7

Terrestrial Plants and Soils

7. Terrestrial Plants and Soils

Introduction

In its 2007 report, the Intergovernmental Panel on Climate Change (IPCC) hardly mentions the beneficial effects of rising atmospheric carbon dioxide (CO_2) concentration on terrestrial plants. In a chapter titled "Changes in Atmospheric Constituents and in Radiative Forcing," the authors write:

> Increased CO_2 concentrations can also "fertilize" plants by stimulating photosynthesis, which models suggest has contributed to increased vegetation cover and leaf area over the 20th century (Cramer *et al.,* 2001). Increases in the Normalized Difference Vegetation Index, a remote sensing product indicative of leaf area, biomass and potential photosynthesis, have been observed (Zhou *et al.,* 2001), although other causes including climate change itself are also likely to have contributed. Increased vegetative cover and leaf area would decrease surface albedo, which would act to oppose the increase in albedo due to deforestation. The RF due to this process has not been evaluated and there is a very low scientific understanding of these effects the following (IPCC 2007, p. 186).

Later in that report, in a chapter titled "Couplings Between Changes in the Climate System and Biogeochemistry," a single paragraph is devoted to the "effects of elevated carbon dioxide" on plants. The paragraph concludes, "it is not yet clear how strong the CO_2 fertilization effect actually is" (p. 527).

The Nongovernmental International Panel on Climate Change (NIPCC) strongly dissented. In a chapter spanning more than 200 pages and citing more than 1,300 peer-reviewed articles, Idso and Singer (2009) contend "the IPCC's failure to report the beneficial effects of rising CO_2 concentrations is surprising when literally thousands of peer-reviewed journal articles exist on the subject. It is also a major defect of the IPCC report and one reason why it is not a reliable summary of the science of climate change."

This chapter begins with a survey of the latest scientific literature on the productivity responses of plants to higher CO_2 concentrations, and then reviews research on other plant responses, responses of plants under stress, effect on biodiversity, carbon sequestion, plant and animal extinction, evolution, food production, the greening of the Earth, and the nitrogen cycle. Like the 2009 report, this survey of the literature confirms what the IPCC so carefully avoids admitting, that atmospheric CO_2 enrichment benefits plant life in many ways.

References

Idso, C.D. and Singer, S.F. 2009. *Climate Change Reconsidered: 2009 Report of the Nongovernmental International Panel on Climate Change (NIPCC).* Chicago, IL: The Heartland Institute.

IPCC. 2007. *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change.* Solomon, S., D. Qin, M. Manning, Z. Chen, M. Marquis, K.B. Averyt, M. Tignor and H.L. Miller. (Eds.) Cambridge University Press, Cambridge, UK.

7.1. Plant Growth Responses to Atmospheric CO_2 Enrichment

7.1.1. C_3 Plants

We begin our review of atmospheric CO_2 enrichment effects on Earth's vegetation with a consideration of C_3 plants—those in which the enzyme RuBisCO is involved in the uptake of CO_2 and the subsequent photosynthetic process, which results in its incorporation into a 3-carbon compound—starting with the study of Norikane et al. (2010). They focused on the genus *Cymbidium*, which comprises about 50 species distributed throughout tropical and subtropical Asia and Oceania.

The four researchers worked with shoots of Music Hour 'Maria,' a type of orchid, possessing two to three leaves, which they obtained from a mass of protocorm-like bodies they derived from shoot-tip culture. They grew them *in vitro* on a modified Vacin and Went medium in air augmented with either 0, 3,000, or 10,000 ppm CO_2 under two photosynthetic photon flux densities (either 45 or 75 µmol m^{-1} s^{-1}) provided by cold cathode fluorescent lamps for a period of 90 days. They then transferred the plants to *ex vitro* culture for 30 more days. Relative to plants grown *in vitro* in ambient air, the percent increases in shoot and root dry weight due to enriching the air in which the plants grew by 3,000 ppm CO_2 were, respectively, 216 percent and 1,956 percent under the low-light regime and 249 percent and 1,591 percent under the high-light regime, while corresponding increases for the plants grown in air enriched with an extra 10,000 ppm CO_2 were 244 percent and 2,578 percent under the low-light regime and 310 percent and 1,879 percent under the high-light regime. Similarly, in the *ex vitro* experiment, the percent increases in shoot and root dry weight due to enriching the air in which the plants grew by 3,000 ppm CO_2 were 223 percent and 436 percent under the low-light regime and 279 percent and 469 percent under the high-light regime, while corresponding increases for the plants grown in air enriched with an extra 10,000 ppm CO_2 were 271 percent and 537 percent under the low-light regime and 332 percent and 631 percent under the high-light regime. Consequently, the Japanese scientists concluded, "super-elevated CO_2 enrichment of in vitro-cultured *Cymbidium* could positively affect the efficiency and quality of commercial production of clonal orchid plantlets."

Turning from ornamental plants to food crops, Vanaja et al. (2010) note grain legumes "provide much needed nutritional security in the form of proteins to the predominant vegetarian populations of India and also the world." They further state that legumes—of which pigeon peas are an important example—"have the potential to maximize the benefit of elevated CO_2 by matching stimulated photosynthesis with increased N_2 fixation," citing Rogers et al. (2009). Therefore, they grew pigeon peas (*Cajanus cajan* L. Millsp.) from seed to maturity outdoors at Hyderabad, India within open-top chambers maintained at atmospheric CO_2 concentrations of either 370 or 700 ppm. They then harvested the plants and measured pertinent productivity parameters.

This work revealed, according to the team of nine Indian scientists, that in the higher of the two CO_2 concentrations, "total biomass recorded an improvement of 91.3%, grain yield 150.1% and fodder yield 67.1%." They also found "the major contributing components for improved grain yield under elevated CO_2 were number of pods, number of seeds and test weight," with these items exhibiting increases of 97.9 percent, 119.5 percent, and 7.2 percent, respectively. In addition, they found there was "a significant positive increase of harvest index at elevated CO_2 with an increment of 30.7% over ambient values," which they say was due to the crop's "improved pod set and seed yield under enhanced CO_2 concentration." These multiple positive findings, according to the scientists from India's Central Research Institute for Dryland Agriculture, illustrate the importance of pigeon peas for "sustained food with nutritional security under a climate change scenario."

In much the same vein, Yang et al. (2009) declared, "rice is unequivocally one of the most important food crops that feed the largest proportion of the world's population," that "the demand for rice production will continue to increase in the coming decades, especially in the major rice-consuming countries of Asia, Africa and Latin America," and that "accurate predictions of rice yield and of the ability of rice crops to adapt to high CO_2 environments are therefore crucial for understanding the impact of climate change on the future food supply." In fact, they forcefully state—and rightly—that "there is a pressing need to identify genotypes which could optimize harvestable yield as atmospheric CO_2 increases."

They set out to do that in a standard paddy culture free-air CO_2 enrichment (FACE) experiment conducted at Yangzhou, Jiangsu, China over the period 2004–2006. The team of eight researchers grew a two-line inter-subspecific hybrid rice variety (Liangyoupeijiu) at ambient and elevated atmospheric CO_2 concentrations of 376 and 568 ppm, respectively, at two levels of field nitrogen (N) application: low N (12.5 g N m^{-2}) and high N (25 g N m^{-2}), measuring numerous aspects of crop growth, development, and final yield production in the process. The Chinese scientists found the 51 percent increase in atmospheric CO_2 concentration employed in their study increased the final grain yield of the low N rice crop by 28 percent and that of the high N rice crop by 32 percent. As a result, and "compared with the two prior rice FACE experiments (Kim et al., 2003; Yang et al., 2006)," they state, "hybrid rice appears to profit much more from CO_2 enrichment than inbred rice cultivars (c. +13 percent)." Yang et al. describe Liangyoupeijiu as "one of the most popular 'super' hybrid rice varieties in China (Peng et al., 2004)," and it appears it will become increasingly "super" as the air's CO_2 content continues to rise, helping China to lead the way in future food production.

References

Kim, H.Y., Lieffering, M., Kobayashi, K., Okada, M., Mitchell, M.W., and Gumpertz, M. 2003. Effects of free-air CO_2 enrichment and nitrogen supply on the yield of temperate paddy rice crops. *Field Crops Research* **83**: 261–270.

Norikane, A., Takamura, T., Morokuma, M., and Tanaka, M. 2010. In vitro growth and single-leaf photosynthetic response of *Cymbidium* plantlets to super-elevated CO_2 under cold cathode fluorescent lamps. *Plant Cell Reports* **29**: 273–282.

Peng, S., Laza, R.C., Visperas, R.M., Khush, G.S., Virk, P., and Zhu, D. 2004. Rice: progress in breaking the yield ceiling. In *New Directions for a Diverse Planet: Proceedings of the Fourth International Crop Science Congress*, 26 Sep-1 Oct 2004, Brisbane, Australia. Gosford, Australia: Regional Institute Ltd.

Rogers, A., Ainsworth, E.A., and Leakey, A.D.B. 2009. Will elevated carbon dioxide concentration amplify the benefits of nitrogen fixation in legumes? *Plant Physiology* **151**: 1009–1016.

Vanaja, M., Reddy, P.R.R., Lakshmi, N.J., Razak, S.K.A., Vagheera, P., Archana, G., Yadav, S.K., Maheswari, M., and Venkateswarlu, B. 2010. Response of seed yield and its components of red gram (*Cajanus cajan* L. Millsp.) to elevated CO_2. *Plant, Soil and Environment* **56**: 458–462.

Yang, L., Liu, H., Wang, Y., Zhu, J., Huang, J., Liu, G., Dong, G., and Wang, Y. 2009. Yield formation of CO_2-enriched inter-subspecific hybrid rice cultivar Liangyoupeijiu under fully open-air condition in a warm sub-tropical climate. *Agriculture, Ecosystems and Environment* **129**: 193–200.

Yang, L.X., Huang, J.Y., Yang, H.J., Zhu, J.G., Liu, H.J., Dong, G.C., Liu, G., Han, Y., and Wang, Y.L. 2006. The impact of free-air CO_2 enrichment (FACE) and N supply on yield formation of rice crops with large panicle. *Field Crops Research* **98**: 141–150.

7.1.2. C_4 Plants

Moving on to C_4 plants—where the enzyme PEP carboxylase allows CO_2 to be taken in very quickly and delivered directly to RuBisCO for photosynthetic incorporation into a 4-carbon compound—Vu and Allen (2009) note such vegetation represents "fewer than 4% of all angiosperm species," yet "their ecological and economic significance is substantial." On a global basis, for example, they write, "up to one-third of terrestrial productivity is provided by C_4 plants," citing Cerling et al. (1997), Ghannoum et al. (1997), and Brown et al. (2005), and they note "in many tropical regions, the food source is primarily based on C_4 crops, among [which] maize, millet, sorghum and sugarcane are the most agriculturally important monocots in terms of production (Brown, 1999)," with "up to 75% of the world sugar production provided by sugarcane (De Souza et al., 2008)." In addition, they indicate the emerging "use of sugarcane as a source for biofuel production has been highly recognized," citing Goldenberg (2007).

So what will happen to the productivity of this important crop as the air's CO_2 content continues its upward climb, especially if global air temperatures rise along with it?

Historically, C_4 crops have been thought to be relatively unresponsive to atmospheric CO_2 enrichment, as they possess a CO_2-concentrating mechanism that allows them to achieve a greater photosynthetic capacity than C_3 plants at the current atmospheric CO_2 concentration, particularly at high growth temperatures (Matsuoka et al., 2001). Thus, simple reasoning might suggest C_4 plants may be little benefited, if at all, in a CO_2-enriched and warmer world of the future. However, in the case of sugarcane, as the research of Vu and Allen demonstrates, simple reasoning would be incorrect, especially with respect to the most important measure of sugarcane's economic value: stem juice production.

The two researchers with the USDA's Agricultural Research Service, who hold joint appointments in the Agronomy Department of the University of Florida (USA), grew two cultivars of sugarcane (*Saccharum officinarum*) for a period of three months in paired-companion, temperature-gradient, sunlit greenhouses under daytime CO_2 concentrations of 360 and 720 ppm and air temperatures of 1.5°C (near ambient) and 6.0°C higher than outside ambient temperature, after which they measured several different plant properties.

"On a main stem basis," Vu and Allen write, "leaf area, leaf dry weight, stem dry weight and stem juice volume were increased by growth at doubled CO_2 [as well as at] high temperature," and they state these increases were even greater under the combination of doubled CO_2 and high temperature, with plants grown under these conditions averaging "50%, 26%, 84% and 124% greater leaf area, leaf dry weight, stem dry weight and stem juice volume, respectively, compared with plants grown at [the] ambient CO_2/near-ambient temperature combination." In addition, they write, "plants grown at [the] doubled CO_2/high temperature combination were 2- to 3-fold higher in stem soluble solids than those at [the] ambient CO_2/near-ambient temperature combination."

Consequently, as Vu and Allen conclude, "sugarcane grown under predicted rising atmospheric CO_2 and temperature in the future may use less water, utilize water more efficiently, and would perform better in sucrose production." This bodes well for tropical-region agriculture, especially, as they note, "with the worldwide continued increase in demand for sugarcane as a source of food and biofuel."

Last, they add that significant "improvements in stem sucrose and biomass through classical breeding and/or new biotechnology" may also be achieved; and, hence, they state, "studies to identify the cultivars with high efficiency in water use and stem sucrose production under future changes in CO_2 and climate are of great importance and should be initiated and explored." Working hand-in-hand with the benefits provided by the ongoing rise in the air's CO_2 content, therefore, as well as those provided by the possibility of still higher air temperatures to come, we may yet be able to meet the increasing food needs of our expanding numbers without taking vast amounts of land and freshwater resources from Earth's natural ecosystems.

Also studying sugarcane, Gouvea et al. (2009) used the agrometeorological model of Doorenbos and Kassam (1994) "to estimate sugarcane yield in tropical southern Brazil, based on future A1B climatic scenarios presented in the fourth Intergovernmental Panel on Climate Change report." They first calculated potential productivity, which considers "the possible impacts caused by changes in temperature, precipitation, sunshine hours and CO_2 concentration in the atmosphere, as well as technological advances," and then actual productivity, which additionally accounts for the yield-reducing effects of water stress.

Based on their calculations, Gouvea et al. determined "potential productivity will increase by 15% in relation to the present condition in 2020, by 33% in 2050 and by 47% in 2080," and "actual productivity will increase by 12% in relation to the present condition in 2020, by 32% in 2050 and by 47% in 2080." They further indicate expected technological advances, including the development of new varieties and best-management practices, will account for 35 percent of the yield gains in 2020, 51 percent in 2050, and 61 percent in 2080. Consequently, and in spite of the gloomy prognostications of the IPCC and its followers, this modeling exercise suggests there will be, in the words of the four researchers, "a beneficial effect of forecasted climate changes on sugarcane productivity, due to the expected increases in temperature and CO_2 concentration."

Finally, in a study of aquatic C_4 vegetation, Mateos-Naranjo et al. (2010) focused their attention on *Spartina maritima*, a cordgrass they say is "an important pioneer and ecosystem engineer in salt marshes on the Atlantic coast of southern Europe," citing Castellanos et al. (1994), noting this particular halophyte "produces extensive stands in a range of marsh environments," citing Castellanos et al. (1998). Working with 15-cm-diameter clumps of the plant obtained from a low-marsh site along the southwest coast of Spain in April 2007, they transplanted them into individual plastic pots filled with pearlite that rested on shallow trays filled with Hoagland's solution of three different salinities (0, 170, or 510 mM NaCl), which they maintained in controlled environment chambers having atmospheric CO_2 concentrations of either 380 ppm or 700 ppm for periods of 30 days, during which time they measured several plant properties and processes.

The four researchers discovered the 84 percent increase in the atmosphere's CO_2 concentration stimulated the growth of *S. maritima* by about 65 percent in all three salinity treatments, while their graphical representation of the halophyte's water use efficiency indicates this important plant property was enhanced by approximately 10 percent, 100 percent, and 160 percent in the 0, 170, and 510 mM salinity treatments, respectively, because, as they describe it, "increasing CO_2 concentration has a positive effect on the photochemical apparatus, helping to counteract salt stress experienced by plants at current CO_2 concentrations." Thus, the U.K. and Spanish scientists concluded the productivity of *S. maritima* "might increase in a future scenario of rising atmospheric CO_2 concentration in environments with salinities as high as that of seawater." That is extremely good news regarding what they describe as "an important pioneer and ecosystem engineer in salt marshes."

References

Brown, R.H. 1999. Agronomic implications of C_4 photosynthesis. In *C_4 Plant Biology*, edited by R.F. Sage and R.K. Monson, 473–507. San Diego, CA: Academic Press.

Brown, N.J., Parsley, K., and Hibberd, J.M. 2005. The future of C_4 research - maize, *Flaveria* or *Cleome*? *Trends in Plant Science* **10**: 215–221.

Castellanos, E.M., Figueroa, M.E., and Davy, A.J. 1994. Nucleation and facilitation in saltmarsh succession: interactions between *Spartina maritima* and *Arthrocnemum perenne*. *Journal of Ecology* **82**: 239–248.

Castellanos, E.M., Heredia, C., Figueroa, M.E., and Davy, A.J. 1998. Tiller dynamics of *Spartina maritima* in successional and non-successional Mediterranean salt marsh. *Plant Ecology* **137**: 213–225.

Cerling, T.E., Harris, J.M., MacFadden, B.J., Leakey, M.G., Quade, J., Eisenmann, V., and Ehleringer, J.R. 1997. Global vegetation change through the Miocene/Pliocene boundary. *Nature* **389**: 153–158.

De Souza, A.P., Gaspar, M., Da Silva, E.A., Ulian, U.C., Waclawovsky, A.J., Nishiyama Jr., M.Y., Dos Santos, R.V., Teixeira, M.M., Souza, G.M., and Buckeridge, M.S. 2008. Elevated CO_2 increases photosynthesis, biomass and productivity, and modifies gene expression in sugarcane. *Plant, Cell and Environment* **31**: 1116–1127.

Doorenbos, J. and Kassam, A.H. 1994. Efeito da agua no rendimento das culturas. Campina Grande: UFPB. Estudos FAO Irrigacao e Drenagem.

Ghannoum, O., von Caemmerer, S., Barlow, E.W.R., and Conroy, J.P. 1997. The effect of CO_2 enrichment and irradiance on the growth, morphology and gas exchange of a C_3 (*Panicum laxum*) and a C_4 (*Panicum antodotale*) grass. *Australian Journal of Plant Physiology* **24**: 227–237.

Goldenberg, J. 2007. Ethanol for a sustainable energy future. *Science* **315**: 808–810.

Gouvea, J.R.F., Sentelhas, P.C., Gazzola, S.T., and Santos, M.C. 2009. Climate changes and technological advances: impacts on sugarcane productivity in tropical southern Brazil. *Scientia Agricola* **66**: 593–605.

Mateos-Naranjo, E., Redondo-Gomez, S. Andrades-Moreno, L., and Davy, A.J. 2010. Growth and photosynthetic responses of the cordgrass *Spartina maritima* to CO_2 enrichment and salinity. *Chemosphere* **81**: 725–731.

Matsuoka, M., Furbank, R.T., Fukayama, H., and Miyao, M. 2001. Molecular engineering of C_4 photosynthesis. *Annual Review of Plant Physiology and Plant Molecular Biology* **52**: 297–314.

Vu, J.C.V. and Allen Jr., L.H. 2009. Stem juice production of the C_4 sugarcane (*Saccharum officinarum*) is enhanced by growth at double-ambient CO_2 and high temperature. *Journal of Plant Physiology* **166**: 1141–1151.

7.1.3. CAM Plants

Concluding this brief review of plant productivity responses to atmospheric CO_2 enrichment, we consider the impact of this phenomenon on Crassulacean Acid Metabolism or CAM plants, where CO_2 enters the plants through their stomata at night and is stored in the form of an acid that is broken down the next day, when its CO_2 is released to RuBisCO for the purpose of participating in the process of photosynthesis.

The first study of this type that we consider deals with the process of micropropagation, which, to quote Yoon et al. (2009), "is an established technique for [the] rapid propagation of uniform plants," although they note leaves formed during *in vitro* growth "may never attain photosynthetic competence." Consequently, to maintain a positive carbon balance over the *in vitro* to *ex vitro* transition, they write, "sugar is supplemented as the source of carbon." They go on to state, however, that "addition of sugar to the culture media [has been] negatively correlated with growth, photosynthesis and expression of enzymes of the carbon assimilation pathway," so the standard cure for the problem is partially self-defeating. Thus, the question arises: Can CO_2 do anything to help?

In investigating this possibility, Yoon et al. grew plantlets of *Phalaenopsis* "Amaglade"—a monopodial epiphytic CAM orchid with succulent leaves—derived from flower stalk cultures and multiplied on a hyponex medium either with or without the addition of 30 g sugar per liter of medium, in air of either 400 or 1,000 ppm CO_2, for a period of 90 days *in vitro* followed by 40 days *ex vitro*, "to identify the more suitable treatments *in vitro* for the best acclimatization of *Phalaenopsis* plantlets to *ex vitro* conditions," which they did by monitoring several plant morphological traits, photosynthetic attributes, and intrinsic elements of the CAM pathway.

The results of these operations indicated the extra CO_2 eliminated the need for any sugar to be supplied to the plantlets, with shoot dry weight in the CO_2-enriched air exceeding that in the ambient air by 120 percent in the nonsweetened treatment at the end of the *in vitro* period, and with root dry weight in the CO_2-enriched air exceeding that in the ambient air by 350 percent. Likewise, at the end of the *ex vitro* period, the CO_2-induced shoot and root dry weight increases in the nonsweetened treatment were 55 percent and 86 percent, respectively. Thus, the four Korean researchers concluded, "plantlets grown under CO_2 enrichment"—and without the help of any applied sugar—"developed completely viable photosynthetic apparatus ready to be efficiently transferred to *ex vitro* conditions," which they state has "far-reaching implications" for the micropropagation of *Phalaenopsis* and possibly other plants as well.

In another pertinent paper, Weiss et al. (2010) introduce their newest work on the subject by noting the CAM cacti *Hylocereus undatus* (red pitaya) and *Selenicereus megalanthus* (yellow pitaya) "are cultivated in a dozen countries around the world and were introduced into and developed in Israel as export fruit crops (Mizrahi et al., 1997)." They write, "both species consist of elongated, three-ribbed stems that cling to trees and rocks in their natural habitat, which, for *S. megalanthus*, is characterized by humid tropical forests (Colombia, Ecuador, Peru and the Amazon Basin." *H. undatus*, on the other hand, grows naturally in the dry forests of Mexico, indicating it is better adapted to semi-arid conditions.

Working in the northern Negev Desert of Israel, the three researchers grew rooted shoot cuttings of the two vine-cactus fruit-crop species in pots filled with volcanic gravel for a period of one full year (August 2006 to August 2007). This was done within vented chambers maintained at either ambient or elevated atmospheric CO_2 concentrations (380 or 1,000 ppm, respectively) in a cooled greenhouse, where the plants were "fertigated" twice weekly with 0.5-strength Hoagland's solution, and where the researchers measured net photosynthesis on four days in mid-April and made final biomass determinations at the conclusion of the study. In addition, they conducted a second one-year study of more-mature, eight-year-old plants in order to investigate their fruit development responses to atmospheric CO_2 enrichment. This work was done in open-top chambers maintained within the same greenhouse.

As Weiss et al. describe it, their results indicated "*H. undatus* plants enriched with CO_2 demonstrated 52%, 22%, 18% and 175% increases, relative to plants measured in ambient CO_2, in total daily net CO_2 uptake, shoot elongation, shoot dry mass, and number of reproductive buds, respectively," while corresponding responses for *S. megalanthus* were 129 percent, 73 percent, 68 percent, and 233 percent. In addition, they found a slight (7 percent) increase in the fruit fresh mass of *H. undatus* and a much greater, 63 percent, increase in the fruit fresh mass of *S. megalanthus*, resulting from the extra 620 ppm of CO_2 enrichment of the air in which the plants had been grown. The three researchers write that, to the best of their knowledge, "this is the first study of the reproductive responses of CAM plants to CO_2 enrichment," and they conclude their experiments demonstrate "the vast potential of possible increases in the yields of CAM crops under CO_2 enrichment."

References

Mizrahi, Y., Nerd, A., and Nobel, P.S. 1997. Cacti as crops. *Horticultural Reviews* **18**: 321–346.

Weiss, I., Mizrahi, Y., and Raveh, E. 2010. Effect of elevated CO_2 on vegetative and reproductive growth characteristics of the CAM plants *Hylocereus undatus* and *Selenicereus megalanthus*. *Scientia Horticulturae* **123**: 531–536.

Yoon, Y.-J., Mobin, M., Hahn, E.-J., and Paek, K.-Y. 2009. Impact of *in vitro* CO_2 enrichment and sugar deprivation on acclamatory responses of *Phalaenopsis* plantlets to *ex vitro* conditions. *Environmental and Experimental Botany* **65**: 183–188.

7.1.4. Ecosystems: Forests

Moving up from individual species and small groups of plants to the ecosystem scale, we consider the case of natural and plantation-type forests, beginning with studies of the latter type, where the air around groups of trees has been experimentally enriched with CO_2, starting with the study of McCarthy et al. (2010). Conducted at the Duke Forest Free-Air CO_2-Enrichment (FACE) facility, this study is a long-term experiment designed to investigate the effects of an extra 200 ppm of atmospheric CO_2 on the growth and development of a plantation of loblolly pine (*Pinus taeda*) trees with an understory of various broadleaf species, including *Liriodendron tulipifera, Liquidambar styraciflua, Acer rubrum, Ulmus alata*, and *Cornus florida*, plus various other trees, shrubs, and vines. All of these were grown on a soil that Finzi and Schlesinger (2003) describe as being in "a state of acute nutrient deficiency that can only be reversed with fertilization." Many researchers had long thought such fertility deficiency would stifle the ability of the extra aerial supply of CO_2 to significantly stimulate the forest's growth on a continuing basis.

Working with data for the years 1996–2004, the team of nine researchers writes, "net primary productivity [NPP] for pines, hardwoods and the entire stand was calculated as the sum of the production of coarse wood (stems, branches, coarse roots), leaf litter (lagged for pines), fine roots and reproductive structures." The results of this protocol indicated "elevated CO_2 increased pine biomass production, starting in 1997 and continuing every year thereafter," and "the CO_2-induced enhancement remained fairly consistent as the stand developed." In addition, they found "elevated CO_2 increased stand (pine plus all other species) biomass production every year from 1997 onwards with no trend over time," while the average yearly increase in NPP caused by the approximate 54 percent increase in the air's CO_2 content was 28 percent. Thus, and in spite of the original belief of many scientists that low levels of soil nitrogen—especially an acute deficiency—would preclude any initial growth stimulation provided by atmospheric CO_2 enrichment from long persisting, the suite of trees, bushes, and shrubs that constitute the Duke Forest has continued to maintain the extra CO_2-enabled vitality it exhibited right from the start of the study, with no sign of it even beginning to taper off.

Further extending the results of the Duke Forest FACE study were Jackson et al. (2009), who describe new belowground data they obtained there, after which they present a synthesis of these and other results obtained from 1996 through 2008, seeking to determine "which, if any, variables show evidence for a decrease in their response to atmospheric CO_2 during that time frame."

Among many other things, Jackson et al. report "on average, in elevated CO_2, fine-root biomass in the top 15 cm of soil increased by 24%," and in recent years the fine-root biomass increase "grew stronger, averaging ~30% at high CO_2." Regarding coarse roots having diameters greater than 2 mm and extending to a soil depth of 32 cm, they report, "biomass sampled in 2008 was twice as great in elevated CO_2." We calculate from the graphical representation of their results that the coarse-root biomass was fully 130 percent greater, which is astounding, particularly given that the extra 200 ppm of CO_2 supplied to the air surrounding the CO_2-enriched trees represented only about a 55 percent increase over ambient conditions. In the concluding sentence of their paper's abstract, Jackson et al. state, "overall, the effect of elevated CO_2 belowground shows no sign of diminishing."

In expanding on this statement, the four researchers note "if progressive nitrogen limitation were occurring in this system, we would expect differences in productivity to diminish for trees in the elevated vs. ambient CO_2 plots," but they state, "in fact there is little evidence from estimates of aboveground or total net primary productivity in the replicated Duke experiment that progressive nitrogen limitation is occurring there or at other forest FACE experiments," even "after more than a decade of manipulation" of the air's CO_2 content, citing in this regard—with respect to the latter portion of their statement—the report of Finzi et al. (2007). Consequently, there is very good reason to believe the "aerial fertilization effect" of atmospheric CO_2 enrichment will continue to benefit Earth's forests significantly as long as the atmosphere's CO_2 concentration continues to rise.

Also studying this important subject were Darbah et al. (2010), who worked with photosynthesis data they and others collected over 11 years at the Aspen

FACE site near Rhinelander, Wisconsin (USA). They too evaluated the progressive nitrogen limitation hypothesis, working with two different quaking aspen (*Populus tremuloides* Michx.) clones (42E and 271), which were exposed to all combinations of ambient and elevated (560 ppm) CO_2 and ambient and elevated (1.5 times ambient) ozone (O_3). As an added bonus, they investigated whether the same principle might apply to leaf stomatal conductance.

In a crisp and clear report of what they learned, the eight researchers state their results "suggest no long-term photosynthetic and stomatal acclimation to elevated CO_2, O_3 or CO_2 + O_3 in aspen trees exposed to elevated CO_2 and/or O_3 gases for 11 years," and that the aspen trees "have sustained their maximum instantaneous photosynthesis stimulation for over a decade." In commenting on their findings, Darbah et al. state they support the observations of (1) Liberloo et al. (2007), who measured a 49 percent increase in net photosynthetic rate in poplar trees after six years of exposure to elevated CO_2, (2) the findings of Sholtis et al. (2004), who reported a 44 percent stimulation of net photosynthesis in sweetgum trees after three years of exposure to elevated CO_2, (3) Crous and Ellsworth (2004), who found a photosynthetic enhancement of 51–69 percent in *Pinus taeda* trees after six years of exposure to elevated CO_2, and (4) Davey et al. (2006) and (5) Paoletti et al. (2007), of whose work Darbah et al. state, "there was no photosynthetic acclimation (down-regulation) occurring in *Quercus ilex* under long-term CO_2 enrichment." In addition, they remark that (6) even in white clover (*Trifolium repens*), Ainsworth et al. (2003) found photosynthetic stimulation "remained after nine years of exposure to elevated CO_2."

Additional support for this upbeat view of the matter is provided by Bader et al. (2010), who, while working at the Swiss Canopy Crane facility in a species-rich deciduous forest 15 km south of Basel, Switzerland, where the 100-year-old stand reaches canopy heights of 30 to 35 meters, measured light-saturated rates of net photosynthesis between 8:30 am and 12:20 pm at ambient (380 ppm) and elevated (550 ppm) atmospheric CO_2 concentrations, the latter of which were maintained throughout all daylight periods over the course of the eighth growing season of their long-term study—just as they had been similarly maintained over the prior seven years—in three *Quercus petraea* trees, three *Carpinus betulus* trees, one *Tilia platyphyllos* tree, and one *Acer campestre* tree.They then compared the results of their measurements with those obtained in earlier years of the experiment.

Bader et al. report the mean net photosynthetic rate of the upper-canopy foliage was 48 percent greater in the CO_2-enriched foliage than in the ambient-treatment foliage in July and 42 percent greater in September, yielding an average increase of 45 percent in response to the 45 percent increase in the air's CO_2 content. They go on to observe, "in the same stand, Zotz et al. (2005) found 36 and 49% photosynthetic enhancement in the mid and late growing season, respectively." This represents a mean response of 42.5 percent, slightly less than what Bader et al. observed most recently.

As for the significance of their findings, the three Swiss scientists write, "the lack of photosynthetic down-regulation is consistent with the findings for mature and understory sweetgum trees growing at the ORNL- and Duke-FACE sites, respectively, and three poplar species growing at short-rotation coppice at the POP-FACE site, as well as for aspen and birch at the ASPEN-FACE stands (Herrick and Thomas, 2001; Sholtis et al., 2004; Liberloo et al., 2007; Uddling et al., 2009)." And in their final comment about their own study, they state their findings suggest "the enhancement of photosynthesis may persist in these mature deciduous trees under high future atmospheric CO_2 concentrations," while adding in the abstract of their paper that they will likely do so "without reductions in photosynthetic capacity."

Kets et al. (2010) also explored the phenomenon of acclimation by investigating diurnal changes in the rate of light-saturated net photosynthesis (Pn) under both ambient and elevated CO_2 and/or ozone (O_3) concentrations over wide ranges of leaf stomatal conductance, leaf water potential, intercellular CO_2 concentration, leaf temperature, and vapor pressure difference between leaf and air in two clones (271 and 42E) of quaking aspen (*Populus tremuloides* Michx.) trees that differed in their sensitivity to ozone and had been growing at the Aspen FACE site for seven to eight years. In describing their findings, they state Pn was typically enhanced by 33–46 percent in the CO_2-enriched treatments over the course of their study, and there was a small increase in leaf chlorophyll concentration as well.

Consequently, and noting that "previous Aspen FACE studies have reported 25–36% increases in Pn (Noormets et al., 2001; Takeuchi et al., 2001; Sharma et al., 2003; Ellsworth et al., 2004)," the six scientists emphasize that the aerial fertilization effect of atmospheric CO_2 enrichment on Pn observed in their study "has rather been increasing in time than decreasing," stating this phenomenon may be caused by the "slight but significant increase in leaf chlorophyll content per leaf area, which is rather positive acclimation in photosynthetic apparatus than negative acclimation." In support of this conclusion they also cite the studies of Centritto and Jarvis (1999) and Eichelmann et al. (2004). Hence, their experiment demonstrated that some of the benefits of elevated atmospheric CO_2 concentrations may actually increase with the passage of time.

Taking the study of this important subject a major step forward, via a totally different approach, Phillips et al. (2008) begin by noting there is "a long held view," as they describe it, that "old trees exhibit little potential for growth." Hence, they write, "it may seem reasonable to conclude that old trees are not responsive to increased CO_2," as some researchers do indeed claim. They go on, however, to demonstrate this view is far from the truth.

The three researchers begin their analysis of the subject by stating, "hydraulic constraints in tall trees," such as those of great age, "constitute a fundamental form of water limitation; indeed, one that is indistinguishable from soil water limitations," citing Koch et al. (2004) and Woodruff et al. (2004). They also report "recent research indicates that tree size and its hydraulic correlates, rather than age per se, controls carbon gain in old trees," as indicated by the study of Mencuccini et al. (2005). These findings imply, in their words, that "factors that alleviate internal or external resource constraints on old trees could improve physiological function and ultimately growth," which is something elevated CO_2 does quite well by increasing plant water use efficiency. They list several phenomena that suggest "a fundamental potential for old growth trees to show greater photosynthesis and growth under industrial age increases in CO_2 than they would under constant, pre-industrial CO_2 levels."

Drawing from their own work, Phillips et al. find "500- and 20-year-old Douglas-fir trees both show high sensitivity of photosynthesis to atmospheric CO_2," presenting data that clearly demonstrate, as they phrase it, "under optimal conditions there exists the potential for an approximately 30% increase in photosynthetic rate with an increase in CO_2 from pre-industrial to current levels [i.e., from 280 to 385 ppm] in old trees." And they go on to note "the phenomenon of twentieth-century ring-width increase," which could thus be expected to accompany the twentieth-century increase in the air's CO_2 content, has in fact been detected in several other studies, including those of LaMarche et al., (1984), Jacoby (1986), Graybill (1987), Kienast and Luxmoore (1988), Graumlich (1991), Knapp et al. (2001), Bunn et al. (2005), and Soule and Knapp (2006), to which could be added the study of Graybill and Idso (1993).

Further commenting on the significance of the findings of these studies, the three researchers write that the results of LaMarche et al. (1984) "could not be explained by temperature or precipitation variation over this time period, but were consistent with, and attributed to, the rise in atmospheric CO_2," which also was the case with the results of Graybill and Idso (1993). Although these data, in their words, "appear to represent compelling circumstantial evidence for carbon fertilization of old growth trees," they note "this possibility has been discounted and climate change has instead been implicated for the observed responses in subsequent research." That invalid discounting is likely based on the erroneous claim that twentieth-century global warming was unprecedented over the past one to two millennia. Instead, it is quite probable that a good portion of the twentieth-century increase in tree growth was a consequence of the growth-promoting and water-use-efficiency-enhancing increase in the air's CO_2 content.

In summation, the analysis of Phillips et al. (2008) provides substantial support for the two-part thesis that (1) old-growth forests can continue to sequester carbon for multiple centuries in the face of ever-increasing atmospheric CO_2 concentrations, and (2) the global temperature history employed by the Intergovernmental Panel on Climate Change depicts an unrealistically large temperature increase over the course of the twentieth century.

Additional evidence for this thesis has recently come from Pan et al. (2010). They examined "how changes in atmospheric composition (CO_2, O_3 and N deposition), climate and land-use affected carbon dynamics and sequestration in Mid-Atlantic temperate forests during the 20th century," by modifying and applying "a well established process-based ecosystem model with a strong foundation of ecosystem knowledge from experimental studies," which they validated "using the U.S. Forest Inventory and Analysis data."

For previously harvested and currently regrowing forests, the calibrated model produced the following percentage changes in net ecosystem productivity (NEP) due to observed changes in N deposition (+32 percent), CO_2 (+90 percent), O_3 (-40 percent), CO_2 + O_3 (+60 percent), CO_2 + N deposition (+184 percent), and CO_2 + N deposition + O_3 (+138 percent), while corresponding changes in NEP for undisturbed forests were +18 percent, +180 percent, -75 percent, +78 percent, +290 percent, and +208 percent. In addition, the results of Pan et al. revealed "the 'fertilization' effect of N deposition mainly stimulates carbon allocation to short-lived tissues such as foliage and fine roots," but "the 'fertilization' effect by elevated CO_2 likely enhances more sustainable carbon storage such as woody biomass (including coarse roots)."

The four USDA Forest Service scientists conclude the evidence indicates "the change in atmospheric composition, particularly elevated CO_2, will gradually account for more of the carbon sink of temperate forests in the Mid-Atlantic region," and they state, "such a significant 'fertilization effect' on the forest carbon sequestration could eventually result in a 'greener world' after a long period of chronic change in atmospheric composition and cumulative impact."

Real-world evidence for this phenomenon is provided by Cole et al. (2010). They begin by noting that quaking aspen (*Populus tremuloides* Michx.) is a dominant forest type in north-temperate, montane, and boreal regions of North America," stating that it is, in fact, "the most widely distributed tree species on the continent," while further noting that aspen—and related poplars—are "quintessential foundation species (Ellison et al., 2005), shaping the structure and function of the communities and ecosystems in which they occur (Whitham et al., 2006; Schweitzer et al., 2008; Madritch et al., 2009)." This being the case, they considered it important to determine how this keystone species may have responded to the increase in atmospheric CO_2 concentration that has occurred over the past several decades, especially within the context of the climatic changes that occurred concurrently.

The four researchers collected branches from 919 trees after their leaves had dropped in the fall, obtaining samples that represented 189 genets or clones (five trees per clone) at 11 sites distributed throughout three regions of Wisconsin (USA). The sampled trees ranged from five to 76 years of age and came from second-growth unmanaged forests south of the areas defoliated by forest tent caterpillars in 1980–1982, 1989–1990, and 2001–2002. In addition, they recorded trunk diameter at breast height for each sampled tree. This parameter, they write, "is very highly correlated with total biomass in aspen," citing Bond-Lamberty et al. (2002).

The Minnesota and Wisconsin scientists learned that "age-specific ring width increased over time" and "the greatest increase occurred for relatively young trees, so that young trees grew faster in recent years than did young trees several decades ago." During the past half-century, for example, they found the growth of trees 11–20 years old rose by 60 percent. In addition, they observed "rising CO_2 causes ring width to increase at all moisture levels, apparently resulting from improved water use efficiency," so that "the overall increase results from historical increases in both CO_2 and water availability." And when they separated out the impacts of the two factors, they found "the effect of rising CO_2 had been to increase ring width by about 53%," as a result of the "19.2% increase in ambient CO_2 levels during the growing season, from 315.8 ppm in 1958 (when CO_2 records began) to 376.4 ppm in 2003."

Cole et al. comment, "the magnitude of the growth increase uncovered by this analysis raises the question of how much other major forest species have responded to the joint effects of long-term changes in CO_2 and precipitation." In this regard, we note many additional tree species may indeed have experienced similar growth stimulation, particularly in light of the analysis of Tans (2009), who demonstrated that Earth's land surfaces were a net source of CO_2 to the atmosphere until about 1940—primarily due to the felling of forests and the plowing of grasslands to make way for expanded agricultural activities—but from 1940 onward the terrestrial biosphere had become, in the mean, an increasingly greater sink for CO_2, and that it has done so even in the face of massive global deforestation, for which it apparently more than compensated. The combined findings of the studies of Tans and Cole et al. clearly testify to the phenomenal ability of the ongoing rise in the air's CO_2 content to transform the face of the Earth.

Other studies complement these findings. For example, Martinez-Vilalta et al.(2008) used tree-ring data from the Catalan Ecological and Forest Inventory "to study the temporal variability of Scots pine stem radial growth (period 1901–1997) across a relatively large region (Catalonia, NE Spain) situated close to the southern limit of the distribution of the species."

This inventory, as they describe it, “included a total of 10,664 plots randomly distributed throughout the forested area of Catalonia,” where Scots pine was present in 30.2 percent of the plots and was the dominant tree species in 18.4 percent of them.

The five researchers’ work revealed, in their words, “an overall increase of 84% in Scots pine BAI [basal area increment] during the 20th century, consistent with most previous studies for temperate forests” and in harmony with the greening of the Earth that has accompanied the historical increase in the air’s CO_2 content. They make a point of stating “this trend was associated with increased atmospheric CO_2 concentration,” which they interpret to be “a fertilization effect,” while observing “there was also a marked increase in temperature across the study region (0.19°C per decade on average).”

Some people, however, worry rising temperatures will lead to greater respiration rates in the world’s forests. Bronson and Gower (2010), for example, write, “the boreal forest historically has been considered a carbon sink,” but “autotrophic respiration is more sensitive than photosynthesis to increases in temperature,” and therefore, in response to global warming “most models predict autotrophic respiration will increase at a greater rate than photosynthesis, which infers decreased carbon use efficiency and net primary production.” This in turn implies “a substantial increase in temperature could turn the boreal forest into a carbon source,” and this positive feedback phenomenon could lead to an intensification of the warming of the globe.

So the argument goes, but the study found otherwise. Working about 20 km south of Thompson, Manitoba, Canada (55°53’N, 98°20’W), within large enclosed greenhouse chambers containing black spruce trees (*Picea mariana* (Mill.) B.S.P.) and the majority of their fine roots, along with soil-heating cables that were used to warm air and soil temperatures about 5°C over ambient control temperatures, Bronson and Gower measured light-saturated net photosynthesis, foliage respiration, and stem respiration in heated and control forest plots during the 2005, 2006, and 2007 growing seasons. Throughout the study, “both the older foliage, which developed before the experiment, and the new foliage, developed during the experiment, had similar rates of light-saturated net photosynthesis, foliage respiration and stem respiration across all treatments.” This they write, “underscores the ability of black spruce to maintain homeostasis in a 5°C warmer environment.” In addition, while noting many global change models predict a doubling of respiration for every 10°C increase in temperature, Bronson and Gower state in the concluding sentence of their paper—and in no uncertain terms—that “the results from this and other whole-ecosystem warming experiments do not support this model assumption.”

In another study utilizing real-world measurements, Lewis et al. (2009) evaluated tropical forest inventory data, plant physiology experiments, ecosystem flux observations, earth observations, atmospheric measurements, and dynamic global vegetation models, which, “taken together,” in their words, “provide new opportunities to cross-validate results.”

According to the five researchers, both theory and experimental findings suggest that over the past several decades “plant photosynthesis should have increased in response to increasing CO_2 concentrations, causing increased plant growth and forest biomass.” In this regard they find “long-term plot data collectively indicate an increase in carbon storage, as well as significant increases in tree growth, mortality, recruitment, and forest dynamism.” They also report that satellite measurements “indicate increases in productivity and forest dynamism” and that “five Dynamic Global Vegetation Models, incorporating plant physiology, competition, and dynamics, all predict increasing gross primary productivity, net primary productivity, and carbon storage when forced using late-twentieth century climate and atmospheric CO_2 concentration data.” In addition, they state “the predicted increases in carbon storage via the differing methods are all of similar magnitude (0.2% to 0.5% per year).”

“Collectively,” Lewis et al. write, “these results point toward a widespread shift in the ecology of tropical forests, characterized by increased tree growth and accelerating forest dynamism, with forests, on average, getting bigger (increasing biomass and carbon storage).” These findings are just the opposite of what some researchers claim will result from the “twin evils” of rising air temperatures and CO_2 concentrations. Instead of being the bane of Earth’s tropical forests, twentieth-century increases in air temperature and atmospheric CO_2 concentrations have been a great boon to the trees of the tropics.

Also studying the effects of rising air temperature and CO_2 concentration on tropical rainforests were Jaramillo et al. (2010), within a much different context: that of the Paleocene-Eocene Thermal

Maximum (PETM) of some 56 million years ago, which they state was "one of the most abrupt global warming events of the past 65 million years (Kennett and Stott, 1991; Zachos et al., 2003; Westerhold et al., 2009)." It was driven, they remark, by "a massive release of ^{13}C-depleted carbon (Pagani et al., 2006; Zeebe et al., 2009)" which led to "an approximate 5°C increase in mean global temperature in about 10,000 to 20,000 years (Zachos et al., 2003)." They note many people argue that during this warm period the Earth's tropical ecosystems "suffered extensively because mean temperatures are surmised to have exceeded the ecosystems' heat tolerance (Huber, 2008)."

To find out whether the ancient warming of the world truly constituted a major problem for the planet's rainforests, the 29 researchers, hailing from eight countries, analyzed pollen and spore contents and the stable carbon isotopic composition of organic materials obtained from three tropical terrestrial PETM sites in eastern Colombia and western Venezuela. Contrary to the prevailing wisdom of the recent past, this work revealed that the onset of the PETM was "concomitant with an increase in diversity produced by the addition of many taxa (with some representing new families) to the stock of preexisting Paleocene taxa." They further determined that this increase in biodiversity "was permanent and not transient."

In discussing their findings, Jaramillo et al. write, "today, most tropical rainforests are found at mean annual temperatures below 27.5°C," and they state several scientists have argued "higher temperatures could be deleterious to the health of tropical ecosystems." In fact, they report that tropical warming during the PETM is believed to have produced intolerable conditions for tropical ecosystems, citing the writings of Huber (2008, 2009). Nevertheless, they reiterate that at the sites they studied, "tropical forests were maintained during the warmth of the PETM (~31° to 34°C)," and they state "it is possible that higher Paleocene CO_2 levels (Royer, 2010) contributed to their success." Such would indeed appear to be the case, in light of the well-established fact that most plants, including trees, tend to exhibit their greatest photosynthetic rates at ever-warmer temperatures as the air's CO_2 content continues to rise (Bjorkman et al., 1978; Nilsen et al., 1983; Jurik et al., 1984; Seeman et al., 1984; Harley et al., 1986; Stuhlfauth and Fock, 1990; McMurtrie et al., 1992; Sage et al., 1995; Ziska and Bunce, 1997; Cowling and Sage, 1998; Lewis et al., 2001; Roberntz, 2001; Borjigidai et al., 2006; Ghannoum et al., 2010).

In light of Jaramillo et al.'s findings, it is becoming increasingly clear that greater warmth and atmospheric CO_2 concentrations are not "twin evils." Quite to the contrary, they are just what the Earth's ecosystems need in order to make them both more stable and more productive, characteristics essential for sustaining the still-expanding human population of the globe while preserving wildlife habitat.

Two other recent studies look beyond the present and contemplate still other factors of potential significance. Doherty et al. (2010) modeled future changes in land biogeochemistry and biogeography in the region bounded by 12.5°N, 12.5°S, 25°E, and 42.5°E, representing the whole of East Africa (Kenya, Tanzania, Uganda, Rwanda, Burundi, Ethiopia, and Somalia), plus portions of Central Africa (the Democratic Republic of Congo and Southern Sudan). They used 18 climate projections derived from nine general circulation models that figured prominently in the IPCC's Fourth Assessment Report, employing the projections as input to the Lund-Potsdam-Jena dynamic global vegetation model that simulates changes in vegetation and ecosystem carbon cycling under future climate conditions, based on what they describe as "a coupled photosynthesis-hydrological scheme [that] computes gross primary productivity, plant respiration, and evapotranspiration on a daily time step based on the current climate, atmospheric CO_2 concentration, vegetation structure and phenological state, and soil water content."

Doherty et al. report "all simulations showed future increases in tropical woody vegetation over the region," noting "regional increases in net primary productivity (18–36%) and total carbon storage (3–13 percent) by 2080–2099 compared with the present-day were common to all simulations," and "seven out of nine simulations continued to show an annual net land carbon sink in the final decades of the 21st century because vegetation biomass continued to increase." The researchers conclude, "overall, our model results suggest that East Africa, a populous and economically poor region, is likely to experience some ecosystem service benefits through increased precipitation, river runoff and fresh water availability," and they state, "resulting enhancements in net primary productivity may lead to improved crop yields in some areas." They specifically state their results "stand in partial contradiction of other studies that suggest possible negative consequences for agriculture, biodiversity and other ecosystem services caused by temperature increases."

Hillstrom et al. (2010) note, "natural forest systems constitute a major portion of the world's land area, and are subject to the potentially negative effects of both global climate change and invasion by exotic insects." In this regard, they report "a suite of invasive weevils has become established in the northern hardwood forests of North America," noting that how these insects will respond to continued increases in the air's CO_2 content is currently "unknown." To examine this subject, they collected 200 mating pairs of *Polydrusus sericeus* weevils—which they describe as "the second most abundant invasive weevil species in northern hardwood forests"—from birch trees growing on the perimeter of the Aspen FACE facility, after which they fed them leaves taken from the birch, aspen, and maple trees growing within either the facility's ambient-air rings or its CO_2-enriched rings (maintained at a target concentration of 560 ppm) under controlled laboratory conditions throughout the summer of 2007, closely monitoring parameters related to weevil longevity and fecundity.

The five researchers, all from the University of Wisconsin's Department of Entomology, report that feeding the weevils with foliage produced on trees in the CO_2-enriched FACE plots had no effect on male longevity but reduced female longevity by 19 percent. Also, "*Polydrusus sericeus* egg production rate declined by 23% and total egg production declined by 29% for females fed foliage produced under elevated CO_2 compared with ambient CO_2." Hillstrom et al. conclude, "concentrations of elevated CO_2 above 500 ppm have the potential to decrease *P. sericeus* populations by reducing female longevity and fecundity," which should benefit the northern hardwood forests of North America.

References

Ainsworth, A.E., Rogers, A., Blum, H., Nosberger, J., and Long, S.P. 2003. Variation in acclimation of photosynthesis in *Trifolium repens* after eight years of exposure to free air CO_2 enrichment (FACE). *Journal of Experimental Botany* **54**: 2769–2774.

Bader, M.K.-F., Siegwolf, R., and Korner, C. 2010. Sustained enhancement of photosynthesis in mature deciduous forest trees after 8 years of free air CO_2 enrichment. *Planta* **232**: 1115–1125.

Bjorkman, O., Badger, M., and Armond, P.A. 1978. Thermal acclimation of photosynthesis: effect of growth temperature on photosynthetic characteristics and components of the photosynthetic apparatus in *Nerium oleander*. *Carnegie Institution of Washington Yearbook* **77**: 262–276.

Bond-Lamberty, B., Wang, C., and Gower, S.T. 2002. Aboveground and belowground biomass and sapwood area allometric equations for six boreal tree species of northern Manitoba. *Canadian Journal of Forest Research* **32**: 1441–1450.

Borjigidai, A., Hikosaka, K., Hirose, T., Hasegawa, T., Okada, M., and Kobayashi, K. 2006. Seasonal changes in temperature dependence of photosynthetic rate in rice under a free-air CO_2 enrichment. *Annals of Botany* **97**: 549–557.

Bronson, D.R. and Gower, S.T. 2010. Ecosystem warming does not affect photosynthesis or aboveground autotrophic respiration for boreal black spruce. *Tree Physiology* **30**: 441–449.

Bunn, A.G., Graumlich, L.J., and Urban, D.L. 2005. Trends in twentieth-century tree growth at high elevations in the Sierra Nevada and White Mountains, USA. *The Holocene* **15**: 481–488.

Centritto, M. and Jarvis, P.G. 1999. Long-term effects of elevated carbon dioxide concentration and provenance on four clones of Sitka spruce (*Picea sitchensis*). II. Photosynthetic capacity and nitrogen use efficiency. *Tree Physiology* **19**: 807–814.

Cole, C.T., Anderson, J.E., Lindroth, R.L., and Waller, D.M. 2010. Rising concentrations of atmospheric CO_2 have increased growth in natural stands of quaking aspen (*Populus tremuloides*). *Global Change Biology* **16**: 2186–2197.

Cowling, S.A. and Sage, R.F. 1998. Interactive effects of low atmospheric CO_2 and elevated temperature on growth, photosynthesis and respiration in *Phaseolus vulgaris*. *Plant, Cell and Environment* **21**: 427–435.

Crous, K.Y. and Ellsworth, D.S. 2004. Canopy position affects photosynthetic adjustments to long-term elevated CO_2 concentration (FACE) in aging needles in a mature *Pinus taeda* forest. *Tree Physiology* **24**: 961–970.

Darbah, J.N.T., Kubiske, M.E., Nelson, N., Kets, K., Riikonen, J., Sober, A., Rouse, L., and Karnosky, D.F. 2010. Will photosynthetic capacity of aspen trees acclimate after long-term exposure to elevated CO_2 and O_3? *Environmental Pollution* **158**: 983–991.

Davey, P.A., Olcer, H., Zakhleniuk, O., Bernacchi, C.J., Calfapietra, C., Long, S.P., and Raines, C.A. 2006. Can fast growing plantation trees escape biochemical down-regulation of photosynthesis when growing throughout their complete production cycle in the open air under elevated carbon dioxide? *Plant, Cell and Environment* **29**: 1235–1244.

Doherty, R.M., Sitch, S., Smith, B., Lewis, S.L., and Thornton, P.K. 2010. Implications of future climate and atmospheric CO_2 content for regional biogeochemistry, biogeography and ecosystem services across East Africa. *Global Change Biology* **16**: 617–640.

Eichelmann, H., Oja, V., Rasulov, B., Padu, E., Bichele, I., Pettai, H., Mols, T., Kasparova, I., Vapaavuori, E., and Laisk, A. 2004. Photosynthetic parameters of birch (*Betula pendula* Roth) leaves growing in normal and in CO_2- and O_3-enriched atmospheres. *Plant, Cell and Environment* **27**: 479–495.

Ellison, A.M., Bank, M.S., Clinton, B.D., Colburn, E.A., Elliott, K., Ford, C.R., Foster, D.R., Kloeppel, B.D., Knoepp, J.D., Lovett, G.M., Mohan, J., Orwig, D.A., Rodenhouse, N.L., Sobczak, W.V., Stinson, K.A., Stone, J.K., Swan, C.M., Thompson, J., Holle, B.V., and Webster, J.R. 2005. Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. *Frontiers in Ecology and the Environment* **3**: 479–486.

Ellsworth, D.S., Reich, P.B., Naumburg, E.S., Koch, G.W., Kubiske, M.E., and Smith, S.D. 2004. Photosynthesis, carboxylation and leaf nitrogen responses of 16 species to elevated pCO_2 across four free-air CO_2 enrichment experiments in forest, grassland and desert. *Global Change Biology* **10**: 2121–2138.

Finzi, A.C., Norby, R.J., Calfapietra, C., Gallet-Budynek, A., Gielen, B., Holmes, W.E., Hoosbeek, M.R., Iversen, C.M., Jackson, R.B., Kubiske, M.E., Ledford, J., Liberloo, M., Oren, R., Polle, A., Pritchard, S., Zak, D.R., Schlesinger, W.H., and Ceulemans, R. 2007. Increases in nitrogen uptake rather than nitrogen-use efficiency support higher rates of temperate forest productivity under elevated CO_2. *Proceedings of the National Academy of Sciences, USA* **104**: 14,014–14,019.

Finzi, A.C. and Schlesinger, W.H. 2003. Soil-nitrogen cycling in a pine forest exposed to 5 years of elevated carbon dioxide. *Ecosystems* **6**: 444–456.

Ghannoum, O., Phillips, N.G., Sears, M.A., Logan, B.A., Lewis, J.D., Conroy, J.P., and Tissue, D.T. 2010. Photosynthetic responses of two eucalypts to industrial-age changes in atmospheric [CO_2] and temperature. *Plant, Cell and Environment* **33**: 1671–1681.

Graumlich, L.J. 1991. Subalpine tree growth, climate, and increasing CO_2: an assessment of recent growth trends. *Ecology* **72**: 1–11.

Graybill, D.A. 1987. A network of high elevation conifers in the western US for detection of tree-ring growth response to increasing atmospheric carbon dioxide. In *Proceedings of the International Symposium on Ecological Aspects of Tree-Ring Analysis*, edited by G.C. Jacoby and J.W. Hornbeck, 463–474. Washington, DC: U.S. Department of Energy Conference Report DOE/CONF8608144.

Graybill, D.A. and Idso, S.B. 1993. Detecting the aerial fertilization effect of atmospheric CO_2 enrichment in tree-ring chronologies. *Global Biogeochemical Cycles* **7**: 81–95.

Harley, P.C., Tenhunen, J.D., and Lange, O.L. 1986. Use of an analytical model to study the limitations on net photosynthesis in *Arbutus unedo* under field conditions. *Oecologia* **70**: 393–401.

Herrick, J.D. and Thomas, R.B. 2001. No photosynthetic down-regulation in sweetgum trees (*Liquidambar styraciflua* L.) after three years of CO_2 enrichment at the Duke forest FACE experiment. *Plant, Cell, and Environment* **24**: 5364.

Hillstrom, M.L., Vigue, L.M., Coyle, D.R., Raffa, K.F., and Lindroth, R.L. 2010. Performance of the invasive weevil *Polydrusus sericeus* is influenced by atmospheric CO_2 and host species. *Agricultural and Forest Entomology* **12**: 285–292.

Huber, M. 2008. A hotter greenhouse? *Science* **321**: 353–354.

Huber, M. 2009. Snakes tell a torrid tale. *Nature* **457**: 669–670.

Jackson, R.B., Cook, C.W., Pippen, J.S., and Palmer, S.M. 2009. Increased belowground biomass and soil CO_2 fluxes after a decade of carbon dioxide enrichment in a warm-temperate forest. *Ecology* **90**: 3352–3366.

Jacoby G.C. 1986. Long-term temperature trends and a positive departure from the climate-growth response since the 1950s in high elevation lodgepole pine from California. In *Proceedings of the NASA Conference on Climate-Vegetation Interactions*, edited by C. Rosenzweig and R. Dickinson, 81–83. Boulder, CO: Office for Interdisciplinary Earth Studies (OIES), University Corporation for Atmospheric Research (UCAR).

Jaramillo, C., Ochoa, D., Conteras, L., Pagani, M., Carvajal-Ortiz, H., Pratt, L.M., Krishnan, S., Cardona, A., Romero, M., Quiroz, L., Rodriguez, G., Rueda, M.J., de la Parra, F., Moron, S., Green, W., Bayona, G., Montes, C., Quintero, O., Ramirez, R., Mora, G., Schouten, S., Bermudez, H., Navarrete, R., Parra, F., Alvaran, M., Osorno, J., Crowley, J.L., Valencia, V., and Vervoort, J. 2010. Effects of rapid global warming at the Paleocene-Eocene boundary on neotropical vegetation. *Science* **330**: 957–961.

Jurik, T.W., Weber, J.A., and Gates, D.M. 1984. Short-term effects of CO_2 on gas exchange of leaves of bigtooth aspen (*Populus grandidentata*) in the field. *Plant Physiology* **75**: 1022–1026.

Kennett, J.P. and Stott, L.D. 1991. Abrupt deep-sea warming, palaeoceanographic changes and benthic extinctions at the end of the Palaeocene. *Nature* **353**: 225–229.

Kets, K., Darbah, J.N.T., Sober, A., Riikonen, J., Sober, J., and Karnosky, D.F. 2010. Diurnal changes in photosynthetic parameters of *Populus tremuloides*, modulated by elevated concentrations of CO_2 and/or O_3 and daily climatic variation. *Environmental Pollution* **158**: 1000–1007.

Kienast, F. and Luxmoore, R.J. 1988. Tree-ring analysis and conifer growth responses to increased atmospheric CO_2 levels. *Oecologia* **76**: 487–495.

Knapp, P.A., Soule, P.T., and Grissino-Mayer, H.D. 2001. Detecting potential regional effects of increased atmospheric CO_2 on growth rates of western juniper. *Global Change Biology* **7**: 903–917.

Koch, G.W., Sillett, S.C., Jennings, G.M., and Davis, S.D. 2004. The limits to tree height. *Nature* **428**: 851–854.

LaMarche Jr., V.C., Graybill, D.A., Fritts, H.C., and Rose, M.R. 1984. Increasing atmospheric carbon dioxide: tree ring evidence for growth enhancement in natural vegetation. *Science* **225**: 1019–1021.

Lewis, S.L., Lloyd, J., Sitch, S., Mitchard, E.T.A., and Laurance, W.F. 2009. Changing ecology of tropical forests: evidence and drivers. *Annual Review of Ecology, Evolution, and Systematics* **40**: 529–549.

Lewis, J.D., Lucash, M., Olszyk, D., and Tingey, D.T. 2001. Seasonal patterns of photosynthesis in Douglas fir seedlings during the third and fourth year of exposure to elevated CO_2 and temperature. *Plant, Cell and Environment* **24**: 539–548.

Liberloo, M., Tulva, I., Raim, O., Kull, O., and Ceulemans, R. 2007. Photosynthetic stimulation under long-term CO_2 enrichment and fertilization is sustained across a closed *Populus* canopy profile (EUROFACE). *New Phytologist* **173**: 537–549.

Madritch, M.D., Greene, S.G., and Lindroth, R.L. 2009. Genetic mosaics of ecosystem functioning across aspen-dominated landscapes. *Oecologia* **160**: 119–127.

Martinez-Vilalta, J., Lopez, B.C., Adell, N., Badiella, L., and Ninyerola, M. 2008. Twentieth century increase of Scots pine radial growth in NE Spain shows strong climate interactions. *Global Change Biology* **14**: 2868–2881.

McCarthy, H.R., Oren, R., Johnsen, K.H., Gallet-Budynek, A., Pritchard, S.G., Cook, C.W., LaDeau, S.L., Jackson, R.B., and Finzi, A.C. 2010. Re-assessment of plant carbon dynamics at the Duke free-air CO_2 enrichment site: interactions of atmospheric [CO_2] with nitrogen and water availability over stand development. *New Phytologist* **185**: 514–528.

McMurtrie, R.E., Comins, H.N., Kirschbaum, M.U.F., and Wang, Y.-P. 1992. Modifying existing forest growth models to take account of effects of elevated CO_2. *Australian Journal of Botany* **40**: 657–677.

Mencuccini, M., Martinez-Vilalta, J., Vanderklein, D., Hamid, H.A., Korakaki, E., Lee, S., and Michiels, B. 2005. Size-mediated ageing reduces vigour in trees. *Ecology Letters* **8**: 1183–1190.

Nilsen, S., Hovland, K., Dons, C., and Sletten, S.P. 1983. Effect of CO_2 enrichment on photosynthesis, growth and yield of tomato. *Scientia Horticulturae* **20**: 1–14.

Noormets, A., Sober, A., Pell, E.J., Dickson, R.E., Podila, G.K., Sober, J., Isebrands, J.G., and Karnosky, D.F. 2001. Stomatal and non-stomatal limitation to photosynthesis in two trembling aspen (*Populus tremuloides* Michx.) clones exposed to elevated CO_2 and O_3. *Plant, Cell and Environment* **24**: 327–336.

Pagani, M., Caldeira, K., Archer, D., and Zachos, J.C. 2006. An ancient carbon mystery. *Science* **314**: 1556–1557.

Pan, Y., Birdsey, R., Hom, J., and McCullough, K. 2010. Separating effects of changes in atmospheric composition, climate and land-use on carbon sequestration of U.S. Mid-Atlantic temperate forests. *Forest Ecology and Management* **259**: 151–164.

Paoletti, E., Seufert, G., Della Rocca, G., and Thomsen, H. 2007. Photosynthetic response to elevated CO_2 and O_3 in *Quercus ilex* leaves at a natural CO_2 spring. *Environmental Pollution* **147**: 516–524.

