Leaves and the Effects of Elevated Carbon Dioxide Levels

Stephen A. Prior
USDA—ARS National Soil Dynamics Laboratory, Auburn, Alabama, U.S.A.

Seth G. Pritchard
Belmont University, Nashville, Tennessee, U.S.A.

G. Brett Runion
USDA—ARS National Soil Dynamics Laboratory, Auburn, Alabama, U.S.A.

INTRODUCTION

Since the onset of the Industrial Revolution, the use of fossil fuel and the clearing of land have led to a dramatic rise in the concentration of carbon dioxide (CO_2) in the atmosphere. This increase has significant implications for green plants because CO_2 is the prime input to photosynthesis. Leaves are the first point of contact for the majority of carbon transfer from atmosphere to biosphere. This capture of carbon by leaves enables the growth of plants, which play a vital role in maintaining the environment and form the base of agriculture. Humans and other organisms depend on this thin layer of leaves for food. Leaves collect highly dilute CO_2 from the atmosphere and concentrate and transform it into organic compounds. These compounds ultimately combine to form useful products (food and fiber). Leaf litter decomposition (by microbes) is a key process in agroecosystems through its role in carbon and nutrient cycling and storage. Leaves and their functions are pivotal in agroecosystems (and are sensitive to environmental change, especially rising CO_2); this article provides a short overview.

PHYSIOLOGICAL PROCESSES IN LEAVES

Changes in atmospheric CO_2 level have been shown to impact two major functions of leaves—photosynthesis and transpiration.[1–3] Crops grown under CO_2 enrichment usually exhibit increased mass, which is attributed to more photosynthetic capacity and enhanced water use efficiency (ratio of CO_2 assimilated to water transpired). There are, however, differences among plants. For example, plants with a C_3 photosynthetic pathway often exhibit a greater response to high CO_2. The CO_2-concentrating mechanism in C_4 species limits the response, but C_4 plants can nevertheless exhibit growth stimulation because elevated CO_2 can increase water use efficiency. The C_3 plant generally benefits from both increased photosynthesis and water use efficiency. Increases in water use efficiency are notable, although the combined effects of CO_2 on decreasing stomatal conductance and increasing leaf area and leaf temperature have resulted in modest reductions in estimated whole plant water use.[3]

An often reported consequence of enhanced photosynthesis is the accumulation of nonstructural carbohydrates.[1,2] Photosynthetic acclimation (a decline in photosynthesis over time) can be related to the buildup of nonstructural carbohydrates in leaves. The coupling of carbohydrate accumulation in leaves and acclimation is probably related to source-sink imbalances, with sink strength an important controlling factor. Some evidence shows a correlation between rooting volume and photosynthetic capacity as well as limitations in resource availability (e.g., soil nitrogen) influencing source-sink activity.[1,2] Increases in soluble carbohydrate concentration may repress photosynthetic gene expression, leading to reductions in photosynthetic pigments (e.g., chlorophyll and carotenoids) and important soluble proteins, including rubisco and antioxidant enzymes.[4] The photosynthetic apparatus may be more susceptible to photodamage due to decreased carotenoid content. There are some indications that increases in carbohydrates and decreases in protein are associated with a slight suppression of growth respiration and construction costs of leaves.[5] Rubisco represents a sizable portion of leaf nitrogen and plays a significant role in the reduction of foliar nitrogen concentration commonly found under high CO_2 conditions.[1,2] Reductions in antioxidant enzyme activities observed under high CO_2 may be reflective of less oxidative stress resulting from growth in CO_2-enriched atmospheres.[4] Furthermore, antioxidant systems can differ according to plant genotype, suggesting differential resistance to biotic and abiotic stresses.

LEAF STRUCTURE AND DEVELOPMENT

Changes in the internal structure of leaves can occur under elevated CO_2 conditions.[6] Consideration of leaf

DOI: 10.1081/E-EPCS 120010613

structural changes may help interpret divergent findings with regard to photosynthetic acclimation. Fixation of CO_2 occurs at specific sites within the chloroplast and, under high CO_2, starch accumulation may change chloroplast structure and function (e.g., altered chloroplast integrity may limit carbohydrate transport to other organs). Both photosynthetic and assimilate transport capacity may also be altered by CO_2-induced shifts in mesophyll and vascular tissue. Leaves grown under elevated CO_2 have exhibited an extra layer (a third layer) of palisade cells as well as increased total mesophyll cross-sectional area and vascular tissue area. Stomatal density has been shown to decrease with elevated CO_2 in some, but not all cases. A further alteration is changes in epicuticular wax on high CO_2-grown leaves.[7,8] Little is known about how CO_2 will affect trichomes. Changes in the leaf surface could affect water relations, susceptibility to pests and diseases, and surface properties that are important in chemical protectant application.

