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Ultra-enhanced spring branch growth in CO₂-enriched trees: can it alter the phase of the atmosphere's seasonal CO₂ cycle?

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Abstract

Since the early 1960s, the declining phase of the atmosphere's seasonal CO₂ cycle has advanced by approximately 7 days in northern temperate latitudes, possibly as a result of increasing temperatures that may be advancing the time of occurrence of what may be called 'climatological spring.' However, just as several different phenomena are thought to have been responsible for the concomitant increase in the amplitude of the atmosphere's seasonal CO₂ oscillation, so too may other factors have played a role in bringing about the increasingly earlier spring drawdown of CO₂ that has resulted in the advancement of the declining phase of the air's CO₂ cycle. One of these factors may be the ongoing rise in the CO₂ content of the air itself; for the aerial fertilization effect of this phenomenon may be significantly enhancing the growth of each new season's initial flush of vegetation, which would tend to stimulate the early drawdown of atmospheric CO₂ and thereby advance the time of occurrence of what could be called 'biological spring.' Working with sour orange (*Citrus aurantium* L.) trees that have been growing out-of-doors in open-top chambers for over 10 years in air of either 400 or 700 ppm CO₂, this hypothesis was investigated by periodically measuring the lengths, dry weights and leaf chlorophyll concentrations of new branches that emerged from the trees at the start of the 1998 growing season. The data demonstrate that the hypothesis is viable, and that it might possibly account for 2 of the 7 days by which the spring drawdown of the air's CO₂ concentration has advanced over the past few decades. © 2000 Published by Elsevier Science B.V.

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1. Introduction

Each spring when the Northern Hemisphere's terrestrial vegetation emerges from the dormancy

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and/or low growth rates typical of winter, it's renewed and/or enhanced growth removes enough CO₂ from the air to reduce the atmosphere's CO₂ concentration by several parts per million (ppm). Then, in the autumn and winter, when much of this vegetation either dies and decays or exhibits much reduced rates of photosynthesis, the air's CO₂ content rises by a small amount. Together, these phenomena produce an oscillation of well-defined waveform that is superimposed upon the yearly rise in the air's mean CO₂ concentration; and the greater the yearly growth of the planet's vegetation, the greater is the amplitude of this seasonal 'breath of the biosphere' (Fung et al., 1983, 1987; Heimann et al., 1989).

Over the period of time for which detailed CO₂ measurements are available, a sizable increase in the annual amplitude of the atmosphere's Northern Hemispheric seasonal CO₂ cycle has been observed. Several studies have attributed a significant portion of this amplitude amplification to the increasing aerial fertilization effect of the steadily rising mean value of the air's CO₂ content (Pearman and Hyson, 1981; Cleveland et al., 1983; Bacastow et al., 1985; Enting, 1987; Kohlmaier et al., 1989; Idso et al., 1999). It has also been suggested that a number of other factors may be involved, including the seasonality of fossil fuel usage (Rotty, 1987; Levin et al., 1989, 1995), seasonal variations in the deposition of fossil fuel-derived nitrogen (Townsend et al., 1996), temporal variations in tropical biomass burning (Hao and Liu, 1994), seasonal shifts of the Intertropical Convergence Zone (Iacobellis et al., 1994), variations in the seasonality of photosynthesis and respiration at high latitudes (Chapin et al., 1996), and changes in the seasonal cycle of ocean-atmosphere CO₂ exchange (Randerson et al., 1997; Heimann et al., 1998).

More recently, a change in a second property of the atmosphere's Northern Hemispheric seasonal CO₂ cycle has been observed. Since the early 1960s, there has been an approximate 7-day advance in the time of occurrence of the declining phase of the oscillation (Keeling et al., 1996). What is more, Myneni et al. (1997) have associated this phase advance with a similar advance in the springtime initiation of plant growth in high

northern latitudes, which they observed in satellite-derived land albedo records spanning the decade 1981–1991.

In announcing the discovery of this phenomenon, Keeling et al. (1996) suggested that the increasingly earlier occurrence of the declining phase of the Northern Hemispheric seasonal CO₂ cycle over this period was due to a contemporaneous increase in Northern Hemispheric springtime temperatures, which would logically be expected to enable spring growth to begin ever earlier, in the mean, each year. Hence, we refer to their hypothesis, with which we are in basic agreement, as a hastening of the time of occurrence of 'climatological spring,' since it is induced by a change in climate.

