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SHORT COMMUNICATION

Effects of atmospheric CO_2 enrichment on biomass accumulation and distribution in Eldarica pine trees

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Abstract

Eight Eldarica pine tree (*Pinus eldarica* L.) seedlings planted directly into the ground at Phoenix, Arizona within four clear-plastic-wall open-top enclosures were grown for a period of 2 years at mean atmospheric CO_2 concentrations of 408, 554, 680, and 812 $\mu L\ L^{-1}$. Biomass accumulations in needles, branches and boles were all linear functions of CO_2 over this concentration range. For a 75% increase in ambient CO_2, i.e. for an increase from 400–700 $\mu L\ L^{-1}$, the trees experienced a 3.42-fold increase in total above-ground biomass; while for a CO_2 concentration doubling from 400–800 $\mu L\ L^{-1}$, they experienced a 4.23-fold increase. Bole biomass responded similarly. Needle biomass, however, increased by a smaller amount (2.84-fold and 3.45-fold, respectively, for 400–700 and 400–800 $\mu L\ L^{-1}$ increases in CO_2); while branch biomass was increased considerably more (by 4.73-fold and 5.97-fold for corresponding increases in CO_2).

Key words: Carbon dioxide, CO_2, forests, pine tree, *Pinus eldarica* L.

Introduction

Terrestrial photosynthesis accounts for roughly 90% of the amplitude of the annual atmospheric CO_2 cycle (Sellers and McCarthy, 1990); and trees account for approximately 75% of the biospheric CO_2 exchange over land (Post *et al.*, 1990). Consequently, earth's forests are responsible for about two-thirds of global photosynthesis and play an important role in the global carbon balance and its response to the rising CO_2 content of the air (Idso, 1991*a*, *b*).

Given the great significance thus attached to the response of tree growth to atmospheric CO_2 enrichment, a number of studies of this phenomenon were conducted during the 1980s. In reviewing that body of work, however, Jarvis (1989) noted that the experiments were 'virtually all short term (less than twelve months) on very young trees that [were] often pot-bound, with growth restricted by the lack of active sinks and in nutrient-deficient condition'. Likewise, in a review of 29 studies describing 61 separate experiments on 49 different woody species, Poorter (1993) reported a mean experimental duration of only 4.5 months. In addition, all of the trees in the studies he reviewed were grown in some type of soil container and it has been demonstrated by Masle *et al.* (1990), Arp (1991) and Thomas and Strain (1991) that the potential root confinement produced by such containers may significantly reduce plant growth responses to atmospheric CO_2 enrichment.

In an attempt to overcome these experimental inadequacies, we initiated a long-term study of the effects of CO_2 enrichment on well-watered and fertilized sour orange trees planted directly into the ground at Phoenix, Arizona and enclosed by open-top chambers with clear plastic walls (Idso *et al.*, 1991). This experiment, begun in November of 1987, is the longest continuous CO_2 enrichment study in existence and it has vindicated Jarvis' criticisms of short-term studies on plants with insufficient rooting volumes. The effects of atmospheric CO_2 enrichment, for example, were found to be much greater than previously believed possible: a 2.75-fold enhancement of both above- and below-ground biomass in response to a 75% (400–700 $\mu L\ L^{-1}$) increase in atmospheric CO_2 concentration (Idso and Kimball, 1991, 1992), as opposed to the 30–40% response observed in most herbaceous plants (Kimball, 1983). In addition, it took fully 18 months for this maximal growth response to be achieved (Idso and Kimball, 1993*b*).

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In view of these remarkable findings and their implications for one of the major environmental concerns of our day, we felt it important to explore their generality. Hence, we initiated a similar CO_2 enrichment study of a totally different tree species (a conifer) that we maintained for a period of 2 years. Although short in terms of the life-span of the tree, this length of time is long enough to reach a growth response plateau, as demonstrated by our sour orange tree study and shown to be true for the trees of this experiment as well.

Materials and methods

On 11 March 1991, sixteen 40 cm-tall *Pinus eldarica* L. seedlings were planted in a field of Avondale loam at Phoenix, Arizona. Shortly thereafter, they were surrounded in pairs by eight clear-plastic-wall open-top enclosures through which air was circulated at a rate of 4 enclosure-volume exchanges per minute, beginning on 18 April 1991. Two of these enclosures received ambient air 24 h d^{-1} that averaged 408 μL of CO_2 L^{-1} of air ($\mu L\ L^{-1}$) over the following 2 years, while three other pairs of enclosures received CO_2 concentrations 24 h per day that averaged 554, 680, and 812 $\mu L\ L^{-1}$, with associated standard errors computed from monthly means of ± 3, ± 3, ± 6, and ± 11 $\mu L\ L^{-1}$, respectively.