Phillips, N.G., Buckley, T.N., and Tissue, D.T. 2008. Capacity of old trees to respond to environmental change. *Journal of Integrative Plant Biology* **50**: 1355–1364.

Roberntz, P. 2001. Atmospheric carbon dioxide concentration, nitrogen availability, temperature and the photosynthetic capacity of current-year Norway spruce shoots. *Tree Physiology* **21**: 931–940.

Royer, D.L. 2010. Fossil soils constrain ancient climate sensitivity. *Proceedings of the National Academy of Sciences, USA* **107**: 517–518.

Sage, R.F., Santrucek, J., and Grise, D.J. 1995. Temperature effects on the photosynthetic response of C_3 plants to long-term CO_2 enrichment. *Vegetatio* **121**: 67–77.

Schweitzer, J.A., Madritch, M.D., Bailey, J.K., LeRoy, C.J., Fischer, D.G., Rehill, B.J., Lindroth, R.L., Hagerman, A.E., Wooley, S.C., Hart, S.C., and Whitham, T.G. 2008. The genetic basis of condensed tannins and their role in nutrient regulation in a *Populus* model system. *Ecosystems* **11**: 1005–1020.

Seemann, J.R., Berry J.A., and Downton, J.S. 1984. Photosynthetic response and adaptation to high temperature in desert plants. A comparison of gas exchange and fluorescence methods for studies of thermal tolerance. *Plant Physiology* **75**: 364–368.

Sharma, P., Sober, A., Sober, J., Podila, G.K., Kubiske, M.E., Mattson, W.J., Isebrands, J.G., and Karnosky, D.F. 2003. Moderation of CO_2-induced gas exchange responses by elevated tropospheric O_3 in trembling aspen and sugar maple. *Ekologia* **22** (S1): 304–317.

Sholtis, J.D., Gunderson, C.A., Norby, R.J., and Tissue, D.T. 2004. Persistent stimulation of photosynthesis by elevated CO_2 in a sweetgum (*Liquidambar styraciflua*) forest stand. *New Phytologist* **162**: 343–354.

Soule, P.T. and Knapp, P.A. 2006. Radial growth rate increases in naturally occurring ponderosa pine trees: a late-20th century CO_2 fertilization effect? *New Phytologist* **171**: 379–390.

Stuhlfauth, T. and Fock, H.P. 1990. Effect of whole season CO_2 enrichment on the cultivation of a medicinal plant, *Digitalis lanata*. *Journal of Agronomy and Crop Science* **164**: 168–173.

Takeuchi, Y., Kubiske, M.E., Isebrands, J.G., Pregitzer, K.S., Hendrey, G., and Karnosky, D.F. 2001. Photosynthesis, light and nitrogen relationships in a young deciduous forest canopy under open-air CO_2 enrichment. *Plant, Cell and Environment* **24**: 1257–1268.

Tans, P. 2009. An accounting of the observed increase in oceanic and atmospheric CO_2 and an outlook for the future. *Oceanography* **22**: 26–35.

Uddling, J., Teclaw, R.M., Pregitzer, K.S., and Ellsworth, D.S. 2009. Leaf and canopy conductance in aspen and aspen-birch forests under free-air enrichment of carbon dioxide and ozone. *Tree Physiology* **29**: 1367–1380.

Westerhold, T., Rohl, U., McCarren, H.K., and Zachos, J.C. 2009. Latest on the absolute age of the Paleocene-Eocene Thermal Maximum (PETM): new insights from exact stratigraphic position of key ash layers + 19 and - 17. *Earth and Planetary Science Letters* **287**: 412–419.

Whitham, T.G., Bailey, J.K., and Schweitzer, J.A. 2006. A framework for community and ecosystem genetics from genes to ecosystems. *Nature Reviews Genetics* **7**: 510–523.

Woodruff, D.R., Bond, J.B., and Meinzer, F.C. 2004. Does turgor limit growth in tall trees? *Plant, Cell and Environment* **27**: 229–236.

Zachos, J.C., Wara, M.W., Bohaty, S., Delaney, M.L., Petrizzo, M.R., Brill, A., Bralower, T.J., and Premoli-Silva, I. 2003. A transient rise in tropical sea surface temperature during the Paleocene-Eocene Thermal Maximum. *Science* **302**: 1551–1554.

Zeebe, R.E., Zachos, J.C., and Dickens, G.R. 2009. Carbon dioxide forcing alone insufficient to explain Palaeocene-Eocene Thermal Maximum warming. *Nature Geoscience* **2**: 576–580.

Ziska, L.H. and Bunce, J.A. 1997. The role of temperature in determining the stimulation of CO_2 assimilation at elevated carbon dioxide concentration in soybean seedlings. *Physiologia Plantarum* **100**: 126–132.

Zotz, G., Pepin, S., and Korner, C. 2005. No down-regulation of leaf photosynthesis in mature forest trees after three years of exposure to elevated CO_2. *Plant Biology* **7**: 369–374.

7.1.5. Ecosystems: Other

Shifting from forests to other ecosystems, we turn to the study of Tian et al. (2010), who like others before them note terrestrial ecosystems provide food, fiber, and various amenities for man and nature alike, and who once again state climate change is typically forecast to negatively affect ecosystem productivity, with potentially disruptive consequences.

Not convinced of the validity of these dire forecasts, Tian et al. used a mechanistic ecosystem model—employing historical (real-world) data for land use, atmospheric CO_2 concentration, nitrogen deposition, fertilization, ozone, and climate—to simulate plant growth responses for multiple biome types (grasslands, forests, wetlands, and agriculture) of the Southern United States at an 8x8-km grid resolution from 1895 to 2007. They found that from Texas through Virginia, net primary productivity rose by 27 percent over the study period (most of it occurring after 1950), with increases in grassland and shrubland (mainly in Texas) and with large increases in cropland. These gains came in spite of increased tropospheric ozone damage.The ten researchers note all biomes showed increases in water use efficiency, contradicting assertions that negative effects of climate change are not only sure to occur but are already apparent.

Contemporaneously, Anderson et al. (2010) studied various root responses of a C_3-C_4 grassland community at Temple, Texas over a CO_2 concentration gradient stretching from 230 to 550 ppm, which they created in two CO_2-gradient above-ground “tunnels” of clear polyethylene film. One of the 60-meter-long and 1.5-meter-wide chambers had ambient air pumped into one end of it, and by the time the air exited the chamber at its other end, its CO_2 concentration was reduced by the photosynthetic activity of the plants within the chamber to a value of approximately 230 ppm. At the same time, the other chamber had air enriched to a CO_2 concentration of 550 ppm pumped into one end of it, and as this air exited the other end of the chamber, its CO_2 concentration was reduced to a value approximately equivalent to that of the ambient air (~380 ppm). Community in-growth root biomass was assessed along the lengths of the tunnels every two to four months from May 1997 through November 1999, with the help of two in-growth cores in each five-meter chamber section, and root biomass response was calculated as the ratio of each measurement date's result to that prevailing at the start of the experiment in May 1997.

Anderson et al. report that based on the linear relationship they derived from all 20 of the in-growth biomass assessments they conducted, there was a 40 percent increase in the in-growth root biomass ratio going from 380 to 480 ppm CO_2, and a 36 percent increase going from 280 to 380 ppm. However, excluding one extremely variable data point and using a power function they fit to the data, the researchers found "the contrast is even greater: a 50% increase from 380 to 480 ppm vs. a 41% increase from 280 to 380 ppm." And in going from the linear relationship to the power function, the r^2 value of the relationship jumped from 0.10 to 0.50, and P dropped from 0.095 to less than 0.001.

Thus the six scientists state their data "suggest that root biomass in grasslands may have changed markedly as atmospheric CO_2 increased since the last glacial period, but more substantial changes are ahead if the air's CO_2 content doubles by the end of this century as predicted."

Moving upward in scale and in latitude, Qian et al. (2010) note it has been hypothesized that if or when the frozen soils of Earth's Northern High Latitudes (NHLs, poleward of 60°N) begin to thaw in response to any new global warming that might occur, the metabolism of soil microbes will be enhanced and the decomposition of soil organic matter will accelerate, and that this, in turn, will lead to an increase in soil organic carbon release to the atmosphere that will amplify global warming. Satellite and phenology studies, however, have shown that during the past several decades the planet's boreal forests have experienced greening and an increase in photosynthetic activity, which extracts carbon (in the form of CO_2) from the atmosphere.

Consequently, and in order to get some indication as to which of these two outcomes might likely predominate over the course of the twenty-first century, Qian et al. explored the potential magnitudes of the two sets of competing processes by analyzing the outputs of ten different models that took part in the Coupled Carbon Cycle Climate Model Intercomparison Project (C4MIP) of the International Geosphere-Biosphere Program and the World Climate Research Program. All of the models, in their words, "used the same anthropogenic fossil fuel emissions from Marland et al. (2005) from the beginning of the industrial period until 2000 and the IPCC SRES A2 scenario for the 2000-2100 period."

According to the three scientists, the ten models predicted a mean warming of 5.6°C from 1901 to 2100 in the NHLs, and they state "the NHLs will be a carbon sink of 0.3 ± 0.3 $PgCyr^{-1}$ by 2100." They also state "the cumulative land organic carbon storage is modeled to increase by 38 ± 20 PgC over 1901 levels, of which 17 ± 8 PgC comes from vegetation [a 43 percent increase] and 21 ± 16 PgC from the soil [an 8 percent increase]," noting "both CO_2 fertilization and warming enhance vegetation growth in the NHLs." Thus over the course of the current century, even the severe warming predicted by current climate models would likely not be a detriment to plant growth and productivity in the NHLs. In fact, it would likely prove a benefit, enhancing plant growth and soil organic carbon storage, which in addition to their own intrinsic virtues would provide a significant negative feedback to global warming.

In a similar study, Friend (2010) calculated the percentage changes in terrestrial plant production that would occur throughout the world in response to (1) projected climate changes alone and (2) projected concurrent changes in climate and atmospheric CO_2 concentration. Friend worked with the *Hybrid6.5* model of terrestrial primary production, which "simulates the carbon, nitrogen, phosphorus, water, and energy fluxes and structural changes in terrestrial ecosystems at hourly to decadal timescales, and at spatial scales ranging from the individual plant to the whole earth," while employing "the climate change anomalies predicted by the GISS-AOM GCM under the A1B emissions scenario for the 2090s [relative] to observed modern climate, and with atmospheric CO_2 increased from 375.7 ppm to 720 ppm."

In response to projected climate changes between 2001–2010 and 2091–2100, the net primary production (NPP) of the planet as a whole was found to be reduced by 2.5 percent, with the largest negative impacts occurring over southern Africa, central Australia, northern Mexico, and the Mediterranean region, where reductions of more than 20 percent were common. At the other extreme, climatic impacts were modestly positive throughout most of the world's boreal forests, as might be expected when these colder regions receive an influx of heat. When both climate and atmospheric CO_2 concentration were changed concurrently, however, the story was vastly different, with a mean *increase* in global NPP of 37.3 percent, driven by mean increases of 43.9–52.9 percent among C_3 plants and 5.9 percent among C_4 species. And in this case of concurrent increases in the globe's air temperature and CO_2 concentration, the largest increases occurred in tropical rainforests and C_3 grass and croplands.

In conclusion, it would appear—at least from climate models—that we can probably expect the historical "greening of the earth" phenomenon to continue.

References

Anderson, L.J., Derner, J.D., Polley, H.W., Gordon, W.S., Eissenstat, D.M., and Jackson, R.B. 2010. Root responses along a subambient to elevated CO_2 gradient in a C_3-C_4 grassland. *Global Change Biology* **16**: 454–468.

Dilley, M., Chen, R.S., Deichmann, U., Lerner-Lam, A.L., and Arnold, M. 2005. *Natural Disaster Hotspots: A Global Risk Analysis.* Washington, DC: The World Bank and Columbia University.

Friend, A.D. 2010. Terrestrial plant production and climate change. *Journal of Experimental Botany* **61**: 1293–1309.

Marland, G., Boden, T.A., and Andres, R.J. 2005. Global, regional, and national CO_2 emissions. In *Trends: A Compendium of Data on Global Change.* Oak Ridge, TN: Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, U.S. Department of Energy. Available at http://cdiac.ornl.gov/trends/emis/overview.html.

Qian, H., Joseph, R., and Zeng, N. 2010. Enhanced terrestrial carbon uptake in the Northern High Latitudes in the 21st century from the Coupled Carbon Cycle Climate Model Intercomparison Project model projections. *Global Change Biology* **16**: 641–656.

Tian, H., Chen, G., Liu, M., Zhang, C., Sun, G., Lu, C., Xu, X., Ren, W., Pan, S., and Chappelka, A. 2010. Model estimates of net primary productivity, evapotranspiration, and water use efficiency in the terrestrial ecosystems of the southern United States during 1895–2007. *Forest Ecology and Management* **259**: 1311–1327.

7.2. Belowground Biotic Responses to Atmospheric CO_2 Enrichment

7.2.1. Soil Fungi

Andrew and Lilleskov (2009) studied sporocarps (the reproductive structures of fungi), which can be significant carbon sinks for the ectomycorrhizal fungi that develop symbiotic relationships with plants by forming sheaths around their root tips, where they are the last sinks for carbon in the long and winding pathway that begins at the source of carbon assimilation in plant leaves. The researchers note "it is critical to understand how ectomycorrhizal fungal sporocarps are affected by elevated CO_2 and ozone," because, they continue, "sporocarps facilitate genetic recombination, permit long-distance dispersal and contribute to food webs," and we need to know how these important processes will be affected by continued increases in the concentrations of these two trace constituents of the atmosphere.

Accordingly, the two researchers evaluated sporocarp biomass for a period of four years at the Aspen free-air CO_2 enrichment (FACE) site near Rhinelander, Wisconsin, which provided, in their words, a "unique opportunity to examine the effects of both elevated CO_2 and O_3 on a forested ecosystem." The examination was conducted during years four through seven of the aspen and aspen-birch forests' exposures to ambient and enriched concentrations of the two gases: CO_2 (350 and 550 ppm) and O_3 (33–67 and 50-–00 ppb). The scientists found total mean sporocarp biomass "was generally lowest under elevated O_3 with ambient CO_2," and it "was greatest under elevated CO_2, regardless of O_3 concentration." They also found "a complete elimination of O_3 effects on sporocarp production when [extra] CO_2 was added." And they state they "expect that the responses seen in the present study were conservative compared to those expected under regional to global changes in CO_2 and O_3." Consequently, by itself or in combination with rising ozone concentrations, the ongoing rise in the atmosphere's CO_2 content appears destined to enhance the genetic recombination and long-distance dispersal of the ectomycorrhizal fungi that form symbiotic relationships with the roots of aspen and birch trees, thereby positively contributing to various food webs that will be found within aspen and aspen-birch forests of the future.

In another study dealing with soil fungi, Alberton et al. (2010) write, "roots of a very large number of plant species are regularly colonized by a group of ascomycete fungi with usually dark-pigmented (melanized) septate hyphae (Mandyam and Jumpponen, 2005; Sieber and Grunig, 2006)" that are referred to as "dark septate root endophytic (DSE) fungi," with "most species belonging to the Leotiomycetes (Kernaghan et al., 2003; Wang et al., 2006)." To study these fungi, the three researchers grew Scots pine (*Pinus sylvestris*) plants from seed for 125 days in Petri dishes—both with and without inoculation with one of seven different species/strains of DSE fungi—within controlled environment chambers maintained at atmospheric CO_2 concentrations of either 350 or 700 ppm, destructively harvesting some of the seedlings at the 98-day point of the experiment and the rest of them at the experiment's conclusion. They found "across all plants (DSE-inoculated and control plants) under elevated CO_2, shoot and root biomass increased significantly by 21% and 19%, respectively, relative to ambient," with "higher values over the final four weeks (increases of 40% and 30% for shoots and roots, respectively)." In addition, they indicate "on average, shoot nitrogen concentration was 57% lower under elevated CO_2," and "elevated CO_2 decreased root nitrogen concentration on average by 16%."

Alberton et al. thus acknowledge their study "did not suggest a role for DSE fungi in increased nutrient uptake." In fact, they emphasize that "under elevated CO_2, DSE fungi even reduced nitrogen content of the pine seedlings." But they also emphasize that "surprisingly, even under reduced nitrogen availability, elevated CO_2 led to increases in both above-ground and below-ground plant biomass."

To explain how that happened, the Brazilian and Dutch scientists write, "a potential mechanism for the increase of plant biomass even when plant nutrient uptake decreases is the production of phytohormones by DSE fungi." They observe that "earlier authors noted that DSE fungi enhance plant growth by producing phytohormones or inducing host hormone production without any apparent facilitation of host nutrient uptake or stimulation of host nutrient metabolism (Addy et al., 2005; Schulz and Boyle, 2005)," further demonstrating that low levels of soil nitrogen availability need not be an insurmountable impediment to significant CO_2-induced increases in plant growth and development.

In another study of note, Compant et al. (2010) write, "virtually all land plant taxa investigated have well-established symbioses with a large variety of microorganisms (Nicolson, 1967; Brundrett, 2009)," some of which "are known to support plant growth and to increase plant tolerance to biotic and abiotic stresses (Bent, 2006)." Many of these microorganisms colonize the rhizosphere (Lugtenberg and Kamilova, 2009), while others "enter the root system of their hosts and enhance their beneficial effects with an endophytic lifestyle (Stone et al., 2000)." This is the case, as they put it, "for plant growth-promoting fungi such as arbuscular mycorrhizae, ectomycorrhizae and other endophytic fungi," as well as for plant growth-promoting bacteria and the more specialized plant growth-promoting rhizobacteria. Many members of the first two categories, they note, "are applied as biocontrol agents, biofertilizers and/or phytostimulators in agriculture (Vessey, 2003; Welbaum et al., 2004) or as degrading microorganisms in phytoremediation applications (Denton, 2007)."

Consequently, and in order to determine how beneficial plant growth-promoting microorganisms might be affected by continued increases in the air's CO_2 content and by possible concomitant changes in climate, Compant et al. reviewed the results of 135 studies that investigated the effects of CO_2 and changes in various climatic factors on "beneficial microorganisms and their interactions with host plants." They found "the majority of studies showed that elevated CO_2 had a positive influence on the abundance of arbuscular and ectomycorrhizal fungi," which, in their words, "is generally in agreement with meta-analyses performed by Treseder (2004) and by Alberton et al. (2005)." But they also found "the effects on plant growth-promoting bacteria and endophytic fungi were more variable." Nevertheless, they state, "in most cases, plant-associated microorganisms had a beneficial effect on plants under elevated CO_2." In addition, they report "numerous studies indicated that plant growth-promoting microorganisms (both bacteria and fungi) positively affected plants subjected to drought stress." Temperature effects, on the other hand, were more of a wash, as Compant et al. state "the effects of increased temperature on beneficial plant-associated microorganisms were more variable, positive and neutral," and "negative effects were equally common and varied considerably with the study system and the temperature range investigated."

In concluding, Compant et al. note the stress of drought is disadvantageous for nearly all terrestrial vegetation, but plant growth-promoting microorganisms should help land plants overcome this potentially negative aspect of future climate change, as long as the air's CO_2 content continues to rise. Temperature effects, on the other hand, would appear to be no more negative than they are positive in a warming world, and when they might be negative, continued atmospheric CO_2 enrichment should prove to be a huge benefit to plants by directly enhancing their growth rates and water use efficiencies. And under the best of climatic conditions, atmospheric CO_2 enrichment should bring out the best of Earth's plants, plus the best of the great majority of plant growth-promoting microorganisms that benefit them biochemically.

References

Addy, H.D., Piercey, M.M., and Currah, R.S. 2005. Microfungal endophytes in roots. *Canadian Journal of Botany* **83**: 1–13.

Andrew, C. and Lilleskov, E.A. 2009. Productivity and community structure of ectomycorrhizal fungal sporocarps under increased atmospheric CO_2 and O_3. *Ecology Letters* **12**: 813–822.

Alberton, O., Kuyper, T.W., and Gorissen, A. 2005. Taking mycocentrism seriously: mycorrhizal fungal and plant responses to elevated CO_2. *New Phytologist* **167**: 859–868.

Alberton, O., Kuyper, T.W., and Summerbell, R.C. 2010. Dark septate root endophytic fungi increase growth of Scots pine seedlings under elevated CO_2 through enhanced nitrogen use efficiency. *Plant and Soil* **328**: 459–470.

Bent, E. 2006. Induced systemic resistance mediated by plant growth-promoting rhizobacteria (PGPR) and fungi (PGPF). In *Multigenic and Induced Systemic Resistance in Plants*, edited by S. Tuzun and E. Bent, 225–258. Berlin, Germany: Springer.

Brundrett, M.C. 2009. Mycorrhizal associations and other means of nutrition of vascular plants: understanding the global diversity of host plants by resolving conflicting information and developing reliable means of diagnosis. *Plant and Soil* **320**: 37–77.

Compant, S., van der Heijden, M.G.A., and Sessitsch, A. 2010. Climate change effects on beneficial plant-microorganism interactions. *FEMS Microbiology Ecology* **73**: 197–214.

Denton, B.D. 2007. Advances in phytoremediation of heavy metals using plant growth promoting bacteria and fungi. *Microbiology and Molecular Genetics* **3**: 1–5.

Kernaghan, G., Sigler, L., and Khasa, D. 2003. Mycorrhizal and root endophytic fungi of containerized *Picea glauca* seedlings assessed by rDNA sequence analysis. *Microbial Ecology* **45**: 128–136.

Lugtenberg, B. and Kamilova, F. 2009. Plant-growth-promoting rhizobacteria. *Annual Review of Microbiology* **63**: 541–556.

Mandyam, K. and Jumpponen, A. 2005. Seeking the elusive function of the root-colonizing dark septate endophytic fungi. *Studies in Mycology* **53**: 173–189.

Nicolson, T.H. 1967. Vesicular-arbuscular mycorrhiza—a universal plant symbiosis. *Science Progress* **55**: 561–581.

Schulz, B. and Boyle, C. 2005. The endophytic continuum. *Mycological Research* **109**: 661–686.

Sieber, T.N. and Grunig, C.R. 2006. Biodiversity of fungal root-endophyte communities and populations, in particular of the dark septate endophyte *Phialocephala fortinii* s.1.In *Microbial Root Endophytes* [of series], edited by B. Schulz, C. Boyle, and T.N. Sieber. *Soil Biology* **9**: 107–132.

Stone, J.K., Bacon, C.W., and White, J.F. 2000. An overview of endophytic microbes: endophytism defined. In *Microbial Endophytes*, edited by C.W. Bacon and J.F. White, 3–29. New York, NY: Marcel Dekker Inc.

Treseder, K.K. 2004. A meta-analysis of mycorrhizal responses to nitrogen, phosphorus and atmospheric CO_2 in field studies. *New Phytologist* **164**: 347–355.

Vessey, J.K. 2003. Plant growth promoting rhizobacteria as biofertilizers. *Plant and Soil* **255**: 571–586.

Wang, Z., Johnston, P.R., Takamatsu, S., Spatafora, J.W., and Hibbett, D.S. 2006. Toward a phylogenetic classification of the Leotiomycetes based on rDNA data. *Mycologia* **98**: 1065–1075.

Welbaum, G., Sturz, A.V., Dong, Z., and Nowak, J. 2004. Fertilizing soil microorganisms to improve productivity of agroecosystems. *Critical Reviews in Plant Sciences* **23**: 175–193.

7.2.2. Plant Roots

Concentrating on plant roots, Wang and Taub (2010) conducted a series of meta-analyses that reveal how differences in the availability of soil fertility and water, as well as the stress of ozone pollution, affect biomass allocation in plants—as expressed by the change in the fraction of root mass to total biomass (root mass fraction, or RMF)—that occurs when plants are exposed to air enriched with CO_2 to levels ranging anywhere from 500 to 1,000 ppm. They used data extracted from 541 peer-reviewed scientific journal articles, which yielded a total of 1,349 RMF observations.

Their analysis determined that lower soil fertility increased RMF, and the magnitude of the increase "was similar for ambient and elevated CO_2-grown plants." They also found that lower soil water content increased RMF, but it did so "to a greater extent at elevated than at ambient CO_2." Finally, they discovered "CO_2 enrichment had little effect on the magnitude of O_3-caused reduction in RMF in herbaceous species," but "it alleviated the adverse effect of higher O_3 on root production in woody species."

Given these findings, the two researchers concluded, "under abiotic stresses, e.g., drought and higher O_3, elevated CO_2-grown plants will likely increase biomass allocation below-ground," where it can be used to construct more roots that can be used to acquire more water and nutrients. However, "because of the non-uniform changes in drought and O_3 projected for different parts of the world," they conclude "elevated CO_2 will have regional, but not global, effects on biomass allocation under various global change scenarios." These responses should make plants—some regionally and some globally—better able to acquire more of the nutrients and water they will need to sustain the increased growth that can be expected in a high-CO_2 world of the future, even in the face of significant ozone pollution.

In another interesting study, Colleen Iversen of the Oak Ridge National Laboratory in Oak Ridge, Tennessee (USA) conducted a review of the pertinent scientific literature "to examine the potential mechanisms for, and consequences of, deeper rooting distributions under elevated CO_2 as they relate to ecosystem carbon and nitrogen cycling," focusing primarily on forests (Iversen, 2010). Iverson found "experimental evidence from a diverse set of forested ecosystems indicates that fine roots of trees exposed to elevated CO_2 are distributed more deeply in the soil profile relative to trees grown under ambient CO_2." As a revealing example, she reports, "in a FACE experiment in a sweetgum (*Liquidambar styraciflua*) plantation, Iversen et al. (2008) found that, over nine years, there was a 220% stimulation in cumulative carbon inputs from fine roots under elevated CO_2 at 45–60 cm soil depth, compared with a 30% stimulation of root carbon inputs at 0–15 cm depth." She also notes "Pritchard et al. (2008a) found a similar response in a CO_2-enriched loblolly pine (*Pinus taeda*) plantation." In fact, she found "of those experiments that examined rooting depth responses to elevated CO_2, 73% found deeper rooting distributions." In addition, she notes, "increased proliferation at depth in the soil has not been limited to fine roots: increased production of mycorrhizas (Pritchard et al., 2008b) and coarse roots (Liberloo et al., 2006) also occurred deeper in the soil under CO_2 enrichment."

Turning to what many have called the progressive nitrogen limitation hypothesis, Iversen notes "a disconnect between observed root dynamics and modeled nutrient availability has confounded projections of forest responses to elevated CO_2," and "while models predict that soil nitrogen availability will limit forest responses to elevated CO_2 (Thornton et al., 2007), many of the forested FACE experiments found a sustained increase in nitrogen uptake from the soil in response to CO_2 enrichment (Finzi et al., 2007)." She then observes, "there has been much speculation on the source of this 'extra' nitrogen (Johnson, 2006), and a greater cumulative amount of nitrogen available at depth in the soil may be the answer (i.e. a 'bigger box' of nitrogen when deeper soil depths are considered)."

In another experiment with implications for the progressive nitrogen limitation hypothesis, McCormack et al. (2010) grew 12 identical mini-ecosystems—each consisting of three longleaf pine (*Pinus palustris*) seedlings, three wiregrass (*Aristida stricta*) C_4 grass plants, two sand post oak (*Quercus margaretta*) seedlings, one rattlebox (*Croatalaria rotundifolia*) C_3 perennial herbaceous legume, and one butterfly weed (*Asclepias tuberose*) herbaceous C_3 dicotyledonous perennial—for three years under natural meteorological conditions in an outdoor soil bin at the National Soil Dynamics Laboratory in Auburn, Alabama (USA) within 12 open-top chambers, half of which were maintained for three years at 365 ppm CO_2 and half of which were maintained at 720 ppm CO_2 for the same period. Throughout this period, the "standing crops" of fine-root length, rhizomorph length, and number of mycorrhizal root tips were assessed in the upper (0–17 cm) and lower (17–34 cm) halves of the plants' root zones at four-week intervals via microvideo cameras installed within each of two mini-rhizotron tubes located within each of the 12 plots into which the soil bin was divided.

The greatest impacts of the 97 percent increase in the air's CO_2 content were generally observed in the lower halves of the ecosystems' root zones, where the standing crops of fine roots, rhizomorphs, and mycorrhizal root tips were increased by 59 percent, 66 percent, and 64 percent, respectively, although the mean standing crop of rhizomorphs in the upper halves of the ecosystems' root zones was increased by 114 percent.

Given these findings, McCormack et al. state that as the atmosphere's CO_2 content continues to rise, "greater biomass production in deeper soils in the coming decades has the potential to contribute to greater carbon storage in forest soils" because "carbon in deeper soil turns over (decomposes) more slowly than litter nearer the soil surface," citing Trumbore (2000) and Schoning and Kogel-Knabner (2006). In addition, they "fungal tissues consist largely of chitin, a potentially recalcitrant compound that may build up soil organic matter and persist for long periods of time relative to more labile carbon," citing Langley and Hungate (2003). Thus they suggest, "regenerating longleaf pine-wiregrass systems may act as a carbon sink as atmospheric CO_2 rises in the coming decades through increased biomass production and potentially through directed allocation of carbon to deeper soils." This, they note, is "consistent with the recent assertion that greater allocation of forest carbon to deeper soil is a general response to atmospheric CO_2-enrichment," citing Iversen (2010). And, very importantly, they state, "significant increases in mycorrhizae and rhizomorphs," as they found in their study, "may explain why the magnitude of the increase in forest net primary productivity caused by elevated CO_2, in several long-term demonstrably nitrogen-limited FACE experiments, has not decreased after nearly a decade (Finzi et al., 2007)." That helps explain why the progressive nitrogen limitation hypothesis has been shown repeatedly to be wrong.

Finally, in a recent review article, Herder et al. (2010) write that humanity "is facing the major challenge of providing food security for an ever growing world population," citing Godfray et al. (2010), while further noting the planet's agricultural area is shrinking, due, in their words, "to erosion of hill-sides, soil degradation, landslides and the increasing demand for biofuels." They indicate the magnitude of the problem is such that currently applied technology and available crop plants "will not be sufficient to feed the rapidly growing world population."

Reviewing potential remedies, the four researchers state, "in the past, improvement of crops and agricultural techniques has mainly focused on increasing shoot biomass and seed yield," but "the relevance of the root system for food production has often been overlooked." This myopic view was unfortunate, for many aspects of root system development are essential for enabling optimal plant growth in the face of numerous belowground environmental stresses such as drought, salinity, and soil-borne pathogenic attacks. They state that achieving improvements in this "hidden half" of a crop's environment represents "an underestimated and not fully exploited area for strategies to enhance yield."

Herder et al.'s analysis indicates crop plants of the future will need "an increased and more efficient root system" that includes "more lateral branches and/or higher number of root hairs," in order to "take up water and nutrients, to fix fertile soil and to prevent soil degradation." These are things that enriching the air with CO_2 helps to bring about. The scientists also note "80% of land plants obtain important mineral nutrition through the ancient arbuscular endomycorrhizal symbiosis with *Glomeromycota* fungi species," which, according to Parniske (2008), are ubiquitous in soils. This, too, is something elevated CO_2 helps to promote. In addition, they note the need for sufficient nitrogen availability to plants, which is provided to legumes by nitrogen-fixing soil bacteria located within nodules on their roots. This need is also met by increasing atmospheric CO_2 concentrations.

References

Finzi, A.C., Norby, R.J., Calfapietra, C., Gallet-Budynek, A., Gielen, B., Holmes, W.E., Hoosbeek, M.R., Iversen, C.M., Jackson, R.B., Kubiske, M.E., Ledford, J., Liberloo, M., Oren, R., Polle, A., Pritchard, S., Zak, D.R., Schlesinger, W.H., and Ceulemans, R. 2007. Increases in nitrogen uptake rather than nitrogen-use efficiency support higher rates of temperate forest productivity under elevated CO_2. *Proceedings of the National Academy of Sciences, USA* **104**: 14,014–14,019.

Godfray, H.C.J., Beddington, J.R., Crute, I.R., Haddad, L., Lawrence, D., Muir, J.F., Pretty, J., Robinson, S., Thomas, S.M., and Toulmin, C. 2010. Food security: the challenge of feeding 9 billion people. *Science* **327**: 812–818.

Herder, G.D., Van Isterdael, G., Beeckman, T., and De Smet, I. 2010. The roots of a new green revolution. *Trends in Plant Science* **15**: 600–607.

Iversen, C.M. 2010. Digging deeper: fine-root responses to rising atmospheric CO_2 concentration in forested ecosystems. *New Phytologist* **186**: 346–357.

Iversen, C.M., Ledford, J., and Norby, R.J. 2008. CO_2 enrichment increases carbon and nitrogen input from fine roots in a deciduous forest. *New Phytologist* **179**: 837–847.

Johnson, D.W. 2006. Progressive N limitation in forests: review and implications for long-term responses to elevated CO_2. *Ecology* **87**: 64–75.

Langley, J.A. and Hungate, B.A. 2003. Mycorrhizal controls on belowground litter quality. *Journal of Ecology* **84**: 2302–2312.

Liberloo, M., Calfapietra, C., Lukac, M., Godbold, D., Luo, Z.-B., Polle, A., Hoosbeek, M.R., Kull, O., Marek, M., Raines, C., Rubino, M., Taylor, G., Scarascia-Mugnozza, G., and Ceulemans, R. 2006. Woody biomass production during the second rotation of a bio-energy *Populus* plantation increases in a future high CO_2 world. *Global Change Biology* **12**: 1094–1106.

McCormack, M.L., Pritchard, S.G., Breland, S., Davis, M.A., Prior, S.A., Runion, G.B., Mitchell, R.J., and Rogers, H.H. 2010. Soil fungi respond more strongly than fine roots to elevated CO_2 in a model regenerating longleaf pine-wiregrass ecosystem. *Ecosystems* **13**: 901–916.

Parniske, M. 2008. Arbuscular mycorrhiza: the mother of plant root endosymbioses. *Nature Reviews Microbiology* **6**: 763–775.

Pritchard, S.G., Strand, A.E., McCormack, M.L., Davis, M.A., Finzi, A.C., Jackson, R.B., Matamala, R., Rogers, H.H., and Oren, R. 2008a. Fine root dynamics in a loblolly pine forest are influenced by free-air-CO_2-enrichment: a six-year-minirhizotron study. *Global Change Biology* **14**: 588–602.

Pritchard, S.G., Strand, A.E., McCormack, M.L., Davis, M.A., and Oren, R. 2008b. Mycorrhizal and rhizomorph dynamics in a loblolly pine forest during 5 years of free-air-CO_2-enrichment. *Global Change Biology* **14**: 1–13.

Schoning, I. and Kogel-Knabner, I. 2006. Chemical composition of young and old carbon pools throughout Camisol and Luvisol profiles under forests. *Soil Biology and Biochemistry* **38**: 2411–2424.

Thornton, P.E., Lamarque, J.F., Rosenbloom, N.A., and Mahowald, N.M. 2007. Influence of carbon-nitrogen cycle coupling on land model response to CO_2 fertilization and climate variability. *Global Biogeochemical Cycles* **21**: 10.1029/2006GB002868.

Trumbore, S. 2000. Age of soil organic matter and soil respiration: radiocarbon constraints on belowground C dynamics. *Ecological Applications* **10**: 399–411.

Wang, X. and Taub, D.R. 2010. Interactive effects of elevated carbon dioxide and environmental stresses on root mass fraction in plants: a meta-analytical synthesis using pairwise techniques. *Oecologia* **163**: 1–11.

7.3. Other Plant Responses to Atmospheric CO_2 Enrichment

7.3.1. Transpiration and Water Use Efficiency

In a study of marsh plants, Li et al. (2010) write, “wetlands evapotranspire more water than other ecosystems, including agricultural, forest and grassland ecosystems,” but the “effects of elevated atmospheric carbon dioxide concentration on wetland evapotranspiration (ET) are largely unknown.” In an effort to help fill this knowledge void, they present the results of “twelve years of measurements of ET, net ecosystem CO_2 exchange (NEE), and ecosystem water use efficiency (EWUE, i.e., NEE/ET) at 13:00–15:00 hours in July and August for a *Scirpus olneyi* (C_3 sedge) community and a *Spartina patens* (C_4 grass) community exposed to ambient and elevated (ambient + 340 ppm) CO_2 in a Chesapeake Bay wetland.”

The results of their study indicate “although a decrease in stomatal conductance at elevated CO_2 in the *S. olneyi* community was counteracted by an increase in leaf area index (LAI) to some extent, ET was still reduced by 19% on average over 12 years,” while “in the *S. patens* community, LAI was not affected by elevated CO_2 and the reduction of ET was 34%.” They found NEE “was stimulated about 36% at elevated CO_2 in the *S. olneyi* community but was not significantly affected by elevated CO_2 in the *S. patens* community.” Merging the ET and NEE responses of the two species, they determined “EWUE was increased about 83% by elevated CO_2 in both the *S. olneyi* and *S. patens* communities.”

Li et al. conclude rising concentrations of atmospheric CO_2 “could have significant impacts on the hydrologic cycles of coastal wetlands,” noting “reduced ET could increase carbon uptake by mitigating the effects of drought on carbon uptake (Rasse et al., 2005),” and it “could also facilitate ground water recharge to counteract salinity intrusion in coastal areas caused by rising sea levels from global warming.” They state salinity intrusion has been identified as "a serious problem in the United States" based on the work of Stevenson et al. (1988) and Day et al. (2000).

Mateos-Naranjo et al. (2010) also worked with a marsh plant—*S. maritima*, which they obtained from a low-marsh site along the southwest coast of Spain. They watered clumps of the plant with Hoagland's solution of three different salinities (0, 170, or 510 mM NaCl), conducting an experiment with the plants in controlled environment chambers maintained at atmospheric CO_2 concentrations of either 380 or 700 ppm for periods of 30 days, during which time they measured several plant properties and processes. They found the 84 percent increase in the atmosphere's CO_2 concentration stimulated the growth of *S. maritima* by about 65 percent in all three salinity treatments, while the halophyte's water use efficiency was increased by about 10 percent, 100 percent, and 160 percent in the 0, 170, and 510 mM salinity treatments, respectively. They conclude, "increasing CO_2 concentration has a positive effect on the photochemical apparatus, helping to counteract salt stress experienced by plants at current CO_2 concentrations."

In another recent study, Shimono et al. (2010) write, "by 2050, the world's population will have increased by about 37%, from the current level of 6.7 billion to an estimated 9.2 billion (UN, 2009), with a corresponding increase in global food demand." They also state "about 0.6 billion Mg of rice is produced annually from an area of 1.5 million km^2, making rice one of the most important crops for supporting human life." As noted by Pritchard and Amthor (2005), rice supplies the planet's human population with an estimated 20 percent of its energy needs (on a caloric basis) and 14 percent of its protein requirements (on a weight basis).

The six scientists further note "rice production depends heavily on water availability," as "irrigated lowlands account for 55% of the total area of harvested rice and typically produce two to three times the crop yield of rice grown under non-irrigated conditions (IRRI, 2002)." And because the demand for ever-greater quantities of water will continue to rise due to the need to feed growing numbers of people, "efficient use of water will thus be essential for future rice production."

In an attempt to determine how agriculture may be affected by the ongoing rise in the air's CO_2 content, the Japanese researchers conducted a two-year free-air CO_2 enrichment (FACE) study in fields at Shizukuishi, Iwate (Japan) to learn how elevated CO_2 may reduce crop water use via its impact on the leaf stomatal conductance (g_s) of three varieties of rice (*Oryza sativa* L.): early-maturing Kirara397, intermediate-maturing Akitakomachi, and latest-maturing Hitomebore.

In response to the 53 percent increase in daytime atmospheric CO_2 concentration employed in their experiments, Shimono et al. report, "the reduction in g_s due to elevated CO_2 was similar across measurements, averaging around 20% in the morning, 24% around noon and 23% in the afternoon across all growth stages." They add "there was no significant CO_2 x cultivar interaction." Consequently, with the concomitant increase in grain yield that also results from atmospheric CO_2 enrichment, it should be apparent that the ongoing rise in the air's CO_2 content will play a major role in enabling a growing world population to meet its food needs.

Moving on from crops to grasslands, we consider Barbosa et al. (2010), who studied an alpine grassland in Switzerland. Citing the principle expressed by DeNiro and Epstein (1978), who coined the phrase "you are what you eat isotopically," they decided to use the horns of numerous deceased alpine ibex (*Capra ibex*) because they are composed of yearly growth layers that possess a temporal archive of the $\delta^{13}C$ values of the alpine grassland plants the animals ate while they were alive. The researchers were given access by the Natural History Museum of Bern to the horns of 24 males that had lived in the grassland they were studying. These horns covered the period from 1938 to 2006 and provided a total of 233 yearly $\delta^{13}C$ data points.

From information obtained from the ibex horns, Barbosa et al. determined the intrinsic water-use efficiency (iWUE) of the alpine grassland plants had increased by approximately 18 percent over the 69-year period from 1938 to 2006, when the atmosphere's CO_2 concentration rose by about 23 percent. Between 1955 and 2006, however, meteorological data indicate the vapor pressure deficit (or evaporative demand) of the air in their study area had risen by about 0.1 kPa, just enough to offset the iWUE benefit provided by the rise in the air's CO_2 content. Thus, although the net effect of the increase in the air's CO_2 content (which tended to reduce plant water loss) and the increase in the air's dryness (which tended to enhance plant water loss) resulted in no net change in plant iWUE, it can be appreciated that had the air's CO_2 content not risen over the period in question, the alpine plants would have fared far worse than they did in reality.

Moving on to trees, we begin with Silva et al. (2009), who studied *Araucaria angustifolia*, which they describe as "an indigenous conifer tree restricted to the southern region of South America that plays a key role in the dynamics of regional ecosystems where forest expansion over grasslands has been observed." Working with various types of tree-ring data obtained from trees growing in both forest and grassland sites in southern Brazil, they compared changes in intrinsic water use efficiency (iWUE)—which they defined as the ratio of the rate of CO_2 assimilation by the trees' needles to their stomatal conductance—with historical changes in temperature, precipitation, and atmospheric CO_2 concentration that occurred in the region over the past century.

The four researchers report that during the past several decades, "iWUE increased over 30% in both habitats," and "this increase was highly correlated with increasing levels of CO_2 in the atmosphere." Over this latter period, however, tree growth remained rather stable, due to lower-than-normal precipitation and higher-than-normal temperatures, which would normally tend to depress the growth of this species: Katinas and Crisci (2008) describe *A. angustifolia* as being "intolerant of dry seasons and requiring cool temperatures." Therefore, Silva et al. conclude the "climatic fluctuations during the past few decades," which would normally be expected to have been deleterious to the growth of *A. angustifolia*, appear to have had their growth-retarding effects "compensated by increases in atmospheric CO_2 and changes [i.e., increases] in iWUE."

Regarding global water scarcity, Kummu et al. (2010) write, "due to the rapidly increasing population and water use per capita in many areas of the world, around one third of the world's population currently lives under physical water scarcity (e.g. Vorosmarty et al., 2000; Alcamo et al., 2003; Oki and Kanae, 2006)." They note that despite the large number of water scarcity studies conducted over the years, "no global assessment is available of how this trend has evolved over the past several centuries to millennia." To fill this void, Kummu et al. conducted a study of AD 0 to 2005. This analysis was carried out for ten different time slices, defined as those times at which the human population of the globe was approximately double the population of the previous time slice. Global population data for these analyses were derived from the 5' latitude x 5' longitude-resolution global HYDE dataset of Klein Goldewijk (2005) and Klein Goldewijk et al. (2010), and evaluation of water resources availability over the same period was based on monthly temperature and precipitation output from the climate model ECBilt-CLIO-VECODE, as calculated by Renssen et al. (2005).

These operations indicated "moderate water shortage first appeared around 1800, but it commenced in earnest from about 1900, when 9% of the world population experienced water shortage, of which 2% was under chronic water shortage (<1000 m^3/capita/year)." Thereafter, from 1960 onwards, "water shortage increased extremely rapidly, with the proportion of global population living under chronic water shortage increasing from 9% (280 million people) in 1960 to 35% (2,300 million) in 2005." Currently, they note, "the most widespread water shortage is in South Asia, where 91% of the population experiences some form of water shortage," while "the most severe shortage is in North Africa and the Middle East, where 77% and 52% of the total population lives under extreme water shortage (<500 m^3/capita/year), respectively."

To alleviate these freshwater shortages, Kummu et al. note measures generally have been taken to increase water availability, such as building dams and extracting groundwater. However, they state, "there are already several regions in which such measures are no longer sufficient, as there is simply not enough water available in some regions." They also note "this problem is expected to increase in the future due to increasing population pressure (e.g. United Nations, 2009), higher welfare (e.g. Grubler et al., 2007), [and] production of water intensive biofuels (e.g. Varis, 2007; Berndes, 2008)." Hence, they conclude there will be an increasing need for many nonstructural measures to be implemented, the first and foremost of which they indicate to be "increasing the efficiency of water use," a property of plants almost universally promoted by atmospheric CO_2 enrichment.

References

Alcamo, J., Doll, P., Henrichs, T., Kaspar, F., Lehner, B., Rosch, T., and Siebert, S. 2003. Global estimates of water withdrawals and availability under current and future 'business-as-usual' conditions. *Hydrological Sciences Journal* **48**: 339–348.

Barbosa, I.C.R., Kohler, I.H., Auerswald, K., Lups, P., and Schnyder, H. 2010. Last-century changes of alpine grassland water-use efficiency: a reconstruction through carbon isotope analysis of a time-series of *Capra ibex* horns. *Global Change Biology* **16**: 1171–1180.

Berndes, G. 2008. Future biomass energy supply: the consumptive water use perspective. *International Journal of Water Resources Development* **24**: 235–245.

Day, J., Shaffer, G., Britsch, L., Reed, D., Hawes, S., and Cahoon, D. 2000. Pattern and processes of land loss in the Mississippi Delta: a spatial and temporal analysis of wetland habitat change. *Estuaries* **23**: 425–438.

DeNiro, M. J. and Epstein, S. 1978. Influence of diet on the distribution of carbon isotopes in animals. *Geochimica et Cosmochimica Acta* **42**: 495–506.

Grubler, A., O'Neill, B., Riahi, K., Chirkov, V., Goujon, A., Kolp, P., Prommer, I., Scherbov, S., and Slentoe, E. 2007. Regional, national, and spatially explicit scenarios of demographic and economic change based on SRES. *Technological Forecasting and Social Change* **74**: 980–1021.

IRRI (International Rice Research Institute). 2002. *Rice Almanac: Source Book for the Most Important Economic Activity on Earth.* Oxfordshire, UK: CABI Publishing.

Katinas, L. and Crisci, J.V. 2008. Reconstructing the biogeographical history of two plant genera with different dispersion capabilities. *Journal of Biogeography* **35**: 1374–1384.

Klein Goldewijk, K. 2005. Three centuries of global population growth: a spatial referenced population (density) database for 1700-2000. *Population and Environment* **26**: 343–367.

Klein Goldewijk, K., Beusen, A., and Janssen, P. 2010. Long-term dynamic modeling of global population and built-up area in a spatially explicit way: HYDE 3.1. *The Holocene* **20**: 565–573.

Kummu, M., Ward, P.J., de Moel, H., and Varis, O. 2010. Is physical water scarcity a new phenomenon? Global assessment of water shortage over the last two millennia. *Environmental Research Letters* **5**: 10.1088/1748-9326/5/3/034006.

Li, J.H., Erickson, J.E., Peresta, G., and Drake, B.G. 2010. Evapotranspiration and water use efficiency in a Chesapeake Bay wetland under carbon dioxide enrichment. *Global Change Biology* **16**: 234–245.

Mateos-Naranjo, E., Redondo-Gomez, S., Andrades-Moreno, L., and Davy, A.J. 2010. Growth and photosynthetic responses of the cordgrass *Spartina maritima* to CO_2 enrichment and salinity. *Chemosphere* **81**: 725–731.

Oki, T. and Kanae, S. 2006. Global hydrological cycles and world water resources. *Science* **313**: 1068–1072.

Pritchard, S.G. and Amthor, J.S. 2005. *Crops and Environmental Change.* New York, NY: Food Production Press.

Rasse, D.P., Peresta, G., Saunders, C.J., and Drake, B.G. 2005. Seventeen years of elevated CO_2 exposure in a Chesapeake Bay Wetland: sustained but contrasting responses of plant growth and CO_2 uptake. *Global Change Biology* **11**: 369–377.

Renssen, H., Goosse, H., Fichefet, T., Brovkin, V., Driesschaert, E., and Wolk, F. 2005. Simulating the Holocene climate evolution at northern high latitudes using a coupled atmosphere-sea-ice-ocean-vegetation model. *Climate Dynamics* **24**: 23–43.

Shimono, H., Okada, M., Inoue, M., Nakamura, H., Kobayashi, K., and Hasegawa, T. 2010. Diurnal and seasonal variations in stomatal conductance of rice at elevated atmospheric CO_2 under fully open-air conditions. *Plant, Cell and Environment* **33**: 322–331.

Silva, L.C.R., Anand, M., Oliveira, J.M., and Pillar, V.D. 2009. Past century changes in *Araucaria angustifolia* (Bertol.) Kuntze water use efficiency and growth in forest and grassland ecosystems of southern Brazil: implications for forest expansion. *Global Change Biology* **15**: 2387–2396.

Stevenson, J., Kearney, M., and Pendleton, E. 1988. Sedimentation and erosion in a Chesapeake Bay brackish marsh system. *Marine Geology* **67**: 213–235.

United Nations. 2009. *The 2006 World Population Prospects. The 2008 Revision Population Database.* New York, NY: United Nations. Available at http://esa.un.org/unpp/.

Varis, O. 2007. Water demands for bioenergy production. *International Journal of Water Resources Development* **23**: 519–535.

Vorosmarty, C.J., Green, P., Salisbury, J., and Lammers, R.B. 2000. Global water resources: vulnerability from climate change and population growth. *Science* **289**: 284–288.

7.3.2. Flowers, Leaves, and Seeds

Focusing on flowers, Johnston and Reekie (2008) state "there have been marked changes in plant phenology over the past century," and they indicate these changes "have been interpreted as a consequence of the increase in temperature that has been observed over this time." However, they add a new twist to the phenomenon, speculating that "the concentration of atmospheric CO_2 may also directly affect time of flowering, even in the absence of temperature change."

In exploring this possibility, the two researchers examined the effects of elevated atmospheric CO_2 concentration by itself (ambient and ambient + 330 ppm), as well as the combined effect of elevated CO_2 and elevated air temperature (ambient + 1.5°C), on the flowering phenology of 22 species of plants in the family Asteraceae, which were grown under natural seasonally varying temperature and daylength in separate compartments of a glasshouse in Wolfville, Nova Scotia, Canada. This work revealed, as they describe it, that "on average, elevated CO_2 by itself advanced flowering by four days," while "increasing temperature as well as CO_2 advanced flowering by an additional three days." They also found "CO_2 was more likely to hasten phenology in long- than in short-day species," and "early- and late-flowering species did not differ in response to elevated CO_2, but the combined effect of elevated CO_2 and temperature hastened flowering more in early- than late-flowering species." In light of their several findings, they concluded that with respect to time of flowering in Asteraceae species, "the direct effect of CO_2 on phenology may be as important as its indirect effect through climate change."

Concentrating on leaves, McGrath et al. (2010) note "early spring leaf-out is critical to the growth and survival of competing trees in deciduous forests (Augspurger, 2008)," and "individuals or genotypes that more quickly reach high LAI [leaf area index] will more successfully compete with neighbors for light energy and space." Therefore, working at the Aspen FACE facility, where aspen clones had been grown since 1997 in conditions simulating CO_2 and O_3 concentrations predicted for the mid-twenty-first century (560 ppm CO_2 and 1.5 times current-ambient O_3), the three researchers documented the history of leaf area development and leaf photosynthetic operating efficiency over the first month of spring leaf-out 11 years later in 2008. They found the trees in the elevated CO_2 plots showed a 36 percent stimulation of leaf area index, whereas the trees in the elevated O_3 plots showed a 20 percent reduction in LAI. In addition, they report the photosynthetic operating efficiency of the CO_2-enriched aspen leaves was enhanced by 51 percent.

Studying seeds at the Duke Forest FACE facility in the Piedmont region of North Carolina, which was established in an unmanaged plantation of 13-year-old loblolly pine (*Pinus taeda* L.) trees, Way et al. (2010) collected in ground traps the seeds released by the trees, counted the number of seeds collected, and analyzed various properties of the seeds over the 12-year period 1997–2008, during which time the trees were growing in either ambient air or air enriched with an extra 200 ppm of CO_2. At the conclusion of their experiment, they determined "the number of mature, viable seeds doubled per unit basal area in high-CO_2 plots from 1997 to 2008 ($P<0.001$)," but "there was no CO_2 effect on mean seed mass, viability, or nutrient content," which they state "is consistent with observations from the few other studies examining reproductive responses to elevated CO_2 in trees," citing the earlier work of LaDeau and Clark (2001, 2006), Stiling et al. (2004), and Kimball et al. (2007). In addition, they report, "the mass of male catkins collected in ground traps was more than doubled over two years in elevated CO_2 plots compared with ambient plots." Based on their and others' findings, the seven scientists concluded, "increased production of high-quality seeds by woody species in response to rising CO_2 would give them a reproductive advantage over herbaceous species that produce more seeds but cannot maintain seed quality," and they suggest this phenomenon "may facilitate woody encroachment into herbaceous communities, a wide-spread phenomenon that has already been linked to rising CO_2 (Bond and Midgley, 2000; Davis et al., 2007)."

In another study, De Frenne et al. (2010) collected seeds of *Anemone nemorosa* L.—a model species for slow-colonizing herbaceous forest plants—found in populations growing along a 2400-km latitudinal gradient stretching from northern France to northern Sweden during three separate growing seasons (2005, 2006, and 2008). They then conducted sowing trials in incubators, a greenhouse, and under field conditions in a forest, where they measured effects of different temperature treatments (growing degree hours, or GDH) on seed and seedling traits. Based on their analyses, they report, "seed mass, germination percentage, germinable seed output and seedling mass all showed a positive response to increased GDH experienced by the parent plant." Seed and seedling mass increased by 9.7 percent and 10.4 percent, respectively, for every 1,000 °C-hours increase in GDH, which they state is equivalent to a 1°C increase in temperature over a 42-day period. As a result, the 19 researchers—from Belgium, Estonia, France, Germany, and Sweden—concluded, "if climate warms, this will have a pronounced positive impact on the reproduction of *A. nemorosa*, especially in terms of seed mass, germination percentage and seedling mass," because "if more seeds germinate and resulting seedlings show higher fitness, more individuals may be recruited to the adult stage." In addition, they write, since "rhizome growth also is likely to benefit from higher winter temperatures (Philipp and Petersen, 2007), it can be hypothesized that the migration potential of *A. nemorosa* may increase as the climate in NW-Europe becomes warmer in the coming decades." And increasing migration potential implies decreasing extinction potential.

In a third seed study, with the help of real-world micrometeorological data measured during the vegetative growth period (May–September) of ten consecutive years (1998–2007) in a boreal forest of southern Finland, Kuparinen et al. (2009) investigated the effects of a warming-induced increase in local convective turbulence (due to a postulated 3°C increase in local temperature) on the long-distance dispersal (LDD) of seeds and pollen based on mechanistic models of wind dispersal (Kuparinen et al., 2007) and population spread (Clark et al., 2001). For light-seeded herbs, they found spread rates increased by 35–42 m/yr (6.--9.2 percent), while for heavy-seeded herbs the increase was 0.01–0.06 m/yr (1.9–6.7 percent). Similarly, light-seeded trees increased their spread rates by 27–39 m/yr (3.5–6.2 percent), while for heavy-seeded trees the increase was 0.2–0.5 m/yr (4.0–8.5 percent). In addition, they discovered "climate change driven advancements of flowering and fruiting phenology can increase spread rates of plant populations because wind conditions in spring tend to produce higher spread rates than wind conditions later in the year."

The four researchers (from France, Germany, Israel, and the United States), write that, in addition to the obvious benefits of greater LLD (being better able to move towards a more hospitable part of the planet), the increased wind dispersal of seeds and pollen may "promote geneflow between populations, thus increasing their genetic diversity and decreasing the risk of inbreeding depression," citing Ellstrand (1992) and Aguilar et al. (2008). They further note "increased gene flow between neighboring populations can accelerate adaptation to environmental change," citing Davis and Shaw (2001) and Savolainen et al. (2007). These phenomena are all very positive developments. In fact, they report the "dispersal and spread of populations are widely viewed as a means by which species can buffer negative effects of climate change."

References

Aguilar, R., Quesada, M., Ashworth, L., Herrerias-Diego, Y., and Lobo, J. 2008. Genetic consequences of habitat fragmentation in plant populations: susceptible signals in plant traits and methodological approaches. *Molecular Ecology* **17**: 5177–5188.

Augspurger, C.K. 2008. Early spring leaf out enhances growth and survival of saplings in a temperate deciduous forest. *Oecologia* **156**: 281–286.

Bond, W.J. and Midgley, G.F. 2000. A proposed CO_2-controlled mechanism of woody plant invasion in grasslands and savannas. *Global Change Biology* **6**: 865f–869.

Clark, J.S., Lewis, M., and Hovarth, L. 2001. Invasion by extremes; population spread with variation in dispersal and reproduction. *American Naturalist* **157**: 537–544.

Davis, M.A., Reich, P.B., Knoll, M.J.B., Dooley, L., Hundtoft, M., and Attleson, I. 2007. Elevated atmospheric CO_2: a nurse plant substitute for oak seedlings establishing in old fields. *Global Change Biology* **13**: 2308–2316.

Davis, M.B. and Shaw, R.G. 2001. Range shifts and adaptive responses to quaternary climate change. *Science* **292**: 673–679.

De Frenne, P., Graae, J.J., Kolb, A., Brunet, J., Chabrerie, O., Cousins, S.A.O., Decocq, G., Dhondt, R., Diekmann, M., Eriksson, O., Heinken, T., Hermy, M., Jogar, U., Saguez, R., Shevtsova, A., Stanton, S., Zindel, R., Zobel, M., and Verheyen, K. 2010. Significant effects of temperature on the reproductive output of the forest herb *Anemone nemorosa* L. *Forest Ecology and Management* **259**: 809–817.

Ellstrand, N.C. 1992. Gene flow by pollen: implications for plant conservation genetics. *Oikos* **63**: 77–86.

Johnston, A. and Reekie, E. 2008. Regardless of whether rising atmospheric carbon dioxide levels increase air temperature, flowering phenology will be affected. *International Journal of Plant Science* **169**: 1210–1218.

Kimball, B.A., Idso, S.B., Johnson, S., and Rillig, M.C. 2007. Seventeen years of carbon dioxide enrichment of sour orange trees: final results. *Global Change Biology* **13**: 2171–2183.

Kuparinen, A., Katul, G., Nathan, R., and Schurr, F.M. 2009. Increases in air temperature can promote wind-driven dispersal and spread of plants. *Proceedings of the Royal Society B* **276**: 3081–3087.

Kuparinen, A., Markkanen, T., Riikonen, H., and Vesala, T. 2007. Modeling air-mediated dispersal of spores, pollen and seeds in forested areas. *Ecological Modelling* **208**: 177–188.

LaDeau, S.L. and Clark, J.S. 2001. Rising CO_2 levels and the fecundity of forest trees. *Science* **292**: 95–98.

LaDeau, S.L. and Clark, J.S. 2006. Elevated CO_2 and tree fecundity: the role of tree size, inter-annual variability and population heterogeneity. *Global Change Biology* **32**: 822–833.

McGrath, J.M., Karnosky, D.F., and Ainsworth, E.A. 2010. Spring leaf flush in aspen (*Populus tremuloides*) clones is altered by long-term growth at elevated carbon dioxide and elevated ozone concentration. *Environmental Pollution* **158**: 1023–1028.

Philipp, M. and Petersen, P.M. 2007. Long-term study of dry matter allocation and rhizome growth in *Anemone nemorosa*. *Plant Species Biology* **22**: 23–31.

Savolainen, O., Pyhajarvi, T., and Knurr, T. 2007. Gene flow and local adaptation in trees. *Annual Review of Ecology, Evolution and Systematics* **38**: 595–619.

Stiling, P., Moon, D., Hymus, G., and Drake, B. 2004. Differential effects of elevated CO_2 on acorn density, weight, germination, and predation among three oak species in a scrub-oak forest. *Global Change Biology* **10**: 228–232.

Way, D.A., LaDeau, S.L., McCarthy, H.R., Clark, J.S., Oren, R., Finzi, A.C., and Jackson, R.B. 2010. Greater seed production in elevated CO_2 is not accompanied by reduced seed quality in *Pinus taeda* L. *Global Change Biology* **16**: 1046–1056.

7.3.3. Secondary Carbon Compounds

Condensed tannins are one example of naturally occurring secondary carbon compounds produced in the leaves of several different plants that often deter herbivorous insects. In New Zealand, the Legume Lotus is a good source of these substances. Scientists with the country's AgResearch Grasslands institute have additionally determined that sheep and cattle feeding on forage that contains this plant may see their methane emissions significantly reduced.

In a study designed to further explore this phenomenon, for a period of four years (2000–2003), Kelly et al. (2010) grew twice-weekly-watered six-year-old quaking aspen (*Populus tremuloides*) clones, two-year-old white willow (*Salix alba*) clones, and two-year-old sugar maple (*Acer saccharum*) siblings outdoors at the University of Michigan Biological Station in northern Michigan (USA) in open-bottom root boxes enclosed within clear-plastic-wall open-top chambers continuously supplied throughout the growing season (from May until leaf senescence in November) with either ambient-CO_2-level air (360 ppm) or elevated-CO_2-air (720 ppm). At the conclusion of the four-year period, the fallen leaves were collected, dried, and analyzed for simple phenolic and condensed tannin concentrations.

From Kelly et al.'s tabular results, it can be calculated that the 360-ppm CO_2 increase employed in their study boosted the simple phenolics concentrations of the aspen, maple, and willow leaves by 16, 30, and 22 percent, respectively, while it boosted their condensed tannin concentrations by 60, 85, and 26 percent, respectively. Because both foliar phenolics and condensed tannins often enhance plant resistance to herbivore and pathogen attack, plus the fact that ruminants browsing on foliage containing condensed tannins may have a tendency to expel less methane (an important greenhouse gas) to the atmosphere, the increased concentrations of these substances in the leaves of trees grown in CO_2-enriched air bodes well for the health of the trees and for people concerned about CO_2- and methane-induced global warming.

In another study dealing with tannins, Huttunen et al. (2009) grew, from seed, well-watered silver birch (*Betula pendula*) plants in small containers filled with peat that were supplied with nitrogen (N) at low, moderate, and high rates equivalent to 0, 150, or 500 kg N per hectare per year, respectively, and maintained within climate-controlled closed-top chambers located outdoors at the University of Joensuu in Finland at either ambient or elevated air temperature (T or T + 2°C), at either ambient or elevated air CO_2 concentrations (360 or 720 ppm), from mid-June 1999 to the end of the 2000 growing season. The researchers then harvested the trees' leaves and determined their insoluble condensed tannin concentrations. As best as can be estimated from the graphical presentations of their results, the doubling of the atmospheric CO_2 concentration they imposed on the tree seedlings led to the following increases in insoluble condensed tannin concentrations: 52 percent (low N), 17 percent (moderate N), and 99 percent (high N) under the ambient air temperature regime, and 61 percent (low N), 67 percent (moderate N), and 20 percent (high N) under the elevated air temperature regime. With all air temperature and soil nitrogen treatments showing

CO_2-induced increases in insoluble condensed tannin concentrations in silver birch leaves, it can be expected that this phenomenon would help to protect the trees' foliage from predation by voracious insect herbivores and reduce methane emissions from ruminants that might eat birch-tree foliage produced in CO_2-enriched air.

Another important group of secondary carbon compounds is that composed of reactive oxygen species (ROS), which can cause severe oxidative damage in plants. To ascertain whether atmospheric CO_2 enrichment could alleviate the harm done by higher plant ROS concentrations caused by the stress of soil salinity, Perez-Lopez et al. (2009) grew two barley (*Hordeum vulgare* L.) cultivars, Alpha and Iranis, within controlled-environment growth chambers at either ambient (350 ppm) or elevated (700 ppm) atmospheric CO_2 concentrations in a 3:1 perlite:vermiculite mixture watered with Hoagland's solution every two days (until the first leaf was completely expanded at 14 days), after which a salinity treatment was administered by adding 0, 80, 160, or 240 m*M* NaCl to the Hoagland's solution every two days for 14 more days. After a total of 28 days, the primary leaf of each barley plant was harvested and assessed for several biochemical properties.

