C}_4 \) photosynthesis.**

\( \text{C}_4 \) plants use a biochemical pump to concentrate \( \text{CO}_2 \) at the locations within the leaf where the \text{RUBISCO} enzyme mediates incorporation of \( \text{CO}_2 \) by the Calvin-Benson photosynthetic cycle. Since \( \text{CO}_2 \) concentrations are already high within the bundle sheath cells, increasing atmospheric \( \text{CO}_2 \) concentrations above current levels has little direct effect on photosynthetic rates for \( \text{C}_4 \) species. \( \text{C}_4 \) species do respond to elevated \( \text{CO}_2 \) by decreasing stomatal conductance; this may lead to some indirect enhancement of photosynthesis by helping avoid water stress under drought conditions (Leakey 2009). In FACE experiments, stimulation of photosynthesis by
elevated CO₂ in C₄ plants is only about one-third of that experienced by C₃ species. C₄ plants also show little or no enhancement of growth (dry matter production) in these studies (Ainsworth & Long 2005). The very limited data available also shows no increase in C₄ crop yield in FACE studies (Long et al. 2006). While there is little FACE data available on effects of elevated CO₂ on plant nitrogen and protein concentrations, data from chamber experiments shows C₄ plants to be much less responsive than C₃ plants in this regard (Cotrufo et al. 1998). The picture that emerges is that C₃ plants are in general relatively unresponsive to elevation of atmospheric CO₂ above current ambient levels.

In contrast to C₄ species, another group of plants, legumes (members of the botanical family Fabaceae) may be especially capable of responding to elevated CO₂ with increased photosynthesis and growth (Rogers et al. 2009). For most plants, growth under elevated CO₂ can alter the internal balance between carbon (obtained in extra quantities through enhanced photosynthesis) and nitrogen (either unaffected or taken up in decreased amounts due to decreased uptake of water). In contrast, most legume species participate in close mutualistic relationships with bacteria that live in nodules formed on the plant’s roots. These bacteria are able to “fix” atmospheric nitrogen, chemically reducing it to a form that can be taken up and used by plants. Under elevated CO₂ conditions, legumes may be able to shunt excess carbon to root nodules where it can serve as a carbon and energy source for the bacterial symbionts. In effect, legumes may be able to exchange the excess carbon for nitrogen and thereby maximize the benefits of elevated atmospheric CO₂. Many studies in controlled environments have shown that, compared to other plant species, legumes show greater enhancement of photosynthesis and growth by elevated CO₂ (Rogers et al. 2009). Decreases in tissue nitrogen concentrations under elevated CO₂ are also smaller for legumes than for other C₃ species (Cotrufo et al. 1988; Jablonski et al. 2002; Taub et al. 2008). In FACE experiments, soybeans (a legume) show a greater response to elevated CO₂ than wheat and rice in photosynthesis and overall growth, although not in harvestable yield (Long et al. 2006).

**Plant Community Interactions under Elevated CO₂**

A number of experiments have found that some plant species that respond positively to elevated CO₂ when grown alone experience decreased growth under elevated CO₂ when grown in mixed plant communities (Poorter & Navas 2003). This effect likely results because the direct positive effects of elevated CO₂ are outweighed by negative effects due to stimulation of the growth of competitors. Rising atmospheric concentrations of CO₂ may therefore lead to changes in the composition of plant communities, as some species reap more of an advantage from the increased CO₂ than do others. In mixed-species experiments under high fertility conditions, C₄ plants decrease as a proportion of the biomass of plant communities under elevated CO₂. Similarly, under low fertility conditions, legumes increase as a proportion of the biomass of plant communities under elevated CO₂ (Poorter & Navas 2003).

**Summary**

Current evidence suggests that that the concentrations of atmospheric CO₂ predicted for the year 2100 will have major implications for plant physiology and growth. Under elevated CO₂ most plant species show higher rates of photosynthesis, increased growth, decreased water use and lowered tissue concentrations of nitrogen and protein. Rising CO₂ over the next century is likely to affect both agricultural production and food quality. The effects of elevated CO₂ are not uniform; some species, particularly those that utilize the C₄ variant of photosynthesis, show less of a
response to elevated CO\textsubscript{2} than do other types of plants. Rising CO\textsubscript{2} is therefore likely to have complex effects on the growth and composition of natural plant communities.

References and Recommended Reading


Ainsworth, E. A. & Long, S. P. What have we learned from 15 years of free-air CO\textsubscript{2} enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy properties and plant production to rising CO\textsubscript{2}. *New Phytologist* 165, 351-372 (2005).


Zvereva, E. L. & Kozlov, M. V. Consequences of simultaneous elevation of carbon dioxide and temperature for plant