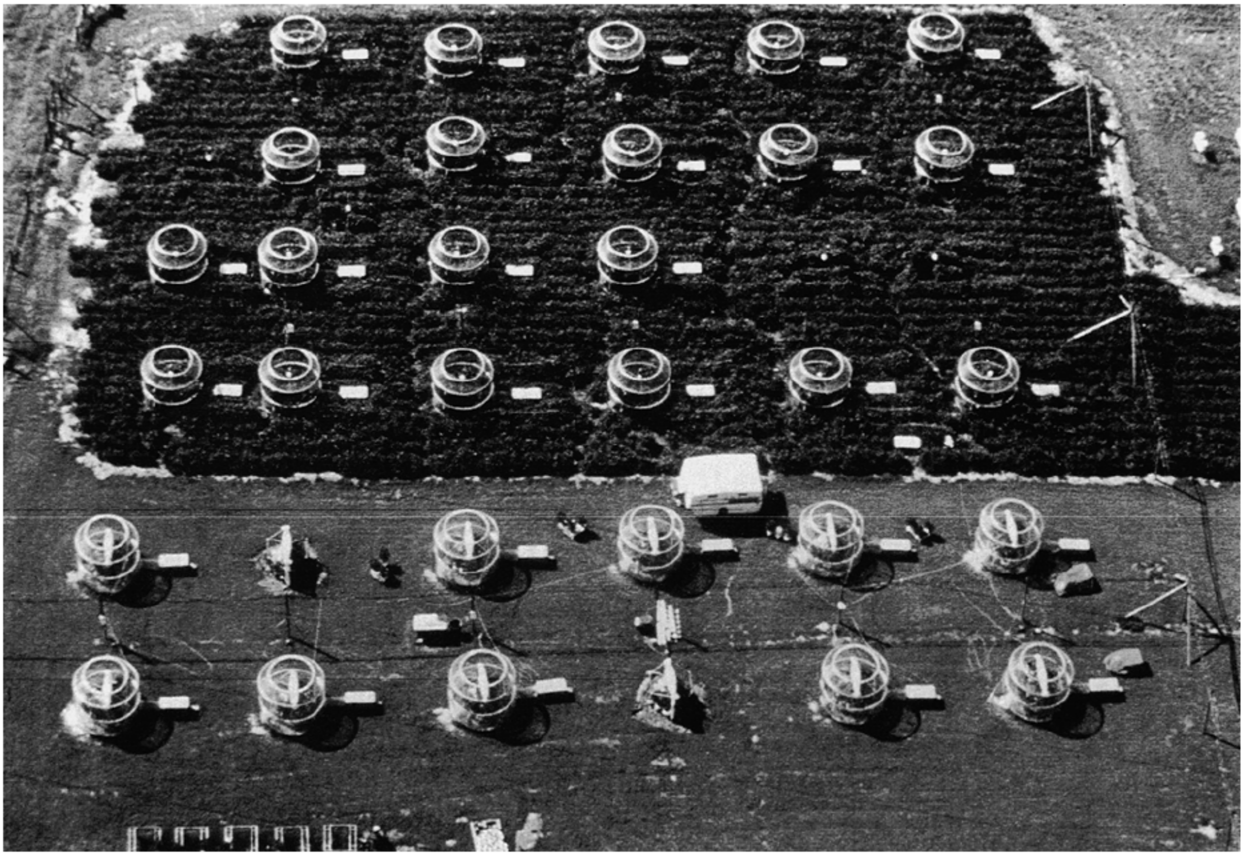

Aerial view of open top chamber system for elevated atmospheric CO_2 studies installed by Rogers and colleagues (ARS-USDA, Raleigh, North Carolina, USA). Upper field: row cropped soybean. Lower field: containerized studies of water stress, nutrition, and nitrogen fixation. (Photo courtesy of Dr. W. W. Cure)

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Crop responses to CO_2 enrichment

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Abstract

Carbon dioxide is rising in the global atmosphere, and this increase can be expected to continue into the foreseeable future. This compound is an essential input to plant life. Crop function is affected across all scales from biochemical to agro-ecosystem. An array of methods (leaf cuvettes, field chambers, free-air release systems) are available for experimental studies of CO_2 effects. Carbon dioxide enrichment of the air in which crops grow usually stimulates their growth and yield. Plant structure and physiology are markedly altered. Interactions between CO_2 and environmental factors that influence plants are known to occur. Implications for crop growth and yield are enormous. Strategies designed to assure future global food security must include a consideration of crop responses to elevated atmospheric CO_2. Future research should include these targets: search for new insights, development of new techniques, construction of better simulation models, investigation of belowground processes, study of interactions, and the elimination of major discrepancies in the scientific knowledge base.

Introduction

Expect the CO_2 concentration in our planet's air (along with radiatively active trace gases) to continue its steady climb, a climb that began with the lighting of the first fires of the Industrial Revolution. The analytical evidence, so clearly tracked over the past three decades by C. D. Keeling, will presumably continue its ascending trajectory (Keeling *et al.* 1989). Please see Figure 1 which provides a 30-year trace that includes Dr. Keeling's latest data. It is perhaps the one global alteration that can be anticipated with certainty. A doubling of CO_2 could occur during the last half of the next century (Bolin *et al.* 1986). The fixation and release of this compound by plants is a two-way bridge linking the atmosphere and biosphere. Regardless of whether there are accompanying climate shifts, as have been predicted (Bolin *et al.* 1986; Idso 1989; Rosenberg *et al.* 1990; Smit *et al.* 1988), CO_2 increases will directly affect growing plants. Not only is CO_2 essential for plant life but it also enhances growth and yield (Warrick 1988; Dahlman *et al.* 1985; Fajer 1989; Rogers *et al.* 1983c). Thus CO_2 is of pivotal significance to both natural plant communities and agro-ecosystems.

What physical climates will prevail and what interactions will occur in a future world are not known. What we can be sure of, however, is that as CO_2 levels climb higher and higher, the growth of vegetation will be stimulated, some plant spe-

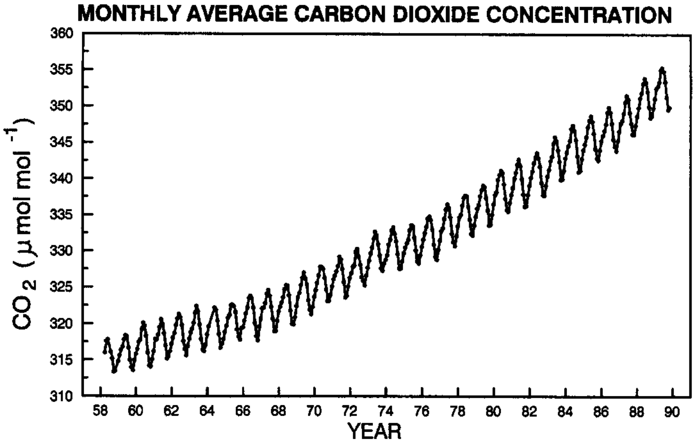

Fig. 1. Original data of C. D. Keeling *et al.* (1989). The steady upward trend of CO_2 in Earth's atmosphere is the most apparent feature; the saw-toothed pattern reflects seasonal biospheric changes.

cies more than others. Most experimental probings have revealed two main responses: (1) increased rates of photosynthesis, i.e., carbon fixation, and (2) enhanced water use efficiency. The proper function of these two vital plant processes can spell the difference between feast and famine. So the potential of elevated CO_2 to positively impact plants – our primary producers of food and fiber – is great. Virtually all works to date have shown enhanced crop growth, the alleviation of some stresses, and substantial boosts of yields.

Plant responses to above-ambient levels of CO_2 have been summarized in several excellent reviews of recent origin, each with its own special intent. Lemon (1983), Waggoner (1984), and Wittwer (1985, 1988) offer a solid background. Thorough syntheses of this topic have been given by Enoch & Zieslin (1988), Gifford (1988), Morison (1988), and Strain (1987). Kimball (1983a, b) provides comprehensive statistical summaries of previous research. Strain and Cure (1985) give in-depth coverage to recent findings. The greenhouse effect in terms of ultraviolet-B radiation, CO_2, and ozone has been discussed by Krupa & Kickert (1989). They underscore the need for multifactor studies. Smith & Tirpak have also provided excellent coverage of climate (1989a) and CO_2 (1989b) relationships to agriculture as have Adams *et al.* (1990) in a more condensed fashion using model output. In their very recent ASA Special Publication, Kimball *et al.* (1990) offer a state-of-the-art report on the impact of CO_2 on global agriculture (including a look at the greenhouse effect, trace gases, and possible influence on soils). In his new book on climate change and world agriculture, Parry (1990) gives a good synopsis of CO_2 enrichment effects and their relationships to other climatic changes. A collection of papers on primary productivity in European agro-ecosystems has just been published (Goudriaan *et al.* 1990). Soils and global change have been discussed (Bouwman 1990; Buol *et al.* 1990; Hatfield 1990).

