

Research on the Response of Vegetation to Elevated Atmospheric Carbon Dioxide¹

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ABSTRACT

The global rise in atmospheric CO₂ is an established phenomenon. Irrespective of whether a CO₂-induced climate change occurs, it is abundantly clear that the earth's mantle of vegetation will be directly affected by increased CO₂ levels. Carbon dioxide is essential for plant growth (plants obtain C from CO₂ in the atmosphere); a higher level of CO₂ will increase the rate of photosynthesis. Quantitative information on the CO₂-induced growth response for field situations is needed for assessments of (i) possible benefits to agriculture, (ii) the amount of fossil C that can be sequestered by CO₂-accelerated growth of the biosphere, and (iii) unknown or unidentified effects of CO₂ on the physiology, structure, and function of plants and ecosystems. Along with knowledge of CO₂ effects on climate and other factors, information on direct plant effects will be used in comprehensive evaluations of policy options related to increasing atmospheric CO₂. Herein, a discussion of the plan by the U.S. Department of Energy (DOE) to address the CO₂ problem is presented along with research results from two programs, one agricultural and the other ecological.

Additional Index Words: CO₂ growth response, field CO₂ data, phytotron CO₂ data, productivity, research plan, water use efficiency.

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The global rise in atmospheric CO₂ is a well-established phenomenon; the preindustrial level of CO₂ was probably between 468 and 504 mg m⁻³ (mg m⁻³ = 1.8 × ppm at 25°C) (Bojkov, 1983); that level has risen to 612 mg m⁻³ and will continue to increase in the future. Irrespective of a frequently discussed CO₂-induced climate

change, it is clear that the earth's mantle of vegetation will directly respond to increased levels of CO₂. Plants form the support system for the rest of the biosphere, producing food by photosynthesis, a solar driven process. Since C is a chief input into this food-producing process, any appreciable response of plants to changing CO₂ levels could have far-reaching implications. Furthermore, the essential role of plants in the global geochemical C system makes them a logical starting point in assessments of the consequences of increased levels of CO₂ from combustion of fossil fuel. An understanding of plant responses to elevated CO₂ is important when considering future energy and food policies.

In a survey of environmental consequences of CO₂, Wittwer (1979) suggested that increased CO₂ would be beneficial to agriculture. Broadly speaking, elevated CO₂ was regarded as a resource rather than a conventional air pollutant, and the challenge was to find ways to capitalize on its value to agriculture. An initial research agenda for investigating direct effects of CO₂ on plants was prepared from a 1980 survey by the U.S. Department of Energy (U.S. DOE, 1980). The agenda

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first called for an international scientific conference to review known and uncertain information about the effects of CO₂ on plants. Accordingly, the Athens Conference was held in May of 1982, and it provided a comprehensive review of CO₂ and Plants edited by Lemon (1983).

About 130 internationally recognized scientists summarized the state of knowledge of C metabolism, physiological effects, plant growth and development, microbial effects, and terrestrial and aquatic plant communities with respect to the direct effects of CO₂.

BACKGROUND

National Research Plan on the Response of Vegetation to Elevated Carbon Dioxide

Expanded interest in the direct effects of CO₂ on plants is related to the potential benefits to agriculture, the need to understand and quantify fundamental effects of CO₂ on plant physiology and growth, and the need to understand ecosystem responses in terms of how plants and communities will change and how much CO₂ can be sequestered by CO₂-enhanced growth of the global biosphere. Based on the 1980 research agenda, and taking into account recommendations of the Athens Conference, the U.S. DOE prepared a research plan (U.S. DOE, 1984) with the following objectives:

1. To determine yield of major crops in relation to CO₂ concentration and other key variables affecting crop productivity
2. To determine fundamental effects of long-term exposure to elevated levels of CO₂ on plant physiology and growth
3. To evaluate ecosystem responses to elevated levels of CO₂ in terms of productivity, altered composition of plant communities, and C change from CO₂ stimulation of growth.

