Name ________________________________

Biology Article Assignment #2 – Rising Carbon Dioxide Levels and Plants

1. What is the atmospheric concentration of CO_2 expected to be by the year 2100? ___________________

2. What percentage of the dry mass of plants is the result of the carbon, hydrogen and oxygen assimilated during photosynthesis? ____

3. What does FACE stand for? How does the FACE technique differ from other studies that have attempted to test the effects of increased CO_2 concentrations on the growth of plants? ________________

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4. What effect did the increased CO_2 concentrations using the FACE technique have on the leaf photosynthetic rates of the plants that were tested? ____

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5. What is stomatal conductance? Explain why plants had an average decrease of 22% in stomatal conductance under elevated CO_2 concentrations? ____

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6. How did the elevated CO_2 concentrations effect the plants growth rate? What effect did the elevated CO_2 concentrations have on the growth of crops lie wheat, rice, and soybean? _______________________

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7. What happened to the nitrogen and protein concentrations in plants under elevated CO_2 concentrations, and how does the nitrogen and protein in the plants effect animals that eat the plants (higher trophic levels)? ____

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8. Explain why the C4 plants respond differently than C3 when exposed to elevated CO_2 concentrations?

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9. How might plants in the bean family (legumes) especially benefit from elevated CO_2 concentrations?

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10. How can an increase in CO_2 concentrations lead to a transformation of plant communities? _________

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Effects of Rising Atmospheric Concentrations of Carbon Dioxide on Plants

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Photosynthetic assimilation of CO2 is central to the metabolism of plants. As atmospheric concentrations of CO2 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_2 are likely to have on global climate, rising CO_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_2 to plant metabolism. As photosynthetic organisms, plants take up atmospheric CO_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_2 for photosynthesis can have profound effects on plant growth and many aspects of plant physiology.

Our knowledge of plant responses to future CO_2 concentrations rests on the results of experiments that have experimentally increased CO_2 and then compared the performance of the experimental plants with those grown under current ambient CO_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_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_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_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.

Figure 1: Free-air carbon dioxide enrichment allows experiments with controlled atmospheric concentrations of carbon dioxide to be conducted in the field and avoids potential experimental artifacts from growing plants in enclosed chambers.
Courtesy of David F. Karnosky.

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 gasses, 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 CO_2, 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 CO_2 in FACE experiments (Ainsworth 2008; Long *et al.* 2006).

Elevated CO_2 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 CO_2 (Ainsworth 2008; Ainsworth & Long 2005). Leaf nitrogen concentrations in plant tissues typically decrease in FACE under elevated CO_2, 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 CO_2 (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 CO_2 (Taub *et al.* 2008). Crop concentrations of nutritionally important minerals including calcium, magnesium and phosphorus may also be decreased under elevated CO_2 (Loladze 2002; Taub & Wang 2008).

Differences among Plant Functional Types in Response to Elevated CO_2

The preceding discussion has presented the average effects of elevated 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 CO_2 is photosynthetic type. Most plant species (~90%) utilize a photosynthetic process known as C_3 photosynthesis. Other species use either of two physiologically distinct processes known as C_4 and CAM photosynthesis (Figure 2). 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 CO_2 in C_4 than in CAM plants.

