THE INCREASING CO_2 CONCENTRATION IN THE ATMOSPHERE AND ITS IMPLICATION ON AGRICULTURAL PRODUCTIVITY

I. Effects on Photosynthesis, Transpiration and Water Use Efficiency[1]

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Abstract. The increasing concentration of CO_2 in the atmosphere should result in a general increase in the net primary productivity of most cultivated species and forest species, assuming no counterproductive climatic changes occur. The photosynthetic rate of C_3 plants is most responsive to increasing concentration of CO_2 in the ambient air. C_4 plants demonstrate a stomatal closure that causes reduced transpiration. In the case of both types of plants, the water use efficiency (photosynthesis/transpiration) is likely to be improved.

It has been suggested that photosynthetic production may be limited today more by shortages of water and nutrients than by shortages of carbon dioxide. The author speculates that the inadvertant 'CO_2-fertilization' now occurring could, in itself, cause a moderate release from these constraints.

Physiological responses to an increased atmospheric CO_2 concentration are easily demonstrated in controlled environment studies. Because of the difficulty in maintaining artifically enriched air near the crop against the forces of turbulent transfer, studies in the open field have been inconclusive. The observation of decreased photosynthetic rate in a perennial crop during that part of the growing season when CO_2 concentration is naturally low suggests a technique by which it may be possible to infer what will happen in the real world of agricultural fields if a CO_2-rich environment, such as is predicted in the coming decades, materializes. Inferences from the very limited set of data available support the view that net photosynthetic production will be increased.

1. Introduction

It is now well known that the concentration of carbon dioxide in the atmosphere has increased significantly since preindustrial times (Machta, 1972) and is continuing to increase at a rate greater than 1 ppm yr^{-1}. This fact is cause for concern since CO_2 is an effective absorber of longwave radiation emitted by the atmosphere and the earth's surfaces. Because of this property of CO_2, it is expected that the mean temperature near the earth's surface will increase and this should lead, ultimately, to significant climatic changes (NAS, 1979). Since the earth's temperature varies from year to year and since natural cooling and warming trends occur over varying periods of years, it is not yet possible to detect, with certainty, any heating effect that may have been caused by the increase in CO_2 concentration ($[CO_2]$) to date. If $[CO_2]$ continues to increase at current or accelerated rates, the warning signal may emerge from the noise of natural variability by the end of this century.

In this paper, I speculate on whether the increasing atmospheric concentration of

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CO_2 will affect world agriculture through a direct influence on photosynthesis (*P*), on evapotranspiration (*ET*) or on water use efficiency (the ratio *P*/*ET*). In a companion paper I will deal with the question of whether an increase in the global atmospheric concentration of CO_2 will affect agricultural production because of the kinds of climatic change that are conceived possible or likely by climate modellers.

Here we will deal, in order, with the physiological evidence of direct $[CO_2]$ effects on photosynthesis and transpiration,[3] and the factors other than $[CO_2]$ that might limit crop production despite increased $[CO_2]$. The results of certain field observations on crop response to natural fluctuations in ambient $[CO_2]$ will be reviewed for the inferential evidence they may provide on future crop responses to a CO_2 enriched atmosphere.

2. Physiological Evidence

2.1. Background

The green plants upon which we depend for food, feed and fiber, and for ground cover to protect the soil, can be classified into three major groups on the basis of their photosynthetic mechanisms. C_4 plants utilize the C_4-dicarboxylic acid chemical pathway for photosynthesis. C_4 species are generally the tropical grasses; e.g., corn, sorghum, millet, sugar cane. C_3 plants utilize a photosynthetic pathway involving a three carbon intermediate product. The C_3 group includes virtually all other species: small grains – e.g., wheat, barley; leguminous species – e.g., alfalfa, soybean and many others. A list of major C_3 and C_4 species is given in Table I. A third, if relatively minor, group of plants accomplish photosynthesis through crassulean acid metabolism (CAM). These plants

TABLE I. Some Common C_3 and C_4 plants.

C_3	C_4
rice (*Oryza sativa* L.)	purple lovegrass (*eragrostis spectabilis* (Pursh) Steud.)
alta fescue (*Festuca arundinacea* Schreb.)	Rhodes grass (*Chloris gayana* Kunth)
bluegrass (*Poa pratensis* L.)	smooth cordgrass (*Spartina alterniflora* Loisel)
oats (*Avena sativa* L.)	pearl millet (*Pennisetum glaucum* (L.) R. Br.)
crested wheatgrass (*Agropyron desertorum* (Fisch.) Schult.)	sugar-cane (*Saccharum officinarum* L.)
barley (*Hordeum vulgare* L.)	sorghum (*Sorghum bicolor* (L.) Moench)
rye (*Secale cereale* L.)	maize (*Zea mays* L.)
wheat (*Triticum aestivum* L.)	red orache (*Atriplex rosea* L.)
sugarbeet (*Beta vulgaris* L.)	
spearscale (*Atriplex patula* L.)	
bean (*Phaseolus vulgaris* L.)	
soybean (*Glycine max* (L.) Merr.)	
alfalfa (*Medicago sativa* L.)	
cotton (*Gossypium hirsutum* L.)	
potato (*Solanum tuberosum* L.)	
tomato (*Lycopersicon esculentum* Mill.)	
sunflower (*Helianthus annuus* L.)	

maintain stomates open at night during which time they fix CO_2 in the form of organic acids. During daytime, the stored CO_2 is reduced photosynthetically. Pineapple is one of the few cultivated CAM plants.

