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Source: *BioScience*, Vol. 31, No. 1 (Jan., 1981), pp. 29-33

Published by: Oxford University Press on behalf of the American Institute of Biological Sciences

Stable URL: <http://www.jstor.org/stable/1308175>

Accessed: 06-01-2017 15:31 UTC

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Carbon Dioxide Concentration, Photosynthesis, and Dry Matter Production

Paul J. Kramer

Many scientists seem to assume that the increasing carbon dioxide concentration of the atmosphere will automatically bring about an increase in global photosynthesis and dry matter (biomass) production. For example, Wittwer (1979) stated that an increase in concentration of atmospheric CO₂ from 330 to 1000 ppm will greatly increase photosynthetic productivity. Some scientists also assert that the increase in carbon fixation by photosynthesis will be large enough to slow down the increase in atmospheric CO₂ produced by burning fossil fuels (Bacastow and Keeling 1973). The validity of these assertions is of great importance to policy makers who need to know the global effects of the increasing use of fossil fuels. However, they are based on the assumptions that the rate of photosynthesis is limited chiefly by CO₂ concentration and that rate of dry matter production is limited chiefly by a low potential rate of photosynthesis. But are these assumptions valid?

CO₂ CONCENTRATION AND RATE OF PHOTOSYNTHESIS

The illustrations presented in plant physiology textbooks suggest that large increases in the rate of photosynthesis occur with increasing CO₂ concentration, at least at high irradiances. However, these illustrations are based on short-term experiments, such as those of Hoover et al. (1933), Thomas and Hill (1949), and Gaastra (1959). Thomas and Hill (1949) reported a linear increase in rate of photosynthesis with increasing CO₂ concentration up to 3500 ppm for al-

falfa, sugarbeet, and tomato in full sun (Figure 1), with exposure to high CO₂ lasting, at most, a few hours. However, leaf injury occurred when they increased the CO₂ concentration to 10 times normal during the middle of the day for two weeks.

Brun and Cooper (1967) found that the rate of photosynthesis of soybean at 1670 ppm and a high irradiance was four times greater than at the normal concentration. However, these data were obtained from plants grown in a greenhouse at ambient CO₂ and brought into the laboratory, where photosynthesis was measured for short periods at high concentrations of CO₂. Green and Wright (1977) reported an average increase in photosynthesis of 84% when branches of conifers were en-

closed in cuvettes and subjected to concentrations of 450 to 500 ppm of CO₂, but again measurements were made for only short periods. The measurements of Moss et al. (1961) showed a 20% increase in photosynthesis of corn at 510 ppm of CO₂, but they were for only one hour so they did not indicate what the long-term behavior may be.

Measurements made over short periods of time do not necessarily provide reliable information concerning what occurs when plants are grown at high concentrations of CO₂ for several weeks. For example, Aoki and Yabuki (1977) grew cucumber plants for up to three weeks in chambers exposed to the sun and subjected to CO₂ concentrations ranging from 300 to 5400 ppm. The rate