The seven scientists report that in the various ambient-air salinity treatments, the deleterious effects of reactive oxygen species (ROS) on barley leaves were made apparent through ion leakage and increases in thiobarbituric acid reactive substances (TBARS), which rose ever-higher as salt concentrations increased. "On the other hand," they continue, "when [the] salinity treatment was imposed under elevated CO_2 conditions, lower solute leakage and TBARS levels were observed, suggesting that the oxidative stress caused by salinity was lower." In interpreting their findings, Perez-Lopez et al. conclude, "elevated CO_2 protects barley cultivars from oxidative stress," noting "the relief of oxidative stress damage observed in our barley leaves grown under [a] CO_2 enriched atmosphere has also been observed in alfalfa (Sgherri et al., 1998), pine (Vu et al., 1999) and oak (Schwanz and Polle, 2001)." Hence, it would appear the ongoing rise in the air's CO_2 content may help a wide variety of plants cope with the many serious problems caused by high soil salinity, and perhaps additional stresses as well.

Still other secondary carbon compounds comprise what are known as biogenic volatile organic compounds or BVOCs. Plants re-emit a substantial portion of their assimilated CO_2 back to the atmosphere as BVOCs, and these substances affect both the chemical and physical properties of the air, where they generate large quantities of organic aerosols that can affect the planet's climate by forming cloud condensation nuclei that may lead to increased cooling during the day by reflecting a greater portion of the incoming solar radiation back to space. In addition, many BVOCs protect plants from a host of insect pests. But not all BVOCs are so helpful.

Isoprene, for example, is a highly reactive non-methane hydrocarbon (NMHC) emitted in copious quantities by vegetation and responsible for the production of vast amounts of tropospheric ozone, which is a debilitating scourge of plant and animal life alike. It has been calculated by Poisson et al. (2000), for example, that current levels of NMHC emissions may increase surface ozone concentrations by up to 40 percent in the marine boundary-layer and by 50–60 percent over land, and that the current tropospheric ozone content extends the atmospheric lifetime of methane—one of the world's most powerful greenhouse gases—by approximately 14 percent. Thus, it is readily understood that anything that reduces isoprene emissions from vegetation is something to be desired.

In a recent paper on the subject, Lathiere et al. (2010) (1) describe the development and analysis of a new model based on the Model of Emissions of Gases and Aerosols from Nature (MEGAN) developed by Guenther et al. (2006) for estimating isoprene emissions from terrestrial vegetation, (2) validate the new model with compilations of published field-based canopy-scale observations, and (3) use the new model to calculate changes in isoprene emissions from the terrestrial biosphere in response to climate change, atmospheric CO_2 increase, and land use change throughout the twentieth century.

The scientists found that between 1901 and 2002, climate change at the global scale "was responsible for a 7% increase in isoprene emissions," but "rising atmospheric CO_2 caused a 21% reduction," and "by the end of the 20th century, anthropogenic cropland expansion had the largest impact, reducing isoprene emissions by 15%," so that "overall, these factors combined to cause a 24% decrease in global isoprene emissions during the 20th century."

These findings represent good news, as the factors identified should reduce the undesirable consequences of increases in tropospheric ozone and methane concentrations. The three scientists warn, however, that "the possible rapid expansion of biofuel production with high isoprene-emitting plant species (e.g., oil palm, willow and poplar) may reverse the trend by which conversion of land to food crops leads to lower isoprene emissions." This provides yet another reason not to force use of biofuels as replacements for fossil fuels.

Finally, the reader is referred to the discussion in Chapter 2, Section 2.1, of papers by Kiendler-Scharr et al., Kiemann, and Ziemann that appeared in *Nature* in 2009. Those authors warned that if vegetative isoprene emissions were to increase, driven directly by rising temperatures and/or indirectly by warming-induced changes in the species composition of boreal forests, the resulting decrease in cloud condensation nuclei "could lead to increased global-warming trends." However, and as almost an afterthought, Ziemann mentions "the potential suppression of terpene emissions by elevated carbon dioxide concentrations." In fact, that suppression is more than sufficient to offset any increase in isoprene emissions from plants, as shown by the literature review of Young et al. (2009), also summarized in Chapter 2.

References

Guenther, A., Karl, T., Harley, P., Wiedinmyer, C., Palmer, P.I., and Geron, C. 2006. Estimates of global terrestrial isoprene emissions using MEGAN (Model of Emissions of Gases and Aerosols from Nature). *Atmospheric Chemistry and Physics* **6**: 3181–3210.

Huttunen, L., Aphalo, P.J., Lehto, T., Niemela, P., Kuokkanen, K., and Kellomaki, S. 2009. Effects of elevated temperature, elevated CO_2 and fertilization on quality and subsequent decomposition of silver birch leaf litter. *Soil Biology & Biochemistry* **41**: 2414–2421.

Kelly, J.J., Bansal, A., Winkelman, J., Janus, L.R., Hell, S., Wencel, M., Belt, P., Kuehn, K.A., Rier, S.T., and Tuchman, N.C. 2010. Alteration of microbial communities colonizing leaf litter in a temperate woodland stream by growth of trees under conditions of elevated atmospheric CO_2. *Applied and Environmental Microbiology* **76**: 4950–4959.

Kiendler-Scharr, A., Wildt, J., Dal Maso, M., Hohaus, T., Kleist, E., Mentel, T.F., Tillmann, R., Uerlings, R., Schurr, U., and Wahner, A. 2009. New particle formation in forests inhibited by isoprene emissions. *Nature* **461**: 381–384.

Lathiere, J., Hewitt, C.N., and Beerling, D.J. 2010. Sensitivity of isoprene emissions from the terrestrial biosphere to 20th century changes in atmospheric CO_2 concentration, climate, and land use. *Global Biogeochemical Cycles* **24**: 10.1029/2009GB003548.

Perez-Lopez, U., Robredo, A., Lacuestra, M., Sgherri, C., Munoz-Rueda, A., Navari-Izzo, F., and Mena-Petite, A. 2009. The oxidative stress caused by salinity in two barley cultivars is mitigated by elevated CO_2. *Physiologia Plantarum* **135**: 29–42.

Poisson, N., Kanakidou, M., and Crutzen, P.J. 2000. Impact of non-methane hydrocarbons on tropospheric chemistry and the oxidizing power of the global troposphere: 3-dimensional modeling results. *Journal of Atmospheric Chemistry* **36**: 157–230.

Schwanz, P. and Polle, A. 2001. Differential stress responses of antioxidative systems to drought in pendunculate oak (*Quercus robur*) and maritime pine (*Pinus pinaster*) grown under high CO_2 concentrations. *Journal of Experimental Botany* **52**: 133–143.

Sgherri, C., Quartacci, M., Menconi, M., Raschi, A., and Navari-Izzo, F. 1998. Interactions between drought and elevated CO_2 on alfalfa plants. *Journal of Plant Physiology* **152**: 118–124.

Vu, J.C., Gesch, R., Allen, L.H., Boote, K., and Bowes, G. 1999. CO_2 enrichment delays a rapid, drought induced decrease in Rubisco small subunit transcript abundance. *Journal of Plant Physiology* **155**: 139–142.

Young, P.J., Arneth, A., Schurgers, G., Zeng, G., and Pyle, J.A. 2009. The CO_2 inhibition of terrestrial isoprene emission significantly affects future ozone projections. *Atmospheric Chemistry and Physics* **9**: 2793–2803.

Ziemann, P.J. 2009. Thwarting the seeds of clouds. *Nature* **461**: 353–354.

7.4. Ecosystem Responses to Elevated Temperature

7.4.1. Respiration

In a recent News & Views item published in *Nature Geoscience*, Agren (2010) states "it is often assumed that warming will stimulate carbon dioxide release from soils," but he notes "soil-warming experiments suggest that warming-induced increases in soil carbon dioxide release are transitory, and that emissions return to pre-warming levels after a period of five to ten years," citing Kirschbaum (2004) and Eliasson et al. (2005). In much the same vein, Bradford et al. (2010) write that in actual field studies "elevated soil respiration rates under experimental warming are relatively short-lived," citing Jarvis and Linder (2000), Oechel et al. (2000), Luo et al. (2001), Rustad et al. (2001), and Melillo et al. (2002).

Similarly, Bronson and Gower (2010) state "the boreal forest historically has been considered a carbon sink," but "autotrophic respiration is [supposedly] more sensitive than photosynthesis to increases in temperature (Ryan, 1991; Amthor, 1994)," and therefore, in response to global warming, "most models predict autotrophic respiration will increase at a greater rate than photosynthesis, which infers decreased carbon use efficiency and net primary production (Ryan, 1995; VEMAP Members, 1995; Ryan et al., 1996)," which implies "a substantial increase in temperature could turn the boreal forest into a carbon source (Goulden et al., 1998)." That positive feedback phenomenon could lead to an intensification of the warming of the globe—if the assumptions are correct, which was tested by the next study.

Working about 20 km south of Thompson, Manitoba, Canada (55°53'N, 98°20'W), within large enclosed greenhouse chambers containing black spruce trees (*Picea mariana* (Mill.) B.S.P.) and the majority of their fine roots, along with soil-heating cables used to warm air and soil temperatures about 5°C over ambient control temperatures, Bronson and Gower (2010) measured light-saturated net photosynthesis, foliage respiration, and stem respiration in heated and control forest plots during the 2005, 2006, and 2007 growing seasons. Throughout the entire study, "both the older foliage, which developed before the experiment, and the new foliage, developed during the experiment, had similar rates of light-saturated net photosynthesis, foliage respiration and stem respiration across all treatments." This, Bronson and Gover write, "underscores the ability of black spruce to maintain homeostasis in a 5°C warmer environment." In addition, while noting many climate change models predict a doubling of respiration for every 10°C increase in temperature, Bronson and Gower state in the concluding sentence of their paper, and in no uncertain terms, that "the results from this and other whole-ecosystem warming experiments do not support this model assumption."

In another study, Mahecha et al. (2010) write, "the respiratory release of carbon dioxide from the land surface is a major flux in the global carbon cycle," and "understanding the sensitivity of respiratory processes to temperature is central for quantifying the climate-carbon cycle feedback." They set out to do that via a complex set of operations that "approximated the sensitivity of terrestrial ecosystem respiration to air temperature (Q_{10}) across 60 FLUXNET sites with the use of a methodology that circumvents confounding effects." The international team of 14 researchers—from Belgium, Canada, Germany, Italy, Norway, Portugal, Switzerland, and the United States—reports their results "may partly explain recent findings indicating a less pronounced climate-carbon cycle sensitivity (Frank et al., 2010) than assumed by current climate-carbon cycle model parameterizations." In fact, "contrary to previous findings," they state their results "suggest that Q_{10} is independent of mean annual temperature, does not differ among biomes, and is confined to values around 1.4 ± 0.1"

Perhaps the most significant consequence of this new assessment was articulated by Reich (2010) in a Perspective article in *Science* that discusses the Mahecha et al. findings; he writes that their new work "reduces fears that respiration fluxes may increase strongly with temperature, accelerating climate change." This concern longer appears to have much support within the community of global-change researchers.

Two years earlier, Burton et al. (2008) also had cited the theory that "increases in terrestrial ecosystem respiration as temperatures warm could create a positive feedback that causes atmospheric CO_2 concentration, and subsequently global temperature, to increase more rapidly," but they suggested "if plant tissue respiration acclimates to temperature over time, this feedback loop will be weakened, reducing the potential temperature increase." And when Burton et al. demonstrated that plant tissue respiration does indeed so acclimate, Bradford et al. (2008) explored the same subject as it pertains to soil microbial respiration, acquiring pertinent data obtained as late as 15 years after the start of a soil-warming experiment established in 1991 on an even-aged mixed-deciduous tract of trees in the Harvard Forest (Massachusetts, USA), where heating cables were used to elevate soil temperatures to 5°C above ambient temperatures measured in non-heated control plots. They discovered—as has been found by many others in long-term field experiments—that "elevated respiration rates under soil warming return to pre-warming values within a few years," citing the corroborative findings of Jarvis and Linder (2000), Oechel et al. (2000), Luo et al.

(2001), Rustad et al. (2001), Melillo et al. (2002), and Eliasson et al. (2005).

In light of this wealth of empirical observations, the nine researchers state, in the concluding sentence of the abstract of their paper, "stimulatory effects of global temperature rise on soil respiration rates may be lower than currently predicted," and in the final sentence of the body of their paper they reiterate, in slightly different language, "the changes in the biomass and physiology of soil microbial communities that we observed may decrease the expected strength of climate warming on soil respiration rates," a state of affairs that ends up "reducing the potential temperature increase."

In a temperate steppe grassland located in Duolun County, Inner Mongolia, China (42°02'N, 116°17'E, 1,324 meters above sea level), Wan et al. (2009) suspended infrared radiators 2.25 meters above the ground over 24 plots divided into four temperature treatments: (1) control, (2) day (06:00–18:00, local time) warming, (3) night (18:00–06:00) warming, and (4) diurnal (24–hour) warming,. They then measured diurnal cycles of net ecosystem gas exchange and daytime ecosystem respiration twice a month over the growing seasons (May–October) of 2006, 2007, and 2008.

The researchers found "nocturnal warming increased leaf respiration of two dominant grass species by 36.3%, enhanced consumption [drawdown] of carbohydrates in the leaves (72.2% and 60.5% for sugar and starch, respectively), and consequently stimulated plant photosynthesis by 19.8% in the subsequent days." In addition, they state "the enhancement of plant photosynthesis overcompensated the increased carbon loss via plant respiration under nocturnal warming and shifted the steppe ecosystem from a minor carbon source (1.87 g C/m^2/year) to a carbon sink (21.72 g C/m^2/year) across the three growing seasons." In addition, the four Chinese researchers note the local climate in their study area "experienced asymmetrical diurnal warming (0.57, 0.45 and 0.30°C increases in daily minimum, mean and maximum temperatures per decade, respectively) over the past half century (1953–2005)," and "similar diurnal scenarios of climate warming have been widely reported at the regional and global scales," citing the studies of Karl et al. (1991), Easterling et al. (1997), Stone and Weaver (2002), Vose et al. (2005), Lobell et al. (2007), and Zhou et al. (2007). Consequently, and in light of the many well-documented "greater increases in daily minimum than maximum temperature" that have been observed throughout the world, Wan et al. conclude, "plant photosynthetic overcompensation may partially serve as a negative feedback mechanism for [the] terrestrial biosphere to climate warming," where "the photosynthetic overcompensation induced by nocturnal warming can ... regulate terrestrial carbon sequestration and negatively feed back to climate change."

References

Agren, G.I. 2010. Microbial mitigation. *Nature Geoscience* **3**: 303–304.

Amthor, J.S. 1994. Scaling CO_2 photosynthesis relationships from the leaf to the canopy. *Photosynthesis Research* **39**: 321–350.

Bradford, M.A., Davies, C.A., Frey, S.D., Maddox, T.R., Melillo, J.M., Mohan, J.E., Reynolds, J.F., Treseder, K.K., and Wallenstein, M.D. 2008. Thermal adaptation of soil microbial respiration to elevated temperature. *Ecology Letters* **11**: 1316–1327.

Bradford, M.A., Watts, B.W., and Davies, C.A. 2010. Thermal adaptation of heterotrophic soil respiration in laboratory microcosms. *Global Change Biology* **16**: 1576–1588.

Bronson, D.R. and Gower, S.T. 2010. Ecosystem warming does not affect photosynthesis or aboveground autotrophic respiration for boreal black spruce. *Tree Physiology* **30**: 441–449.

Burton, A.J., Melillo, J.M., and Frey, S.D. 2008. Adjustment of forest ecosystem root respiration as temperature warms. *Journal of Integrative Plant Biology* **50**: 1467–1483.

Easterling, D.R., Horton, B., Jones, P.D., Peterson, T.C., Karl, T.R., Parker, D.E., Salinger, M.J., Razuvayev, V., Plummer, N., Jamason, P., and Folland, C.K. 1997. Maximum and minimum temperature trends for the globe. *Science* **277**: 364–367.

Eliasson, P.E., McMurtrie, R.E., Pepper, D.A., Stromgren, M., Linder, S., and Agren, G.I. 2005. The response of heterotrophic CO_2 flux to soil warming. *Global Change Biology* **11**: 167–181.

Frank, D.C., Esper, J., Raible, C.C., Büntgen, U., Trouet, V., Stocker, B., and Joos, F. 2010. Ensemble reconstruction constraints on the global carbon cycle sensitivity to climate. *Nature* **463**: 527–530.

Goulden, M.L., Wofsy, S.C., and Harden, J.W. 1998. Sensitivity of boreal forest carbon balance to soil thaw. *Science* **279**: 214–217.

Jarvis, P. and Linder, S. 2000. Constraints to growth of boreal forests. *Nature* **405**: 904–905.

Karl, T.R., Kukla, G., Razuvayev, N., Changery, M.J., Quayle, R.G., Heim, R.R., Easterling, D.R., and Fu, C.B. 1991. Global warming—evidence for asymmetric diurnal temperature-change. *Geophysical Research Letters* **18**: 2253–2256.

Kirschbaum, M.U.F. 2004. Soil respiration under prolonged soil warming: are rate reductions caused by acclimation or substrate loss? *Global Change Biology* **10**: 1870–1877.

Lobell, D.B., Bonfils, C., and Duffy, P.B. 2007. Climate change uncertainty for daily minimum and maximum temperatures: a model inter-comparison. *Geophysical Research Letters* **34**: 10.1029/2006GL028726.

Luo, Y.Q., Wan, S.Q., Hui, D.F., and Wallace, L.L. 2001. Acclimation of soil respiration to warming in a tall grass prairie. *Nature* **413**: 622–625.

Mahecha, M.D., Reichstein, M., Varvalhais, N., Lasslop, G., Lange, H., Seneviratne, S.I., Vargas, R., Ammann, C., Arain, M.A., Cescatti, A., Janssens, I.A., Migliavacca, M., Montagnani, L., and Richardson, A.D. 2010. Global convergence in the temperature sensitivity of respiration at ecosystem level. *Science* **329**: 838–840.

Melillo, J.M., Steudler, P.A., Aber, J.D., Newkirk, K., Lux, H., Bowles, F.P., Catricala, C., Magill, A., Ahrens, T., and Morrisseau, S. 2002. Soil warming and carbon-cycle feedbacks to the climate system. *Science* **298**: 2173–2176.

Oechel, W.C., Vourlitis, G.L., Hastings, S.J., Zulueta, R.C., Hinzman, L., and Kane, D. 2000. Acclimation of ecosystem CO_2 exchange in the Alaskan Arctic in response to decadal climate warming. *Nature* **406**: 978–981.

Reich, P.B. 2010. The carbon dioxide exchange. *Science* **329**: 77–-775.

Rustad, L., Campbell, J.L., Marion, G.M., Norby, R.J., Mitchell, M.J., Hartley, A.E., Cornelissen, J.H.C., and Gurevitch, J. 2001. A meta-analysis of the response of soil respiration, net nitrogen mineralization, and above-ground plant growth to experimental ecosystem warming. *Oecologia* **126**: 543–562.

Ryan, M.G. 1991. Effects of climate change on plant respiration. *Ecological Applications* **1**: 157–167.

Ryan, M.G. 1995. Foliar maintenance respiration of sub-alpine and boreal trees and shrubs in relation to nitrogen-content. *Plant, Cell and Environment* **18**: 765-772.

Ryan, M.G., Hunt, E.R., McMurtrie, R.E., Agren, G.I., Aber, J.D., Friend, A.D., Rastetter, E.B., Pulliam, W.M., Raison, R.J., and Linder, S. 1996. Comparing models of ecosystem function for temperate conifer forests. In *Global Change: Effects on Coniferous Forests and Grasslands*, edited by A.I. Greymeyer, D.O. Hall, G.I. Agren, and J.M. Melillo, 313–361. New York, NY: John Wiley.

Stone, D.A. and Weaver, A.J. 2002. Daily maximum and minimum temperature trends in a climate model. *Geophysical Research Letters* **29**: 10.1029/2001GL014556.

VEMAP Members. 1995. Vegetation Ecosystem Modeling and Analysis Project: comparing biogeography and biogeochemistry models in a continental-scale of terrestrial ecosystem response to climate change and CO_2 doubling. *Global Biogeochemical Cycles* **9**: 407–437.

Vose, R.S., Easterling, D.R., and Gleason, B. 2005. Maximum and minimum temperature trends for the globe: an update through 2004. *Geophysical Research Letters* **32**: 10.1029/2005GL024379.

Wan, S., Xia, J., Liu, W., and Niu, S. 2009. Photosynthetic overcompensation under nocturnal warming enhances grassland carbon sequestration. *Ecology* **90**: 2700–2710.

Zhou, L., Dickinson, R.E., Tian, Y., Vose, R.S., and Dai, Y. 2007. Impact of vegetation removal and soil aridation on diurnal temperature range in a semiarid region: application to the Sahel. *Proceedings of the National Academy of Sciences USA* **104**: 17,937–17,942.

7.4.2. Agricultural Crops

In a controversial study published in the *Proceedings of the National Academy of Sciences* (USA), Schlenker and Roberts (2009) compared U.S. county-level yields of corn, soybeans, and cotton for the years 1950–2005 with fine-scale weather datasets that incorporated the entire distribution of temperatures that occurred within each day and across all days of the crops' growing seasons, in order to determine yield responses to the range of temperatures experienced by the crops. They then used the yield vs. temperature relationships they had thereby derived to estimate yield changes expected throughout the remainder of the twenty-first century, based on temperatures predicted to occur by the Hadley III climate model.

The first stage of the scientists' research indicated yields had historically increased as temperatures rose to an optimum value of 29°C for corn, 30°C for soybeans, and 32°C for cotton. At temperatures above these optimum values, crop yields declined, and they did so with slopes that were significantly steeper than the upward slopes that had preceded them. Then, in the second stage of their research, Schlenker and Roberts found, "holding current growing regions fixed, area-weighted average yields are predicted to decrease by 30–46% before the end of the century under the slowest warming scenario and decrease by 63–82% under the most rapid warming scenario under the Hadley III model."

This was not good news, but on the upside, it was much too bad to be true. About six weeks later, the *Proceedings* published a letter by Meerburg et al. (2009) that provided a new perspective on the issue.

The seven Dutch scientists began their critique of Schlenker and Roberts' study by noting that yields of the crops in question will continue to increase in years to come, because of "the development and adoption of new technologies and improved farm management," citing Ewert et al. (2005), who found that continuing advances in technology historically have been the most important driver of productivity change, outweighing the negative effects of detrimental climate change. And in further illustration of this phenomenon, Meerburg et al. report that between 1961 and 2007, "average US corn yields increased by 240%, from 3.9 tons per hectare per year to 9.4 tons per hectare per year (FAO, 2009)," while noting some researchers have predicted "advances in agronomics, breeding, and biotechnology will lead to an average corn yield in the US of just over 20 tons per hectare per year in 2030," citing Duvick (2005).

Meerburg et al. also make note of the fact that farmers in Brazil successfully increased the productivity of soybeans, maize, and cotton during the past decade even though the cumulative number of days of exposure to temperatures above the three crops' optimum values "is far greater than in the US." In the Brazilian state of Mato Grosso, for example, "maximum average day temperature exceeds 35°C for 118 days per year, of which 75 days are in the average soybean-growing season." Nevertheless, they report, in 2008 average production of soybeans was about 3.1 tons per hectare per year in Mexico, while the average yield in the US was 2.8 tons per hectare per year. Similarly, they note the mean cotton yield in Brazil in 2006/2007 was 1.4 tons per hectare per year, while in the U.S. it was only 0.9 tons per hectare per year.

The seven scientists thus conclude "temperatures higher than currently experienced in the US do not necessarily need to coincide with lower crop yields and that already existing technology and future advances (new varieties, optimized farm management, biotechnology, etc.) can overrule the negative effect of increasing temperatures on yield," as has in fact been observed in the historical crop yield data of the United States.

A final flaw in the analysis of Schlenker and Roberts (2009) is their acknowledged "inability to account for CO_2 concentrations," the increasing levels of which, in their own words, "might spur plant growth and yields," such that "yield declines stemming from warmer temperatures therefore may be offset by CO_2 fertilization." This has been found to be the case by many different studies, as we recount in Section 5.5 of this report.

In light of Schlenker and Roberts' stated admissions, therefore, as well as the facts cited by Meerburg et al.—which should have been known by the two U.S. researchers as well as the communicator of their paper to the *Proceedings of the National Academy of Sciences* and the editorial staff of the journal—it is clear their paper never should have been published, especially with a title that proclaims as fact that "nonlinear temperature effects indicate severe damages to U.S. crop yields under climate change."

References

Duvick, D.N. 2005. The contribution of breeding to yield advances in maize (*Zea mays* L.). *Advances in Agronomy* **86**: 83–145.

Ewert, F., Rounsevell, M.D.A., Reginster, I., Metzger, M.J., and Leemans, R. 2005. Future scenarios of European agricultural land use: I. Estimating changes in crop productivity. *Agriculture, Ecosystems and Environment* **107**: 101–116.

FAO (Food and Agriculture Organization). 2009. FAOSTAT Database. United Nations Food and Agriculture Organization. Available at www.fao.org. Accessed 8 September 2009.

Meerburg, B.G., Verhagen, A., Jongschaap, R.E.E., Franke, A.C., Schaap, B.F., Dueck, T.A., and van der Werf, A. 2009. Do nonlinear temperature effects indicate severe damages to US crop yields under climate change? *Proceedings of the National Academy of Sciences USA* **106**: 10.1073 pnas.0910618106.

Schlenker, W. and Roberts, M.J. 2009. Nonlinear temperature effects indicate severe damages to U.S. crop yields under climate change. *Proceedings of the National Academy of Sciences USA* **106**: 15,594–15,598.

7.5. Responses of Plants Under Stress to Atmospheric CO_2 Enrichment

7.5.1. The Stress of Disease

Eastburn et al. (2010) note, "globally, soybean is the most widely planted dicot crop and has economic significance due to its wide variety of uses, ranging from food and health products to printing inks and biodiesel," but "little to no work has evaluated the influence of future atmospheric conditions on soybean diseases." This is particularly surprising given that "worldwide yield losses to all soybean diseases combined are about 11% (Wrather et al., 1997), which is equivalent to more than 24 million metric tons based on current production." In an attempt to begin to fill this knowledge void, Eastburn et al. evaluated the individual and combined effects of elevated carbon dioxide (CO_2, 550 ppm) and ozone (O_3, 1.2 times ambient) on three economically important soybean diseases—downy mildew, *Septoria* brown spot, and sudden death syndrome (SDS)—over the three-year period 2005–2007 under natural field conditions at the soybean free-air CO_2-enrichment (SoyFACE) facility on the campus of the University of Illinois (USA).

The five researchers found "elevated CO_2 alone or in combination with O_3 significantly reduced downy mildew disease severity by 39–66% across the three years of the study." On the other hand, they state "elevated CO_2 alone or in combination with O_3 significantly increased brown spot severity in all three years," but "the increase was small in magnitude." Finally, they state "the atmospheric treatments had no effect on the incidence of SDS." Taken in their entirety, these findings thus suggest, on balance, that elevated CO_2 should provide a net benefit to soybean productivity throughout the world, as its concentration continues to rise in the years and decades to come.

In the introduction to another soybean study, Kretzschmar et al. (2009) write, "isoflavonoids constitute a group of natural products derived from the phenylpropanoid pathway, which is abundant in soybeans," and they state "the inducible accumulation of low molecular weight antimicrobial pterocarpan phytoalexins, the glyceollins, is one of the major defense mechanisms implicated in soybean resistance." Thus, in their study, as they describe it, they "evaluated the effect of an elevated CO_2 atmosphere on the production of soybean defensive secondary chemicals induced by nitric oxide and a fungal elicitor." They did this in a glasshouse where they grew soybeans from seed for a period of nine days in large, well-watered pots placed within open-top chambers that were maintained at atmospheric CO_2 concentrations of either 380 or 760 ppm, while they examined changes in the production of phytoalexins and some of their precursors.

This work revealed that elevated CO_2 "resulted in an increase of intermediates and diverted end products (daidzein by 127%, coumestrol by 93%, genistein by 93%, luteolin by 89% and apigenin by 238%) with a concomitant increase of 1.5–3.0 times in the activity of enzymes related to their biosynthetic routes." The Brazilian researchers state these findings "indicate changes in the pool of defense-related flavonoids in soybeans due to increased carbon availability, which may differentially alter the responsiveness of soybean plants to pathogens in CO_2 atmospheric concentrations such as those predicted for future decades." Or to put it more simply, the ongoing rise in the air's CO_2 content will likely increase the ability of soybeans to withstand the attacks of various plant diseases in the years and decades to come.

In a very different type of study, AL-Kayssi (2009) investigated soil solarization, "a method of heating the soil by using polyethylene sheets as mulching over moistened soil, to retain solar radiation during the hot season," so that "soil-borne pathogens may be killed by lethal heat (>40°C) and weakened by sub-lethal heat (<38-40°C) to the extent that they are unable to cause damage to plants or they are more susceptible to chemical toxicants." This technique, the Iraqi researcher writes, "has been successfully used to control soil-borne pathogens and weeds," as observed in the studies of Katan et al. (1976), Mahrer (1979), Grinstein et al. (1979), Katan (1981), Mahrer et al. (1984), Avissar et al. (1986), AL-Karaghouli et al. (1990), and AL-Kayssi and AL-Karaghouli (1991).

Against this background, AL-Kayssi conducted a laboratory experiment where "clay soil samples infested with *Verticillium dahliae* were exposed to different CO_2 concentrations (350, 700, 1050, 1400, 1750 ppm air) and incubated in hot water baths at 35, 40, 45, 50 and 55°C," while "field plots were exposed to the same CO_2 levels during soil solarization in three periods (1st of July to 30th of September, 1st of August to 30th of September, and 1st to 30th of September)." He found that higher than normal CO_2 contents in the soil increased maximum soil temperatures while reducing the length of time required to kill 90 percent of the propagules of *V. dahliae* in natural field soil with moisture content at field capacity. As an example, he notes this killing time parameter in soil heated to 35°C was reduced from 24 days at the normal ambient CO_2 concentration to 15 days at 1,750 ppm CO_2, and he states sub-lethal soil temperatures were raised to lethal levels as the soil's CO_2 content was raised. In a high-CO_2 world of the future, therefore, soil solarization could become an even more viable method of controlling soil-borne pathogens and weeds than it is today.

We next consider leaf spot disease, which is characterized by chlorotic to necrotic localized leaf lesions caused by the *Cercospora* (a large genus of ascomycete fungi) that affect, in the words of McElrone et al. (2010), "numerous economically important plant species around the world, including grapes, cereals, soybeans, peanuts, orchids, coffee, alfalfa and potatoes (Sinclair et al., 1987)," as well as redbud (*Cercis canadensis*) and sweetgum (*Liquidambar styraciflua*) trees, such as those growing at the Duke Forest FACE Facility in Orange County, North Carolina (USA), where McElrone et al. studied the disease throughout the growing seasons of five different years (2000, 2001, 2002, 2003, 2005). The six scientists assessed how elevated CO_2 (to 200 ppm above the ambient air's CO_2 concentration) and natural interannual climatic variability affected the incidence and severity of leaf spot disease among the sweetgum and redbud trees growing in the several FACE rings. In order "to determine how photosynthetic capacity surrounding pathogen damage was affected by CO_2 exposure, the spatial pattern of photosystem II operating efficiency was quantified on *C. canadensis* leaves still attached to plants with an imaging chlorophyll fluorometer."

By these means, McElrone et al. found "disease incidence and severity for both species were greater in years with above average rainfall," while "in years with above average temperatures, disease incidence for *Liquidambar styraciflua* was decreased significantly." On the other hand, they found elevated CO_2 increased disease incidence and severity "in some years." However, they state the "chlorophyll fluorescence imaging of leaves revealed that any visible increase in disease severity induced by elevated CO_2 was mitigated by higher photosynthetic efficiency in the remaining undamaged leaf tissue and in a halo surrounding lesions." Consequently, even in a situation where atmospheric CO_2 enrichment was observed to increase the incidence and severity of leaf spot disease, the photosynthesis-enhancing effect of the extra CO_2 was found to compensate for the photosynthetic productivity lost to the disease by enhancing productivity in healthy portions of diseased leaves and in leaves without lesions, for no net ill effect.

As for what has been observed in other studies of this nature, McElrone et al. report that disease incidence or severity also has been observed to be enhanced by elevated CO_2 in four other "pathosystems" (Thompson and Drake, 1994; Mitchell et al., 2003; Kobayashi et al., 2006; Eastburn et al., 2010), that disease incidence or severity has been observed to be unaffected by elevated CO_2 in another four pathosystems (Hibberd et al., 1996; Tiedemann and Firsching, 2000; Percy et al., 2002; Eastburn et al., 2010), and that the two disease parameters have been reduced by elevated CO_2 in another seven pathosystems (Thompson et al., 1993; Thompson and Drake, 1994; Chakraborty et al., 2000b; Jwa and Walling, 2001; Pangga et al., 2004; McElrone et al., 2005; Eastburn et al., 2010). Among the numerous pertinent studies conducted to date, elevated CO_2 has been found, generally speaking to lead to (1) no net loss in the productivity of disease-infected plants in 31 percent of the studies, (2) a moderate increase in the productivity of disease-infected plants in 25 percent of the studies, and (3) a large increase in productivity in 44 percent of the studies, while the study of McElrone et al. (2010) suggests concomitant warming may further enhance the productivity of infected plants.

As a prelude to another analysis of CO_2 effects on diseased plants, Runion et al. (2010) note obligate pathogens "have a more intimate relationship with their host and must have the host to survive," whereas facultative pathogens "live saprophytically and generally result in disease (or tend to be more severe) under conditions of plant stress such as low nutrition or water." In their experiment, well-watered and -fertilized seedlings of loblolly pine (*Pinus taeda*) and northern red oak (*Quercus rubra*) were grown outdoors in open-top chambers constructed within large soil bins located at the USDA-ARS National Soil Dynamics Laboratory in Auburn, Alabama (USA), where they were exposed to atmospheric CO_2 concentrations of either 360 or 720 ppm with or without being infected by the fusiform rust fungus (the obligate pathogen *Cronartium quercuum* f.sp. *fusiforme*), and where the pines were also grown with or without being infected by the pitch canker fungus (the facultative pathogen *Fusarium circinatum*) for various lengths of time that ranged from weeks to a full year, with each of the three experiments being conducted twice.

Regarding the pine *Fusarium* rust study, Runion et al. report "percent infection was not significantly affected by CO_2 concentration," but in spite of this fact "the percentage of loblolly pine seedlings which died as a result of rust infection was generally significantly lower under elevated CO_2 in both runs of the experiment." In the oak *Fusarium* rust study, they state "the percent of oak seedlings with uredia was consistently lower for seedlings exposed to elevated CO_2 in both runs," and "the percent of oak seedlings with telia was significantly lower for seedlings exposed to elevated CO_2 at the 16 and 19 days evaluations in both runs of the experiment." In the pine pitch canker study, the four researchers indicate "the percent of loblolly pine seedlings which developed cankers following inoculation with the pitch canker fungus was consistently lower for seedlings grown under elevated CO_2 in both runs of the experiment ... with infection in elevated CO_2-grown seedlings remaining about half that of ambient-grown seedlings." In light of these results, Runion et al. state "disease incidence—regardless of pathogen type—may be reduced as atmospheric CO_2 concentration continues to rise," a phenomenon that should significantly benefit the two species of trees they studied in the high-CO_2 world of the future.

Rounding out our review of diseased-plant responses to atmospheric CO_2 enrichment, we focus on the *Phytophthora citricola* pathogen, which can infect the roots and trunks of European Beech (*Fagus sylvatica* L.) trees. Introducing their study of the subject, Fleischmann et al. (2010) state that several reviews of the effects of elevated atmospheric CO_2 on plant parasite interactions—including those of Manning and Tiedemann (1995), Chakraborty et al. (2000b), and Garrett et al. (2006)—conclude "it is uncertain whether elevated CO_2 favors or suppresses pathogens in herbaceous or woody plants."

Therefore, in an attempt to obtain additional pertinent data, Fleischmann et al. grew well-watered *Fagus sylvatica* plants from seed in several 40-cm by 60-cm containers—which were 30 cm deep and filled with natural forest soil—for four years within growth chambers maintained at either 400 or 700 ppm CO_2 within a greenhouse. During this period, the trees received an adequate supply of all essential nutrients, but in the case of nitrogen (N), there were low-N and high-N treatments, with the high-N treatment receiving twice as much nitrogen as the low-N treatment. Finally, half of the seedlings were infected with *P. citricola* in the early summer of the third year of the study, and half of the trees in each treatment were harvested at the ends of the third and fourth years of the experiment.

The three German researchers found "chronic elevation of atmospheric CO_2 increased the susceptibility of beech seedlings towards the root pathogen *P. citricola*, while additional nitrogen supply reduced susceptibility." In fact, they found 27 percent of the infected plants in the low-N high-CO_2 treatment were killed by the pathogen by the end of their study, whereas only 9 percent of the infected plants in the high-N high-CO_2 treatment died. In terms of the bigger picture, they found surviving beech seedlings of the low-N high-CO_2 treatment "managed to tolerate the root infection by (a) increasing their carbon gain, (b) improving their fine root functionality and (c) changing their allometric relation between below-ground and above-ground biomass." Thus, Fleischmann et al. concluded infected beech seedlings in the low-N high-CO_2 treatment rose to the challenge presented by the pernicious pathogen and "enhanced [their] primary production rates in the second year of the experiment and increased above-ground biomass significantly as compared to control trees."

References

AL-Karaghouli, A.A., AL-Kayssi, A.W., and Hasson, A.M. 1990. The photometric properties of different colored plastic mulches used for soil solarization. *Solar and Wind Technology* **7**: 119–123.

AL-Kayssi, A.W. 2009. Impact of elevated CO_2 concentrations in the soil on soil solarization efficiency. *Applied Soil Ecology* **43**: 150–158.

AL-Kayssi, A.W. and AL-Karaghouli, A.A. 1991. Influence of different colored plastic mulches used for soil solarization on the effectiveness of soil heating. *Soil Solarization* **109**: 297–308.

Avissar, R., Mahrer, Y., Margulies, L., and Katan, J. 1986. Field aging of transparent polyethylene mulch: I. Photometric properties. *Soil Science Society of America Journal* **50**: 202–205.

Chakraborty, S., Pangga, I.B., Lupton, J., Hart, L., Room, P.M., and Yates, D. 2000a. Production and dispersal of

Colletotrichum gloeosporiodies spores on *Stylosanthes scabra* under elevated CO_2. *Environmental Pollution* **108**: 381–387.

Chakraborty, S., Tiedeman, A.V., and Teng, P.S. 2000b. Climate change: potential impact on plant diseases. *Environmental Pollution* **108**: 317–326.

Eastburn, D.M., Degennaro, M.M., DeLucia, E.H., Dermody, O., and McElrone, A.J. 2010. Elevated atmospheric carbon dioxide and ozone alter soybean diseases at SoyFACE. *Global Change Biology* **16**: 320–330.

Fleischmann, F., Raidl, S., and Osswald, W.F. 2010. Changes in susceptibility of beech (*Fagus sylvatica*) seedlings towards *Phytophthora citricola* under the influence of elevated atmospheric CO_2 and nitrogen fertilization. *Environmental Pollution* **158**: 1051–1060.

Garrett, K.A., Dendy, S.P., Frank, E.E., Rouse, M.N., and Travers, S.E. 2006. Climate change effects on plant disease: genomes to ecosystems. *Annual Review of Phytopathology* **44**: 489–509.

Grinstein, A., Orion, D., Greenberger, A., and Katan, J. 1979. Solar heating of the soil for the control of *Verticillium dahliae* and *Pratylenchus thornei* in potatoes. In *Soilborne Plant Pathogens*, edited by B. Shippers and W. Gams, 431–438. London, UK: Academic Press.

Hibberd, J.M., Whitbread, R., and Farrar, J.F. 1996. Effect of elevated concentrations of CO_2 on infection of barley by *Erysiphe graminis*. *Physiological and Molecular Plant Pathology* **48**: 37–53.

Jwa, N.S. and Walling, L.L. 2001. Influence of elevated CO_2 concentration on disease development in tomato. *New Phytologist* **149**: 509–518.

Katan, J. 1981. Solar heating (solarization) of soil for control of soilborne pests. *Annual Review of Phytopathology* **19**: 211–236.

Katan, J., Greenberger, A., Alon, H., and Grinstein, A. 1976. Solar heating by polyethylene mulching for the control of diseases caused by soilborne pathogens. *Phytopathology* **66**: 683–688.

Kobayashi, T., Ishiguro, K., Nakajima, T., Kim, H.Y., Okada, M., and Kobayashi, K. 2006. Effects of elevated atmospheric CO_2 concentration on the infection of rice blast and sheath blight. *Phytopathology* **96**: 425–431.

Kretzschmar, F. d S., Aidar, M.P.M., Salgado, I., and Braga, M.R. 2009. Elevated CO_2 atmosphere enhances production of defense-related flavonoids in soybean elicited by NO and a fungal elicitor. *Environmental and Experimental Botany* **65**: 319–329.

Mahrer, Y. 1979. Prediction of soil temperatures of a soil mulched with transparent polyethylene. *Journal of Applied Meteorology* **18**: 1263–1267.

Mahrer, Y., Naot, O., Rawitz, E., and Katan, J. 1984. Temperature and moisture regimes in soils mulched with transparent polyethylene. *Soil Science Society of America Journal* **48**: 362–367.

Manning, W.J. and Tiedemann, A. 1995. Climate change: potential effects of increased atmospheric carbon dioxide (CO_2), ozone (O_3), and ultraviolet-B (UV-B) radiation on plant diseases. *Environmental Pollution* **88**: 219–245.

McElrone, A.J., Hamilton, J.G., Krafnick, A.J., Aldea, M., Knepp, R.G., and DeLucia, E.H. 2010. Combined effects of elevated CO_2 and natural climatic variation on leaf spot diseases of redbud and sweetgum trees. *Environmental Pollution* **158**: 108–114.

McElrone, A.J., Reid, C.D., Hoye, K.A., Hart, E., and Jackson, R.B. 2005. Elevated CO_2 reduces disease incidence and severity of a red maple fungal pathogen via changes in host physiology and leaf chemistry. *Global Change Biology* **11**: 1828–1836.

Mitchell, C.E., Reich, P.B., Tilman, D., and Groth, J.V. 2003. Effects of elevated CO_2, nitrogen deposition, and decreased species diversity on foliar fungal plant disease. *Global Change Biology* **9**: 438–451.

Pangga, I.B., Chakraborty, S., and Yates, D. 2004. Canopy size and induced resistance in *Stylosanthes scabra* determine anthracnose severity at high CO_2. *Phytopathology* **94**: 221–227.

Percy, K.E., Awmack, C.S., Lindroth, R.L., Kopper, B.J., Isebrands, J.G., Pregitzer, K.S., Hendrey, G.R., Dickson, R.E., Zak, D.R., Oksanen, E., Sober, J., Harrington, R., and Karnosky, D.F. 2002. Altered performance of forest pests under atmospheres enriched by CO_2 and O_3. *Nature* **420**: 403–407.

Runion, G.B., Prior, S.A., Rogers, H.H., and Mitchell, R.J. 2010. Effects of elevated atmospheric CO_2 on two southern forest diseases. *New Forests* **39**: 275–285.

Sinclair, W.A., Lyon, H.H., and Johnson, W.T. 1987. *Diseases of Trees and Shrubs.* Ithaca, NY: Cornell University Press.

Thompson, G.B., Brown, J.K.M., and Woodward, F.I. 1993. The effects of host carbon dioxide, nitrogen and water supply on the infection of wheat by powdery mildew and aphids. *Plant, Cell and Environment* **16**: 687–694.

Thompson, G.B. and Drake, B.G. 1994. Insects and fungi on a C_3 sedge and a C_4 grass exposed to elevated atmospheric CO_2 concentrations in open-top chambers in the field. *Plant, Cell and Environment* **17**: 1161–1167.

Tiedemann, A.V. and Firsching, K.H. 2000. Interactive effects of elevated ozone and carbon dioxide on growth and yield of leaf rust-infected versus non-infected wheat. *Environmental Pollution* **108**: 357–363.

Wrather, J.A., Anderson, T.R., Arsyad, D.M., Gai, J., Ploper, L.D., Porta-Puglia, A., Ram, H.H., and Yourinori, J.T. 1997. Soybean disease loss estimates for the top 10 soybean producing countries in 1994. *Plant Disease* **81**: 107–110.

7.5.2. Nitrogen Insufficiency

Since nitrogen is one of the plant world's most important nutrients, a lack of sufficient nitrogen for maximum growth can be thought of as a significant environmental stress. This is especially important in the case of rice. As Feng et al. (2009) write, rice fields "represent the most important agricultural ecosystems in Asia since rice and wheat are the main source for food supply, and more than 90% of rice fields around the world are located in Asia." In this context, they note "purple phototrophic bacteria (PPB) are thought to be crucial in the nutrient cycling of rice fields." The Chinese researchers state PPB "thrive in the anaerobic portions of all kinds of aquatic environments, and have long been recognized as one of the key players in global carbon and nitrogen cycles."

Against this backdrop, in a FACE study conducted within a rice/wheat rotation system at the Nianyu Experimental Station in Jiangsu Province, China, Feng et al. grew rice (*Oryza sativa* L.) plants under standard paddy culture at two levels of soil nitrogen (N) fertility—low (150 kg N/hectare) and high (250 kg N/hectare)—at ambient and ambient plus 200 ppm CO_2 concentrations, throughout which period they measured several characteristics of PPB within the rhizosphere and bulk soils of the two CO_2 treatments. The seven scientists found (1) "based on denaturant gradient gel electrophoresis (DGGE) analysis of *pufM* gene encoding the M subunit of anoxygenic PPB light reaction center, elevated CO_2 appeared to enhance the biodiversity of PPB in flooded paddy soils," (2) "this was further supported by canonical correspondence analysis (CCA) of DGGE fingerprinting pattern of *pufM* genes in paddy soils as well as Shannon diversity indices," (3) "real-time quantitative PCR analysis of *pufM* gene further indicated that PPB abundance was stimulated by elevated CO_2 in bulk soil," and (4) "N fertilization enhanced the biodiversity of PPB under elevated atmospheric CO_2."

The significance of Feng et al.'s findings—especially the positive synergism of atmospheric CO_2 enrichment and N fertilization working together—is brought into perspective by their noting it has been found that "PPB inoculation into the flood water [in rice paddy culture] could lead to grain yield increase by 29% (Elbadry et al., 1999; Harada et al., 2005)." Therefore, the ongoing rise in the air's CO_2 content in the presence of adequate N availability—which can itself be improved by atmospheric CO_2 enrichment, as Feng et al. state "PPB are thought to be capable of fixing nitrogen"—can help provide the boost in food production that will be needed to feed the planet's still-expanding human population in the decades ahead.

Finally, Churkina et al. (2009) state "to investigate feedbacks between climate, atmospheric CO_2, atmospheric nitrogen deposition and carbon uptake of the land over almost two centuries [1860–2030]," they coupled "an earth system model of intermediate complexity" with "a biogeochemical process model" used with a "carbon and nitrogen allocation routine" that was "parameterized for seven vegetation types" including "deciduous broadleaf forest, evergreen needleleaf forest, evergreen broadleaf forest, evergreen deciduous forest, shrubland, C_4 and C_3 grasslands." They initialized the system by running the model "to a steady state to obtain the size of the ecosystem's carbon and nitrogen pools" under the assumption the ecosystem was "in equilibrium with the long-term climate," utilizing "daily climate data from NCEP Reanalysis for 1968–1977, constant preindustrial atmospheric nitrogen deposition, and CO_2 concentration."

The scientists first determined their global- and continental-scale estimates of land carbon uptake in the 1990s were "consistent with previously reported data." This comparison with the real world gave them confidence in the results their modeling exercise projected for the future, namely that "increasing nitrogen deposition and the physiological effect of elevated atmospheric CO_2 on plants have the potential to increase the land carbon sink, to offset the rise of CO_2 concentration in the atmosphere, and to reduce global warming." Specifically, they found that predicted changes in climate, CO_2, and nitrogen deposition for the year 2030 were sufficient to offset atmospheric CO_2 by a sizable 41 ppm. And if likely land use changes were included in the calculations, the offset rose to 76 ppm. The six scientists who conducted the work conclude their study suggests "reforestation and sensible ecosystem management in industrialized regions may have larger potential for climate change mitigation than anticipated."

References

Churkina, G., Brovkin, V., von Bloh, W., Trusilova, K., Jung, M., and Dentener, F. 2009. Synergy of rising nitrogen depositions and atmospheric CO_2 on land carbon uptake moderately offsets global warming. *Global Biogeochemical Cycles* **23**: 10.1029/2008GB003291.

Elbadry, M., Gamal-Eldin, H., and Elbanna, K. 1999. Effects of *Rhodobacter capsulatus* inoculation in combination with graded levels of nitrogen fertilizer on growth and yield of rice in pots and lysimeter experiments. *World Journal of Microbiology and Biotechnology* **15**: 393–395.

Feng, Y., Lin, X., Wang, Y., Zhang, J., Mao, T., Yin, R., and Zhu, J. 2009. Free-air CO_2 enrichment (FACE) enhances the biodiversity of purple phototrophic bacteria in flooded paddy soil. *Plant and Soil* **324**: 317–328.

Harada, N., Nishiyama, M., Otsuka, S., and Matsumoto, S. 2005. Effects of inoculation of phototrophic bacteria on grain yield of rice and nitrogenase activity of paddy soil in a pot experiment. *Soil Science and Plant Nutrition* **51**: 361–367.

7.5.3. Ozone Pollution

Logan et al. (2010) describe and discuss what was revealed at a "Tropospheric Ozone Changes Workshop" held in Boulder, Colorado (USA) on 14–16 October 2009: "long-term ozone records from regionally representative surface and mountain sites, ozonesondes, and aircraft were reviewed by region." In brief, they report, "in the Southern Hemisphere, surface measurements from South Africa and Tasmania and sonde data from New Zealand show a significant increase over the past 25 years." North of the equator, on the other hand, the story is different. In western Europe, for example, they write, "several time series of ~15-40 years ... show a rise in ozone into the middle to late 1990s and a leveling off, or in some cases declines, in the 2000s, in general agreement with precursor emission changes." Similarly, they state "surface measurements within North America show a pattern of mostly unchanged or declining ozone over the past two decades that [also] seems broadly consistent with decreases in precursor emissions," while noting "the Japanese sonde record suggests rising ozone into the 1980s and small changes thereafter."

The spatial and temporal distributions of these observations would seem to suggest that, whereas increasing industrialization initially tends to increase the emissions of precursor substances that lead to the creation of greater tropospheric ozone pollution, subsequent technological advances tend to ameliorate that phenomenon, as they appear gradually to lead to (1) a leveling off of the magnitude of precursor emissions and (2) an ultimately decreasing trend in tropospheric ozone pollution. In light of these observations, it can be appreciated that when atmospheric ozone and CO_2 concentrations both rise together, the plant-growth-enhancing effect of atmospheric CO_2 enrichment is significantly muted by the plant-growth-retarding effect of contemporaneous increases in ozone pollution, but as the troposphere's ozone concentration gradually levels off and then declines—as it appears to be doing with the development of new and better antipollution technology in the economically advanced countries—we should begin to see faster-than-usual increases in the planet's vegetative productivity, which should promote a further acceleration of the greening of the earth phenomenon.

Exploring this relationship, Tu et al. (2009) examined what happens when agricultural crops exposed to various degrees of ozone pollution are grown in CO_2-enriched air. The researchers grew peanut (*Arachis hypogaea* L.) plants from seed to maturity outdoors near Raleigh, North Carolina (USA) in open-top chambers under adequately watered and fertilized conditions, while exposing the plants to (1) charcoal-filtered air, which was thus ozone-free, (2) ambient air of unaltered ozone (O_3) concentration, and (3) air containing 1.6 times the ambient O_3 concentration. All of the O_3 treatments were exposed to air of 376, 550, and 730 ppm CO_2. Throughout the study period, the researchers made many different plant physiological measurements, and at the end of the period they harvested the crop and measured its final stem, leaf, and pod biomass.

Tu et al. state, "elevated CO_2 generally increased biomass production while O_3 suppressed it, and CO_2 ameliorated the O_3 effect." In terms of the season-long mean of midday net photosynthesis, for example, the 94 percent increase in the atmosphere's CO_2 concentration experienced in going from the lowest to the highest CO_2 treatment resulted in a 25 percent increase in net photosynthesis in the charcoal-filtered air, a 50 percent increase in the nonfiltered air, and a 104 percent increase in the ozone-polluted air. For the final aboveground biomass produced, the corresponding CO_2-induced increases were 10 percent, 41 percent, and 105 percent.

On the other hand, the four researchers found "at mid-vegetative growth, elevated CO_2 significantly reduced leaf nitrogen concentrations by up to 44%," but "plant nitrogen concentrations only differed by 8% among CO_2 treatments at harvest while N_2 fixation was increased," and they state data from their experiment suggest "symbiotic N_2 fixation is important for maintaining seed N concentrations and that CO_2 enhancement of symbiotic N_2 fixation may compensate for low soil N availability."

Tu et al. additionally note several experiments, like theirs, "have shown that elevated CO_2 can offset the adverse effects of O_3 on crop biomass production and yield," citing Olszyk et al. (2000), Fuhrer (2003), and Fiscus et al. (2005). In addition, they note "the protective effect of elevated CO_2 against O_3 injury has been observed in several C_3 plant species, including cotton, peanut, rice, soybean, and wheat, due in large part to a reduction in O_3 uptake from reduced stomatal conductance and possibly from increases in photoassimilation rates and antioxidant metabolism," citing McKee et al. (2000), Booker and Fiscus (2005), Fiscus et al. (2005), and Booker et al. (2007).

Clearly, therefore, and contrary to the contention of the U.S. Environmental Protection Agency, CO_2 is *not* a pollutant. On the contrary, it is a pollution *fighter* that reduces the negative effects of true pollutants (such as ozone) on important agricultural crops and replaces them with positive effects of great worth to mankind.

In a study of what atmospheric CO_2 enrichment can do for trees growing in ozone-polluted air, Vapaavuori et al. (2009) grew 20 initially-seven-year-old trees of each of two different silver birch (*Betula pendula* Roth) clones—4 and 80 (V5952 and K1659, respectively, in the Finnish forest genetic register)—outdoors at the Suonenjoki Research Unit site of the Finnish Forest Research Institute for three years (1999–2001) within individual open-top chambers maintained at all combinations of (1) ambient CO_2 and ambient O_3, (2) ambient CO_2 and double O_3, (3) double CO_2 and ambient O_3, and (4) double CO_2 and double O_3. CO_2 treatments were imposed 24 hours per day, and O_3 treatments were imposed for 12, 12, and 14 hours per day in 1999, 2000, and 2001, respectively. Throughout the course of the experiment they measured a variety of plant physiological responses to the four different treatments, including net photosynthesis, leaf stomatal conductance, leaf soluble proteins, leaf phenolic compounds, leaf nutrient concentrations, trunk and branch growth, physiology of the foliage and root systems, crown structure, wood properties, and interactions with folivorous insects. The many results they thus obtained indicated, in general, that the negative effects of elevated O_3 on the various growth parameters and properties of the trees "were mainly found in ambient CO_2," and elevated CO_2 typically "reversed or diminished the effects of elevated O_3.".

In a similar study conducted at the Aspen FACE facility, where aspen clones had been grown since 1997 in conditions simulating atmospheric CO_2 and O_3 concentrations predicted for the mid-twenty-first century (560 ppm CO_2 and 1.5 times the current ambient O_3 concentration), McGrath et al. (2010) documented the history of leaf area index (LAI) development and leaf photosynthetic operating efficiency over the first month of spring leaf-out 11 years later in 2008, at a time when the yearly growth-season CO_2 fumigation had begun but before O_3 fumigation was started. The trees in the elevated CO_2 plots showed a 36 percent stimulation of leaf area index, while the trees in the elevated O_3 plots showed a 20 percent reduction in LAI. In addition, the photosynthetic operating efficiency of the CO_2-enriched aspen leaves was enhanced by 51 percent. Given these findings, atmospheric CO_2 enrichment would appear to be capable of providing young aspen trees with a great head start on the growing season, even in the debilitating presence of elevated ozone concentrations.

In studying others' experimental work, Wang and Taub (2010) conducted a series of meta-analyses that reveal how differences in the availability of soil fertility and water, as well as the stress of ozone (O_3) pollution, affect the biomass allocation in plants—as expressed by the change in the fraction of root mass to total biomass (i.e., *root mass fraction* or RMF)—that occurs when plants are exposed to air enriched with CO_2 to levels ranging anywhere from 500 to 1,000 ppm. Using data extracted from 541 peer-reviewed scientific journal articles, which yielded a total of 1,349 RMF observations, the researchers discovered that lower soil fertility increased RMF, and the magnitude of the increase "was similar for ambient and elevated CO_2-grown plants." They also discovered that lower soil water content also increased RMF, but in this case they report it did so "to a greater extent at elevated than at ambient CO_2." Finally, they discovered "CO_2 enrichment had little effect on the magnitude of O_3-caused reduction in RMF in herbaceous species," but "it alleviated the adverse effect of higher O_3 on root production in woody species."

Given these findings, the two researchers conclude, "under abiotic stresses, e.g., drought and higher O_3, elevated CO_2-grown plants will likely increase biomass allocation below-ground," where it can be used to construct more roots that can be used to acquire more water and nutrients. However, "because of the non-uniform changes in drought and O_3 projected for different parts of the world," they state "elevated CO_2 will have regional, but not global, effects on biomass allocation under various global change scenarios."

In one final CO_2 vs. O_3 study, Andrew and Lilleskov (2009) note sporocarps (the reproductive structures of fungi) can be significant carbon sinks for the ectomycorrhizal fungi that develop symbiotic relationships with plants by forming sheaths around their root tips, where they are the last sinks for carbon in the long and winding pathway that begins at the source of carbon assimilation in plant leaves. They also note "it is critical to understand how ectomycorrhizal fungal sporocarps are affected by elevated CO_2 and O_3" because, as they continue, "sporocarps facilitate genetic recombination, permit long-distance dispersal and contribute to food webs," and we need to know how these important processes will be affected by continued increases in the concentrations of these two trace constituents of the atmosphere.

In an effort to find some answers, the authors sampled aboveground sporocarps for four years at the Aspen FACE site, which provided, in their words, a "unique opportunity to examine the effects of both elevated CO_2 and O_3 on a forested ecosystem." The examination was conducted during years four through seven of the aspen and aspen-birch forests' exposures to ambient and enriched concentrations of the two gases: CO_2 (350 and 550 ppm) and O_3 (33–67 and 50–100 ppb).

The two researchers found total mean sporocarp biomass "was generally lowest under elevated O_3 with ambient CO_2," and it "was greatest under elevated CO_2, regardless of O_3 concentration." They also state there was "a complete elimination of O_3 effects on sporocarp production when [extra] CO_2 was added." Finally, they say they "expect that the responses seen in the present study were conservative compared to those expected under regional to global changes in CO_2 and O_3."

Consequently, by itself or in combination with rising ozone concentrations, the ongoing rise in the air's CO_2 content can be expected to enhance the genetic recombination and long-distance dispersal of the ectomycorrhizal fungi that form symbiotic relationships with the roots of aspen and birch trees, thereby positively contributing to various food webs found within aspen and aspen-birch forests.

References

Andrew, C. and Lilleskov, E.A. 2009. Productivity and community structure of ectomycorrhizal fungal sporocarps under increased atmospheric CO_2 and O_3. *Ecology Letters* **12**: 813–822.

Booker, F.L., Burkey, K.O., Pursley, W.A., and Heagle, A.S. 2007. Elevated carbon dioxide and ozone effects on peanut: I. Gas-exchange, biomass, and leaf chemistry. *Crop Science* **47**: 1475–1487.

Booker, F.L. and Fiscus, E.L. 2005. The role of ozone flux and antioxidants in the suppression of ozone injury by elevated CO_2 in soybean. *Journal of Experimental Botany* **56**: 2139–2151.

Fiscus, E.L., Booker, F.L., and Burkey, K.O. 2005. Crop responses to ozone: uptake, modes of action, carbon assimilation and partitioning. *Plant, Cell and Environment* **28**: 997–1011.

Fuhrer, J. 2003. Agroecosystem responses to combinations of elevated CO_2, ozone, and global climate change. *Agriculture, Ecosystems and Environment* **97**: 1–20.

Logan, J., Schultz, M., and Oltmans, S. 2010. Observing and understanding tropospheric ozone changes. *EOS, Transactions, American Geophysical Union* **91**: 119.

McGrath, J.M., Karnosky, D.F., and Ainsworth, E.A. 2010. Spring leaf flush in aspen (*Populus tremuloides*) clones is altered by long-term growth at elevated carbon dioxide and elevated ozone concentration. *Environmental Pollution* **158**: 1023–1028.

McKee, I.F., Mulholland, B.J., Craigon, J., Black, C.R., and Long, S.P. 2000. Elevated concentrations of atmospheric CO_2 protect against and compensate for O_3 damage to photosynthetic tissues of field-grown wheat. *New Phytologist* **146**: 427–435.

Olszyk, D.M., Tingey, D.T., Watrud, L., Seidler, R., and Andersen, C. 2000. Interactive effects of O_3 and CO_2:

implications for terrestrial ecosystems. In *Trace Gas Emissions and Plants*, edited by S.N. Singh, 97–136. Dordrecht: Netherlands.

Tu, C., Booker, F.L., Burkey, K.O., and Hu, S. 2009. Elevated atmospheric carbon dioxide and O_3 differentially alter nitrogen acquisition in peanut. *Crop Science* **49**: 1827–1836.

Vapaavuori, E., Holopainen, J.K., Holopainen, T., Julkunen-Titto, R., Kaakinen, S., Kasurien, A., Kontunen-Soppela, S., Kostiainen, K., Oksanen, E., Peltonen, P., Riikonen, J., and Tulva, I. 2009. Rising atmospheric CO_2 concentration partially masks the negative effects of elevated O_3 in silver birch (*Betula pendula* Roth). *Ambio* **38**: 418–424.

Wang, X. and Taub, D.R. 2010. Interactive effects of elevated carbon dioxide and environmental stresses on root mass fraction in plants: a meta-analytical synthesis using pairwise techniques. *Oecologia* **163**: 1–11.

7.5.4. Phosphorus Insufficiency

With respect to the CO_2-induced increase in the growth of plants generally observed in atmospheric CO_2 enrichment experiments, Khan et al. (2010) write, “if faster and more vigorous plant growth is to be sustained,” such as in the case of trees that may live for many decades or even centuries, “a sufficient nutrient supply must be available” to sustain that growth. This concept underlies the well-known but long-discredited progressive nitrogen limitation hypothesis. And since the researchers note “phosphorus is one of the key elements often considered to limit productivity in terrestrial ecosystems,” they state its gradual depletion in the soil may also “act as a negative feedback to increased growth.”

In a test of this hypothesis regarding phosphorus, Khan et al. grew three species of poplar trees (*Populus alba*, *P. nigra* and *P. x euramericana*) at ambient and elevated (550 ppm) CO_2 concentrations at the EuroFACE facility in Viterbo (Central Italy) in a low-nitrogen soil for a period of five years. Started as stem cuttings in 1999, the trees experienced a significant CO_2-induced stimulation of biomass production over the first three years of the study, at which point they were coppiced and allowed to grow for two more years. During that period, they continued to exhibit a significant CO_2-induced enhancement of growth. Afterward, numerous soil samples were taken to a depth of 60 cm under each species and analyzed for phosphorus (P) availability. This work revealed that rather than decreasing under elevated CO_2, and contrary to their own initial hypothesis, “the plant available, the weatherable mineral P pool and degradable organic P pools increased under FACE.” This, they state, suggests “the availability of P can actually increase in elevated CO_2, forming a positive feedback with increased biomass production on P limited soils.”

In the last paragraph of their paper, Khan et al. conclude their study “shows that increased tree growth under elevated CO_2 has not resulted in depletion of P pools in soils, but rather in replenishment and increased storage of P in the rooting zone.” Therefore, and contrary to even their own expectations before beginning their experiment, they conclude “phosphorus limitation may therefore not reduce tree growth in a high CO_2 world.”

Reference

Khan, F.N., Lukac, M., Miglietta, F., Khalid, M., and Godbold, D.L. 2010. Tree exposure to elevated CO_2 increases availability of soil phosphorus. *Pakistan Journal of Botany* **42**: 907–916.

7.5.5. Salinity Stress

Soil salinity stress, according to Perez-Lopez et al. (2010), results from a buildup of salt in soils, which “can inhibit the growth of valuable crops such as barley” because the “osmotic stress caused by low water potential in salinized soils reduces the availability of water for uptake by plants.” This stress, however, may be mitigated by plants actively decreasing their osmotic potential via a phenomenon known as osmotic adjustment, but the processes involved in this adjustment require extra energy that often leads to a reduction in plant growth. This penalty, or tax, is sometimes referred to as “the cost of salt tolerance.”

