NUTRIENT ACQUISITION IN A CO_2 ENRICHED WORLD

Will plants be able to sustain their enhanced growth?

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With respect to acquiring nitrogen, Zak *et al*. (2000)[1] found that aspen seedlings grown for 2.5 years at twice-ambient CO_2 concentrations displayed an average total seedling nitrogen content that was 13% greater than that displayed by control seedlings grown in ambient air, in spite of an average reduction in tissue nitrogen concentration of 18%. Thus, elevated CO_2 enhanced total nitrogen uptake from the soil, even though tissue nitrogen concentrations in the CO_2-enriched plants were diluted by the enhanced biomass of the much larger CO_2-enriched seedlings.

On a per-unit-biomass basis, Smart *et al*. (1998)[2] noted there were no differences in the total amounts of nitrogen within CO_2-enriched and ambiently-grown wheat seedlings after three weeks of exposure to atmospheric CO_2 concentrations of 360 and 1,000 ppm. Nevertheless, the CO_2-enriched seedlings exhibited greater rates of soil nitrate extraction than did the ambient-grown plants. Similarly, BassiriRad *et al*. (1998)[3] reported that a doubling of the atmospheric CO_2 concentration doubled the uptake rate of nitrate in the C_4 grass *Bouteloua eriopoda*. However, they also reported that elevated CO_2 had no effect on the rate of nitrate uptake in *Prosopis*, and that it actually decreased the rate of nitrate uptake by 55% in *Larrea*. Nonetheless, atmospheric CO_2 enrichment increased total biomass in these two species by 55 and 69%, respectively. Thus, although the uptake rate of this nutrient was depressed under elevated CO_2 conditions in the latter species, the much larger CO_2-enriched plants likely still extracted more *total* nitrate from the soil than did the ambient-grown plants of the experiment.

It is interesting to note that trees, grasses and shrubs can all absorb significant amounts of organic nitrogen from soils. Thus, plants do not have to wait for the mineralization of organic nitrogen before they extract the nitrogen they need from soils to support their growth and development.

Hence, the forms of nitrogen removed from soils by plants (nitrate vs. ammonium) and their abilities to remove different forms may not be as important as was once thought.

1 http://www.co2science.org/articles/V3/N8/B4.php.
2 http://www.co2science.org/articles/V2/N16/B3.php.
3 http://www.co2science.org/articles/V2/N6/B3.php.

It is also interesting to note that Nasholm *et al*. (1998)[4] determined that trees, grasses and shrubs can all absorb significant amounts of organic nitrogen from soils. Thus, plants do not have to wait for the mineralization of organic nitrogen before they extract the nitrogen they need from soils to support their growth and development. Hence, the forms of nitrogen removed from soils by plants (nitrate vs. ammonium) and their abilities to remove different forms may not be as important as was once thought.

In another tree study, Finzi *et al*. (2002)[5] found that, on average, loblolly pine that were exposed to an extra 200 ppm CO_2 maintained rates of net primary productivity that were 25% greater, and produced 32% more biomass, than the trees growing in ambient air. Moreover, the elevated CO_2 also increased the total amount of nitrogen present in the trees' biomass. In fact, the average annual requirement for nitrogen rose by 16% for the trees growing in the air enriched with CO_2. In order to compensate for this increased nitrogen demand, the average uptake of nitrogen from the soil was enhanced by 28% in the CO_2-enriched plot, which says a lot considering that soils in the study region are characteristically low in available nitrogen. In addition, average nitrogen-use efficiency rose by approximately 10% with atmospheric CO_2 enrichment.

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With respect to the uptake of phosphate, Staddon *et al*. (1999)[6] reported that *Plantago lanceolata* and *Trifolium repens* plants grown at 650 ppm CO_2 for 2.5 months exhibited total plant phosphorus contents that were much greater than those displayed by plants grown at 400 ppm CO_2, due to the fact that atmospheric CO_2 enrichment significantly enhanced plant biomass. Similarly, Rouhier and Read (1998)[7] reported that enriching the air around *Plantago lanceolata* plants with an extra 190 ppm of CO_2 for a period of three months led to increased uptake of phosphorus and greater tissue phosphorus concentrations than were observed in plants growing in ambient air.

Greater uptake of phosphorus can also occur due to CO_2-induced increases in root absorptive surface area or enhancements in specific enzyme activities. In addressing the first of these phenomena, BassiriRad *et al*. (1998) reported that a doubling of the atmospheric CO_2 concentration significantly increased the belowground biomass of *Bouteloua eriopoda* and doubled its uptake rate of phosphate. However, elevated CO_2 had no effect on uptake rates of phosphate in *Larrea* and *Prosopis*. Because the CO_2-enriched plants grew so much bigger, however, they still removed more phosphate from the soil on a per-plant basis. With respect to the second phenomenon, phosphatase - which is the primary enzyme responsible for the

[4] http://www.co2science.org/articles/V2/N8/B3.php.
[5] http://www.co2science.org/articles/V5/N43/B1.php.
[6] http://www.co2science.org/articles/V2/N18/B2.php.
[7] http://www.co2science.org/articles/V2/N2/B4.php.

conversion of organic phosphate into usable inorganic forms - had its activity increased by 30 to 40% in wheat seedlings growing at twice-ambient CO_2 concentrations (Barrett *et al*., 1998[8]).