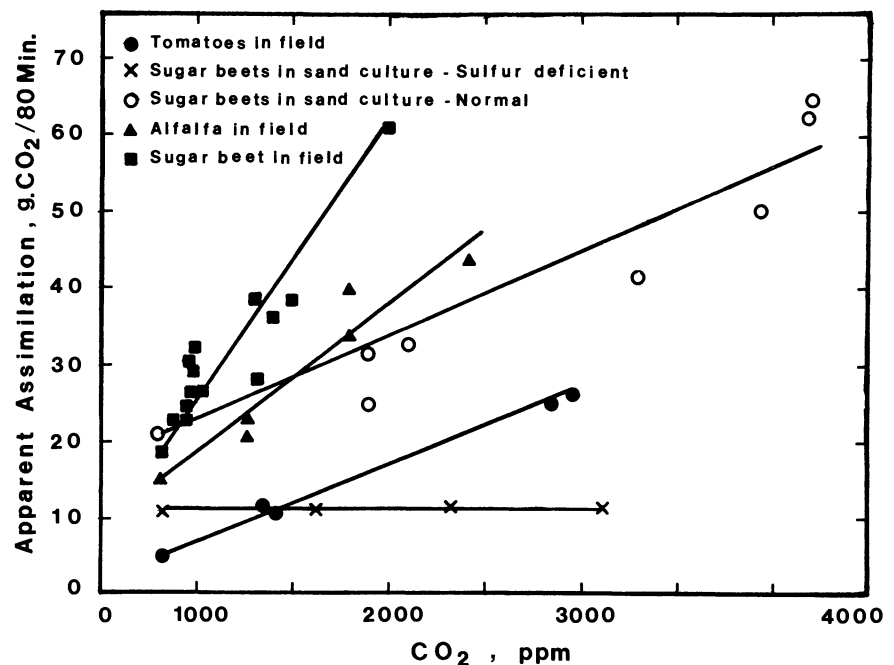


FIGURE 1. Rate of photosynthesis of alfalfa, sugarbeets, and tomatoes exposed to high concentrations of CO₂ for 80 minutes in full sun. Note that the sulfur-deficient sugarbeets did not respond to increased concentration of CO₂. (Adapted from Thomas and Hill 1949)

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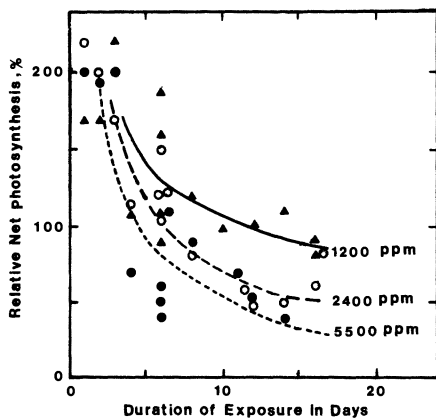


FIGURE 2. Decrease in rate of photosynthesis in full sun with duration of exposure to high concentrations of CO₂. Rates are expressed as percentages of rates at 300 ppm. (Adapted from Aoki and Yabuki 1977)

of photosynthesis was measured at frequent intervals at the concentrations in which the plants were growing. Although the initial rates of photosynthesis in the higher CO₂ concentrations were about twice those at 300 ppm, they decreased rapidly; in 5 days the rates in 5500 and 2400 ppm had fallen below the control rate, and in 15 days the rate at 1200 ppm was below the control rate (Figure 2). Raper and Peedin (1978) grew two cultivars of tobacco at 400 and 1000 ppm of CO₂ for 35 days after transplanting. At this time the leaf area of the high CO₂ plants was larger, but the rate of photosynthesis per unit of leaf area of the high CO₂ plants was only 70 to 80% of the rate of plants kept at 400 ppm. Hicklenton and Joliffe (1980) found that the rate of photosynthesis per unit of leaf area of plants of *Pharbitis nil*, after 14 days in 1.0% CO₂, was lower than the rate of plants kept at 0.03%, when measured at various concentrations from 0.03 to 2.5%. Clough and Peet¹ found that the rate of photosynthesis of high sink soybeans kept at 1000 ppm of CO₂ decreased steadily with time over a period of 20 days, while the rate of high sink plants kept at 350 ppm remained unchanged for 15 days before beginning to decrease. However, the absolute rate of photosynthesis was always higher at 1000 ppm than at 350 ppm.

Thomas et al. (1975) suggested that the decrease in rate of photosynthesis following prolonged exposure to high CO₂ concentration is caused by accumulation of starch in the leaves, a phenomenon

observed in other experiments. Madsen (1975), for example, reported that, at 1000 ppm or more of CO₂, so much starch accumulates in tomato leaves that the chloroplasts and leaves are deformed, and the leaves finally begin to wither. Mauney et al. (1979) also reported that accumulation of starch in cotton leaves reduced the rate of photosynthesis.