To further investigate this penalty, Perez-Lopez et al. (2009) grew two barley (*Hordeum vulgare* L.) cultivars, Alpha and Iranis, within controlled-environment growth chambers at either ambient (350 ppm) or elevated (700 ppm) atmospheric CO_2 concentrations in a 3:1 perlite:vermiculite mixture watered with Hoagland’s solution every two days (until the first leaf was completely expanded at 14 days), after which a salinity treatment was administered by adding 0, 80, 160, or 240 m*M* NaCl to the Hoagland’s solution every two days for 14 more days. Then, after a total of 28 days, the primary leaf of each barley plant was harvested and assessed for several biochemical properties.

The seven scientists determined that in the various ambient-air salinity treatments, the deleterious effects of reactive oxygen species (ROS) on barley leaves were made apparent through ion leakage and increases in thiobarbituric acid reactive substances (TBARS), which rose ever-higher as salt concentrations increased. "On the other hand," they continue, "when [the] salinity treatment was imposed under elevated CO_2 conditions, lower solute leakage and TBARS levels were observed, suggesting that the oxidative stress caused by salinity was lower." In discussing their findings, Perez-Lopez et al. write, "elevated CO_2 protects barley cultivars from oxidative stress," and they note "the relief of oxidative stress damage observed in our barley leaves grown under [a] CO_2 enriched atmosphere has also been observed in alfalfa (Sgherri et al., 1998), pine (Vu et al., 1999) and oak (Schwanz and Polle, 2001)." Hence, it would appear the ongoing rise in the air's CO_2 content may help a wide variety of Earth's plants cope with the serious problems caused by high soil salinity.

One year later, Perez-Lopez et al. (2010) once again grew two barley cultivars under well-watered and -fertilized conditions in pots placed within controlled-environment chambers they maintained at atmospheric CO_2 concentrations of either 350 or 700 ppm for a period of 28 days. During this time, midday leaf water potential, osmotic potential, osmotic potential at full turgor, dehydration, and osmotic adjustment were routinely measured, after which the primary leaf of each plant was harvested and assessed for the concentrations of various minerals and organic compounds it contained. The scientists found "elevated CO_2 permitted plant metabolism to be maintained at a better status under salt stress than did ambient CO_2," noting "growth was reduced more at ambient than at elevated CO_2." In addition, they determined "elevated CO_2 widens the range of salt concentrations at which osmotic adjustment continues to be efficient by providing the greater supply of carbon and ATP [Adenosine-5'-triphosphate]," which is a multifunctional nucleotide that transports chemical energy within cells for metabolism and is, in their words, "needed to perform the energetically expensive salt tolerance mechanisms." Given these findings, the Spanish scientists state their data suggest "under future environmental conditions, barley species will be able to succeed in salinized areas in which growth is not currently possible."

Turning our attention to halophytes, Geissler et al. (2009) note they are "naturally salt tolerant plants which are able to complete their life cycle on a substrate rich in NaCl," and that cash-crop halophytes "can be used for various economical and ecological purposes, e.g. for food, fodder, for obtaining timber, fibers, reeds or chemicals, as ornamental plants, for coastal protection, land reclamation or greenification of deserts." They note that *Aster tripolium*, in particular, "can be used for food (the leaves have a high nutritional value and can be eaten as salad or vegetable), for fodder and as an ornamental plant."

In their study of this plant, Geissler et al. grew adequately fertilized two-month-old seedlings for an additional month within open-top chambers maintained at atmospheric CO_2 concentrations of either 370 or 520 ppm inside a controlled-environment greenhouse, where they were irrigated with water having a salt (NaCl) content equivalent to 0, 50, or 100 percent sea water salinity (SWS), while monitoring several plant properties and processes. This work revealed, first, that the 40 percent increase in the air's CO_2 content increased the light-saturated rate of net photosynthesis by 56 percent, 82 percent, and 71 percent, respectively, in the plants irrigated with water of 0, 50, and 100 percent SWS, while it increased their water use efficiencies by 14, 26, and 61 percent at the same respective SWS percentages. Other positive impacts of the CO_2-enriched air were "an enhanced synthesis of proline, carbohydrates and proteins." The three researchers state "these mechanisms led to a higher survival rate under saline conditions, i.e. to an improved salt tolerance." Geissler et al. conclude their paper by stating, "*A. tripolium* is a promising cash crop halophyte which will probably benefit from rising atmospheric CO_2 concentrations in the future," and "its sustainable use can help feeding the growing world population and counteracting the greenhouse effect."

In another study of a halophyte, Mateos-Naranjo et al. (2010) note the cordgrass *Spartina maritima* "is an important pioneer and ecosystem engineer in salt marshes on the Atlantic coast of southern Europe," citing Castellanos et al. (1994). They state that "using the C_4 pathway," this halophyte "produces extensive stands in a range of marsh environments," citing Castellanos et al. (1998). Working with 15-cm-diameter clumps of *S. maritima* they obtained from a low-marsh site along the southwest coast of Spain in

April 2007, which they transplanted into individual plastic pots filled with pearlite that rested on shallow trays filled with Hoagland's solution of three different salinities (0, 170, or 510 mM NaCl), Mateos-Naranjo et al. conducted an experiment in which they maintained the plants in controlled environment chambers having atmospheric CO_2 concentrations of either 380 ppm or 700 ppm (an increase of 84 percent) for 30 days, during which time they measured several plant properties and processes.

The 84 percent increase in the atmosphere's CO_2 concentration stimulated the growth of *S. maritima* by about 65 percent in all three salinity treatments, while the halophyte's water use efficiency was enhanced by approximately 10 percent, 100 percent, and 160 percent in the 0, 170, and 510 mM salinity treatments, respectively, because "increasing CO_2 concentration has a positive effect on the photochemical apparatus, helping to counteract salt stress experienced by plants at current CO_2 concentrations." Therefore, the U.K. and Spanish scientists state their results suggest the productivity of *S. maritima* "might increase in a future scenario of rising atmospheric CO_2 concentration in environments with salinities as high as that of seawater," which is good news, indeed, about what they describe as "an important pioneer and ecosystem engineer in salt marshes."

References

Castellanos, E.M., Figueroa, M.E., and Davy, A.J. 1994. Nucleation and facilitation in saltmarsh succession: interactions between *Spartina maritima* and *Arthrocnemum perenne*. *Journal of Ecology* **82**: 239–248.

Castellanos, E.M., Heredia, C., Figueroa, M.E., and Davy, A.J. 1998. Tiller dynamics of *Spartina maritima* in successional and non-successional Mediterranean salt marsh. *Plant Ecology* **137**: 213–225.

Geissler, N., Hussin, S. and Koyro, H.-W. 2009. Interactive effects of NaCl salinity and elevated atmospheric CO_2 concentration on growth, photosynthesis, water relations and chemical composition of the potential cash crop halophyte *Aster tripolium* L. *Environmental and Experimental Botany* **65**: 220-231.

Mateos-Naranjo, E., Redondo-Gomez, S., Andrades-Moreno, L., and Davy, A.J. 2010. Growth and photosynthetic responses of the cordgrass *Spartina maritima* to CO_2 enrichment and salinity. *Chemosphere* **81**: 725–731.

Perez-Lopez, U., Robredo, A., Lacuesta, M., Munoz-Rueda, A., and Mena-Petite, A. 2010. Atmospheric CO_2 concentration influences the contributions of osmolyte accumulation and cell wall elasticity to salt tolerance in barley cultivars. *Journal of Plant Physiology* **167**: 15–22.

Perez-Lopez, U., Robredo, A., Lacuestra, M., Sgherri, C., Munoz-Rueda, A., Navari-Izzo, F., and Mena-Petite, A. 2009. The oxidative stress caused by salinity in two barley cultivars is mitigated by elevated CO_2. *Physiologia Plantarum* **135**: 29–42.

Schwanz, P. and Polle, A. 2001. Differential stress responses of antioxidative systems to drought in pendunculate oak (*Quercus robur*) and maritime pine (*Pinus pinaster*) grown under high CO_2 concentrations. *Journal of Experimental Botany* **52**: 133–143.

Sgherri, C., Quartacci, M., Menconi, M., Raschi, A., and Navari-Izzo, F. 1998. Interactions between drought and elevated CO_2 on alfalfa plants. *Journal of Plant Physiology* **152**: 118–124.

Vu, J.C., Gesch, R., Allen, L.H., Boote, K., and Bowes, G. 1999. CO_2 enrichment delays a rapid, drought induced decrease in Rubisco small subunit transcript abundance. *Journal of Plant Physiology* **155**: 139–142.

7.5.6. Temperature Stress

Focusing on an agricultural crop, Xiong et al. (2009) write, "rice is an essential component of the diet in more than half the world's population, and it is the most socially and economically important crop in China," where they indicate it "contributes 43.7% of total national grain production," citing Yao et al. (2007). In light of this importance, Xiong et al. assess "the effect of greenhouse gas-induced climate change, as well as the direct fertilization effect of CO_2, on rice yields and production in China," by coupling "the regional climate model PRECIS (Providing Regional Climates for Impacts Studies) with the CERES (Crop Environment Resources Synthesis) rice crop model to simulate current (1961–1990) and future (2011–2100) rice yields and production under [the] A2 and B2 climate change scenarios" of the Intergovernmental Panel on Climate Change, which include significant global warming.

The four researchers report that with anticipated climate changes, "single rice cropping may expand further north in China, and double rice cropping may move to the northern portion of the Yangtze River basin." In addition, they write, "the national mean rice production is estimated to increase by 2.7 to 19.2% considering the combined effects of climate change,

CO_2 and shifting rice-producing areas." Therefore, even considering the inflated temperature increases predicted by the IPCC, the estimated net effect of global warming and concomitant growth in anthropogenic CO_2 emissions ends up producing an increase in rice production in the world's most populous country, where it is the people's single most important food source. This is a benefit of the ongoing rise in the air's CO_2 content that simply cannot be ignored.

Noting "responses to elevated CO_2 may differ at different temperature levels and that a potential reduction in yield due to high temperatures" is "very relevant," Yoon et al. (2009) grew well-watered and -fertilized cotton (*Gossypium hirsutum* L.) plants from seed to maturity—one plant to each container of washed sand, with spacing between plants similar to the plant spacing found in typical cotton fields—within the University of Georgia's Envirotron, where they were placed within chambers maintained at all combinations of two day/night air temperature regimes (25/15°C and 35/25°C) and three atmospheric CO_2 concentrations (400, 600, and 800 ppm), during which time, as well as at the end of the study, various plant properties were measured.

Describing the final yield obtained, Yoon et al. report that at the lower of the two air temperature regimes, "final boll weight at harvest was 1.59 times (at 600 ppm) and 6.3 times (at 800 ppm) higher compared to ambient CO_2," and "increasing the temperature increased this difference, as the final boll weight was 34.1 times (at 600 ppm) and 23.3 times (at 800 ppm) higher compared to ambient CO_2." In addition, they state "the response of final lint yield to CO_2 was more or less similar to the response of boll weight."

Clearly, both higher air temperatures and higher atmospheric CO_2 concentrations—individually and in combination—were a great boon to cotton productivity in this well-controlled study, indicating that in this experiment not only were the twin evils of the radical environmentalist movement not detrimental to cotton growth and development, they were incredibly beneficial, demonstrating the enormous disconnect between forecasts of biospheric doom and experimental studies of how various species of both plants and animals actual to respond to changes in climate.

The study of Wertin et al. (2010) demonstrates that disconnect in the case of loblolly pine. The commercial forestry industry in the Southeast United States depends heavily on loblolly pine, and this part of the country is forecast to become warmer and perhaps slightly drier over time as the air's CO_2 content continues to increase. Any climate-induced damage to this tree would thus have a huge negative impact on the region's economy. Therefore, the three researchers set out to evaluate the effects of elevated CO_2, elevated temperature, and moisture stress on loblolly pine trees in a full-factorial experiment replicated at three sites spanning most of the north-south range of Georgia. Few studies have evaluated all three factors in this way, but Wertin et al. were able to do so using controlled-environment chambers that could not only keep the air's CO_2 concentration continuously elevated at 700 ppm but could also keep its temperature a constant 2°C above ambient.

The study revealed there was essentially no effect of temperature on net assimilation rate (A_{net}), which the researchers attribute to the very broad temperature optimum of loblolly pine, which extends from about 20 to 35°C. Thus, there is no realistically possible global warming scenario under which a direct warming-induced negative effect would be detectable on this important commercial tree species.

The CO_2 effect, on the other hand, was substantial. A_{net} in the CO_2-enriched trees was 43 percent higher than in the ambient-air trees in June in the high-water treatment and 79 percent higher in the low-water treatment. The critical interaction between water stress and CO_2 also showed the low-water with high-CO_2 treatment had equal or higher A_{net} than the high-water with ambient-CO_2 treatment at all sites and during all seasons, indicating even a substantial decrease in moisture in this region would be compensated for by the positive A_{net} response to increased atmospheric CO_2 under future warmer conditions. Even under the worst-case predicted scenario, the dominant tree species in the Southeastern United States—loblolly pine—will grow as well as, or even better than, it does at present. And if the increases in precipitation forecast by some climate models come to pass, these climate conditions would lead to even greater growth enhancements.

In another illuminating study, Darbah et al. (2010) report that an unusual heat wave and drought occurred in northern Wisconsin (USA) during the summer of 2006, leading to maximum leaf temperatures that varied between 30 and 38°C and drought-exacerbated heat stress on the leaves of most trees. The scientists measured leaf gas exchange characteristics and several other plant physiological properties of the leaves of paper birch trees (*Betula papyrifera*) and two clones (271 and 42E) of quaking aspen trees (*Populus tremuloides* Michx) exposed to either ambient or elevated (ambient + 200 ppm) atmospheric CO_2 concentrations at the Aspen FACE facility before, during, and after the highest air temperatures recorded during that period of extreme heat. The four researchers discovered, "elevated CO_2 protected photosynthesis of both species against moderate heat stress" by increasing "carboxylation capacity, photosynthetic electron transport capacity and triose phosphate use." In addition, they "observed significant increases in transpiration rates in both aspen clones and the birch trees under elevated CO_2," the cooling effect of which decreased the leaf temperatures of the aspen trees by 1.9°C in clone 42E and by 2.7°C in clone 171, while the leaf temperatures of the birch trees were decreased by 3.1°C.

As for how this cooling could have occurred, Darbah et al. note under normal, less-stressful conditions, atmospheric CO_2 enrichment typically does just the opposite: It reduces transpiration and increases leaf temperature. This behavior earlier in the growing season in the elevated CO_2 treatment may have left more water in the soil, enabling the trees to transpire at a greater rate and thereby cool their leaves when it was most needed (during the subsequent heat wave and drought). They describe this phenomenon as "one part of the increased thermotolerance of the plants under high CO_2."

As a result of these various stress-relieving phenomena, Darbah et al.'s CO_2 gas exchange data indicated that whereas the CO_2-induced stimulation of net photosynthesis in aspen clone 42E was about 31 percent over the leaf temperature range 32–35°C, it was approximately 218 percent over the temperature range 36–39°C, while for aspen clone 171 the corresponding CO_2-induced net photosynthesis enhancements were 38 and 199 percent, and for the birch trees they were 95 and 297 percent.

In discussing their findings, Darbah et al. state they agree with those of Veteli et al. (2007), who "reported that elevated CO_2 ameliorated the negative effects of high temperature in three deciduous tree species," as well as those of Wayne et al. (1998), who "reported that elevated CO_2 ameliorated high temperature stress in yellow birch trees," and that all of these observations are "in agreement with Idso and Kimball (1992), who reported that elevated CO_2 (ambient + 300 ppm) increased net photosynthetic rate in sour orange tree leaves exposed to full sunlight by 75, 100 and 200% compared to those in ambient CO_2 concentration at temperatures of 31, 35 and 42°C, respectively, suggesting that elevated CO_2 ameliorates heat stress in tree leaves." Hence, they conclude, "in the face of rising atmospheric CO_2 and temperature (global warming), trees will benefit from elevated CO_2 through increased thermotolerance."

References

Darbah, J.N.T., Sharkey, T.D., Calfapietra, C., and Karnosky, D.F. 2010. Differential response of aspen and birch trees to heat stress under elevated carbon dioxide. *Environmental Pollution* **158**: 1008–1014.

Idso, S.B. and Kimball, B.A. 1992. Effects of atmospheric CO_2 enrichment on photosynthesis, respiration and growth of sour orange trees. *Plant Physiology* **99**: 341–343.

Veteli, T.O., Mattson, W.J., Niemela, P., Julkunen-Tiitto, R., Kellomaki, S., Kuokkanen, K., and Lavola, A. 2007. Do elevated temperature and CO_2 generally have counteracting effects on phenolic phytochemistry of boreal trees? *Journal of Chemical Ecology* **33**: 287–296.

Wayne, P.M., Reekie, E.G., and Bazzaz, F.A. 1998. Elevated CO_2 ameliorates birch response to high temperature and frost stress: implications for modeling climate-induced geographic range shifts. *Oecologia* **114**: 335–342.

Wertin, T.M., McGuire, M.A., and Teskey, R.O. 2010. The influence of elevated temperature, elevated atmospheric CO_2 concentration and water stress on net photosynthesis of loblolly pine (*Pinus taeda* L.) at northern, central and southern sites in its native range. *Global Change Biology* **16**: 2089–2103.

Xiong, W., Conway, D., Lin, E., and Holman, I. 2009. Potential impacts of climate change and climate variabiity on China's rice yield and production. *Climate Research* **40**: 23–35.

Yao, F.M., Xu, Y.L., Lin, E.D., Yokozawa, M., and Zhang, J.H. 2007. Assessing the impacts of climate change on rice yields in the main rice areas of China. *Climatic Change* **80**: 395–409.

Yoon, S.T., Hoogenboom, G., Flitcroft, I., and Bannayan, M. 2009. Growth and development of cotton (*Gossypium hirsutum* L.) in response to CO_2 enrichment under two different temperature regimes. *Environmental and Experimental Botany* **67**: 178–187.

7.5.7. Water Insufficiency and Over-Sufficiency

In a study of the more common type of extreme water availability (insufficiency), Wertin et al. (2010) used controlled-environment chambers that maintained the air's CO_2 concentration at either normal or elevated (700 ppm) values and its temperature either normal or elevated (2°C above ambient), while they studied the photosynthetic responses of loblolly pine trees growing in both high-water and low-water conditions in a full-factorial experiment replicated at three sites spanning most of the north-south range of Georgia (USA). This work revealed the net assimilation rate ($A_{\mathbf{net}}$) in the CO_2-enriched trees was 43 percent higher than in the ambient-air trees in June in the high-water treatment, but 79 percent higher in the low-water treatment, and that the low-water with high-CO_2 treatment had equal or higher $A_{\mathbf{net}}$ than the high-water with ambient-CO_2 treatment at all sites and during all seasons, indicating even a substantial decrease in moisture in this region would be compensated for by the positive $A_{\mathbf{net}}$ response to increased atmospheric CO_2 under future warmer conditions.

In a pertinent contemporaneous study, Wyckoff and Bowers (2010) write, "with continued increases in global greenhouse gas emissions, climate models predict that, by the end of the 21st century, Minnesota [USA] summer temperature will increase by 4–9°C and summer precipitation will slightly decrease," citing in this regard Kling et al. (2003) and Christensen et al. (2007); and they state certain "forest models and extrapolations from the paleoecological record suggest that, in response to increased temperature and/or drought, forests may retreat to the extreme north-eastern parts of the state," citing Pastor and Post (1998), Hamilton and Johnson (2002), and Galatowitsch et al. (2009).

Working with bur oak trees (*Quercus macrocarpa*), Wyckoff and Bowers evaluated the drought effect by: "(i) using tree rings to establish the relationship between drought and *Q. macrocarpa* growth for three sites along Minnesota's prairie-forest border, (ii) calculating the current relationship between growth and mortality for adult *Q. macrocarpa* and (iii) using the distributions of current growth rates for *Q. macracarpa* to predict the susceptibility of current populations to droughts of varying strength." In addition, they looked for "temporal trends in the correlation between *Q. macrocarpa* growth and climate, hypothesizing that increases in CO_2 may lead to weaker relationships between drought and tree growth over time," because atmospheric CO_2 enrichment typically leads to increases in plant water use efficiency, which generally makes them less susceptible to the deleterious impact of drought on growth.

The two University of Minnesota researchers discovered "the sensitivity of annual growth rates to drought has steadily declined over time as evidenced by increasing growth residuals and higher growth rates for a given PDSI [Palmer Drought Severity Index] value after 1950 [when the atmosphere's CO_2 concentration rose by 57 ppm from 1950 to 2000] compared with the first half of the century [when the CO_2 increase was only 10 ppm]." In addition, Wyckoff and Bowers write, "for *Q. macrocarpa*, declining sensitivity of growth to drought translates into lower predicted mortality rates at all sites" and "at one site, declining moisture sensitivity yields a 49% lower predicted mortality from a severe drought (PDSI = -8, on a par with the worst 1930s 'American Dust Bowl' droughts)." Hence, they conclude "the decreasing drought sensitivity of established trees may act as a buffer and delay the movement of the prairie-forest ecotone for many decades even in the face of climate change."

At the other end of the moisture spectrum, we confront the problem of an over-sufficiency of water, which we equate with complete submergence in water. This phenomenon was recently studied by Pedersen et al. (2010), who write, with respect to terrestrial plants in general, that complete submergence in water "impedes exchange of O_2 and CO_2 with shoots (Voesenek et al., 2006)," and that underwater photosynthesis "is limited by CO_2 availability owing to slow diffusion in water, and stomatal closure (Mommer and Visser, 2005)." These submergence-induced phenomena—if long sustained—typically lead to plant death.

To learn how the wetland plant *Hordeum marinum* Huds. would respond when fully submerged in water, Pedersen et al. grew several 28-day-old plants consisting of three Nordic Gene Bank accessions (H21, H90, and H546) for seven additional days while exposing them to four different treatments: "aerated root zone controls with shoots in air; stagnant root zone with shoots in air; stagnant root zone with shoots also completely submerged with 18 µM CO_2 (air equilibrium); stagnant root zone with shoots also completely submerged with 200 µM CO_2 (simulating CO_2 enrichment in many natural flood waters)," while measuring numerous plant responses.

This revealed, as they describe it, that "plants submerged for 7 days in water at air equilibrium (18 µM CO_2) suffered loss of biomass, whereas those with 200 µM CO_2 continued to grow." In addition, "higher underwater net photosynthesis at 200 µM CO_2 increased by 2.7- to 3.2-fold sugar concentrations in roots of submerged plants, compared with at air equilibrium CO_2." They state this phenomenon "is likely to have contributed to the greater root growth in submerged plants with the higher CO_2 supply." Finally, they note the latter CO_2-enriched plants "tillered similarly to plants with shoots in air."

Pedersen et al. further report that CO_2 enrichment of submerging water to ~290 µM enhanced by twofold the growth of two cultivars of rice, compared to plants submerged with water in equilibrium with normal ambient air (Setter et al., 1989), and they state such elevated CO_2 concentrations "have been reported at various field sites," citing Setter et al. (1987) and Ram et al. (1999). Thus, they indicate plants experiencing total submergence during floods typically lose mass and die under normal conditions, but when the water is supersaturated with CO_2, they can not only survive, they actually continue to grow.

References

Christensen, J.H., et al.. 2007. Regional climate projections. In Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change, edited by S. Solomon, et al., 847–940. Cambridge, UK: Cambridge University Press.

Galatowitsch, S., Frelich, L., and Phillips-Mao, L. 2009. Regional climate change adaptation strategies for biodiversity conservation in a mid-continental region of North America. *Biological Conservation* **142**: 2012–2022.

Hamilton, J.D. and Johnson, S. 2002. *Playing with Fire: Climate Change in Minnesota.* St. Paul, MN: Minnesotans for an Energy-Efficient Economy.

Kling, G.W., et al. 2003. *Confronting Climate Change in the Great Lakes Region: Impacts on our Communities and Ecosystems.* Washington, DC: Union of Concerned Scientists and Ecological Society of America.

Mommer, L. and Visser, E.J.W. 2005. Underwater photosynthesis in flooded terrestrial plants: a matter of leaf plasticity. *Annals of Botany* **96**: 581–589.

Pastor, J. and Post, W.M. 1988. Response of northern forests to CO_2-induced climate change. *Nature* **334**: 55–58.

Pedersen, O., Malik, A., and Colmer, T.D. 2010. Submergence tolerance in *Hordeum marinum*: dissolved CO_2 determines underwater photosynthesis and growth. *Functional Plant Biology* **37**: 524–531.

Ram, P.C., Singh, A.K., Singh, B.B., Singh, V.K., Singh, H.P., Setter, T.L., Singh, V.P., and Singh, R.K. 1999. Environmental characterization of floodwater in Eastern India: relevance to submergence tolerance of lowland rice. *Experimental Agriculture* **35**: 141–152.

Setter, T.L., Kupkanchanakul, T., Kupkanchankul, K., Bhekasut, P., Wiengweera, A., and Greenway, H. 1987. Concentrations of CO_2 and O_2 in floodwater and in internodal lacunae of floating rice growing at 1–2 meter water depths. *Plant, Cell and Environment* **10**: 767–776.

Setter, T.L., Waters, I., Wallace, I., Bhekasut, P., and Greenway, H. 1989. Submergence of rice. I. Growth and photosynthetic response to CO_2 enrichment of floodwater. *Australian Journal of Plant Physiology* **16**: 251–263.

Voesenek, L.A.C.J., Colmer, T.D., Pierik, R., Millenaar, F.F., and Peeters, A.J.M. 2006. How plants cope with complete submergence. *New Phytologist* **170**: 213–226.

Wertin, T.M., McGuire, M.A., and Teskey, R.O. 2010. The influence of elevated temperature, elevated atmospheric CO_2 concentration and water stress on net photosynthesis of loblolly pine (*Pinus taeda* L.) at northern, central and southern sites in its native range. *Global Change Biology* **16**: 2089–2103.

Wyckoff, P.H. and Bowers, R. 2010. Response of the prairie-forest border to climate change: impacts of increasing drought may be mitigated by increasing CO_2. *Journal of Ecology* **98**: 197–208.

7.6. Ecosystem Biodiversity

How will the biodiversity of Earth's ecosystems respond to predicted changes in the planet's climate? This question is among the top concerns about potential CO_2-induced global warming, and it has been addressed in several different ways.

Studying the direct effects of elevated CO_2 itself, Lau et al. (2010) grew thale cress (*Arabidopsis thaliana*) either alone or together with the C_3 grass *Bromus inermis* or the C_4 grass *Andropogon gerardii* in small pots placed within open-field FACE arrays at the Cedar Creek Ecosystem Science Reserve, Minnesota (USA). These were maintained at atmospheric CO_2 concentrations of either 368 or 560 ppm from the time of emergence to the time of plant senescence. At the time of harvest, the CO_2-induced stimulation of *A. thaliana* biomass was approximately 42 percent when it was grown alone, but 46 percent when it was grown together with *A. gerardii* and 50 percent when grown together with *B. inermis,* while corresponding stimulation values were 1 percent, 3 percent, and 4 percent for leaf number; 15 percent, 17 percent, and 21 percent for plant height; 11 percent, 21 percent, and 20 percent for stem number; and 25 percent, 43 percent, and 39 percent for fruit number. All of this indicates greater CO_2-induced benefits for *A. thaliana* when grown in competitive mixtures with other species. Lau et al. conclude, "elevated CO_2 reduces the effects of competition on mean fitness ... and minimizes the strength of competition as a selective agent." Therefore, it may logically be expected (all else being equal) that ecosystem species richness or biodiversity should at least remain stable, or possibly even increase, in response to continued increases in the air's CO_2 content.

In a related study, Peter B. Reich of the University of Minnesota (2009) wrote, "levels of N [nitrogen] deposition and CO_2 have risen in recent decades and are expected to increase further," and in the case of natural ecosystems, he writes, "the suppression of diversity by increasing N availability is almost ubiquitous," while stating "evidence of CO_2 effects on species richness is scarce and shows mixed results, with positive, neutral, and negative responses seen in the few published reports."

In what Collins (2009) appropriately describes as "a rare gem in long-term ecological research," Reich presided over the ten-year-long BioCON study conducted at the Cedar Creek Long-Term Ecological Research site, where, as Reich describes it, "species richness was measured in 48 experimental grassland plots (each 2 m by 2 m) planted in 1997 with 16 perennial species [four species from each of four functional groups (C_4 grasses, C_3 grasses, legumes and non-legume forbs)] and treated since 1998 with all combinations of ambient and elevated atmospheric CO_2 (ambient and +180 ppm delivered by means of a free-air CO_2 enrichment technique) and ambient and enriched N (ambient and +4 g N m^{-2} $year^{-1}$ delivered as ammonium nitrate in three equal doses each year)," while several plant physiological processes and properties were measured throughout each growing season.

Reich found that at the ambient soil N concentration, elevated CO_2 had minimal impact on observed species richness (-2 percent), while at the ambient atmospheric CO_2 concentration, elevated N decreased species richness by fully 15 percent over the last seven years of the ten-year-long study. But when the elevated soil N concentration was combined with the elevated atmospheric CO_2 concentration, species richness declined by only 5 percent, leading Reich to conclude, "elevated CO_2 reduces losses of plant diversity caused by nitrogen deposition." This was such an important finding that he made it the title of his paper. With levels of nitrogen deposition "expected to increase further," as Reich notes, the Earth's natural ecosystems will benefit from the fact that the atmosphere's CO_2 concentration is rising in tandem with the increasing level of N deposition that is being experienced throughout the world.

Regarding possible indirect effects of rising CO_2 concentrations, some researchers contend that CO_2-induced global warming will be so fast and furious that many species of plants will not be able to migrate poleward in latitude or upward in altitude at rates required to keep them within the geographically shifting temperature regimes to which they have been adapted. Thus, they claim, many species will be driven to extinction, and the species richness of various ecosystems will be greatly reduced.

As some examples of these contentions, Dyer (1995) wrote, "the magnitude of the projected warming is considerable" and "the rate at which it is predicted to occur is unprecedented," and consequently, "there is genuine reason for concern that the extent of range shifts will exceed the dispersal abilities of many plant species." Malcolm and Markham (2000) similarly wrote, "rapid rates of global warming are likely to increase rates of habitat loss and species extinction," and "many species may be unable to shift their ranges fast enough to keep up with global warming." Malcolm et al. (2002) added, "migration rates required by the warming are unprecedented by historical standards, raising the possibility of extensive, and in many cases, catastrophic, species loss." In his 26 April 2007 testimony to the Select Committee of Energy Independence and Global Warming of the United States House of Representatives, NASA's James Hansen echoed these fears, saying "greenhouse gas emissions threaten many ecosystems," contending "very little additional forcing is needed ... to cause the extermination of a large fraction of plant and animal species," claiming "polar species can be pushed off the planet, as they have no place else to go," and stating “life in alpine regions ... is similarly in danger of being pushed off the planet.”

An enlightening reality check on these doomsday scenarios was provided by Le Roux and McGeoch (2008), who examined patterns of altitudinal range changes in the totality of the native vascular flora of sub-Antarctic Marion Island (46°54’S, 37°45’E) in the southern Indian Ocean, which warmed by 1.2°C between 1965 and 2003. These South African researchers found that between 1966 and 2006, there was “a rapid expansion in altitudinal range,” with species expanding their upper elevational boundaries by an average of 70 meters. And because, as they describe it, “the observed upslope expansion was not matched by a similar change in lower range boundaries,” they emphasize “the flora of Marion Island has undergone range expansion rather than a range shift,” noting “the expansion of species distributions along their cooler boundaries in response to rising temperatures appears to be a consistent biological consequence of recent climate warming,” citing references to several other studies that have observed the same type of response.

An important consequence of the stability of lower-range boundaries of species together with expanding upper-range boundaries is a greater overlapping of ranges, which results in greater local species richness or biodiversity everywhere up and down various altitudinal transects. As a further consequence, le Roux and McGeoch indicate “the present species composition of communities at higher altitudes is not an analogue of past community composition at lower altitudes, but rather constitutes a historically unique combination of species,” a new world significantly richer in species in a greater number of locations than in the recent past.

Working on the outskirts of Jena, Germany, Steinbeiss et al. (2008) sowed 20-m by 20-m plots of soil with seeds of either one, two, four, eight, 16, or 60 species of either one, two, three, or four plant functional groups (grasses, small herbs, tall herbs, and legumes), creating 16 replicate plots per species level except for the 16-species level plots (14 replicates) and the 60-species level plots (four replicates) in April 2002, just before soil carbon content sampling was performed, and after which similar sampling was repeated in April 2004 and April 2006.

During the first two years of their study, soil carbon storage was limited to the top 5 cm of soil, while below 10 cm depth, carbon was actually lost. After four years, however, carbon stocks had increased significantly within the top 20 cm of the soil. However, and “more importantly,” in the words of Steinbeiss et al., “carbon storage significantly increased with sown species richness in all depth segments and even carbon losses were significantly smaller with higher species richness.” Consequently, they concluded, “plant species richness ... accelerate[d] the build-up of new carbon pools within four years,” and “higher plant diversity mitigated soil carbon losses in deeper horizons.”

The researchers state their findings suggest “higher biodiversity might lead to higher soil carbon sequestration in the long-term,” and, therefore, “the conservation of biodiversity might play a role in greenhouse gas mitigation.” It also should be added that this phenomenon represents a previously unrecognized negative feedback, since studies such as that of Le Roux and McGeoch have demonstrated global warming typically leads to higher local and regional biodiversity wherever the process has been studied throughout the world.

The study of Odland et al. (2010) provides what can be seen as the icing on the cake when it comes to refuting James Hansen’s wild contention of mountaintop species being “pushed off the planet” by global warming. Based on their documentation of plant species diversity on 13 mountain summits in southern Norway—in a reenactment of what Lye (1973) had done more than three decades earlier—and their assessment of regional warming over the intervening years, the three scientists sought to ascertain how plant species richness may have changed in response to what turned out to have been a significant increase in local temperatures. They found average summer temperatures had risen by approximately 1.3°C between the times of the two studies, and over that period plant taxa richness had risen by an average of 90 percent, with two of the summits experiencing increases of fully 200 percent.

Odland et al. state the average rise they identifed “is in accordance with similar studies in both Scandinavia and southern Europe (Kullman, 2007a,b; Parmesan, 2005; Pauli et al., 2007),” but the 200 percent increase in taxa richness they documented on two of the summits “is exceptional.” And because the latter result is also true, it can validly be called an exceptional truth. And giving credit where credit is due, the three Norse researchers conclude “the present increase in species richness is mainly a result of recent climatic change.”

Not all ecosystems, however, respond so dramatically to warming, though still positively, as evidenced by the study of Hudson and Henry (2010). They employed open-top chambers to passively warm an evergreen-shrub heath, which was dominated by several shrub species and bryophytes, by 1.0–1.3°C over a period of 15 years (when there was also a significant background warming) in the vicinity of Alexandra Fiord, Nunavut, Canada (79°N). In what they describe as "the longest-running passive warming experiment in the Canadian Arctic," the two University of British Columbia researchers found "experimental warming did not strongly affect vascular plant cover, canopy height or species diversity, but it did increase bryophyte cover by 6.3% and decrease lichen cover by 3.5%," although they note "temporal changes in plant cover were more frequent and of greater magnitude than changes due to experimental warming." These findings thus prompted them to state, "this evergreen-shrub heath continues to exhibit community-level resistance to long-term experimental warming."

In about the only logical conclusion that could be reached on the basis of their observations, Hudson and Henry state their findings "support the view that only substantial climatic changes will alter unproductive ecosystems," such as the one they studied. In further support of this statement they note other plant communities also have "exhibited strong resistance to simulated climate change manipulations (e.g. Grime et al., 2008), where resistance is defined as the ability of a community to maintain its composition and structure in the face of environmental change." They amplify this conclusion by stating, "at other Arctic sites, lichen, bryophyte and evergreen-shrub dominated heaths were [also] less responsive to experimental warming than other plant communities," citing the studies of Hollister et al. (2005), Jonsdottir et al. (2005), and Wahren et al. (2005).

In the first of two studies of an agricultural crop that looks at the phenomenon in question from a very different point of view, Yang et al. (2009) write, "rice (*Oryza sativa* L.) is unequivocally one of the most important food crops that feed the largest proportion of the world's population," and they note "the demand for rice production will continue to increase in the coming decades, especially in the major rice-consuming countries of Asia, Africa and Latin America, due to the population explosion and cropland reduction." Hence, they state "as sufficient intraspecific variation in yield response [of rice] exists under field conditions, there is a pressing need to identify genotypes which would produce maximum grain yield under projected future CO_2 levels." In other words, they are looking to go beyond nature in determining what will grow where, in order to take best advantage of what Earth's changing environment has to offer.

Working with that same goal in mind at the National Institute for Agro-Environmental Sciences in Tsukuba, Japan, Lou et al. (2008) grew plants of four different rice cultivars—Dular (a traditional indica variety), IR72 (an improved indica variety), Koshihikari (a temperate japonica variety), and IR65598 (a new variety not yet released to farmers)—within growth chambers in submerged pots filled with a fertilized soil collected from the plough layer of a paddy field in Chiba Prefecture, Japan, at two atmospheric CO_2 concentrations: ambient (~370 ppm) and elevated (~570 ppm). This protocol revealed the extra 200 ppm of CO_2 reduced the ultimate grain yield of Dular (by 0.7 percent), while it increased the final grain yield of IR72 by 8.0 percent, that of Koshihikari by 13.4 percent, and that of IR65598 by 17.7 percent.

Shortly thereafter—working at the FACE facility at Yangzhou City, Jiangsu Province, China—Yang et al. (2009) focused on a single two-line inter-subspecific hybrid rice variety (Liangyoupeijiu), produced as part of "a nationwide mega project" to develop what they call "super" hybrid cultivars that would "further break the yield ceiling." In their three-year CO_2-enrichment study, which employed the same CO_2 levels as the study of Lou et al., they found a much greater grain yield stimulation: a 28.4 percent CO_2-induced increase under a low nitrogen fertility treatment of 12.5 g N m^{-2} and a 31.7 percent CO_2-induced increase under a high nitrogen fertility treatment of 25 g N m^{-2}.

In discussing their findings, Yang et al. state their hybrid cultivar "appears to profit much more from elevated CO_2 than inbred japonica cultivars," which does indeed seem to be the case, as both Japanese and Chinese FACE studies of inbred japonica cultivars have found CO_2-induced grain yield enhancements only on the order of 13 percent for a 200 ppm increase in the air's CO_2 concentration. Therefore, noting "there is a pressing need to identify genotypes which could optimize harvestable yield as atmospheric CO_2 increases," Yang et al. conclude, "on the basis of available FACE data on rice," the hybrid rice cultivar Liangyoupeijiu "appears to be particularly promising."

References

Collins, S.L. 2009. Biodiversity under global change. *Science* **326**: 1353–1354.

Dyer, J.M. 1995. Assessment of climatic warming using a model of forest species migration. *Ecological Modelling* **79**: 199–219.

Grime, J.P., Fridley, J.D., Askew, A.P., Thompson, K., Hodgson, J.G. and Bennett, C.R. 2008. Long-term resistance to simulated climate change in an infertile grassland. *Proceedings of the National Academy of Sciences of the United States ofAmerica* **105**: 10028–10032.

Grime, J.P., Brown, V.K., Thompson, K., Masters, G.J., Hillier, S.H., Clarke, I.P., Askew, A.P., Corker, D., and Kielty, J.P. 2000. The response of two contrasting limestone grasslands to simulated climate change. *Science* **289**: 762–765.

Hollister, R.D., Webber, P.J., and Tweedie, C.E. 2005. The response of Alaskan arctic tundra to experimental warming: differences between short- and long-term responses. *Global Change Biology* **11**: 525–536.

Hudson, J.M.G. and Henry, G.H.R. 2010. High Arctic plant community resists 15 years of experimental warming. *Journal of Ecology* **98**: 1035–1041.

Jonsdottir, I.S., Magnusson, B., Gudmundsson, J., Elmarsdottir, A., and Hjartarson, H. 2005. Variable sensitivity of plant communities in Iceland to experimental warming. *Global Change Biology* **11**: 553–563.

Kullman, L. 2007a. Long-term geobotanical observations of climate change impacts in the Scandes of West-Central Sweden. *Nordic Journal of Botany* **24**: 445–467.

Kullman, L. 2007b. Modern climate change and shifting ecological sates of the subalpine/alpine landscape in the Swedish Scandes. *Geooko* **28**: 187–221.

Lau, J.A., Shaw, R.G., Reich, P.B., and Tiffin, P. 2010. Species interactions in a changing environment: elevated CO_2 alters the ecological and potential evolutionary consequences of competition. *Evolutionary Ecology Research* **12**: 435–455.

Le Roux, P.C. and McGeoch, M.A. 2008. Rapid range expansion and community reorganization in response to warming. *Global Change Biology* **14**: 2950–2962.

Lou, Y., Inubushi, K., Mizuno, T., Hasegawa, T., Lin, Y., Sakai, H., Cheng, W., and Kobayashi, K. 2008. CH_4 emission with differences in atmospheric CO_2 enrichment and rice cultivars in a Japanese paddy soil. *Global Change Biology* **14**: 2678–2687.

Lye, K.A. 1973. The vascular plants on alpine peaks at Filefjell, south Norway. *Norwegian Journal of Botany* **20**: 51–55.

Malcolm, J.R., Liu, C., Miller, L.B., Allnutt, T., and Hansen, L. 2002. *Habitats at Risk: Global Warming and Species Loss in Globally Significant Terrestrial Ecosystems.* Gland, Switzerland: World Wide Fund for Nature.

Malcolm, J.R. and Markham, A. 2000. *Global Warming and Terrestrial Biodiversity Decline.* Gland, Switzerland: World Wide Fund for Nature.

Odland, A., Hoitomt, T., and Olsen, S.L. 2010. Increasing vascular plant richness on 13 high mountain summits in southern Norway since the early 1970s. *Arctic, Antarctic, and Alpine Research* **42**: 458–470.

Parmesan, C. 2005. Biotic response: range and abundance changes. In *Climate Change and Biodiversity*, edited by T.E. Lovejoy and H. Lee, H. 41–55. New Haven, CT and London, UK: Yale University Press.

Pauli, H., Gottfried, M., Reiter, K., and Grabherr, G. 2007. Signals of range expansions and contractions of vascular plants in the high Alps: observations 1994–2004 at the GLORIA master site Schrankogel, Tyrol, Austria. *Global Change Biology* **13**: 147–156.

Reich, P.B. 2009. Elevated CO_2 reduces losses of plant diversity caused by nitrogen deposition. *Science* **326**: 1399–1402.

Steinbeiss, S., Bessler, H., Engels, C., Temperton, V.M., Buchmann, N., Roscher, C., Kreutziger, Y., Baade, J., Habekost, M., and Gleixner, G. 2008. Plant diversity positively affects short-term soil carbon storage in experimental grasslands. *Global Change Biology* **14**: 2937–2949.

Wahren, C.H.A., Walker, M.D., and Bret-Harte, M.S. 2005. Vegetation responses in Alaskan arctic tundra after 8 years of a summer warming and winter snow manipulation experiment. *Global Change Biology* **11**: 537–552.

Yang, L., Liu, H., Wang, Y., Zhu, J., Huang, J., Liu, G., Dong, G., and Wang, Y. 2009. Yield formation of CO_2-enriched inter-subspecific hybrid rice cultivar Liangyoupeijiu under fully open-air condition in a warm sub-tropical climate. *Agriculture, Ecosystems and Environment* **129**: 193–200.

7.7. Soil Carbon Sequestration

7.7.1. Agricultural Crops

According to Martens et al. (2009), "the generally higher above and belowground productivity of C_3 plants under elevated CO_2 leads to the conclusion that more rhizodepositions (roots and exudates) are transferred into soils, potentially increasing soil carbon content," but they note most free-air CO_2-enrichment (FACE) and outdoor chamber studies have failed to detect significant changes in soil organic carbon (SOC) due to the typically large amount and spatially heterogeneous nature of pre-existing SOC. In an attempt to overcome these difficulties, they cultivated well-watered and -fertilized spring wheat (cv. Minaret) within stainless steel cylinders forced into the soil of control and free-air CO_2-enriched (to 180 ppm above ambient) FACE plots at the experimental farm of the Federal Research Institute in Braunschweig, Germany. Between stem elongation and beginning of ripening the plants were repeatedly pulse-labelled with $^{14}CO_2$ and thereafter monitored daily for soil-borne total CO_2 and $^{14}CO_2$ until harvest, after which the distribution of ^{14}C was analyzed in all plant parts, soil, soil mineral fractions, and soil microbial biomass.

The researchers found, "in comparison to ambient conditions, 28% more $^{14}CO_2$ and 12% more total CO_2 was evolved from soil under elevated CO_2," and "in the root-free soil 27% more residual ^{14}C was found in the free-air CO_2-enriched soil than in the soil from the ambient treatment." In addition, in soil samples from both treatments about 80 percent of residual ^{14}C was "integrated into the stable, clay bound soil organic matter pool," which suggests, in the researchers' words, that "under FACE conditions a considerable contribution was made to the long-term storage of soil carbon in this soil." By these means, Martens et al. state they were able to "show for the first time," as they describe it, "that a crop plant grown under FACE conditions deposited significantly more carbon to soil than those grown under ambient CO_2 in the field," and "the additional carbon input under elevated CO_2 did not induce an accelerated degradation of pre-existing soil organic matter (no positive priming effect)," thereby indicating "wheat plants grown under elevated CO_2 can contribute to an additional net carbon gain in soils."

Reference

Martens, R., Heiduk, K., Pacholski, A., and Weigel, H.-J. 2009. Repeated $^{14}CO_2$ pulse-labelling reveals an additional net gain of soil carbon during growth of spring wheat under free air carbon dioxide enrichment (FACE). *Soil Biology & Biochemistry* **41**: 2422–2429.

7.7.2. Grasslands

Shifting from agricultural fields to grasslands, Adair et al. (2009) employed mass balance calculations to quantify the effects of biodiversity, atmospheric CO_2 concentration, and soil nitrogen content on the total amount of carbon (C) allocated belowground by plants (total belowground C allocation or TBCA), as well as ecosystem C storage, in an eight-year experiment that was part of the BioCON study of a periodically burned Minnesota grassland. They found annual TBCA increased in response to all three treatment variables—"elevated CO_2, enriched N, and increasing diversity"—and it also was "positively related to standing root biomass." Upon removing the influence of root biomass, however, they found the effects of N and diversity became neutral or even negative (depending on the year), but "the effect of elevated CO_2 remained positive." In the case of years with fire, they found "greater litter production in high diversity, elevated CO_2, and enhanced nitrogen treatments increased annual ecosystem C loss." Given these findings, it would appear that under normal, non-fire conditions, increasing CO_2 concentrations, nitrogen deposition, and increasing biodiversity generally tend to increase ecosystem carbon gain; but if grasslands are frequently burned, they could remain neutral in this regard.

Halfway around the world, in a temperate steppe grassland located in Duolun County, Inner Mongolia, China, Wan et al. (2009) suspended infrared radiators 2.25 meters above the ground over 24 plots divided into four temperature treatments—(1) control, (2) day (06:00–18:00, local time) warming, (3) night (18:00–06:00) warming, and (4) diurnal (24-hour) warming—after which they measured diurnal cycles of net ecosystem gas exchange and daytime ecosystem respiration twice a month over the growing seasons (May–October) of 2006, 2007, and 2008. They found "nocturnal warming increased leaf respiration of two dominant grass species by 36.3%, enhanced consumption [drawdown] of carbohydrates in the leaves (72.2% and 60.5% for sugar and starch, respectively), and consequently stimulated plant photosynthesis by 19.8% in the subsequent days." In addition, they write, "the enhancement of plant photosynthesis overcompensated the increased carbon loss via plant respiration under nocturnal warming and shifted the steppe ecosystem from a minor carbon source (1.87 g C/m^2/year) to a carbon sink (21.72 g C/m^2/year) across the three growing seasons."

In addition, the four researchers report the local climate in their study area "experienced asymmetrical diurnal warming (0.57, 0.45 and 0.30°C increases in daily minimum, mean and maximum temperatures per decade, respectively) over the past half century (1953–2005)," and "similar diurnal scenarios of climate warming have been widely reported at the regional and global scales," citing the studies of Karl et al. (1991), Easterling et al. (1997), Stone and Weaver (2002), Vose et al. (2005), Lobell et al. (2007), and Zhou et al. (2007). Consequently, and in light of the many well-documented cases of "greater increases in daily minimum than maximum temperature" that they say have been observed throughout the world, Wan et al. conclude, "plant photosynthetic overcompensation may partially serve as a negative feedback mechanism for [the] terrestrial biosphere to climate warming," where "the photosynthetic overcompensation induced by nocturnal warming can ... regulate terrestrial carbon sequestration and negatively feed back to climate change."

Also working in China, Yang et al. (2010) conducted five consecutive regional soil surveys of that country's grasslands during 2001–2005 and sampled 981 soil profiles from 327 sites across the northern part of the country. They then compared their results with data of 275 soil profiles derived from China's National Soil Inventory during the 1980s. This work indicated the organic carbon stock in the upper 30 cm of soil in northern China's grasslands "did not show significant association with mean annual temperature, but was positively correlated with mean annual precipitation," reaching a plateau when soil moisture was above 30 percent. And in perhaps their most important observation, they found "grassland soil organic carbon stock did not change significantly over the past two decades, with a change of 0.08 kg carbon per m^2, ranging from -0.30 to +0.46 kg carbon per m^2 at 95% confidence interval."

In discussing their findings, Yang et al. write, "it has been often asserted that soil will act as a carbon source because of its sensitivity to global environmental change (e.g., Melillo et al., 2002; Bellamy et al., 2005; Schipper et al., 2007)," but "in contrast to these previous reports, our results indicate that soil organic carbon stock in northern China's grasslands has not experienced significant changes during the past two decades, despite measureable climate change," i.e., global warming. Hence, there is very good reason (i.e., real-world data) not to believe "climate warming is likely to accelerate the decomposition of soil organic carbon which could lead to increased carbon release from soils, providing a positive feedback to climate change," as some have suggested based primarily on theoretical considerations.

In one final study of carbon sequestration in the soils of grasslands, Belay-Tedla et al. (2009) write, "the stability of carbon (C) and nitrogen (N) in soil organic matter (SOM) to perturbations such as global warming is critically important," because "on a global scale, the soil contains 1500 Pg (1 Pg = 10^{15} g) of organic carbon and 300 Pg of total nitrogen" in its uppermost meter, so that "relatively small changes in the amounts of soil C and N may therefore bring about substantial effects on atmospheric concentrations," which in the case of the carbon contained in CO_2 may feed back either positively or negatively to enhance or reduce the original warming of the air.

In an experiment designed to explore these interactions within a specific biome, Belay-Tedla et al. "used sulfuric acid hydrolysis to quantify changes in labile and recalcitrant C and N fractions of soil in a tallgrass prairie ecosystem that had been continuously warmed with or without clipping for about 2.5 years," conducting their work in "an old-field tallgrass prairie abandoned from agriculture 30 years ago and without grazing during the past 20 years" at a location within the Great Plains Apiaries of McClain County, Oklahoma, USA, where infrared heaters suspended 1.5 m above the ground warmed half of the plots 24 hours a day, 365 days a year, for the 2.5-year period, increasing the daily mean air temperature at 25 cm above the ground by 1.1°C and soil temperature at 2.5 cm depth by 2.0°C.

The work of the five researchers revealed, as they describe it, "significant increases in both labile C and N (including microbial biomass) pools in response to experimental warming," which "largely resulted from increased above- and below-ground biomass." They also observed "a possible shift to a fungi-dominated microbial community," noting "such a shift could favor soil C storage" as well. In addition, they found evidence suggesting "warming increased the percentage of total N for microbial biomass N," and they state this enhanced N use efficiency "may be conducive for a continued supply of organic inputs." As a result, Belay-Tedla et al. conclude their combined findings favor "long-term N retention and C accumulation in soils, leading to negative feedbacks of terrestrial ecosystems to climate warming."

References

Adair, E.C., Reich, P.B., Hobbie, S.E., and Knops, J.M.H. 2009. Interactive effects of time, CO_2, N, and diversity on total belowground carbon allocation and ecosystem carbon storage in a grassland community. *Ecosystems* **12**: 1037–1052.

Belay-Tedla, A., Zhou, X., Su, B., Wan, S., and Luo, Y. 2009. Labile, recalcitrant, and microbial carbon and nitrogen pools of a tallgrass prairie soil in the US Great Plains subjected to experimental warming and clipping. *Soil Biology & Biochemistry* **41**: 110–116.

Bellamy, P.H., Loveland, P.J., Bradley, R.I., Lark, R.M., and Kirk, G.J.D. 2005. Carbon losses from all soils across England and Wales 1978-2003. *Nature* **437**: 245–248.

Easterling, D.R., Horton, B., Jones, P.D., Peterson, T.C., Karl, T.R., Parker, D.E., Salinger, M.J., Razuvayev, V., Plummer, N., Jamason, P., and Folland, C.K. 1997. Maximum and minimum temperature trends for the globe. *Science* **277**: 364–367.

Karl, T.R., Kukla, G., Razuvayev, N., Changery, M.J., Quayle, R.G., Heim, R.R., Easterling, D.R., and Fu, C.B. 1991. Global warming—evidence for asymmetric diurnal temperature-change. *Geophysical Research Letters* **18**: 2253–2256.

Lobell, D.B., Bonfils, C., and Duffy, P.B. 2007. Climate change uncertainty for daily minimum and maximum temperatures: a model inter-comparison. *Geophysical Research Letters* **34**: 10.1029/2006GL02872.

Melillo, J.M., Steudler, P.A., Aber, J.D., Newkirk, K., Lux, H., Bowles, F.P., Catricala, C., Magill, A., Ahrens, T., and Morrisseau, S. 2002. Soil warming and carbon-cycle feedbacks to the climate system. *Science* **298**: 2173–2176.

Schipper, L.A., Baisden, T., Parfitt, R.L., Ross, C., and Claydon, J.J. 2007. Large losses of soil C and N from soil profiles under pasture in New Zealand during the past 20 years. *Global Change Biology* **13**: 1138–1144.

Stone, D.A. and Weaver, A.J. 2002. Daily maximum and minimum temperature trends in a climate model. *Geophysical Research Letters* **29**: 10.1029/2001GL014556.

Vose, R.S., Easterling, D.R., and Gleason, B. 2005. Maximum and minimum temperature trends for the globe: an update through 2004. *Geophysical Research Letters* **32**: 10.1029/2005GL024379.

Wan, S., Xia, J., Liu, W., and Niu, S. 2009. Photosynthetic overcompensation under nocturnal warming enhances grassland carbon sequestration. *Ecology* **90**: 2700–2710.

Yang, Y., Fang, J., Ma, W., Smith, P., Mohammat, A., Wang, S., and Wang, W. 2010. Soil carbon stock and its changes in northern China's grasslands from 1980s to 2000s. *Global Change Biology* **16**: 3036–3047.

Zhou, L., Dickinson, R.E., Tian, Y., Vose, R.S., and Dai, Y. 2007. Impact of vegetation removal and soil aridation on diurnal temperature range in a semiarid region: application to the Sahel. *Proceedings of the National Academy of Sciences USA* **104**: 17,937–17,942.

7.7.3. Forests

Moving up from grasslands to forests—literally—Hoosbeek and Scarascia-Mugnozza (2009) report the final soil carbon sequestration results of the POP-EuroFACE experiment conducted on a poplar plantation established in early 1999 on former agricultural fields near Biterbo, Italy, where three control plots and three CO_2-enriched plots (to a target atmospheric concentration of 560 ppm) were each planted with equal-area sections of three *Populus* genotypes: *P. x euramericana* Dode (Guinier) genotype I-214, *P. nigra* L. (Jean Pourtet), and *P. alba* L. (genotype 2AS11). Their final analysis indicated over the course of the six-year study there was an additional mean carbon (C) sink of 32 g C m^{-2} $year^{-1}$ in the forest floor litter layer. In the case of the soil itself, they found over the first half of the experiment the increase in soil carbon was suppressed under FACE, but over the second half of the study they measured an additional mean sink of 54 g C m^{-2} $year^{-1}$ in the top 10 cm of the FACE treatment's mineral soil. This expanded sink was not statistically significant, however, because of a combination of high soil spatial variability and the low number of treatment replicates. Nevertheless, it suggested that if the experiment had been allowed to continue for a longer period of time, the difference likely would have become significant. Last, they report the amount of stabilized soil organic matter increased significantly under FACE. Thus, the two researchers conclude the forest floor as a whole "will serve as an additional carbon sink under future increased atmospheric CO_2 concentrations in poplar stands," which should help to mitigate further increases in the air's CO_2 content and whatever increase in global temperature might possibly cause to occur.

One year later, in the United States, Thomas et al. (2010) wrote, "human activities have greatly accelerated emissions of both carbon dioxide and biologically reactive nitrogen to the atmosphere," and "as nitrogen availability often limits forest productivity, it has long been expected that anthropogenic nitrogen deposition could stimulate carbon sequestration in forests." However, they noted spatially extensive evidence for this phenomenon "has been lacking," and they proceeded to provide some, using "spatially extensive forest inventory data to discern the effect of nitrogen deposition on the growth and survival of the 24 most common tree species of the northeastern and north-central US, as well as the effect of nitrogen deposition on carbon sequestration in trees across the breadth of the northeastern US."

They found "nitrogen deposition (which ranged from 3 to 11 kg ha^{-1} yr^{-1}) enhanced the growth of 11 species and decreased the growth of three species," while it "enhanced growth of all tree species with arbuscular mycorrhizal fungi associations," leading to "a 40% enhancement over pre-industrial conditions." This response "includes the direct effects of nitrogen deposition on tree growth through soil fertilization, foliar nitrogen uptake and other potential interactions between nitrogen deposition and other environmental changes, including CO_2 fertilization." To give some idea of the magnitude of this response, they state it "exceeds the 23% enhancement of net primary production anticipated for the year 2050 from a doubling of atmospheric CO_2 over preindustrial levels, as estimated using free-air CO_2 enrichment studies," citing in this regard Norby et al. (2005).

Thomas et al. thus conclude "nitrogen deposition is an important mechanism contributing to carbon sequestration within these temperate forests," but this phenomenon is still "unlikely to explain all of the observed terrestrial carbon sink." Nevertheless, it does go a long way toward doing so, and it demonstrates the major benefits of the concomitant increases in (1) the air's CO_2 content and (2) the air's temperature, with which (3) the increase in nitrogen deposition interacted over the course of the Industrial Revolution and its aftermath. Therefore, whereas the IPCC considers the increases in the air's CO_2 content and temperature to be two of the worst things ever to have happened to the biosphere, they clearly were not. And neither was the increase in anthropogenic nitrogen deposition, for all three of these phenomena interacted with each other in such a way as to greatly increase the productivity of the Earth's forests.

Finally, in a study of a process that is changing the face of much of the planet, Springsteen et al. (2010) write, "woody plant expansion within grassland ecosystems is a worldwide phenomenon, and dramatic vegetation shifts from grassland to savanna/woodlands have occurred over the past 50–100 years in North America." They note one of the chief factors that has contributed to this phenomenon is believed by many to have been the historical increase in the air's carbon dioxide concentration, as suggested by the studies of Archer et al. (1995), Polley (1997), Bond and Midgley (2000), and Bond et al. (2003). They also indicate that once shrublands are established, they tend to persist for several possible reasons, one of which is a type of feedback phenomenon referred to as islands of fertility, which "occurs when resources accumulate in soils beneath woody plants due to litterfall, interception of wet and dry deposition, nitrogen fixation, and animal droppings," as described by Schlesinger et al. (1990), Archer et al. (1995), Reynolds et al. (1999), and Lopez-Pintor et al. (2006). Springsteen et al. report in this regard, "changes in soil attributes under woody vegetation have been documented in the arid grasslands of the southern Great Plains, including increases in soil carbon and nitrogen," citing Reynolds et al. (1999), Hibbard et al. (2001, 2003), McCulley et al. (2004), Schade and Hobbie (2005), and Liao et al. (2006).

Considering these findings, while working at the USDA-ARS Northern Great Plains Research Laboratory near Mandan, North Dakota (USA), Springsteen et al. examined near-surface (upper 15 cm) soil biogeochemistry along a 42-year (1963–2005) chronosequence, which encompassed grassland, woodland, and grassland-woodland transition zones in a northern Great Plains grassland, to determine the influence of woody plant expansion on soil carbon and nitrogen contents. They report total soil carbon content rose by 26 percent across the chronosequence from grassland to woodland within the 0–15 cm soil depth, while total soil nitrogen content rose by 31 percent. And they observe the rate of woody shrub expansion from 1963 to 1988 (25 years) was ~1,800 m^2 per year at their study site, whereas from 1988 to 2005 (17 years) it was ~3,800 m^2 per year, just a little more than double the rate of the earlier period.

Therefore, as more experiments of this nature are conducted at more sites around the world, it is becoming increasingly evident that soil carbon sequestration driven by woody-plant invasions of grasslands (driven to a significant degree by the ongoing rise in the air's CO_2 content), as well as the increases in soil nitrogen content required to sustain them, are growing with the passage of time as the greening of the Earth continues.

References

Archer, S., Schimel, D.S., and Holland, E.A. 1995. Mechanisms of shrubland expansion: land use, climate or CO_2? *Climatic Change* **29**: 91–99.

Bond, W.J. and Midgley, G.F. 2000. A proposed CO_2-controlled mechanism of woody plant invasion in grasslands and savannas. *Global Change Biology* **6**: 865–869.

Bond, W.J., Midgley, G.F., and Woodward, F.I. 2003. The importance of low atmospheric CO_2 and fire in promoting the spread of grasslands and savannas. *Global Change Biology* **9**: 973–982.

Hibbard, K.A., Archer, S., Schimel, D.S., and Valentine, D.W. 2001. Biogeochemical changes accompanying woody plant encroachment in a subtropical savanna. *Ecology* **82**: 1999–2011.

Hibbard, K.A., Schimel, D.S., Archer, S., Ojima, D.S., and Parton, W. 2003. Grassland to woodland transitions: integrating changes in landscape structure and biogeochemistry. *Ecological Applications* **13**: 911–926.

Hoosbeek, M.R. and Scarascia-Mugnozza, G.E. 2009. Increased litter build up and soil organic matter stabilization in a poplar plantation after 6 years of atmospheric CO_2 enrichment (FACE): final results of POP-EuroFACE compared to other forest FACE experiments. *Ecosystems* **12**: 220–239.

Liao, J.D., Boutton, T.W., and Jastrow, J.D. 2006. Storage and dynamics of carbon and nitrogen in soil physical fractions following woody plant invasion of grassland. *Soil Biology and Biochemistry* **38**: 3184–3196.

Lopez-Pintor, A., Sal, A.G., and Benayas, J.M. R. 2006. Shrubs as a source of spatial heterogeneity—the case of *Retama sphaerocarpa* in Mediterranean pastures of central Spain. *Acta Oecologia* **29**: 247–255.

McCulley, R.L., Archer, S.R., Boutton, T.W., Hons, F.M., and Zuberer, D.A. 2004. Soil respiration and nutrient cycling in wooded communities developing in grassland. *Ecology* **85**: 2804–2817.

Norby, R.J., DeLucia, E.H., Gielen, B., Calfapietra, C., Giardina, C.P., King, S.J., Ledford, J., McCarthy, H.R., Moore, D.J.P., Ceulemans, R., De Angelis, P., Finzi, A.C., Karnosky, D.F., Kubiske, M.E., Lukac, M., Pregitzer, K.S., Scarasci-Mugnozza, G.E., Schlesinger, W.H., and Oren, R. 2005. Forest response to elevated CO_2 is conserved across a broad range of productivity. *Proceedings of the National Academy of Sciences* **102**: 18,052–18,056.

Polley, H.W. 1997. Implications of rising atmospheric carbon dioxide concentration for rangelands. *Journal of Range Management* **50**: 561–577.

Reynolds, J.F., Virginia, R.A., Kemp, P.R., de Soyza, A.G., and Tremmel, D.C. 1999. Impact of drought on desert shrubs: effects of seasonality and degree of resource island development. *Ecological Monographs* **69**: 69–106.

Schade, J.D. and Hobbie, S.E. 2005. Spatial and temporal variation in islands of fertility in the Sonoran Desert. *Biogeochemistry* **73**: 541–553.