Enhancement of photosynthesis by increased levels of CO₂ is a common thread that connects these objectives, and the principal components of this research are shown in Fig. 1. The general logic is to determine the effects on physiology and fundamental growth processes. In addition, yield and productivity of crops and species growth differences within ecosystems are evaluated. Crop yield and ecosystem response models are needed for predictions of crop and ecosystem responses at the twofold elevated CO₂ levels expected within the next 100 yr. Detailed structure and logic of the research on vegetation responses to CO₂ are described in Fig. 2.

The relationship of vegetation response research to other key components of the government's comprehensive CO₂ research program is given in Fig. 3. The U.S. DOE is the lead agency for coordinating research on CO₂, and this function is conducted by the Carbon Dioxide Research Division in the Office of Energy Research, Basic Energy Sciences. This program, summarized in Fig. 3 and described in more detail in the U.S. DOE (1983) Summary Research Plan, is developing the scientific understanding for evaluating possible policy options and government actions in connection with atmospheric CO₂ changes. Emphasis presently is placed on activities covered in the cross-hatched region of Fig. 3.

Integrated approaches for achieving the plan's research objectives require acquisition of laboratory and field data on the effects of CO₂ on plant physiology and growth. Simultaneously, models will be developed for predicting responses directly related to CO₂, as well as the combined effects of CO₂ and other environmental variables affecting plant growth. Emphasis will be placed on field research when this approach holds promise for achieving objectives. Scientific understanding of CO₂-induced effects is a first priority followed by interpretations and assessments of economic benefits and costs to agriculture, as well as potential impacts on ecosystems. The general priorities are (i) to evaluate crop response in relation to increased atmospheric CO₂, including studies of the CO₂ enhancement or reduction of photosynthesis in relation to other environmental stresses (water/nutrients) for both crop and noncrop plants; (ii) to estimate ecosystem productivity and net C storage related to photosynthetic enhancement; and (iii) as data become available, to begin evaluating effects of CO₂ on com-

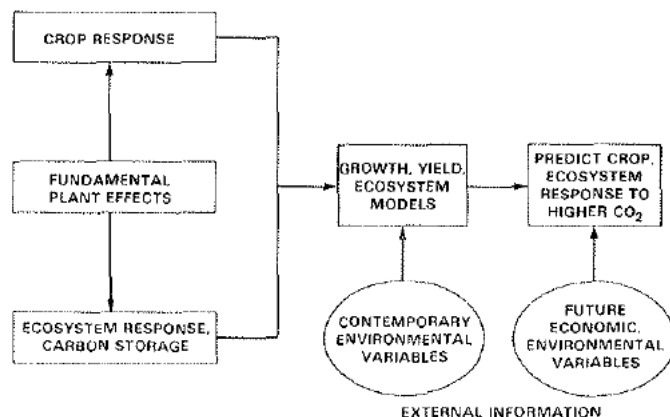


Fig. 1. Components of research on responses of plants to CO₂.

petition, composition, and other species relationships of crops and natural communities.

The plan places considerable emphasis on modeling plant responses to CO₂. Not only are models needed for predictive purposes, but they are also useful as a conceptual framework for evaluating existing data; model experiments and sensitivity analysis also help define critical data needs. Model validation is emphasized to improve confidence and credibility of predictions.

The short-range product of the research is the information required for a 1985 state-of-the-art report on the response of vegetation to CO₂. Over the longer range (5–15 yr), improved understanding of CO₂ effects on crops and ecosystems will foster better predictions of future vegetation responses in a higher CO₂ world. Periodic evaluations of the state-of-the-art in CO₂ research will be incorporated into comprehensive assessments related to energy policy, as shown in Fig. 3.