From the start of the experiment, the trees were flood irrigated every 3–6 d to ensure that they were never short of water. After the first summer of the study, this frequency was reduced to every 2–3 weeks. Under these protocols, there were never any visual indications of water stress throughout the entire period of the study.

At the midpoint of each month, we measured the height of each tree's bole and its diameter every 20 cm, starting 20 cm above the soil surface, and extending to the top of the tree. From these data we calculated monthly values of each tree's total bole volume (from 10 cm above the soil surface to its top) by summing the volumes of all of the tree's 20-cm bole segments, which we treated as cylinders with diameters equal to those measured at their midpoints.

Eleven months into the experiment (on 18 March 1992), one tree was cut and removed from each chamber to provide intermediate harvest data and to prevent shading of the remaining eight trees (2 replicates of 4 treatments), whose growth we followed for an additional year. Then, at the end of the study, each tree was cut at a height of 10 cm above the soil surface, after which we made separate dry weight (biomass) measurements of each tree's needles, branches and bole (from 10 cm above the soil surface to its top).

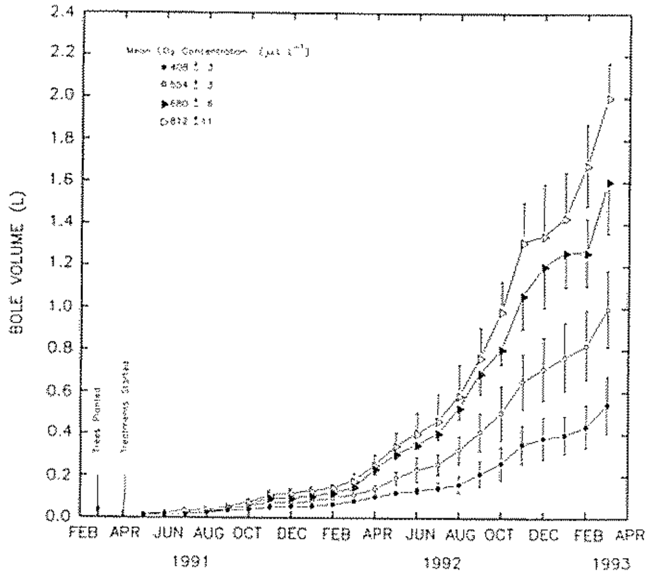

Fig. 1. A two-year record of monthly mean values of bole volumes of Eldarica pine trees (two per treatment) grown in air having mean CO_2 concentrations of 408, 554, 680, and 812 $\mu L\ L^{-1}$ over the period of measurement. Standard errors are shown wherever they do not overlap those of an adjacent treatment.

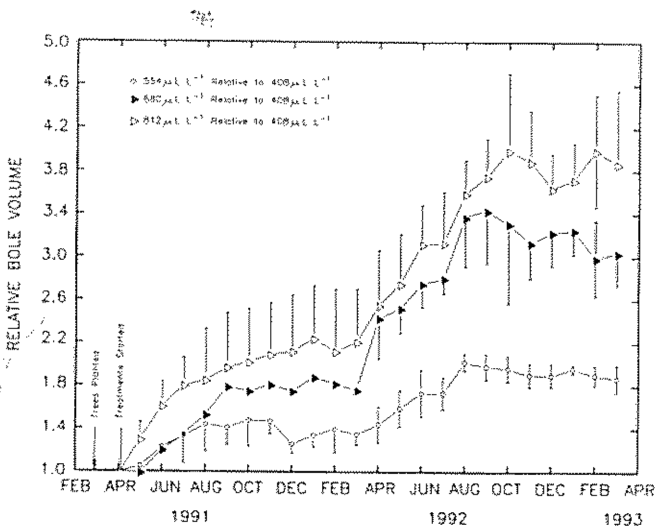

Fig. 2. A two-year record of monthly mean values of bole volumes of Eldarica pine trees grown in air having mean CO_2 concentrations of 554, 680 and 812 $\mu L\ L^{-1}$ relative to bole volumes of trees growing in ambient air containing 408 $\mu L\ L^{-1}$ of CO_2. Standard errors are shown wherever they do not overlap those of an adjacent treatment.