Schlesinger, W.H., Reynolds, J.F., Cunningham, G.L., Huenneke, L.F., Jarrell, W.M., Ross, V.A., and Whitford, W.G. 1990. Biological feedbacks in global desertification. *Science* **247**: 1043–1048.

Springsteen, A., Loya, W., Liebig, M., and Hendrickson, J. 2010. Soil carbon and nitrogen across a chronosequence of woody plant expansion in North Dakota. *Plant and Soil* **328**: 369–379.

Thomas, R.Q., Canham, C.D., Weathers, K.C., and Goodale, C.L. 2010. Increased tree carbon storage in response to nitrogen deposition in the US. *Nature Geoscience* **3**: 13–17.

7.7.4. Tundra

It has been hypothesized that if—or when—the frozen soils of Earth's Northern High Latitudes (NHLs, land poleward of 60°N) begin to thaw in response to any new global warming that might occur, the metabolism of soil microbes will be accelerated and the decomposition of soil organic matter will speed up; and it has been further postulated that this, in turn, will lead to an increase in soil organic carbon release to the atmosphere that will amplify global warming.

On the other hand, satellite and phenology studies have shown that during the past several decades the planet's boreal forests have experienced greening and an increase in photosynthetic activity, which extracts carbon (in the form of CO_2) from the atmosphere.

To find some indication as to which of these two outcomes might likely predominate over the course of the twenty-first century, Qian et al. (2010) explored the potential magnitudes of the two competing sets of processes by analyzing the outputs of ten models that took part in the Coupled Carbon Cycle Climate Model Intercomparison Project (C4MIP) of the International Geosphere-Biosphere Program and the World Climate Research Program, all of which, in their words, "used the same anthropogenic fossil fuel emissions from Marland et al. (2005) from the beginning of the industrial period until 2000 and the IPCC SRES A2 scenario for the 2000–2100 period."

According to the three researchers, the ten C4MIP models predicted a mean warming of 5.6°C from 1901 to 2100 in the NHLs, and they state "the NHLs will be a carbon sink of 0.3 ± 0.3 $PgCyr^{-1}$ by 2100." They also state "the cumulative land organic carbon storage is modeled to increase by 38 ± 20 PgC over 1901 levels, of which 17 ± 8 PgC comes from vegetation [a 43 percent increase] and 21 ± 16 PgC from the soil [an 8 percent increase]," noting "both CO_2 fertilization and warming enhance vegetation growth in the NHLs." Consequently, over the course of the current century even the severe warming predicted by current climate models would likely not be a detriment to plant growth and productivity in the NHLs. In fact, it would likely be a benefit, enhancing plant growth and soil organic carbon storage, which (in addition to their own virtues) would provide a significant negative feedback to global warming.

As background for their study of the subject, Bao et al. (2010) write that peatland ecosystems "play a key role in the global carbon cycle and are influenced by global climate change," within which context the some researchers say the ongoing warming of the planet will lead to great releases of previously sequestered carbon to the atmosphere in the form of CO_2 and methane. This, they argue, will greatly exacerbate global warming, as was declared quite prominently and publicly to be a confirmed fact by former U.S. Vice President Al Gore in his 21 March 2007 testimony before the U.S. Senate's Environment and Public Works Committee. But, of course, he was wrong, as is clear from the work cited above and will be clear from the work cited below.

Working in the Changbai mountain region that runs along the boundary between China and North Korea, Bao et al. extracted eight peat cores they analyzed for numerous parameters, among which were those required to calculate the recent rate of carbon accumulation (RERCA) in the peatlands of that region over the past two centuries. The four researchers report "obvious increasing trends in RERCA were observed in all peat cores," as "organic carbon content declined from the top to the substrate." What is more, they state the temporal increase in RERCA in the upper regions of the cores—which likely corresponded to the warmest segment of their two-century study period—"changed to a much greater extent in recent decades than in the earlier period of peat formation."

Consequently, this study indicates that researchers who raise concerns over warming peatlands have got things 180 degrees out of phase with reality. Earth's peatlands provide a *negative* feedback to global warming, whereby when they warm, they extract more—not less—CO_2 from the atmosphere, applying a brake on rising temperatures.

Blok et al. (2010) likewise note there are "fears" that if Earth's permafrost thaws, "much of the carbon stored will be released to the atmosphere," as will great quantities of the greenhouse gas methane, further exacerbating warming, as has been claimed is already happening—and at an accelerating rate—by Michael Mann and Lee Kump (2008) in their *Dire Predictions* book. Quite to the contrary, however, Blok et al. state "it has been demonstrated that increases in air temperature sometimes lead to vegetation changes that offset the effect of air warming on soil temperature," citing the research of Walker et al. (2003) and Yi et al. (2007) as specific examples of this phenomenon.

Exploring the subject in real-world experimentation, Blok et al. conducted a study within the Kytalyk nature reserve in the Indigirka lowlands of northeastern Siberia (Russia), where they measured the thaw depth or active layer thickness (ALT) of the soil, the ground heat flux, and the net radiation in ten-meter-diameter plots either possessing or not possessing a natural cover of bog birch (*Betula nana*) shrubs, the latter of which set of plots had all *B. nana* shrubs removed from their native tundra vegetation in 2007.

The Dutch, Swiss, and Russian researchers state the "experimental *B. nana* removal had increased ALT significantly by an average of 9% at the end of the 2008 growing season, compared with the control plots," which implies reduced warming in the more shrub-dominated plots, and "in the undisturbed control plots with varying natural *B. nana* cover, ALT decreased with increasing *B. nana* cover," also "showing a negative correlation between *B. nana* cover and ALT," which again implies reduced warming in the more shrub-dominated plots.

Blok et al. state their results suggest "the expected expansion of deciduous shrubs in the Arctic region, triggered by climate warming, may reduce summer permafrost thaw," and the "increased shrub growth may thus partially offset further permafrost degradation by future temperature increases." In further support of their conclusion, the six scientists note (1) permafrost temperature records "do not show a general warming trend during the last decade (Brown and Romanovsky, 2008), despite large increases in surface air temperature," (2) during the decade before that, "data from several Siberian Arctic permafrost stations do not show a discernible trend between 1991 and 2000 (IPCC, 2007)," and (3) "a recent discovery of ancient permafrost that survived several warm geological periods suggests that vegetation cover may help protect permafrost from climate warming (Froese et al., 2008)." And finally, they note this phenomenon "could feedback negatively to global warming, because the lower soil temperatures in summer would slow down soil decomposition and thus the amount of carbon released to the atmosphere."

Zhuang et al. (2010) used a process-based biogeochemistry model—the Terrestrial Ecosystem Model or TEM, which also employed a soil thermal model—to examine permafrost dynamics and their effects on the carbon dynamics of the Tibetan Plateau over the past century. This was done by "parameterizing and verifying" the TEM using existing real-world data for soil temperature, permafrost distribution, and carbon and nitrogen distributions throughout the region, and then extrapolating the model and its parameters to the whole of the plateau. The six scientists found "during the 20th century, the Tibetan Plateau changed from a small carbon source or neutral in the early part of the century to a sink later," such that "net primary production and soil respiration increased by 0.52 and 0.22 Tg C/year, respectively, resulting in a regional carbon sink increase of 0.3 Tg C/year." Thus, "by the end of the century, the regional carbon sink reached 36 Tg C/year," and carbon storage in vegetation and soils was 32 and 16 Pg C, respectively.

In explaining their findings, Zhuang et al. state the "increasing soil temperature and deepening active layer depth enhanced soil respiration, increasing the net nitrogen mineralization rate," and "together with the [positive] effects of warming air temperature and rising CO_2 concentrations on photosynthesis, the stronger plant nitrogen uptake due to the enhanced available nitrogen stimulate[d] plant carbon uptake, thereby strengthening the regional carbon sink as the rate of increase in net primary production was faster than that of soil respiration." Thus, they state their study implies "future warming will increase thawing of the permafrost, increase soil temperature and dry up soil moisture," and "these physical dynamics may enhance [the] future strength of the regional carbon sink, since the rate of increase of net primary production is higher than that of soil respiration on the Tibetan Plateau."

References

Bao, K., Yu, X., Jia, L., and Wang, G. 2010. Recent carbon accumulation in Changbai Mountain peatlands, northeast China. *Mountain Research and Development* **30**: 33–41.

Blok, D., Heijmans, M.M.P.D., Schaepman-Strub, G., Kononov, A.V., Maximov, T.C., and Berendse, F. 2010. Shrub expansion may reduce summer permafrost thaw in Siberian tundra. *Global Change Biology* **16**: 1296–1305.

Brown, J. and Romanovsky, V.E. 2008. Report from the International Permafrost Association: state of permafrost in the first decade of the 21st century. *Permafrost and Periglacial Processes* **19**: 255–260.

Froese, D.G., Westgate, J.A., Reyes, A.V., Enkin, R.J., and Preece, S.J. 2008. Ancient permafrost and a future, warmer Arctic. *Science* **321**: 1648.

IPCC. 2007. In *Intergovernmental Panel on Climate Change. Fourth Assessment Report: Working Group I Report "The Physical Science Basis,"* edited by S. Solomon, et al. Cambridge, UK: Cambridge University Press.

Mann, M.E. and Kump, L.R. 2008. *Dire Predictions: Understand Global Warming.* New York, NY: DK Publishing Inc.

Marland, G., Boden, T.A., and Andres, R.J. 2005. Global, regional, and national CO_2 emissions. In *Trends: A Compendium of Data on Global Change.* Oak Ridge, TN: Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, U.S. Department of Energy. Available at http://cdiac.ornl.gov/trends/emis/overview.html.

Qian, H., Joseph, R., and Zeng, N. 2010. Enhanced terrestrial carbon uptake in the Northern High Latitudes in the 21st century from the Coupled Carbon Cycle Climate Model Intercomparison Project model projections. *Global Change Biology* **16**: 641–656.

Walker, D.A., Jia, G.J., Epstein, H.E., Raynolds, M.K., Chapin III, F.S., Copass, C., Hinzman, L.D., Knudson, J.A., Maier, H.A., Michaelson, G.J., Nelson, F., Ping, C.L., Romanovsky, V.E., and Shiklomanov, N. 2003. Vegetation-soil-thaw-depth relationships along a low-arctic bioclimate gradient, Alaska: synthesis of information from the ATLAS studies. *Permafrost and Periglacial Processes* **14**: 103–123.

Yi, S., Woo, M., and Arain, M.A. 2007. Impacts of peat and vegetation on permafrost degradation under climate warming. *Geophysical Research Letters* **34**: 10.1029/2007GL030550.

Zhuang, Q., He, J., Lu, Y., Ji, L., Xiao, J., and Luo, T. 2010. Carbon dynamics of terrestrial ecosystems on the Tibetan Plateau during the twentieth century: an analysis with a process-based biogeochemical model. *Global Ecology and Biogeography* **19**: 649–662.

7.7.5. Urban Areas

Working in Europe, Trusilova and Churkina (2008) analyzed carbon sink dynamics driven by urbanization-induced changes in land use, climate, atmospheric CO_2 concentration, and nitrogen deposition. They used the BIOME-BGC terrestrial ecosystem model to calculate responses of the local biosphere to these several “urban changes” applied individually and together. Some examples of the four classes of urban-induced environmental changes considered in this approach are (1) for land use, pristine soils and their associated vegetation being replaced by buildings, roads, parking lots, etc.; (2) for climate, increases in temperature due to the urban heat island phenomenon, together with associated changes in local precipitation; (3) for atmospheric CO_2 concentration, increases in the air’s CO_2 content from vehicle exhaust and other combustion processes that produce the urban CO_2 dome phenomenon; and (4) for nitrogen deposition, many of the same processes that simultaneously release nitrogen to the air.

Trusilova and Churkina found “fertilization effects from the elevated CO_2 and atmospheric nitrogen deposition made the strongest positive contributions to the carbon uptake (0.023 PgC per year and 0.039 PgC per year, respectively), whereas the impervious urban land and local urban meteorological conditions resulted in a reduction of carbon uptake (-0.005 PgC per year and -0.007 PgC per year, respectively).” The synergetic effect of the four urbanization-induced changes, however, “was an increase of the carbon sequestration in Europe of 0.058 PgC per year,” a result greater than the algebraic sum of the four individual components of the carbon sequestration equation. This amplification of the two positive responses (which manifests itself when the two phenomena occur in unison) happens because “atmospheric CO_2 and soil nitrogen availability co-limit [the] productivity of land ecosystems,” as the two researchers describe it, so that if more nitrogen becomes available to plants, the aerial fertilization effect of the elevated CO_2 concentration is generally magnified. Another reason for the dominance of the CO_2- and nitrogen-induced phenomena is that “the land use and urban climate changes affect rather small land areas while the urban CO_2 and nitrogen pollution spread over larger areas.”

When all is said and done, therefore, it is clear—although perhaps not intuitively so—that the urbanization process actually leads to an amplification of carbon sequestration in the vegetation and soils of urban ecosystems, which in the words of Trusilova and Churkina has “led to a net increase of [the] carbon sink in Europe.”

Reference

Trusilova, K. and Churkina, G. 2008. The response of the terrestrial biosphere to urbanization: land cover conversion, climate, and urban pollution. *Biogeosciences* **5**: 1505–1515.

7.7.6. Entire Earth

Gloor et al. (2010) note the ratio of CO_2 accumulating in the atmosphere to the CO_2 flux into the atmosphere due to human activities—which is known as the airborne fraction (AF)—is central to predicting changes in Earth’s surface temperature due to greenhouse gas-induced warming, and they note this ratio has remained remarkably constant over the past five decades. However, they report Canadell et al. (2007) and Raupach et al. (2008) claim to have detected a long-term increasing trend in the airborne fraction, which they interpret as being indicative of “a decreasing trend in the efficiency of the ocean and land carbon sinks.”

Gloor et al. note Knorr (2009) already had challenged Canadell et al. and Raupach et al. over their detection of a positive AF trend, "arguing that given the noise in the data, the trend is not detectable." Thus, they challenged the second claim of Canadell et al. and Raupach et al., that a positive AF trend is indicative of a decreasing planetary carbon sink efficiency, by investigating "the question of what controls trends and decadal scale variations in CO_2 airborne fraction using simple linear models describing the evolution of an atmospheric perturbation in CO_2."

The three researchers determined, first of all, that there is no one-to-one association between positive trends in CO_2 flux to the atmosphere (due to fossil fuel emissions and changes in land use) and negative trends in Earth's carbon sink efficiency. Second, they found that in order to detect trends in sink efficiencies from the time course of fossil fuel-derived CO_2 emissions and temporal changes in land use, "it is necessary to disentangle the spin-up time and fossil fuel growth rate variation signatures in the airborne fraction from signatures due to other causes."

And when they make the pertinent calculations for fossil-fuel and land-use changes, they state they "do indeed find a positive trend in the residuals," but they argue this trend "is not statistically significant after correcting for known events such as the temporal distribution of the extrinsic forcings and likely omissions in the emissions (particularly from land-use change)." They further note their analysis suggests "trends in airborne fraction are not a very good diagnostic to detect changes in carbon sink efficiency because variations in the signal are complex and the signal-to-noise ratio is small."

Thus Gloor et al. conclude "atmospheric data, if analyzed adequately, do not yet reveal a statistically significant signal," which suggests it's too soon to say whether the carbon sink efficiency of the Earth is increasing, decreasing, or remaining relatively constant.

References

Canadell, J.G., Le Quere, C., Raupach, M.R., Field, C.B., Buitenhuis, E.T., Ciais, P., Conway, T.J., Gillett, N.P., Houghton, R., and Marland, G. 2007. Contributions to accelerating atmospheric CO_2 growth from economic activity, carbon intensity, and efficiency of natural sinks. *Proceedings of the National Academy of Sciences USA* **104**: 18,866–18,870.

Gloor, M., Sarmiento, J.L. and Gruber, N. 2010. What can be learned about carbon cycle climate feedbacks from the CO_2 airborne fraction? *Atmospheric Chemistry and Physics* **10**: 7739-7751.

Knorr, W. 2009. Is the airborne fraction of anthropogenic CO_2 emissions increasing? *Geophysical Research Letters* **36**: 10.1029/2009GL040613.

Raupach, M.R., Canadell, J.G. and Le Quere, C. 2008. Anthropogenic and biophysical contributions to increasing atmospheric CO_2 growth rate and airborne fraction. *Biogeosciences* **5**: 1601-1613.

7.8. Extinction

Scherrer and Korner (2010) write, "climate warming scenarios predict higher than average warming in most alpine areas," and therefore, they state, "alpine regions are often considered as particularly threatened." In testimony presented to the Select Committee on Energy Independence and Global Warming of the United States House of Representatives on 26 April 2007, NASA's James Hansen declared life in alpine regions is in danger of being "pushed off the planet" as the Earth warms, since it has "no place else to go."

In a study designed to test this contention, Scherrer and Korner employed thermal imagery and microloggers to assess the fine-scale detail of both surface and root zone temperatures in three temperate-alpine and subarctic-alpine regions: one in the Swiss Alps, one in Northern Sweden, and one in Northern Norway. All of these sites were located on steep mountain slopes above the climatic tree line that exhibited a rich microtopography but no significant change in macroexposure. The two Swiss scientists report observing, "microclimatic variation on clear sky days was strong within all slopes, with 8.4 ± 2.5°C (mean ± SD) surface temperature differences persisting over several hours per day along horizontal (i.e., equal elevation) transects." These differences, as they describe them, "are larger than the temperature change predicted by the IPCC."

These findings, in the words of Scherrer and Korner, are "important in the context of climate change" because they show "species do not necessarily need to climb several hundred meters in elevation to escape the warmth." Quite often, in fact, a "few meters of horizontal shift will do," so that for plants "unable or too slow to adapt to a warmer climate, thermal microhabitat mosaics offer both refuge habitats as well as stepping stones as atmospheric temperatures rise.” Discussing the greater implications of their results, the Swiss scientists state their data “challenge the stereotype of particularly sensitive and vulnerable alpine biota with respect to climatic warming,” noting “high elevation terrain may in fact be more suitable to protect biodiversity under changing climatic conditions than most other, lower elevation types of landscapes.” Thus, in what would appear to be a bit of good advice to all—and James Hansen in particular—the two researchers state they “advocate a more cautious treatment of this matter.”

In another report on the status of alpine communities, this one in the Swedish Scandes, Kullman (2010) writes, “alpine plant life is proliferating, biodiversity is on the rise, and the mountain world appears more productive and inviting than ever,” which is about as far from being “pushed off the planet” as one could imagine. The professor of physical geography at Sweden’s Umea University states this particular course of biotic landscape evolution “has reached historical dimensions and broken a multi-millennial trend of plant cover retrogression, alpine tundra expansion, floristic and faunal impoverishment, all imposed by progressive and deterministic neoglacial climate cooling.” And he concludes “continued modest warming over the present century will likely be beneficial to alpine biodiversity, geoecological stability, resilience, sustainable reindeer husbandry and aesthetic landscape qualities.” He came to these conclusions, he writes, via “an integrative review of results from long-term monitoring of subalpine/alpine vegetation.”

Enlarging on some of these positive warming-induced impacts, Kullman writes, “plant species diversity will further increase, both in remaining treeless alpine areas and emerging forest outliers on the former alpine tundra,” and this “new alpine landscape may come to support a previously unseen mosaic of richly flowering and luxuriant plant communities of early Holocene character,” citing the works of Smith (1920), Iversen (1973), and Birks (2008). In describing what already has been documented, he states, “in contrast to model predictions, no single alpine plant species has become extinct, neither in Scandinavia nor in any other part of the world, in response to climate warming over the past century,” citing the studies of Pauli et al. (2001, 2007), Theurillat and Guisan (2001), and Birks (2008).

Tracing the evidence to the source of all these warming-induced ecological benefits, Kullman writes, “many alpine species are extremely tolerant of high temperatures per se,” citing Dahl (1998) and Birks (2008), as indicated “by their prospering and spread along roadsides far below the treeline, where emerging trees and shrubs are regularly mechanically exterminated (Kullman, 2006; Westerstrom, 2008).” He notes “another argument against the much-discussed option of pending mass-extinction of alpine species in a warmer future is that some alpine and arctic plant species contain a variety of ecotypes, pre-adapted to quite variable microclimatic and edaphic conditions, which could buffer against extinction in a possibly warmer future (Crawford, 2008).” In addition, he writes, this view is supported “by the fact that in the early Holocene, alpine plants survived, reproduced and spread in accordance with higher and more rapidly rising temperatures than those projected for the future by climate models (Oldfield, 2005; Birks, 2008).”

Kullman observes the “extended ranges of many flowering species and increasing plant species richness and habitat diversity imply a highly variable and aesthetically appealing mountain landscape, which should be positive from a nature conservation point of view (Jurasinski and Kreyling, 2007).” In fact, he states “such a course of landscape evolution adds to physical and ecological stability, functional efficiency, resilience and assures against ‘system failure’,” citing McCann (2000), Korner (2002), and McLaren (2006). Therefore, as Kullman concludes, “continued warming throughout the present century would be potentially and predominantly advantageous for alpine flora and vegetation.”

In a very different type of study, Willis et al. (2010) identified past historical periods in which climate was either similar to that projected by global climate models for the next century or so, or in which the rate of temperature change was unusually rapid. They examined these real-world periods to see if any real-world climate-related extinctions occurred.

The first period they examined was the Eocene Climatic Optimum (53–51 million years ago), when the atmosphere’s CO_2 concentration exceeded 1,200 ppm and tropical temperatures were 5–10°C warmer than modern values. Yet far from causing extinctions of the tropical flora (where the data are best), the four researchers report “all the evidence from low-latitude records indicates that, at least in the plant fossil record, this was one of the most biodiverse intervals of time in the Neotropics.” They also note “ancestors of many of our modern tropical and temperate plants evolved ...when global temperatures and CO_2 were much higher than present ... indicating that they have much wider ecological tolerances than are predicted based on present-day climates alone.”

The second period they examined included two rapid-change climatic events in the Holocene—one at 14,700 years ago and one at 11,600 years ago—when temperatures increased in the mid- to high-latitudes of the Northern Hemisphere by up to 10°C over periods of less than 60 years. There is evidence from many sites for rapid plant responses to rapid warming during these events. The researchers note “at no site yet studied, anywhere in the world, is there evidence in the fossil record for large-scale climate-driven extinction during these intervals of rapid warming.” On the other hand, they report extinctions did occur due to the cold temperatures of the glacial epoch, when subtropical species in southern Europe were driven out of their comfort zone.

The Willis et al. study also makes use of recent historical data, as in the case of the 3°C rise in temperature at Yosemite Park over the past 100 years. In comparing surveys of mammal fauna conducted near the beginning and end of this period, they detected some changes but no local extinctions. Thus they determined that for all of the periods they studied, with either very warm temperatures or very rapid warming, there were no detectable species extinctions.

In a study that may help explain how some researchers could have gotten things so wrong in predicting massive extinctions of both plants and animals in response to projected future warming, Nogues-Bravo (2009) explains the climate envelope models (CEMs)—often employed to predict species responses to global warming (and whether or not a species will be able to survive projected temperature increases)—“are sensitive to theoretical assumptions, to model classes and to projections in non-analogous climates, among other issues.” To determine how appropriate these models are for determining whether a particular species will be driven to extinction by hypothesized planetary warming, Nogues-Bravo reviewed the scientific literature pertaining to the subject and found several flaws. Nogues-Bravo writes, “the studies reviewed: (1) rarely test the theoretical assumptions behind niche modeling such as the stability of species climatic niches through time and the equilibrium of species with climate; (2) they only use one model class (72% of the studies) and one palaeoclimatic reconstruction (62.5%) to calibrate their models; (3) they do not check for the occurrence of non-analogous climates (97%); and (4) they do not use independent data to validate the models (72%).” Nogues-Bravo writes, “ignoring the theoretical assumptions behind niche modeling and using inadequate methods for hindcasting” can produce “a cascade of errors and naïve ecological and evolutionary inferences.” Hence, he concludes, “there are a wide variety of challenges that CEMs must overcome in order to improve the reliability of their predictions through time.” Until these challenges are met, contentions of impending species extinctions must be considered little more than guesswork (see also Chapman, 2010).

Employing yet another way of assessing the potential for plants to avoid extinction in a warming world, De Frenne et al. (2010) collected seeds of *Anemone nemorosa* L.—a model species for slow-colonizing herbaceous forest plants—found in populations growing along a 2,400-km latitudinal gradient stretching from northern France to northern Sweden during three separate growing seasons (2005, 2006, and 2008). They then conducted sowing trials in incubators, in a greenhouse, and under field conditions in a forest, where they measured the effects of different temperature treatments (growing degree hours or GDHs) on various seed and seedling traits.

The 19 researchers—from Belgium, Estonia, France, Germany, and Sweden—determined “seed mass, germination percentage, germinable seed output and seedling mass all showed a positive response to increased GDHs experienced by the parent plant,” noting seed and seedling mass increased by 9.7 percent and 10.4 percent, respectively, for every 1,000 °C-hours increase in GDHs, which they say is equivalent to a 1°C increase in temperature over a 42-day period. Therefore, they conclude, “if climate warms, this will have a pronounced positive impact on the reproduction of *A. nemorosa*, especially in terms of seed mass, germination percentage and seedling mass,” because “if more seeds germinate and resulting seedlings show higher fitness, more individuals may be recruited to the adult stage.” In addition, since “rhizome growth also is likely to benefit from higher winter temperatures (Philipp and Petersen, 2007), it can be hypothesized that the migration potential of *A. nemorosa* may increase as the climate in NW-Europe becomes warmer in the coming decades."

And, we would add, increasing migration potential implies a decreasing chance of extinction.

References

Birks, H.H. 2008. The late-quaternary history of arctic and alpine plants. *Plant Ecology and Diversity* **1**: 135–146.

Chapman, D.S. 2010. Weak climatic associations among British plant distributions. *Global Ecology and Biogeography* **19**: 831–841.

Crawford, R.M.M. 2008. Cold climate plants in a warmer world. *Plant Ecology and Diversity* **1**: 285–297.

Dahl, E. 1998. *The Phytogeography of Northern Europe.* Cambirdge, UK: Cambridge University Press.

De Frenne, P., Graae, J.J., Kolb, A., Brunet, J., Chabrerie, O., Cousins, S.A.O., Decocq, G., Dhondt, R., Diekmann, M., Eriksson, O., Heinken, T., Hermy, M., Jogar, U., Saguez, R., Shevtsova, A., Stanton, S., Zindel, R., Zobel, M.. and Verheyen, K. 2010. Significant effects of temperature on the reproductive output of the forest herb *Anemone nemorosa* L. *Forest Ecology and Management* **259**: 809–817.

Iversen, J. 1973. The development of Denmark's nature since the last glacial. *Danmarks Geologiske Undersogelse Series V. Raeeke* **7-C**: 1–126.

Jurasinski, G. and Kreyling, J. 2007. Upward shift of alpine plants increases floristic similarity of mountain summits. *Journal of Vegetation Science* **18**: 711–718.

Korner, C. 2002. Mountain biodiversity, its causes and function: an overview. In *Mountain Biodiversity, a Global Assessment*, edited by C. Korner and E.M. Spehn, 3–20. Boca Raton, FL: The Parthenon Publishing Group.

Kullman, L. 2006. Transformation of alpine and subalpine vegetation in a potentially warmer future, the Anthropocene era. Tentative projections based on a long-term observations and paleovegetation records. *Current Trends in Ecology* **1**: 1–16.

Kullman, L. 2010. A richer, greener and smaller alpine world: review and projection of warming-induced plant cover change in the Swedish Scandes. *Ambio* **39**: 159–169.

McCann, K.S. 2000. The diversity-stability debate. *Nature* **405**: 228–233.

McLaren, J.R. 2006. Effects of plant functional groups on vegetation dynamics and ecosystems properties. *Arctic* **59**: 449–452.

Nogues-Bravo, D. 2009. Predicting the past distribution of species climatic niches. *Global Ecology and Biogeography* **18**: 521–531.

Oldfield, F. 2005. Environmental Change. Key Issues and Alternative Perspectives. Cambridge , UK: Cambridge University Press.

Pauli, H., Gottfried, M., and Grabherr, G. 2001. High summits of the Alps in a changing climate. In *Fingerprints of Climate Change*, edited by G.-R. Walther, C.A. Burga, and P.J. Edwards, 139–149. New York, NY: Kluwer.

Pauli, H., Gottfried, M., Reiter, K., Klettner, C., and Grabherr, G. 2007. Signals of range expansions and contractions of vascular plants in the high Alps: observations (1994–2004) at the GLORIA master site Schrankogel, Tyrol, Austria. *Global Change Biology* **13**: 147–156.

Philipp, M. and Petersen, P.M. 2007. Long-term study of dry matter allocation and rhizome growth in *Anemone nemorosa*. *Plant Species Biology* **22**: 23–31.

Scherrer, D. and Korner, C. 2010. Infra-red thermometry of alpine landscapes challenges climatic warming projections. *Global Change Biology* **16**: 2602–2613.

Smith, H. 1920. *Vegetationen och dess Utvecklingshistoria i det Centralsvenska Hogfjallsomradet*. Uppsala, Sweden: Almqvist och Wiksell.

Theurillat, J.-P. and Guisan, A. 2001. Potential impacts of climate change on vegetation in the European Alps: a review. *Climatic Change* **50**: 77–109.

Westerstrom, G. 2008. Floran i tre socknar i nordvastra Angermanland. *Svensk Botanisk Tidskrift* **102**: 225–261.

Willis, K.J., Bennett, K.D., Bhagwat, S.A., and Birks, H.J.B. 2010. Perspective: 4 deg C and beyond: what did this mean for biodiversity in the past? *Systematics and Biodiversity* **8**: 3–9.

7.9. Evolution

One of the most powerful means plant and animal species have for avoiding extinction during climate change is the ability to evolve in ways that enable them to deal with the change. Several studies have demonstrated the abilities of numerous plants and animals to do just that.

Working in the Swiss Alps, Stocklin et al. (2009) studied the consequences of the highly structured alpine landscape for evolutionary processes in four different plants (*Epilobium fleischeri*, *Geum reptans*, *Campanula thyrsoides*, and *Poa alpina*), testing for whether genetic diversity within their populations was related to altitude and land use, while seeking to determine whether genetic differentiation among populations was related more to different land use or to geographic distances. In pursuit of these goals, the three Swiss scientists determined that within-population genetic diversity of the four species was high and mostly not related to altitude and population size, while genetic differentiation among populations was pronounced and strongly increased with distance, implying "considerable genetic drift among populations of alpine plants."

Based on these findings and the observations of others, Stocklin et al. write, "phenotypic plasticity is particularly pronounced in alpine plants," and "because of the high heterogeneity of the alpine landscape, the pronounced capacity of a single genotype to exhibit variable phenotypes is a clear advantage for the persistence and survival of alpine plants." Hence they conclude, "the evolutionary potential to respond to global change is mostly intact in alpine plants, even at high altitude." This result makes it much easier to understand why—even in the face of significant twentieth-century global warming—no species of plants have been observed to have been "pushed off the planet" in alpine regions. This has been shown to be the case in several pertinent studies, including Walther et al. (2005), Kullman (2007), Holzinger et al. (2008), Randin et al. (2009), and Erschbamer et al. (2009).

Describing another approach to the subject, Franks and Weis (2009) note a "rigorous way to determine if evolution has occurred in a natural population is to collect propagules before and after an environmental change and raise them under common conditions." They state "this approach was used previously to show that *Brassica rapa* [a self-incompatible weedy winter annual] evolved drought escape through earlier flowering following a series of recent dry years in Southern California, and that early flowering results in higher fitness under drought conditions (Franks et al., 2007)." They also note "a related study showed that multiple phenological traits and their interactions evolved in response to the drought (Franks and Weis, 2008)."

Working with the same pre- and post-drought collection lines from their earlier experiment (Franks et al., 2007), the two researchers estimated the amount of assortative mating within, and the degree of phenological isolation between, two *B. rapa* populations. Their results indicated "climate change can alter plant phenology, which can change patterns of assortative mating within populations," and "this assortative mating can directly change genotype frequencies and can also increase the rate of evolution by interacting with selection." In addition, they demonstrated "climatically driven changes in phenology can potentially influence gene flow among populations due to changes in overlap in flowering schedules," and "these changes in gene flow can also influence both the rate and pattern of evolutionary change."

Given these findings, the two scientists conclude "the high degree of interdependence of flowering time, assortative mating, selection and gene flow make predicting evolutionary responses to changes in climate particularly complex and challenging." This great degree of complexity suggests that among the multiplicity of outcomes, there is a good chance one or more will be just what the plants need to respond successfully to the climate change that elicited the outcomes.

Finally, Kuparinen et al. (2010) note "climate change is predicted to increase average air surface temperatures by several degrees in this century," and "species exposed to changes in the environmental conditions may first show plastic phenotypic responses (e.g. Rehfeldt et al., 2002); but, in the long term, rapid climate change raises the question how quickly species can evolutionarily adapt to future climates in their habitats." Against this backdrop, therefore, the authors investigated "the adaptation of Scots pine (*Pinus sylvestris*) and Silver birch (*Betula pendula*) to climate change induced prolongation of the thermal growing season," using "quantitative genetic individual-based simulations to disentangle the relative roles of mortality, dispersal ability and maturation age for the speed of adaptation."

The three scientists state their simulations predict "after 100 years of climate change, the genotypic growth period length of both species will lag more than 50% behind the climatically determined optimum," but "this lag is reduced by increased mortality of established trees," in conformity with the prior suggestion of Savolainen et al. (2004) and Kramer et al. (2008) that "the persistence of maladapted old trees preventing the establishment of seedlings better adapted to a changed environment" is not helpful to their long-term survival.

In addition, and in light of the fact that Kuparinen et al.'s findings suggest, as they put it, "adaptation might be sped up if mortality factors such as storms, fires, or insect outbreaks get more common in the future," it could actually turn out to be a positive thing—in this particular instance, at least, and for these specific species—if some of the envisioned negative consequences of global warming were ever to become a reality.

References

Erschbamer, B., Kiebacher, T., Mallaun, M., and Unterluggauer, P. 2009. Short-term signals of climate change along an altitudinal gradient in the South Alps. *Plant Ecology* **202**: 79–89.

Franks, S.J., Sim, S., and Weis, A.E. 2007. Rapid evolution of flowering time by an annual plant in response to a climate fluctuation. *Proceedings of the National Academy of Sciences USA* **104**: 1278–1282.

Franks, S.J. and Weis, A.E. 2008. A change in climate causes rapid evolution of multiple life-history traits and their interactions in an annual plant. *Journal of Evolutionary Biology* **21**: 1321–1334.

Franks, S.J. and Weis, A.E. 2009. Climate change alters reproductive isolation and potential gene flow in an annual plant. *Evolutionary Applications* **2**: 481–488.

Holzinger, B., Hulber, K., Camenisch, M., and Grabherr, G. 2008. Changes in plant species richness over the last century in the eastern Swiss Alps: elevational gradient, bedrock effects and migration rates. *Plant Ecology* **195**: 179–196.

Kramer, K., Bulteveld, J., Forstreuter, M., Geburek, T., Leonardi, S., Menozzi, P., Povillon, F., Scherlhaas, M.J., Teissier du Cros, E., Vendramin, G.G., and van der Werf, D.C. 2008. Bridging the gap between ecophysiological and genetic knowledge to assess the adaptive potential of European beech. *Ecological Modelling* **216**: 333–353.

Kullman, L. 2007. Long-term geobotanical observations of climate change impacts in the Scandes of West-Central Sweden. *Nordic Journal of Botany* **24**: 445–467.

Kuparinen, A., Savolainen, O., and Schurr, F.M. 2010. Increased mortality can promote evolutionary adaptation of forest trees to climate change. *Forest Ecology and Management* **259**: 1003–1008.

Randin, C.F., Engler, R., Normand, S., Zappa, M., Zimmermann, N.E., Pearman, P.B., Vittoz, P., Thuiller, W., and Guisan, A. 2009. Climate change and plant distribution: local models predict high-elevation persistence. *Global Change Biology* **15**: 1557–1569.

Rehfeldt, G.R., Tchebakova, N.M., Parfenova, Y.I., Wykoff, W.R., Kuzmina, N.A., and Milyutin, L.I. 2002. Intraspecific responses to climate change in *Pinus sylvestris*. *Global Change Biology* **8**: 912–929.

Savolainen, O., Bokma, F., Garcia-Gil, R., Komulainen, P., and Repo, T. 2004. Genetic variation in cessation of growth and frost hardiness and consequences for adaptation of *Pinus sylvestris* to climatic changes. *Forest Ecology and Management* **197**: 79–89.

Stocklin, J., Kuss, P., and Pluess, A.R. 2009. Genetic diversity, phenotypic variation and local adaptation in the alpine landscape: case studies with alpine plant species. *Botanica Helvetica* **119**: 125–133.

Walther, G.-R., Beissner, S., and Burga, C.A. 2005. Trends in the upward shift of alpine plants. *Journal of Vegetation Science* **16**: 541–548.

7.10. Food Production

7.10.1. Meeting Global Food and Water Needs

Several years ago, Waggoner (1995) rhetorically asked: How much land can ten billion people spare for nature? That was the title of an essay he wrote to illuminate the dynamic tension between the need for land to support the agricultural enterprises that sustain mankind and the need for land to support the natural ecosystems that sustain all other creatures. As noted by Huang et al. (2002), human populations "have encroached on almost all of the world's frontiers, leaving little new land that is cultivatable." And in consequence of humanity's ongoing usurpation of this most basic of natural resources, Raven (2002) has noted "species-area relationships, taken worldwide in relation to habitat destruction, lead to projections of the loss of fully two-thirds of all species on earth by the end of this century." In addition, Wallace (2000) has calculated we will need to divert essentially all usable non-saline water on the face of the Earth to the agricultural enterprises that will be required to meet the food and fiber needs of humanity's growing numbers well before that.

So what parts of the world are likely to be hit hardest by the great land-grabbing and water-consuming machine of humanity? Tilman et al. (2001) report developed countries are expected to withdraw large areas of land from farming between now and the middle of the century (2050), leaving developing countries to shoulder essentially all of the growing burden of feeding our expanding population. In addition, they calculate the loss of these countries' natural ecosystems to crops and pasture represent about half of all potentially suitable remaining land, which "could lead to the loss of about a third of remaining tropical and temperate forests, savannas, and grasslands," along with the many unique species they support.

If one were to pick the most significant problem currently facing the biosphere, this would probably be it: a single species of life, *Homo sapiens*, is on course to annihilate two-thirds of the ten million or so other species with which we share the planet within the next several decades, simply by taking their land and water. Global warming, by comparison, pales in significance, as its impact is nowhere near as severe and in fact may be neutral or even positive. In addition, its chief cause is highly debated, and actions to thwart it are much more difficult, if not impossible, to define and implement. Furthermore, what many people believe to be the main cause of global warming—anthropogenic CO_2 emissions—may actually be a powerful force for preserving land and water for nature.

In an analysis of the problem of human land-use expansion, Tilman et al. (2002) introduced a few more facts before suggesting some solutions. They noted, for example, that by 2050 the human population of the globe is projected to be 50 percent larger than it was in 2000, and that global grain demand could double because of expected increases in per-capita real income and dietary shifts toward a higher proportion of meat. Hence, they stated the obvious when they concluded, "raising yields on existing farmland is essential for 'saving land for nature'."

So how is it to be done? Tilman et al. (2002) suggested a strategy built around three essential tasks: (1) increasing crop yield per unit land area, (2) increasing crop yield per unit of nutrients applied, and (3) increasing crop yield per unit of water used.

Regarding the first of these requirements, Tilman et al. note that in many parts of the world the historical rate of increase in crop yields is declining, as the genetic ceiling for maximal yield potential is being approached. This observation, in their words, "highlights the need for efforts to steadily increase the yield potential ceiling." With respect to the second requirement, they indicate, "without the use of synthetic fertilizers, world food production could not have increased at the rate it did [in the past] and more natural ecosystems would have been converted to agriculture." Hence, they state the solution "will require significant increases in nutrient use efficiency, that is, in cereal production per unit of added nitrogen, phosphorus," and so forth. Finally, as to the third requirement, Tilman et al. remind us "water is regionally scarce," and "many countries in a band from China through India and Pakistan, and the Middle East to North Africa either currently or will soon fail to have adequate water to maintain per capita food production from irrigated land." Increasing crop water use efficiency, therefore, is also a must.

Although the impending biological crisis and several important elements of its potential solution are thus well defined, Tilman et al. (2001) noted "even the best available technologies, fully deployed, cannot prevent many of the forecasted problems." This was also the conclusion of Idso and Idso (2000), who stated that although "expected advances in agricultural technology and expertise will significantly increase the food production potential of many countries and regions," these advances "will not increase production fast enough to meet the demands of the even faster-growing human population of the planet."

Fortunately, we have a powerful ally in the ongoing rise in the air's CO_2 content that can provide what we can't. Since atmospheric CO_2 is the basic "food" of essentially all plants, the more of it there is in the air, the bigger and better they grow. For a nominal doubling of the air's CO_2 concentration, for example, the productivity of Earth's herbaceous plants rises by 30 to 50 percent (Kimball, 1983; Idso and Idso, 1994), and the productivity of its woody plants rises by 50 to 80 percent or more (Saxe et al. 1998; Idso and Kimball, 2001). Hence, as the air's CO_2 content continues to rise, the land use efficiency of the planet will rise right along with it. In addition, atmospheric CO_2 enrichment typically increases plant nutrient use efficiency and plant water use efficiency. Thus, with respect to all three of the major needs identified by Tilman et al. (2002), increases in the air's CO_2 content pay huge dividends, helping to increase agricultural output without the taking of new land and water from nature.

Many other researchers have broached this subject. In a paper recently published in the *Annual Review of Plant Biology*, three scientists associated with the Institute of Genomic Biology at the University of Illinois at Urbana-Champaign (USA) write that meeting the global increase in agricultural demand during this century "is predicted to require a doubling of global production," but "the world has limited capacity to sustainably expand cropland," and this capacity is actually "shrinking in many developed countries." Thus, Zhu et al. (2010) state, "meeting future increases in demand will have to come from a near doubling of productivity on a land area basis," and they conclude "a large contribution will have to come from improved photosynthetic conversion efficiency," estimating "at least a 50% improvement will be required to double global production."

The researchers' reason for focusing on photosynthetic conversion efficiency derives from the experimentally observed facts that increases in the atmosphere's CO_2 concentration increase the photosynthetic rates of nearly all plants, and those rate increases generally lead to equivalent—or only slightly smaller—increases in plant productivity on a land area basis. That provides a solid foundation for their enthusiasm in this regard. In their review of the matter, however, they examine the prospects for boosting photosynthetic conversion efficiency in an entirely different way: genetically, without increasing the air's CO_2 content.

"Improving photosynthetic conversion efficiency will require," the three scientists state, "a full suite of tools including breeding, gene transfer, and synthetic biology in bringing about the designed alteration to photosynthesis." For some of these "near-term" endeavors, they indicate "implementation is limited by technical issues that can be overcome by sufficient investment," meaning they can "be bought." But several "mid-term" goals could take 20 years or more to achieve; and they state "even when these improvements are achieved, it may take an additional 10–20 years to bring such innovations to farms in commercial cultivars at adequate scale." And if that is not bad enough, they say of still longer-term goals that "too little of the science has been undertaken to identify what needs to be altered to effect an increase in yield," while in some cases they acknowledge that what they envision may not even be possible, as in developing a form of RuBisCO that exhibits a significant decrease in oxygenation activity, or in designing C_3 crops to utilize the C_4 form of photosynthetic metabolism.

Clearly, we do not have the time to gamble on our ability to accomplish what needs to be done in order to forestall massive human starvation of global dimensions within the current century. Therefore—in addition to trying what Zhu et al. suggest—we must rely on the "tested and true": the CO_2-induced stimulation of plant photosynthesis and crop yield production. And all we need to do in this regard is to refrain from interfering with the natural evolution of the Industrial Revolution, which is destined to be carried for some time yet on the backs of fossil-fuel-driven enterprises that can provide the atmosphere with the extra carbon dioxide that will be needed to provide the extra increase in crop growth that may mean the difference between global food sufficiency and human starvation on a massive scale a mere few decades from now.

Another take on the matter has been provided by Hanjra and Qureshi (2010). They begin their treatment of the subject by quoting Benjamin Franklin's well-known homily, "When the well is dry, we know the worth of water," and they write we "must not lose sight of surging water scarcity." Noting "population and income growth will increase the demand for food and water," they contend "irrigation will be the first sector to lose water, as water competition by non-agricultural uses increases and water scarcity intensifies." As "increasing water scarcity will have implications for food security, hunger, poverty, and ecosystem health and services," they report "feeding the 2050 population will require some 12,400 km^3 of water, up from 6800 km^3 used today." This huge increase, they continue, "will leave a water gap of about 3300 km^3 even after improving efficiency in irrigated agriculture, improving water management, and upgrading of rainfed agriculture," as per the findings of de Fraiture et al. (2007), Molden (2007), and Molden et al. (2010).

This water deficiency, according to Hanjra and Qureshi, "will lead to a food gap unless concerted actions are taken today." Some of the measures they propose are to conserve water and energy resources, develop and adopt climate-resilient crop varieties, modernize irrigation, shore up domestic food supplies, reengage in agriculture for further development, and reform the global food and trade markets. To achieve these goals, they write, "unprecedented global cooperation is required," which by the looks of today's world is an exceedingly remote possibility.

What, then, can we do to defuse the ticking time-bomb of this looming food and water crisis? One option is to do nothing: don't mess with the normal, unforced evolution of civilization's means of acquiring energy. This is because on top of everything else we may try to do to conserve both land and freshwater resources, we will still fall short of what is needed to be achieved unless the air's CO_2 content rises significantly and thereby boosts the water use efficiency of Earth's crop plants and that of the plants that provide food and habitat for what could be called "wild nature," enabling both sets of plants to produce more biomass per unit of water used.

To ensure this happens, we will need all of the CO_2 that will be produced by the burning of fossil fuels, until other forms of energy truly become more cost-efficient than coal, gas, and oil. In fact, these other energy sources will have to become much more cost-efficient before fossil fuels are phased out, because the positive externality of the CO_2-induced increase in plant water use efficiency provided by the steady rise in the atmosphere's CO_2 concentration due to the burning of fossil fuels will be providing a most important service in helping us feed and sustain our own species without totally decimating what yet remains of wild nature.

In yet another paper to address this important issue—this one published in the *Journal of Proteome Research*—Sarkar et al. (2010) write, "increasing population and unsustainable exploitation of nature and natural resources have made 'food security' a burning issue in the 21st century," echoing the sentiments expressed by Farrell (2009), who noted "the alarming increase in biofuel production, the projected demand for livestock products, and the estimated food to feed the additional 700 million people who will arrive here by 2016, will have unprecedented consequences," among which are likely to be that "arable land, the environment, water supply and sustainability of the agricultural system will all be affected," and not in a positive way. Furthermore, when the human population of the globe reaches 8.7–11.3 billion by the year 2050 (Bengtsson et al., 2006), the situation will become truly intolerable, unless something is done, far in advance of that date, to mitigate the situation dramatically. Thus, as Sarkar et al. suggest, "a normal approach for any nation/region is to strengthen its agricultural production for meeting future demands and provide food security." But a major difficulty, which could spoil mankind's ability to do so, is the ongoing rise in the atmosphere's ozone concentration. This is the subject of Sarkar et al.'s new paper.

In a study designed to elucidate the many ways in which ozone (O_3) is harmful to plants, the eight researchers grew two high-yielding cultivars (Sonalika and HUW 510) of wheat (*Triticum aestivum* L.) outdoors at the Agriculture Research Farm of India's Banaras Hindu University. This was done within open-top chambers maintained at the ambient O_3 concentration and at elevated O_3 concentrations of 25 percent and 50 percent above ambient during the peak O_3 period of the day (10:00 to 15:00 hours local time) for a total of 50 days, during which time they measured numerous responses of the plants to the two levels of ozone enrichment.

Sarkar et al. determined, among several other things, that the moderate increases in the air's O_3 concentration resulted in higher foliar injury, a reduction in photosynthetic efficiency, induced inhibition in photochemical efficacy of photosystem II, lowered concentrations of photosynthetic pigments and proteins, and what they describe as "drastic reductions" in RuBisCO large and small subunits, while noting major leaf photosynthetic proteins and important energy metabolism proteins were also "drastically reduced."

Discussing the results, the scientists from India, Japan, and Nepal remark that anthropogenic activities have made ozone a "major environmental pollutant of our time," while noting some are predicting it to be an even "greater problem for the future." Adding this dilemma to the problem of feeding the world over the next few decades and beyond makes humanity's future look incredibly bleak. Thus, Sarkar et al. suggest we focus on "engineering crops for future high O_3," concentrating on maintaining "effective stomatal conductance of plants which can avoid O_3 entry but not hamper their productivity." We agree.

But not knowing to what extent we will be successful in this endeavor, we also need to do something we know will work: allowing the air's CO_2 content to rise, unimpeded by the misguided efforts of those who would curtail anthropogenic CO_2 emissions in the guise of fighting what they claim is anthropogenic-induced global warming. This contention is largely theoretical and wholly unproven, but we know, as a result of literally hundreds, if not thousands, of real-world experiments, that atmospheric CO_2 enrichment increases both the productivity and water-use efficiency of nearly all plants, and that it often more than compensates for the negative effects of O_3 pollution.

Introducing another review of food security studies pertinent to the challenge of feeding 9 billion people just four decades from now, Godfray et al. (2010) note "more than one in seven people today still do not have access to sufficient protein and energy from their diet and even more suffer some form of micronutrient malnourishment," citing the FAO (2009). Although "increases in production will have an important part to play" in correcting this problem and keeping it from worsening in the future, mankind "will be constrained by the finite resources provided by the earth's lands, oceans and atmosphere," This set of difficulties they describe at the end of their review as constituting a "perfect storm."

In considering ways to mitigate these problems, the first question they ask is: "How can more food be produced sustainably?" They state the primary solution to food shortages of the past was "to bring more land into agriculture and to exploit new fish stocks," but they note there is precious little remaining of either of these pristine resources. Thus, they conclude "the most likely scenario is that more food will need to be produced from the same or less land." As they suggest, "we must avoid the temptation to sacrifice further the earth's already hugely depleted biodiversity for easy gains in food production, not only because biodiversity provides many of the public goods upon which mankind relies, but also because we do not have the right to deprive future generations of its economic and cultural benefits." And, we might add, because we should be enlightened enough to realize we have a moral responsibility to drive no more species to extinction than we already have sent to that sorry state.

So how can these diverse requirements all be met simultaneously? A clue comes from Godfray et al.'s statement that "greater water and nutrient use efficiency, as well as tolerance of abiotic stress, are likely to become of increasing importance." And what is there that can bring about these changes in mankind's crops? You guessed it: carbon dioxide.

Rising concentrations of atmospheric CO_2 increase the photosynthetic prowess of essentially all of the Earth's plants, while generally reducing the rate at which they transfer water from the soil to the air. In addition, more CO_2 in the air tends to enhance the efficiency with which plants utilize nutrients in constructing their tissues and producing the edible portions that we and all of Earth's animals depend upon for our very existence.

Focusing on the water scarcity aspect of the food shortage problem, Kummu et al. (2010) write, "due to the rapidly increasing population and water use per capita in many areas of the world, around one third of the world's population currently lives under physical water scarcity (e.g. Vorosmarty et al., 2000; Alcamo et al., 2003; Oki and Kanae, 2006)." But despite the large number of water scarcity studies conducted over the years, "no global assessment is available of how this trend has evolved over the past several centuries to millennia." Thus they conducted a study covering AD 0 to 2005. This analysis was carried out for ten different time slices, defined as those times at which the human population of the globe was approximately double the population of the previous time slice. Global population data for these analyses were derived from the 5' latitude x 5' longitude-resolution global HYDE dataset of Klein Goldewijk (2005) and Klein Goldewijk et al. (2010), while evaluation of water resources availability over the same period was based on monthly temperature and precipitation output from the climate model ECBilt-CLIO-VECODE, as calculated by Renssen et al. (2005).

After completing these assessments, the four researchers found "moderate water shortage first appeared around 1800, but it commenced in earnest from about 1900, when 9% of the world population experienced water shortage, of which 2% was under chronic water shortage (<1000 m^3/capita/year)." Thereafter, from 1960 onwards, they write, "water shortage increased extremely rapidly, with the proportion of global population living under chronic water shortage increasing from 9% (280 million people) in 1960 to 35% (2300 million) in 2005." And currently, they continue, "the most widespread water shortage is in South Asia, where 91% of the population experiences some form of water shortage," while "the most severe shortage is in North Africa and the Middle East, where 77% and 52% of the total population lives under extreme water shortage (<500 m^3/capita/year), respectively."

To alleviate these freshwater shortages, Kummu et al. state measures generally have been taken to increase water availability, such as building dams and extracting groundwater. But they note "there are already several regions in which such measures are no longer sufficient, as there is simply not enough water available in some regions." In addition, they observe, "this problem is expected to increase in the future due to increasing population pressure (e.g. United Nations, 2009), higher welfare (e.g. Grubler et al., 2007) [and] production of water intensive biofuels (e.g. Varis, 2007, Berndes, 2008)." Hence, they conclude there will be an increasing need for many nonstructural measures, the first and foremost of which they indicate to be "increasing the efficiency of water use." This characteristic of nearly all of Earth's plants is almost universally promoted by atmospheric CO_2 enrichment.

References

Alcamo, J., Doll, P., Henrichs, T., Kaspar, F., Lehner, B., Rosch, T., and Siebert, S. 2003. Global estimates of water withdrawals and availability under current and future 'business-as-usual' conditions. *Hydrological Sciences Journal* **48**: 339–348.

Bengtsson, M., Shen, Y., and Oki, T. 2006. A SRES-based gridded global population dataset for 1990-2100. *Population & Environment* **28**: 113–131.

Berndes, G. 2008. Future biomass energy supply: the consumptive water use perspective. *International Journal of Water Resources Development* **24**: 235–245.

de Fraiture, C., Wichelns, D., Rockstrom, J., Kemp-Benedict, E., Eriyagama, N., Gordon, L.J., Hanjra, M.A., Hoogeveen, J., Huber-Lee, A., and Karlberg, L. 2007. Looking ahead to 2050: scenarios of alternative investment approaches. In *Comprehensive Assessment of Water Management in Agriculture. Water for Food, Water for Life: A Comprehensive Assessment of Water Management*, edited by D. Molden, 91–145. London, UK: Earthscan and Colombo, Sri Lanka: International Water Management Institute.

FAO (Food and Agriculture Organization). 2009. *State of Food Insecurity in the World 2009.* Rome, Italy: Food and Agriculture Organization.

Farrell, D. 2009. Feeding the future. *Livestock Research for Rural Development* **21**: 219. http://www.lrrd.org/lrrd21/12/farr21219.htm.

Godfray, H.C.J., Beddington, J.R., Crute, I.R., Haddad, L., Lawrence, D., Muir, J.F., Pretty, J., Robinson, S., Thomas, S.M., and Toulmin, C. 2010. Food security: the challenge of feeding 9 billion people. *Science* **327**: 812–818.

Grubler, A., O'Neill, B., Riahi, K., Chirkov, V., Goujon, A., Kolp, P., Prommer, I., Scherbov, S., and Slentoe, E. 2007. Regional., national, and spatially explicit scenarios of demographic and economic change based on SRES. *Technological Forecasting and Social Change* **74**: 980–1021.

Hanjra, M.A. and Qureshi, M.E. 2010. Global water crisis and future food security in an era of climate change. *Food Policy* **35**: 365–377.

Huang, J., Pray, C., and Rozelle, S. 2002. Enhancing the crops to feed the poor. *Nature* **418**: 678–684.

Idso, C.D. and Idso, K.E. 2000. Forecasting world food supplies: the impact of the rising atmospheric CO_2 concentration. *Technology* **7S**: 33–55.

Idso, K.E. and Idso, S.B. 1994. Plant responses to atmospheric CO_2 enrichment in the face of environmental constraints: a review of the past 10 years' research. *Agricultural and Forest Meteorology* **69**: 153–203.

Idso, S.B. and Kimball, B.A. 2001. CO_2 enrichment of sour orange trees: 13 years and counting. *Environmental and Experimental Botany* **46**: 147–153.

Kimball, B.A. 1983. Carbon dioxide and agricultural yield: an assemblage and analysis of 430 prior observations. *Agronomy Journal* **75**: 779–788.

Klein Goldewijk, K. 2005. Three centuries of global population growth: a spatial referenced population (density) database for 1700-2000. *Population and Environment* **26**: 343–367.

Klein Goldewijk, K., Beusen, A., and Janssen, P. 2010. Long-term dynamic modeling of global population and built-up area in a spatially explicit way: HYDE 3.1. *The Holocene* **20**: 565–573.

Kummu, M., Ward, P.J., de Moel, H., and Varis, O. 2010. Is physical water scarcity a new phenomenon? Global assessment of water shortage over the last two millennia. *Environmental Research Letters* **5**: 10.1088/1748-9326/5/3/034006.

Molden, D. 2007. Water responses to urbanization. *Paddy and Water Environment* **5**: 207–209.

Molden, D., Oweis, T., Steduto, P., Bindraban, P., Hanjra, M.A., and Kijne, J. 2010. Improving agricultural water productivity: between optimism and caution. *Agricultural Water Management* **97**: 528–535.

Oki, T. and Kanae, S. 2006. Global hydrological cycles and world water resources. *Science* **313**: 1068–1072.

Raven, P.H. 2002. Science, sustainability, and the human prospect. *Science* **297**: 954–959.

Renssen, H., Goosse, H., Fichefet, T., Brovkin, V., Driesschaert, E., and Wolk, F. 2005. Simulating the Holocene climate evolution at northern high latitudes using a coupled atmosphere-sea-ice-ocean-vegetation model. *Climate Dynamics* **24**: 23–43.

Sarkar, A., Rakwal, R., Agrawal, S.B., Shibato, J., Ogawa, Y., Yoshida, Y., Agrawal, G.K., and Agrawal, M. 2010. Investigating the impact of elevated levels of ozone on tropical wheat using integrated phenotypical, physiological, biochemical, and proteomics approaches. *Journal of Proteome Research* **9**: 4565–4584.

Saxe, H., Ellsworth, D.S., and Heath, J. 1998. Tree and forest functioning in an enriched CO_2 atmosphere. *New Phytologist* **139**: 395–436.

Tilman, D., Cassman, K.G., Matson, P.A., Naylor, R., and Polasky, S. 2002. Agricultural sustainability and intensive production practices. *Nature* **418**: 671–677.

Tilman, D., Fargione, J., Wolff, B., D'Antonio, C., Dobson, A., Howarth, R., Schindler, D., Schlesinger, W.H., Simberloff, D., and Swackhamer, D. 2001. Forecasting agriculturally driven global environmental change. *Science* **292**: 281–284.

United Nations. 2009. *World Population Prospects: The 2008 Revision.* Population Division of the Department of Economic and Social Affairs of the United Nations Secretariat. http://esa.un.org/unpp.

Varis, O. 2007. Water demands for bioenergy production. *International Journal of Water Resources Development* **23**: 519–535.

Vorosmarty, C.J., Green, P., Salisbury, J., and Lammers, R.B. 2000. Global water resources: vulnerability from climate change and population growth. *Science* **289**: 284–288.

Waggoner, P.E. 1995. How much land can ten billion people spare for nature? Does technology make a difference? *Technology in Society* **17**: 17–34.

Wallace, J.S. 2000. Increasing agricultural water use efficiency to meet future food production. *Agriculture, Ecosystems & Environment* **82**: 105–119.

Zhu, X.-G., Long, S.P., and Ort, D.R. 2010. Improving photosynthetic efficiency for greater yield. *Annual Review of Plant Biology* **61**: 235–261.

7.10.2. Prospects for Rice

Shimono et al. (2010) write, "by 2050, the world's population will have increased by about 37%, from the current level of 6.7 billion to an estimated 9.2 billion (United Nations, 2009), with a corresponding increase in global food demand." They note "about 0.6 billion Mg of rice is produced annually from an area of 1.5 million km^2, making rice one of the most important crops for supporting human life"; as noted by Pritchard and Amthor (2005), it supplies the planet's human population with an estimated 20 percent of its energy needs (on a caloric basis) and 14 percent of its protein requirements (on a weight basis).

The six scientists further note "rice production depends heavily on water availability," stating "irrigated lowlands account for 55% of the total area of harvested rice and typically produce two to three times the crop yield of rice grown under non-irrigated conditions (IRRI, 2002)." With the demand for water continuing to rise in order to feed our growing numbers, they conclude, "efficient use of water will thus be essential for future rice production."

To determine how agricultural productivity may be impacted by the ongoing rise in the air's CO_2 content, the Japanese researchers conducted a two-year free-air CO_2 enrichment (FACE) study in fields at Shizukuishi, Iwate (Japan) to learn how elevated CO_2 might reduce crop water use via its impact on the leaf stomatal conductance (g_s) of three varieties of rice (*Oryza sativa* L.): early maturing Kirara397, intermediate-maturing Akitakomachi, and latest-maturing Hitomebore.

In response to the 53 percent increase in daytime atmospheric CO_2 concentration employed in their experiments, Shimono et al. found "the reduction in g_s due to elevated CO_2 was similar across measurements, averaging around 20% in the morning, 24% around noon and 23% in the afternoon across all growth stages." They also note "there was no significant CO_2 x cultivar interaction."

Also focusing on rice were Xiong et al. (2009), who began their study by noting "rice is an essential component of the diet in more than half the world's population, and it is the most socially and economically important crop in China," where they say it "contributes 43.7% of total national grain production," citing Yao et al. (2007). Xiong et al. "assessed the effect of greenhouse gas-induced climate change, as well as the direct fertilization effect of CO_2, on rice yields and production in China," by coupling "the regional climate model PRECIS (Providing Regional Climates for Impacts Studies) with the CERES (Crop Environment Resources Synthesis) rice crop model to simulate current (1961–1990) and future (2011–2100) rice yields and production under [the] A2 and B2 climate change scenarios" of the Intergovernmental Panel on Climate Change.

The four researchers report that with anticipated climate changes, "single rice cropping may expand further north in China, and double rice cropping may move to the northern portion of the Yangtze River basin." In addition, they state "the national mean rice production is estimated to increase by 2.7 to 19.2% considering the combined effects of climate change, CO_2 and shifting rice-producing areas." Thus, even considering the inflated temperature increases predicted by the IPCC, the estimated net effect of global warming and concomitant growth in anthropogenic CO_2 emissions ends up producing an increase in rice production in the world's most populous country, where it is the people's single most important food source.

In another study of rice's role in world food security, Yang et al. (2009) begin by noting (1) "rice is unequivocally one of the most important food crops that feed the largest proportion of the world's population," (2) "the demand for rice production will continue to increase in the coming decades, especially in the major rice-consuming countries of Asia, Africa and Latin America," and (3) "accurate predictions of rice yield and of the ability of rice crops to adapt to high CO_2 environments are therefore crucial for understanding the impact of climate change on the future food supply." They forcefully declare, "there is a pressing need to identify genotypes which could optimize harvestable yield as atmospheric CO_2 increases."

They set out to do so in a standard paddy culture FACE experiment conducted at Yangzhou, Jiangsu, China, in 2004–2006. Yang et al. grew a two-line inter-subspecific hybrid rice variety (Liangyoupeijiu) at ambient and elevated atmospheric CO_2 concentrations of 376 and 568 ppm, respectively, at two levels of field nitrogen (N) application: low N (12.5 g N m^{-2}) and high N (25 g N m^{-2}), measuring numerous aspects of crop growth, development, and final yield production in the process. Their "bottom-line" finding was that the 51 percent increase in atmospheric CO_2 concentration increased the final grain yield of the low N rice crop by 28 percent and that of the high N rice crop by 32 percent. As a result, and "compared with the two prior rice FACE experiments (Kim et al., 2003; Yang et al., 2006)," they report "hybrid rice appears to profit much more from CO_2 enrichment than inbred rice cultivars (c. +13%)." Little wonder, then, that Yang et al. describe Liangyoupeijiu as "one of the most popular 'super' hybrid rice varieties in China (Peng et al., 2004)."

Highlighting an especially important aspect of the role of atmospheric CO_2 enrichment in promoting rice production, Feng et al. (2009) write, "purple phototrophic bacteria (PPB) are thought to be crucial in the nutrient cycling of rice fields." The Chinese researchers note PPB "thrive in the anaerobic portions of all kinds of aquatic environments, and have long been recognized as one of the key players in global carbon and nitrogen cycles." Against this backdrop, therefore, in a FACE study conducted within a rice/wheat rotation system at the Nianyu Experimental Station in Jiangsu Province, China, they grew rice (*Oryza sativa* L.) plants under standard paddy culture at two levels of soil nitrogen (N) fertility—low (150 kg N/hectare) and high (250 kg N/hectare)—at ambient and ambient plus 200 ppm CO_2 concentrations, while measuring several characteristics of PPB within the rhizosphere and bulk soils of the two CO_2 treatments.