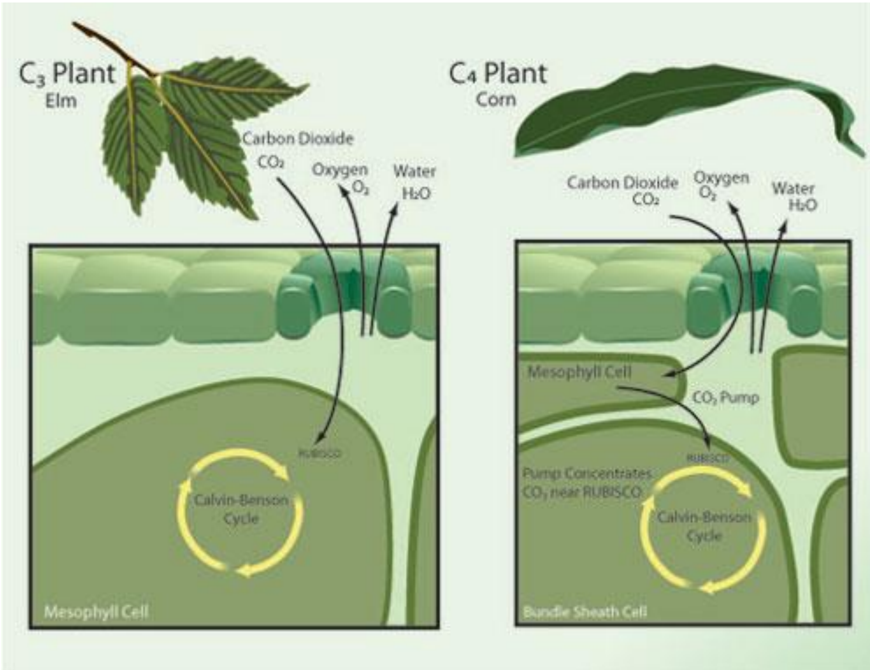

Figure 2: Each plant species utilizes one of several distinct physiological variants of photosynthesis mechanisms, including the variants known as C3 and C4 photosynthesis.

C_4 plants use a biochemical pump to concentrate CO_2 at the locations within the leaf where the RUBISCO enzyme mediates incorporation of CO_2 by the Calvin-Benson photosynthetic cycle. Since CO_2 concentrations are already high within the bundle sheath cells, increasing atmospheric CO_2concentrations above current levels has little direct effect on photosynthetic rates for C_4 species. C_4 species do respond to elevated 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 CO_2 in C_4 plants is only about one-third of that experienced by C_3 species. C_4plants 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 C_4 crop yield in FACE studies (Long *et al.* 2006). While there is little FACE data available on effects of elevated CO_2 on plant nitrogen and protein concentrations, data from chamber experiments shows C_4 plants to be much less responsive than C_3 plants in this regard (Cotrufo *et al.* 1998). The picture that emerges is that C_4 plants are in general relatively unresponsive to elevation of atmospheric CO_2 above current ambient levels.

In contrast to C_4 species, another group of plants, legumes (members of the botanical family Fabaceae) may be especially capable of responding to elevated CO_2 with increased photosynthesis and growth (Rogers *et al.* 2009). For most plants, growth under elevated CO_2 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 CO_2 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 CO_2. Many studies in controlled environments have shown that, compared to other plant species, legumes show greater enhancement of photosynthesis and growth by elevated CO_2 (Rogers *et al.* 2009). Decreases in tissue nitrogen concentrations under elevated CO_2 are also smaller for legumes than for other C_3 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 CO_2 than wheat and rice in photosynthesis and overall growth, although not in harvestable yield (Long *et al.* 2006).

Plant Community Interactions under Elevated CO_2

A number of experiments have found that some plant species that respond positively to elevated CO_2 when grown alone experience decreased growth under elevated CO_2 when grown in mixed plant communities (Poorter & Navas 2003). This effect likely results because the direct positive effects of elevated CO_2 are outweighed by negative effects due to stimulation of the growth of competitors. Rising atmospheric concentrations of CO_2 may therefore lead to changes in the composition of plant communities, as some species reap more of an advantage from the increased CO_2 than do others. In mixed-species experiments under high fertility conditions, C_4 plants decrease as a proportion of the biomass of plant communities under elevated CO_2. Similarly, under low fertility conditions, legumes increase as a proportion of the biomass of plant communities under elevated CO_2 (Poorter & Navas 2003).

Summary

Current evidence suggests that that the concentrations of atmospheric CO_2 predicted for the year 2100 will have major implications for plant physiology and growth. Under elevated CO_2 most plant species show higher rates of photosynthesis, increased growth, decreased water use and lowered tissue concentrations of nitrogen and protein. Rising CO_2 over the next century is likely to affect both agricultural production and food quality. The effects of elevated CO_2 are not uniform; some species, particularly those that utilize the C_4 variant of photosynthesis, show less of a response to elevated CO_2 than do other types of plants. Rising CO_2 is therefore likely to have complex effects on the growth and composition of natural plant communities.

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