The potential effect of increased global CO_2 will be different for C_3 and C_4 species. All plants consume, by respiration, some portion of the photosynthate they produce. Respiration proceeds in both C_3 and C_4 species by an essentially identical biochemical pathway throughout the day and night. However, the C_3 plants have an additional respiratory mechanism that is controlled by light and the availability of oxygen. The respiratory mechanism common to C_3 and C_4 plants is called *dark respiration* since it occurs regardless of light. The additional respiratory mechanism of C_3 plants is called *photorespiration* and occurs only during daytime.

Charateristics of C_3 and C_4 plants are given in Table II (from Goudriaan and Ajtay, 1979). At the light compensation point (that level of irradiance at which photosynthesis and respiration are in balance) the internal CO_2 concentration is considerably greater in the leaves of C_3 plants – due to the rapid release of CO_2 in photorespiration. The CO_2 compensation point (leaf internal CO_2 concentration at high irradiance) is considerably greater in the C_3 than in C_4 plants.

TABLE II. Some characteristics of C_3 and C_4 plants.

	C_3	C_4
CO_2 assimilation rate in high light	2-4 g CO_2 m^2 h^{-1}	4-7 g CO_2 m^2 h^{-1}
Temperature optimum	20-25 C	30-35 C
CO_2 compensation point in high light	50 ppm	10 ppm
Photorespiration	present	not present

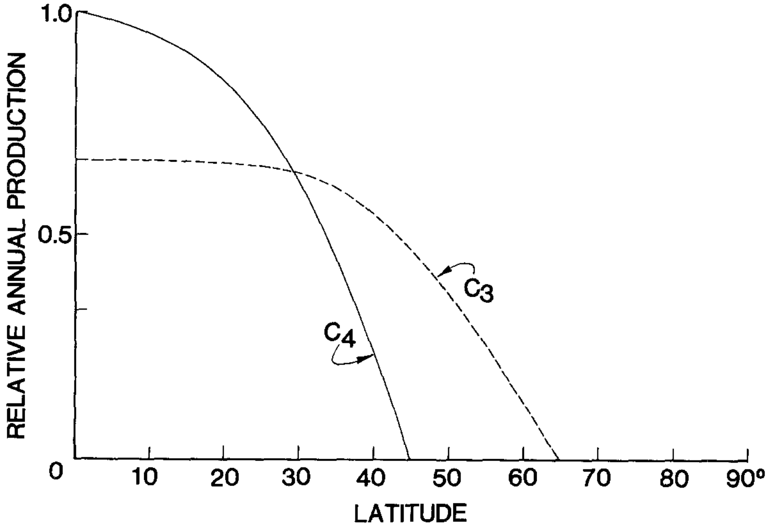

Fig. 1. Potential production of C_3 and C_4 crop species (after Loomis and Gerakis, 1975).

C_4 plants have a greater photosynthetic potential under their optimum conditions which involve strong illumination and high temperatures. C_3 plants, given their optima of lower irradiance and temperature, produce photosynthate at about half the rate of C_4 plants. However, as Figure 1 (from Loomis and Gerakis, 1975) shows, in generality, the relative annual production of C_4 plants falls off very sharply in the midlatitudes. Beyond latitude 45°, the C_4 plants are generally ill adapted. It is true, of course, that certain C_3 plants, e.g., cotton are best adapted to the lower latitudes.

In order to better understand the mechanisms of photosynthesis and evapotranspiration, as these may be affected by increasing CO_2 concentration in the atmosphere, we may use Ohm's law as a starting point:

$$I = \frac{V}{R} \tag{1}$$

where I is electrical current flow, V is voltage and R is resistance. Transpiration is the flux of water vaporized within the leaf into the atmosphere. The transpiration process (T) may be treated as an analog of the flow of electric current:

$$T = (C)\,\frac{e_1 - e_a}{r_a + r_s} \tag{2}$$

where e_a is vapor pressure of the air in contact with the leaf and e_1 is the vapor pressure within the leaf's substomatal cavities and (C) represents a group of physical constants. Thus, the driving force or voltage for transpiration is the difference or gradient in vapor pressure from leaf to air. Vapor leaving the leaf must pass through the stomates. Stomates exert a resistance (r_s) to the passage of vapor which depends on their degree of openness. The air itself exerts a resistance (r_a) to further passage of the vapor molecules. If the air is still, vapor can move only by molecular diffusion – a very slow process compared to the turbulent diffusion that occurs when the air is in motion; with increasing windspeed the aerial resistance is reduced.

Similarly, photosynthesis (P) can be approximated by the flux of carbon dioxide (F_c) which is given as a functional analogue of Ohm's Law:

$$P \cong F_c = (C')\,\frac{[CO_2]_a - [CO_2]_g}{r_a' + r_s' + r_m'} \tag{3}$$

Here the driving force is the CO_2 concentration gradient between air, $[CO_2]_a$, and the leaf internal CO_2 concentration $[CO_2]_g$, (g for grana – the subcellular organelle where the photosynthetic reaction takes place). Since $[CO_2]$ is greater in the atmosphere than it is within the leaf during daylight, CO_2 diffuses from the air into the plant leaf. This diffusion is resisted by air itself (r_a') and a further resistance is exerted by the stomata (r_s'). The primes are used to indicate that the constants and resistances to diffusion of H_2O and CO_2 are numerically different because of physical differences between these molecules.