Plants grown under high CO_2 often exhibit increased area per leaf, greater leaf thickness, more leaves per plant, and higher total leaf area per plant,[6] but effects on leaf area index are variable.[2,3] Exposure to elevated CO_2 is thought to have little impact on rates of leaf initiation. Reported increases in leaf thickness and decreases in specific leaf area (leaf area/total leaf dry weight) are often the result of altered anatomy or increased starch accumulation. Although highly variable, increases in cell expansion may contribute to larger leaf size more than increased cell division. Increased expansion appears to result from greater cell wall relaxation and/or greater cell turgor. There is little information on how high CO_2 will affect leaf shape or duration.

ENVIRONMENTAL CONSIDERATIONS

CO_2-induced increases in leaf production and changes in leaf composition can significantly affect other trophic level organisms that utilize leaf tissue as a food substrate. The nitrogen concentration of green leaf material is often lower under high CO_2, whereas leaf carbon:nitrogen ratio, nonstructural carbohydrates, and secondary defense compounds can be increased. Effects on senescent leaf quality are more variable, but tend to be lower in magnitude.[1,3,5] Changes in green leaves are relevant to phyllosphere organisms (fungi and bacteria living on leaf surfaces) and grazers (insects and livestock). The reproductive success of insects may be altered by diets of high CO_2-leaf tissue. However, the sparseness of information prevents generalization concerning the life cycle strategies of these organisms in a high CO_2 world. Information on this topic is critical for effective pest management (rates, timing, and number of pesticide applications may change under higher CO_2 environments). Trace gas emission (e.g., methane) associated with cattle production is related to low forage quality, thus any CO_2-induced downward shift in leaf nitrogen concentration may be significant.

Senesced leaves are a food source for soil organisms and a major component of carbon inputs for agroecosystems.[9] Leaf litter input can be increased by high CO_2, but decomposition rates will vary by crop species. Some decomposition work suggests that CO_2-enriched cropping systems may store more carbon, decomposition may be limited by nitrogen, and nitrogen release from litter may be slowed. A more thorough understanding of carbon and nitrogen cycling is needed to predict the potential for soil carbon storage in agroecosystems.[1,9] Green leaf material can also contribute to litter production in systems using cover crops. Plant growth stage and leaf tissue nitrogen need to be considered for cover crop termination to optimize resource availability (nitrogen and/or water) to the following crop. There are some indications that CO_2 can alter crop phenology,[3] which may alter kill time for cover crops and subsequent timing of farm operations, including planting. Another complication is that herbicide efficacy can vary by weed species under elevated CO_2.[10] This has important implications for future weed management (frequency of spraying/rate adjustments), including control of invasive species, and also raises questions about herbicide efficacy on cover crops.

CONCLUSION

Leaf responses to elevated atmospheric CO_2 will need to be further elucidated if we are to accurately understand and predict the development and growth of crops under future environmental conditions. Future research will need to address:

1. How alterations in leaf structure are related to both cellular and higher-level growth processes;
2. Whether increased cell division is driven by greater rates of cell expansion or by molecular cues;
3. The role of ultrastructural, anatomical, and morphological leaf adjustments in photosynthetic acclimation;
4. How CO_2-induced changes in leaf structure and leaf function will alter the degree of impact of multiple crop stresses (abiotic and biotic);
5. How CO_2-induced shifts in leaf quality and/or changes in leaf surface features (e.g., epicuticular waxes, trichomes) will alter herbivore and pathogen attacks;
6. Mechanisms for herbicide tolerance of plants grown under high CO_2;
7. How CO_2 alters leaf nutrient composition of cover crops over time (growth stage and phenology); and

8. With regard to leaf residue (green and senesced) supplying carbon and nitrogen to the soil, how elevated CO_2 will affect available crop nitrogen and the residence time of leaf-derived carbon in the soil.