Long-term experiments with high concentrations of CO₂ give different results for various species. Mauney et al. (1978) grew four species of plants for 12 weeks or more in air-conditioned glasshouses in Arizona with 330 and 660 ppm of CO₂. The rate of photosynthesis per unit of leaf area, measured at frequent intervals on single leaves over a 12-week period on plants grown in 660 ppm of CO₂, showed increases of 41% for soybean and 15% for cotton above plants grown at 330 ppm, but increases of only 7% for sunflower and 2% for sorghum (Table 1). Moreover, the net assimilation rate (NAR, or dry weight increase in g dm⁻²day⁻¹) was increased by high CO₂ in the juvenile stage (10–30 days), but not in the mature stage.

Patterson and Flint (1980) did not measure CO₂ uptake directly, but they presented data for NAR for four species grown for 45 days at 350, 600, and 1000 ppm of CO₂. Increase in CO₂ concentration produced little change in NAR of corn and itchgrass (*Rottboellia exaltata*), which are C₄ plants, but the NAR of the two C₃ plants, soybean and velvetleaf (*Abutilon theophrasti*), was significantly increased at the two higher concentrations of CO₂ (Table 2). In all four species at all concentrations of CO₂, the NAR decreased as the plants grew older.

There are important differences among species in the response of photosynthesis to enhanced CO₂; plants with the C₃ carbon pathway usually show a greater increase in rate than plants with the C₄ pathway. Furthermore, over the long term, exposure to high concentrations of CO₂ often results in only a temporary in-

TABLE 1. Effects of 660 ppm of CO₂ on rate of photosynthesis (CER), leaf area (LA), and dry weight (DW) accumulation after 12 weeks. Values are percentage increases above values for plants grown in 330 ppm. (From Table 1 of Mauney et al. 1978)

Species	CER	LA	DW
Cotton	15	91	109
Soybean	41	180	382
Sunflower	7	142	60
Sorghum	1.5	15	18

crease in rate of photosynthesis. The high rate observed in the seedling stage disappears, and the rate often falls lower than the rate in plants kept at the ambient concentration. Thus, it is doubtful if a global doubling of the atmospheric CO₂ concentration will bring about a large sustained increase in rate of photosynthesis per unit of leaf surface. However, this does not necessarily mean that it could not result in some increase in dry matter production by plants of some species.

CO₂ CONCENTRATION, GROWTH, AND DRY MATTER PRODUCTION

In greenhouses and experimental conditions where other factors such as water and mineral nutrients are seldom limiting, an increase in CO₂ concentration usually is accompanied by at least a temporary increase in growth. Wittwer and Robb (1964) reported increases in fresh weight for lettuce, cucumbers, and tomatoes grown in greenhouses, and similar increases have been reported for other kinds of plants. Allen (1979) summarized considerable data on the effects of enhanced CO₂ concentration on plant growth; in most experiments, growth was increased, but in a few instances it was decreased. In most of the experiments only the economic yield was reported, with no data on total dry

TABLE 2. Effects of enhanced CO₂ on net assimilation rate (NAR), leaf area duration (LAD), and dry weight accumulation (DW) for the period 24 to 45 days after germination. Data are for values at 600 and 1000 ppm expressed as percentage increases above values for 350 ppm. (From Patterson and Flint 1980)

Species	NAR		LAD		DW	
	600	1000	600	1000	600	1000
Corn	4	-11	3	-1	-1	-13
Itchgrass	-1	-8	23	7	18	-19
Soybean	17	34	10	28	22	72
Velvetleaf	24	35	7	13	32	52

¹John M. Clough, Jr. and Mary Peet, Department of Botany, Duke University, personal communication, April 1980.

weight. Experiments with white pine (Funsch et al. 1970) and crabapple seedlings (Krizek et al. 1971) indicated that increased CO₂ concentration caused increase in height and amount of lateral branching, but no information was given concerning total dry weight. Tinus (1972) reported that exposure of ponderosa and table mountain pine seedlings to 1200 ppm of CO₂ for 12 months resulted in nearly a 50% increase in dry weight above controls grown at 325 ppm.