Here we provide a short overview of the influence of more CO_2 on crops. First, a brief look at current research methods will show how most plant effects data have been gathered. And in the discussion that follows, crop responses to elevated CO_2 will be viewed in three contexts: (1) at several hierarchical scales, from biochemical through physiological, individual plant types (C_3, C_4, and CAM), the cell, leaf, to agro-ecosystem, (2) interactively with other environmental factors, and (3) at the species level a brief look at 10 major crops, with special emphasis on water use, carbon fixation, biomass, and yield. Implications for crop agriculture will be presented. Finally, a few specific targets of future research will be proposed.

Research methods

In the past decade and a half, technology has provided several approaches to the study of plant response to rising CO_2, primarily in the form of various configurations of containment structures. A comprehensive evaluation of exposure techniques has been presented by Drake *et al.* (1985). Much of the current data base has come from greenhouses where CO_2 is often added to boost commercial production. Research greenhouses with better regulation of test variables have also been employed in CO_2 experiments (Enoch & Kimball 1986; Mortensen 1987). Environmental rooms where basic physical factors are controlled probably constitute the second largest source of CO_2/vegetation information. One specialized example is the sunlit SPAR (soil-plant-atmosphere-research) system where conditions are tightly regulated (Jones *et al.* 1984). Leaf cuvettes are another common category; these vary from no control to highly sophisticated conditioning and come in a variety of sizes and shapes, many custom-made (Sinclair *et al.* 1979). A second cousin to cuvettes, the branch exposure chamber (BEC) is especially useful in tree research; the unit envelops a whole branch and allows maximum experimental flexibility (CO_2 and air pollutant addition, gas exchange measurement, and use of tracers, even in tall trees). Dr. Jim Houpis and his colleagues at the Lawrence Livermore National Laboratory have recently developed an excellent version of the BEC (Houpis *et al.* 1991). A widely used plant exposure chamber in air quality and gas kinetics work (i.e., uptake by and release from plants) is the continuous stirred tank reactor or CSTR (Rogers *et al.* 1977). The unique feature of this chamber, besides offering a uniform and highly characterizable environment, is that it provides direct kinetic data.

In the field, two principal avenues have been taken: (1) open top chambers (OTC) in two versions, round (Heagle *et al.* 1973; Rogers *et al.* 1983b) and square (Kimball *et al.* 1983), and (2) free-air CO_2 enrichment (FACE) (Hendrey *et al.* 1988). Both OTC types have been used over several years in CO_2 efforts. The square type is much cheaper but probably would not withstand stormy weather as well as the round type. Sometimes a simple portable enclosure is used in short-term measurements. A far more advanced system, the field tracking chamber, simulates outdoor conditions but permits the introduction of test variables such as CO_2 (Prudhomme *et al.* 1984). None of these, however, provide ideal field meteorology, which has led to attempts to release gases in various patterns over and within open fields (Allen *et al.* 1985). At present, the most promising approach appears to be FACE, a recent innovative technique. In practice, a large diameter (23 m) PVC doughnut from which a uniformly spaced series of vertical vent pipes arise is used; vent pipes are ported by drilling holes at vertical intervals. A circular array of stand pipes is thus created; a sophisticated programmer (based on an algorithm keyed to wind) controls the release of CO_2 into the ring; CO_2 is dumped upwind from open sectors of the vertical pipes in amounts equivalent to windspeed such that a circular plot is uniformly fumigated. Dr. George Hendrey and his team from the Brookhaven National Laboratory have done a remarkable job over the past two years in designing and perfecting this system (Hendrey *et al.* 1988).

Beyond the special ways in which controlled test atmospheres of CO_2 are generated, virtually all categories of classical botanical methodology have been considered and many used in CO_2 effects research, particularly sequential determinations of plant extension and mass, often for input to simulation models. Physiologically, water use and net photosynthesis have frequently been assessed; water use in terms of stomatal conductance, water potential, or soil water content, and net photosynthesis by mass balance or radiolabeling. Newer, more novel techniques have also been applied. For example, we have used nuclear magnetic resonance (NMR) imaging to ascertain short-term water flow dynamics in root systems of plants exposed to CO_2-enriched air. Stable isotopic ratios have been used to excellent advantage in both photosynthetic and water use investigations (Rundel *et al.* 1989). Dynamic tracing with short-lived isotopes such as ^{11}C and ^{13}N has provided new insight into plant metabolic functions (Goeschl *et al.* 1988).

To integrate and utilize these incoming streams of physicochemical and biological data, crop simulation models are used (Dahlman 1985; Harvey 1989; King *et al.* 1985; Reynolds & Acock 1985a, b). Due to the highly complex nature of crop response to CO_2 in the presence of fluctuating atmospheric and edaphic factors over the growing season continuum, models are extremely valuable, both as research tools and as methods of prediction. Several models being constructed for crops are expected to treat physiological effects of variable CO_2 concentration. These models show great promise, but much remains to be done, particularly with respect to new experimental parameters, data inputs, and verification. They are essential to our work since trajectories of response must be projected in the most reliable way.

Scales of crop response

The experimental assessment of crop response to more atmospheric CO_2 takes several scales: biochemical, physiological, cellular level, organ (leaves, stems, roots, and reproductive structures), individual plants, canopies, and whole cropping regions. Economic yield is often the main point of agronomic research, and likewise is the central focus of most CO_2/crop assessments.

Biochemical. At the biochemical level, there are three main plant groups, so-called C_3, C_4, and CAM. Three and four refer to the number of carbon atoms in the first molecules formed at the end of the photosynthetic pathway. Soybean, wheat, rice, and potato are examples of C_3 plants. The C_4 pathway is found in tropical grass crops like corn, sugarcane, and sorghum. The C_4 type metabolism is almost never found in woody species. The C_4's are more efficient in photosynthesis than the C_3's. The CAM (Crassulacean acid metabolism) plants are a form of C_4 except that CO_2 is fixed at night and then processed via a C_3 pathway during the day. They are succulent plants such as cacti and are highly efficient users of water. High levels of CO_2 stimulate photosynthesis, particularly in C_3 plants. The C_4 types are much less affected. Growth tends to respond similarly (Warrick 1988; Kramer 1981). Limited data on CAM plants suggest that night enrichment would be beneficial (Black 1986). In his just-completed review (which includes a discussion of leaf metabolism), Allen (1990) concludes that direct biochemical effects do not appear to be the cause of enhanced photosynthesis. It is simply an increase in the carbon (i.e., CO_2) feedstream to photosynthesis. A substantial amount of work has focused on net photosynthesis at higher concentrations of CO_2 (Allen *et al.* 1990b; Besford *et al.* 1990; Gifford & Morison 1985; Huber *et al.* 1984a, b; Radin *et al.* 1987).

Physiological/cellular. At the cellular level, elevated CO_2 slows transpiration rate by inducing the partial closure of guard cells that form stomates on leaf surfaces. This contributes to an increase in water use efficiency (WUE, the ratio of carbon fixed to water transpired). Physiologically, WUE increase represents one of the most significant crop responses identified thus far. Both the suppressed use of water and the rise in photosynthetic rate go toward pushing this important ratio upwards. Table 1, presented by Acock and Allen (1985) from the data of Wong (1980) and Valle *et al.* (1985), shows the relative contributions of each of these two processes. It is readily apparent that the positive change in transpiration rate is most important for a C_4 plant like corn in contrast to C_3 types where both carbon fixation and transpiration are important. Figure 2 shows WUE for field-grown corn and soybean over a

Table 1. Relative contribution (%) of changes in net photosynthesis and transpiration rate to a CO_2-induced, approximate doubling of leaf water use efficiency for four species.