Key Literature

In addition to the Athens Conference (Lemon, 1983), other recent publications about CO₂ and plant growth include the National Research Council Report (NRC, 1983) on *Changing Climate*, Kimball's review (1983) of responses of crop plants to increased CO₂, and Kramer's (1981) generalizations about the growth of plants exposed to enhanced levels of CO₂. In the NRC study, Woodwell noted that photosynthesis of ecosystems is difficult to measure, and that both photosynthesis and growth are governed by complex influences of light, water, nutrients, space, CO₂, and other factors. He concludes that there is essentially no database for treating direct CO₂ effects and that these interactions and long-term responses of ecosystems cannot be predicted at this time. In the same NRC study, Waggoner conservatively estimated nominal effects of CO₂ on crop yields. Waggoner's (1984; NRC, 1983) analysis relied heavily on Kimball's (1983) review, which reported yield responses ranging from 0.1 to 0.9% per 1.8 mg m⁻³ (1 ppm) increase. Even for controlled glasshouse and growth chamber conditions, considerable variability apparently exists in the yield responses of crop and horticultural species. Waggoner's comparative low value evidently was used for the estimates of future CO₂ effect on yield, apparently because plants experience various stresses under field conditions, whereas experimental data summarized by Kimball conventionally represent more or less ideal growth conditions of optimal temperature, water, nutrients, and pest control. Most of the CO₂-effect-on-yield literature reported by Kimball is based on indoor experiments. More recently, Rogers and coworkers (1983a, b, c; 1984a), Thomas (1984), and Thomas and Harvey (1983) obtained data with open-top chambers under field conditions.

Kramer's (1981) review posed tentative generalizations about growth responses of plants to enhanced concentrations of CO₂: (i) large differences exist among various species; (ii) responses are greater with indeterminate plants [e.g., cotton (*Gossypium hirsutum* L.), soybean [*Glycine max* (L.) Merr.]] than determinate plants [e.g., corn (*Zea mays* L.), sorghum [*Sorghum bicolor* (L.) Moench], sunflower (*Helianthus annuus* L.)]; (iii) plants with C₃ metabolism [e.g., soy-