It is possible, however, that just as the change in the amplitude of the atmosphere's Northern Hemispheric seasonal CO₂ oscillation may have multiple causes, so too may the shift in the phase of the cycle have its origin in more than one factor. For example, the ever-increasing aerial fertilization effect of the ongoing rise in the air's CO₂ content may be stimulating Northern Hemispheric terrestrial vegetation to begin to grow earlier and/or more robustly each succeeding spring. This phenomenon would clearly lead to a hastening of the time of occurrence of what we call 'biological spring' (since it is unrelated to climatic factors), which may also play a significant role in the phase advance of the atmosphere's Northern Hemispheric seasonal CO₂ cycle.

Our initial thoughts on this subject were based on the simple but fundamental fact that CO₂ is the primary raw material used by plants to produce the organic matter out of which they construct their tissues, plus the well-documented observations that: (1) plants generally grow better with more CO₂ in the air (Kimball, 1983a,b; Poorter, 1993); and (2) plants are typically more robust in the face of environmental stresses when they are exposed to elevated levels of atmospheric CO₂ (Idso and Idso, 1994). It was thus hypothesized that as CO₂-enriched plants experience the waning of winter, they may be relieved of this major environmental 'stress' more readily than plants growing in ambient air, and they might therefore begin to grow earlier and/or more ro-

bustly in the spring. Hence, an ongoing experiment designed to reveal the long-term effects of atmospheric CO₂ enrichment on the growth and development of sour orange trees was utilized to investigate this idea.

2. Materials and methods

2.1. *The trees*

Since mid-November of 1987, eight sour orange (*Citrus aurantium* L.) trees that are planted in the ground, where their unrestricted roots are free to explore the natural soil environment, have been growing out-of-doors at Phoenix, Arizona in four clear-plastic-wall open-top enclosures (Idso and Kimball, 1997). Two of these enclosures (each of which contains two trees) have been continuously maintained at the local ambient CO₂ concentration of approximately 400 ppm, while the other two enclosures have been maintained at a CO₂ concentration of approximately 700 ppm. Under these circumstances, both sets of trees are acclimated to the two CO₂ regimes; and they have grown large enough — over 7 m tall — to accommodate the removal of the large amounts of branch tissue needed to assess the validity of the hypothesis.

2.2. *Branch length and biomass measurements*

The study was initiated on 4 January 1998 — day-of-year (DOY) 4 — when we began examining each tree on a daily basis for signs of new spring growth. When the first signs of new branch emergence were observed — which occurred in both the CO₂-enriched and ambient-treatment trees on DOY 21 — we began to measure the lengths of seven new terminal branches and seven new non-terminal branches on both the north and south sides of each of the eight trees every Monday, Wednesday and Friday. To be as objective as possible in this regard, we consistently looked for the largest new branches we could find over the first 3 m distance above the ground, which we could reach without a ladder. We felt that this protocol would be much more accurate than at-

tempting to select average-size branches. Indeed, the trees were so big it was impossible to measure enough branches to determine their average length.

At weekly intervals, beginning DOY 31 through DOY 94 (after which we continued at increasingly longer intervals), we harvested one new terminal branch and one new non-terminal branch from the north and south sides of each tree from the portions of the trees that were located more than three meters above the ground (so we would not harvest the lower branches we regularly used for length determinations). For this purpose, we selected new branches that were of the same lengths as the north and south terminal and non-terminal CO₂ treatment means determined below the 3-m height level. These branches, with their associated leaves, were oven dried and weighed. For the first half of the experiment, when the new branches were relatively small, all branches from all four trees of each CO₂ treatment were pooled before drying and, hence, weighed together. Over the last half of the study, however, data were obtained for each of the two replications of each CO₂ treatment separately.

2.3. *Leaf chlorophyll concentration measurements*

Once the first leaves of the new branches were large enough to sample with a leaf chlorophyll meter, we began a Monday–Wednesday–Friday regimen of leaf chlorophyll concentration measurements, as per the procedure outlined by Idso et al. (1996). These measurements were made with a hand-held Minolta SPAD 502 chlorophyll meter (Minolta Corporation, Ramsey, NJ) on leaves located within the first three meters above the ground, where we sampled one leaf on each of seven new terminal and seven new non-terminal branches on both the north and south sides of each tree.