Crop	Photosynthesis	Transpiration
Corn	27	73
Cotton	60	40
Snow gum	75	25
Soybean	90	10

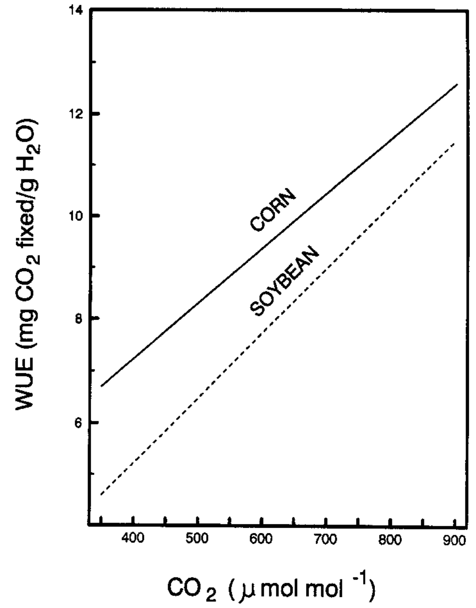

Fig. 2. Water use efficiencies for corn and soybean at various CO_2 concentrations. Values were fitted by the method of least squares and are based on 50 observations for corn and 46 for soybean.

range of CO_2 concentrations (Rogers *et al.* 1983a).

That WUE is boosted by CO_2 enrichment of experimentally tested crops has often been reported (Baker *et al.* 1990b; Morison 1985; Sionit *et al.* 1984). However, discrepancy does exist. Some claim that larger plant size offsets the reduction in water use resulting in no change. Others suggest that the landscape's response is not adequately reflected by studies of small numbers of plants in artificial enclosures. At least one recently completed simulation, which included climate change, predicts a rise in plant water needs (Curry *et al.* 1990). But by and large, most studies have reported enhancements. In their comprehensive summary of the topic, Kimball and Idso (1983) cited 46 observations showing that transpiration would be lowered an average of 34% which when coupled with an economic yield enhancement of 33% (over 500 observations) suggested a doubling of water use efficiency for a doubling of CO_2 level.

There have been no *in situ*, non-invasive field studies of CO_2 effects on plant water use published to date. In the field, water availability will depend upon rainfall distribution, leaf and canopy structure, extent and depth of crop rooting, and the various weather variables. For an accurate assessment, the test crops must be unencumbered by our experimental gear, i.e., micrometeorology must be normal for the crop to be representative of what happens on the farm.

Another important reaction in some crop plants, the legumes, is nitrogen fixation. Legume/bacterial symbiosis is significantly increased by elevated CO_2 levels (Reardon *et al.* 1990; Reddy *et al.* 1989a). The increase appears to be mainly due to larger biomass (Acock 1990), i.e., bigger plants, more carbon allocation for nitrogen fixation.

Organ level. Individual plant organs have often been observed to enlarge proportionally with added CO_2. Lengths of stems and roots increase (Allen *et al.* 1990a; Rogers *et al.* 1987). The expanse and thickness of leaves increase (Thomas & Harvey 1983). Shifts in stomatal density have also been seen (Rowland-Bamford *et al.* 1990). In their study of leaf ultrastructure, Vu *et al.* (1989) observed larger starch grains but no appreciable alteration of chloroplasts. Enhanced numbers of specific parts (stems, branches, tillers, and flowers) are often seen. Two authors have presented new data on crop roots and CO_2 enrichment (Chaudhuri *et al.* 1986, 1990; Del Castillo 1989). Our laboratory has observed a significant enhancement of root development in both the laboratory (Rogers *et al.* 1987) and field (Rogers *et al.* 1989). A theoretical framework has been developed for the growth and carbon economy of wheat seedlings as affected by soil resistance to penetration and CO_2 level (Masle *et al.* 1990). Acceleration of development and a shortening of total growth duration has been recorded for rice (Baker *et al.* 1990a). Reproductive structures (which are often the marketable product) may increase in size or number (Acock & Allen 1985). Figure 3 provides an example of partitioning in corn (a C_4 plant) and Figure 4 soybean (C_3) over a range of CO_2 exposure concentrations (Rogers *et al.* 1982). Shifts in overall plant structure may

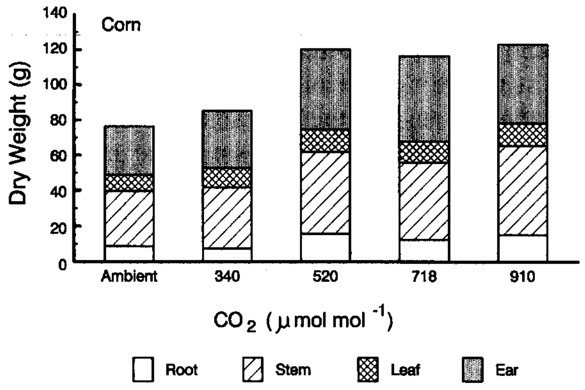

Fig. 3. Partitioning of dry weight components of corn: roots, stems, leaves, and ears (n = 6). 'Ambient' refers to control plots outside of open top chambers used for season-long CO_2 exposure.

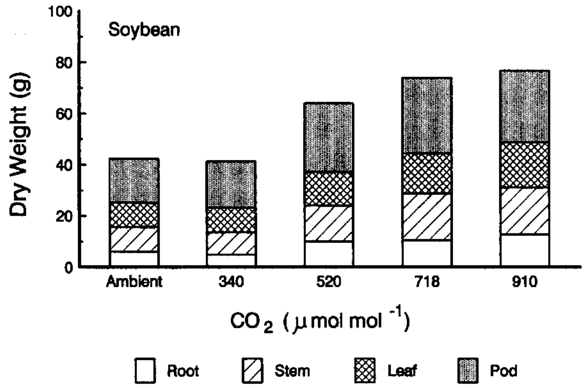

Fig. 4. Partioning of dry weight components of soybean: roots, stems, leaves, and pods (n = 6). 'Ambient' refers to control plots outside of open top chambers used for season-long CO_2 exposure.

be of much less consequence to crop production where the rule is monoculture than in natural ecosystems which are highly diverse. Natural interspecific competition is intense and is believed to be strongly influenced by canopy architecture, root distribution, and environmental conditions. Harsh stresses are common in these native plant communities.

A so-called 'luxury consumption' of carbon can occur when extra CO_2 from the air is available. This can translate into plant parts with higher densities than might actually be required (Acock & Allen 1985). This can also lead to taller, denser canopies and greater root length densities. Such changes may enhance the plant's capacity to harvest light, water, and nutrients. Practically speaking, this capacity to gather raw materials can become crucial over the cropping cycle.

Plant/canopy. Single plants provide integrated values for what goes on at the process level. Many individual crop plants have been evaluated for their response to CO_2. Groups of plants or segments of crop rows have also been studied. Such findings have contributed substantially to our data base, but for analysis of broad questions of food productivity and sustainable agriculture, there must be extrapolation to the agro-ecosystem level and then to cropping regions. This will require improved models tested with field data.

Cropping system/region. Agro-ecosystems within specific geographic regions should respond in a generally uniform pattern since the atmospheric CO_2 level is globally determined. Specific long-range predictions will have to await the refinement of crop simulation and climate models; for, as yet, model resolution is not fine enough to describe regional weather patterns. Current crop models can not treat highly variable physical forcing functions such as temperature, precipitation, and CO_2 concentration at the required scales. Nevertheless, at present our best bet is the use of models which help organize myriads of facts and lead to intelligent and, hopefully, realistic output. On a regional scale, one system where agro-ecosystems and natural ecosystems meld is in the rangelands that are used for livestock grazing. Research needs were highlighted in a 1982 report to DOE (Pendleton & van Dyne 1982). Recently Dr. Clenton Owensby and his colleagues (1989) at Kansas State University provided the first and only study of rangeland/grazing responses to elevated CO_2. In their report, rangeland biomass was observed to increase with extra CO_2 but individual species response varied, suggesting that over time community composition might shift. The methodology needed to investigate grazing of CO_2-affected rangeland was developed. With rangelands occupying 47% of the world's land area, such research is indeed important.

Economic yield, the bottom line of all farming, has been seen to increase. Kimball's excellent compilation and analysis of hundreds of prior studies (1983a) suggests an enhancement factor of 1.32 (99.9% confidence interval: 1.24 to 1.43) if ambient CO_2 were doubled. Allen *et al.* (1987) have discussed yield in relation to CO_2- enhanced photosynthesis and biomass accumulation. In another crop analysis, Kimball *et al.* (1989) considered both direct CO_2 effects and changing climate. We are not aware of major studies on the alteration of quality or desirability of agricultural products produced at high levels of CO_2. Virtually all authors dealing with direct effects of CO_2 have concluded that the impact on crops will be positive.