The seven scientists found "elevated CO_2 appeared to enhance the biodiversity of PPB in flooded paddy soils"; "PPB abundance was stimulated by elevated CO_2 in bulk soil"; and "N fertilization enhanced the biodiversity of PPB under elevated atmospheric CO_2." Feng et al. highlight the significance of these findings by noting "PPB inoculation into the flood water [in rice paddy culture] could lead to grain yield increase by 29% (Elbadry et al., 1999; Harada et al., 2005)," and "PPB are thought to be capable of fixing nitrogen." Thus these two phenomena—enhanced by the ongoing rise in the air's CO_2 content—can help provide the boost in food production that will be needed to feed the planet's still-growing human population in the years and decades ahead.

Turning to the effect of warming on cultivation, Dong et al. (2009) state "the annual mean surface air temperature in China has increased 1.1°C over the past 50 years," adding that "striking warming has occurred since the mid-1980s, particularly in northern China." Noting annual accumulated temperatures greater than 10°C (AAT10) represent "an important indicator of thermal conditions in crop ecology (Qiu and Lu, 1980; Bai et al., 2008)," which "affects the choice of crop varieties, the crop calendar, cropping systems and crop patterns (Zheng et al., 2008)," the five Chinese scientists decided to "assess the relationship between accumulated temperature change and cultivated land use in China from the late 1980s to 2000," in order to determine the impact of the dramatic warming on the nation's agriculture.

They found "since the late 1980s, AAT10 has noticeably risen in most of China." More specifically, Dong et al. indicate 1.22×10^{15} km^2 of land moved from the potato accumulated temperature zone (ATZ) to the spring wheat ATZ, that 3.16×10^{15} km^2 of land moved from the spring wheat ATZ to the winter wheat ATZ, and that 1.64×10^{15} km^2 of land moved from the winter wheat ATZ to the rice ATZ. In addition, they determined "because of improved thermal conditions since the late 1980s," farmers changed from a single crop per year to three crops in two years in many regions, while "the growth boundary of winter wheat moved northward."

With respect to the cropping index, which they define as the number of crops grown per year on a given area of land, the researchers from the Chinese Academy of Sciences state, "as a result of climate warming on a national scale, it is feasible for the cropping index to improve." They report that, indeed, "cropping indices have improved in many regions since the 1980s," citing the studies of Yan et al. (2005) and Li et al. (2008). Hence, they indicate "to acquire higher yields of food and income, people have improved the cropping index in regions that had previously been difficult to crop and also in some areas where the index was low."

The past century's increasing temperature and atmospheric CO_2 concentration have not in any way hurt the people of China. Quite to the contrary, they have improved the country's capacity to provide the quantities of food needed to support its population.

Much the same can be said of Canada. Working with a homogenized temperature dataset consisting of daily maximum and minimum air temperatures for the period 1895–2007 obtained from 210 meteorological stations distributed across the country, plus an adjusted precipitation dataset developed at the Climate Research Division of Environment Canada, Qian et al. (2010) derived a set of agroclimatic indices that are sure to prove useful for agricultural production planning purposes for many years to come. They report, for example, that their results indicate "a significant lengthening of the growing season due to a significantly earlier start and a significantly later end of the growing season," and they state "significant positive trends are also observed for effective growing degree-days and crop heat units at most locations across the country." They also report "the occurrence of extremely low temperatures has become less frequent during the non-growing season, implying a more favorable climate for overwinter survival," and "the total numbers of cool days, frost days, and killing-frost days within a growing season have a decreasing trend," so "crops may also be less vulnerable to cold stress and injury during the growing season." They also found "extreme daily precipitation amounts and 10-day precipitation totals during the growing season have been increasing," and "significant trends associated with increased availability of water during the growing season are identified."

These desirable results clearly indicate the global warming that brought an end to the debilitating cold of the Little Ice Age and ushered the planet into the Current Warm Period is proving to be a real boon to Canada, as well as to the rest of the world, which may have to depend upon North America's northernmost country to supply a significant portion of the food that will be required to support Earth's burgeoning human population in the decades to come.

References

Bai, Q.F., Huo, Z., Li, S., Du, H., He, N., and Jiang, Y. 2008. Comparison of accumulated temperature above 10°C before and after the year 1978 in China. *Chinese Journal of Applied Ecology* **19**: 1810–1816.

Dong, J., Liu, J., Tao, F., Xu, X., and Wang, J. 2009. Spatio-temporal changes in annual accumulated temperature in China and the effects on cropping systems, 1980s to 2000. *Climate Research* **40**: 37–48.

Elbadry, M., Gamal-Eldin, H., and Elbanna, K. 1999. Effects of *Rhodobacter capsulatus* inoculation in combination with graded levels of nitrogen fertilizer on growth and yield of rice in pots and lysimeter experiments. *World Journal of Microbiology and Biotechnology* **15**: 393–395.

Feng, Y., Lin, X., Wang, Y., Zhang, J., Mao, T., Yin, R., and Zhu, J. 2009. Free-air CO_2 enrichment (FACE) enhances the biodiversity of purple phototrophic bacteria in flooded paddy soil. *Plant and Soil* **324**: 317–328.

Harada, N., Nishiyama, M., Otsuka, S., and Matsumoto, S. 2005. Effects of inoculation of phototrophic bacteria on grain yield of rice and nitrogenase activity of paddy soil in a pot experiment. *Soil Science and Plant Nutrition* **51**: 361–367.

IRRI (International Rice Research Institute). 2002. *Rice Almanac: Source Book for the Most Important Economic Activity on Earth.* Oxfordshire, UK: CABI Publishing.

Kim, H.Y., Lieffering, M., Kobayashi, K., Okada, M., Mitchell, M.W., and Gumpertz, M. 2003. Effects of free-air CO_2 enrichment and nitrogen supply on the yield of temperate paddy rice crops. *Field Crops Research* **83**: 261-270.

Li, J., Gao, P., Chen, Y.C., Chen, H., and Yang, T.M. 2008. Relationships between farming system and effective accumulated temperature in East China. *Chinese Journal of Ecology* **27**: 361–368.

Peng, S., Laza, R.C., Visperas, R.M., Khush, G.S., Virk, P., and Zhu, D. 2004. Rice: progress in breaking the yield ceiling. In *New Directions for a Diverse Planet: Proceedings of the Fourth International Crop Science Congress*, 26 Sep-1 Oct 2004, Brisbane, Australia. Gosford, Australia: Regional Institute Ltd.

Pritchard, S.G. and Amthor, J.S. 2005. *Crops and Environmental Change.* New York, NY: Food Production Press.

Qian, B., Zhang, X., Chen, K., Feng, Y., and O'Brien, T. 2010. Observed long-term trends for agroclimatic conditions in Canada. *Journal of Applied Meteorology and Climatology* **49**: 604–618.

Qiu, B. and Lu, Q. 1980. A tentative regionalization of agroclimate of China. *Acta Geographica Sinica* **35**: 116–125.

Shimono, H., Okada, M., Inoue, M., Nakamura, H., Kobayashi, K., and Hasegawa, T. 2010. Diurnal and seasonal variations in stomatal conductance of rice at elevated atmospheric CO_2 under fully open-air conditions. *Plant, Cell and Environment* **33**: 322–331.

United Nations. 2009. *The 2006 World Population Prospects. The 2008 Revision Population Database.* New York, NY: United Nations. Available at http://esa.un.org/unpp/.

Xiong, W., Conway, D., Lin, E., and Holman, I. 2009. Potential impacts of climate change and climate variabiity on China's rice yield and production. *Climate Research* **40**: 23–35.

Yan, H., Liu, J., and Cao, M. 2005. Remotely sensed multiple cropping index variations in China during 1981–2000. *Acta Geographica Sinica* **60**: 559–566.

Yang, L., Liu,. H., Wang, Y., Zhu, J., Huang, J., Liu, G., Dong, G., and Wang, Y. 2009. Yield formation of CO_2-enriched inter-subspecific hybrid rice cultivar Liangyoupeijiu under fully open-air condition in a warm sub-tropical climate. *Agriculture, Ecosystems and Environment* **129**: 193–200.

Yang, L.X., Huang, J.Y., Yang, H.J., Zhu, J.G., Liu, H.J., Dong, G.C., Liu, G., Han, Y., and Wang, Y.L. 2006. The impact of free-air CO_2 enrichment (FACE) and N supply on yield formation of rice crops with large panicle. *Field Crops Research* **98**: 141–150.

Yao, F.M., Xu, Y.L., Lin, E.D., Yokozawa, M., and Zhang, J.H. 2007. Assessing the impacts of climate change on rice yields in the main rice areas of China. *Climatic Change* **80**: 395–409.

Zheng, D., Ou, Y., and Zhou, C.H. 2008. Understanding of and thinking over geographical regionalization methodology. *Acta Geographica Sinica* **63**: 563–573.

7.10.3. Pigeon Peas

Citing Sinha et al. (1998), Vanaja et al. (2010) write, "food grain requirements of India (both human and cattle) are estimated at 300 Mt in 2020," and they note "grain legumes are one of the mainstays of the drylands, as these crops provide much needed nutritional security in the form of proteins to the predominant vegetarian populations of India and also the world." They state that legumes, of which pigeon peas are an important example, "have the potential to maximize the benefit of elevated CO_2 by matching stimulated photosynthesis with increased N_2 fixation," citing Rogers et al. (2009).

With this in mind, Vanaja et al. grew pigeon peas (*Cajanus cajan* L. Millsp.) from seed to maturity outdoors at Hyderabad (India) within open-top chambers maintained at atmospheric CO_2 concentrations of either 370 or 700 ppm (ambient or enriched, respectively). They then harvested them and measured several pertinent productivity parameters. The team of nine Indian scientists from their country's Central Research Institute for Dryland Agriculture determined "total biomass recorded an improvement of 91.3%, grain yield 150.1% and fodder yield 67.1%." They also state "the major contributing components for improved grain yield under elevated CO_2 were number of pods, number of seeds and test weight," which exhibited increases of 97.9 percent, 119.5 percent, and 7.2 percent, respectively. In addition, they found there was "a significant positive increase of harvest index at elevated CO_2 with an increment of 30.7% over ambient values," which they say was due to the crop's "improved pod set and seed yield under enhanced CO_2 concentration." These very positive findings, in the words of Vanaja et al., illustrate the importance of pigeon peas for "sustained food with nutritional security under a climate change scenario."

References

Rogers, A., Ainsworth, E.A., and Leakey A.D.B. 2009. Will elevated carbon dioxide concentration amplify the benefits of nitrogen fixation in legumes? *Plant Physiology* **151**: 1009–1016.

Sinha, S.K., Kulshreshtha, S.M., Purohit, A.N., and Singh, A.K. 1998. Base Paper. *Climate Change and Perspective for Agriculture*, 20. New Delhi, India: National Academy of Agricultural Sciences.

Vanaja, M., Reddy, P.R.R., Lakshmi, N.J., Razak, S.K.A., Vagheera, P., Archana, G., Yadav, S.K., Maheswari, M., and Venkateswarlu, B. 2010. Response of seed yield and its components of red gram (*Cajanus cajan* L. Millsp.) to elevated CO_2. *Plant, Soil and Environment* **56**: 458–462.

7.10.4. CO_2 Enrichment for Crops

Noting the CO_2 concentrations in greenhouses may range from 100 to 250 ppm during the day due to their being tightly sealed (concentrations that are suboptimal for growth), Jin et al. (2009) proposed "a new strategy of CO_2 enrichment," wherein they compost crop residues and animal manure (CRAM) "directly in the greenhouse." The composting units they designed to demonstrate this low-tech approach to enriching greenhouse air with CO_2 were made of wood and had a height of 1.2 meters and diameter of 0.6 meter. The unit's bottom was constructed of 6-cm-wide wood bars with a 2-cm-wide interval between them that ensured sufficient aeration. The composting material consisted of 25 kg of crop residue (rice straw, in their case) and 8 kg of moist manure, to which mixture 90 liters of water were added initially, after which the mixture was kept at a moisture content of approximately 70 percent. Then the CRAM mixture was inoculated with three different species of fungi (*Panusconclmtw* zj3, *Trichoderma viride* zj2, and *Aspergillas niger* zj1), to increase CO_2 production via accelerated fermentation. And "to prevent NH_3 emission from the compost into the greenhouse," as they describe it, "a sponge layer permeated with 2 M H_2SO_4 was placed on top of the composting mixture to trap volatizing NH_3."

The six scientists tested their technique in three pairs of greenhouses placed over a uniform soil surface, in which they planted celery (*Apium graveolens* L.), leaf lettuce (*Lactuca virosa* L.), stem lettuce (*Lactuca saiva* L.), oily sowthistle (*Sonchus oleraceus* L.), and Chinese cabbage (*Brassica chinensis* L.). One of each of these greenhouse pairs acted as a control, while the other housed one of their low-tech CO_2 generators, which they emptied every 21 days onto an adjacent field to provide it with an organic fertilizer over the course of their 63-day growing season. As best as can be determined from Jin et al.'s graphs of the hourly CO_2 measurements they made on specific days, as well as every-day or every-other-day measurements of CO_2 made at one specific time of day, mean daylight CO_2 concentrations in the CO_2-enriched greenhouses were just a little over twice as great as those measured in the control greenhouses. As for the effects of this slightly more than doubling of the air's CO_2 content, they report, "the average percentage of yield increases of all three sites were 270%, 257%, 87%, 140% and 227% for celery, leaf lettuce, stem lettuce, oily sowthistle, and Chinese cabbage, respectively." In addition, they state the extra CO_2 from the composting units increased the concentration of vitamin C in all five species: "by 13%, 39%, 25%, 72% and 37% for celery, leaf lettuce, stem lettuce, oily sowthistle, and Chinese cabbage, respectively."

The five Chinese researchers and their Australian collaborator conclude their CRAM procedure "is an efficient way to elevate CO_2 concentrations," that it "represents a simple, cheap and adoptable management tool for use in greenhouse vegetable production," and that its "use of crop residues and animal manures decreases the possible environmental problems caused by burning and [other less-than-desirable] practices of disposal of these agricultural by-products." Considering these environmental benefits, the increased crop yields, and the increased nutritive value of the edible produce they harvested, Jin et al.'s low-tech approach to enriching greenhouse air with CO_2 would appear to be a winning proposition, especially where it may not feasible to employ more sophisticated techniques.

Reference

Jin, C., Du, S., Wang, Y., Condon, J., Lin, X., and Zhang, Y. 2009. Carbon dioxide enrichment by composting in greenhouses and its effect on vegetable production. *Journal of Plant Nutrition and Soil Science* **172**: 418–424.

7.11. Greening of the Earth

In light of what we know about the aerial fertilization and anti-transpirant effects of atmospheric CO_2 enrichment, we would expect Earth's terrestrial plant life to become increasingly productive as the air's CO_2 content continues to rise, even in the face of rising air temperatures. The following sections highlight real-world evidence about plant productivity as CO_2 increases.

7.11.1. Africa

Ciais et al. (2009) modeled the terrestrial carbon balance of Africa over the past century (1901–2002) using a spatially resolved, process-based vegetation model (ORCHIDEE), which is forced by changing climate, human-induced changes in land use, and a parameterization of natural fires. They found "the African net terrestrial carbon (C) balance increased from a net CO_2 source to the atmosphere of 0.14 Pg C per year in the 1980s to a net sink of 0.15 Pg C per year in the 1990s." In addition, they state the land use flux due to deforestation was "a source of 0.13 Pg C per year," and "this implies that climatic trends (mainly increasing precipitation) and CO_2 increase (the fertilization effect), are causing a sink of 0.28 Pg C per year which offsets the land-use source."

The five researchers also indicate "the trend of gross primary production is closely matching the trend in satellite observed NDVI," or Normalized Difference Vegetation Index, and they note their simulated trend in gross primary production "is also consistent with an increased vegetation activity over [the] Sahel reported by Eklundh and Olsson (2003) and Olsson et al. (2005)," while at the continental scale the gross primary production trend can be largely (70 percent) explained by the CO_2 fertilization effect. Primarily in response to the ongoing rise in the air's CO_2 content, therefore, it would appear from the results of this study that the African continent is significantly "greening up," and that it has been doing so recently at a significantly enhanced rate.

Examining what might be next for Africa, Doherty et al. (2010) modeled future changes in land biogeochemistry and biogeography in the region bounded by 12.5°N, 12.5°S, 25°E, and 42.5°E, representing most of East Africa (Kenya, Tanzania, Uganda, Rwanda, Burundi, Ethiopia, and Somalia), and portions of Central Africa (the Democratic Republic of Congo and Southern Sudan). They did this using 18 future climate projections derived from nine general circulation models that figured prominently in the IPCC's Fourth Assessment Report, employing the projections as input to the Lund-Potsdam-Jena dynamic global vegetation model that simulates changes in vegetation and ecosystem carbon cycling under future climate conditions, based on what they describe as "a coupled photosynthesis-hydrological scheme [that] computes gross primary productivity, plant respiration, and evapotranspiration on a daily time step based on the current climate, atmospheric CO_2 concentration, vegetation structure and phenological state, and soil water content."

Doherty et al. report "all simulations showed future increases in tropical woody vegetation over the region at the expense of grasslands," noting "regional increases in net primary productivity (18–36%) and total carbon storage (3–13%) by 2080–2099 compared with the present-day were common to all simulations," and "seven out of nine simulations continued to show an annual net land carbon sink in the final decades of the 21st century because vegetation biomass continued to increase." The researchers conclude "overall, our model results suggest that East Africa, a populous and economically poor region, is likely to experience some ecosystem service benefits through increased precipitation, river runoff and fresh water availability," and they state "resulting enhancements in net primary productivity may lead to improved crop yields in some areas." They specifically state their results "stand in partial contradiction of other studies that suggest possible negative consequences for agriculture, biodiversity and other ecosystem services caused by temperature increases."

Regarding the continent as a whole, Scheiter and Higgins (2009) write, "recent IPCC projections suggest that Africa will be subject to particularly severe changes in atmospheric conditions" in the decades ahead, and these changes could have severe repercussions for its flora and fauna. However, they say that how the continent's "grassland-savanna-forest complex will respond to these changes has rarely been investigated," and "most studies on global carbon cycles use vegetation models that do not adequately account for the complexity of the interactions that shape the distribution of tropical grasslands, savannas and forests."

In an attempt to overcome these shortcomings, the two scientists developed a new vegetation model—the adaptive dynamic global vegetation model (aDGVM)—that employs established sub-models for photosynthesis, respiration, canopy scaling, competition for water, competition for light, reproduction, and mortality, and which additionally contains the novel elements of dynamic carbon allocation and phenology functions. They also employed a fire model that estimates fire intensity as a function of fuel biomass, fuel moisture, and wind speed and simulates topkill (stem mortality) as a function of individual tree size and fire intensity. All of these phenomena are related to the individual plant's physiological state and the environmental conditions surrounding it.

Forward simulations to the year 2100 with this model suggest, in the words of the two researchers, that "grasslands will spread into the Sahara and into the horn of Africa, such that the total area covered by deserts or bare soil decreases by 5.7%." In addition, they write, "it is predicted that 34.6% of today's grasslands are transformed into savannas" and "45.3% of today's savannas are transformed into deciduous woodlands." Hence, "the total biomass stored in each of the biomes increases, with high relative changes in grasslands and savannas (by 256% and 241%, respectively)" and a 102 percent increase in tree biomass.

In conclusiuon, the CO_2- and warming-induced greening of the Earth, which has been manifest throughout the world over the past few decades, seems destined to continue through the twenty-first century in Africa with positive results for plant and animal life.

References

Ciais, P., Piao, S.-L., Cadule, P., Friedlingstein, P., and Chedin, A. 2009. Variability and recent trends in the African terrestrial carbon balance. *Biogeosciences* **6**: 1935–1948.

Doherty, R.M., Sitch, S., Smith, B., Lewis, S.L., and Thornton, P.K. 2010. Implications of future climate and atmospheric CO_2 content for regional biogeochemistry, biogeography and ecosystem services across East Africa. *Global Change Biology* **16**: 617–640.

Eklundh, L. and Olsson, L. 2003. Vegetation index trends for the African Sahel 1982–1999. *Geophysical Research Letters* **30**: 10.1029/2002GL016772.

Olsson, L., Eklundh, L., and Ardo, J. 2005. A recent greening of the Sahel, trends, patterns and potential causes. *Journal of Arid Environments* **63**: 556–566.

Scheiter, S. and Higgins, S.I. 2009. Impacts of climate change on the vegetation of Africa: an adaptive dynamic vegetation modeling approach. *Global Change Biology* **15**: 2224–2246.

7.11.2. Forests

McMahon et al. (2010) note "there are indications that forest biomass accumulation may be accelerating where nutrients and water are not limiting," citing Myneni et al. (1997), Lewis et al. (2004), Lewis et al. (2009a), Boisvenue and Running (2006), Delpierre et al. (2009), Salzer et al. (2009), and Chave et al. (2008). They further investigate the subject because of the great significance such a phenomenon would hold for the planet's carbon balance and the future course of potential CO_2-induced global warming. Using unique datasets of tree biomass collected over the past 22 years from 55 temperate forest plots with known land-use histories and stand ages ranging from five to 250 years—which were derived from knowledge of when the stands had begun to regrow following major disturbances such as significant logging, various natural disasters that had decimated large patches of trees, or the clearing of trees to make room for agriculture that was ultimately abandoned—McMahon et al. "estimated biomass change, while controlling for stand regeneration." They did this within various parts of a temperate deciduous forest in the vicinity of the Smithsonian Environmental Research Center, Edgewater, Maryland (USA) by comparing recent (last 22 years or less) rates of biomass accumulation of the various stands with rates predicted for those age intervals by the overall growth function derived from the combined data of all of the stands. Finally, they compared their findings with "over 100 years of local weather measurements and 17 years of on-site atmospheric CO_2 measurements."

The three researchers report "recent biomass accumulation greatly exceeded the expected growth caused by natural recovery," noting that in stands younger than 50 years the observed increase was generally at least one-third of total growth, and in older stands it typically was "the majority of growth," even though past experience and the ensemble relationship of growth vs. age derived from the totality of their data suggest "old forests should grow very little as they approach equilibrium." As for what could have caused the tremendous recent increases in forest plot growth rates detected by the Smithsonian scientists, they state "increases in temperature, growing season [which is largely driven by temperature], and atmospheric CO_2 have documented influences on tree physiology, metabolism, and growth," and they state these global-change factors—the magnitudes of which rose significantly over the course of their study—may have been "critical to changing the rate of stand growth observed across stands." Such findings and this explanation provide additional important evidence for the greening of the Earth phenomenon that is transforming the face of the planet as the air's CO_2 content continues to rise.

Further north, satellite studies based on Normalized Difference Vegetation Index (NDVI) data have produced conflicting trend estimates, ranging from greening to browning, for the boreal forest zone of Canada. In an attempt to resolve this disagreement, Alcaraz-Segura et al. (2010) argue that a significant factor not considered in past studies is fire history. If points in time are compared before and after a fire, for example, NDVI will be seen to have decreased, but not for the reason for which the data were sought.

Similarly, trends that begin right after a fire will show increasing NDVI that is unrelated to climate factors, as the vegetation recovers from fire. Hence, they use this latter phenomenon of vegetation recovery after fire as a ground-truth test for two satellite datasets.

Working with GIMMS satellite data that represent 64-km^2 cells and newly available CCRS data that represent 1-km^2 cells, the five researchers used an algorithm shown to detect recent fires to correctly classify pixels as burned or not-burned, comparing the performance of the two datasets for detecting trends. They found the GIMMS data were unable to properly detect increases in NDVI over time in burned areas compared to the CCRS data, and that GIMMS data are thus a poor choice for this type of study. The CCRS data, on the other hand, detected strong greening in burned areas (as expected) and a weaker but consistent greening in unburned forest areas over 1996 to 2006. As a result, Alcaraz-Segura et al. suggest (1) the widely-used GIMMS data may have produced false results in other studies and should be used with caution, (2) satellite data need to be better calibrated with ground data before use, and (3) the greening of the Canadian boreal forest is probably real for the most recent decades.

Although many high-latitude regions may indeed be experiencing greening due to increases in the air's CO_2 content, as well as concomitant warming that allows crops and forests to grow where it has previously been too cold for them to survive, some researchers worry about Earth's tropical regions, where they claim just a little extra warming may spell disaster for local forests. Consequently, in a thorough review of the scientific literature on this important subject, Lewis et al. (2009b) evaluated tropical forest inventory data, plant physiology experiments, ecosystem flux observations, Earth observations, atmospheric measurements, and dynamic global vegetation models, which "taken together," in their words, "provide new opportunities to cross-validate results."

The five researchers note both theory and experiments suggest over the past several decades "plant photosynthesis should have increased in response to increasing CO_2 concentrations, causing increased plant growth and forest biomass." And they did indeed find "long-term plot data collectively indicate an increase in carbon storage, as well as significant increases in tree growth, mortality, recruitment, and forest dynamism." They also state satellite measurements "indicate increases in productivity and forest dynamism," and five Dynamic Global Vegetation Models, incorporating plant physiology, competition, and dynamics, all predict increasing gross primary productivity, net primary productivity, and carbon storage when forced using late-twentieth century climate and atmospheric CO_2 concentration data. In addition, they state "the predicted increases in carbon storage via the differing methods are all of similar magnitude (0.2% to 0.5% per year)."

"Collectively," they conclude, "these results point toward a widespread shift in the ecology of tropical forests, characterized by increased tree growth and accelerating forest dynamism, with forests, on average, getting bigger (increasing biomass and carbon storage)." Far from being the bane of the Earth's tropical forests, twentieth-century increases in air temperature and atmospheric CO_2 concentration—which have returned these meteorological parameters to more normal post-Little Ice Age values—have been a great boon to the trees of the tropics.

Commenting on this state of affairs, Gloor et al. (2009) reiterated that "large-scale changes in forest dynamics are currently occurring in Amazonia (Phillips and Gentry, 1994; Phillips et al., 2004), and that an increase in aboveground biomass has occurred, with increases in mortality tending to lag increases in growth (Phillips et al., 1998; Baker et al., 2004a,b; Lewis et al., 2004)." However, they state this conclusion has been challenged recently by an overzealous application of the "Slow in, Rapid out" dictum, which recognizes that forest growth is a slow process, whereas mortality can be dramatic and singular in time, such that sampling over relatively short observation periods may miss these more severe events, leading to positively biased estimates of aboveground biomass trends, when either no trend or negative trends actually exist.

To test this claim, Gloor et al. statistically characterized "the disturbance process in Amazon old-growth forests as recorded in 135 forest plots of the RAINFOR network up to 2006, and other independent research programs, and explore the consequences of sampling artifacts using a data-based stochastic simulator." They found "over the observed range of annual aboveground biomass losses, standard statistical tests show that the distribution of biomass losses through mortality follow an exponential or near-identical Weibull probability distribution and not a power law as assumed by others." In addition, they state "the simulator was parameterized using both an exponential disturbance probability distribution as well as a mixed exponential-power law distribution to account for potential large-scale blow-down events," and they report "in both cases, sampling biases turn out to be too small to explain the gains detected by the extended RAINFOR plot network."

Gloor et al. therefore conclude their results lend "further support to the notion that currently observed biomass gains for intact forests across the Amazon are actually occurring over large scales at the current time, presumably as a response to climate change," which in many of their earlier papers is explicitly stated to include the aerial fertilization effect of the historical increase in the air's CO_2 content.

In another of several contemporaneous studies, Silva et al. (2009) describe *Araucaria angustifolia* as "an indigenous conifer tree restricted to the southern region of South America that plays a key role in the dynamics of regional ecosystems where forest expansion over grasslands has been observed." Working with various types of tree-ring data obtained from such trees growing in both forest and grassland sites in southern Brazil, they compared changes in intrinsic water use efficiency—iWUE, defined as the ratio of the rate of CO_2 assimilation by the trees' needles to their stomatal conductance—with concomitant historical changes in temperature, precipitation, and atmospheric CO_2 concentration over the past century.

They found "iWUE increased over 30% in both habitats" over the past several decades, and "this increase was highly correlated with increasing levels of CO_2 in the atmosphere." Tree growth, however, remained rather stable, due to lower-than-normal precipitation and higher-than-normal temperatures, which would normally tend to depress the growth of this species—Katinas and Crisci (2008) describe *A. angustifolia* as being "intolerant of dry seasons and requiring cool temperatures." Therefore, Silva et al. conclude the "climatic fluctuations during the past few decades," which would have been expected to have been deleterious to the growth of *A. angustifolia*, seem to have had their growth-retarding effects "compensated by increases in atmospheric CO_2 and changes [i.e., increases] in iWUE."

Also dealing with the expansion of forests onto grasslands were Springsteen et al. (2010), who write, "woody plant expansion within grassland ecosystems is a worldwide phenomenon, and dramatic vegetation shifts from grassland to savanna/woodlands have occurred over the past 50–100 years in North America," while noting one of the chief factors that has contributed to this phenomenon is believed by many to have been the increase in the air's CO_2 content, as suggested by Archer et al. (1995), Polley (1997), Bond and Midgley (2000), and Bond et al. (2003). They also note once shrublands are established, they tend to persist for several different reasons, one of which is a type of feedback phenomenon referred to as islands of fertility, which "occurs when resources accumulate in soils beneath woody plants due to litterfall, interception of wet and dry deposition, nitrogen fixation, and animal droppings," as described by Schlesinger et al. (1990), Archer et al. (1995), Reynolds et al. (1999), and Lopez-Pintor et al. (2006). They report "changes in soil attributes under woody vegetation have been documented in the arid grasslands of the southern Great Plains, including increases in soil carbon and nitrogen," citing Reynolds et al. (1999), Hibbard et al. (2001, 2003), McCulley et al. (2004), Schade and Hobbie (2005), and Liao et al. (2006).

For their part of this massive undertaking—while working at the USDA-ARS Northern Great Plains Research Laboratory near Mandan, North Dakota (USA)—Springsteen et al. examined near-surface (upper 15 cm) soil biogeochemistry along a 42-year (1963–2005) chronosequence that encompassed grassland, woodland, and grassland-woodland transition zones in a northern Great Plains grassland, in order to determine the influence of woody plant expansion on soil carbon and nitrogen contents. They found total soil carbon content rose by 26 percent across the chronosequence from grassland to woodland within the 0–15 cm soil depth, and total soil nitrogen content rose by 31 percent. The rate of woody shrub expansion from 1963 to 1988 (25 years) was ~1,800 m^2 per year at their study site, whereas from 1988 to 2005 (17 years) it was ~3,800 m^2 per year, or a little more than double the initial rate, as the greening of the Earth accelerated to keep pace with the accelerating increase of the air's CO_2 content.

In the U.S. mid-Atlantic region, Pan et al. (2010) examined "how changes in atmospheric composition (CO_2, O_3 and N deposition), climate and land-use affected carbon dynamics and sequestration in Mid-Atlantic temperate forests during the 20th century." They modified and applied "a well established process-based ecosystem model with a strong foundation of ecosystem knowledge from experimental studies," which they validated "using the U.S. Forest Inventory and Analysis (FIA) data."

For previously harvested and currently regrowing forests, the calibrated model produced the following percentage changes in net ecosystem productivity (NEP) due to observed changes in N deposition (+32 percent), CO_2 (+90 percent), O_3 (-40 percent), CO_2 + O_3 (+60 percent), CO_2 + N deposition (+184 percent), and CO_2 + N deposition + O_3 (+138 percent), while corresponding changes in NEP for undisturbed forests were +18 percent, +180 percent, -75 percent, +78 percent, +290 percent, and +208 percent. The model results also revealed "the 'fertilization' effect of N deposition mainly stimulates carbon allocation to short-lived tissues such as foliage and fine roots," but "the 'fertilization' effect by elevated CO_2 likely enhances more sustainable carbon storage such as woody biomass (including coarse roots)." The four USDA Forest Service scientists state their findings indicate "the change in atmospheric composition, particularly elevated CO_2, will gradually account for more of the carbon sink of temperate forests in the Mid-Atlantic region," and they conclude "such a significant 'fertilization effect' on the forest carbon sequestration could eventually result in a 'greener world' after a long period of chronic change in atmospheric composition and cumulative impact."

Martinez-Vilalta et al. (2008) used tree-ring data from the Catalan Ecological and Forest Inventory "to study the temporal variability of Scots pine stem radial growth (period 1901–1997) across a relatively large region (Catalonia, NE Spain) situated close to the southern limit of the distribution of the species." This inventory "included a total of 10,664 plots randomly distributed throughout the forested area of Catalonia," where Scots pine was present in 30.2 percent of the plots and was the dominant tree species in 18.4 percent of the plots. The inventory "showed an overall increase of 84% in Scots pine BAI [basal area increment] during the twentieth century, consistent with most previous studies for temperate forests." The scientists state "this trend was associated with increased atmospheric CO_2 concentration," which they interpret as "a fertilization effect." In addition, over the same time period, the five researchers note "there was also a marked increase in temperature across the study region (0.19°C per decade on average)," and they report "this warming had a negative impact on radial growth, particularly at the drier sites," but "its magnitude was not enough to counteract the fertilization effect."

Cole et al. (2010) introduce their study of the subject by noting that quaking aspen (*Populus tremuloides* Michx.) is a dominant forest type in north-temperate, montane and boreal regions of North America," stating it is, in fact, "the most widely distributed tree species on the continent." They also note that aspen—and related poplars—are "quintessential foundation species (Ellison et al., 2005), shaping the structure and function of the communities and ecosystems in which they occur (Whitham et al., 2006; Schweitzer et al., 2008; Madritch et al., 2009)." This being the case, they attempted to determine how this keystone species may have responded to the twentieth-century increase in atmospheric CO_2 concentration.

The four researchers collected branches from 919 trees after their leaves had dropped in the fall, obtaining samples that represented 189 genets or clones (five trees per clone) at 11 sites distributed throughout three regions of Wisconsin (USA). The sampled trees ranged from five to 76 years of age and came from second-growth unmanaged forests south of the areas defoliated by forest tent caterpillars in 1980–1982, 1989–1990, and 2001–2002. In addition, they recorded trunk diameter at breast height for each sampled tree, which parameter, in their words, "is very highly correlated with total biomass in aspen," citing Bond-Lamberty et al. (2002).

The Minnesota and Wisconsin scientists determined "age-specific ring width increased over time," and "the greatest increase occurred for relatively young trees, so that young trees grew faster in recent years than did young trees several decades ago." They found, for example, that during the past half-century the growth of trees 11–20 years old rose by 60 percent. In addition, they observed "rising CO_2 causes ring width to increase at all moisture levels, apparently resulting from improved water use efficiency," so "the overall increase results from historical increases in both CO_2 and water availability." And when they separated the impacts of the two factors, they found "the effect of rising CO_2 had been to increase ring width by about 53%," as a result of "a 19.2% increase in ambient CO_2 levels during the growing season, from 315.8 ppm in 1958 (when CO_2 records began) to 376.4 ppm in 2003."

Cole et al. state "the magnitude of the growth increase uncovered by this analysis raises the question of how much other major forest species have responded to the joint effects of long-term changes in CO_2 and precipitation." Indeed, there is reason to believe many other tree species may have experienced similar large growth stimulation, particularly in light of the analysis of Tans (2009), who demonstrated the Earth's land surfaces were a net source of CO_2 to the atmosphere until about 1940—primarily due to the felling of forests and the plowing of grasslands to make way for expanded agricultural activities—but from 1940 onward the terrestrial biosphere had become, in the mean, an increasingly greater sink for CO_2 and had done so even in the face of massive global deforestation, for which it apparently more than compensated.

References

Alcaraz-Segura, D., Chuvieco, E., Epstein, H.E., Kasischke, E.S., and Trishchenko, A. 2010. Debating the greening vs. browning of the North American boreal forest: differences between the satellite datasets. *Global Change Biology* **16**: 760–770.

Archer, S., Schimel, D.S., and Holland, E.A. 1995. Mechanisms of shrubland expansion: land use, climate or CO_2? *Climatic Change* **29**: 91–99.

Baker, T.R., Phillips, O.L., Malhi, Y., Almeida, S., Arroyo, L., Di Fiore, A., Erwin, T., Higuchi, N., Killeen, T.J., Laurance, S.G., Laurance, W.F., Lewis, S.L., Monteagudo, A., Neill, D.A., Núñez Vargas, P., Pitman, N.C.A., Silva, J.N.M., and Vásquez Martinez, R. 2004a. Increasing biomass in Amazonian forest plots. *Philosophical Transactions of the Royal Society of London Series B - Biological Sciences* **359**: 353–365.

Baker, T.R., Phillips, O.L., Malhi, Y., Almeida, S., Arroyo, L., Di Fiore, A., Erwin, T., Killeen, T.J., Laurance, S.G., Laurance, W.F., Lewis, S.L., Lloyd, J., Monteagudo, A., Neil, D.A., Patiño, S., Pitman, N.C.A., Silva, N.M., and Vásquez Martinez, R. 2004b. Variation in wood density determines spatial patterns in Amazonian forest biomass. *Global Change Biology* **10**: 545–562.

Boisvenue, C. and Running, S. 2006. Impacts of climate change on natural forest productivity—evidence since the middle of the 20th century. *Global Change Biology* **12**: 862–882.

Bond, W.J. and Midgley, G.F. 2000. A proposed CO_2-controlled mechanism of woody plant invasion in grasslands and savannas. *Global Change Biology* **6**: 865–869.

Bond, W.J., Midgley, G.F., and Woodward, F.I. 2003. The importance of low atmospheric CO_2 and fire in promoting the spread of grasslands and savannas. *Global Change Biology* **9**: 973–982.

Bond-Lamberty, B., Wang, C., and Gower, S.T. 2002. Aboveground and belowground biomass and sapwood area allometric equations for six boreal tree species of northern Manitoba. *Canadian Journal of Forest Research* **32**: 1441–1450.

Chave, J., Condit, R., Muller-Landau, H.C., Thomas, S.C., Ashton, P.S., Bunyavejchewin, S., Co, L.L., Dattaraja, H.S., Davies, S.J., Esufali, S., Ewango, C.E.N., Feeley, K.J., Foster, R.B., Gunatilleke, N., Gunatilleke, S., Hall, P., Hart, T.B., Hernández, C., Hubbell, S.P., Itoh, A., Kiratiprayoon, S., LaFrankie, J.V., de Lao, S.L., Makana, J.-R., Noor, Md.N.S., Kassim, A.R., Samper, C., Sukumar, R., Suresh, H.S., Tan, S., Thompson, J., Tongco, Ma.D.C., Valencia, R., Vallejo, M., Villa, G., Yamakura, T., Zimmerman, J.K., and Losos, E.C. 2008. Assessing evidence for a pervasive alteration in tropical tree communities. *PLoS Biology* **6**: 10.1371/journal.pbio.0060045.

Cole, C.T., Anderson, J.E., Lindroth, R.L., and Waller, D.M. 2010. Rising concentrations of atmospheric CO_2 have increased growth in natural stands of quaking aspen (*Populus tremuloides*). *Global Change Biology* **16**: 2186–2197.

Delpierre, N., Soudani, K., Francois, C., Kostner, B., Pontailler, J.-Y., Nikinmaa, E., Misson, L., Aubinet, M., Bernhofer, C., Granier, A., Grunwald, T., Heinesch, B., Longdoz, B., Ourcival, J.-M., Rambal, S., Vesala, T., and Dufrene, E. 2009. Exceptional carbon uptake in European forests during the warm spring of 2007: A data-model analysis. *Global Change Biology* **15**: 1455–1474.

Ellison, A.M., Bank, M.S., Clinton, B.D., Colburn, E.A., Elliott, K., Ford, C.R., Foster, D.R., Kloeppel, B.D., Knoepp, J.D., Lovett, G.M., Mohan, J., Orwig, D.A., Rodenhouse, N.L., Sobczak, W.V., Stinson, K.A., Stone, J.K., Swan, C.M., Thompson, J., Holle, B.V., and Webster, J.R. 2005. Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. *Frontiers in Ecology and the Environment* **3**: 479–486.

Gloor, M., Phillips, O.L., Lloyd, J.J., Lewis, S.L., Malhi, Y., Baker, T.R., Lopez-Gonzalez, G., Peacock, J., Almeida, S., Alves de Oliveira, A.C., Alvarez, E., Amaral, I., Arroyo, L., Aymard, G., Banki, O., Blanc, L., Bonal, D., Brando, P., Chao, K.-J., Chave, J., Davila, N., Erwin, T., Silva, J., DiFiore, A., Feldpausch, T.R., Freitzs, A., Herrera, R., Higuchi, N., Honorio, E., Jimenez, E., Killeen, T., Laurance, W., Mendoza, C., Monteagudo, A., Andrade, A. Neill, D., Nepstad, D., Nunez Vargas, P., Penuela, M.C., Pena Cruz, A., Prieto, A., Pitman, N., Quesada, C., Salomao, R., Silveira, M., Schwarz, M., Stropp, J., Ramirez, F., Ramirez, H., Rudas, A., ter Steege, H., Silva, N., Torres, A., Terborgh, J., Vasquez, R., and van der Heijden, G. 2009. Does the disturbance hypothesis explain the biomass increase in basin-wide Amazon forest plot data? *Global Change Biology* **15**: 2418–2430.

Hibbard, K.A., Archer, S., Schimel, D.S., and Valentine, D.W. 2001. Biogeochemical changes accompanying woody plant encroachment in a subtropical savanna. *Ecology* **82**: 1999–2011.

Hibbard, K.A., Schimel, D.S., Archer, S., Ojima, D.S., and Parton, W. 2003. Grassland to woodland transitions: integrating changes in landscape structure and biogeochemistry. *Ecological Applications* **13**: 911–926.

Katinas, L. and Crisci, J.V. 2008. Reconstructing the biogeographical history of two plant genera with different dispersion capabilities. *Journal of Biogeography* **35**: 1374–1384.

Lewis, S.L., Lloyd, J., Sitch, S., Mitchard, E.T.A., and Laurance, W.F. 2009b. Changing ecology of tropical forests: Evidence and drivers. *Annual Review of Ecology, Evolution, and Systematics* **40**: 529–549.

Lewis, S.L., Lopez-Gonzalez, G., Sonke, B., Affum-Baffoe, K., Baker, T.R., Ojo, L.O., Phillips, O.L., Reitsma, J.M., White, L., Comiskey, J.A., Djuikouo Kamden, M.-N., Ewango, C.E.N., Feldpausch, T.R., Hamilton, A.C., Gloor, M., Hart, T., Hladik, A., Lloyd, J., Lovett, J.C., Makana, J.-R., Malhi, Y., Mbago, F.M., Ndangalasi, H.J., Peacock, J., Peh, K. S.-H., Sheil, D., Sunderland, T., Swaine, M.D., Taplin, J., Taylor, D., Thomas, S.C., Votere, R., and Woll, H. 2009a. Increasing carbon storage in intact African tropical forests. *Nature* **457**: 1003–1006.

Lewis, S.L., Phillips, O.L., Baker, T.R., Lloyd, J., Malhi, Y., Almeida, S., Higuchi, N., Laurance, W.F., Neill, D.A., Silva, J.N.M., Terborgh, J., Lezama, A.T., Vasquez Martinez, R., Brown, S., Chave, J., Kuebler, C., Núñez Vargas, P., and Vinceti, B. 2004. Concerted changes in tropical forest structure and dynamics: evidence from 50 South American long-term plots. *Philosophical Transactions of the Royal Society of London Series B - Biological Sciences* **359**: 421–436.

Liao, J.D., Boutton, T.W., and Jastrow, J.D. 2006. Storage and dynamics of carbon and nitrogen in soil physical fractions following woody plant invasion of grassland. *Soil Biology and Biochemistry* **38**: 3184–3196.

Lopez-Pintor, A., Sal, A.G., and Benayas, J.M. R. 2006. Shrubs as a source of spatial heterogeneity—the case of *Retama sphaerocarpa* in Mediterranean pastures of central Spain. *Acta Oecologia* **29**: 247–255.

Madritch, M.D., Greene, S.G., and Lindroth, R.L. 2009. Genetic mosaics of ecosystem functioning across aspen-dominated landscapes. *Oecologia* **160**: 119–127.

Martinez-Vilalta, J., Lopez, B.C., Adell, N., Badiella, L., and Ninyerola, M. 2008. Twentieth century increase of Scots pine radial growth in NE Spain shows strong climate interactions. *Global Change Biology* **14**: 2868–2881.

McCulley, R.L., Archer, S.R., Boutton, T.W., Hons, F.M., and Zuberer, D.A. 2004. Soil respiration and nutrient cycling in wooded communities developing in grassland. *Ecology* **85**: 2804–2817.

McMahon, S.M., Parker, G.G., and Miller, D.R. 2010. Evidence for a recent increase in forest growth. *Proceedings of the National Academy of Sciences USA* **107**: 3611–3615.

Myneni, R., Keeling, C., Tucker, C., Asrar, G., and Nemani, R. 1997. Increased plant growth in the northern high latitudes from 1981 to 1991. *Nature* **386**: 698–702.

Pan, Y., Birdsey, R., Hom, J., and McCullough, K. 2010. Separating effects of changes in atmospheric composition, climate and land-use on carbon sequestration of U.S. Mid-Atlantic temperate forests. *Forest Ecology and Management* **259**: 151–164.

Phillips, O.L., Baker, T.R., Arroyo, L., Higuchi, N., Killeen, T.J., Laurance, W.F., Lewis, S.L., Lloyd, J., Malhi, Y., Monteagudo, A., Neill, D.A., Núñez Vargas, P., Silva, J.N.M., Terborgh, J., Vásquez Martinez, R., Alexiades, M., Almeida, S., Brown, S., Chave, J., Comiskey, J.A., Czimczik, C.I., Di Fiore, A., Erwin, T., Kuebler, C., Laurance, S.G., Nascimento, H.E.M., Olivier, J., Palacios, W., Patiño, S., Pitman, N.C.A., Quesada, C.A., Saldias, M., Torres Lezama, A.B., and Vinceti, B. 2004. Pattern and process in Amazon tree turnover: 1976–2001. *Philosophical Transactions of the Royal Society of London Series B - Biological Sciences* **359**: 381–407.

Phillips, O.L. and Gentry, A.H. 1994. Increasing turnover through time in tropical forests. *Science* **263**: 954–958.

Phillips, O.L., Malhi, Y., Higuchi, N., Laurance, W.F., Nunez, P.V., Vasquez, R.M., Laurance, S.G., Ferreira, L.V., Stern, M., Brown, S., and Grace, J. 1998. Changes in the carbon balance of tropical forests: evidence from long-term plots. *Science* **282**: 439–442.

Polley, H.W. 1997. Implications of rising atmospheric carbon dioxide concentration for rangelands. *Journal of Range Management* **50**: 561–577.

Reynolds, J.F., Virginia, R.A., Kemp, P.R., de Soyza, A.G., and Tremmel, D.C. 1999. Impact of drought on desert shrubs: effects of seasonality and degree of resource island development. *Ecological Monographs* **69**: 69–106.

Salzer, M., Hughes, M., Bunn, A., and Kipfmueller, K. 2009. Recent unprecedented tree-ring growth in bristlecone pine at the highest elevations and possible causes. *Proceedings of the National Academies of Science USA* **106**: 20,346–20,353.

Schade, J.D. and Hobbie, S.E. 2005. Spatial and temporal variation in islands of fertility in the Sonoran Desert. *Biogeochemistry* **73**: 541–553.

Schlesinger, W.H., Reynolds, J.F., Cunningham, G.L., Huenneke, L.F., Jarrell, W.M., Ross, V.A., and Whitford, W.G. 1990. Biological feedbacks in global desertification. *Science* **247**: 1043–1048.

Schweitzer, J.A., Madritch, M.D., Bailey, J.K., LeRoy, C.J., Fischer, D.G., Rehill, B.J., Lindroth, R.L., Hagerman, A.E., Wooley, S.C., Hart, S.C., and Whitham, T.G. 2008. The genetic basis of condensed tannins and their role in nutrient regulation in a *Populus* model system. *Ecosystems* **11**: 1005–1020.

Silva, L.C.R., Anand, M., Oliveira, J.M., and Pillar, V.D. 2009. Past century changes in *Araucaria angustifolia* (Bertol.) Kuntze water use efficiency and growth in forest and grassland ecosystems of southern Brazil: implications for forest expansion. *Global Change Biology* **15**: 2387–2396.

Springsteen, A., Loya, W., Liebig, M., and Hendrickson, J. 2010. Soil carbon and nitrogen across a chronosequence of woody plant expansion in North Dakota. *Plant and Soil* **328**: 369–379.

Tans, P. 2009. An accounting of the observed increase in oceanic and atmospheric CO_2 and an outlook for the future. *Oceanography* **22**: 26–35.

Whitham, T.G., Bailey, J.K., and Schweitzer, J.A. 2006. A framework for community and ecosystem genetics from genes to ecosystems. *Nature Reviews Genetics* **7**: 510–523.

7.11.3. High Latitudes

In the introduction to their report on the response of High Arctic tundra vegetation to the warming experienced in that part of the world over the past quarter-century, Hudson and Henry (2009) note the Arctic warmed by about 1.6°C over the past four decades, citing McBean et al. (2005). They state this temperature increase “led the Arctic Climate Impact Assessment (ACIA) and Intergovernmental Panel on Climate Change (IPCC) to predict that tundra ecosystems will be particularly threatened by climate change [i.e., warming] over the next century.” To test this prediction, the authors set out to find if plants of the High Arctic tundra have been growing more or less vigorously or abundantly during the recent warming period.

At an 8-km^2 coastal lowland adjacent to Alexandra Fiord on the east-central coast of Ellesmere Island, Nunavut, Canada, Hudson and Henry measured biomass and composition changes in a heath community dominated by several vascular plants and bryophytes. They did this over a period of 13 years (1995–2007), using a point-intercept method in permanent plots, and over a period of 27 years (1981–2008) using a biomass harvest comparison. “Results from both methods,” in the words of the Canadian scientists, “indicate that the community became more productive over time.” The note “bryophyte and evergreen shrub abundances increased,” while “deciduous shrub, forb, graminoid, and lichen cover did not change,” so that “species diversity also remained unchanged.” All of these changes—and non-changes—are a far cry from the “particularly threatened” view of the ACIA and IPCC.

In further support of their findings, Hudson and Henry report “satellite-based remote sensing models, such as green trends derived from the normalized difference vegetation index (NDVI; e.g., Myneni et al., 1997; Zhou et al., 2001; Stow et al., 2004; Verbyla, 2008), and global vegetation and ecosystem process simulations of the terrestrial carbon cycle (e.g., Kimball et al., 2006; Zhang et al., 2008), indicate increasing trends in vegetation photosynthetic activity and net primary production in the Arctic over the past several decades.” As for what drove this welcome transformation of the tundra, Hudson and Henry say “it is likely that warming directly increased plant growth and reproduction and indirectly increased resource supply,” while “increased temperatures also lengthened the growing season, increased soil temperature, deepened the active [soil] layer, and consequently may have influenced nutrient uptake in the plant community.”

Nevertheless, some people continue to claim anthropogenic global warming will have widespread adverse effects on ecosystems, and one of the regions they claim to be most vulnerable is the Arctic. Jia et al. (2009) utilized 25 years of satellite data covering the period of most rapid recent warming (1982 to 1996) to evaluate this contention via NDVI data obtained from the GIMMS dataset, which consists of 64-km^2 cells minus those cells with too much open water or bare ground within them that are known to inject significant bias into NDVI data analyses. This study showed tundra ecosystems exhibited an average increase in greenness of 5.6 percent per decade over 96 percent of the pixels evaluated, which was proportional to the rate of summer warming as measured by growing degree days. The three researchers state the decadal increases of vegetation greenness over the tundra biome in summer “reflect increasing vegetation productivity during the growing season.”

Working at a site just three kilometers from the Abisko Scientific Research Station (68°21’N, 18°49’E) in the Northern Swedish Scandes, Hallinger et al. (2010) studied male plants of the medium-sized *Juniperus nana* shrub, collecting the main stems of five to eight shrubs every hundred meters of elevation until the shrub zone ended. They then performed ring-width measurements on these stems, “to measure radial and vertical growth, to track growth changes over time, to age the shrub individuals and to correlate annual shrub growth with climate.” Data for the latter factor were derived from records of the nearby Abisko Station. By these means the three researchers identified “a distinct increase in radial and vertical growth rates of *J. nana* shrubs during recent decades in the subalpine zone of North Sweden,” and they state “the age structure of shrubs along the elevational gradient provides evidence that an upslope advance of the altitudinal shrubline is underway.” In addition, they state they observed “significant, strong and stable correlations between annual ring width and summer temperatures (June, July, August),” and “the acceleration of radial and vertical growth since 1970 also coincides with the recent three decades of rising arctic air temperatures and the warming trend of 0.2°C per decade for the average temperature since 1956 at Abisko.” Thus, the German scientists’ study adds to what they call the “mounting evidence that shrubs are expanding into alpine and arctic areas because of climate warming,” and they note “this expansion occurs in both evergreen and deciduous shrub types,” citing Forbes et al. (2010).

Other remote-sensing data suggest tundra vegetation in North America may be responding to recent warming via increased photosynthetic activity (Goetz et al., 2005; Verbyla , 2008). Forbes et al. (2010) write, “at a circumpolar scale, the highest photosynthetic activity and strongest growth trends are reported in locations characterized by erect shrub tundra (Reynolds et al., 2006),” noting “live leaf phytomass from deciduous shrubs, shown to have increased in northern Alaska during the second half of the last century (Sturm et al., 2001; Tape et al., 2006), is believed to be a key driver of the observed trends (Jia et al., 2003; Goetz et al., 2005; Verbyla, 2008).” Therefore, working with *Salix lanata* L. (*sensu latu*)—an abundant deciduous dioecious willow with nearly circumpolar geographic distribution from the northern boreal forest to the northern limits of the Low Arctic—Forbes et al. analyzed annual ring growth for 168 stem slices of 2- to 3-cm thickness collected from 40 discrete individuals spread across 15 sample sites within an area of approximately 3 x 2.3 km, located at about 68°40’N, 58°30’E, to further examine this phenomenon.

The three scientists state they detected “a clear relationship with photosynthetic activity for upland vegetation at a regional scale for the period 1981–2005, confirming a parallel ‘greening’ trend reported for similarly warming North American portions of the tundra biome,” and they state “the standardized growth curve suggests a significant increase in shrub willow growth over the last six decades.” Additionally noting “the quality of the chronology as a climate proxy is exceptional,” Forbes et al. go on to state their findings “are in line with field and remote sensing studies that have assigned a strong shrub component to the reported greening signal since the early 1980s,” adding the growth trend agrees with the qualitative observations of nomadic reindeer herders, which suggest there have been “recent increases in willow size in the region.” They state their analysis “provides the best proxy assessment to date that deciduous shrub phytomass has increased significantly in response to an ongoing summer warming trend.”

Contemporaneously, Zhuang et al. (2010) used a process-based biogeochemistry model—the Terrestrial Ecosystem Model or TEM, which also employed a soil thermal model—to examine permafrost dynamics and their effects on the carbon dynamics of the Tibetan Plateau over the past century. This was done by “parameterizing and verifying” the TEM using existing real-world data for soil temperature, permafrost distribution, and carbon and nitrogen distributions throughout the region, and then extrapolating the model and its parameters to the whole of the plateau. The six scientists found, “during the 20th century, the Tibetan Plateau changed from a small carbon source or neutral in the early part of the century to a sink later.” They note “net primary production and soil respiration increased by 0.52 and 0.22 Tg C/year, respectively, resulting in a regional carbon sink increase of 0.3 Tg C/year,” so that “by the end of the century, the regional carbon sink reached 36Tg C/year and carbon storage in vegetation and soils is 32 and 16 Pg C, respectively.”

Zhuang et al. state the “increasing soil temperature and deepening active layer depth enhanced soil respiration, increasing the net nitrogen mineralization rate,” and “together with the [positive] effects of warming air temperature and rising CO_2

concentrations on photosynthesis, the stronger plant nitrogen uptake due to the enhanced available nitrogen stimulated plant carbon uptake, thereby strengthening the regional carbon sink as the rate of increase in net primary production was faster than that of soil respiration." Thus, they conclude "future warming will increase thawing of the permafrost, increase soil temperature and dry up soil moisture," and "these physical dynamics may enhance [the] future strength of the regional carbon sink, since the rate of increase of net primary production is higher than that of soil respiration on the Tibetan Plateau."

References

Forbes, B.C., Fauria, M., and Zetterberg, P. 2010. Russian Arctic warming and 'greening' are closely tracked by tundra shrub willows. *Global Change Biology* **16**: 1542–1554.

Goetz, S.J., Bunn, A.G., Fiske, G.J., and Houghton, R.A. 2005. Satellite-observed photosynthetic trends across boreal North America associated with climate and fire disturbance. *Proceedings of the National Academy of Sciences USA* **102**: 13,521–13,525.

Hallinger, M., Manthey, M., and Wilmking, M. 2010. Establishing a missing link: warm summers and winter snow cover promote shrub expansion into alpine tundra in Scandinavia. *New Phytologist* **186**: 890–899.

Hudson, J.M.G. and Henry, G.H.R. 2009. Increased plant biomass in a High Arctic heath community from 1981 to 2008. *Ecology* **90**: 2657–2663.

Jia, G.J., Epstein, H.E., and Walker, D.A. 2003. Greening of arctic Alaska, 1981–2001. *Geophysical Research Letters* **30**: 31–33.

Jia, G.J., Epstein, H.E., and Walker, D.A. 2009. Vegetation greening in the Canadian Arctic related to decadal warming. *Journal of Environmental Monitoring* **11**: 2231–2238.

Kimball, J.S., Zhao, M., Mcguire, A.D., Heinsch, F.A., Clein, J., Calef, M.P., Jolly, W.M., Kang, S., Euskirchen, S.E., McDonald, K.C., and Running, S.W. 2006. Recent climate-driven increases in vegetation productivity for the Western Arctic: evidence for an acceleration of the northern terrestrial carbon cycle. *Earth Interactions* **11**: 1–23.

McBean, G., Alekseev, G., Chen, D., Forland, E., Fyfe, J., Groisman, P.Y., King, R., Melling, H., Vose, R., and Whitfield, P.H. 2005. Arctic climate: past and present. In *Arctic Climate Impact Assessment: Scientific Report*, 21–60. Cambridge, UK: Cambridge University Press.

Myneni, R.B., Keeling, C.D., Tucker, C.J., Asrar, G., and Nemani, R.R. 1997. Increased plant growth in the northern high latitudes from 1981 to 1991. *Nature* **386**: 698–702.

Reynolds, M.K., Walker, D.A., and Maier, H.A. 2006. NDVI patterns and phytomass distribution in the circumpolar Arctic. *Remote Sensing of Environment* **102**: 271–281.

Stow, D.A., Hope, A., McGuire, D., Verbyla, D., Gamon, J., Huemmrich, F., Houston, S., Racine, C., Sturm, M., Tape, K., Hinzman, L., Yoshikawa, K., Tweedie, C., Noyle, B., Silapaswan, C., Douglas, D., Griffith, B., Jia, G., Epstein, H., Walker, D., Daeschner, S., Petersen, A., Liming, Z., and Myneni, R. 2004. Remote sensing of vegetation and land-cover change in Arctic tundra ecosystems. *Remote Sensing of Environment* **89**: 281–308.

Sturm, M., Racine, C., and Tape, K. 2001. Increasing shrub abundance in the Arctic. *Nature* **411**: 546–547.

Tape, K., Sturm, M., and Racine, C.H. 2006. The evidence for shrub expansion in northern Alaska and the Pan-Arctic. *Global Change Biology* **32**: 686–702.

Verbyla, D. 2008. The greening and browning of Alaska based on 1982–2003 satellite data. *Global Ecology and Biogeography* **17**: 547–555.

Zhang, K., Kimball, J.S., Hogg, E.H., Zhao, M.S., Oechel, W.C., Cassano, J.J., and Running, S.W. 2008. Satellite-based model detection of recent climate-driven changes in northern high-latitude vegetation productivity. *Journal of Geophysical Research-Biogeosciences* **113**: G03033.

Zhou, L.M., Tucker, C.J., Kaufmann, R.K., Slayback, D., Shabanov, N.V., and Myneni, R.B. 2001. Variations in northern vegetation activity inferred from satellite data of vegetation index during 1981 to 1999. *Journal of Geophysical Research* **106**: 20,069–20,083.

Zhuang, Q., He, J., Lu, Y., Ji, L., Xiao, J., and Luo, T. 2010. Carbon dynamics of terrestrial ecosystems on the Tibetan Plateau during the 20th century: an analysis with a process-based biogeochemical model. *Global Ecology and Biogeography* **19**: 649–662.

7.11.4. The Globe

Periodically, even in some of the world's most prestigious scientific journals, it is said the natural sinks of Earth's carbon cycle are becoming decreasingly effective in removing from the atmosphere the CO_2 released to it as a result of humanity's energy-intensive activities (Canadell et al., 2007; LeQuere et al., 2007). This myth, however, has been put to rest once and for all by a new analysis of real-world data.

In a study published in the December 2009 issue of *Oceanography* that considered several related topics, Pieter Tans of the National Oceanic and Atmospheric Administration (NOAA) employed measurements of atmospheric and oceanic carbon contents, along with reasonably constrained estimates of global anthropogenic CO_2 emissions, to calculate the residual fluxes of carbon (in the form of CO_2) from the terrestrial biosphere to the atmosphere (+) or from the atmosphere to the terrestrial biosphere (-), obtaining the results depicted in Figure 7.11.1.

As the figure illustrates, Earth's land surfaces were a net source of CO_2-carbon to the atmosphere until about 1940, primarily due to the felling of forests and the plowing of grasslands to make way for expanded agricultural activities. From 1940 onward, however, the terrestrial biosphere has become, in the mean, an increasingly greater sink for CO_2-carbon, and it has done so even in the face of massive global deforestation, for which it has more than compensated. These findings do "not depend on models" but "only on the observed atmospheric increase and estimates of fossil fuel emissions," Tans notes.

Tans concludes, "suggestions that the carbon cycle is becoming less effective in removing CO_2 from the atmosphere (e.g., LeQuere et al., 2007; Canadell et al., 2007) can perhaps be true locally, but they do not apply globally, not over the 50-year atmospheric record, and not in recent years." In fact, he adds, "to the contrary" and "despite global fossil fuel emissions increasing from 6.57 GtC in 1999 to 8.23 in 2006, the five-year smoothed global atmospheric growth rate has not increased during that time, which requires more effective uptake [of CO_2] either by the ocean or by the terrestrial biosphere, or both, to satisfy atmospheric observations." Tans' results, depicted in Figure 6.11.1, clearly indicate this "more effective uptake" of CO_2-carbon has occurred primarily over land.

This observation-based analysis of real-world data provides strong evidence for both the reality and the tremendous strength of the CO_2-induced greening of the Earth phenomenon, which has been observed in numerous independent studies conducted throughout the world. In addition, it refutes the unfounded arguments that various environmental stresses and resource limitations will not allow the full potential of the aerial fertilization effect of atmospheric CO_2 enrichment to be manifest in nature. This phenomenon is itself a "force of nature" that can be neither hindered nor halted.

