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LETTERS TO THE EDITOR

Comment on "Modelling the seasonal contribution of a CO_2 fertilization effect of the terrestrial vegetation to the amplitude increase in atmospheric CO_2 at Mauna Loa Observatory" by G. H. Kohlmaier et al.*

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Kohlmaier et al. (1989) present a detailed analysis of the increasing amplitude of the atmosphere's seasonal CO_2 cycle at Mauna Loa, Hawaii, finding that the aerial fertilization effect of atmospheric CO_2 enrichment on the terrestrial biota accounts for only about a quarter of the observed amplitude increase between 1958 and 1987. In discussing various ways of resolving this dilemma, they note that a quadrupling of the CO_2 fertilization factor (β) observed in phytotrons, greenhouses, and open-top chambers over exposure times of less than 1 year would provide the needed amplitude amplification; but they also note that a β factor of this magnitude would be 4 × higher than most ecologists are willing to support. Nevertheless, there are a number of reasons for believing that β may be considerably greater than has historically been assumed.

First of all, phytotron and greenhouse experiments generally restrict root growth, so that plants suffer a reduction in available carbon sinks (Jarvis, 1989); and it is a well-established fact that carbon sink limitations generally reduce plant photosynthetic rates (Herold, 1980; Azcon-Bieto, 1983). Hence, such experiments may yield a β factor much smaller than that likely to be experienced in nature because of end-product inhibition of photosynthesis (Guinn and Mauney, 1980; Von Caemmerer and Farquhar, 1981). In addition, restricted rooting volumes reduce the potential for the roots of CO_2-enriched plants to mine essential nutrients from greater soil depths (Luxmoore et al., 1986; Norby et al., 1986).

Second, vesicular-arbuscular mycorrhizal fungi, which are generally present in all terrestrial ecosystems (Gerdemann, 1968; Read et al., 1976), tend to expand the effective root zones of naturally-occurring plants still more. Growing outward from their hosts' roots, they effectively increase the area of root surface available for nutrient uptake (Harley, 1975), and they extend the life of absorptive roots beyond the few days that root hairs are normally active (Fogel, 1983). Serving as biological filters, these fungi not only increase the absorption of water and nutrients by the plants they "service," they also protect their hosts from soil-borne diseases and reduce the incidence of nematode infection of roots (Ingham, 1988). In addition, they typically produce hormones (Slankis, 1973) that enhance root growth (Simmons and Pope, 1987, 1988). But, again, if available rooting volume is limited, or if the plants do not have access to such symbionts, as is often the case in phytotron and greenhouse experiments, these many additional benefits—all of which are enhanced by the enhanced vigor of their hosts (Johnson and McGraw, 1988), such as would be produced by atmospheric CO_2 enrichment (Idso, 1989)—may be forfeited and the real-world β factor thereby underestimated.

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Third, short-term experiments, even those conducted under field conditions, cannot reveal the importance of the subtle and long-term soil rhizosphere improvements likely to be conferred by atmospheric CO_2 enrichment. For example, photosynthetically-stimulated phospho-microbes (Tiwari et al., 1989) secrete a number of organic acids that help solubilize tri-calcium phosphate and organic and rock phosphate (Ortuno et al., 1978; Molla et al., 1984; Babenko et al., 1985). Hence, as noted by Rosenberg et al. (1983), "CO_2 "fertilization" may initiate or stimulate an acceleration of soil formation through enhanced biological activity" so that a "more rapid release of many essential nutrients might follow." In addition, augmented populations of soil microorganisms—"all [of which] will be enhanced by the larger photosynthetic activity of plants at higher CO_2" (Lamborg et al., 1983)—should lead to a more thorough bio-detoxification of polluted soil water (Alexander, 1981, 1985; Hutchins et al., 1985). And both of these phenomena have a cumulative impact that builds up over a period of many years.

Fourth, good earthworm populations also require considerable time to be established; and they, too, are not generally included in phytotron and greenhouse experiments. Their significance, of course, arises from their fabled soil-forming activities (Darwin, 1881) and the major role they play "in improving and maintaining the fertility, structure, aeration, and drainage of agricultural soil" (Edwards, 1988). And, again, as Edwards has made very clear, "the most important factor in maintaining good earthworm populations in agricultural soils is that there be adequate availability of organic matter," such as is known to be provided by direct stimulatory action of atmospheric CO_2 enrichment.