Interaction with other environmental factors

Virtually any factor that affects plant growth can influence its reaction to elevated CO_2. From a different vantage point, it is also known that CO_2 can ameliorate certain environmental stresses. The role of CO_2 as a chief input to plant life may become especially significant in view of predicted future climate effects on crops (Bolin *et al.* 1986; Idso 1989). Water, temperature, light, nutrients, salinity, and air pollutants have all been observed to interact with CO_2 concentration. In addition, biological interactions with crops have been seen in the form of altered weed competition and crop pests relationships.

Water. Water stress has been repeatedly observed to be ameliorated by increased concentration of CO_2 (Gifford 1979; Morison & Gifford 1984a, b; Schonfeld *et al.* 1989; Sionit *et al.* 1980, 1981d). Our laboratory observed this with soybean (Rogers *et al.* 1984; Prior *et al.* 1991). Reports that it occurs with other plant species are not uncommon (Lemon 1983; Acock & Allen 1985; Wong 1980). By inducing the partial closure of stomates, water is conserved. To date the role of plant roots, the primary extractors of soil water, has not been elucidated. This protection from water stress phenomena could help relieve negative impacts of drier future climates.

Temperature. Baker *et al.* (1989) substantiated a high degree of temperature dependence in soybean growth response to elevated CO_2. Jones *et al.* (1985) have provided response curves for photosynthesis and transpiration under various levels of both CO_2 and temperature. Idso *et al.* (1987) reported results suggesting that for a 3 degree C rise in mean surface air temperature, plant growth enhancement would increase from 30% to 56%. Their results also showed that at cooler temperatures (<18.5 degrees C, daily mean) elevated CO_2 tends to reduce plant growth. The authors aptly pointed out that this temperature dependence would make the prediction of CO_2 response far more complex than first thought. Both Potvin (1985) and Sionit *et al.* (1981b) saw alleviation of chilling effects by CO_2 enrichment. Potvin observed a buffering of physiological shifts due to cold while Sionit *et al.* saw an elevated CO_2 compensation for chilling in the common garden vegetable okra. The life cycle of the plant could be completed several degrees lower with added CO_2. The interaction of CO_2 and temperature is not well understood; there is some conflict in the experimental data base.

Light. Light and CO_2 have been long known to interact. Both affect the plant through the photosynthetic process. Brun and Cooper (1967) have provided a full spectrum of their interactions with soybean leaves. A maxima for net photosynthesis was reached which fell if either light level or CO_2 concentration was lowered. Sionit *et al.* (1982) reported similar findings for soybean, radish, sugarbeet, and corn; total dry matter production was highest at the highest values of CO_2 and light tested. It has been concluded that, at least in part, elevated CO_2 can compensate for reduced light (Acock & Allen 1985; Hurd 1968; Mortensen & Ulsaker 1985).

Nutrition. Positive plant response to CO_2 appears to occur under a wide range of nutrient availability (Sionit *et al.* 1981a; Sionit 1983; Cure *et al.* 1988). Studies (with soybean, corn, rice, cotton, wheat, and a few weed species) have, however, demonstrated diminished growth responses due to nitrogen limitation (Cure *et al.* 1988; Goudriaan & de Ruiter 1983). One study has shown this with several plant types over a range of dilutions of a complete nutrient solution (Patterson & Flint 1982). In other words, with increasing nutrient availability, the CO_2 stimulation response appears to grow larger.

Salinity. Relief from the effects of salinity has been seen in some studies (Schwarz & Gale 1984). Salt tolerance increases as CO_2 concentration goes up (Zeroni & Gale 1989). There are two possible explanations. Extra supplies of photosynthate may help to offset increased respiration demands. Less water throughput in the transpiration stream (rate lowered by extra CO_2) could lessen the quantity of salt taken up (Acock & Allen 1985).

Air pollutants. The narrowing of stomates by increased levels of CO_2 immediately infers the possibility of protection from air pollutants that enter leaves by this route. In fact it has been experimentally demonstrated. A few laboratories have shown a lessening of injury by O_3, SO_2, NO, and NO_2 on several common crops (Allen 1990; Reddy *et al.* 1989b). Allen's recently published review (1990) of the topic revealed a paucity of data and concluded further studies were needed.

Weed competition. Weeds are important since they suppress crops in a variety of ways by competing for raw materials. The differential responses of plant species to rising CO_2 suggest that relative competitiveness may be altered. This has been found to be the case. Studies by Patterson and Flint (1990) have shown that weeds with the C_3 pathway would probably outcompete C_4 crops but that C_4 weeds would be less competitive against C_3 crops. Other studies have substantiated this (Patterson *et al.* 1988; Sasek & Strain 1989). Zangerl & Bazzaz (1984) have noted an unusually high stimulation of growth in one common C_4 weed species. Potential shifts in weed growth will be important in terms of farm practice and economics.

Pests. The interaction of high CO_2 and plant insect pests has been shown (Osbrink *et al.* 1987; Fajer *et al.* 1989). First Lincoln *et al.* (1984) showed that insect (butterfly larvae) feeding rates rose as CO_2 in the plant growth atmosphere was increased. This was related to the nitrogen and water content of soybean leaves. More recent studies have suggested that leaf-feeding caterpillars do not do as well on plants grown at high CO_2, presumably due to increased carbon:nitrogen ratio (nutritive value lower) (Akey & Kimball 1989).

Effects on specific crop species

Different species respond differently. This is a chief concern with respect to natural plant community response (where competition governs composition) to global CO_2 rises. It is not so much an issue in crop monoculture, except for weeds which must be controlled. Major world crops have been researched to varying degrees with respect to CO_2. An idea of the relative thoroughness with which 10 major crops have been studied may be gleaned from a tally of the entries in the comprehensive CDIAC bibliography provided by Strain & Cure (1986). Please see Table 2 which shows number of studies as well as world rank, photosynthetic type, and selected references by species. Table 3 provided the response of four key variables of these same 10 crops to a doubling of ambient CO_2 (Cure & Acock 1986). The extent of crop response could eventually influence their selection for the farm.

Implications for agriculture

Previous discussions of the agricultural implications of more atmospheric CO_2 have been presented (Strain & Cure 1985; Kimball *et al.* 1989; Rosenberg 1981, 1982). Table 4 lists specific implications with the authors' perception of importance, relative knowledge base, and degree of confidence. Available data suggest that the direct effects of CO_2 alone will have a positive effect on

Table 2. World rank, photosynthetic type, number of CO_2 studies, and selected references for 10 major crops.

Crop	World rank (acreage)	Photosynthetic pathway	Number of CO_2 studies*	Selected references
Wheat	1	C_3	48	Havelka *et al.* 1984a, Sionit *et al.* 1981c
Rice	2	C_3	12	Imai *et al.* 1985, Yoshida 1973
Corn	3	C_4	57	King & Greer 1986, Surano & Shinn 1984
Barley	4	C_3	10	Ford & Thorne 1967
Sorghum	6	C_4	10	Chaudhuri *et al.* 1986, Mauney *et al.* 1979
Soybean	7	C_3	89	Acock & Allen 1985, Havelka *et al.* 1984b
Cotton	9	C_3	29	Kimball *et al.* 1989
White potato	12	C_3	12	Goudriaan & de Ruiter 1983
Sweet potato	16	C_3	8	Bhattacharya *et al.* 1985
Alfalfa	–	C_3	8	Goudriaan & de Ruiter 1983, Morison & Gifford 1984

* This column updated; all other information, Cure and Acock (1986).

Table 3. Percent change ± 95% confidence limits in four key variables of 10 major crops due to a doubling of ambient CO_2 concentration. Data from Cure and Acock (1986) computed by regression analysis; N numbers and references were provided.

Crop	Transpiration	Photosynthesis	Biomass	Yield
Corn	- 26 ± 6	+ 4 ± 13	+ 9 ± 5	+ 29 ± 64
Wheat	- 17 ± 17	+ 27 ± 20	+ 31 ± 16	+ 35 ± 14
Soybean	- 23 ± 5	+ 42 ± 10	+ 39 ± 5	+ 29 ± 8
Sorghum	- 27 ± 16	+ 6 ± 16	+ 9 ± 29	–
Barley	- 19 ± 6	+ 14 ± *	+ 30 ± 17	+ 70 ± *
Cotton	- 18 ± 17	+ 13 ± 19	+ 84 ± 126	+ 209 ± *
Rice	- 16 ± 9	+ 46 ± *	+ 27 ± 7	+ 15 ± 3
White potato	- 51 ± 24	–	- 15 ± *	+ 51 ± 111
Sweet potato	–	–	+ 59 ± 18	+ 83 ± 12
Alfalfa	–	–	+ 57 ± 277	–

* Data points too few to calculate.

crop yield, all other factors remaining the same. Once-in-a-while a reported experiment shows little or no effect, but these are few and far between. As crop simulation models mature over the next decade, we should be in an excellent position to predict and even take advantage of direct response of crops to CO_2. In his 1989 address before the Agricultural Science Centennial in Steinkjer, Norway, Dr. J. E. Newman (1989) concluded that rising atmospheric CO_2 should provide benefits to agriculture through direct fertilization and enhanced water use efficiency on local, regional, and global scales. Increased CO_2 is an important aspect of the future, and farmers, growers, and producers of foods are expected to adjust their practices to take advantage of this CO_2 subsidy. Based on current projections, there is every reason to believe that this will occur. Strategies designed to assure future global food security must include a consideration of crop responses to elevated atmospheric CO_2.