Several investigators have reported substantial increases in dry matter production by herbaceous plants grown for several weeks to several months in above ambient CO₂ concentrations. Cooper and Brun (1967) found an increase in seed weight of 40% in one variety of soybean and 57% in another when grown to maturity in 1350 ppm of CO₂. In another experiment, Hardman and Brun (1971) found that 1200 ppm of CO₂ increased the seed yield of soybeans about 40%. Unpublished data of Sionit² show a 40% increase in dry weight of wheat, including grain, grown at 1000 ppm. Mauney et al. (1978) reported that plants of four species, grown to maturity in controlled environment greenhouses in 660 ppm of CO₂, showed widely different reactions to increased concentration of CO₂. At maturity, soybean showed an increase in dry weight of 382%, cotton 110%, and sunflower only 60%, but there was no statistically significant increase in dry weight of sorghum above plants grown in 330 ppm.

The absence of larger increases in sorghum and sunflower was attributed to the fact that they are determinate plants, whereas soybean and cotton are indeterminate, branch more, and grow longer. However, the lack of response of sorghum may also be related to the fact that it is a C₄ plant. According to Patterson and Flint (1980), the dry weight of soybean, velvetleaf, maize, and itchgrass was increased in the seedling stage by high CO₂ concentration, but the increase was less in 1000 ppm than in 600 ppm. However, the situation changed as the plants grew older because, after 45 days, the dry weight of the C₄ corn and itchgrass was less at 1000 ppm than at 350 ppm. The dry weight of the C₃ soybeans and velvetleaf increased with higher CO₂ concentration, being 72% and 54% greater respectively at 1000 than at 350 ppm (Table 2).

Thomas et al. (1975) reported that the

relative growth rate of tobacco seedlings was increased in 1000 ppm of CO₂, but in the post-transplant stage it decreased below the rate at 400 ppm. Mauney et al. (1978) also reported a higher relative growth rate in the seedling stage of soybean, cotton, sorghum, and sunflower at 630 ppm than at 330 ppm, but not later. However, the high CO₂ cotton and soybeans maintained their larger size beyond the juvenile stage, as did the tobacco studied by Thomas et al. (1975). This probably occurred because the high CO₂ seedlings had a larger leaf area at the beginning of the steady-state stage of growth (see Raper and Peedin 1978).

Thus, certain tentative generalizations can be made concerning the growth response of plants to enhanced concentration of CO₂:

- There are large differences in amount of growth among plants of various species when subjected to high concentrations of CO₂.

- The response is greater in indeterminate plants such as cotton and soybean than in determinate plants such as corn, sorghum, sunflower, Alaska pea, and tobacco.

- It is greater in C₃ plants such as soybean, sunflower, and velvetleaf than in C₄ plants such as corn, itchgrass, and sorghum.

- The largest growth response appears to occur in seedlings, and it decreases or ceases as plants grow older.

These generalizations are tentative and may require revision when data from more kinds of plants become available. However, the increase in dry weight often observed when plants are grown in high concentrations of CO₂ is not always caused by a long-term increase in rate of photosynthesis per unit of leaf area.

SPECIAL EFFECTS OF HIGH CO₂ CONCENTRATION

Exposure of plants to high concentrations of CO₂ produces effects on growth in addition to those caused directly by in-

crease in rate of photosynthesis. Among the morphological effects are increase in branching of both woody and herbaceous plants, greater stem elongation, and increase in root/shoot ratio. Exposure of roots of potato plants to high CO₂ greatly increased tuber formation (Arteca et al. 1979). In some experiments there was a significant increase in leaf area in the seedling stage, which increased subsequent growth. The data summarized in Tables 1 and 3 show large increases in leaf area of plants grown in high concentrations of CO₂. Moreover, exposure of young tomato plants to 1000 ppm of CO₂ caused a 24% increase in leaf area of mature plants and a 20% increase in thickness (Ho 1977). These modifications in pattern of growth indicate significant modification in the allocation or partitioning of photosynthate to various plant organs. Study of the mechanism by which this is brought about might contribute information concerning the control of phloem transport in plants.

The time of flowering is affected differently by high CO₂ in various kinds of plants. Floral initiation was greatly delayed at 1000 ppm of CO₂ in four cultivars of sorghum, but only slightly in corn, sunflowers, and cotton (Hesketh and Hellmers 1973), but flower bud initiation and flowering were hastened in Alaska pea (Paez et al. 1980). According to Hicklenton and Joliffe (1980), high concentrations of CO₂ cause *Pharbitis* to flower under noninductive, long-day conditions, but delay flowering under short days.