Most recently, Lin et al. (2010) noted "most models predict that climate warming will increase the

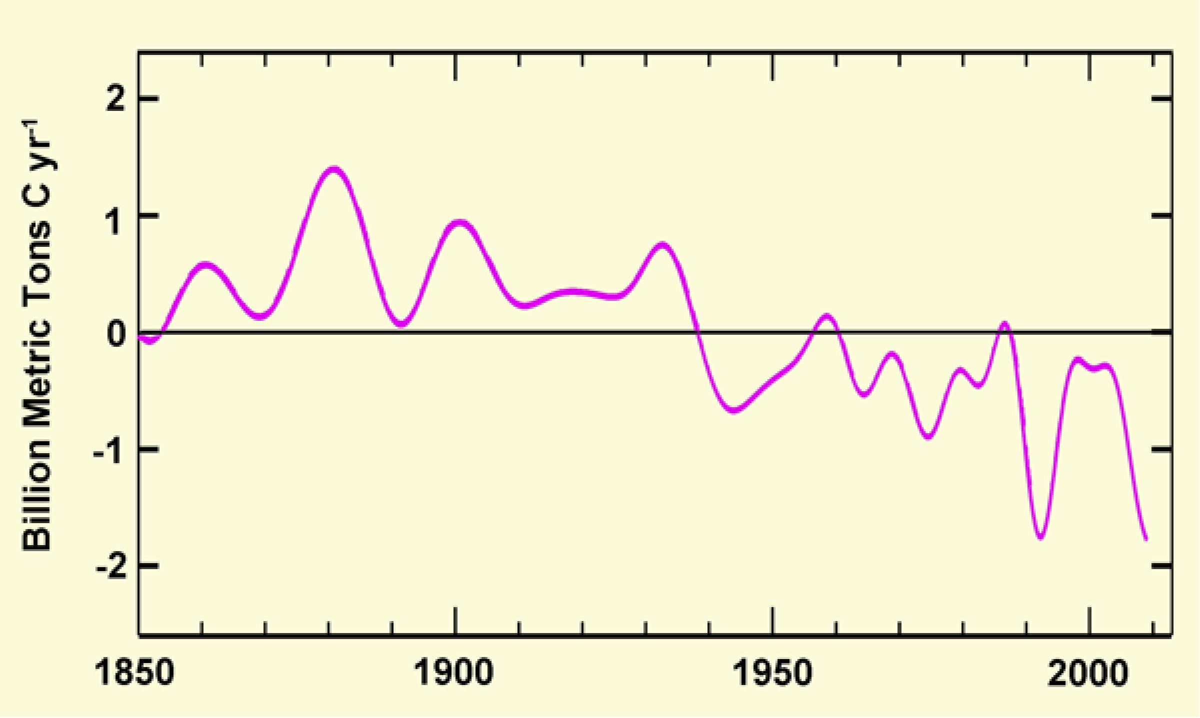

Figure 7.11.1. Five-year smoothed rates of global carbon transfer from land to air (+) or from air to land (-) vs. time. Adapted from Tans (2009).

release of carbon dioxide from the terrestrial biosphere into the atmosphere, thus triggering positive climate-terrestrial carbon feedback which leads to a warmer climate." However, they state the "stimulation of biomass accumulation and net primary productivity of terrestrial ecosystems under rising temperature (Rustad et al., 2001; Melillo et al., 2002; Luo et al., 2009) may enhance carbon sequestration and attenuate the positive feedback between climate warming and the terrestrial biosphere."

In an effort to find out which view is correct, Lin et al. conducted a meta-analysis of pertinent data from 127 individual studies published before June 2009, in order to ascertain whether the overall impact of a substantial increase in the air's CO_2 concentration on terrestrial biomass production would likely be positive or negative. The three scientists determined that for the totality of terrestrial plants included in their analysis, "warming significantly increased biomass by 12.3%," and there was a "significantly greater stimulation of woody (+26.7%) than herbaceous species (+5.2%)." They also found the warming effects on plant biomass production "did not change with mean annual precipitation or experimental duration," and "other treatments, including CO_2 enrichment, nitrogen addition, drought and water addition, did not alter warming responses of plant biomass."

The Chinese researchers thus conclude "results in this and previous meta-analyses (Arft et al., 1999; Rustad et al., 2001; Dormann and Woodin, 2002; Walker et al., 2006) have revealed that warming generally increases terrestrial plant biomass, indicating enhanced terrestrial carbon uptake via plant growth and net primary productivity." Thus, we can logically expect that the ongoing rise in the air's CO_2 content will soften its tendency to increase global temperatures while causing greater growth rates and biomass production of terrestrial vegetation.

References

Arft, A.M., Walker, M.D., Gurevitch, J., Alatalo, J.M., Bret-Harte, M.S., Dale, M., Diemer, M., Gugerli, F., Henry, G.H.R., Jones, M.H., Hollister, R.D., Jonsdottir, I.S., Laine, K., Levesque, E., Marion, G.M., Molau, U., Molgaard, P., Nordenhall, U., Raszhivin, V., Robinson, C.H., Starr, G., Stenstrom, A., Stenstrom, M., Totland, O., Turner, P.L., Walker, L.J., Webber, P.J., Welker, J.M., and Wookey, P.A. 1999. Responses of tundra plants to experimental warming: meta-analysis of the international tundra experiment. *Ecological Monographs* **69**: 491–511.

Canadell, J.G., LeQuere, C., Raupach, M.R., Field, C.B., Buitenhuis, E.T,., Ciais, P., Conway, T.J., Gillett, N.P., Houghton, R.A., and Marland, G. 2007. Contributions to accelerating atmospheric CO_2 growth from economic activity, carbon intensity, and efficiency of natural sinks. *Proceedings of the National Academy of Sciences of the United States of America* **104**: 18,866–18,870.

Dormann, C.F. and Woodin, S.J. 2002. Climate change in the arctic: using plant functional types in a meta-analysis of field experiments. *Functional Ecology* **16**: 4–17.

LeQuere, C., Rodenbeck, C., Buitenhuis, E.T., Conway, T.J., Langenfelds, R., Gomez, A., Labuschagne, C., Ramonet, M., Nakazawa, T., Metzl, N., Gillett, N., and Heimann, M. 2007. Saturation of the Southern Ocean CO_2 sink due to recent climate change. *Science* **316**: 1735–1738.

Lin, D., Xia, J., and Wan, S. 2010. Climate warming and biomass accumulation of terrestrial plants: a meta-analysis. *New Phytologist* **188**: 187–198.

Luo, Y.Q., Sherry, R., Zhou, X.H., and Wan, S.Q. 2009. Terrestrial carbon-cycle feedback to climate warming: experimental evidence on plant regulation and impacts of biofuel feedstock harvest. *Global Change Biology Bioenergy* **1**: 62–74.

Melillo, J.M., Steudler, P.A., Aber, J.D., Newkirk, K., Lux, H., Bowles, F.P., Catricala, C., Magill, A., Ahrens, T., and Morrisseau, S. 2002. Soil warming and carbon-cycle feedbacks to the climate system. *Science* **298**: 2173–2176.

Rustad, L.E., Campbell, J.L., Marion, G.M., Norby, R.J., Mitchell, M.J., Hartley, A.E., Cornelissen, J.H.C., Gurevitch, J., and GCTE-NEWS. 2001. A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. *Oecologia* **126**: 543–562.

Tans, P. 2009. An accounting of the observed increase in oceanic and atmospheric CO_2 and an outlook for the future. *Oceanography* **22**: 26–35.

Walker, M.D., Wahren, C.H., Hollister, R.D., Henry, G.H.R., Ahlquist, L.E., Alatalo, J.M., Bret-Harte, M.S., Calef, M.P., Callaghan, T.V., Carroll, A.B., Epstein, H.E., Jonsdottir, I.S., Klein, J.A., Magnusson, B., Molaug, U., Oberbauer, S.F., Rewan, S.P., Robinson, C.H., Shaver, G.R., Suding, K.N., Thompson, C.C., Tolvanen, A., Totland, O., Turner, P.L., Tweedie, C.E., Webber, P.J., and Wookey, P.A. 2006. Plant community responses to experimental warming across the tundra biome. *Proceedings of the National Academy of Sciences USA* **103**: 1342–1346.

7.11.5. Miscellaneous

Logan et al. (2010) describe and discuss what was revealed at a Tropospheric Ozone Changes Workshop in Boulder, Colorado (USA) on 14–16 October 2009, where "long-term ozone records from regionally representative surface and mountain sites, ozonesondes, and aircraft were reviewed by region." They report, "in the Southern Hemisphere, surface measurements from South Africa and Tasmania and sonde data from New Zealand show a significant increase over the past 25 years." North of the equator, on the other hand, the story is somewhat different. In western Europe, for example, "several time series of ~15-40 years ... show a rise in ozone into the middle to late 1990s and a leveling off, or in some cases declines, in the 2000s, in general agreement with precursor emission changes." Similarly, they state "surface measurements within North America show a pattern of mostly unchanged or declining ozone over the past two decades that seems broadly consistent with decreases in precursor emissions," while noting "the Japanese sonde record suggests rising ozone into the 1980s and small changes thereafter."

The spatial and temporal distributions of these observations would seem to suggest: Whereas increasing industrialization originally tends to increase the emissions of precursor substances that lead to the creation of greater tropospheric ozone pollution, subsequent technological advances tend to ameliorate that phenomenon as they gradually lead to (1) a leveling off of the magnitude of precursor emissions and (2) an ultimately decreasing trend in tropospheric ozone pollution. This suggests that when atmospheric ozone and CO_2 concentrations both rise together, the plant-growth-enhancing effect of atmospheric CO_2 enrichment is significantly muted by the plant-growth-retarding effect of contemporaneous increases in ozone pollution, but as the troposphere's ozone concentration gradually levels off and declines—as it appears to be doing with the development of new and better anti-pollution technology in the planet's more economically advanced countries—we should begin to see more-rapid-than-usual increases in Earth's vegetative productivity, which should promote an acceleration of the greening of the Earth.

Contemporaneously, Lazzarotto et al. (2010) note "white clover (*Trifolium repens* L.) is the most important pasture legume grown in temperate climates in association with a variety of grasses, notably perennial ryegrass (*Lolium perenne* L.)." They explain "white clover improves the nutritional quality and digestibility of the herbage" and "contributes substantially to the nitrogen status of the sward through biological nitrogen fixation." They state, however, that there is some concern future drought predicted to occur in tandem with CO_2-induced global warming will hurt clover more than the grass with which it is intermingled, thereby degrading the nutritional quality and digestibility of pasture swards.

To test this mix of facts and presumptions, Lazzarotto et al. planned and conducted a study in which "mechanisms controlling transient responses to elevated CO_2 concentration and climate change in an unfertilized grassland on the Swiss Plateau were examined in light of simulations with PROGRASS," a process-based model of grass-clover interactions developed by Lazzarotto et al. (2009) in which "daily weather for a series of transient climate scenarios spanning the 21st century were developed for the study site with the help of the LARS-WG weather generator," which is described by Semenov and Barrow (1997) and Semenov et al. (1998). In addition, "changes in the length of dry and wet spells, temperature, precipitation and solar radiation defining the scenarios were obtained from regional climate simulations carried out in the framework of the PRUDENCE project," which is described by Christensen and Christensen (2007).

"Compared to 1961–1990," the Swiss and UK scientists write, the climate scenarios they developed for a CO_2 increase from 370 to 860 ppm "indicated that for 2071–2100 there would be a noticeable increase in temperature (roughly 3°C in winter and 5°C in summer), a significant drop in summer precipitation (of the order of -30%), and a nearly 2-fold increase in the length of dry spells." The four researchers report these significant climate changes had no projected negative effect on the grass-clover swards: "clover abundance did not decline even in the absence of CO_2 stimulation." And when the atmospheric CO_2 concentration was programmed to gradually rise from an initial value of 370 ppm to a final value of 860 ppm, they found "clover development benefited from the overall positive effects of CO_2 on nitrogen acquisition," which they report was also "the reason for increasing productivity of the [entire] sward."

For Swiss grass-clover swards, therefore, the rather large predicted increases in temperature and decreases in precipitation predicted for the remainder of the twenty-first century will not have much of an effect, but the concomitant increase in the air's CO_2 content will be of considerable benefit. In addition, Lazzarotto et al. state it is likely "technical progress in the management of grasslands and pastures," which will surely occur, will help such pastures even more.

In a similar type of study, Friend (2010) used an advanced mechanistic physiological model (Hybrid6.5) of leaf and whole-plant canopy response to climate for basically the same purposes as Lazzarotto et al. This model considers light extinction within the leaf and through the canopy, the gradient of nitrogen content through the canopy, and other factors. It also distinguishes between C_3 and C_4 plants, broadleaf and conifer trees, and other life forms; and it has been verified by close matches to local, regional, and global net primary production (NPP) data. The model was run with current global vegetation distributions and the GISS-AOM climate model using the IPCC A1B scenario, with CO_2 rising to 720 ppm by AD 2100. When it was run with only climate change (CO_2 fixed at current levels), it showed a 2.5 percent reduction in global NPP, but when CO_2 change was added to the model, global NPP increased 37.3 percent to 80.7 Pg C/year.

This rise was most evident in absolute terms in tropical rainforests. In percentage terms, temperate and boreal forests and tundra showed the largest increases, along with C_3 grasslands and agricultural lands. C_4 grasses and crops showed only a 5.9 percent increase in NPP, because of the less-responsive photosynthetic pathway in C_4 plants. Only very small areas of the globe showed any decrease in NPP with this model. The results therefore suggest elevated CO_2 will help plants cope with the modest changes in climate that might otherwise be slightly harmful to their growth. The study also confirms past work showing that as models of plant growth become more realistic and mechanistic, they tend to predict positive responses to CO_2 and climate changes over the next 100 years in most regions and ecosystems.

References

Christensen, J.H. and Christensen, O.B. 2007. A summary of the PRUDENCE model projections of changes in European climate by the end of this century. *Climatic Change* **81**: 7–30.

Friend, A.D. 2010. Terrestrial plant production and climate change. *Journal of Experimental Botany* **61**: 10.1093/jxb/erq019.

Lazzarotto, P., Calanca, P., and Fuhrer, J. 2009. Dynamics of grass-clover mixtures—an analysis of the response to management with the PROductive GRASsland Simulator (PROGRASS). *Ecological Modelling* **220**: 703–724.

Lazzarotto, P., Calanca, P., Semenov, M., and Fuhrer, J. 2010. Transient responses to increasing CO_2 and climate change in an unfertilized grass-clover sward. *Climate Research* **41**: 221–232.

Logan, J., Schultz, M., and Oltmans, S. 2010. Observing and understanding tropospheric ozone changes. *EOS, Transactions, American Geophysical Union* **91**: 119.

Semenov, M.A. and Barrow, E.M. 1997. Use of a stochastic weather generator in the development of climate change scenarios. *Climatic Change* **35**: 397–414.

Semenov, M.A., Books, R.J., Barrow, E.M., and Richardson, C.W. 1998. Comparison of the WGEN and LARS-WG stochastic weather generators for diverse climates. *Climate Research* **10**: 95–107.

7.12. Nitrogen

7.12.1. Nitrogen Cycling

Jin and Evans (2010) write, "resource limitations, such as the availability of soil nitrogen (N), are expected to constrain continued increases in plant productivity under elevated atmospheric carbon dioxide." This is a common belief. Providing a glimmer of hope, however, they state, "one potential but under-studied N source for supporting increased plant growth under elevated CO_2 is soil organic N." They report, "in arid ecosystems, there have been no studies examining plant organic N uptake to date."

To help remedy this situation, Jin and Evans grew seedlings of the desert shrub *Larrea tridentata* in environmentally controlled chambers in ambient or CO_2-enriched air (380 or 600 ppm) in pots filled with Mojave Desert (Nevada, USA) soils injected with isotopically labeled ^{15}N obtained from one of three different organic and inorganic sources—(1) organic ^{15}N glycine, (2) inorganic $^{15}NH_4^+$, or (3) inorganic $^{15}NO_3^-$. They then destructively harvested the plants following zero, two, ten, 24, and 49 additional days of growth and determined the amounts of soil N they had taken up from each of the three N sources. The scientists found "elevated CO_2 positively affected root uptake of N derived from all three N forms by day 10, with NO_3^--derived N taken up at the highest rates," and "added glycine was taken up as intact amino acid within one hour of treatment application, indicating that *L. tridentata* can directly utilize soil organic sources.” They note, “to date, this study is the first to report organic N uptake by a plant species from a hot, arid ecosystem.”

In further discussing their findings, Jin and Evans state “there is increasing consensus that organic N uptake could be a major plant N acquisition pathway (Lipson and Nasholm, 2001; Schimel and Bennett, 2004), with 10–90% of the total annual plant N requirement potentially met by the uptake of external soil organic N (Chapin et al., 1993; Kielland, 1994; Jones and Darrah, 1994).” In addition, they note “long-term exposure to elevated CO_2 has altered the quality and quantity of plant-derived carbon inputs into Mojave Desert soils, leading to higher extracellular enzyme activities indicative of a greater or more active soil fungal component (Jin and Evans, 2007),” such that “increased soil fungi may lead to the greater release of monomeric organic N under elevated CO_2, enhancing substrate availability for soil microbes as well as for plant uptake.” Hence, they found several encouraging indications that the ongoing rise in the air’s CO_2 content will significantly increase the vitality of arid-land ecosystems, just as it does for other ecosystems.

In a related study, Brantly and Young (2010) note woody plant encroachment in herbaceous ecosystems “represents a key shift in community structure that has [the] potential to alter regional and global C and N cycling.” However, they write, “there is considerable uncertainty regarding the effects of woody [plant] encroachment on global terrestrial C storage,” due to the possibility that “increases in C sequestration in woody biomass may be offset by associated increases in soil CO_2 efflux (i.e., combined heterotrophic respiration and root respiration) resulting from increased litterfall, increased soil moisture, and associated increases in microbial activity that often accompany woody [plant] encroachment.”

To further investigate this situation by determining “if young, sandy soils on a barrier island became a sink for C after encroachment of the nitrogen-fixing shrub *Morella cerifera*, or if associated stimulation of soil CO_2 efflux mitigated increased litterfall,” Brantley and Young “monitored variations in litterfall in shrub thickets across a chronosequence of shrub expansion and compared those data to previous measurements of ANPP [annual net primary production] in adjacent grasslands,” after which they “quantified standing litter C and N pools in shrub thickets and soil organic matter (SOM) , soil organic carbon (SOC), soil total nitrogen (TN) and soil CO_2 efflux in shrub thickets and adjacent grasslands,” This field work was conducted on the north end of Hog Island (37°27’N, 75°40’W), a barrier island just east of the Virginia portion of the DelMarVa peninsula, USA.

The two researchers discovered that although soil CO_2 efflux was indeed stimulated by shrub encroachment in the younger soils, “soil CO_2 efflux did not vary between shrub thickets and grasslands in the oldest soils, and increases in CO_2 efflux in shrub thickets did not offset contributions of increased litterfall to SOC.” In fact, they found “SOC was 3.6–9.8 times higher beneath shrub thickets than in grassland soils, and soil TN was 2.5–7.7 times higher under shrub thickets.” These facts led them to conclude the expansion of shrubs on barrier islands—which often have low levels of soil carbon but a high potential for ANPP—can “significantly increase ecosystem C sequestration.” In addition, “stimulation of N storage beneath shrub thickets will also favor future growth of species with lower nutrient use efficiencies than native grasses, including climax maritime forest species that could sequester additional C in biomass,” citing Ehrenfeld (1990) and Vitousek et al. (2002). The phenomena presaged by their work bode well for barrier islands and the planet’s less-productive grasslands.

References

Brantley, S.T. and Young, D.R. 2010. Shrub expansion stimulates soil C and N storage along a coastal soil chronosequence. *Global Change Biology* **16**: 2052–2061.

Chapin III, F.S., Moilanen, L., and Kielland, K. 1993. Preferential use of organic nitrogen for growth by a non-mycorrhizal arctic sedge. *Nature* **361**: 150–153.

Ehrenfeld, J.G. 1990. Dynamics and processes of barrier island vegetation. *Reviews in Aquatic Sciences* **2**: 437–480.

Jin, V.L. and Evans, R.D. 2007. Elevated CO_2 increases microbial carbon substrate use and N cycling in Mojave Desert soils. *Global Change Biology* **13**: 452–465.

Jin, V.L. and Evans, R.D. 2010. Elevated CO_2 increases plant uptake of organic and inorganic N in the desert shrub *Larrea tridentata*. *Oecologia* **163**: 257–266.

Jones, D.L. and Darrah, P.R. 1994. Amino-acid influx at the soil-root interface of *Zea mays* L. and its implications in the rhizosphere. *Plant and Soil* **163**: 1–12.

Kielland, K. 1994. Amino acid absorption by arctic plants: implications for plant nutrition and nitrogen cycling. *Ecology* **75**: 2373–2383.

Lipson, D.A. and Nasholm, T. 2001. The unexpected versatility of plants: organic nitrogen use and availability in terrestrial ecosystems. *Oecologia* **128**: 305–316.

Schimel, J.A. and Bennett, J. 2004. Nitrogen mineralization: challenges of a changing paradigm. *Ecology* **85**: 591–602.

Vitousek, P.M., Cassman, K., Cleveland, C., Crews, T., Field, C.B., Grimm, N.B., Howarth, R.W., Marino R., Martinelli, L., Rastetter, E.B., and Sprent, J.I. 2002. Towards an ecological understanding of biological N fixation. *Biogeochemistry* **57**: 1–45.

7.12.2. Nitrogen Deposition

Noting "human activities have greatly accelerated emissions of both carbon dioxide and biologically reactive nitrogen to the atmosphere," Thomas et al. (2010) report, "as nitrogen availability often limits forest productivity, it has long been expected that anthropogenic nitrogen deposition could stimulate carbon sequestration in forests." However, they note geographically extensive evidence for this phenomenon "has been lacking," and, therefore, they proceeded to provide some, using "spatially extensive forest inventory data to discern the effect of nitrogen deposition on the growth and survival of the 24 most common tree species of the northeastern and north-central US, as well as the effect of nitrogen deposition on carbon sequestration in trees across the breadth of the northeastern US."

They determined that "nitrogen deposition (which ranged from 3 to 11 kg ha^{-1} yr^{-1}) enhanced the growth of eleven species and decreased the growth of three species," while it "enhanced growth of all tree species with arbuscular mycorrhizal fungi associations," leading to "a 40% enhancement over pre-industrial conditions," This response "includes the direct effects of nitrogen deposition on tree growth through soil fertilization, foliar nitrogen uptake and other potential interactions between nitrogen deposition and other environmental changes, including CO_2 fertilization." To provide a sense of the significance of this response, they note it "exceeds the 23% enhancement of net primary production anticipated for the year 2050 from a doubling of atmospheric CO_2 over preindustrial levels, as estimated using free-air CO_2 enrichment studies," citing Norby et al. (2005).

Thomas et al. thus conclude "nitrogen deposition is an important mechanism contributing to carbon sequestration within these temperate forests," though this phenomenon is still "unlikely to explain all of the observed terrestrial carbon sink."

In a study described previously in Section 7.6, Reich (2009) states, "levels of nitrogen deposition and CO_2 have risen in recent decades and are expected to increase further." He notes that in the case of natural ecosystems, the subsequent suppression of diversity by increasing N availability "is almost ubiquitous," while "evidence of CO_2 effects on species richness is scarce and shows mixed results, with positive, neutral, and negative responses seen in the few published reports." So Reich explored what is most likely to happen when the two phenomena occur together using the ten-year-long BioCON study conducted at the Cedar Creek Long-Term Ecological Research site.

According to Reich, at the ambient soil nitrogen concentration, elevated CO_2 had reduced observed species richness by 2 percent while at the ambient atmospheric CO_2 concentration elevated nitrogen decreased species richness by 15 percent over the last seven years of the ten-year-long study. When the elevated soil N concentration was combined with the elevated atmospheric CO_2 concentration, however, species richness declined by only 5 percent, leading Reich to conclude, "elevated CO_2 reduces losses of plant diversity caused by nitrogen deposition." With nitrogen deposition "expected to increase further," as Reich notes, Earth's many natural ecosystems will be protected by the rise in the air's CO_2 content that is expected to accompany it.

References

Norby, R.J., DeLucia, E.H., Gielen, B., Calfapietra, C., Giardina, C.P., King, S.J., Ledford, J., McCarthy, H.R., Moore, D.J.P., Ceulemans, R., De Angelis, P., Finzi, A.C., Karnosky, D.F., Kubiske, M.E., Lukac, M., Pregitzer, K.S., Scarasci-Mugnozza, G.E., Schlesinger, W.H., and Oren, R. 2005. Forest response to elevated CO_2 is conserved across a broad range of productivity. *Proceedings of the National Academy of Sciences* **102**: 18,052–18,056.

Reich, P.B. 2009. Elevated CO_2 reduces losses of plant diversity caused by nitrogen deposition. *Science* **326**: 1399–1402.

Thomas, R.Q., Canham, C.D., Weathers, K.C., and Goodale, C.L. 2010. Increased tree carbon storage in response to nitrogen deposition in the US. *Nature Geoscience* **3**: 13–17.

7.12.3. Nitrogen Fixation

Tu et al. (2009) grew peanut (*Arachis hypogaea* L.) plants from seed to maturity outdoors near Raleigh, North Carolina (USA) in open-top chambers under adequately watered and fertilized conditions, while exposing the plants to (1) charcoal-filtered air, which was thus ozone-free, (2) ambient air of unaltered ozone (O_3) concentration, and (3) air containing 1.6 times the ambient O_3 concentration. All of these O_3 treatments were exposed to air of 376, 550, and 730 ppm CO_2, while the researchers made many plant physiological measurements. At the end of the period they harvested the crop and measured its final steam, leaf, and pod biomass. The four researchers found "at mid-vegetative growth, elevated CO_2 significantly reduced leaf nitrogen concentrations by up to 44%," but "plant nitrogen concentrations only differed by 8% among CO_2 treatments at harvest while N_2 fixation was increased." They state their findings suggest "symbiotic N_2 fixation is important for maintaining seed N concentrations and that CO_2 enhancement of symbiotic N_2 fixation may compensate for low soil N availability."

One year later, Prevost et al. (2010) grew soybean (*Glycine max* [L.] Merr. cv. *Lotus*) plants from seed in 24-cm-deep pots filled with a sandy loam soil that was watered and fertilized according to standard agricultural procedures for a period of six weeks within controlled-environment chambers maintained at atmospheric CO_2 concentrations of either 400 or 800 ppm, after inoculating either the soil or the seeds with either a reference strain (532c) of the nitrogen-fixing bacteria *Bradyrhizobium japonicum*, which is widely used in commercial operations in Canada, or with one of two strains of *B. japonicum* that are indigenous to the soils of Quebec (5Sc2 or 12NS14). They found "elevated CO_2 increased mass (+63%) and number (+50%) of soybean nodules, particularly medium and large, allowed a deeper nodule development, and increased shoot dry weight (+30%), shoot carbon uptake (+33%) and shoot nitrogen uptake (+78%), compared to ambient CO_2."

The four Canadian scientists state their results "constitute the first report showing that elevated CO_2 affects nodule size by allowing a greater production of large nodules, and influences nodule localization by favoring deeper nodule development on roots." Regarding the significance of these findings, they write, "medium and/or large nodules may confer advantages to legumes," since "they have been shown to improve drought tolerance of soybean (King and Purcell, 2001) and to exhibit higher nitrogenase activity in peanut (Tajima et al., 2007)." Also, they say their finding that "both shoot nitrogen and carbon uptakes are stimulated by elevated CO_2 agrees with Rogers et al. (2009), who stated that photosynthetic activity in legumes under elevated CO_2 does not acclimate [decrease with time] under optimal growing conditions, since the additional photosynthates produced are allocated to root nodules for N_2 fixation." And they note similar increases in nodule mass and number have been observed "with other legume species (Schortemeyer et al., 2002; Cabrerizo et al., 2001; Haase et al., 2007)," as well as "with soybean under drought (Serraj et al., 1998)." These findings bode well for legume farmers of the future and for the people and livestock that will consume their produce.

References

Cabrerizo, P.M., Gonzalez, E.M., Aparico-Tejo, P.M., and Aresse-Igor, C. 2001. Continuous CO_2 enrichment leads to increased nodule biomass, carbon availability to nodules and activity of carbon-metabolizing enzymes but does not enhance specific nitrogen fixation in pea. *Physiologia Plantarum* **113**: 33–40.

Haase, S., Neumann, G., Kania, A., Kuzyakov, Y., Romheld, V., and Kandeler, E. 2007.

Elevation of atmospheric CO_2 and N-nutritional status modify nodulation, nodule-carbon supply, and root exudation of *Phaseolus vulgaris* L. *Soil Biology & Biochemistry* **39**: 2208–2221.

King, C.A. and Purcell, L.C. 2001. Soybean nodule size and relationship to nitrogen fixation response to water deficit. *Crop Science* **41**: 1099–1107.

Prevost, D., Bertrand, A., Juge, C., and Chalifour, F.P. 2010. Elevated CO_2 induces differences in nodulation of soybean depending on bradyrhizobial strain and method of inoculation. *Plant and Soil* **331**: 115–127.

Rogers, A., Ainsworth, E.A., and Leakey, A.D.B. 2009. Will elevated carbon dioxide concentration amplify the benefits of nitrogen fixation in legumes? *Plant Physiology* **151**: 1009–1016.

Shortemeyer, M., Atkin, O.K., McFarlane, N., and Evans, J.R. 2002. N_2 fixation by *Acacia* species increases under elevated atmospheric CO_2. *Plant, Cell and Environment* **25**: 567–579.

Serraj, R., Sinclair, T.R., and Allen, L.H. 1998. Soybean nodulation and N_2 fixation response to drought under carbon dioxide enrichment. *Plant, Cell and Environment* **21**: 491–500.

Tajima, R., Lee, O.N., Abe, J., Lux, A., and Morita, S. 2007. Nitrogen-fixing activity of root nodules in relation to their size in peanut (*Arachis hypogaea* L.). *Plant Production Science* **10**: 423–429.

Tu, C., Booker, F.L., Burkey, K.O., and Hu, S. 2009. Elevated atmospheric carbon dioxide and O_3 differentially alter nitrogen acquisition in peanut. *Crop Science* **49**: 1827–1836.

7.12.4. The Progressive Nitrogen Limitation Hypothesis (Part 1)

In an article published in the *Los Angeles Times* on May 14, 2010, headlined "Plant Study Dims Silver Lining to Global Warming," Amina Khan wrote "some biologists had theorized earlier that rising greenhouse gas levels would encourage plant growth over the long term because of the increased amount of carbon dioxide in the atmosphere," but she went on to say "plant physiologists from UC Davis may have dashed those hopes." She quoted the principal investigator of the research project that prompted her article as stating, "we thought rising carbon dioxide levels might actually have some benefit, but it proves to be wrong. ... Over a period of time, be it weeks or years, that stimulation [of photosynthetic and growth rates] disappears."

In the scientific paper describing the research, published the same day as the Khan article, Bloom et al. (2010) claimed to have used "five independent methods with wheat and *Arabidopsis* to show that atmospheric carbon dioxide enrichment inhibited the assimilation of nitrate into organic nitrogen compounds," and "this inhibition may be largely responsible for carbon dioxide acclimation, the decrease in photosynthesis and growth of plants conducting C_3 carbon fixation after long exposures (days to years) to carbon dioxide enrichment."

Interestingly, this concept had a nearly identical incarnation eight years earlier in the *Proceedings of the National Academy of Sciences, USA*, wherein Bloom and three other collaborators (Bloom et al., 2002) made essentially the same claims as Bloom and his second set of associates in 2010. And what was wrong then remains wrong now.

In the earlier study, Bloom et al. (2002) analyzed the ability of two-week-old seedlings of hydroponically grown wheat to respond to a near-doubling of the air's CO_2 content when their roots were bathed in a non-nitrogen-limiting solution of either ammonium (NH_4^+) or nitrate (NO_3^-). The results of that experiment demonstrated that the 94 percent increase in the air's CO_2 content enhanced the biomass of the young wheat plants by 44 percent when the seedlings received their nitrogen in the form of NO_3^-. This result was a significant positive response. Nevertheless, the study's findings were widely portrayed by various organizations, Web sites, and publications as presaging significant negative consequences in the years and decades to come for almost all of Earth's vegetation, including both agricultural crops and natural ecosystems.

One reason for the negativism may have been that the positive result obtained for the plants whose roots were bathed in the NH_4^+ solution was even more impressive. Instead of "just" a 44 percent increase in plant biomass, these plants exhibited a 78 percent increase. And thus it was that on February 4, 2002—one day before the Bloom et al. (2002) paper appeared in print—that NASA's Earth Observatory News posted an article on its Web site titled "High CO_2 Levels Hamper Nitrate Incorporation by Plants," in which it was claimed "nitrate fertilizer is not nearly as efficient as ammonium fertilizer when atmospheric carbon dioxide levels are unusually high." This is quite an expansive conclusion to draw from a study that lasted only two weeks, dealt with only one species, and utilized only seedlings growing only in nutrient solution.

This report was followed by several similar stories of much the same negative bent. *Scientific American* introduced its take on the Bloom et al. (2002) paper with an equally expansive title, stating "Rising CO_2 Levels Could Force Shift in Fertilizer Use," which was reproduced the same day by the Climate Ark organization. Simultaneously, AmeriScan displayed an article titled "Rising CO_2 Hampers Fertilizers," which began with the declaration that "as carbon dioxide levels rise, plant life around the globe may lose the ability to incorporate certain forms of nitrogen, like those found in most fertilizers." It ended by stating, "as atmospheric CO_2 levels continue to rise, nitrate-sensitive plant and tree species in the wild could be at a competitive disadvantage," and "this could change the distribution of plants in natural ecosystems."

Eerily, several press reports also said that "for many years, scientists believed ... rising levels of carbon dioxide would actually benefit plants," as if to suggest that was no longer the case. They also matter-of-factly stated that the initial positive growth response to atmospheric CO_2 enrichment observed in most experiments "wasn't sustained," dropping back to just a few percent above normal "within a few days or weeks," but which Bloom et al. (2010) have now extended to "days to years."

It was also interesting—but not unexpected—that the environmental press highly hyped so many of the presumed negative ramifications of the Bloom et al. (2002) experiment for both agricultural and natural ecosystems, when the experiment upon which those presumptions were based lasted only 14 days and had been performed under sterile laboratory conditions that included no soil, no competing plants, and a totally unnatural mix of antibiotics in the water surrounding the seedlings' roots. These antibiotics were introduced to suppress naturally occurring nitrogen-transforming processes that Bloom et al. (2002) admitted are "rapid in nonsterile cultures (Padgett and Leonard, 1993) and sensitive to atmospheric CO_2 (Smart et al., 1997)," which made the experimental conditions very different from the real world of nature.

It should not surprise us, then, that longer experiments conducted under more realistic conditions have refuted the claims made by the press. We first consider the three-part claim—which, to be fair to the press, was actually made by Bloom et al. (2002)—that (1) "a doubling of CO_2 level initially accelerates carbon fixation in C_3 plants by about 30%," (2) this growth stimulation "after days to weeks" dramatically declines, and (3) the CO_2-induced growth enhancement thereafter "stabilizes at a rate that averages 12% above ambient controls."

All three parts of this contention are inadequate generalizations of what is called acclimation to CO_2 enrichment. In the first instance, a doubling of the air's CO_2 content often will accelerate biomass production in young C_3 plants in the early stages of CO_2 enrichment by much more than 30 percent. Even in their own experiment, Bloom et al. (2002) found that slightly less than a doubling of the air's CO_2 content increased the biomass of their NO_3^--treated plants by fully 44 percent, and it increased the biomass of their NH_4^+-treated plants by 78 percent. In addition, the mini-review of Idso (1999) cites at least 20 experiments where the initial growth stimulation exceeded 100 percent.

With respect to the decline in growth stimulation claimed by Bloom et al. to follow hard on the heels of the initial CO_2-induced growth enhancement, we note it in some cases it never occurs (Gunderson et al., 1993; Fernandez et al., 1998; Garcia et al., 1998). In other instances, the reverse occurs: The CO_2-induced growth stimulation increases over time (Arp and Drake, 1991; Vogel and Curtis, 1995; Jacob et al., 1995). And in those cases where there is a decline in the strength of the CO_2 aerial fertilization effect, it sometimes does not begin until one or more years after the initiation of the experiment. In the long-term sour orange tree study of Idso and Kimball (2001), for example, a decline in the CO_2-induced growth stimulation did not begin until the 2.5-year point of the experiment.

Finally, the degree of CO_2-induced growth stimulation at which the aerial fertilization effect of atmospheric CO_2 enrichment eventually stabilizes is often significantly larger than the 12 percent value suggested by Bloom et al. (2002) for a doubling of the air's CO_2 content. In their summary report of the Phoenix, Arizona sour orange tree study, for example, Kimball et al. (2007) write that rather than "a continual acclimation" or neverending long-term decline in the strength of the CO_2-induced aerial fertilization effect, there was a "sustained enhancement," a near-constant 70 percent increase in total yearly biomass production over the entire last decade of the 17-year study in response to the 75 percent increase in the air's CO_2 content employed throughout the experiment, which for a doubling of the air's CO_2 content implies there would have been a CO_2-induced productivity enhancement on the order of 93 percent, nearly eight times greater than what Bloom et al. (2002) declared to be typical.

Having thus clarified the record with respect to the erroneously summarized aspects of the CO_2 acclimation phenomenon presented in the Bloom et al. (2002) article, there is a need to address their contention that plants respond better to atmospheric CO_2 enrichment when they obtain their nitrogen in the ammonium form as opposed to the nitrate form. For in spite of their claim that theirs may have been "the first study to examine CO_2 responses under controlled levels of NH_4^+ vs. NO_3^- as sole N sources," there have in fact been many other studies, some of which are briefly highlighted below, that provide important—and vastly different—information about this topic.

Bauer and Berntson (2001) grew seedlings of *Betula alleghanienis* and *Pinus strobus* for 15 weeks—as opposed to the abbreviated two weeks of the Bloom et al. (2002) experiment—in growth chambers maintained at atmospheric CO_2 concentrations of 400 and 800 ppm, while the seedlings' roots were suspended in nutrient solutions whose sole sources of N were, as in the study of Bloom et al. (2002), either NO_3^- or NH_4^+. In this experiment, the extra CO_2 did not have any effect on the growth of the *Pinus* species in either solution, but it increased total seedling dry weight in the *Betula* species by 61 percent in the nitrate treatment and by 79 percent in the ammonium treatment. Although this result is qualitatively the same as that obtained by Bloom et al., the ammonium/nitrate (A/N) response ratio, i.e., 79%/61% = 1.30, was much lower than the A/N response ratio of the Bloom et al. (2002) experiment, i.e., 78%/44% = 1.77, suggesting perhaps the A/N response ratio could be undergoing a type of acclimation as experimental duration lengthens. That suggests the possibility that for still longer (and more realistic) periods of differential CO_2 exposure, there may be little or no plant preference for a particular N source.

Van der Merwe and Cramer (2000) grew tomato seedlings for two weeks—bringing them to the same age as the wheat plants studied by Bloom et al. (2002)—in air of 360 ppm CO_2, while the roots of the seedlings were enclosed in sealed vessels containing either NO_3^- or NH_4^+ solutions, after which the solutions were equilibrated with air as high in CO_2 concentration as 20,000 ppm. This rhizospheric CO_2 enrichment had no effect on the uptake of NH_4^+ by the tomato seedlings, but it resulted in an enhanced uptake of NO_3^-, with the maximum effect occurring at a rhizospheric CO_2 concentration of 5,000 ppm, which is to be compared to a normal root-zone CO_2 concentration of something less than 5,000 ppm but more than 1,000 ppm, as is typical of soil airspace in most outdoor environments. Although we cannot be confident about all the possible implications of this observation, it does indicate a preferential plant uptake of nitrate N at higher-than-normal rhizospheric CO_2 concentrations, which is difficult to understand if plants are supposed to prefer ammonium N at high CO_2 concentrations, as suggested by Bloom et al. (2002).

It can be additionally noted, at this point, that attempting to discern and characterize a possible CO_2-mediated plant preference for a particular form of nitrogen must involve considerably more complex investigations than simple laboratory experiments with individual plants whose roots never have been exposed to anything other than sterile nutrient solutions. Actual nonsterile soils are required to host the plants if one is ever going to learn how plants operate in the world of nature. Hence, this aspect of our investigation begins with a brief review of an intermediate sort of study conducted by Constable et al. (2001). Although not using totally natural soil, they at least got beyond the hydroponic stage of investigation for the major portion of their experiment, and they also dealt with the added complexity supplied by the presence of two types of fungal symbionts, which often live in close association with the roots of plants in their normal habitats and serve as a living link between them and the soil environment.

Constable et al. studied mycorrhizal- and non-mycorrhizal-infected seedlings of both sweetgum and loblolly pine seedlings rooted in pots filled with fine sand above a layer of mycorrhizal inoculum, or clay lacking such inoculum, and grown for six months outdoors in open-top chambers maintained at atmospheric CO_2 concentrations of either 350 or 700 ppm. They then brought the seedlings into the laboratory, washed the sand from their roots and from the fungal hyphae associated with the roots of half of the plants, and placed the roots and root/hyphae systems in hydroponic solutions of NO_3^- and NH_4^+ for N uptake evaluations conducted within controlled environment chambers maintained at the same atmospheric CO_2 concentrations to which the seedlings had been exposed while growing outside.

In this part of the experiment, both tree species exhibited a greater preference for NH_4^+ than for NO_3^-, regardless of mycorrhizal treatment, as is commonly reported for trees exposed to normal atmospheric CO_2 concentrations (Gessler et al., 1998; Wallenda and Read, 1999). Nevertheless, the presence of mycorrhizae clearly improved nitrogen acquisition in both species at both CO_2 concentrations; and, as the researchers reported, "this increase in uptake capacity was preferentially for NO_3^- as opposed to NH_4^+." Furthermore, they noted "in loblolly pine, the relative enhancement of NO_3^- uptake capacity by ectomycorrhizal fungi was significantly higher at elevated CO_2 compared with ambient CO_2," in direct opposition to what would be expected on the basis of the Bloom et al. (2002) experiment. In sweetgum, however, the reverse was true. Thus the authors urged caution in concluding too much from observations derived from too few species of both plants and mycorrhizae—a caution, we might add, that seems not to have occurred to either Bloom et al. (2002) or the members of the press who wrote so confidently about the global applicability of the results of their highly artificial wheat experiment.

In a still more realistic set of experiments, BassiriRad et al. (1999) grew two tree species—red maple and sugar maple—for close to 1.5 years outdoors in open-top chambers (OTCs) maintained at atmospheric CO_2 concentrations of ambient and ambient plus 300 ppm, as well as two crop species—soybean and sorghum—studied for one full growing season in OTCs maintained at atmospheric CO_2 concentrations of ambient and ambient plus 360 ppm. The trees were planted directly into the natural soil upon which the OTCs of their experiment were constructed, while the crops were planted in natural soil that filled a 2-meter-deep bin, measuring 6 meters wide and 76 meters long, upon which the OTCs of their experiment were constructed.

In both sets of experiments, small groups of fine roots were carefully exposed, cleaned, and inserted into tubes containing known volumes of 25, 50, 75, 100, 150, and 200 µM solutions of NH_4NO_3, after which the roots were allowed to take up whatever amounts of each form of N they preferred over periods of 30 to 60 minutes. The roots were then removed from the tubes and the portions that had been immersed in the nutrient solution excised, dried, and weighed. The volume of the remaining solution in each tube was stored for later assessment of the amounts of NH4+ and NO3- that had not been removed by the roots.

All four species exhibited a distinct preference for NH_4^+ uptake over NO_3^- uptake when grown in air of normal atmospheric CO_2 concentration, but this preference was only to be expected, because the energy requirements associated with the uptake and assimilation of NO_3^- are considerably greater than those associated with the uptake and assimilation of NH_4^+, as demonstrated by Haynes and Goh (1978), Blacquiere (1987), and Glass and Siddiqi (1995). BassiriRad et al. also noted "the greater preference for NH_4^+ vs. NO_3^- is almost a universal root characteristic in tree species and is often associated with an adaptation to forest soils that are relatively low in NO_3^-."

So what happened with the plants in the CO_2-enriched chambers? Red maple exhibited a slight increase of its ambient-air preference for NH_4^+. The other three species showed no change in N preference at the higher CO_2 concentration. Hence, one of the four species studied provided weak support for the hypothesis of the Bloom et al. (2002) study, and the other three species provided no support.

Where does all of this discussion lead? For one thing, the body of literature discussed above suggests different species may behave differently with respect to the effects of atmospheric CO_2 enrichment on their N uptake kinetics. BassiriRad et al. additionally note, for example, that "using potted seedlings we have shown elsewhere (BassiriRad et al., 1997a, b) that high CO_2 increased, decreased or had no significant effect on NO_3^- uptake kinetics depending upon species tested." They also note that in a hydroponic experiment using soybean and sunflower, they found "root N uptake kinetics response to CO_2 enrichment was highly dependent on the stages of development and root age." Hence, they state "a 'one point in time' determination"—such as that which comprised the study of Bloom et al. (2002)—"is not adequate," and "more measurements of root N uptake kinetics are necessary to draw valid conclusions about possible effects of CO_2."

Clearly, the Bloom et al. (2002) experiment in no way supports any of the monumental biospheric problems that they and many in the press have attempted to convince us will occur on the basis of their severely restricted study. The newer study of Bloom et al. (2010) likewise provides no support for their equally wild speculations about the future of Earth's biosphere. In all five of their newest experiments, for example, the plants they studied were grown (1) hydroponically in (2) isolation under (3) sterile laboratory conditions for (4) only a few weeks, while measurements of the key processes they made were generally conducted over (5) only a matter of hours.

That is not the way to ascertain what might happen over the long haul in the real world. The way to find out what really happens in the real world is to conduct long-term studies in as natural a setting as possible. For many people this means working outdoors in open-top chambers with plants rooted directly in the ground, which is how the 17-year Phoenix, Arizona sour orange tree study was conducted. For others it likewise means working outside but doing so within the context of free-air CO_2 enrichment experiments.

Summarizing nine years of such work at the Duke Forest FACE facility in North Carolina (USA), where portions of an aggrading loblolly pine plantation had been continuously exposed to an extra 200 ppm of CO_2 since 1996, Lichter et al. (2008) reported the CO_2-induced increase in productivity there had amounted to about 30 percent annually—which roughly equates to a 45 percent increase for a 300 ppm increase in CO_2, and even more for a true doubling of the air's CO_2 content. The scientists add there is "little evidence to indicate a diminished response through time," citing, in this regard, Finzi et al. (2007), who found the same to be true at three other long-term forest FACE studies conducted at Rhinelander, Wisconsin (USA), Oak Ridge National Laboratory (USA), and Tuscania (Italy).

As but one example, after working at the EuroFACE facility in Central Italy for a period of several years, Davey et al. (2006) published their observations in a paper titled "Can fast-growing plantation trees escape biochemical down-regulation of photosynthesis when grown throughout their complete production cycle in the open air under elevated carbon dioxide?" They report that poplar trees exposed to a 50 percent increase in atmospheric CO_2 concentration over four growing seasons "showed a sustained increase in photosynthesis of between 35 and 60 percent prior to coppicing," and "this increase in daily photosynthesis [was] maintained during the re-growth," such that "no long-term photosynthetic acclimation to CO_2 occurred in these plants." They note "poplar trees are able to 'escape' from long-term, acclamatory down-regulation of photosynthesis" and "the acclamatory loss of the initial increase in photosynthetic rate under elevated CO_2 is not inevitable." In their report of another study conducted on the same trees, Calfapietra et al. (2005) write, "photosynthetic acclimation of poplar plantations is unlikely to occur in an atmosphere enriched in CO_2 and thereby will not influence the response of poplar plantations to increasing atmospheric CO_2 concentrations either over the long term or under conditions of nitrogen deposition."

But perhaps the most amazing example of avoiding long-term photosynthetic acclimation in the real world comes from Paoletti et al. (2007). They measured rates of net photosynthesis during a two-week period in June 2002 "at the end of the spring rains" when midday air temperatures rose above 40°C in upper sunlit leaves of mature holm oak trees growing close to (5 m) and further away from (130 m) a natural CO_2-emitting spring near Laiatico (Pisa, Italy), where the trees had experienced lifetime exposure to atmospheric CO_2 concentrations of approximately 1,500 and 400 ppm, respectively. They found the net photosynthetic rates of the leaves on the trees growing closest to the CO_2 spring were approximately 250 percent greater than those of the leaves on the trees growing 125 meters further away, where the atmospheric CO_2 concentration was 1,100 ppm lower than it was in the vicinity of the trees nearest the spring. The four Italian researchers thus concluded, "the considerable photosynthetic stimulation at the very high CO_2 site suggests no photosynthetic down-regulation over long-term CO_2 enrichment." This real-world finding demonstrates the truly amazing potential for very large increases in the air's CO_2 content to greatly stimulate photosynthesis and significantly enhance the growth and development of plants over the very long term.

Contrary to the claims of Bloom et al. (2002) and Bloom et al. (2010), trees—including those thought to have access to less-than-adequate soil nitrogen supplies—are entirely capable of maintaining the sizable increases in their growth rates that are made possible by elevated concentrations of atmospheric CO_2. In the case of North Carolina's Duke Forest, for example, "even after nine years of experimental CO_2 fertilization," as Lichter et al. (2008) state, "attenuation of the CO_2-induced productivity enhancement has not been observed." This also has been noted to be the case by Finzi et al. (2006). This finding at this particular location is significant because the growth of pine-hardwood forests in the southeastern United States often removes so much nitrogen from the soils in which they grow that they induce what Finzi and Schlesinger (2003) have described as "a state of acute nutrient deficiency that can only be reversed with fertilization." This operation, however, has not been employed in the Duke Forest FACE study, which makes it about as challenging a situation as there could be for the long-term persistence of the growth-promoting aerial fertilization effect of atmospheric CO_2 enrichment. Yet the phenomenon does precisely that: It persists.

References

Arp, W.J. and Drake, B.G. 1991. Increased photosynthetic capacity of Scirpus olneyi after 4 years of exposure to elevated CO_2. *Plant, Cell and Environment* **14**: 1003–1006.

BassiriRad, H., Griffin, K.L., Reynolds, J.F., and Strain, B.R. 1997a. Changes in root NH_4^+ and NO_3^- absorption rates of loblolly and ponderosa pine in response to CO_2 enrichment. *Plant and Soil* **190**: 1–9.

BassiriRad, H., Prior, S.A., Norby, R.J., and Rogers, H.H. 1999. A field method of determining NH_4^+ and NO_3^- uptake kinetics in intact roots: Effects of CO_2 enrichment on trees and crop species. *Plant and Soil* **217**: 195–204.

BassiriRad, H., Reynolds, J.F., Virginia, R.A., and Brunelle, M.H. 1997b. Growth and root NO_3^- and PO_3^- uptake capacity of three desert species in response to atmospheric CO_2 enrichment. *Australian Journal of Plant Physiology* **24**: 353–358.

Bauer, G.A. and Berntson, G.M. 2001. Ammonium and nitrate acquisition by plants in response to elevated CO_2 concentration: the roles of root physiology and architecture. *Tree Physiology* **21**: 137–144.

Blacquiere, T. 1987. Ammonium and nitrate nutrition in Plantago lanceolata and P. major ssp. major. II. Efficiency of root respiration and growth. Comparison of measured and theoretical values of growth respiration. *Plant Physiology and Biochemistry* **25**: 1775–1785.

Bloom, A.J., Burger, M., Asensio, J.S.R., and Cousins, A.B. 2010. Carbon dioxide enrichment inhibits nitrate assimilation in wheat and Arabidopsis. *Science* **328**: 899–903.

Bloom, A.J., Smart, D.R., Nguyen, D.T., and Searles, P.S. 2002. Nitrogen assimilation and growth of wheat under elevated carbon dioxide. *Proceedings of the National Academy of Sciences, USA* **99**: 1730–1735.

Calfapietra, C., Tulva, I., Eensalu, E., Perez, M., De Angelis, P., Scarascia-Mugnozza, G., and Kull, O. 2005. Canopy profiles of photosynthetic parameters under elevated CO_2 and N fertilization in a poplar plantation. *Environmental Pollution* **137**: 525–535.

Constable, J.V.H., BassiriRad, H., Lussenhop, J., and Zerihun, A. 2001. Influence of elevated CO_2 and mycorrhizae on nitrogen acquisition: contrasting responses in Pinus taeda and Liquidambar styraciflua. *Tree Physiology* **21**: 83–91.

Davey, P.A., Olcer, H., Zakhleniuk, O., Bernacchi, C.J., Calfapietra, C., Long, S.P., and Raines, C.A. 2006. Can fast-growing plantation trees escape biochemical down-regulation of photosynthesis when grown throughout their complete production cycle in the open air under elevated carbon dioxide? *Plant, Cell and Environment* **29**: 1235–1244.

Finzi, A.C., Moore, D.J.P., DeLucia, E.H., Lichter, J., Hofmockel, K.S., Jackson, R.B., Kim, H.-S., Matamala, R., McCarthy, H.R., Oren, R., Pippen, J.S., and Schlesinger, W.H. 2006. Progressive nitrogen limitation of ecosystem processes under elevated CO_2 in a warm-temperate forest. *Ecology* **87**: 15–25.

Finzi, A.C., Norby, R.J., Calfapietra, C., Gallet-Budynek, A., Gielen, B., Holmes, W.E., Hoosbeek, M.R., Iversen, C.M., Jackson, R.B., Kubiske, M.E., Ledford, J., Liberloo, M., Oren, R., Polle, A., Pritchard, S., Zak, D.R., Schlesinger, W.H., and Ceulemans, R. 2007. Increases in nitrogen uptake rather than nitrogen-use efficiency support higher rates of temperate forest productivity under elevated CO_2. *Proceedings of the National Academy of Sciences, USA* **104**: 14,014–14,019.

Finzi, A.C. and Schlesinger, W.H. 2003. Soil-nitrogen cycling in a pine forest exposed to 5 years of elevated carbon dioxide. *Ecosystems* **6**: 444–456.

Fernandez, M.D., Pieters, A., Donoso, C., Tezara, W., Azuke, M., Herrera, C., Fengifo, E., and Herrera, A. 1998. Effects of a natural source of very high CO_2 concentration on the leaf gas exchange, xylem water potential and stomatal characteristics of plants of Spatiphylum cannifolium and Bauhinia multinervia. *New Phytologist* **138**: 689–697.

Garcia, R.L., Long, S.P., Wall, G.W., Osborne, C.P., Kimball, B.A., Nie, G.Y., Pinter Jr., P.J., LaMorte, R.L., and Wechsung, F. 1998. Photosynthesis and conductance of spring-wheat leaves: field response to continuous free-air atmospheric CO_2 enrichment. *Plant, Cell and Environment* **21**: 659–669.

Gessler, A., Schneider, S., Von Sengbusch, D., Weber, P., Hanemann, W., Huber, C., Rothe, A., Kreutzer, K., and Rennenberg, H. 1998. Field and laboratory experiments on net uptake of nitrate and ammonium by the roots of spruce (Picea abies) and beech (Fagus sylvatica) trees. *New Phytologist* **138**: 275–285.

Glass, A.D.M. and Siddiqi, M.Y. 1995. Nitrogen absorption by plant roots. In *Nitrogen Nutrition in Higher Plants*, edited by H.S. Srivastava and R.P. Singh, 21–56. New Delhi, India: Associated Publishing Co.

Gunderson, C.A., Norby, R.J., and Wullschleger, S.D. 1993. Foliar gas exchange responses of two deciduous hardwoods during three years of growth in elevated CO_2: no loss of photosynthetic enhancement. *Plant, Cell and Environment* **16**: 797–807.

Haynes, R.J. and Goh, K.M. 1978. Ammonium and nitrate nutrition of plants. *Biological Reviews* **53**: 465–510.

Idso, S.B. 1999. The long-term response of trees to atmospheric CO_2 enrichment. *Global Change Biology* **5**: 493–495.

Idso, S.B. and Kimball, B.A. 2001. CO_2 enrichment of sour orange trees: 13 years and counting. *Environmental and Experimental Botany* **46**: 147–153.

Jacob, J., Greitner, C., and Drake, B.G. 1995. Acclimation of photosynthesis in relation to Rubisco and non-structural carbohydrate contents and in situ carboxylase activity in Scirpus olneyi grown at elevated CO_2 in the field. *Plant, Cell and Environment* **18**: 875–884.

Kimball, B.A., Idso, S.B., Johnson, S., and Rillig, M.C. 2007. Seventeen years of carbon dioxide enrichment of sour orange trees: final results. *Global Change Biology* **13**: 2171–2183.

Lichter, J., Billings, S.A., Ziegler, S.E., Gaindh, D., Ryals, R., Finzi, A.C., Jackson, R.B., Stemmler, E.A., and Schlesinger, W.H. 2008. Soil carbon sequestration in a pine forest after 9 years of atmospheric CO_2 enrichment. *Global Change Biology* **14**: 2910–2922.

Padgett, P.E. and Leonard, R.T. 1993. Contamination of ammonium-based nutrient solutions by nitrifying organisms and the conversion of ammonium to nitrate. *Plant Physiology* **101**: 141–146.

Paoletti, E., Seufert, G., Della Rocca, G., and Thomsen, H. 2007. Photosynthetic responses to elevated CO_2 and O3 in Quercus ilex leaves at a natural CO_2 spring. *Environmental Pollution* **147**: 516–524.

Smart, D.R., Ritchie, K., Stark, J.M., and Bugbee, B. 1997. Evidence that elevated CO_2 levels can indirectly increase rhizosphere denitrifier activity. *Applied and Environmental Microbiology* **63**: 4621–4624.

Van der Merwe, C.A and Cramer, M.D. 2000. Effect of enriched rhizosphere carbon dioxide on nitrate and ammonium uptake in hydroponically grown tomato plants. *Plant and Soil* **221**: 5–11.

Vogel, C.S. and Curtis, P.S. 1995. Leaf gas exchange and nitrogen dynamics of N2-fixing, field-grown Alnus glutinosa under elevated atmospheric CO_2. *Global Change Biology* **1**: 55–61.

Wallenda, T. and Read, D.J. 1999. Kinetics of amino acid uptake by ectomycorrhizal roots. *Plant, Cell and Environment* **22**: 179–187.

7.12.5. The Progressive Nitrogen Limitation Hypothesis (Part 2)

Land plants grow best when supplied with optimum levels of soil nitrogen. When this reactive nitrogen (Nr) is present in soils in concentrations that are less than optimal, terrestrial vegetation grows less vigorously and removes less CO_2 from the atmosphere. As a result, there have been claims that less-than-optimal soil nitrogen concentrations will eventually cause a significant reduction in the strength of the growth stimulation provided by the aerial fertilization effect of the ongoing rise in the air's CO_2 content because the limited amount of Nr in the soil simply cannot supply enough of this essential nutrient to maintain the increase in growth stimulated by the rising CO_2. This string of suppositions has come to be called the progressive nitrogen limitation hypothesis (Hungate et al., 2003; Luo et al., 2004).

Expressing the opposite concern about Nr are scientists such as Fujimaki et al. (2009), who contend "anthropogenic addition of reactive nitrogen to the biosphere"—"through production of fertilizers, cultivation of N-fixing plants, and utilization of fossil fuels"—"is increasing globally and some terrestrial ecosystems are suffering from a state of excess Nr." They contend "excess Nr has a harmful impact on vegetation cover and species diversity," as a result of "increasing competitive abilities for a small number of nitrophilic species, increase of herbivory, decreases in mutualistic fungi, increases in pathogenic fungi, and enhanced invasibility by exotic species that are highly competitive under conditions of high soil nitrate." Both sides of this debate feel strongly about their positions, and both foresee undesirable consequences in the fairly near future if certain aspects of the way modern societies operate are not radically changed.

What neither side seems to consider, however, is that the two extreme phenomena might work together to produce a harmonious outcome. Instead of suppressing economic activity (to reduce CO_2 emissions) and agricultural production (to reduce addition of nitrogen to the soil), we could simply let each phenomenon proceed unimpaired by overt human intervention. Thus the addition of nitrogen to the soil should provide what is needed (more reactive nitrogen) to enable the world's terrestrial vegetation to capture and sequester more of the carbon supplied to the air by anthropogenic CO_2 emissions. This will be needed to increase the productivity of the world's cropped and naturally vegetated land in order to feed the still-growing human population.

Evidence that such a laissez-faire approach to the two concerns is indeed reasonable is provided by the fact that even Fujimaki et al. admit "ecosystem net primary production seems to be under N limitation," and "in global trends to date, plant growth itself tends to be stimulated with increase of N deposition." This observation leads them to conclude, "if N deposition continues at the present rates in the next few decades, ecosystem net primary production would be released from the limitation of N availability." Better yet, there is evidence that vegetation growing in CO_2-enriched air can find the nitrogen it needs even when it seems not to be there.

Consider the Duke Forest free-air CO_2-enrichment (FACE) study: a long-term experiment designed to investigate the effects of an extra 200 ppm of atmospheric CO_2 on the growth and development of a plantation of loblolly pine (*Pinus taeda*) trees with an understory of various broadleaf species (*Liriodendron tulipifera, Liquidambar styraciflua*, *Acer rubrum*, *Ulmus alata*, and *Cornus florida*), plus various other trees, shrubs, and vines, all growing on a soil that Finzi and Schlesinger (2003) have described as being in "a state of acute nutrient deficiency that can only be reversed with fertilization." Many people had long thought this fertility deficiency would stifle the ability of the extra aerial supply of CO_2 to significantly stimulate the forest's productivity on a continuing basis. Based on data for the years 1996–2004, however, McCarthy et al. (2010) calculated the net primary productivity (NPP) for the pines, the hardwoods, and the entire stand as the sum of the production of coarse wood (stems, branches, and coarse roots), leaf litter (lagged for pines), fine roots, and reproductive structures. They found "elevated CO_2 increased pine biomass production, starting in 1997 and continuing every year thereafter," and "the CO_2-induced enhancement remained fairly consistent as the stand developed."

They also found "elevated CO_2 increased stand (pine plus all other species) biomass production every year from 1997 onwards with no trend over time," such that the average yearly increase in NPP caused by the approximate 54 percent increase in the air's CO_2 content was a solid 28 percent. Thus, and in spite of the original belief of many scientists that low levels of soil nitrogen—especially an acute deficiency—would preclude the persistence of any growth stimulation provided by atmospheric CO_2 enrichment, the suite of trees, bushes, and shrubs that constitute the Duke Forest has continued to maintain the extra CO_2-enabled vitality exhibited right from the start of the study, with no sign of it even beginning to taper off.

Also working at the Duke Forest FACE facility, Jackson et al. (2009) described belowground data they obtained there, after which they presented a synthesis of these and other results they obtained between 1996 and 2008, seeking to determine "which, if any, variables show evidence for a decrease in their response to atmospheric CO_2 during that time frame."

Among many other things, Jackson et al. report "on average, in elevated CO_2, fine-root biomass in the top 15 cm of soil increased by 24%," and in recent years the fine-root biomass increase "grew stronger, averaging ~30% at high CO_2." Regarding coarse roots having diameters greater than 2 mm and extending to a soil depth of 32 cm, they report "biomass sampled in 2008 was twice as great in elevated CO_2." We calculate from the graphical representation of their results that the coarse-root biomass was fully 130 percent greater, while the extra 200 ppm of CO_2 supplied to the air surrounding the CO_2-enriched trees represented an enhancement of only about 55 percent above ambient conditions. In the concluding sentence of their paper's abstract, they state, "overall, the effect of elevated CO_2 belowground shows no sign of diminishing."

The four researchers thus conclude, "if progressive nitrogen limitation were occurring in this system, we would expect differences in productivity to diminish for trees in the elevated vs. ambient CO_2 plots," but "there is little evidence from estimates of aboveground or total net primary productivity in the replicated Duke experiment that progressive nitrogen limitation is occurring there or at other forest FACE experiments," even "after more than a decade of manipulation" of the air's CO_2 content, citing, with respect to the latter portion of their statement, Finzi et al. (2007). Consequently, there is good reason to believe the "aerial fertilization effect" of atmospheric CO_2 enrichment will continue to significantly benefit Earth's forests as long as the atmosphere's CO_2 concentration continues to rise.

Working with photosynthesis data they and others collected over 11 years at the Aspen FACE site near Rhinelander, Wisconsin (USA), Darbah et al. (2010) evaluated the merits of the progressive nitrogen limitation hypothesis for two different quaking aspen (*Populus tremuloides* Michx.) clones (42E and 271) exposed to all combinations of ambient and elevated (560 ppm) CO_2 and ambient and elevated (1.5 times ambient) ozone (O_3). They also investigated whether the same hypothesis applied to leaf stomatal conductance.

The eight researchers say their results "suggest no long-term photosynthetic and stomatal acclimation to elevated CO_2, O_3 or $CO_2 + O_3$ in aspen trees exposed to elevated CO_2 and/or O_3 gases for 11 years," adding the aspen trees "have sustained their maximum instantaneous photosynthesis stimulation for over a decade." Commenting further, they say their findings support the observations of (1) Liberloo et al. (2007), who measured a 49 percent increase in net photosynthetic rate in poplar trees after six years of exposure to elevated CO_2, (2) Sholtis et al. (2004), who reported a 44 percent stimulation of net photosynthesis in sweetgum trees after three years of exposure to elevated CO_2, (3) Crous and Ellsworth (2004), who found a photosynthetic enhancement of 51–69 percent in *Pinus taeda* trees after six years of exposure to elevated CO_2, as well as (4) Davey et al. (2006) and (5) Paoletti et al. (2007), of whose work Darbah et al. state "there was no photosynthetic acclimation (down-regulation) occurring in *Quercus ilex* under long-term CO_2 enrichment." In addition, Darbah et al. remark that (6) even in white clover (*Trifolium repens*), Ainsworth et al. (2003) found photosynthetic stimulation "remained after nine years of exposure to elevated CO_2."