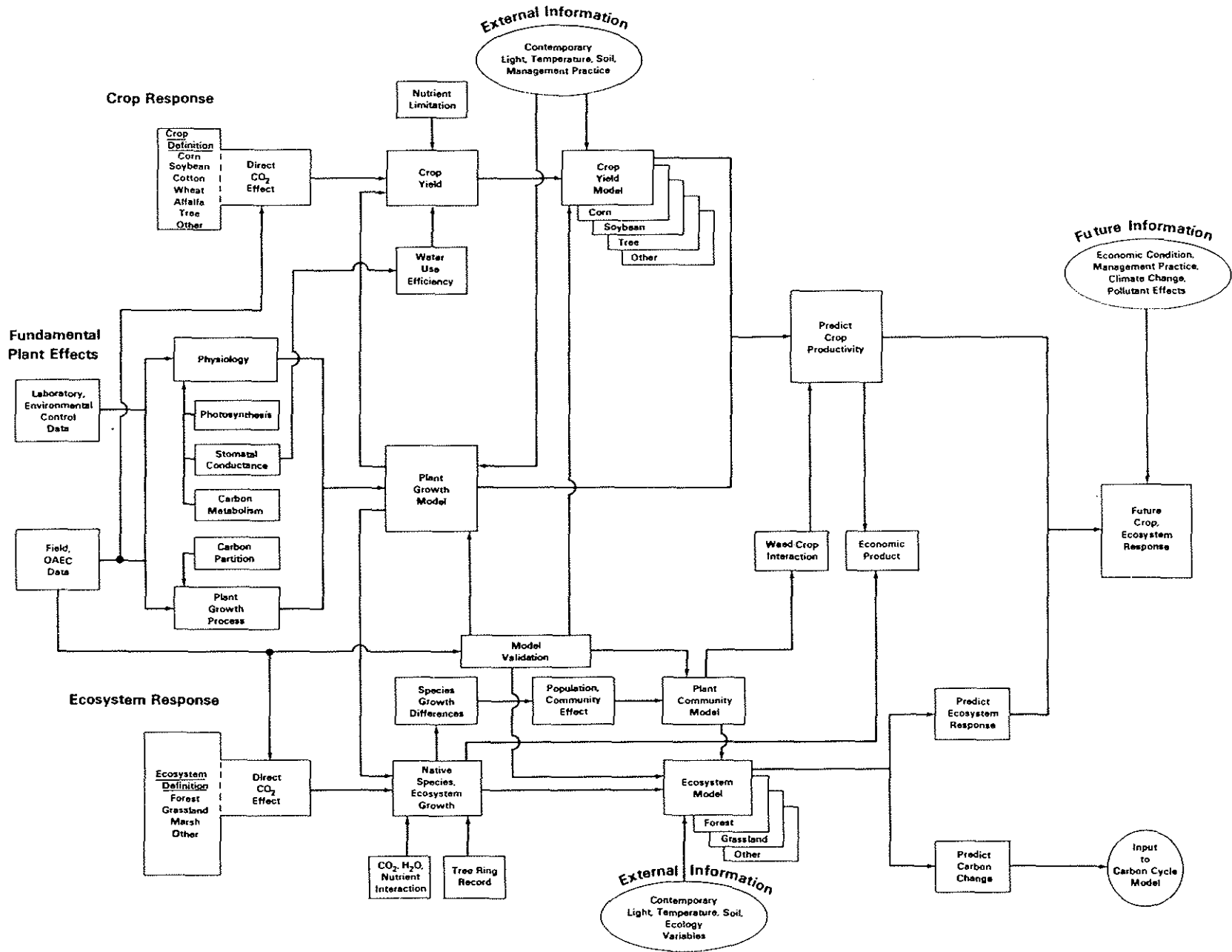


Fig. 2. Detailed logic of research on responses of plants to CO₂.

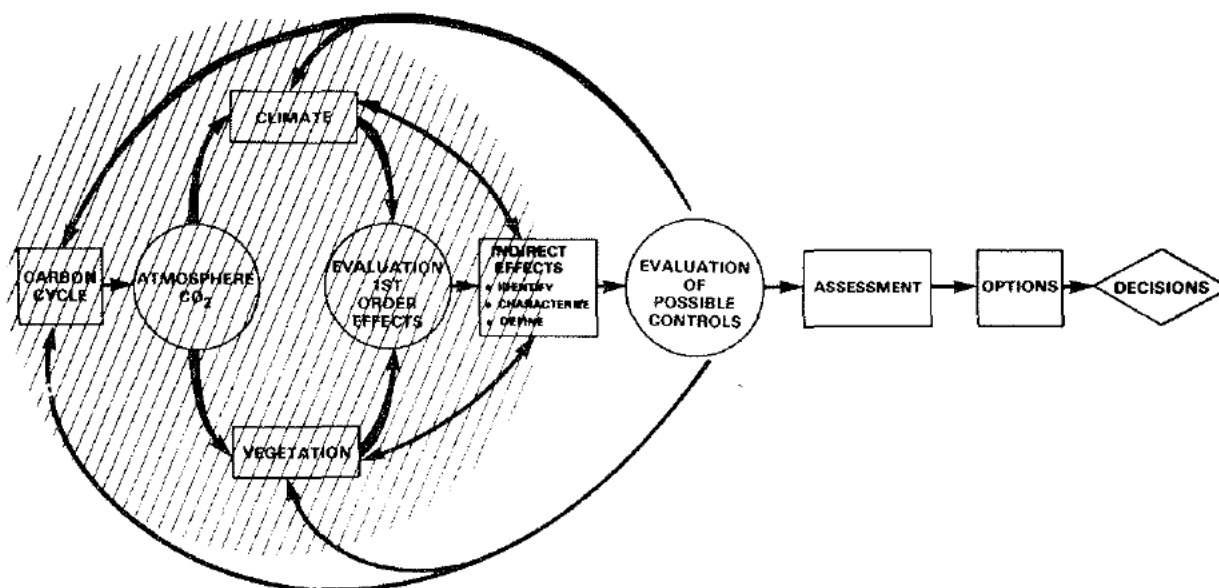


Fig. 3. Structure of the Carbon Dioxide Research Program.

bean, sunflower, velvetleaf (*Abutilon theophrasti* Medic.) respond more than plants with C₄ metabolism [corn, sorghum, itchgrass (*Rottboellia exaltata* L.f.)]; and (iv) the largest response occurs in seedlings and decreases or ceases as plants grow older. Most of the data are from monoculture-type experiments; essentially no data are available on growth responses for mixtures of species and assemblages of plants at the ecosystem scale of organization. Kramer's review also drew attention to many uncertainties, especially for perennial species where responses to long-term CO₂ exposure has not been determined. Complex interactions between CO₂-induced growth and the effects of water, nutrients, temperature, and other stresses affecting plant growth are not adequately documented.