Table 4. Implications of more atmospheric CO_2 for agriculture ranked by overall importance to crop production, based on authors' interpretation of the available literature base.

Rank	Implication for agriculture	Relative size of knowledge base*	Degree of confidence*
1	Increased yields	VH	VH
2	Aboveground crop processes	VH	VH
3	Belowground crop processes	VL	VL
4	Shift in water use, probably a savings	H	I
5	Amelioration of some environmental stresses	H	I
6	Nutrient needs may change	L	L
7	Grazingland composition and quality could change	L	L
8	New weed problems may arise	I	I
9	Degree of disease (including insects)susceptibility	L	L
10	Farmers might switch species (e.g., $C_3 > C_4$) in some cases	I	L
11	Potential change in geographic range of given crops	L	VL
12	Possibility of crop quality alteration	L	VL

* Ratings: Very High, High, Intermediate, Low, & Very Low (VH, H, I, L, & VL).

Future research targets

Research needs have been delineated by previous authors (Dahlman *et al.* 1985; Strain & Cure 1985; White 1985). Certainly any data that would shed light on the CO_2/crops question would be welcomed. Below are a few critical goals which we have prioritized in descending order:

(1) Search for new insights and opportunities.
(2) Develop novel techniques.
(3) Construct better simulation models.
(4) Investigate belowground processes.
(5) Study interactions of CO_2 and other environmental factors.
(6) Eliminate major discrepancies in scientific knowledge base.

Exploring for new insights and opportunities is particularly significant since we are dealing with a global function. Novel techniques, e.g., both stable and short-lived isotopes, non-invasive exposure methods, and *in situ* plant probes such as NMR (spectroscopy and imaging), would certainly improve our research arsenal. More complete data inputs and improved field verification procedures are essential if our models are to provide greater reliability. Belowground processes (which include plant root systems, the rhizosphere, and the soil) have been too long ignored due to lack of methodology and difficulty in data collection; they must be investigated. Interactions of CO_2 (an area where data are sparse) with climatic change variables, ozone, and ultraviolet-B radiation need to be examined. And finally, we must research and seek to eliminate major discrepancies, e.g., the influence of elevated CO_2 on plant water use.

A lot has been accomplished, but as most authors have concluded, a lot remains to be done. We agree. We must continue to develop a sound and complete knowledge base. Crop responses to CO_2 enrichment offer fertile ground for enormous strides to be made in world food production. It is essential that we understand and best utilize this and other future potentials.

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References

Acock, B. 1990. Effects of CO_2 on photosynthesis, plant growth and other processes. In: Kimball, B. A., Rosenberg, N. J. & Allen, L. H. (eds), Impact of CO_2, trace gases, & climate change on global agriculture. ASA Special Publication No. 53. pp. 45–60. Am. Soc. Agron., Madison, WI.

Acock, B. & Allen, L. H., Jr. 1985. Crop responses to elevated carbon dioxide concentrations. In: Strain, B. R. & Cure, J. D. (eds), Direct effects of increasing carbon dioxide on vegetation. DOE/ER-0238. pp. 53–97. Office of Energy Research. U.S. Dept. of Energy, Washington, DC.

Adams, R. A., Rosenzweig, C., Peart, R. M., Ritchie, J. T., McCarl, B. A., Glyer, J. D., Curry, R. B., Jones, J. W., Boote, K. J. & Allen, L. H., Jr. 1990. Global climate change and US agriculture. Nature 345: 219–224.

Akey, D. H. & Kimball, B. A. 1989. Growth and development of the beet armyworm on cotton grown in an enriched carbon dioxide atmosphere. Southwestern Entomol. 14: 255–260.

Allen, L. H., Jr. 1990. Plant responses to rising carbon dioxide and potential interactions with air pollutants. J. Environ. Qual. 19: 15–34.

Allen, L. H., Jr., Beladi, S. E. & Shinn, J. H. 1985. Modeling the feasibility of free-air carbon dioxide releases for vegetation response research. 17th Conf. on Agriculture and Forest Meteorology, Am. Meteorol. Soc. Boston, MA.

Allen, L. H., Jr., Boote, K. J., Jones, J. W., Jones, P. H., Valle, R. R., Vu, C. V., Acock, B., Rogers, H. H. & Dahlman, R. C. 1987. Response of vegetation to rising carbon dioxide: photosynthesis, biomass, and seed yield of soybean. Global Biogeochem. Cycles 1: 1–14.

Allen, L. H., Jr., Bisbal, E. C., Campbell, W. J. & Boote, K. J. 1990a. Carbon dioxide effects on soybean developmental stages and expansive growth. Soil & Crop Sci. Soc. Fla. Proc. 49: 124–131.

Allen, L. H., Jr., Valle, R. R., Mishoe, J. W., Jones, J. W. & Jones, P. H. 1990b. Soybean leaf gas exchange responses to CO_2 enrichment. Soil & Crop Sci. Soc. Fla. Proc. 49: 192–198.

Baker, J. T., Allen, L. H., Jr., Boote, K. J., Jones, P. & Jones, J. W. 1989. Response of soybean to air temperature and carbon dioxide concentration. Crop Sci. 29: 98–105.

Baker, J. T., Allen, L. H., Jr., Boote, K. J., Jones, P. & Jones, J. W. 1990a. Developmental responses of rice to photoperiod and carbon dioxide concentration. Agric. & Forest Meteorol. 50: 201–210.

Baker, J. T., Allen, L. H., Jr., Boote, K. J., Jones, P. & Jones, J. W. 1990b. Rice photosynthesis and evapotranspiration in subambient, ambient, and superambient carbon dioxide concentrations. Agron. J. 82: 834–840.

Besford, R. T., Ludwig, L. J. & Withers, A. C. 1990. The greenhouse effect: Acclimation of tomato plants growing in high CO_2, photosynthesis and ribulose-1, 5-*bis* phosphate carboxylase protein. J. Exp. Bot. 41: 925–931.

Bhattacharya, N. C., Biswas, P. K., Bhattacharya, S., Sionit, N. & Strain, B. R. 1985. Growth and yield response of sweet potato to atmospheric CO_2 environment. Crop Sci. 25: 975–981.

Black, C. C., Jr. 1986. Effects of CO_2 concentration on photosynthesis and respiration of C_4 and CAM plants. In: Enoch, H. Z. & Kimball, B. A. (eds), Carbon dioxide enrichment of greenhouse crops, Vol. II: Physiology, yield, and economics. pp. 29–40. CRC Press, Boca Raton, FL.

Bolin, B., Doos, B. R., Jager, J. & Warrick, R. A. 1986. Scope 29 – The greenhouse effect, climate change, and ecosystems. John Wiley & Sons, NY. 541 pp.

Boone, M. Y. L., Rickman, R. W. & Whisler, F. D. 1990. Leaf appearance rates of two winter wheat cultivars under high carbon dioxide conditions. Agron. J. 82: 718–724.

Bouwman, A. F. (ed). 1990. Soils and the greenhouse effect. John Wiley & Sons, NY. 567 pp.

Brun, W. A. & Cooper, R. L. 1967. Response of soybeans to a carbon dioxide-enriched atmosphere. Crop Sci. 7: 455–467.

Buol, S. W., Sanchez, P. A., Kimble, J. M. & Weed, S. B. 1990. Predicted impact of climate warming on soil properties and use. In: Kimball, B. A., Rosenberg, N. J. & Allen, L. H., Jr. (eds), Impact of carbon dioxide, trace gases, and climate change on global agriculture. ASA Special Publication No. 53, pp. 71–82. Am. Soc. Agron., Madison, WI.

Chaudhuri, U. N., Burnett, R. B., Kirkham, M. B. & Kanemasu, E. T. 1986. Effect of carbon dioxide on sorghum yield, root growth, and water use. Agric. For. Meteorol. 37: 109–122.