3. Results

3.1. *Branch biomass*

Mean results of the new-branch biomass me-

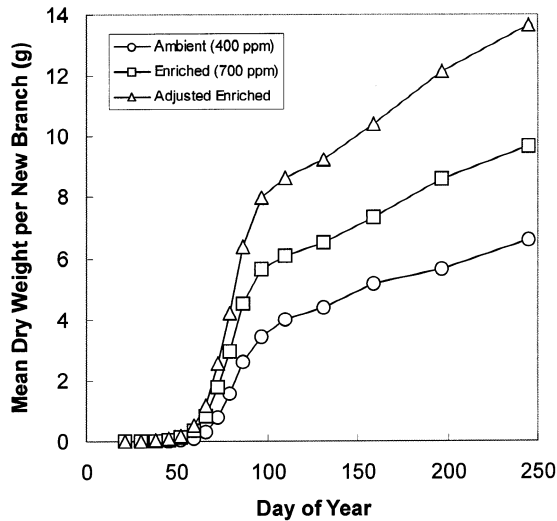


Fig. 1. New-branch dry weight plotted as a function of time for: (1) the mean of the seven largest new terminal branches and seven largest new non-terminal branches on all of the ambient-treatment trees (\circ), (2) the same for all of the CO_2 -enriched trees (\square), and (3) the same as (2), but multiplied by the factor 1.42 (see text) to express the result on a relative 'per tree' basis as opposed to the 'per branch' basis of the first two plots (\triangle). Standard errors of the means were too small to show on the graph (see text).

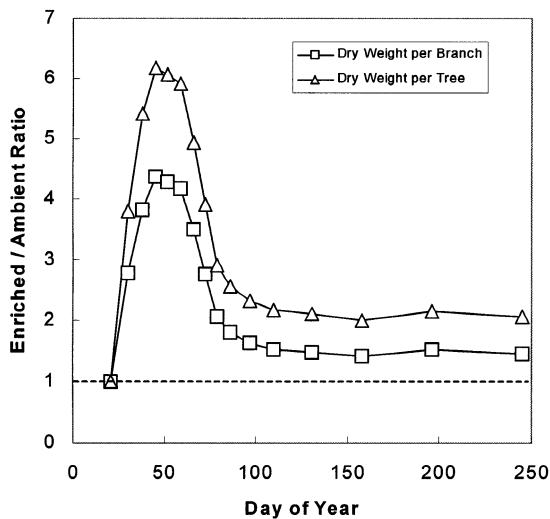


Fig. 2. The CO_2 -enriched/ambient-treatment ratios of new-branch mean biomass and new-branch mean biomass per tree plotted as functions of time. Standard errors were too small to show on the graph.

asurements are shown in Fig. 1. Standard errors of the means over the last half of the study averaged ± 0.27 g/branch in both CO_2 treatments, graphical representations of which (if plotted) would extend a mere 0.05 unit above and below each symbol of the figure and, hence, are not plotted.

The open-circle and open-square symbols of Fig. 1 represent the mean per-branch dry weights of the ambient and CO_2 -enriched trees, respectively. To compare these results on a per-tree basis, it was necessary to know how many more branches there were on the much larger CO_2 -enriched trees. Since it was impossible to count all of the branches on the trees, this CO_2 -induced branch-number-enhancement factor was calculated via a relationship between branch numbers and trunk cross-sectional area that had been developed for these specific trees by Idso and Kimball (1992). Based on the trees' trunk cross-sectional areas as measured at the start of data acquisition, it was thus determined that the CO_2 -enriched trees had 1.42 times more branches than the ambient treatment trees at that time. Consequently, the open-triangle plot of Fig. 1, which allows a per-tree comparison to be made, was simply obtained by multiplying the open-square plot of this figure by this factor, i.e. by 1.42.

Dividing the CO_2 -enriched per-branch and per-tree results of Fig. 1 by the corresponding ambient-treatment results produces the CO_2 -enriched/ambient-treatment ratios of new-branch biomass portrayed in Fig. 2. These results demonstrate that, from the first day of new-branch emergence, which occurred on DOY 21 in both CO_2 treatments, the CO_2 -enriched trees produced new-branch tissue at a much faster rate than the ambient-treatment trees. By DOY 45, in fact, the new branches of the CO_2 -enriched trees were, on average, 4.4 times more massive than the new branches of the trees growing in ambient air; and the total new-branch tissue produced on the CO_2 -enriched trees to that point in time was over six times greater than that produced on the ambient-treatment trees.