Previous observations clearly suggest that CO₂ plays a central role in photosynthesis and plant growth. Possible future effects on crop productivity and ecosystem change could be significant, but the database is very limited for making quantitative estimates of crop and ecosystem productivity, especially under field conditions. Much of the existing information provides qualitative insight about plant growth in relation to increasing CO₂ levels, but presently neither data nor models are adequate to quantify and predict key physiological and structural responses to enriched CO₂ atmospheres. Presently, potential long-term implications for agriculture, forestry, and native ecosystems are based on data from short-term experiments. Very few observations of responses for the entire life cycle of plants are available. Because of these uncertainties and apparent deficiencies in the database, systematic research on crop and native species has been initiated. A plan (U.S. DOE, 1984) has been formulated for expanding the research, and the balance of this report provides examples of initial research findings.

RESULTS AND DISCUSSION

Research in the Field

The small amount of available data collected under actual field conditions (Kramer, 1981) has prompted additional research in this area. The rationale is that by exposing plants to known concentrations of CO₂ under as near field conditions as feasible, a realistic description of plant responses to CO₂ could be made.

At the outset of these field studies, which extended over four growing seasons (1980-1983), techniques were developed for the generation of large-scale test atmospheres in the field (Rogers et al., 1983b). Open-top ex-

posure chambers, which are essentially open-ended baffles, were ventilated at about 1.06 m³ s⁻¹ using a plenum box equipped with a 0.75-HP fan and a particulate filter. Each chamber (2.4 m high by 3.0 m in diam) was constructed of a structural aluminum frame covered by clear polyvinyl chloride (PVC) film. Pure CO₂ from a receiver (capacity: 12 700 kg) was continuously injected, day and night, into the ventilation air stream from planting until final harvest. This air stream was distributed from the plenum box into the chamber through the perforated inner wall of the double-walled bottom half of the cover. Five CO₂ concentrations, including ambient and ranging from 612 to 1710 mg m⁻³, were continually monitored and held at the predetermined levels above ambient.

Plants were grown either in large containers (16.5 L) or in the ground using standard plant culture practices. During the first season, corn ('Golden Bantam'), soybean ('Ransom'), loblolly pine (*Pinus taeda* L.), and sweetgum (*Liquidambar styraciflua* L.) were studied. During the next three seasons, in-depth studies were conducted on soybean ('Bragg').

STRUCTURE

Soybean growth increased with CO₂ concentration (Fig. 4). Greater node number, height, stem diameter and length, branching, and leaf area and number were observed. Rooting appeared to increase both in density and depth. Pod number also increased. Similar enhancement of growth in corn plant parts was observed. In the two trees, pine and sweetgum, wood volume and density were greater at high CO₂ concentrations.

In the more detailed studies of soybean plants, the rate of leaf development was again shown to be increased by high levels of CO₂. Increased development of intercellular spaces in the spongy mesophyll was responsible for the greater thickness of soybean leaves at high CO₂ levels. Changes in the spongy mesophyll also

accounted for diurnal fluctuations in total leaf thickness. Leaves were generally thinnest in early morning and thickest late at night, except the leaves from chambers at 1161 and 1703 mg m⁻³ CO₂ concentrations, which exhibited a drastic reduction in thickness at 1600 h EDT (Thomas, 1984).