In the case of photosynthesis, an additional resistance affects the pathway since the

CO_2 molecule must diffuse to the grana against certain physical and chemical barriers. This combined resistance is termed the mesophyll resistance (r_m'). The resistances to water vapor and CO_2 flux under normal conditions are about 0.1-0.3; 0.2-5.0; 4-10 s cm^{-1} for r_a, r_s, and r_m, respectively.

2.2 *Effects on Photosynthesis*

Let us now address the direct effects on photosynthesis of an increasing atmospheric CO_2 concentration. In its simplest manifestation, augmented $[CO_2]_a$ increases the gradient or 'driving force' in the numerator of Equation (3). This will be true regardless of species. However, the effect is of greater relative significance in C_3 species because $[CO_2]_g$ is greater in plants having photorespiration (Table II) and the gradient is normally smaller than in C_4 species. Other more subtle influences of $[CO_2]$ on the physiological mechanisms of the plant and on its net photosynthesis are known but these do not counter the effects described above.

Figure 2 (from Brown and Rosenberg, 1971) summarizes experimental evidence from

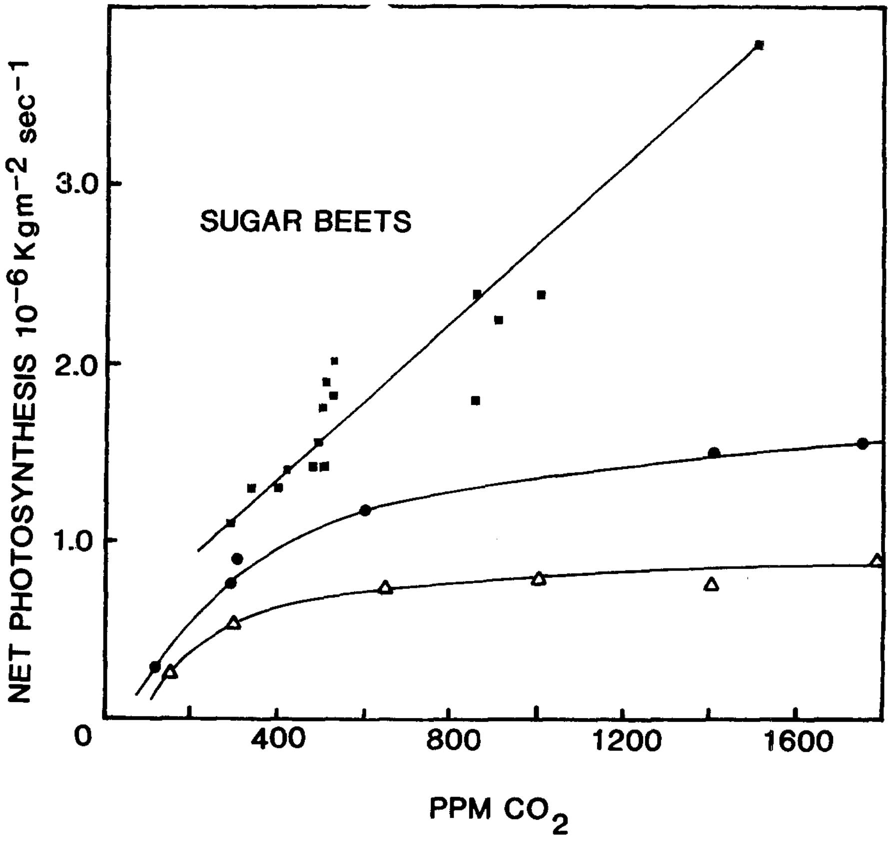

Fig. 2. Sugar beet net photosynthesis as a function of CO_2 concentration in the ambient air (see Brown and Rosenberg, 1971 for details on sources of the data).

a number of sources showing that an increase in ambient [CO_2] leads to a direct increase in photosynthetic rate of sugar beet. The increase is especially marked in the range of 200-600 ppm CO_2. In the case of C_3 species, the increase in ambient [CO_2] may also act to suppress photorespiration since that process proceeds at a rate which depends upon competition between oxygen molecules and CO_2 molecules for enzymatic sites (Cholett, 1977 and Ehleringer and Bjorkman, 1977).

The [CO_2] increase in the ambient air has a lesser effect on the photosynthetic rate of C_4 than of C_3 plants. Moss *et al* (1961), for example, have shown small increases in maize photosynthesis with increasing [CO_2] in the range 200 to 400 ppm.

Other direct effects of ambient CO_2 concentration on photosynthesis will occur through its impact on r_s'. [CO_2] affects stomatal closure in both C_3 and C_4 species. However, r_a', a function of windspeed is not directly affected by ambient [CO_2] and r_m', a function of plant morphology and physiology, may be slightly responsive. Since r_s' is relatively small compared to the sum of r_a' and r_m', its influence on photosynthesis will also be relatively small, unless a severe stomatal closure is induced. It is important to emphasize here that the influence of [CO_2] on stomatal mechanics is not yet well understood and a considerable amount of physiological research on the subject is now underway.