ARTICLES OF FURTHER INTEREST

Air Pollutants: Interactions with Elevated Carbon Dioxide, p. 17
Crop Responses to Elevated Carbon Dioxide, p. 346
Crops and Environmental Change, p. 370
Ecophysiology, p. 410
Environmental Concerns and Agricultural Policy, p. 418
Leaf Cuticle, p. 635
Leaf Structure, p. 638
Leaves and Canopies: Physical Environment, p. 646
Photosynthate Partitioning and Transport, p. 897
Starch, p. 1175
Sucrose, p. 1179
Trichomes, p. 1254
Water Deficits: Development, p. 1284
Water Use Efficiency Including Carbon Isotope Discrimination, p. 1288

REFERENCES

1. Amthor, J.S. Terrestrial higher-plant response to increasing atmospheric [CO_2] in relation to the global carbon cycle. Glob. Chang. Biol. **1995**, *1*, 243–274.
2. Drake, B.G.; Gonzalez-Meler, M.A. More efficient plants: A consequence of rising atmospheric CO_2? Annu. Rev. Plant Physiol. Plant Mol. Biol. **1997**, *48*, 609–639.
3. Kimball, B.A.; Kobayashi, K.; Bindi, M. Responses of agricultural crops to free-air CO_2 enrichment. Adv. Agron. **2002**, *77*, 293–368.
4. Pritchard, S.G.; Ju, Z.; Van Santen, E.; Qui, J.; Weaver, D.B.; Prior, S.A.; Rogers, H.H. The influence of elevated CO_2 on the activities of antioxidative enzymes in two soybean genotypes. Aust. J. Plant Physiol. **2000**, *27*, 1061–1068.
5. Poorter, H.; Van Berkel, Y.; Baxter, R.; Den Hertog, J.; Dijkstra, P.; Gifford, R.M.; Griffin, K.L.; Roumet, C.; Roy, J.; Wong, S.C. The effect of elevated CO_2 on the chemical composition and construction costs of leaves of 27 C_3 species. Plant Cell Environ. **1997**, *20*, 472–482.
6. Pritchard, S.G.; Rogers, H.H.; Prior, S.A.; Peterson, C.M. Elevated CO_2 and plant structure: A review. Glob. Chang. Biol. **1999**, *5*, 807–837.
7. Prior, S.A.; Pritchard, S.G.; Runion, G.B.; Rogers, H.H.; Mitchell, R.J. Influence of atmospheric CO_2 enrichment, soil N, and water stress on needle surface wax formation in *Pinus palustris* (Pinaceae). Am. J. Bot. **1997**, *84*, 1070–1077.
8. Thomas, J.F.; Harvey, C.N. Leaf anatomy of four species grown under continuous CO_2 enrichment. Bot. Gaz. **1983**, *144*, 303–309.
9. Torbert, H.A.; Prior, S.A.; Rogers, H.H.; Wood, C.W. Elevated atmospheric CO_2 effects on agro-ecosystems: Residue decomposition processes and soil C storage. Plant Soil **2000**, *224*, 59–73.
10. Ziska, L.H.; Teasdale, J.R.; Bunce, J.A. Future atmospheric carbon dioxide may increase tolerance to glyphosate. Weed Sci. **1999**, *47*, 608–615.

Request Permission or Order Reprints Instantly!

Interested in copying and sharing this article? In most cases, U.S. Copyright Law requires that you get permission from the article's rightsholder before using copyrighted content.

All information and materials found in this article, including but not limited to text, trademarks, patents, logos, graphics and images (the "Materials"), are the copyrighted works and other forms of intellectual property of Marcel Dekker, Inc., or its licensors. All rights not expressly granted are reserved.

Get permission to lawfully reproduce and distribute the Materials or order reprints quickly and painlessly. Simply click on the "Request Permission/ Order Reprints" link below and follow the instructions. Visit the U.S. Copyright Office for information on Fair Use limitations of U.S. copyright law. Please refer to The Association of American Publishers' (AAP) website for guidelines on Fair Use in the Classroom.

The Materials are for your personal use only and cannot be reformatted, reposted, resold or distributed by electronic means or otherwise without permission from Marcel Dekker, Inc. Marcel Dekker, Inc. grants you the limited right to display the Materials only on your personal computer or personal wireless device, and to copy and download single copies of such Materials provided that any copyright, trademark or other notice appearing on such Materials is also retained by, displayed, copied or downloaded as part of the Materials and is not removed or obscured, and provided you do not edit, modify, alter or enhance the Materials. Please refer to our Website User Agreement for more details.

Request Permission/Order Reprints

Reprints of this article can also be ordered at
http://www.dekker.com/servlet/product/DOI/101081EEPCS120010613