PHYSIOLOGY

Field studies showed that elevated CO₂ ameliorates plant water stress. Decreased stomatal conductance with increasing CO₂ was documented for corn, soybean, and sweetgum (Rogers et al., 1983a). Leaf water potentials and leaf starch, sugar, and chlorophyll contents of stressed soybean plants all confirmed that plants grown in high CO₂ levels could avoid mild stress through reduced water consumption (Rogers, 1984b). During water stress, soybeans grown in lower CO₂ treatments showed greater leaf tissue damage, lower leaf water potential, and lower stomatal conductance than did plants grown at higher CO₂ levels. Plants grown in low CO₂ environments showed stomatal closure at lower leaf water potentials than high CO₂ level plants. Even with greater growth from high CO₂ levels, their lower rate of water use delayed, and thus prevented, severe water stress during conditions of low moisture availability. The effects of CO₂ on growth appeared to be greatest during water stress.

The effect of CO₂ on field-grown soybean nodulated with either of two *Rhizobium* strains has been studied (Israel & Rogers, 1984). No strain by CO₂ interaction was observed. The ratio of whole plant N to whole-plant dry matter decreased as CO₂ increased. Although nodule mass increased with high CO₂ levels, there was no significant increase in N₂-fixing activity, with the result that specific N₂-fixing activity of nodules actually dropped.

Net photosynthesis increased with higher CO₂ levels for soybean and sweetgum (C₃ plants), but remained constant or decreased slightly for corn (a C₄ plant).

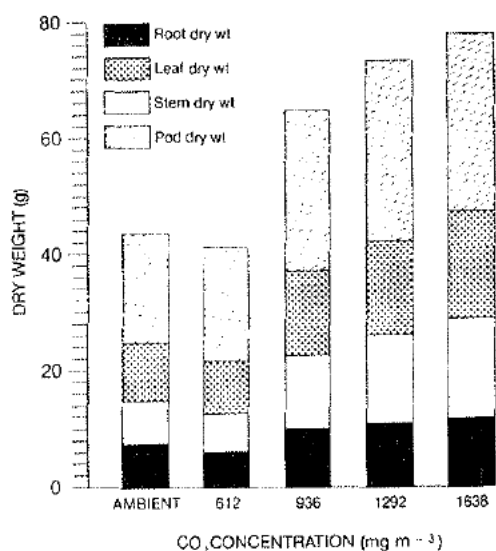


Fig. 4. Carbon dioxide vs. total dry wt of roots, stems, leaves, and pods of soybean at 11 weeks from planting ($n = 6$).

Gross photosynthesis also increased for soybean, but remained nearly constant or increased slightly for corn. Water use efficiency (ratio of C fixed to water consumed) was shown to increase for all three species (Rogers et al., 1983c).

In a study of carbohydrate partitioning, data suggested that the capacity for formation of sucrose (the transport carbohydrate) is limiting even at ambient CO₂, and that this capacity is reduced further by elevated CO₂ (Huber et al., 1984). Extra C fixed at elevated CO₂ levels is partitioned entirely into starch. Plant growth increased when some of the additional starch was mobilized at night. Current soybean varieties may be unable to maximize the benefits of elevated CO₂, a limitation that the science of plant breeding and genetic modification or development should take into account.

YIELD

Soybean seed yield increases with increasing CO₂ levels. Seed quality (such as fat, protein, fiber, and moisture) was generally unaffected by rises in CO₂ level. Germination and early development of the seeds produced in field chambers under different CO₂ regimes showed no significant differences (Rogers et al., 1984a).

Information on soybean productivity from the open-top chamber experiments has been combined with other data to form generalized yield-response functions (Allen et al., 1983). Composite soybean seed yield data from four locations (Acock, 1982; Allen, 1982; DeWitt & Lambert, 1982; Rogers, 1981; Rogers & Bingham, 1983) across the southeastern USA are summarized in Fig. 5 (Allen et al., 1984). In these experiments the desired CO₂ levels (range: 612–1910 mg m⁻³) were maintained with controlled environment, soil-plant-atmosphere research units, or with open-top chambers. Relative