Results and discussion

Figure 1 portrays the results of the monthly bole volume measurements. Dividing each of the CO_2-enriched bole volumes by the corresponding ambient treatment bole volumes produces the *relative* bole volume trends we have plotted in Fig. 2. As can be seen, it took approximately 16 months for the maximal growth enhancement of the 554 $\mu L\ L^{-1}$ treatment to be realized, about 17 months for the 680 $\mu L\ L^{-1}$ treatment, and as much as 18 months for the 812 $\mu L\ L^{-1}$ treatment, which is comparable to that previously observed in sour orange trees.

Figure 3 depicts the relationships obtained for the final dry weights of the needles, branches and boles of the harvested trees as functions of the mean CO_2 concentrations to which the trees were exposed over the course of the 23-month experiment, along with the corresponding final (23-month) and 11-month *total* dry weight (biomass) results. In viewing these latter relationships, it can again be seen that 11 months of differential CO_2 exposure was insufficient to reveal the full potential of atmospheric CO_2 enrichment to stimulate growth in Eldarica pine trees. At

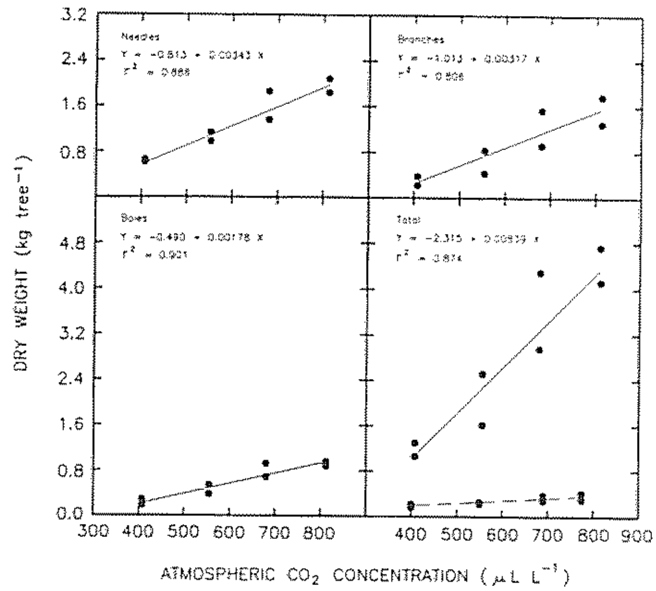

Fig. 3. The final dry weights of the needles, branches and boles of eight Eldarica pine trees grown for two years in air of four different atmospheric CO_2 concentrations plotted as a function of the atmospheric CO_2 content within which they were grown, along with the intermediate total dry weight results obtained after 11 months of the experiment (dashed line result).

the final harvest after 23 months of exposure, however, the effect was strong and clear: the total above-ground biomass of the trees rose 3.42-fold for a 75% (400–700 μL L^{-1}) increase in the CO_2 content of the air, while for a doubling of the CO_2 content from 400–800 μL L^{-1}, it rose 4.22-fold.

These total biomass increases were driven by nearly identical increases in bole biomass (3.40-fold and 4.21-fold increases in biomass for 400–700 and 400–800 μL L^{-1} increases in atmospheric CO_2 concentration, respectively), by slightly smaller increases in needle biomass (corresponding 2.84-fold and 3.45-fold increases in biomass), and by significantly larger increases in branch biomass (corresponding 4.73-fold and 5.97-fold increases). These observations suggest that bole measurements alone, such as those of Figs 1 and 2, may be adequate for characterizing total above-ground biomass responses of pine trees to atmospheric CO_2 enrichment. They also demonstrate, however, that there are significant differences in the distribution of biomass under conditions of elevated atmospheric CO_2, with relatively more going into branches and less into needles in our experiment.

All of these increases in biomass are much larger than those typically observed in shorter term studies of trees growing in pots or other containers. However, they are similar to the large growth responses we have documented for sour orange trees and three Australian tree species growing out-of-doors and rooted in the natural soil environment (Idso and Kimball, 1993*a*).