Increasing CO₂ concentration might increase the water use efficiency of plants, because partial closure of stomata reduces transpiration more than photosynthesis. According to Goudrian and van Laar (1978), the stomatal conductivity of corn and bean is reduced by an increasing CO₂ concentration, but not that of sunflower. They state that corn uses water much more efficiently than sunflower. Gifford (1979) reported that increasing the CO₂ concentration 250 ppm above the ambient concentration in-

TABLE 3. Effect of nitrogen supply and CO₂ concentration on rate of photosynthesis (CER), leaf area (LA), and rate (CER) per plant after 35 days in enhanced CO₂ at 730 μE m⁻²s⁻¹ in the PAR. Values are percentages of values at 400 ppm and high N. (From Raper and Peedin 1978)

CO ₂ conc.	N supply	CER	LA	CER/plant
400 ppm	High	100	100	100
400 ppm	Low	91	70	64
1000 ppm	High	80	132	106
1000 ppm	Low	65	96	63

²Nasser Sionit, Department of Botany, Duke University, personal communication, April 1980.

creased the yield of water-stressed wheat above that of stressed plants grown at the normal concentration of CO₂, resulting in increased water use efficiency. He claimed that enhancing the CO₂ concentration might be increasing wheat yields in Australia.

One of the most striking effects of increased CO₂ concentration is on nitrogen fixation by soybeans. According to Hardy and Havelka (1975), soybeans normally fix only about 25% of the nitrogen found in mature plants. However, when supplied with three times the ambient concentration in full sun, they fix about five times as much nitrogen and are heavier and produce a much larger yield of beans. Thus, nitrogen fixation may normally be limited by the carbohydrate supply. These results are in accord with data presented earlier indicating that soybeans respond better to CO₂ enhancement than almost any other crop. Unfortunately, enrichment of CO₂ in the field probably is not profitable (Allen 1979, p. 511).

PHOTOSYNTHESIS AND BIOMASS PRODUCTION

Growth and increase in dry weight (biomass) are not necessarily closely correlated with the rate of photosynthesis measured over short periods of time. Mauney et al. (1978) (Table 1) revealed that doubling the CO₂ concentration for 12 weeks increased the rate of photosynthesis of soybean 41%, leaf area 180%, and dry weight 382%, whereas in sunflower the increases were 7%, 142%, and 60%. In the experiments of Raper and Peedin (1978), after 35 days in 1000 ppm of CO₂, the rate of photosynthesis per unit of leaf area of the high nitrogen tobacco plants was only 80% of the rate of plants in 400 ppm, but the leaf area of the high CO₂ plants was 30% larger, and the increase in photosynthetic surface compensated for the decrease in rate per unit of surface (Table 3). The data of Patterson and Flint (summarized in Table 2), presented differently and for a shorter period of time, show considerable variation among species in the relationship between rate of photosynthesis, leaf area, and dry weight accumulation. More long-term research is needed to establish how much of the response to enhanced CO₂ concentration is caused by increase in leaf area, how much by increase in rate of photosynthesis, and how much by other factors.

There seems to be no clear correlation between rate of photosynthesis per unit

of leaf area and dry matter production. As a result, most attempts to select high-yielding crop plants on the basis of the rate of photosynthesis have been unsuccessful. Evans (1975, p. 334) stated that "there is little evidence of any positive relationship between them nor any instance where selection for a greater rate of photosynthesis has led to an increase in yield." Loomis et al., Moss, and Wallace et al. (in Burris and Black 1975) all stress the difficulties inherent in attempting to relate yield to photosynthesis. The same problems exist with respect to predicting growth and dry matter production of forest trees from rates of photosynthesis (Kramer and Kozlowski 1979, pp. 219-221). Plants ranging from apples and maize to soybeans and wheat have more capacity to carry on photosynthesis than is generally used partly because rate of photosynthesis is controlled by "sink strength" in a complex manner (Peet and Kramer 1980) and partly because the rate is often limited by environmental factors.