With respect to another nutrient, iron, Jin *et al*. (2009)[9] grew twenty-day-old plants for an additional seven days within controlled-environment chambers maintained at atmospheric CO_2 concentrations of either 350 or 800 ppm in an iron (Fe)-sufficient medium with a soluble Fe source or under Fe-limited conditions in a medium containing the sparingly soluble hydrous Fe(III)-oxide, while measuring a number of pertinent plant parameters. Results indicated that plant growth was increased by the elevated CO_2 in both the Fe-sufficient and Fe-limited media, with shoot fresh weight increasing by 22% and 44%, respectively, and root fresh weight increasing by 43% and 97%, respectively. In addition, Jin *et al*. report that "the elevated CO_2 under Fe-limited conditions enhance[d] root growth, root hair development, proton release, root FCR [ferric chelate reductase] activity, and expressions of *LeFR01* and *LeIRT1* genes [which respectively encode FCR and the Fe(II) transporter in tomato], all of which enable plants to access and accumulate more Fe." And they add, as would be expected, that "the associated increase in Fe concentrations in the shoots and roots alleviated Fe-deficiency-induced chlorosis."

In considering their results, Jin *et al*. write that the bioavailability of iron to terrestrial plants "is often limited (Guerinot and Yi, 1994), particularly in calcareous soils, which represent 30% of the earth's surface (Imsande, 1998)," and they thus conclude that "Fe nutrition in plants is likely to be affected by the continued elevation of atmospheric CO_2, which, in turn, will affect crop production." And as their work strongly suggests, those important effects should be highly beneficial, while even *wider* biospheric benefits are suggested by the work of Sasaki *et al*. (1998), who demonstrated that both the ferric reductase activity and Fe uptake capacity of the marine alga *Chlorococcum littorale* cultured in Fe-limited media have been significantly enhanced by elevated CO_2 concentrations.

In another study, Haase *et al*. (2008)[10] grew barley (*Hordeum vulgare* L. cv. Europa) plants from seed for four weeks - both hydroponically in nutrient solution having adequate or less-than-adequate iron (Fe) concentrations (+Fe and -Fe, respectively), as well as in rhizobox microcosms filled with soil under the same two conditions of iron availability - in controlled-environment chambers maintained at atmospheric CO_2 concentrations of either 400 or 800 ppm, while they measured a number of pertinent plant physiological parameters. This work revealed that the elevated atmospheric CO_2 treatments stimulated biomass production in both Fe-sufficient and Fe-deficient barley plants, in both hydroponics and soil culture. In addition, they say there were three different CO_2-induced modifications in plant activity: "(i) increased internal Fe use efficiency, (ii) stimulation of root growth, and (iii) increased root exudation of Fe-mobilizing phytosiderophores in the sub-apical root zones." And since phytosiderophores act as metal chelators that mobilize sparingly soluble inorganic forms of iron and zinc and make them more readily available to plants, the researchers suggest that atmospheric CO_2 enrichment increases the competitiveness of plants such as barley with rhizosphere microorganisms in their quest for

8 http://www.co2science.org/articles/V2/N8/B1.php.
9 http://www.co2science.org/articles/V12/N30/B3.php.
10 http://www.co2science.org/articles/V11/N30/B1.php.

these often difficult-to-obtain trace elements, which phenomenon helps to explain the strong growth response of barley to atmospheric CO_2 enrichment, even when iron availability is low.

As for studies dealing with multiple nutrients, Schaffer *et al*. (1997)[11] grew two mango ecotypes, one evolving from a warm, humid tropical climate, and the other from a cool, dry subtropical region, for 12 months in glasshouses with atmospheres of either 350 or 700 ppm CO_2 to determine the effects of CO_2 enrichment on plant growth and leaf mineral nutrient concentrations. According to the researchers, although atmospheric CO_2 enrichment led to partial photosynthetic acclimation in both ecotypes, greater net carbon gains were still achieved with elevated CO_2, as indicated by greater plant dry mass values for trees grown at 700 ppm CO_2. Elevated CO_2 also tended to decrease foliar concentrations of mineral nutrients (N, P, K, Ca, Mg, S, Cl, Fe, Zn, Mn, Cu and B) in both mango cultivars, most likely due to a dilution effect, since atmospheric CO_2 enrichment increased leaf dry mass. Yet, although the instantaneous doubling of the atmospheric CO_2 content in this experiment reduced concentrations of leaf mineral elements, the authors stated that "given the slow rate at which global atmospheric CO_2 concentration is increasing, it is possible that plants will adapt to elevated ambient CO_2 concentrations over time with respect to mineral nutrition," as did sour orange trees after 85 months of exposure to elevated CO_2 (Penuelas *et al*., 1997).