In addition to the typically longer time-period of CO_2 enrichment and the lack of root restrictions in our studies, another reason for the large growth responses we have generally observed in trees is likely to be the high air temperature of Phoenix in summer (mean temperatures of 26 °C with average afternoon maximums approaching 40 °C). In a review of 30 studies of 34 different species of plants, for example, Idso and Idso (1994) found that the relative or percentage growth enhancement produced by atmospheric CO_2 enrichment rose with air temperature over the entire range investigated, from 8–36 °C. They also found seven studies that reported a mean rise of 5.9 °C in the optimum temperature for plant growth in response to a 300 μL L^{-1} increase in the CO_2 content of the air. As has been elegantly demonstrated by Long (1991), both of these phenomena are due to the fact that atmospheric CO_2 enrichment significantly reduces rates of photorespiration, which under ambient CO_2 concentrations typically increases with increasing temperature.

In view of these observations, there is a real possibility that some trees, particularly those in warmer climates, may remove considerably more carbon from the atmosphere than most people have previously thought possible. More research should thus be directed towards investigating the significance and extent of this important phenomenon, and whether it results in an ultimate increase in carbon sequestration in the soil.

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References

Arp WJ. 1991. Effects of source–sink relations on photosynthetic acclimation to elevated CO_2. *Plant, Cell and Environment* **14**, 869–75.

Idso KE, Idso SB. 1994. Plant responses to atmospheric CO_2 enrichment in the face of environmental constraints: A review of the past ten years' research. *Agricultural and Forest Meteorology* **69**, 153–203.

Idso SB. 1991*a*. The aerial fertilization effect of CO_2 and its implications for global carbon cycling and maximum greenhouse warming. *Bulletin of the American Meteorological Society* **72**, 962–5.

Idso SB. 1991*b*. Reply. *Bulletin of the American Meteorological Society* **72**, 1910–14.

Idso SB, Kimball BA. 1991. Effects of two and a half years of atmospheric CO_2 enrichment on the root density distribution of three-year-old sour orange trees. *Agricultural and Forest Meteorology* **55**, 345–9.

Idso SB, Kimball BA. 1992. Above-ground inventory of sour orange trees exposed to different atmospheric CO_2 concentrations for three full years. *Agricultural and Forest Meteorology* **60**, 145–51.

Idso SB, Kimball BA. 1993*a*. Effects of atmospheric CO_2

enrichment on net photosynthesis and dark respiration rates of three Australian tree species. *Journal of Plant Physiology* **141**, 166–71.

Idso SB, Kimball BA. 1993*b*. Tree growth in carbon dioxide enriched air and its implications for global carbon cycling and maximum levels of atmospheric CO_2. *Global Biogeochemical Cycles* **7**, 537–55.

Idso SB, Kimball BA, Allen SG. 1991. CO_2 enrichment of sour orange trees: 2.5 years into a long-term experiment. *Plant, Cell and Environment* **14**, 351–3.

Jarvis PG. 1989. Atmospheric carbon dioxide and forests. *Philosophical Transactions of the Royal Society of London* **324B**, 369–92.

Kimball BA. 1983. Carbon dioxide and agricultural yield: An assemblage and analysis of 330 prior observations. *Agronomy Journal* **75**, 779–88.

Long SP. 1991. Modification of the response of photosynthetic productivity to rising temperature by atmospheric CO_2 concentrations: Has its importance been underestimated? *Plant, Cell and Environment* **14**, 729–39.

Masle J, Farquhar GD, Gifford RM. 1990. Growth and carbon economy of wheat seedlings as affected by soil resistance to penetration and ambient partial pressure of CO_2. *Australian Journal of Plant Physiology* **17**, 465–87.

Poorter H. 1993. Interspecific variation in the growth response of plants to an elevated ambient CO_2 concentration. *Vegetatio* **104/105**, 77–97.

Post WM, Peng TG, Emanuel WR, King AW, Dale VH, De-Angelis DL. 1990. The global carbon cycle. *American Scientist* **78**, 310–26.

Sellers P, McCarthy JJ. 1990. Planet Earth: Part III. Biosphere interactions. *EOS: Transactions of the American Geophysical Union* **71**, 1883–4.

Thomas RB, Strain BR. 1991. Root restriction as a factor in photosynthetic acclimation of cotton seedlings grown in elevated carbon dioxide. *Plant Physiology* **96**, 627–34.