2.3. *Effects on Transpiration*

The influence of [CO_2] on stomatal closure is more consequential in the process of transpiration than it is in photosynthesis. Reference to Equation (2) will show that, except in almost windless conditions, r_s is the primary determinant of the resistance to

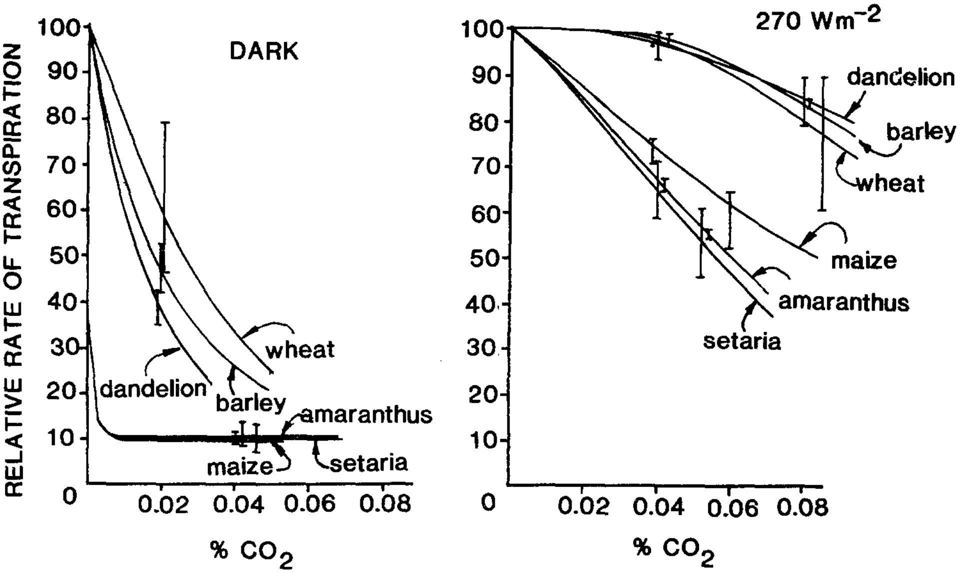

Fig. 3. Effect of CO_2 concentration on transpiration of C_3 and C_4 species in light and darkness (after Akita and Moss, 1972).

vapor transport from plant to atmosphere. Any significant increase in r_s should then lead to a reduction in transpiration rate.

Experimental evidence supports this hypothesis. Figure 3 (from Akita and Moss, 1972) illustrates the relative decrease in transpiration rate for three C_3 and three C_4 species that occurs with increasing $[CO_2]$. The transpiration of these plants was observed in a leaf chamber in the dark and under strong illumination. Clearly, stomates of the C_4 species respond more sharply and this response holds true in the range of CO_2 concentrations currently found in the field air and anticipated in the foreseeable future. In Figure 3 it is seen that, in the light, the response of the C_3 species to realistic ambient $[CO_2]$ is very slight. The response is considerably greater in the dark. Since most transpiration occurs during the daytime, however, the response in darkness is probably of minor importance.

2.4. *Effects on Water Use Efficiency*

Data summarized above indicate that increasing $[CO_2]$ in the ambient air will lead to an increase in photosynthetic activity, especially in C_3 species, and to a decrease in transpiration, especially in C_4 species. Thus, the water use efficiency (P/T) – the photosynthetic production per unit of water consumed by the plant through transpiration – should, if the physiological responses observed under controlled conditions hold true in the field, be increased in both C_3 and C_4 species, although for different reasons in each case. This predicted effect on water use efficiency may be of particular importance in the semiarid and arid regions where limitations in natural rainfall or irrigation limit current agricultural productivity.

3. Some Questions Concerning Applicability of the Physiology Evidence

It is important to realize that the analyses given above, while optimistic concerning the overall impact of a $[CO_2]$ increase in the ambient air, are incomplete. It is possible, for example, that elevated CO_2 concentration could affect the timing of phenological events – e.g., time of flowering, maturation – in certain species or affect certain developmental processes – e.g., root ramification, numbers of florets, etc. Such phenological or morphological changes might increase the vulnerability of crops to certain hazards such as late spring frost or prolonged drought. No convincing evidence of such effects, at concentrations considered possible within the next century or so, are known to this writer. At very extreme concentrations, however, there is evidence of deleterious effects. Aoki and Yabuki (1977) found, for example, that dry matter production and photosynthetic rate of cucumber increased with exposure to CO_2 concentrations up to 2400 ppm. Exposure to 5000 ppm of CO_2 decreased dry weight gains below those achieved at lower concentrations.

Others have argued, e.g. Botkin *et al.* (1973), that a changing CO_2 regime could lead to changes in species composition and succession in forests or other unmanaged ecological associations. Such effects, however, would not be consequential in most agricultural ecosystems.