Fifth, short-term and confined laboratory and field experiments are not well suited for detecting any "compound interest effect" that may be manifest in either individual plants or their progeny. In a 21-month study of water lilies, for example, Idso et al. (1990) observed a 49% increase in leaf net photosynthesis produced by a 300 ppm enrichment of the air's CO_2 content that operated upon a greatly augmented population of significantly larger and longer-lived leaves to ultimately produce a 270% increase in total plant dry matter. Another example of this effect would be the spreading of mesic vegetation into more xeric environments as plant water use efficiencies improve (Idso and Quinn, 1983), so that more of the Earth's surface becomes more densely vegetated. This process, in turn, should lead to reductions in soil erosion caused by the ravages of wind and rain, as well as to the many other soil-improving phenomena discussed previously.

Sixth, on-going studies of in situ vegetation are beginning to reveal much larger growth responses to long-term atmospheric CO_2 enrichment than have historically been observed in phytotron and greenhouse experiments. At our laboratory in Phoenix, Arizona, for example, we are following the growth and development of a number of sour orange trees planted directly into the ground as seedlings and then enclosed by open-top polyethylene chambers, half of which are maintained at ambient CO_2 concentrations and half of which receive an extra 300 ppm of CO_2. After $2\frac{1}{2}$ years of growth, the trees in the CO_2-enriched chambers have approximately twice as much leaf and fine root biomass as the trees growing in normal air; and their trunk and branch volumes are fully $2.8\times$ greater than those of their ambient-CO_2-treatment counterparts (Idso and Kimball, 1991; Idso et al., 1991), which is three to five times more than what would be expected on the basis of most short-term greenhouse and phytotron studies. And in a similar open-top chamber study of natural wetlands near Chesapeake Bay, Drake et al. (1989) have documented CO_2-induced increases in net ecosystem productivity that have also exceeded 100% over a three-year period.

Last of all, and perhaps demonstrating the significance of some of the phenomena enumerated above, Tans et al. (1990) have recently utilized observations of atmospheric CO_2 concentrations and partial pressures of CO_2 in surface ocean waters to demonstrate the existence of a Northern Hemispheric terrestrial sink for CO_2 that is *much* larger than anyone had previously suspected. Consequently, in view of all the available physical and biological evidence, as well as the fact that the primary driving force of the seasonal atmospheric CO_2 cycle is universally acknowledged to be the seasonal growth and decay of the Northern Hemispheric terrestrial vegetation (Pearman and Hyson, 1981; Cleveland et al., 1983; Keeling et al., 1985; Bacastow et al., 1985; Enting, 1987), it would appear that the real-world β factor may well

be three to four or possibly even five times greater than what has heretofore been believed.

It is also interesting to note in this regard that Kohlmaier et al. (1989) found the mean increase in the seasonal CO_2 cycle amplitude within the first half of the Mauna Loa record to be "considerably lower than the mean increase over the entire period" and that "global surface temperatures fell during the first half of the Mauna Loa record, while they increased over the second half," suggestive of the likelihood that "climatic variability is the most likely cause for such a behavior." This conclusion is precisely what is predicted by the results of a number of recent studies of the effects of temperature variability on the strength of the CO_2 fertilization factor. Independently suggested by Mortensen (1987) and Idso et al. (1987), who also demonstrated the reality of the phenomenon, it is now generally accepted that the positive effects of atmospheric CO_2 enrichment decrease with decreasing temperatures and that they increase when temperatures rise (Sage and Sharkey, 1987; Allen et al., 1988, 1990 a, b; Idso and Kimball, 1989). Hence, it would indeed be expected that the mean increase in the amplitude of the seasonal CO_2 cycle would be considerably lower over the first half of the Mauna Loa record, when global temperatures were falling, than over the second half of the record, when temperatures rose, giving further credence to the primary point of this comment: that naturally-occurring vegetation may be much more responsive to atmospheric CO_2 enrichment than has previously been believed.

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