Focusing her efforts belowground, Colleen Iversen of the Oak Ridge National Laboratory in Oak Ridge, Tennessee (USA) reviewed the pertinent scientific literature "to examine the potential mechanisms for, and consequences of, deeper rooting distributions under elevated CO_2 as they relate to ecosystem carbon and nitrogen cycling," focusing primarily on forests (Iversen, 2010). She found "experimental evidence from a diverse set of forested ecosystems indicates that fine roots of trees exposed to elevated CO_2 are distributed more deeply in the soil profile relative to trees grown under ambient CO_2." As an example, she reports, "in a FACE experiment in a sweetgum (*Liquidambar styraciflua*) plantation, Iversen et al. (2008) found that, over nine years, there was a 220% stimulation in cumulative carbon inputs from fine roots under elevated CO_2 at 45-60 cm soil depth, compared with a 30% stimulation of root carbon inputs at 0-15 cm depth," and she notes "Pritchard et al. (2008a) found a similar response in a CO_2-enriched loblolly pine (*Pinus taeda*) plantation." In fact, she found, "of those experiments that examined rooting depth responses to elevated CO_2, 73% found deeper rooting distributions." In addition, she notes "increased proliferation at depth in the soil has not been limited to fine roots: increased production of mycorrhizas (Pritchard et al., 2008b) and coarse roots (Liberloo et al., 2006) also occurred deeper in the soil under CO_2 enrichment."

Regarding the progressive nitrogen limitation hypothesis, therefore, Iversen writes, "a disconnect between observed root dynamics and modeled nutrient availability has confounded projections of forest responses to elevated CO_2." She notes "while models predict that soil nitrogen availability will limit forest responses to elevated CO_2 (Thornton et al., 2007), many of the forested FACE experiments found a sustained increase in nitrogen uptake from the soil in response to CO_2 enrichment (Finzi et al., 2007)." She goes on to state "there has been much speculation on the source of this 'extra' nitrogen (Johnson, 2006), and a greater cumulative amount of nitrogen available at depth in the soil may be the answer (i.e. a 'bigger box' of nitrogen when deeper soil depths are considered)."

Shifting from forests to grasslands, Dijkstra et al. (2008) used open-top chambers to examine the effects of elevated atmospheric CO_2 concentration (720 vs. 368 ppm) on nitrogen dynamics in a semi-arid grassland ecosystem in northeastern Colorado (USA), where they studied the impacts of elevated CO_2 on nitrogen mineralization and plant N uptake by tracking initially applied ^{15}N and total N in both plants and soil over a period of five years. This work revealed an increase in aboveground biomass on the order of 40 percent in response to their specific degree of elevated CO_2; and they state it "did not lead to a progressive decline in soil N availability." On the contrary, the six scientists write, "soil N availability remained higher after 5 years of elevated than ambient CO_2," likely due to "a greater mineralization rate under elevated CO_2." As for why this was so, they speculate the "elevated CO_2 increased soil moisture due to decreased plant transpiration at [their] site (Nelson et al., 2004), which could have stimulated microbial activity and N mineralization."

In another illuminating experiment, McCormack et al. (2010) constructed 12 identical mini-ecosystems—each consisting of three longleaf pine (*Pinus palustris*) seedlings, three wiregrass (*Aristida stricta*) C_4 grass plants, two sand post oak (*Quercus margaretta*) seedlings, one rattlebox (*Croatalaria rotundifolia*) C_3 perennial herbaceous legume, and one butterfly weed (*Asclepias tuberose*) herbaceous C_3 dicotyledonous perennial—which they allowed to grow for three years in an outdoor soil bin at the National Soil Dynamics Laboratory in Auburn, Alabama (USA), within 12 open-top chambers (half of which were maintained for three years at 365 ppm CO_2 and half of which were maintained at 720 ppm CO_2 for the same period). During this time the "standing crops" of fine-root length, rhizomorph length, and number of mycorrhizal root tips were assessed in the upper (0–17 cm) and lower (17–34 cm) halves of the plants' root zones at four-week intervals via microvideo cameras installed within each of two mini-rhizotron tubes located within each of the 12 plots into which the soil bin was divided.

They found the greatest impacts of the 97 percent increase in the air's CO_2 content were generally observed in the lower halves of the ecosystems' root zones, where the standing crops of fine roots, rhizomorphs, and mycorrhizal root tips were increased, respectively, by 59 percent, 66 percent, and 64 percent, although the mean standing crop of rhizomorphs in the upper halves of the ecosystems' root zones was increased by 114 percent.

Based on these findings, McCormack et al. state that as the atmosphere's CO_2 concentration continues to rise, "greater biomass production in deeper soils in the coming decades has the potential to contribute to greater carbon storage in forest soils," because "carbon in deeper soil turns over (decomposes) more slowly than litter nearer the soil surface," citing Trumbore (2000) and Schoning and Kogel-Knabner (2006). In addition, they note "fungal tissues consist largely of chitin, a potentially recalcitrant compound that may build up soil organic matter and persist for long periods of time relative to more labile carbon," citing Langley and Hungate (2003). Thus they suggest "regenerating longleaf pine-wiregrass systems may act as a carbon sink as atmospheric CO_2 rises in the coming decades through increased biomass production and potentially through directed allocation of carbon to deeper soils," This, they note, is "consistent with the recent assertion that greater allocation of forest carbon to deeper soil is a general response to atmospheric CO_2-enrichment," citing Iversen (2010). And, very importantly, they state "significant increases in mycorrhizae and rhizomorphs," as they found in their study, "may explain why the magnitude of the increase in forest net primary productivity caused by elevated CO_2, in several long-term demonstrably nitrogen-limited FACE experiments, has not decreased after nearly a decade (Finzi et al., 2007)." This observation helps explain why the progressive nitrogen limitation hypothesis repeatedly has been shown to be wrong.

Also studying roots were Alberton et al. (2010), who write, "roots of a very large number of plant species are regularly colonized by a group of ascomycete fungi with usually dark-pigmented (melanized) septate hyphae (Mandyam and Jumpponen, 2005; Sieber and Grunig, 2006)" that are referred to as "dark septate root endophytic (DSE) fungi," with "most species belonging to the Leotiomycetes (Kernaghan et al., 2003; Hambleton and Sigler, 2005; Wang et al., 2006)." To study these fungi further, the authors grew Scots pine (*Pinus sylvestris*) plants from seed for 125 days in Petri dishes—both with and without inoculation with one of seven different species/strains of DSE fungi—within controlled environment chambers maintained at atmospheric CO_2 concentrations of either 350 or 700 ppm, destructively harvesting some of the seedlings at the 98-day point of the study and the rest at the end of the experiment.

At the conclusion of their study, the three researchers found, "across all plants (DSE-inoculated and control plants) under elevated CO_2, shoot and root biomass increased significantly by 21% and 19%, respectively, relative to ambient," with "higher values over the final four weeks (increases of 40% and 30% for shoots and roots, respectively)." In addition, they state "on average, shoot nitrogen concentration was 57% lower under elevated CO_2," and "elevated CO_2 decreased root nitrogen concentration on average by 16%." Nevertheless, they emphasize that "surprisingly, even under reduced nitrogen availability, elevated CO_2 led to increases in both above-ground and below-ground plant biomass."

In explaining how this happened, the Brazilian and Dutch researchers write, "a potential mechanism for the increase of plant biomass even when plant nutrient uptake decreases is the production of phytohormones by DSE fungi." They report "earlier authors noted that DSE fungi enhance plant growth by producing phytohormones or inducing host hormone production without any apparent facilitation of host nutrient uptake or stimulation of host nutrient metabolism (Addy et al., 2005; Schulz and Boyle, 2005)," further demonstrating that low levels of nitrogen availability need not impede significant CO_2-induced increases in plant growth and development.

In another pertinent study, Langley et al. (2009) once again state "it has been suggested that stimulation of productivity with elevated CO_2 ties up nitrogen in plant litter, which, if not offset by increases in N-use efficiency or N supply, will limit the ecosystem CO_2 response (Reich et al., 2006).” To test this hypothesis, they used “an acid-hydrolysis-incubation method and a net nitrogen-mineralization assay to assess stability of soil carbon pools and short-term nitrogen dynamics in a Florida scrub-oak ecosystem after six years of exposure to elevated CO_2,” This work was conducted at a multiple open-top-chamber facility on a barrier island located at NASA’s Kennedy Space Center on the east coast of central Florida, USA.

The researchers found elevated atmospheric CO_2 (to 350 ppm above ambient concentrations) tended to increase net N mineralization in the top 10 cm of the soil, but it also decreased total soil organic carbon content there by 21 percent. However, that loss of carbon mass was equivalent only to “roughly one-third of the increase in plant biomass that occurred in the same experiment.” In addition, they state the strongest increases in net N mineralization were observed in the 10–30 cm depth increment, and “release of N from this depth may have allowed the sustained CO_2 effect on productivity in this scrub-oak forest,” which over the four years leading up to their study “increased litterfall by 19–59%,” citing Hungate et al. (2006) for the latter figures. This is yet another experimental demonstration that plants are generally able to find the extra nitrogen they need to take full advantage of the aerial fertilization effect of elevated atmospheric CO_2 concentrations, which increases total ecosystem carbon content and thus results in a negative feedback to anthropogenic CO_2 emissions.

We conclude our review of the progressive nitrogen limitation hypothesis with a brief analysis of the paper of Thornton et al. (2009), who provided powerful political fodder for the claim that there will be even greater global warming in the future than the amount that already has been predicted by climate models, due to the supposedly smaller amount of CO_2 being removed from the air by the supposedly less-vigorously growing vegetation, due to the imagined gradual weakening of CO_2’s aerial fertilization effect on plants growing in nitrogen-limited soils.

As for why we should believe this model-based projection, the ten authors of the study state their conclusion “is supported by previous studies,” including “stand-alone ecosystem models (McGuire et al., 2001), [an] offline land component of a coupled climate model (Thornton et al., 2007), [a] coupled model of intermediate complexity (Sokolov et al., 2008), and now here for the case of a fully-coupled climate system model.” In addition, they state, “each of these studies is based on either the TEM or the CLM-CN model.”

You may get the impression that Thornton et al.’s work depends just a little too heavily on models, as compared to real-world experimental data. That is indeed the case, as numerous experimental studies provide no evidence for the progressive nitrogen limitation hypothesis, even in plants growing in soils of extremely low nitrogen content, where evidence for it surely would be expected to be found if the hypothesis were correct.

Historically, far too many falsehoods have been foisted on the world by mere hypotheses and models to justify accepting the outcome of Thornton et al.’s study, especially when the numerous results of the many real-world experiments reviewed here clearly indicate the study’s conclusion is false. As ever-more long-term experiments are conducted on long-lived plants growing outdoors and rooted in the earth, where their roots are not artificially confined to a limited volume of soil, it is becoming abundantly clear that plants generally do not experience any significant decline in the initial photosynthetic stimulation provided them by the extra CO_2 to which they are exposed in CO_2 enrichment studies.

References

Addy, H.D., Piercey, M.M., and Currah, R.S. 2005. Microfungal endophytes in roots. *Canadian Journal of Botany* **83**: 1–13.

Ainsworth, A.E., Rogers, A., Blum, H., Nosberger, J., and Long, S.P. 2003. Variation in acclimation of photosynthesis in *Trifolium repens* after eight years of exposure to free air CO_2 enrichment (FACE). *Journal of Experimental Botany* **54**: 2769–2774.

Alberton, O., Kuyper, T.W., and Summerbell, R.C. 2010. Dark septate root endophytic fungi increase growth of Scots pine seedlings under elevated CO_2 through enhanced nitrogen use efficiency. *Plant and Soil* **328**: 459–470.

Crous, K.Y. and Ellsworth, D.S. 2004. Canopy position affects photosynthetic adjustments to long-term elevated CO_2 concentration (FACE) in aging needles in a mature *Pinus taeda* forest. *Tree Physiology* **24**: 961–970.

Darbah, J.N.T., Kubiske, M.E., Nelson, N., Kets, K., Riikonen, J., Sober, A., Rouse, L., and Karnosky, D.F. 2010. Will photosynthetic capacity of aspen trees acclimate after long-term exposure to elevated CO_2 and O_3? *Environmental Pollution* **158**: 983–991.

Davey, P.A., Olcer, H., Zakhleniuk, O., Bernacchi, C.J., Calfapietra, C., Long, S.P., and Raines, C.A. 2006. Can fast growing plantation trees escape biochemical down-regulation of photosynthesis when growing throughout their complete production cycle in the open air under elevated carbon dioxide? *Plant, Cell and Environment* **29**: 1235–1244.

Dijkstra, F.A., Pendall, E., Mosier, A.R., King, J.Y., Milchunas, D.G., and Morgan, J.A. 2008. Long-term enhancement of N availability and plant growth under elevated CO_2 in a semi-arid grassland. *Functional Ecology* **22**: 975–982.

Finzi, A.C., Norby, R.J., Calfapietra, C., Gallet-Budynek, A., Gielen, B., Holmes, W.E., Hoosbeek, M.R., Iversen, C.M., Jackson, R.B., Kubiske, M.E., Ledford, J., Liberloo, M., Oren, R., Polle, A., Pritchard, S., Zak, D.R., Schlesinger, W.H., and Ceulemans, R. 2007. Increases in nitrogen uptake rather than nitrogen-use efficiency support higher rates of temperate forest productivity under elevated CO_2. *Proceedings of the National Academy of Sciences, USA* **104**: 14,014–14,019.

Finzi, A.C. and Schlesinger, W.H. 2003. Soil-nitrogen cycling in a pine forest exposed to 5 years of elevated carbon dioxide. *Ecosystems* **6**: 444–456.

Fujimaki, R., Sakai, A., and Kanedo, N. 2009. Ecological risks in anthropogenic disturbance of nitrogen cycles in natural terrestrial ecosystems. *Ecological Research* **24**: 955–964.

Hambleton, S. and Sigler, L. 2005. *Meliniomyces*, a new anamorph genus for root-associated fungi with phylogenetic affinities to *Rhizoscyphus ericae* (= *Hymenoscyphus ericae*), *Leotiomycetes*. *Studies in Mycology* **53**: 1–27

Hungate, B.A., Dukes, J.S., Shaw, M.R., Luo, Y., and Field, C.B. 2003. Nitrogen and climate change. *Science* **302**: 1512–1513.

Hungate, B.A., Johnson, D.W., Dijkstra, P., Hymus, G., Stiling, P., Megonigal, J.P., Pagel, A.L., Moan, J.L., Day, F., Li, J., Hinkle, C.R., and Drake, B.G. 2006. Nitrogen cycling during seven years of atmospheric CO_2 enrichment in a scrub oak woodland. *Ecology* **87**: 26–40.

Iversen, C.M. 2010. Digging deeper: fine-root responses to rising atmospheric CO_2 concentration in forested ecosystems. *New Phytologist* **186**: 346–357.

Iversen, C.M., Ledford, J., and Norby, R.J. 2008. CO_2 enrichment increases carbon and nitrogen input from fine roots in a deciduous forest. *New Phytologist* **179**: 837–847.

Jackson, R.B., Cook, C.W., Pippen, J.S., and Palmer, S.M. 2009. Increased belowground biomass and soil CO_2 fluxes after a decade of carbon dioxide enrichment in a warm-temperate forest. *Ecology* **90**: 3352–3366.

Johnson, D.W. 2006. Progressive N limitation in forests: review and implications for long-term responses to elevated CO_2. *Ecology* **87**: 64–75.

Kernaghan, G., Sigler, L., and Khasa, D. 2003. Mycorrhizal and root endophytic fungi of containerized *Picea glauca* seedlings assessed by rDNA sequence analysis. *Microbial Ecology* **45**: 128–136.

Langley, J.A. and Hungate, B.A. 2003. Mycorrhizal controls on belowground litter quality. *Journal of Ecology* **84**: 2302–2312.

Langley, J.A., McKinley, D.C., Wolf, A.A., Hungate, B.A., Drake, B.G., and Megonigal, J.P. 2009. Priming depletes soil carbon and releases nitrogen in a scrub-oak ecosystem exposed to elevated CO_2. *Soil Biology & Biochemistry* **41**: 54–60.

Liberloo, M., Calfapietra, C., Lukac, M., Godbold, D., Luo, Z.-B., Polle, A., Hoosbeek, M.R., Kull, O., Marek, M., Raines, C., Rubino, M., Taylor, G., Scarascia-Mugnozza, G., and Ceulemans, R. 2006. Woody biomass production during the second rotation of a bio-energy *Populus* plantation increases in a future high CO_2 world. *Global Change Biology* **12**: 1094–1106.

Liberloo, M., Tulva, I., Raim, O., Kull, O., and Ceulemans, R. 2007. Photosynthetic stimulation under long-term CO_2 enrichment and fertilization is sustained across a closed *Populus* canopy profile (EUROFACE). *New Phytologist* **173**: 537–549.

Luo, Y., Su, B., Currie, W.S., Dukes, J.S., Finzi, A., Hartwig, U., Hungate, B., McMurtrie, R.E., Oren, R., Parton, W.J., Pataki, D.E., Shaw, M.R., Zak, D.R., and Field, C.B. 2004. Progressive nitrogen limitation of ecosystem responses to rising atmospheric carbon dioxide. *BioScience* **54**: 731–739.

Mandyam, K. and Jumpponen, A. 2005. Seeking the elusive function of the root-colonizing dark septate endophytic fungi. *Studies in Mycology* **53**: 173–189.

McCarthy, H.R., Oren, R., Johnsen, K.H., Gallet-Budynek, A., Pritchard, S.G., Cook, C.W., LaDeau, S.L., Jackson, R.B., and Finzi, A.C. 2010. Re-assessment of plant carbon dynamics at the Duke free-air CO_2 enrichment site: interactions of atmospheric [CO_2] with nitrogen and water availability over stand development. *New Phytologist* **185**: 514–528.

McCormack, M.L., Pritchard, S.G., Breland, S., Davis, M.A., Prior, S.A., Runion, G.B., Mitchell, R.J., and Rogers, H.H. 2010. Soil fungi respond more strongly than fine roots to elevated CO_2 in a model regenerating longleaf pine-wiregrass ecosystem. *Ecosystems* **13**: 901–916.

McGuire, A.D., Sitch, S., Clein, J.S., Dargaville, R., Esser, G., Foley, J., Heimann, M., Joos, F., Kaplan, J., Kicklighter, D.W., Meier, R.A., Melillo, J.M., Moore III, B., Prentice, I.C., Ramankutty, N., Reichenau, T., Schloss, A., Tian, H., Williams, L.J., and Wittenberg, U. 2001. Carbon balance of the terrestrial biosphere in the twentieth century: analyses of CO_2, climate and land use effects with four process-based ecosystem models. *Global Biogeochemical Cycles* **15**: 183–206.

Nelson, J.A., Morgan, J.A., LeCain, D.R., Mosier, A., Milchunas, D.G., and Parton, B.A. 2004. Elevated CO_2 increases soil moisture and enhances plant water relations in a long-term field study in semi-arid shortgrass steppe of Colorado. *Plant and Soil* **259**: 169–179.

Paoletti, E., Seufert, G., Della Rocca, G., and Thomsen, H. 2007. Photosynthetic response to elevated CO_2 and O_3 in *Quercus ilex* leaves at a natural CO_2 spring. *Environmental Pollution* **147**: 516–524.

Pritchard, S.G., Strand, A.E., McCormack, M.L., Davis, M.A., Finzi, A.C., Jackson, R.B., Matamala, R., Rogers, H.H., and Oren, R. 2008a. Fine root dynamics in a loblolly pine forest are influenced by free-air-CO_2-enrichment: a six-year-minirhizotron study. *Global Change Biology* **14**: 588–602.

Pritchard, S.G., Strand, A.E., McCormack, M.L., Davis, M.A., and Oren, R. 2008b. Mycorrhizal and rhizomorph dynamics in a loblolly pine forest during 5 years of free-air-CO_2-enrichment. *Global Change Biology* **14**: 1–13.

Reich, P.B., Hungate, B.A., and Luo, Y. 2006. Carbon-nitrogen interactions in terrestrial ecosystems in response to rising atmospheric carbon dioxide. *Annual Review of Ecology, Evolution and Systematics* **37**: 611–636.

Schoning, I. and Kogel-Knabner, I. 2006. Chemical composition of young and old carbon pools throughout Camisol and Luvisol profiles under forests. *Soil Biology and Biochemistry* **38**: 2411–2424.

Schulz, B. and Boyle, C. 2005. The endophytic continuum. *Mycological Research* **109**: 661–686.

Sholtis, J.D., Gunderson, C.A., Norby, R.J., and Tissue, D.T. 2004. Persistent stimulation of photosynthesis by elevated CO_2 in a sweetgum (*Liquidambar styraciflua*) forest stand. *New Phytologist* **162**: 343–354.

Sieber, T.N. and Grunig, C.R. 2006. Biodiversity of fungal root-endophyte communities and populations, in particular of the dark septate endophyte *Phialocephala fortinii* s.1.In *Microbial Root Endophytes* [of series], edited by B. Schulz, C. Boyle, and T.N. Sieber. *Soil Biology* **9**: 107–132.

Sokolov, A.P., Kicklighter, D.W., Melillo, J.M., Felzer, B.S., Schlosser, C.A., and Cronin, T.W. 2008. Consequences of considering carbon-nitrogen interactions on the feedbacks between climate and the terrestrial carbon cycle. *Journal of Climate* **21**: 3776–3796.

Thornton, P.E., Doney, S.C., Lindsay, K., Moore, J.K., Mahowald, N., Randerson, J.T., Fung, I., Lamarque, J.-F., Feddema, J.J., and Lee, Y.-H. 2009. Carbon-nitrogen interactions regulate climate-carbon cycle feedbacks: results from an atmosphere-ocean general circulation model. *Biogeosciences* **6**: 2120–2120.

Thornton, P.E., Lamarque, J.F., Rosenbloom, N.A., and Mahowald, N.M. 2007. Influence of carbon-nitrogen cycle coupling on land model response to CO_2 fertilization and climate variability. *Global Biogeochemical Cycles* **21**: 10.1029/2006GB002868.

Trumbore, S. 2000. Age of soil organic matter and soil respiration: radiocarbon constraints on belowground C dynamics. *Ecological Applications* **10**: 399–411.

Wang, Z., Johnston, P.R., Takamatsu, S., Spatafora, J.W., and Hibbett, D.S. 2006. Toward a phylogenetic classification of the Leotiomycetes based on rDNA data. *Mycologia* **98**: 1065–1075.

7.13. Phenology

The progressively earlier arrival of spring with each succeeding year is widely viewed as an indicator of global warming. Scheifinger et al. (2002) and Schaber and Badeck (2005) claim to have detected earlier spring arrival in Europe over the course of the twentieth century.

A difficulty with such studies, however, is the lack of a commonly agreed-upon metric for the arrival of spring. Therefore, White et al. (2009) compared ten algorithms for processing satellite Normalized Difference Vegetaton Index (NDVI) data for this purpose, based on the expectation that satellite data, with their continental coverage, should allow such trends to be more easily detected. A question that remains, however, is whether the various methods employed measure the same things or correspond to on-the-ground measurements.

White et al.'s study covered the period of most rapid global warming (1982–2006), and a unique aspect of it was their use of 16,000 ground-based phenological measurements from across North America, as well as data on snow melt and hydrology. They found the ten methods of extracting a start-of-spring (SOS) signal from the satellite data differed widely, yielding a range of 60 days around the ten-model mean estimate. The methods also tended to be biased toward detecting SOS earlier than ground-based phenology data indicated, and to have weak correlations with the ground data, perhaps because there were difficulties classifying pixels in some cases, particularly for desert, semi-tropical, and Mediterranean (California) zones in which the arrival of "spring" is not a well-defined phenomenon.

In the end, therefore, the 21 researchers say they "found no evidence for time trends in spring arrival from ground- or model-based data," and "using an ensemble estimate from two methods that were more closely related to ground observations than other methods, SOS trends could be detected for only 12% of North America," with 7 percent of them showing a trend to earlier spring and 5 percent exhibiting a trend toward later spring. Thus, the possibility arises that the wide range of results obtained by most past and current methods of detecting the start of spring may have led to premature claims of spring's increasingly earlier annual occurrence over the latter part of the twentieth century. That finding, in turn, raises significant concerns about the validity of near-surface air temperature measurements that suggest that North America has warmed significantly over the past several decades.

In the introduction to their study of the subject, however, Johnston and Reekie (2008) write there have indeed "been marked changes in plant phenology over the past century," and they say these changes "have been interpreted as a consequence of the increase in temperature that has been observed over this time." But in an added twist to the subject, they speculate "the concentration of atmospheric CO_2 may also directly affect time of flowering, even in the absence of temperature change."

In exploring these possibilities, the two researchers examined the effect of elevated atmospheric CO_2 concentration by itself (ambient and ambient + 330 ppm), as well as the combined effect of elevated CO_2 and elevated air temperature (ambient + 1.5°C), on the flowering phenology of 22 species of plants in the Asteraceae family. These were grown under natural, seasonally varying temperature and daylength in separate compartments of a glasshouse in Wolfville, Nova Scotia, Canada. The researchers found, "on average, elevated CO_2 by itself advanced flowering by four days," while "increasing temperature as well as CO_2 advanced flowering by an additional three days." They also found "CO_2 was more likely to hasten phenology in long- than in short-day species," and "early- and late-flowering species did not differ in response to elevated CO_2, but the combined effect of elevated CO_2 and temperature hastened flowering more in early- than late-flowering species." As a result of these findings, they conclude, with respect to time of flowering in Asteraceae species, "the direct effect of CO_2 on phenology may be as important as its indirect effect through climate change," further complicating the interpretation of a progressively earlier start of spring as an indication of regional or global warming.

Another concern about global warming possibly hastening various types of biological activity associated with the arrival of spring is that various links of certain food chains may not respond in a compatible manner in terms of the temporal development of the different stages of their life cycles, leading to a serious mismatch among the unique needs of different ecosystem trophic levels that could spell disaster for some species. This concept has been said by Visser and Both (2005) to constitute an "insufficient adjustment" to climate change.

In a study designed to discover whether this phenomenon actually occurs in the real-world of nature for certain elements of an important ecosystem of Central Europe, Bauer et al. (2010) studied the effect of 47 years of warming (1961–2007) on (1) the time of leafing-out of dominant English Oak (*Quercus robur*) trees at four different research sites in the Czech Republic located in full-grown, multi-aged floodplain forests that had been under no forestry management, (2) the time of appearance of the two most abundant species of caterpillars in the floodplain forests, the Winter Moth (*Operophtera brumata*) and the Tortrix Moth (*Tortrix viridana*), and (3) the first and mean laying dates of two of the ecosystem's most common birds: Great Tits (*Parus major*) and Collared Flycatchers (*Ficedula albicollis*).

According to the seven scientists, "mean annual temperature showed a significant increase of 0.27–0.33°C per decade, with approximately the same magnitude of change during spring at all sites." They also found "on average (all four sites), the bud burst date for English Oak has advanced by 7.9 days and full foliage by 8.9 days, with approximately the same shifts being recorded for the peak of the beginning and end of frass for herbivorous caterpillars." This was the observational variable they used to characterize the caterpillars' presence. Last, they determined "the first laying date of Great Tits has advanced by between 6.2 to 8.0 days," while "the mean laying date has advanced by 6.4 to 8.0 days." Likewise, they found the "Collared Flycatcher first laying date has advanced by 8.5 to 9.2 days over the past 47 years, and the mean laying date by 7.7 to 9.6 days."

As to the importance of their findings, Bauer et al. state that because "trends in the timing of reproduction processes of both bird species are coherent with the trends in development of English Oak and with peak herbivorous caterpillar activity," it is apparent that in this specific food chain the common temporal shifting of the different organisms' phenological stages toward the beginning of the year "does not appear to have led to mistiming in the trophic food chain." Hence, there is reason to believe other food chains also may not be as seriously disrupted by global warming as many have postulated they could be. Of course, more work of this nature is needed before any generalizations are warranted.

References

Bauer, Z., Trnka, M., Bauerova, J., Mozny, M., Stepanek, P., Bartosova, L., and Zalud, Z. 2010. Changing climate and the phenological response of great tit and collared flycatcher populations in floodplain forest ecosystems in Central Europe. *International Journal of Biometeorology* **54**: 99–111.

Johnston, A. and Reekie, E. 2008. Regardless of whether rising atmospheric carbon dioxide levels increase air temperature, flowering phenology will be affected. *International Journal of Plant Science* **169**: 1210–1218.

Schaber, J. and Badeck, F. 2005. Plant phenology in Germany over the 20th Century. *Regional Environmental Change* **5**: 37–46.

Scheifinger, H., Menzel, A., Koch, E., Peter, C., and Ahas, R. 2002. Atmospheric mechanisms governing the spatial and temporal variability of phenological phases in central Europe. *International Journal of Climatology* **22**: 1739–1755.

Visser, M.E. and Both, C. 2005. Shifts in phenology due to global climate change: the need for yardstick. *Proceedings of the Royal Society B* **272**: 2561–2569.

White, Michael A., de Beurs, K.M., Kidan, K., Inouye, D.W., Richardson, A.D., Jensen, O.P., O'Keefe, J., Zhang, G., Nemani, R.R., van Leeuwen, W.J.D., Brown, J.F., de Wit, A., Schaepman, M., Lin, X., Dettinger, M., Bailey, A.S., Kimball, J., Schwartz, M.D., Baldocchi, D.D., Lee, J.T., and Lauenroth, W.K. 2009. Intercomparison, interpretation, and assessment of spring phenology in North America estimated from remote sensing for 1982–2006. *Global Change Biology* **15**: 2335–2359.

7.14. Range Expansion

When the air's CO_2 content is experimentally increased, the vast majority of Earth's plants lose less water to the atmosphere via transpiration while producing more biomass. The latter phenomenon is generally more strongly expressed in woody perennial species than in annual herbaceous plants. Consequently, and in concert with future increases in the atmosphere's CO_2 concentration, Earth's bushes, shrubs, and trees will likely grow better than non-woody species will. In addition, the increase in the air's CO_2 content will make many plants of all types actually prefer warmer temperatures, as reported by Idso and Idso (1994), which suggests that if air temperatures continue to rise, global warming will cause both woody and non-woody plants to grow more vigorously and expand their ranges, but with woody plants doing so in much more dramatic fashion.

In this summary, we review some of the more recent evidence for this phenomenon as it has operated among a wide variety of plants, beginning with trees.

Citing Bowman et al. (2001), Banfai and Bowman (2006), Bowman and Dingle (2006), and Brook and Bowman (2006), Bowman et al. (2010) write, "a large research program in the Australian monsoon tropics has concluded that monsoon rainforests have expanded within the savanna matrix" since "the middle of the last century," while noting a similar trend "has been emulated throughout the tropics worldwide," citing Schwartz et al. (1996), Guillet et al. (2001), Puyravaud et al. (2003), and Wigley et al. (2009). They say this phenomenon has been "suggested to be linked to a long-term trend towards wetter climates, atmospheric CO_2 enrichment, and changed fire regimes," although they remark that the observed forest expansion in Australia "is remarkable, being contrary to the widely accepted view that fire limits the extent of rainforests."

Following this introduction to the subject, Bowman et al. (2010) further discuss this suite of findings, paying particular attention to their "analytical and evidentiary basis and plausibility." And at the conclusion of their review, they note they "consider it most likely that the expansion of rainforest patches is related to global climate change via increased rainfall and/or the CO_2 'fertilizer effect'," since the expansion of Australia's monsoon rainforests occurred "despite hostile fire regimes." And they note this conclusion "is consistent with the recent finding from South Africa that strongly contrasting localized land management practices had little effect on the dramatic expansion of forest patches into the surrounding savanna in the latter half of the 20th century, strongly implicating global environmental change." This study confirms evidence that atmospheric CO_2 enrichment is the cause of the range expansion of woody plants that has been occurring around the world.

In a contemporary paper published in *Austral Ecology*, Kgope et al. (2010) similarly write, "over the last century, there has been a trend of increasing woody biomass in many savanna regions (Polley et al., 2002; Ward, 2005)," which is "generally attributed to changes in land use practice, particularly grazing and fire use, and to episodes of high or low rainfall." But they state "the phenomenon may also have been influenced by increasing atmospheric CO_2," citing the papers of Idso (1992), Polley (1997), and Polley et al. (1999). Consequently, in an investigation into the strength of the latter hypothesis, the three South African researchers conducted an experiment where they monitored "photosynthetic, growth and carbon allocation responses of African savanna trees (*Acacia karroo* and *Acacia nilotica*) and a C_4 grass, *Themeda triandra*, exposed to a gradient of CO_2 concentrations from 180 (typical of the Last Glacial Maximum) to 1000 ppm in open-top chambers in a glasshouse," as well as intermediate concentrations of 280, 370 (representing the present), 550, and 700 ppm.

The well-watered and -fertilized nitrogen-fixing *Acacia* trees they studied were started from seed and grown under the above-described conditions from the age of one week for a period of two years, at the midpoint of which time interval they were cut back and allowed to regrow for a second season, while the *T. triandra* plants they evaluated—which constitute "the dominant grass species in many frequently burnt grasslands and savannas in South Africa," as they describe them—were established from tillers obtained from a C_4 grassland in southern Kwa-Zulu-Natal, South Africa.

As a result of their efforts, Kgope et al. determined "photosynthesis, total stem length, total stem diameter, shoot dry weight and root dry weight of the acacias increased significantly across the CO_2 gradient, saturating at higher CO_2 concentrations." And they say "after clipping to simulate fire, plants showed an even greater response in total stem length, total stem diameter and shoot dry weight, signaling the importance of re-sprouting following disturbances such as fire or herbivory in savanna systems." However, and "in contrast to the strong response of tree seedlings to the CO_2 gradient," the three researchers found "grass productivity showed little variation."

Kgope et al. report, "at the end of the first growing season, SDW [shoot dry weight] had increased by 529% in *A. karroo* and 110% on average in *A. nilotica* under ambient relative to sub-ambient CO_2 treatments," and "a further increase in CO_2 from ambient to elevated CO_2 significantly increased SDW of *A. nilotica* by 86%." As for the second-season results, they found the SDW of re-sprouted *A. karoo* shoot material increased by 366 percent from sub-ambient to ambient CO_2, while that of *A. nilotica* increased by 133 percent on average. The South African scientists state, "changes in CO_2 from pre-industrial times to the present have effectively produced acacia 'super seedlings' in relation to their growth potential over the past several million years."

In light of these findings, Kgope et al. conclude, "where fires once killed seedlings, they are unlikely to do so today, resulting in much higher seedling recruitment rates," and they write "the rate of sapling release to adult height classes will also be greatly enhanced because they are able to grow out of the fire trap more rapidly." In addition, they state the trees "should also be better defended against mammal browsers and insect herbivores." And citing yet-to-be-published results, they state "both structural (spines) and chemical (tannins) defenses showed significant increases with increasing CO_2."

As for the implications of these several observations, the three researchers write they "provide experimental support for suggestions and simulation studies predicting that reductions in CO_2 alone could have led to loss of tree cover in grassy environments in the last glacial (Bond et al., 2003; Harrison and Prentice, 2003)," and they state "the large increases in CO_2 from industrial emissions over the last century would now favor trees at the expense of grasses." This conclusion is supported by palaeo-records that indicate "trees disappeared from current savanna sites in South Africa during the Last Glacial Maximum (Scott, 1999), re-appeared in the Holocene, and have rapidly increased over the last half century."

Addressing the same subject, Springsteen et al. (2010) write, "woody plant expansion within grassland ecosystems is a worldwide phenomenon, and dramatic vegetation shifts from grassland to savanna/woodlands have occurred over the past 50–100 years in North America," while noting one of the chief factors that has contributed to this phenomenon is believed by many to have been the concomitant historical increase in the air's carbon dioxide concentration, as suggested by the studies of Archer et al. (1995), Polley (1997), Bond and Midgley (2000), and Bond et al. (2003). They also indicate once shrublands are established, they tend to persist for several different reasons, one of which is a type of feedback phenomenon that "occurs when resources accumulate in soils beneath woody plants due to litterfall, interception of wet and dry deposition, nitrogen fixation, and animal droppings," as described by Schlesinger et al. (1990), Archer et al. (1995), Reynolds et al. (1999), and Lopez-Pintor et al. (2006). And they report in this regard that "changes in soil attributes under woody vegetation have been documented in the arid grasslands of the southern Great Plains, including increases in soil carbon and nitrogen," citing Reynolds et al. (1999), Hibbard et al. (2001, 2003), McCulley et al. (2004), Schade and Hobbie (2005), and Liao et al. (2006).

While working at the USDA-ARS Northern Great Plains Research Laboratory near Mandan, North Dakota (USA), Springsteen et al. examined near-surface (upper 15 cm) soil biogeochemistry along a 42-year (1963–2005) chronosequence, which encompassed grassland, woodland, and grassland-woodland transition zones in a northern Great Plains grassland, in order to determine the influence of woody plant expansion on soil carbon and nitrogen contents. The four researchers found total soil carbon content rose by 26 percent across the chronosequence from grassland to woodland within the 0–15 cm soil depth, while total soil nitrogen content rose by 31 percent. They add the rate of woody shrub expansion from 1963 to 1988 was ~1,800 m^2 per year, while from 1988 to 2005 it was ~3,800 m^2 per year, or a little more than double the rate of what it was in the first period.

In another pertinent paper, Souza et al. (2010) describe "how elevated CO_2 affects aboveground biomass within the understory community of a temperate deciduous forest at the Oak Ridge National Laboratory sweetgum (*Liquidambar styraciflua*) free-air carbon dioxide enrichment (FACE) facility in eastern Tennessee, USA," where growing-season (April to November) CO_2 treatments—ambient (aCO_2) and enriched (eCO_2)—were initiated in 1998. For the years 2001–2003 and 2008, when total understory aboveground biomass was assessed, the dominant sweetgum trees were approximately 16 meters tall during the first period and 18 meters tall in the second; and for these four years the daytime aCO_2 and eCO_2 concentrations in the forest understory averaged 474 and 577 ppm, respectively, for an eCO_2-aCO_2 difference (103 ppm) that was considerably less than that experienced in the sweetgum canopy above (161 ppm).

Under these conditions, Souza et al. report, "across years, aboveground biomass of the understory community was on average 25% greater in eCO_2 than in aCO_2 plots." In addition, they found "in 2001–03, little of the understory biomass was in woody species." In fact, they report "herbaceous species made up 94% of the total understory biomass across CO_2 treatments." In 2008, however, they discovered the contribution of herbaceous species to total understory biomass had dropped to 61 percent in the aCO_2 plots and had declined all the way to 33 percent in the eCO_2 plots.

In considering these results, the growth stimulation provided to the understory plants in the sweetgum plantation was truly outstanding: a 25 percent increase for a mere 103 ppm increase in the CO_2 concentration of the air to which they were exposed. Likewise, the rapid shift from a predominantly herbaceous understory to one that was fully two-thirds woody in the eCO_2 plots a mere five years later was also rather amazing, indicating, in the words of the five researchers, a "more rapid development of the tree regeneration layer and faster successional development of the stand," which they state could "influence long-term forest dynamics." In addition, the researchers' findings provide support for the theory that atmospheric CO_2 enrichment is enabling woody plants to expand their ranges into areas that previously had supported primarily herbaceous plants.

Still more recently, Keenan et al. (2011) note climate models "consistently project significant increases in temperature and decreases in precipitation in the Mediterranean basin," and they state these changes may have a large impact on current Mediterranean forests and the related ecosystem services they provide. In addition, they note niche-based models—also known as bioclimatic envelope models or habitat models—are by far the most commonly used method for predicting potential species distribution responses to future climatic changes. These models typically predict significant negative consequences for terrestrial plants in the face of continued increases in atmospheric CO_2 concentrations.

Keenan et al., however, prefer process-based models, which describe eco-physiological processes ranging from purely empirical relationships to mechanistic descriptions based on physical laws. They note these models—supported by experiments and growth and yield surveys—"suggest that global warming will have a positive impact on forest productivity (van der Meer et al., 2002; Nigh et al., 2004; Norby and Luo, 2004; Briceño-Elizondo et al., 2006; Gaucharel et al., 2008), due to the direct fertilization effect of increased CO_2 and indirect effects such as lengthening of the growing period."

To elucidate the difference in results obtained when employing these two approaches to forecasting the future, the five researchers assessed and compared the projections of each of them when applied to stands of three forest species (*Quercus ilex, Pinus halepensis,* and *Pinus sylvestris*) with widely contrasting distributions in continental Spain. They found "CO_2 fertilization through projected increased atmospheric CO_2 concentrations is shown to increase forest productivity in the mechanistic process-based model (despite increased drought stress) by up to three times that of the non-CO_2 fertilization scenario by the period 2050–2080, which is in stark contrast to projections of reduced habitat suitability from the niche-based models."

Given these findings, the Spanish and U.S. scientists say their results show "previous reports of species decline in continental Spain (e.g. Benito-Garzon et al., 2008) may be overestimated due to two reasons: the use of only one predictive niche-based model, and the failure to account for possible effects of CO_2 fertilization." They add "similar studies in other regions, which do not consider these two aspects, are also potentially overestimating species decline due to climate change." Furthermore, they suggest "niche-based model results also likely overestimate the decline in [habitat] suitability," and they therefore conclude "an organism's niche must be modeled mechanistically if we are to fully explain distribution limits," additionally citing Kearney (2006) in this regard.

In another intriguing study, a review of all large FACE studies conducted over the prior 15 years, Ainsworth and Long (2005) reported the greatest CO_2-induced benefits were accrued by trees, which experienced a mean biomass increase of 42 percent in response to a 300 ppm increase in the atmosphere's CO_2 concentration. In comparison, they found C_4 sorghum posted a yield increase of only 7 percent, while the C_3 crops rice and wheat exhibited yield increases of 16 percent and 22 percent, respectively. Thus, it is only natural to presume that as the air's CO_2 content continues to climb ever-higher, Earth's woody plants gradually will encroach upon areas where herbaceous plants previously ruled the landscape. Such is typically observed to be the case throughout the entire world. However, as noted by Wilcox and Huang (2010), trees typically use deeper water than grasses, and consequently they say the "prevailing belief is that woody plant encroachment leads to declining groundwater recharge and, therefore, to lower groundwater contributions to streams."

That typically would be an undesirable outcome, and in a study they designed to explore whether the declining-groundwater hypothesis is correct, the Texas A & M University researchers analyzed the long-term (85-year) trends of both baseflow (groundwater-derived) and stormflow (precipitation-derived) streamflow components of four major rivers in the Edwards Plateau region of Texas (USA)—the Nueces, Frio, Guadalupe, and Llano Rivers—over which time period the region experienced a significant increase in the presence of woody plants. The results of their analysis indicated "contrary to widespread perceptions," streamflows in their study region "have not been declining." In fact, they write, "the contribution of baseflow has doubled—even though woody cover has expanded and rainfall amounts have remained constant."

Noting their findings "run counter to current thinking in both lay and scientific circles," the Texas researchers speculate that "baseflows are higher now than in pre-settlement times, because rooting by trees has facilitated groundwater recharge." In addition, the transpiration-reducing effect of atmospheric CO_2 enrichment also may have played a role in this regard, as has been suggested by several prior studies of river basin hydrology (Idso and Brazel, 1984; Gedney et al., 2006; Betts et al., 2007). Whatever the answer or answers may be, it would appear good things have been happening to degraded grasslands throughout the world as the atmosphere's CO_2 concentration has been rising and woody plants have been extending their ranges and growing where they previously had been unable to survive, thus helping to make more water available for many other uses by man and nature alike.

Shifting from trees to shrubs, Brantly and Young (2010) note woody plant encroachment in herbaceous ecosystems "represents a key shift in community structure that has [the] potential to alter regional and global carbon and nitrogen cycling." However, they state "there is considerable uncertainty regarding the effects of woody [plant] encroachment on global terrestrial C storage," because of the possibility that "increases in C sequestration in woody biomass may be offset by associated increases in soil CO_2 efflux (i.e., combined heterotrophic respiration and root respiration) resulting from increased litterfall, increased soil moisture, and associated increases in microbial activity that often accompany woody [plant] encroachment."

In an attempt to determine "if young, sandy soils on a barrier island became a sink for C after encroachment of the nitrogen-fixing shrub *Morella cerifera*, or if associated stimulation of soil CO_2 efflux mitigated increased litterfall," the two researchers "monitored variations in litterfall in shrub thickets across a chronosequence of shrub expansion and compared those data to previous measurements of ANPP [annual net primary production] in adjacent grasslands." They then "quantified standing litter C and N pools in shrub thickets and soil organic matter (SOM), soil organic carbon (SOC), soil total nitrogen (TN) and soil CO_2 efflux in shrub thickets and adjacent grasslands." They conducted this field work on the north end of a barrier island just east of the Virginia portion of the DelMarVa peninsula, USA.

The two researchers report that although soil CO_2 efflux was indeed stimulated by shrub encroachment in the younger soils, "soil CO_2 efflux did not vary between shrub thickets and grasslands in the oldest soils, and increases in CO_2 efflux in shrub thickets did not offset contributions of increased litterfall to SOC." In fact, they found "SOC was 3.6–9.8 times higher beneath shrub thickets than in grassland soils, and soil TN was 2.5–7.7 times higher under shrub thickets." Thus Brantly and Young determined the expansion of shrubs on barrier islands has the ability "to significantly increase ecosystem C sequestration." What is more, they write, "stimulation of N storage beneath shrub thickets will also favor future growth of species with lower nutrient use efficiencies than native grasses, including climax maritime forest species that could sequester additional C in biomass," citing Ehrenfeld (1990) and Vitousek et al. (2002). All of these phenomena presaged by their work bode well for Earth's barrier islands and the woody plants they have the potential to support.

Continuing in much the same vein, and in light of the planet's significant warming over the last few decades of the twentieth century, it is only natural to presume many plants have concurrently expanded their ranges in a northward direction, providing for more overlapping of individual ranges and concomitant increases in local species diversity. One way of documenting this northward expansion of vegetation is what Hallinger et al. (2010) call "the long tradition of tree-line research." Now, however, they augment that older approach with an analogous study of the range expansion of shrubs.

Working at a site just three kilometers from the Abisko Scientific Research Station (68°21'N, 18°49'E) in the Northern Swedish Scandes, Hallinger et al. studied male plants of the medium-sized *Juniperus nana* shrub, collecting the main stems of five to eight shrubs every hundred meters of elevation until the shrub zone ended. Ring-width measurements on these stems were then performed, as they describe it, "to measure radial and vertical growth, to track growth changes over time, to age the shrub individuals and to correlate annual shrub growth with climate." The climate data were derived from records of the nearby Abisko Station.

The three researchers report they "documented a distinct increase in radial and vertical growth rates of *J. nana* shrubs during recent decades in the subalpine zone of North Sweden," and they state "the age structure of shrubs along the elevational gradient provides evidence that an upslope advance of the altitudinal shrubline is underway." In addition, they "observed significant, strong and stable correlations between annual ring width and summer temperatures (June, July, August)," and "the acceleration of radial and vertical growth since 1970 also coincides with the recent three decades of rising arctic air temperatures and the warming trend of 0.2°C per decade for the average temperature since 1956 at Abisko." Thus, the fruits of the German scientists' work add to what they call the "mounting evidence that shrubs are expanding into alpine and arctic areas because of climate warming," and they note "this expansion occurs in both evergreen and deciduous shrub types," citing the additional findings of Forbes et al. (2010).

Examining what happens even further north, Prach et al. (2010) studied a site in the High Arctic located at 78°38'N, 16°45'E, near Brucebyen at the

Adolfbukta Bay in central Spitsbergen (Svalbard), where the vegetation had been carefully surveyed, identified, and mapped in the 1930s and the results published by Acock (1940). In the summer of 2008, Prach et al. repeated the vegetation mapping and identification of species "on the same strip of land 2,042 x 521 meters in size, as surveyed by Acock in 1936–1937 and using the same methods." According to the four researchers, all from the Czech Republic, their work "did not reveal any changes in vegetation, since [the] previous study in 1936–1937, that could be attributed to climate change." Therefore, they "endorse the opinion that the vegetation on Svalbard is still resistant to climate fluctuations, in line with a statement of Jonsdottir (2005): 'Svalbard ecosystems are adapted to extreme fluctuations in climate on different temporal scales and can thus be regarded as rather robust'." Then, quoting Parmesan (2006), who had said "nearly every Arctic ecosystem shows marked shifts due to climate change," they concluded their paper by writing, "based on the results presented here, we wanted to note that some Arctic ecosystems still show no evident change." This lack of change may simply be because it may not have warmed as much in this High Arctic land as some researchers would have us believe, which also is suggested by Prach et al.

Also concerned about the future of Earth's biosphere, and especially the Arctic, Geml et al. (2010) note "the ability to migrate is of particular importance, because climate warming is expected to cause a northward shift in the distribution of many Arctic species, and the long-distance dispersal capability of individual species will greatly influence the composition of future Arctic communities." To assess the ability of two Arctic-alpine lichens to cope with such an eventuality, they examined the genetic structure and long-distance gene flow in two lichenized ascomycetes—*Flavocetraria cucullata* and *F. nivalis*—which are widespread in Arctic and alpine tundra. They did this via DNA sequencing of 49 specimens of *F. cucullata* and 41 of *F. nivalis* collected from various locations throughout Europe, Asia, and North America, employing "phylogenetic, nonparametric permutation methods and coalescent analyses" to assess "population divergence and to estimate the extent and direction of migration among continents."

The four researchers discovered both *F. cucullata* and *F. nivalis* had "high and moderately high intraspecific genetic diversity, respectively," and "clades within each species contained specimens from both North America and Eurasia." Thus, they concluded "at least some Arctic lichens have strong potential to adapt to the changing Arctic by tracking their ecological niche and to maintain high genetic diversity through intercontinental dispersal and sexual reproduction." As a result, whatever nature—or man—ultimately may send their way in terms of global warming, Arctic-alpine lichens should be good to go, wherever it is they need to go.

Another enlightening look at how plants have been responding to recent warming was provided by Le Roux and McGeoch (2008), who examined patterns of altitudinal range changes in the totality of the native vascular flora of sub-Antarctic Marion Island (46°54'S, 37°45'E) in the southern Indian Ocean, which warmed by 1.2°C between 1965 and 2003. The work of these South African researchers revealed between 1966 and 2006 there was "a rapid expansion in altitudinal range," with species expanding their upper elevational boundaries by an average of 70 meters. And because, as they describe it, "the observed upslope expansion was not matched by a similar change in lower range boundaries," they emphasize "the flora of Marion Island has undergone range expansion rather than a range shift." And an important consequence of the stability of lower-range boundaries together with expanding upper-range boundaries is that there is now a greater overlapping of ranges, resulting in greater local species richness or biodiversity everywhere up and down various altitudinal transects of the island. As a further consequence of this fact, Le Roux and McGeoch indicate "the present species composition of communities at higher altitudes is not an analogue of past community composition at lower altitudes, but rather constitutes a historically unique combination of species," or what we could truly call a "brave new world" significantly richer in variety than that of the recent past.

Finally, based on their documentation of plant species diversity on 13 mountain summits in southern Norway (61°06'–61°14'N, 7°52'–8°15'E)—in a reenactment of what Lye (1973) had done more than three decades earlier—as well as their assessment of regional warming over the intervening years, Odland et al. (2010) sought to see how plant species richness may have changed in response to what turned out to have been a significant increase in local temperature between the times of the two studies. Average summer temperatures, for example, increased by approximately 1.3°C over the time interval between the two studies. Over the same time period, they found plant taxa richness rose by an average of 90 percent, with two of the summits experiencing increases of fully 200 percent.

Of these results, Odland et al. state the average "is in accordance with similar studies in both Scandinavia and southern Europe (Kullman, 2007a,b; Parmesan, 2005; Pauli et al., 2007)," but they state the 200 percent increase in taxa richness they documented on two of the summits "is exceptional." And to make their view of the issue perfectly clear, the three Norse researchers conclude, "the present increase in species richness is mainly a result of recent climatic change."

References

Acock, A.M. 1940. Vegetation of a calcareous inner fjord region in Spitsbergen. *Journal of Ecology* **28**: 81–106.

Ainsworth, E.A. and Long, S.P. 2005. What have we learned from 15 years of free-air CO_2 enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy properties and plant production to rising CO_2. *New Phytologist* **165**: 351–372.

Archer, S., Schimel, D.S., and Holland, E.A. 1995. Mechanisms of shrubland expansion: land use, climate or CO_2? *Climatic Change* **29**: 91–99.

Banfai, D.S. and Bowman, D.M.J.S. 2006. Forty years of lowland monsoon rainforest expansion in Kakadu National Park, northern Australia. *Biological Conservation* **131**: 553–565.

Benito-Garzon, M., Sanchez de Dios, R., and Sainz Ollero, H. 2008. Effects of climate change on the distribution of Iberian tree species. *Applied Vegetation Science* **11**: 169–178.

Betts, R.A., Boucher, O., Collins, M., Cox, P.M., Falloon, P.D., Gedney, N., Hemming, D.L., Huntingford, C., Jones, C.D., Sexton, D.M.H., and Webb, M.J. 2007. Projected increase in continental runoff due to plant responses to increasing carbon dioxide. *Nature* **448**: 1037–1041.

Bond, W.J. and Midgley, G.F. 2000. A proposed CO_2-controlled mechanism of woody plant invasion in grasslands and savannas. *Global Change Biology* **6**: 865–869.

Bond, W.J., Midgley, G.F., and Woodward, F.I. 2003. The importance of low atmospheric CO_2 and fire in promoting the spread of grasslands and savannas. *Global Change Biology* **9**: 973–982.

Bowman, D.M.J.S. and Dingle, J.K. 2006. Late 20th century landscape-wide expansion of *Allosyncarpia ternata* (Myrtaceae) forests in Kakadu National Park, northern Australia. *Australian Journal of Botany* **54**: 707–715.

Bowman, D.M.J.S., Murphy, B.P., and Banfai, D.S. 2010. Has global environmental change caused monsoon rainforests to expand in the Australian monsoon tropics? *Landscape Ecology* **25**: 1247–1260.

Bowman, D.M.J.S., Walsh, A., and Milne, D.J. 2001. Forest expansion and grassland contraction within a *Eucalyptus savanna* matrix between 1941 and 1994 at Litchfield National Park in the Australian monsoon tropics. *Global Ecology and Biogeography* **10**: 535–548.

Brantley, S.T. and Young, D.R. 2010. Shrub expansion stimulates soil C and N storage along a coastal soil chronosequence. *Global Change Biology* **16**: 2052–2061.

Briceño-Elizondo, R., Garcia-Gonzalo, J., Peltola, H., Matala, J., and Kellomaki, S. 2006. Sensitivity of growth of Scots pine, Norway spruce and silver birch to climate change and forest management in boreal conditions. *Forest Ecology and Management* **232**: 152–167.

Brook, B.W. and Bowman, D.M.J.S. 2006. Postcards from the past: charting the landscape-scale conversion of tropical Australian savanna to closed forest during the 20th century. *Landscape Ecology* **21**: 1253–1266.

Ehrenfeld, J.G. 1990. Dynamics and processes of barrier island vegetation. *Reviews in Aquatic Sciences* **2**: 437–480.

Forbes, B.C., Fauria, M., and Zetterberg, P. 2010. Russian Arctic warming and 'greening' are closely tracked by tundra shrub willows. *Global Change Biology* **16**: 1542–1554.

Gaucharel, C., Guiot, J., and Misson, L. 2008. Changes of the potential distribution area of French Mediterranean forests under global warming. *Biogeosciences* **5**: 1493–1503.

Gedney, N., Cox, P.M., Betts, R.A., Boucher, O., Huntingford, C., and Stott, P.A. 2006. Detection of a direct carbon dioxide effect in continental river runoff records. *Nature* **439**: 835–838.

Geml, J., Kauff, F., Brochmann, C., and Taylor, D.L. 2010. Surviving climate changes: high genetic diversity and transoceanic gene flow in two arctic-alpine lichens, *Flavocetraria cucullata* and *F. nivalis* (Parmeliaceae, Ascomycota). *Journal of Biogeography* **37**: 1529–1542.

Guillet, B., Achoundong, G., Happi, J.Y., Beyala, V.K.K., Bonvallot, J., Riera, B., Mariotti, A., and Schwartz, D. 2001. Agreement between floristic and soil organic carbon isotope ($^{13}C/^{12}C$, ^{14}C) indicators of forest invasion of savannas during the last century in Cameroon. *Journal of Tropical Ecology* **17**: 809–832.

Hallinger, M., Manthey, M., and Wilmking, M. 2010. Establishing a missing link: warm summers and winter snow cover promote shrub expansion into alpine tundra in Scandinavia. *New Phytologist* **186**: 890–899.

Harrison, S.P. and Prentice, I.C. 2003. Climate and CO_2 controls on global vegetation distribution at the last glacial maximum: analysis based on paleovegetation data, biome modeling and paleoclimate simulations. *Global Change Biology* **9**: 983–1004.

Hibbard, K.A., Archer, S., Schimel, D.S., and Valentine, D.W. 2001. Biogeochemical changes accompanying woody plant encroachment in a subtropical savanna. *Ecology* **82**: 1999–2011.

Hibbard, K.A., Schimel, D.S., Archer, S., Ojima, D.S., and Parton, W. 2003. Grassland to woodland transitions: integrating changes in landscape structure and biogeochemistry. *Ecological Applications* **13**: 911–926.

Idso, K.E. and Idso, S.B. 1994. Plant responses to atmospheric CO_2 enrichment in the face of environmental constraints: a review of the past 10 years' research. *Agricultural and Forest Meteorology* **69**: 153–203.

Idso, S.B. 1992. Shrubland expansion in the American southwest. *Climatic Change* **22**: 85–86.

Idso, S.B. and Brazel, A.J. 1984. Rising atmospheric carbon dioxide concentrations may increase streamflow. *Nature* **312**: 51–53.

Jonsdottir, I.S. 2005. Terrestrial ecosystems on Svalbard: heterogeneity, complexity and fragility from an Arctic island perspective. *Biology and Environment: Proceedings of the Royal Irish Academy* **105B**: 155–165.

Kearney, M. 2006. Habitat, environment and niche: what are we modeling? *Oikos* **115**: 186–191.

Keenan, T., Serra, J.M., Lloret, F., Ninyerola, M., and Sabate, S. 2011. Predicting the future of forests in the Mediterranean under climate change, with niche- and process-based models: CO_2 matters! *Global Change Biology* **17**: 565–579.

Kgope, B.S., Bond, W.J., and Midgley, G.F. 2010. Growth responses of African savanna trees implicate atmospheric [CO_2] as a driver of past and current changes in savanna tree cover. *Austral Ecology* **35**: 451–463.

Kullman, L. 2007a. Long-term geobotanical observations of climate change impacts in the Scandes of West-Central Sweden. *Nordic Journal of Botany* **24**: 445–467.

Kullman, L. 2007b. Modern climate change and shifting ecological sates of the subalpine/alpine landscape in the Swedish Scandes. *Geooko* **28**: 187–221.

Le Roux, P.C. and McGeoch, M.A. 2008. Rapid range expansion and community reorganization in response to warming. *Global Change Biology* **14**: 2950–2962.

Liao, J.D., Boutton, T.W., and Jastrow, J.D. 2006. Storage and dynamics of carbon and nitrogen in soil physical fractions following woody plant invasion of grassland. *Soil Biology and Biochemistry* **38**: 3184–3196.

Lopez-Pintor, A., Sal, A.G., and Benayas, J.M. R. 2006. Shrubs as a source of spatial heterogeneity—the case of *Retama sphaerocarpa* in Mediterranean pastures of central Spain. *Acta Oecologia* **29**: 247–255.

Lye, K.A. 1973. The vascular plants on alpine peaks at Filefjell, south Norway. *Norwegian Journal of Botany* **20**: 51–55.

McCulley, R.L., Archer, S.R., Boutton, T.W., Hons, F.M., and Zuberer, D.A. 2004. Soil respiration and nutrient cycling in wooded communities developing in grassland. *Ecology* **85**: 2804–2817.

Nigh, G.D., Ying, C.C., and Qian, H. 2004. Climate and productivity of major conifer species in the interior of British Columbia, Canada. *Forest Science* **50**: 659–671.

Norby, R.J. and Luo, Y. 2004. Evaluating ecosystem responses to rising atmospheric CO_2 and global warming in a multi-factor world. *New Phytologist* **162**: 281–293.

Odland, A., Hoitomt, T., and Olsen, S.L. 2010. Increasing vascular plant richness on 13 high mountain summits in southern Norway since the early 1970s. *Arctic, Antarctic, and Alpine Research* **42**: 458–470.

Parmesan, C. 2005. Biotic response: range and abundance changes. In *Climate Change and Biodiversity*, edited by T.E. Lovejoy and H. Lee, 41–55. New Haven, CT and London, UK: Yale University Press.

Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution and Systematics* **37**: 637–669.

Pauli, H., Gottfried, M., Reiter, K., and Grabherr, G. 2007. Signals of range expansions and contractions of vascular plants in the high Alps: observations 1994–2004 at the GLORIA master site Schrankogel, Tyrol, Austria. *Global Change Biology* **13**: 147–156.

Polley, H.W. 1997. Implications of rising atmospheric carbon dioxide concentration for rangelands. *Journal of Range Management* **50**: 562–577.

Polley, H.W., Tischler, C.R., Johnson, H.B., and Derner, J.D. 2002. Growth rate and survivorship of drought: CO_2 effects on the presumed tradeoff in seedlings of five woody legumes. *Tree Physiology* **22**: 383–391.

Polley, H.W., Tischler, C.R., Johnson, H.B., and Pennington, R.E. 1999. Growth, water relations, and survival of drought-exposed seedlings from six maternal families of honey mesquite (*Prosopis glandulosa*): responses to CO_2 enrichment. *Tree Physiology* **19**: 359–366.

Prach, K., Kosnar, J., Klimesova, J., and Hais, M. 2010. High Arctic vegetation after 70 years: a repeated analysis from Svalbard. *Polar Biology* **33**: 635–639.

Puyravaud, J.-P., Dufour, C., and Aravajy, S. 2003. Rainforest expansion mediated by successional processes in vegetation thickets in the Western Ghats of India. *Journal of Biogeography* **30**: 1067–1080.

Reynolds, J.F., Virginia, R.A., Kemp, P.R., de Soyza, A.G., and Tremmel, D.C. 1999. Impact of drought on desert shrubs: effects of seasonality and degree of resource island development. *Ecological Monographs* **69**: 69–106.

Schade, J.D. and Hobbie, S.E. 2005. Spatial and temporal variation in islands of fertility in the Sonoran Desert. *Biogeochemistry* **73**: 541–553.

Schlesinger, W.H., Reynolds, J.F., Cunningham, G.L., Huenneke, L.F., Jarrell, W.M., Ross, V.A., and Whitford, W.G. 1990. Biological feedbacks in global desertification. *Science* **247**: 1043–1048.

Schwartz, D., de Foresta, H., Mariotti, A., Balesdent, J., Massimba, J.P., and Girardin, C. 1996. Present dynamics of the savanna-forest boundary in the Congolese Mayombe: a pedological, botanical and isotopic (^{13}C/ and ^{14}C) study. *Oecologia* **106**: 516–524.

Scott, L. 1999. Vegetation history and climate in the Savanna biome of South Africa since 190,000 ka: a comparison of pollen data from the Tswaing Crater (the Pretoria Saltpan) and Wonderkrater. *Quaternary International* **57/58**: 517–544.

Souza, L., Belote, R.T., Kardol, P., Weltzin, J.F., and Norby, R.J. 2010. CO_2 enrichment accelerates successional development of an understory plant community. *Journal of Plant Ecology* **3**: 33–39.

Springsteen, A., Loya, W., Liebig, M., and Hendrickson, J. 2010. Soil carbon and nitrogen across a chronosequence of woody plant expansion in North Dakota. *Plant and Soil* **328**: 369–379.

van der Meer, P.J., Jorritsma, I.T.M., and Kramer, J.K. 2002. Assessing climate change effects on long-term forest development: adjusting growth, phenology and seed production in a gap model. *Forest Ecology and Management* **162**: 39–52.

Vitousek, P.M., Cassman, K., Cleveland, C., Crews, T., Field, C.B., Grimm, N.B., Howarth, R.W., Marino R., Martinelli, L., Rastetter, E.B., and Sprent, J.I. 2002. Towards an ecological understanding of biological N fixation. *Biogeochemistry* **57**: 1–45.

Ward, D. 2005. Do we understand the causes of bush encroachment in African savannas? *African Journal of Range and Forage Science* **22**: 101–105

Wigley, B.J., Bond, W.J., and Hoffmann, M.T. 2009. Thicket expansion in a South African savanna under divergent land use: local vs. global drivers? *Global Change Biology* **16**: 964–976.

Wilcox, B.P. and Huang, Y. 2010. Woody plant encroachment paradox: rivers rebound as degraded grasslands convert to woodlands. *Geophysical Research Letters* **37**: 10.1029/2009GL041929.