One of the strongest arguments against the hypothesis that an atmospheric CO_2 increase will lead to improved photosynthesis and/or water use efficiency has been proposed by Lemon (1976) and is supported by Goudriaan and Ajtay (1979). They argue that net primary productivity (photosynthesis less respiratory loss) is now limited by shortages in water supply and nutrient availability – not by the CO_2 concentration of the atmosphere. The shortage of water and nutrients, they argue, and such climatic limitations as insufficient length of the growing season explain the fact that the world's vegetation does not even now achieve its potential net primary productivity. On a global scale it does, indeed, seem unlikely that radical increases in photosynthesis rate and net primary productivity will occur quickly as the CO_2 concentration continues to increase.

Such arguments, however, as those of Lemon (1976) assume a static ecology. Let us speculate on what might happen in, for example, a northern (Boreal) forest under a regime of CO_2 enriched air if nutrients are not strongly limiting. Assuming no beneficial climatic change induced by the increasing $[CO_2]$ but depending on the evidence of physiological experiments alone, it seems likely that CO_2 fertilization would cause an incremental increase in the rate of photosynthesis in an association of C_3 species. This would, in turn, lead to a greater dry-matter production – perhaps to larger trees and greater standing biomass. Larger trees should produce denser and, perhaps, deeper root systems. In turn these root systems should senesce to yield greater accumulations of soil organic matter. A heavier leaf litter might also occur.

Soil forming processes, according to Jenny (1941) depend upon a number of factors: parent materials, topography, climate, biology (vegetation, soil flora and fauna) and time. Thus, it is not inconceivable that, even if climate does not change, CO_2 'fertilization' may initiate or stimulate an acceleration of soil formation through enhanced biological activity. A more rapid release of many essential nutrients might follow. Further, a reduction in transpiration rate may have the effect of reducing the severity of moisture shortages, at least occasionally. This, too, might favor biological activity in the soil. Soil forming processes are perpetual and occur in soils used for agriculture as well as in natural ecosystems.

It should be clear to the reader that the arguments posed in this section – both optimistic and pessimistic – are, at best, speculations.

4. Natural Cycles and Field Responses to $[CO_2]$ Fluctuations

4.1. Annual Cycles

Information on the annual range of $[CO_2]$ from the ground surface to about 16 km at 30° N latitude is provided by Bolin (1970) in Figure 4. In the northern hemisphere summer, considerable amounts of CO_2 are extracted from the atmosphere, most likely by terrestrial vegetation. The oceans may also be involved in this capture – with some involvement of photosynthetically active marine vegetation. During winter a net release of CO_2 occurs because of the respiration by living vegetation, consumption of the products of photosynthesis and oxidation of soil carbon and fossil fuels.

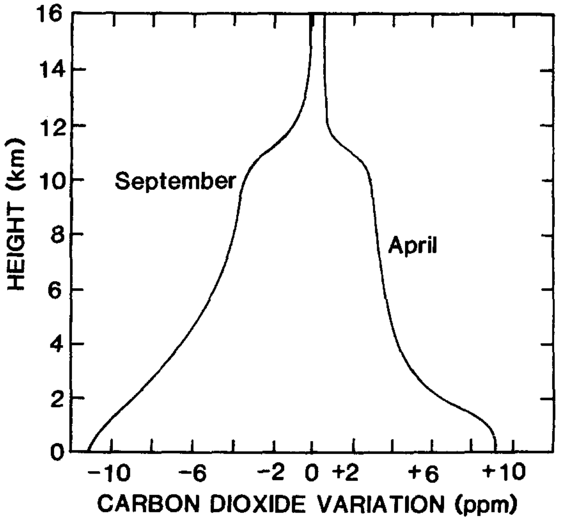

Fig. 4. Seasonal variations in carbon dioxide concentration north of latitude 30° (after Bolin, 1970).

This annual concentration cycle is demonstrated in a different way by Verma and Rosenberg (1976). At a site typical of agricultural land use in the eastern Great Plains of North America (Mead, Nebraska, lat. 41°09′ N; long. 96°30′ W, elev. 354 m above m.s.l.) the mean daily CO_2 concentration at 16 m above ground level varied from about 340 ppm in winter to a minimum of about 328 ppm in early August of 1972 (Figure 5). The