Chaudhuri, U. N., Kirkham, M. B. & Kanemasu, E. T. 1990. Root growth of winter wheat under elevated carbon dioxide and drought. Crop Sci. 30: 853–857.

Cure, J. D. & Acock, B. 1986. Crop responses to carbon dioxide doubling: A literature survey. Agric. & Forest Meteorol. 38: 127–145.

Cure, J. D., Israel, D. W. & Rufty, T. W., Jr. 1988. Nitrogen stress effects on growth and seed yield of nonnodulated soybean exposed to elevated carbon dioxide. Crop Sci. 28: 671–677.

Curry, R. B., Peart, R. M., Jones, J. W., Boote, K. J. & Allen, L. H., Jr. 1990. Response of crop yield to predicted changes in climate and atmospheric CO_2 using simulation. Trans. ASAE 33: 1383–1389.

Dahlman, R. C., 1985. Modeling needs for predicting responses to CO_2 enrichment: Plants, communities and ecosystems. Ecol. Model. 29: 77–106.

Dahlman, R. C., Strain, B. R. & Rogers, H. H. 1985. Research on the response of vegetation to elevated atmospheric carbon dioxide. J. Environ. Qual. 14: 1–8.

Del Castillo, D. B., Acock, B., Reddy, V. R. & Acock, M. C. 1989. Elongation and branching of roots on soybean plants in a carbon dioxide-enriched aerial environment. Agron. J. 81: 692–695.

Drake, B. G., Rogers, H. H. & Allen, Jr., L. H. 1985. Methods of exposing plants to elevated CO_2 concentrations. In: Strain, B. R. & Cure, J. D. (eds), Direct effects of CO_2 on vegetation. DOE/ER-0238. pp. 112–31. Office of Energy Research. U.S. Dept. of Energy, Washington, DC.

Enoch, H. Z. & Kimball, B. A. (eds). 1986. CO_2 enrichment of greenhouse crops: Vol. II, Physiology, yield and economics. CRC Press, Boca Raton, FL. 230 pp.

Enoch, H. Z. & Zieslin, N. 1988. Growth and development of plants in response to carbon dioxide concentrations. Applied Agric. Res., 3: 248–256.

Fajer, E. D. 1989. How enriched carbon dioxide environments may alter biotic systems even in the absence of climatic changes. Conservation Biol. 3: 318–320.

Fajer, E. D., Bowers, M. D. & Bazzaz, F. A. 1989. The effects of enriched carbon dioxide atmospheres on plant-insect herbivore interactions. Sci. 243: 1198–1200.

Ford, M. A. & Thorne, G. N. 1967. Effect of carbon dioxide concentration on growth of sugar-beet, barley, kale, and maize. Ann. Bot. 31: 629–644.

Gifford, R. M. 1988. Direct effects of higher carbon dioxide concentrations on vegetation. In: Pearman, G. I. (ed), Green: Planning for climate change. pp. 506–519. E. J. Brill Co., NY.

Gifford, R. M. 1979. Growth and yield of carbon dioxide-enriched wheat under water-limited conditions. Aust. J. Plant Physiol. 6: 367–378.

Gifford, R. M. & Morison, J. I. L. 1985. Photosynthesis, water use and growth of a C_4 grass stand at high CO_2 concentration. Photosyn. Res. 7: 69–76.

Goeschl, J. D., Fares, Y., Magnuson, C. E., Schield, H. W., Strain, B. R., Jaeger, C. H. & Nelson, C. E. 1988. Short-lived isotope kinetics: A window to the inside. In: Beecher, G. R. (ed), Research instrumentation for the 21st century. pp. 21–53. Martinus Nijhoff.

Goudriaan, J. & de Ruiter, H. E. 1983. Plant growth in response to CO_2 enrichment, at two levels of nitrogen and phosphorus supply. I. Dry matter, leaf area and development. Neth. J. Agric. Sci. 31: 157–169.

Goudriaan, J., van Keulen, H. & van Laar, H. H. (eds). 1990. The greenhouse effect and primary productivity in European agro-ecosystems. Pudoc, Wageningen. 90 pp.

Harvey, L. D. D. 1989. Effect of model structure on the response of terrestrial biosphere models to CO_2 and temperature increases. Global Biogeochem. Cycles 3: 137–153.

Hatfield, J. L. 1990. Climate change and the potential impact on the soil resource. J. Iowa Acad. Sci. 97: 82–83.

Havelka, U. D., Wittenbach, V. A. & Boyle, M. G. 1984a. CO_2-enrichment effects on wheat yield and physiology. Crop Sci. 24: 1163–1168.

Havelka, U. D., Ackerson, R. C., Boyle, M. G. & Wittenback, V. A. 1984b. CO_2-enrichment effects on soybean physiology. I. Effects of long-term CO_2 exposure. Crop Sci. 24: 1146–1150.

Heagle, A. S., Body, D. E. & Heck, W. W. 1973. An open top field chamber to assess the impact of air pollution on plants. J. Environ. Qual. 2: 365–368.

Hendrey, G. R., Lewin, K. F., Kolber, Z. & Daum, M. 1988. Free-air carbon dioxide enrichment (FACE) facility development: I. Concept, prototype design, and performance. Series 045, Response of vegetation to carbon dioxide, BNL-42338, Brookhaven National Laboratory, Upton, NY. Office of Energy Research. U.S. Dept. of Energy, Washington, DC. 36 pp.

Houpis, J. L., Costello, M. T. & Cowles, S. 1991. A branch exposure chamber for fumigating *Pinus ponderosa* to atmospheric pollution. J. Environ. Qual. 20: 467–474.

Huber, S. C., Rogers, H. H. & Israel, D. W. 1984a. Effects of CO_2 enrichment on photosynthesis and photosynthate partitioning in soybean (*Glycine max*) leaves. Physiol. Plant. 62: 95–101.

Huber, S. C., Rogers, H. H. & Mowry, F. L. 1984b. Effects of water stress on photosynthesis and carbon partitioning in soybean [*Glycine max* (L.) *Merr.*] plants grown in the field at different CO_2 levels. Plant Physiol. 76: 244–249.

Hurd, R. G. 1968. Effects of carbon dioxide-enrichment on the growth of young tomato plants in low light. Ann. Bot. 32: 531–542.

Idso, S. B. 1989. Carbon dioxide and global change: Earth in transition. IBR Press, Tempe, AZ. 292 pp.

Idso, S. B., Kimball, B. A., Anderson, M. G. & Mauney, J. R. 1987. Effects of atmospheric CO_2 enrichment on plant growth: the interactive role of air temperature. Agric., Ecosys. & Environ. 20: 1–10.

Imai, K., Coleman, D. F. & Yanagisawa, T. 1985. Increase in atmospheric partial pressure of carbon dioxide and growth and yield of rice (*Oryza sativa* L.). Japan J. Crop Sci 54: 413–418.

Jones, P., Allen, L. H., Jr. & Jones, J. W. 1985. Responses of a soybean canopy photosynthesis and transpiration to whole-day temperature changes in different CO_2 environments. Agron. J. 77: 242–249.

Jones, P., Jones, J. W., Allen, L. H., Jr. & Mishoe, J. W. 1984. Dynamic computer control of closed environmental plant growth chambers. Design and verification. Trans. ASAE 27: 879–888.

Keeling, C. D., Bacastow, R. B., Carter, A. F., Piper, S. C., Whorf, T. P., Heimann, M., Mook, W. G. & Roeloffzen, H. 1989. A three dimensional model of atmospheric CO_2 transport based on observed winds: observational data and preliminary analysis. In: Peterson, D. H. (ed), Aspects of climate variability in the Pacific and the Western Americas. Geophysical Monograph 55: 165–235.

Kimball, B. A. 1983a. Carbon dioxide and agricultural yield: An assemblage and analysis of 430 prior observations. Agron. J. 75: 779–788.

Kimball, B. A. 1983b. Carbon dioxide and agricultural yield: An assemblage and analysis of 770 prior observations. WCL Report 14, U.S. Dept. of Agric., Agric. Res. Serv., 71 pp.

Kimball, B. A. & Idso, S. B. 1983. Increasing atmospheric CO_2: Effects on crop yield, water use, and climate. Agric. Water Man. 7: 55–72.

Kimball, B. A., Mauney, J. R., Guinn, G., Nakayama, F. S., Pinter, Jr., P. J., Clawson, K. L., Reginato, R. J. & Idso,

S. B. 1983. Series 021, Effects of increasing atmospheric CO_2 on yield and water use of crops. Office of Energy Research. U.S. Dept. of Energy, Washington, DC. 37 pp.