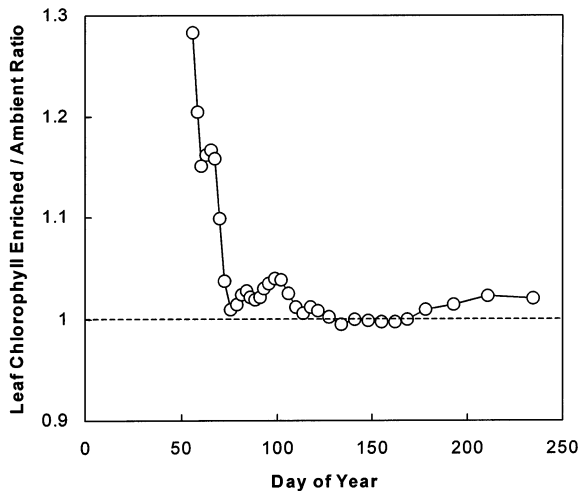


Fig. 3. The CO_2 -enriched/ambient-treatment ratio of the chlorophyll concentrations in the leaves of the new branches of the sour orange trees plotted as a function of time. Standard errors were too small to show on the graph.

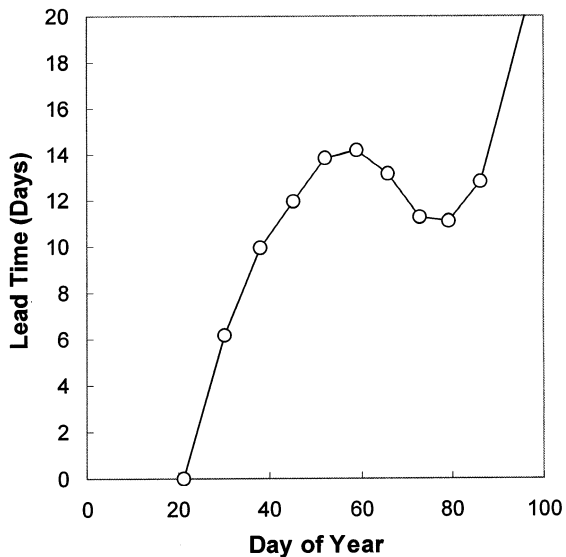


Fig. 4. The days by which the new-branch dry weight of the CO_2 -enriched trees leads the new-branch dry weight of the ambient-treatment trees over the first 2 months of the growing season.

These extremely high new-branch biomass ratios were maintained for a period of approximately 2 weeks, whereupon they began to fall at approximately the same rate they had risen ini-

tially. About 2.5 months into the growing season, however, this decline subsided; and the per-tree new-branch CO_2 -enriched/ambient-treatment biomass ratio thereafter leveled off at a constant value commensurate with the seasonal standing biomass and fruit production ratios maintained by the trees over the past few years (Idso and Kimball, 1997).

3.2. Leaf chlorophyll concentration

The new-leaf chlorophyll data also suggested an enhanced early development in the CO_2 -enriched foliage. As shown in Fig. 3, at the time when the leaf chlorophyll data first became available — which coincides with the time of peak CO_2 -enriched/ambient-treatment new-branch biomass ratio — the leaves on the new branches of the CO_2 -enriched trees contained approximately 25% more chlorophyll per unit area than the leaves on the trees growing in ambient air. From that point on, however, the CO_2 -enriched/ambient-treatment leaf chlorophyll ratio dropped rapidly, leveling off at a value that hovered just above unity for most of the rest of the growing season.

4. Discussion

4.1. Implications for the atmosphere's seasonal CO_2 cycle

What do our results imply about the behavior of the declining phase of the atmosphere's seasonal CO_2 cycle over the past few decades?

In viewing Fig. 1 it can be seen that, starting at each ambient-treatment data point, one can move horizontally to the left to determine how much earlier the CO_2 -enriched trees had produced the same amount of new-branch biomass as that of the ambient-treatment trees at the particular time represented by the ambient-treatment data point at which this procedure is started. The resulting parameter — days by which the new-branch dry weight of the CO_2 -enriched trees leads the new-branch dry weight of the ambient-treatment trees — can then be plotted as a function of time to produce the graph shown in Fig. 4.