Growth and yield depend on many factors in addition to rate of photosynthesis, such as dark respiration, nitrogen metabolism, translocation, and the partitioning of photosynthate to the various organs of plants. Plant growth also is affected by environmental factors such as water, mineral nutrition, temperature, and light, and these affect growth through other processes in addition to photosynthesis. For example, water stress causes closure of stomata, which reduces the rate of photosynthesis, but it also reduces cell enlargement, which reduces both the photosynthetic surface and the demand for photosynthate. Nitrogen deficiency limits the formation of new tissue and, thus, the demand for photosynthate, and the experiments of Mauney et al. (1978) and Raper and Peedin (1978) (Table 3) indicate the need for adequate mineral nutrition to obtain large increases in yield from CO₂ enhancement. Further, sulfur deficiency prevented photosynthesis of sugarbeet from responding to an increase in CO₂ concentration (Figure 1).

In nature, the rate of photosynthesis and biomass production probably is limited more often by water and nitrogen deficiency than by the low CO₂ concentration of the air. Increasing the CO₂ concentration will have little effect if the stomata already are closed, the cell enlargement is inhibited by water stress, or the use of photosynthate is limited by lack of nitrogen. Where good farming practices are used, yield is controlled largely by "weather," chiefly rainfall

and temperature. This is equally true of forests, where 80% of the year-to-year fluctuation in diameter growth can be explained by variations in rainfall (Zahner 1968).

Enhancement of CO₂ concentration can be regarded as analogous to fertilization, which often operates largely by increasing the leaf area. For example, Brix and Ebell (1969) reported that the only factor associated with increased diameter growth of a 20-year-old Douglas fir stand fertilized with nitrogen was increased leaf area. In another experiment on Douglas fir, Brix (1971) reported that, although rates of photosynthesis and dark respiration increased after nitrogen fertilization, most of the increase in diameter growth was caused by the increase in leaf area. Fertilization was most effective in open stands where the leaf area was below the optimum and water supply was not limiting. Tamm (1979) also reported that the close correlation between leaf area and stem growth observed in young conifer stands decreased as the stands closed and shading effects increased in importance. In general, increase in CO₂ concentration will probably have least effect on growth of plants in closed stands where light, water, and mineral nutrition, separately or collectively, already are limiting the rate of photosynthesis.

In view of these observations, even though increasing the concentration of CO₂ to 600 ppm increases the rate of photosynthesis of many plants in phytotron and greenhouse experiments, there is no assurance that similar increases will occur on a global scale where water and nitrogen already often limit growth. Thus, it is uncertain whether there will be a sufficient increase in carbon fixation on a global scale to reduce significantly the rate of increase in global CO₂ concentration caused by combustion of fossil fuels. On the other hand, a doubling of CO₂ concentration might cause significant differences in rates of growth of various kinds of plants, which may affect their relative success in competition. The experiments of Mauney et al. (1978) and Patterson and Flint (1980) revealed important differences in the response of C₃ versus C₄ plants and determinate versus indeterminate plants to high CO₂. These differences may affect crop-weed competition and, in the long term, might produce changes in species composition of some ecosystems. Extensive experiments are needed to learn how long-term enhancement of CO₂ affects the relative growth rates of competing species.

Overall, there seems to be a tendency to overestimate the effects on vegetation of doubling the CO₂ concentration of the atmosphere. This is so because present knowledge of the effects of CO₂ concentration is based chiefly on short-term laboratory experiments and measurements of plant growth made in greenhouses, where water and mineral nutrition are seldom limiting. We cannot make reliable predictions concerning the global effects of increasing CO₂ concentration until we have information based on long-term measurements of plant growth from experiments in which high CO₂ concentration is combined with water and nitrogen stress on a wide range of species.

Information concerning the reaction of forest trees to high CO₂ concentration is particularly important because forests cover about one-third of the land area and carry on about two-thirds of the global photosynthesis. To obtain the information needed to assess the role of forests in stabilizing the global CO₂ concentration would require a large research program with approximately the scope of the U.S. effort in the International Biological Programme. Meantime, much useful information can be obtained from small-scale experiments in controlled environments.

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