Kimball, B. A., Mauney, J. R., Nakayama, F. S. & Idso, S. B. 1989. Effects of CO_2 and changing climate variables on plants. In: Proc. of 20th annual anniversary meeting of Canada Grains Council. pp. 116–139. Winnipeg, Canada, 4–5 April 1989.

Kimball, B. A., Rosenberg, N. J. & Allen, L. H., Jr. (eds). 1990. Impact of CO_2, trace gases, and climate change on global agriculture. ASA Special Publication No. 53, Am. Soc. Agron., Madison, WI. 133 pp.

King, D. A., Bingham, G. E. & Kercher, J. R. 1985. Estimating the direct effect of CO_2 on soybean yield. J. Environ. Man. 20: 51–62.

King, K. M. & Greer, D. H. 1986. Effects of carbon dioxide enrichment and soil water on maize. Agron. J. 78: 515–521.

Kramer, P. J. 1981. Carbon dioxide concentration, photosynthesis, and dry matter production. Biosci. 31: 29–33.

Krupa, S. V. & Kickert, R. N. 1989. The greenhouse effect: impact of ultraviolet-B (UV-B) radiation, carbon dioxide (CO_2), and ozone (O_3) on vegetation. Environ. Pollut. 61: 263–393.

Lemon, E. R. (ed). 1983. CO_2 and plants: the response of plants to rising levels of atmospheric carbon dioxide. AAAS Selected Symposium 84. Westview Press, Boulder, Co. 280 pp.

Lincoln, D. E., Sionit, N. & Strain, B. R. 1984. Growth and feeding responses of *Pseudoplusia includens* (Lepidoptera: Noctuidae) to host plants grown in controlled carbon dioxide atmospheres. Environ. Entomol. 13: 1527–1530.

Masle, J., Farquhar, G. D. & Gifford, R. M. 1990. Growth and carbon economy of wheat seedlings as affected by soil resistance to penetration and ambient partial pressure of CO_2. Aust. J. Plant Physiol. 17: 445–487.

Mauney, J. R., Guinn, K. E., Fry, E. & Hesketh, J. D. 1979. Correlation of photosynthetic carbon dioxide uptake and carbohydrate accumulation in cotton, soybean, sunflower and sorghum. Photosyn. 13: 260–266.

Morison, J. I. L. 1988. Effect of increasing atmospheric CO_2 on plants and their responses to other pollutants, climatic and soil factors. Aspect. App. Biol. 17: 113–122.

Morison, J. I. L. 1985. Sensitivity of stomata and water use efficiency to high CO_2. Plant, Cell & Environ. 8: 467–474.

Morison, J. I. L. & Gifford, R. M. 1984a. Plant growth and water use with limited water supply in high CO_2 concentrations. I. Leaf area, water use and transpiration. Aust. J. Plant Physiol. 11: 361–374.

Morison, J. I. L. & Gifford, R. M. 1984b. Plant growth and water use with limited water supply in high CO_2 concentrations. II. Plant dry weight, partitioning and water use efficiency. Aust. J. Plant Physiol. 11: 375–384.

Mortensen, L. M. 1987. Review: CO_2 enrichment in greenhouses. Crop responses. Sci. Hort. 33: 1–25.

Mortensen, L. M. & Ulsaker, R. 1985. Effect of CO_2 concentration and light levels on growth, flowering and photosynthesis of *Begonia x hiemalis* fotsch. Sci. Hort. 27: 133–141.

Newman, J. E. 1989. The direct and indirect impacts of climate change on crop production. In: Proceedings for agricultural science centennial. pp. 101–129. Central Agric. Expt. Sta., Steinkjer, Norway. August 9–11, 1989.

Osbrink, W. L. A., Trumble, J. T. & Wagner, R. E. 1987. Host suitability of *Phaseolus lunata* for *Trichoplusia ni* (Lepidoptera: Noctuidae) in controlled carbon dioxide atmospheres. Environ. Entomol. 16: 639–644.

Owensby, C. E., Coyne, P. I. & Allen, L. M. 1989. I. Rangeland-Plant response to elevated CO_2. II. Large-Chamber system. Series 054, Response of vegetation to carbon dioxide. Office of Energy Research, U.S. Dept. of Energy, Washington, DC. 42 pp.

Parry, M. 1990. Climate change and world agriculture. Earthscan Pub. Ltd., London, 157 pp.

Patterson, D. T. & Flint, E. P. 1990. Implications of increasing CO_2 and climate change for plant communities and competition in natural and managed ecosystems. In: Kimball, B. A., Rosenberg, N. J. & Allen, Jr., L. H. (eds), Impact of CO_2, trace gases, and climate change on global agriculture. ASA Special Publication No. 53. pp. 83–110. Am. Soc. Agron., Madison, WI.

Patterson, D. T. & Flint, E. P. 1982. Interacting effects of CO_2 and nutrient concentration. Weed Sci. 30: 389–394.

Patterson, D. T., Highsmith, M. T. & Flint, E. P. 1988. Effects of temperature and CO_2 concentration on the growth of cotton (*Gossypium hirsutum*), spurred anoda (*Anoda cristata*), and velvetleaf (*Abutilon theophrasti*). Weed Sci. 36: 751–757.

Pendleton, D. F. & van Dyne, G. M. 1982. Research issues in grazinglands under changing climate. Carbon dioxide effects research and assessment program 013. Vol. II, Part 16. Environmental and social consequences of a possible CO_2-induced climate change. Dept. of Energy, Washington, DC. DOE/EV/10019-16. 43 pp.

Potvin, C. 1985. Amelioration of chilling effects by CO_2 enrichment. Physiol. Veg. 23: 345–352.

Prior, S. A., Rogers, H. H., Sionit, N. & Patterson, R. P. 1991. Effects of elevated atmospheric CO_2 on water relations of soybean. Agric., Ecosystems & Environ. 35: 13–25.

Prudhomme, T. I., Oechel, W. C., Hastings, S. J. & Lawrence, W. T. 1984. Net ecosystem gas exchange at ambient and elevated CO_2 concentrations in the tussock tundra at Tolik Lake, Alaska: An evaluation of methods and initial results. In: McBeath, J. H. (ed), Potential effects of carbon dioxide induced climatic changes in Alaska. No. 8–31. pp. 155–162. Univ. of Alaska, Fairbanks, AK, USA.

Radin, J. W., Kimball, B. A., Hendrix, D. L. & Mauney, J. R. 1987. Photosynthesis of cotton plants exposed to elevated levels of CO_2 in the field. Photosyn. Res. 12: 191–203.

Reardon, J. C., Lambert, J. R. & Acock, B. 1990. The influence of carbon dioxide enrichment on the seasonal patterns of nitrogen fixation in soybeans. Series 016, Response of vegetation to carbon dioxide. Office of Energy Research, U.S. Dept. Energy, Washington, DC. 94 pp.

Reddy, V. R., Acock, B. & Acock, M. C. 1989a. Seasonal carbon and nitrogen accumulation in relation to net carbon dioxide exchange in a carbon dioxide-enriched soybean canopy. Agron. J. 81: 78–83.

Reddy, V. R., Baker, D. N. & McKinion, J. M. 1989b. Analysis of effects of atmospheric carbon dioxide and ozone on cotton yield trends. J. Environ. Qual. 18: 427–432.

Reynolds, J. F. & Acock, B. 1985a. Modelling approaches for evaluating vegetation responses to carbon dioxide concentration. In: Strain, B. R. & Cure, J. D. (eds), Direct effects of increasing carbon dioxide on vegetation. DOE/ER-0238. pp. 33–51. Office of Energy Research, U.S. Dept. of Energy. Washington, DC.

Reynolds, J. F. & Acock, B. 1985b. Predicting the response of plants to increasing carbon dioxide: a critique of plant growth models. Ecol. Model. 29: 107–129.

Rogers, H. H., Bingham, G. E., Thomas, J. F., Smith, J. M., Israel, D. W. & Surano, K. A. 1982. Effects of long-term CO_2 concentrations on field-grown crops and trees. In: Brown, S. (ed), Global dynamics of biospheric carbon. pp. 9–45. U.S. Dept. of Energy, Washington, DC.

Rogers, H. H., Jeffries, H. E., Stahel, E. P., Heck, W. W., Ripperton, L. A. & Witherspoon, H. E. 1977. Measuring air pollutant uptake by plants: a direct kinetic technique. J. Air Poll. Control Assoc. 27: 1192–1197.