By comparing the results of Fig. 4 with those of Fig. 1, it can be seen that at the time at which the new-branch biomass of the CO₂-enriched trees began its rapid ascent phase (at approximately DOY 60, as is evident in Fig. 1), it was approximately two weeks ahead of the new-branch biomass of the ambient-treatment trees, as is evident in Fig. 4. This observation suggests that, although new-branch growth began on the same day in both of the CO₂ treatments, the start of significant spring drawdown of atmospheric CO₂ — which is the parameter of primary importance to the phase behavior of the atmosphere's seasonal CO₂ cycle — began about 14 days earlier in response to the 300 ppm increase in the air's CO₂ concentration that is maintained between the open-top enclosures of the two CO₂ treatments.

For the approximate 43 ppm increase in atmospheric CO₂ experienced between 1960 and 1994, which is the period of time investigated by Keeling et al. (1996), we could therefore expect an advancement in the declining phase of the atmosphere's seasonal CO₂ oscillation of approximately 2 days — $(14 \text{ days}/300 \text{ ppm}) \times 43 \text{ ppm} = 2.01 \text{ days}$ — but only if all terrestrial vegetation responded to atmospheric CO₂ enrichment as sour orange trees do. Since this assumption could well prove incorrect, the calculation based on it may also be incorrect. We consequently emphasize that the assumption and calculation are made solely for the purpose of exploring the potential for earth's terrestrial vegetation to influence the phenomenon we are studying; they are not to be interpreted as being accurate representations of all of earth's vegetation or its combined effect on the air's CO₂ cycle.

Considered in this light, our hypothesized CO₂-induced hastening of 'biological spring' might possibly account for as much as 25–30% of the advancement in the declining phase of the atmosphere's seasonal CO₂ cycle that has been observed over the past few decades. As we want to emphasize, however, this conclusion can only be valid if the great bulk of earth's woody plants respond to atmospheric CO₂ enrichment as sour orange trees do, which has yet to be determined. Nevertheless, there are some indications that this assumption may not be unreasonable.

It is interesting to note, for example, that of 180 CO₂ enrichment experiments on woody plants described in the reviews of Poorter (1993), Ceulemans and Mousseau (1994) and Wullschlegel et al. (1995, 1997), the trees and shrubs of 176 of them were grown in various types of root-restricting containers, most often located in growth chambers or greenhouses. In an analysis of these 176 experiments, Idso (1999) found that 'it is possible to get almost any response conceivable' to atmospheric CO₂ enrichment. For the four groups of trees that were grown out-of-doors under natural conditions with their roots in the ground, however, a single common growth response was observed; and it was basically identical to that of the sour orange trees with which we worked.

4.2. *Prior discoveries related to our hypothesis*

A number of atmospheric CO₂ enrichment experiments reported in the literature shed additional light on the mechanisms that may be involved in the CO₂-induced hastening of the major spring growth surge we have observed in sour orange trees. Specifically, several studies indicate that elevated levels of atmospheric CO₂ tend to: (1) enhance plant growth at low temperatures, such as are experienced in early spring; and (2) stimulate growth profoundly at the very beginning of a plant's life cycle.

With respect to the first of these phenomena, more than a quarter of a century ago Rowley and Taylor (1972) observed that sorghum plants exposed to 1000 ppm CO₂ were better able to withstand a drop in air temperature from 25 to 10°C than were similar plants grown in air of 300 ppm CO₂. More importantly from our perspective, when air temperature was returned to 25°C (reminiscent of a winter-to-spring transition), the photosynthetic rates in the CO₂-enriched plants recovered more rapidly and to a greater degree than the photosynthetic rates of the plants growing in ambient air, which would be expected to produce a growth response much like that observed in the sour orange trees.

Sionit et al. (1981) observed a similar phenomenon in okra, where atmospheric CO₂ enrich-

ment made plants more vigorous and productive at low temperatures. In controlled environment chambers with day/night temperatures of 17/11, 20/14 and 23/17°C, for example, all newly-emerged seedlings exposed to ambient air died by 17, 35 and 44 days after emergence, respectively, while all plants in atmospheres of 450, 675 and 1000 ppm CO₂ grew to maturity and produced fruit.