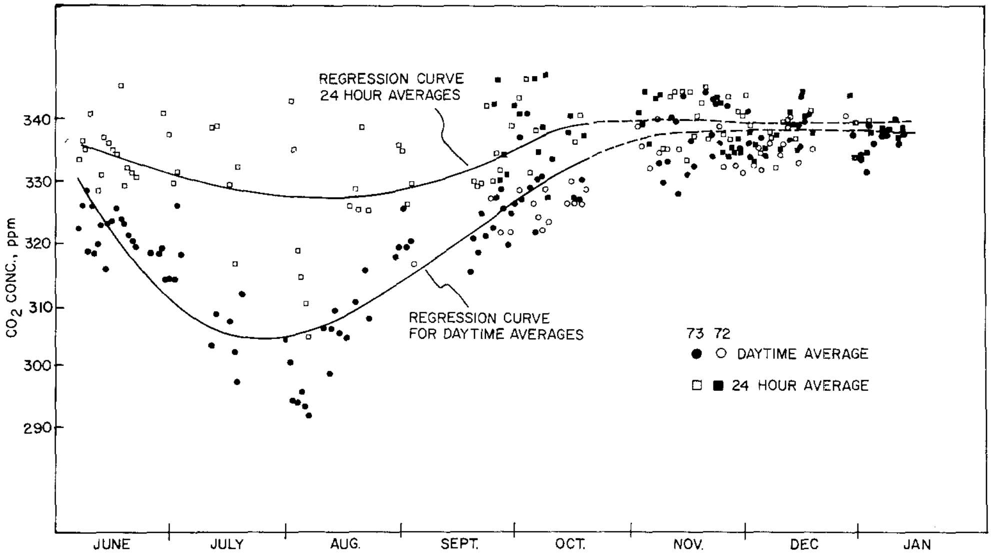

Fig. 5. Daytime and 24-hr means of CO_2 concentration at 16 m above ground during the periods September 1972 to January 1973 and June-December 1973 at Mead, NE. The curvilinear regressions are fitted to the data for only the period of the year shown by the solid lines (after Verma and Rosenberg, 1976).

annual range for daytime concentrations was much greater – from about 339 ppm in winter to about 305 ppm in late July and early August when photosynthetic activity in this region is greatest. Note in Figure 5 that on many days the concentration was lower than 300 ppm. These data demonstrate that agricultural lands provide a strong sink for CO_2 and this sink strength is easily detected 16 m above the ground. A diurnal effect on CO_2 concentration was detected at about 150 m above corn land in Iowa by Chapman *et al.* (1954).

Near the ground the midday concentrations are normally even lower since it is the growing plants that extract CO_2 from the air. In Figure 6 (from Verma and Rosenberg, 1979) it is seen that low growing crops such as alfalfa typically encounter a CO_2 concentration range from about 400 ppm at night (respiration dominates and little turbulent mixing occurs) to 290 ppm during midday (photosynthesis dominates and turbulence quickly transfers CO_2 from the bulk air to the plant). The data in Figures 5 and 6 illustrate the fact that annual and, especially, perennial plants experience a very wide range of ambient $[CO_2]$ in the course of their life cycles.

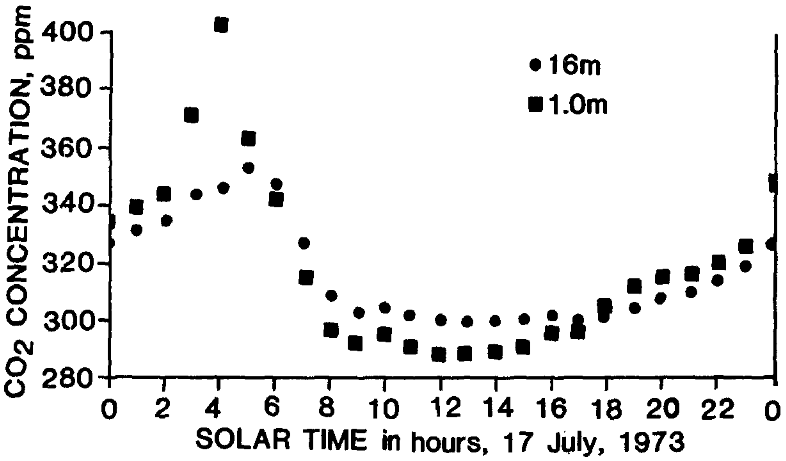

Fig. 6. Typical diurnal pattern of CO_2 concentration at 1 and 16 m above ground during the growing season at Mead, Nebraska (after Verma and Rosenberg, 1979).

4.2 *Field Response of Fluctuating* $[CO_2]$

Are current concentrations of CO_2 limiting? The results of growth chamber research reported above would indicate that the answer is affirmative. Direct field evidence supporting this observation is much more difficult to obtain, however. Allen *et al.* (1974) and Harper *et al.* (1973) have, literally, fertilized field crops by injecting CO_2 into the air.[4] Results have been disappointing or inconclusive, primarily because of the difficulty of maintaining high concentrations of CO_2 in the face of turbulence that tends to disperse it quickly.

Figure 7 from Verma and Rosenberg (1981) shows that crops growing in the vicinity of Mead, Nebraska reach their maximal photosynthetic activity (indicated by maximal

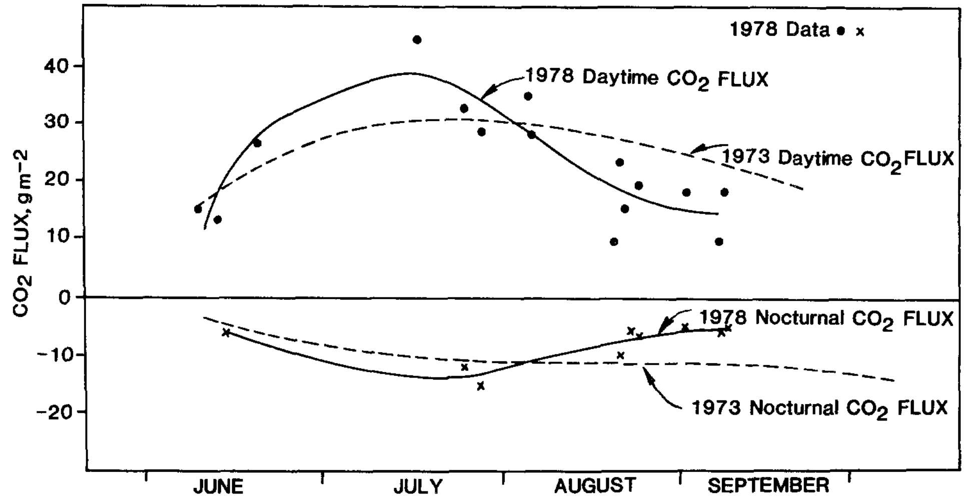

Fig. 7. Growing season CO_2 flux 1973 and 1978 at Mead, NE (after Verma and Rosenberg, 1981).