Rogers, H. H., Peterson, C. M., McCrimmon, J. N. & Cure, J. D. 1987. Response of soybean roots to elevated atmospheric carbon dioxide. Agron. Abst. pp. 100.

Rogers, H. H., Prior, S. A. & O'Neill, E. G. 1989. Response of roots in field grown cotton subjected to free air CO_2 enrichment (FACE). Am. Soc. Plant Physiol. Abstr. Adden. 1: 4.

Rogers, H. H., Sionit, N., Cure, J. D., Smith, J. M. & Bingham, G. E. 1984. Influence of elevated carbon dioxide on water relations of soybeans. Plant Physiol. 74: 233–238.

Rogers, H. H., Bingham, G. E., Cure, J. D., Smith, J. M. & Surano, K. A. 1983a. Responses of selected plant species to elevated CO_2 in the field. J. Environ. Qual. 12: 569–574.

Rogers, H. H., Heck, W. W. & Heagle, A. S. 1983b. A field technique for the study of plant responses to elevated carbon dioxide concentrations. J. Air Pollut. Contr. Assoc. 33: 42–44.

Rogers, H. H., Thomas, J. F. & Bingham, G. E. 1983c. Response of agronomic and forest species to elevated atmospheric carbon dioxide. Sci. 220: 428–429.

Rosenberg, N. J. 1981. The increasing CO_2 concentration in the atmosphere and its implication on agricultural productivity. I. Effects on photosynthesis, transpiration and water use efficiency. Clim. Change 3: 265–279.

Rosenberg, N. J. 1982. The increasing carbon dioxide concentration in the atmosphere and its implication on agricultural productivity. II. Effects through carbon dioxide induced climatic change. Clim. Change 4: 239–254.

Rosenberg, N. J., Kimball, B. A., Martin, P. & Cooper, C. F. 1990. From climate and CO_2 enrichment to evapotranspiration. In: Waggoner, P. E. (ed), Climate change in U.S. water resources. pp. 151–175. John Wiley and Sons, NY.

Rowland-Bamford, A., Nordenbrock, C., Baker, J. T., Bowes, G. & Allen, Jr., L. H. 1990. Changes in stomatal density in rice grown under various CO_2 regimes with natural solar irradiance. Environ. Exper. Bot. 2: 175–180.

Rundel, P. W., Ehleringer, J. R. & Nagy, K. A. (eds). 1989. Stable isotopes in ecological research. Springer-Verlag, NY. 525 pp.

Sasek, T. W. & Strain, B. R. 1989. Effects of carbon dioxide enrichment on the expansion and size of kudzu (*Pueraria lobata*) leaves. Weed Sci. 37: 23–28.

Schonfeld, M., Johnson, R. C. & Ferris, D. M. 1989. Development of winter wheat under increased atmospheric CO_2 and water limitation at tillering. Crop. Sci. 29: 1093–1086.

Schwarz, M. & Gale, J. 1984. Growth response to salinity at high levels of carbon dioxide. J. Exp. Bot. 35: 193–196.

Sinclair, T. R., Johnson, M. N., Drake, G. M. & Van Houtte, R. C. 1979. Mobile laboratory for continuous, long-term gas exchange measurements of 39 leaves. Photosyn. 4: 446–453.

Sionit, N. 1983. Response of soybean to two levels of mineral nutrition in CO_2-enriched atmosphere. Crop Sci. 23: 329–333.

Sionit, N., Hellmers, H. & Strain, B. R. 1982. Interaction of atmospheric carbon dioxide enrichment and irradiance on plant growth. Agron. J. 74: 721–725.

Sionit, N., Hellmers, H. & Strain, B. R. 1980. Growth and yield of wheat under carbon dioxide enrichment and water stress conditions. Crop Sci. 20: 687–690.

Sionit, N., Rogers, H. H., Bingham, G. E. & Strain, B. R. 1984. Photosynthesis and stomatal conductance with CO_2-enrichment of container- and field-grown soybeans. Agron. J. 76: 447–451.

Sionit, N., Mortensen, D. A., Strain, B. R. & Hellmers, H. 1981a. Growth responses of wheat to carbon dioxide enrichment with different levels of mineral nutrition. Agron. J. 73: 1023–1027.

Sionit, N., Strain, B. R. & Beckford, H. A. 1981b. Environmental controls on the growth and yield of okra. I. Effects of temperature and carbon dioxide enrichment at cool temperature. Crop Sci. 21: 885–888.

Sionit, N., Strain, B. R. & Hellmers, H. 1981c. Effects of different concentrations of atmospheric CO_2 on growth and yield components of wheat. J. Agric. Sci. 79: 335–339.

Sionit, N., Strain, B. R., Hellmers, H. & Kramer, P. J. 1981d. Effects of atmospheric carbon dioxide concentration and water stress on water relations of wheat. Bot. Gaz. 142: 191–196.

Smit, B., Ludlow, L. & Brklacich, M. 1988. Implications of a global climatic warming for agriculture: a review and appraisal. J. Environ. Qual. 17: 519–527.

Smith, J. B. & Tirpak, D. A. (eds). 1989a. The potential effects of global climate change on the United States. Appendix C – Agriculture, Vols. I & II. EPA, Office of Policy, Planning and Evaluation, Washington, DC.

Smith, J. B. & Tirpak, D. A. (eds). 1989b. The potential effects of global climate change on the United States. Report to Congress. EPA, Office of Policy, Planning and Evaluation, Washington, DC. 413 pp.

Strain, B. R. 1987. Direct effect of increasing atmospheric CO_2 on plants and ecosystems. Trend. Ecol. Evol. 2: 18–21.

Strain, B. R. & Cure, J. D. (eds). 1985. Direct effects of increasing carbon dioxide on vegetation. DOE/ER-0238. Office of Energy Research, U.S. Dept. of Energy. Washington, DC. 286 pp.

Strain, B. R. & Cure, J. D. 1986. Direct effect of atmospheric CO_2 on plants and ecosystems: a bibliography with abstracts. ORNL/CDIC-13. The Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, Oak Ridge, TN. 1032 entires.

Surano, K. A. & Shinn, J. H. 1984. A field study of elevated atmospheric CO_2 effects on yield, water use efficiency, and dry matter partitioning in *Zea mays*. UCRL Preprint 90771. Lawrence Livermore National Laboratory, Livermore, CA. 30 pp.

Thomas, J. F. & Harvey, C. N. 1983. Leaf anatomy of four species grown under continuous CO_2 enrichment. Bot. Gaz. 144: 303–309.

Valle, R., Mishoe, J. W., Jones, J. W. & Allen, Jr., L. H. 1985. Transpiration rate and water use efficiency of soybean leaves adapted to different CO_2 environments. Crop Sci. 25: 477–482.

Vu, J. C. V., Allen, Jr., L. H. & Bowes, G. 1989. Leaf ultrastructure, carbohydrates and protein of soybeans grown under CO_2 enrichment. Environ. & Exper. Bot. 29: 141–147.

Warrick, R. A. 1988. Carbon dioxide, climatic change and agriculture. The Geographical J. 154: 221–223.

Waggoner, P. E. 1984. Agriculture and carbon dioxide. Amer. Sci. 72: 179–184.

White, M. R. (ed). 1985. Characterization of information requirements for studies of CO_2 effects: Water resources, agriculture, fisheries, forests and human health. DOE/ER-0236. Office of Energy Research, U.S. Dept. of Energy, Washington, DC. 235 pp.

Wittwer, S. H. 1988. The greenhouse effect. No. 163. Carolina Biological Supply Co., Burlington, NC. 16 pp.

Wittwer, S. H. 1985. Carbon dioxide levels in the biosphere: Effects on plant productivity. CRC Press 2: 171–198.

Wong, S. C. 1980. Effects of elevated partial pressures of CO_2 on rate of CO_2 assimilation and water use efficiency in plants. In: Pearman, G. I. (ed), Carbon dioxide and climate: Australian research. pp. 159–166. Australian Academy of Science, Canberra.

Yoshida, S. 1973. Effects of CO_2 enrichment at different stages of panicle development on yield components and yield of rice (*Oryza sativa* L.). Soil Sci. Plant Nutr. 19: 311–316.

Zangerl, A. R. & Bazzaz, F. A. 1984. The response of plants to elevated CO_2. II. Competitive interactions between annual plants under varying light and nutrients. Oecologia 62: 412–417.

Zeroni, M. & Gale, J. 1989. Response of 'Sonia' roses to salinity at three levels of ambient CO_2. J. Hort. Sci. 64: 503–511.