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Several years later, Lieffering *et al*. (2004)[12] analyzed the elemental concentrations of archived grain samples from temperate rice (*Oryza sativa* L. cv. Akitakomachi) crops they had grown previously under FACE conditions out-of-doors in a fertile agricultural field (Okada *et al*., 2001), where an approximate 200-ppm increase in the air's CO_2 concentration increased rice grain yields by about 14% (Kim *et al*., 2003a,b).

Of the five macro-nutrients they measured (N, P, K, Mg, S), Lieffering *et al*. report that "only N showed a decrease in concentration with elevated CO_2 in both years," while all six of the micro-nutrients studied (Zn Mn, Fe, Cu, B, Mo) exhibited concentration *increases*. For Zn and Mn, in particular, they say "there was a strong tendency [for concentrations] to increase," while the same could also have been said of Fe, which in the second year of the study exhibited a CO_2-induced concentration increase on the order of 68%, as best as can be determined from Lieffering *et al*.'s bar graphs.

11 http://www.co2science.org/articles/V2/N17/B1.php.
12 http://www.co2science.org/articles/V7/N31/EDIT.php.

In concluding their paper, Lieffering *et al*. note that their study of the effects of elevated CO_2 on grain elemental concentrations under real-world field conditions is "the first such report for a staple food crop: all other previously reported data were obtained from plants growing in pots and in some kind of enclosure." In contrast to the results obtained in most of these latter root-confining experiments, they note that, other than for N, "no dilution of [the] elements in the grain was observed, contrary to the general conclusions of Loladze (2002)." Hence, they conclude that "as long as there is a readily available supply of nutrients and that the nutrient uptake capacity response to elevated CO_2 is equal [to] or greater than the whole plant biomass response [which was the case in their experiment, except for N], then no dilution should be observed."

Noting that "increased production of fine roots with CO_2 enrichment (Norby *et al*., 2004; Pritchard *et al*., 2008) may allow plants to match increased carbon assimilation with increased uptake of soil-derived elements," Natali *et al*. (2009)[13] "examined CO_2 effects of a suite of metal micronutrients and contaminants in forest trees and soils at two free-air CO_2 enrichment sites - a loblolly pine forest in North Carolina (Duke) and a sweetgum plantation in Tennessee [Oak Ridge National Laboratory (ORNL)] - and an open-top chamber experiment in a scrub-oak community in Florida [Smithsonian Environmental Research Center (SERC)]."

The three U.S. researchers report that they "did not find an overall decline in foliar metal concentrations with CO_2 enrichment," but that they *did* find that dilution effects for metal micronutrients were generally "less than for non-essential trace metals," and that "some essential plant metals were greater under elevated CO_2 (for example, 28% increase in Mn across species and sites)." Natali *et al*. conclude that their results "should alleviate some concerns that rising CO_2 concentrations will result in broad-scale decreases in the concentrations of all elements essential for plant function and animal nutrition," as proposed by Loladze (2002). They also say their generally opposite results for non-essential trace elements (some of which can be toxic) "may be applicable to contaminated systems," stating that "elevated CO_2 may, through dilution effects, alleviate aluminum toxicity." In general, therefore, one could say that elevated CO_2 tends to increase the availability of helpful trace elements, while it tends to decrease the availability of harmful ones.

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In general, therefore, one could say that elevated CO_2 tends to *increase* the availability of *helpful* trace elements, while it tends to *decrease* the availability of *harmful* ones.

[13] http://www.co2science.org/articles/V12/N49/B3.php.

Finally, in a somewhat different type of study, Urabe and Waki (2009)[14] grew three algal species -- *Scenedesmus obliquus* (green algae), *Cyclotella* sp. (diatoms) and *Synechococcus* sp. (cyanobacteria) -- in mono- and mixed cultures at ambient (360 ppm) and high (2000 ppm) CO_2 levels, and allowed a planktonic herbivore (*Daphnia*) to feed on the different algal populations thereby produced either individually or in various mixtures, to see if there was any CO_2-induced effect on herbivore growth. In so doing, the two researchers report that "both in the mono- and mixed cultures, algal steady state abundance increased but algal P:C and N:C ratios decreased when they were grown at high CO_2." They also found that "*Daphnia* fed monospecific algae cultured at high CO_2 had decreased growth rates despite increased algal abundance." But "when fed mixed algae cultured at high CO_2, especially consisting of diatoms and cyanobacteria or the three algal species," they found that "*Daphnia* maintained high growth rates despite lowered P and N contents relative to C in the algal diets." Such findings, in the words of Urabe and Waki, imply that "algal diets composed of multiple species can mitigate the adverse effects of elevated CO_2 on herbivore performance," and that "in environments with high CO_2, herbivores may find a new diet producer or a combination of producer species to best meet their nutritional demands."

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In summary, as the CO_2 content of the air increases, the experimental data that have been accumulated to date suggest that much of Earth's vegetation will likely display increases in biomass; and there is considerable evidence suggestive of the further likelihood that the larger plants thereby produced will develop more extensive root systems and extract greater amounts of mineral nutrients from the soils in which they are rooted, enabling them to sustain their enhanced growth.

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[14] http://www.co2science.org/articles/V12/N18/B2.php.

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