daytime CO_2 flux) in mid to late July when the ambient CO_2 concentration is at its lowest. This figure is based upon fluxes measured between 5.6 and 16 m above the ground and, as such, the data represent an integration of the photosynthetic activity occuring in an undefined zone including many surrounding fields. Most of these fields were planted to annual crops – predominantly soybeans and maize.

Figure 8 (from Baldocchi *et al.* 1981a) indicates that a depression in photosynthetic

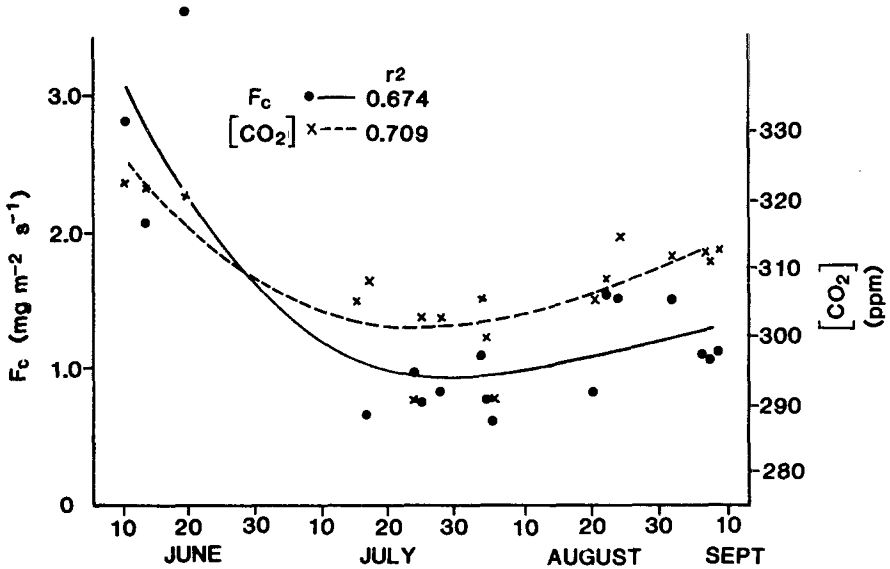

Fig. 8. Seasonal variation in canopy CO_2 flux (F_c) and $[CO_2]$ at 1 m over alfalfa at Mead, NE. Data were fitted with a second order polynomial regression (after Baldocchi *et al.*, 1981a).

rate of field-grown alfalfa occurs when the regional ambient CO_2 concentration is at its lowest. [CO_2] should explain this effect in part, but it is likely that the high temperatures occuring in midsummer are more directly involved since alfalfa photosynthesis is reduced considerably by high temperatures (see Baldocchi *et al.* (1981b) for a discussion of this effect). Low rates of photosynthesis may also be due, under strong irradiance to an accumulation of starch in the leaves, a 'sink-limiting' situation that can occur if the plant is unable to translocate photosynthate rapidly into storage organs. Despite these confounding factors, a low photosynthetic rate in a perennial vegetative crop coincident with the seasonal low in ambient [CO_2] provides an intriguing opportunity to observe (albeit in reverse) the possible effects of the projected long term changes in atmospheric [CO_2] on net photosynthesis.

To test these speculations data assembled by Baldocchi[5] were used to calculate the effect of ambient [CO_2] on F_c which is proportional to the net photosynthesis. Data were selected from periods when the crop suffered no moisture stress and when a moderate range of temperatures (15 to 28 C) prevailed. The selection was further confined to mid-morning periods when photosynthetic rates were not likely to be sink-limited. The range of net radiation flux densities in mid-morning was about 320 to 375 W m^{-2}. This data selection procedure provided a set of 12 items and a range of [CO_2] from 312 to 332 ppm.

The data were subjected to multiple regression with F_c the dependent and temperature, net radiation and ambient [CO_2] the independent variables. The resulting statistics are used to predict the influence of [CO_2] alone on F_c with temperature and net radiation held constant (Figure 9).