In terms of specific physiological processes that may contribute to these responses, Potvin et al. (1984, 1985) found that a doubling of the air's CO₂ content ameliorated the low-temperature-induced reduction in metabolite translocation in a C₄ grass; while Potvin (1985) observed that atmospheric CO₂ enrichment reduced the amount of low-temperature-induced chlorosis in its leaves. More recently, Boese et al. (1997) demonstrated that elevated atmospheric CO₂ levels mitigated chilling-induced water stress and photosynthetic reductions in bean, cucumber and corn, problems that are often associated with reduced hydraulic conductivity of root membranes (McWilliam et al., 1982; Markhart, 1984) and/or stomatal dysfunction (Eamus et al., 1983; Pardossi et al., 1992).

In addition to helping plants cope with the challenges of low air temperatures, atmospheric CO₂ enrichment tends to give them a significant advantage early in their life cycles (Garbutt et al., 1990; Den Hertog et al., 1993; Farage et al., 1998). In a study of the impact of elevated CO₂ on the growth and development of *Arabidopsis thaliana* (L.), for example, Van Der Kooij and De Kok (1996) found that the CO₂-induced increase in shoot biomass after one week of plant exposure to elevated CO₂ was primarily due to an increase in plant relative growth rate that occurred on the first day of the study. Jitla et al. (1997) similarly found that a doubling of the air's CO₂ content significantly increased the height and diameter of the apical domes and the lengths of rice leaf primordia and tiller buds only 8 days after planting (DAP). Reminiscent of our branch length results, they observed more than a 3-fold increase in the length of the first growing tiller at 16 DAP; but by 26 DAP, this length advantage had declined to only 11%. Also, in a study of *Nicotiana*

tabacum (L.), Miller et al. (1997) noted that peak photosynthetic rates in plants grown in ambient air were generally not observed until leaf expansion was complete; but in CO₂-enriched plants it occurred when leaf expansion was only 50% complete.

With respect to trees, which have been estimated to account for about 70% of the terrestrial CO₂ exchange with the atmosphere (Waring and Schlesinger, 1985), Wang et al. (1996) observed that atmospheric CO₂ enrichment resulted in a significant increase in the cold-adaptability of photosynthesis in Scots pine (*Pinus sylvestris* L.), although Guak et al. (1997) did not observe such an effect in Douglas fir (*Pseudotsuga menziesii*). Likewise, Murthy et al. (1996) demonstrated that a CO₂ concentration doubling can enhance wintertime photosynthesis in loblolly pine trees even when low winter temperatures cause a greater-than-50% reduction in stomatal conductance. Murthy et al. (1997) showed that this phenomenon leads to an accelerated rate of increase in photosynthesis during the winter-to-early-spring transition period, which allows foliage recovering from low winter photosynthesis to rapidly enhance its carbon fixation potential to attain a higher rate of photosynthesis at the time of bud-break.

The latter two studies describe a physiological response to atmospheric CO₂ enrichment that could well produce the results we observed in sour orange trees. It is also possible that the spring rise in air temperature may stimulate the efflux of nutrients and/or carbohydrates from tree reserves, which would be expected to be more substantial in trees grown the previous season in an atmosphere of elevated CO₂ than in trees continuously exposed to the ambient atmosphere (Lovelock et al., 1999); and the enhanced availability of these and other stored substances may have provided the basis for the tremendous early enhancement of new-branch growth observed in the CO₂-enriched trees. On the other hand, the mechanism responsible for ultra-enhanced spring growth in CO₂-enriched sour orange trees may well be something totally different from anything suggested to date.

4.3. Tentative conclusions

Although we are unable to specify the precise mechanism or mechanisms by which atmospheric CO₂ enrichment induces a large but transient increase in early spring branch growth in sour orange trees, the results of our experiment demonstrate that it is possible — but only if other trees respond similarly — that with each passing year, the ongoing rise in the air's CO₂ content may be inducing terrestrial vegetation in temperate northern latitudes to remove CO₂ from the air at an increasingly faster rate at the beginning of the growing season, leading to a noticeable advancement in the declining phase of the atmosphere's seasonal CO₂ cycle. Based on the results of the experiment and the observations of Keeling et al. (1996), however, this CO₂-induced stimulation of spring plant growth cannot currently be demonstrated to be the major determinant of the increasingly earlier occurrence of biological/climatological spring over the past few decades. Nevertheless, this newly-discovered phenomenon is clearly substantial enough — at least in the sour orange trees we studied — to warrant further experimental scrutiny.

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