It may be seen that the slope of the curve is in the direction that theory and experiment indicate. Statistically, the slope can be said to differ from zero only at a probability

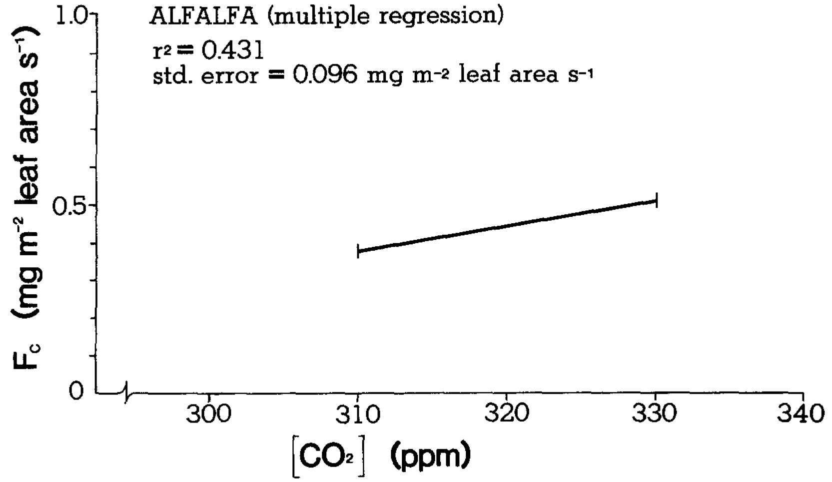

Fig. 9. Flux of atmospheric CO_2 into an alfalfa canopy at selected times during the 1978 growing season at Mead, NE as a function of ambient CO_2 concentration. Data from Baldocchi, 1979.[5] (See text for details).

level of $p = 0.2$. This less than satisfactory result may be due to the very small population of observations or to counfounding factors other than those removed by the selection process and multiple regression.

These data and Figure 9 are presented only to suggest a possible approach to analysis of the potential impacts of an increasing atmospheric $[CO_2]$ upon net photosynthesis in the real agricultural environment. It seems possible that the records of agronomic and agrometeorological field experiments may contain similar sets of consistent measurements of photosynthetic rates made over a long enough portion of the growing season to encompass a significant segment of the annual $[CO_2]$ wave. I hope, too, that other researchers, taking note of the possibility described above, may be encouraged to design new studies or to adapt ongoing research so that the needed observations can be made.

5. Summary and Conclusion

The increasing concentration of CO_2 in the atmosphere should result in a general increase in net primary photosynthetic productivity in most cultivated species of crops and probably in forests as well. C_4 plants experience a slight increase in photosynthetic rate when exposed to CO_2 concentrations in the range anticipated within the next century. The rate of transpiration is significantly reduced in C_4 plants because high concentrations induce partial stomatal closure.

The stomatal mechanism of C_3 plants is less sharply affected by high concentrations of CO_2 but the gradient of CO_2 between air and the internal leaf tissues is significantly increased when the concentration of CO_2 rises. Photorespiration in C_3 species is also suppressed by increasing $[CO_2]$. Hence photosynthetic activity is favored in C_3 species. The water use efficiency (P/T) is favored in both C_3 and C_4 species by increasing CO_2 concentration in the ambient air.

Arguments against a significant change in P, T or their ratio are based on the view that photosynthetic production is limited by insufficiency in available nutrients and/or available water for crop growth. I speculate that the dynamics of all terrestrial ecosystems (the agricultural as well as the unmanaged) may be changed as a result of CO_2-fertilization even to the extent of accelerated soil forming processes. If so, nutrient shortages may be alleviated through acceleration of certain chemical processes in the soil; water shortages may be moderated because an increased organic matter content improves water holding capacity in soil. Deeper rooting may also occur in crops if they grow larger because of increased net primary production.

Clearly, terrestrial vegetation provides a major sink for atmospheric CO_2 (and a source through respiration). It has been very difficult to provide direct evidence of the effects of increasing $[CO_2]$ on photosynthesis in the field situation. Experiments to increase photosynthesis by directly fertilizing the air in open fields with CO_2 have not been succesful because turbulence quickly disperses the added CO_2. It *has* been demonstrated, however, that photosynthetic rate of alfalfa, a perennial crop maintained in the vegetative state, is lowest during that period of the growing season when ambient $[CO_2]$ is lowest. Although other factors are involved in this suppression of photosynthetic rate the evidence suggests that the role of [CO_2] is discernible. This 'negative' evidence may provide a tool for evaluating the possible effects on photosynthesis when [CO_2] increases to the extent projected for the coming decades.

If only the direct effects of increased CO_2 concentration in the global atmosphere are considered, I speculate, with others (e.g., Loomis, 1977), that net photosynthetic productivity in agricultural crops will increase. Water use efficiency will be improved in both C_3 and C_4 species.

Assuming no climate change attendant on the increased global [CO_2], these direct effects, described above, should lead to a significant improvement in agricultural productivity worldwide. However, climatic changes are predicted and in a companion paper, I will examine the direct implications of these predicted changes on agricultural potential in certain select regions.

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Notes

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[3] In this section we will consider only the plant transpiration which is directly affected by ambient CO_2 concentration. Evaporation from the soil surface may also be affected, but indirectly, if a CO_2 induced climate change occurs.

[4] I refer here only to those experiments in which CO_2 has been released into the air in uncovered fields. Some confusion exists in the literature since the term 'field study' is often used by experimenters (and later by the compilers of review articles) to describe studies in which sealed chambers enclose plants growing in the field. The latter generally support the results of growth chamber and laboratory studies of the effects of CO_2 enrichment.

[5] Baldocchi, D. D. 1979. Environmental and physiological effects on the carbon exchange rate and water use efficiency of alfalfa. Center for Agricultural Meteorology and Climatology Progress Report 79-1 on NSF Grant ATM 77-27533. Univ. of Nebraska-Lincoln, Lincoln, NE U.S.A.

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