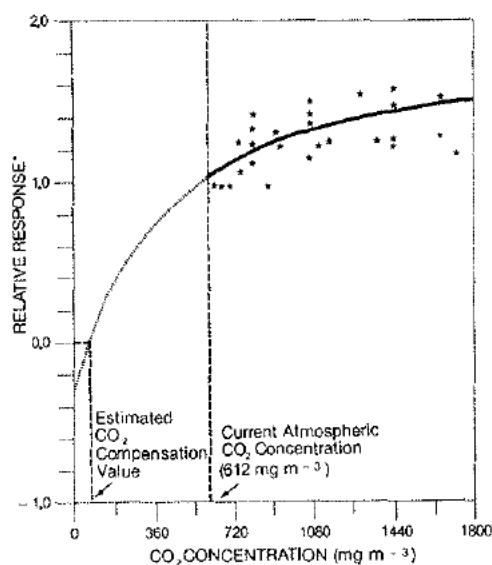


Fig. 5. Carbon dioxide vs. relative seed yield response for 'Ransom', 'Bragg', and 'Forest' varieties (Allen et al., 1983). Data obtained from Gainesville soil-plant-atmosphere (SPAR) experiments (Allen, 1982); From Mississippi State SPAR experiments (Acock, 1982); from Clemson SPAR experiments (DeWitt & Lambert, 1982); and from Raleigh open-top chamber experiments (Rogers, 1981; Rogers & Bingham, 1983). All data were normalized to 340 ppm = 1.0.

seed yield (value at elevated CO₂ divided by value at ambient CO₂) ranged from about 1.1 times the ambient at +135 mg m⁻³ to about 1.5 times the ambient at +1080 mg m⁻³ of CO₂. This unique data set on the effect of increased CO₂ concentrations on harvestable yield suggests a productivity increase of 30% for a CO₂ doubling. This level of atmospheric CO₂ is expected 75 yr from now if present rates of fossil fuel CO₂ emission remain unchanged.

An important objective of the CO₂ program is the development of methods or models for predicting growth and yield of various crop and native plants in relation to rising atmospheric CO₂. The soybean seed yield data were fit by Allen et al. (1984) with a nonlinear model (e.g., rectangular hyperbola) of the Michaelis-Menton (MM) form to describe the range of yield-CO₂ relationships; the model can also predict an asymptotic response of about 1.83 (relative to the response at ambient CO₂) at infinite atmospheric CO₂ concentration (Allen et al., 1984). Using the equation derived from the modeled response, seed yield response can be calculated for other atmospheric CO₂ concentrations (e.g., at 1800 mg m⁻³, the yield is 1.48 times that for soybeans grown at 594 to 612 mg m⁻³). Also, solving the Michaelis-Menten equation when the yield response is zero computes the CO₂ crop compensation point (i.e., 70 mg m⁻³ at the zero intercept, Fig. 5). At 70 mg m⁻³, the value registers on the low end of the range measured for soybean photosynthesis and would be a reasonable first approximation for seed yield.

Research in Phytotron-Controlled Environments

It is clear from the above results that plants in single-species stands will respond directly and indirectly to modest increases in the CO₂ content of the global atmosphere. Responses will be specific to each type of organism, and different responses by different species growing side by side make it probable that ecosystems will change structurally and functionally in the future. The rate and magnitude of change will certainly depend on the amount of CO₂ injected into the atmosphere. The database, however, does not now exist on which predictions can be made for ecosystem responses to changing global CO₂ concentration (Strain & Bazzaz, 1983).

Research at the Duke University Phytotron has focused on whole plant responses, with attention to physiological measurements of net photosynthesis, stomatal conductance, tissue water potential, chlorophyll, and starch concentration. In addition, much effort has been directed to developing the talent, techniques, and hardware for laboratory studies of direct, long-term effects of increasing atmospheric CO₂ levels on plants.

GROWTH RESPONSES

It is clear that increasing CO₂ concentration affects the growth form of some species. Alaska pea plants (*Pisum sativum* L.) grown at 630 and 1800 mg m⁻³ CO₂ showed that a 1800 mg m⁻³ CO₂ atmosphere significantly increased the rate of lateral branch, flower bud, and flower and fruit development over an environment with 630 mg m⁻³ CO₂ (Paez et al., 1980, 1983).

Most of the C₃ species that have been measured have shown substantially increased root/shoot ratios with increased CO₂ concentrations. Leaf area per plant increased with increasing CO₂, while crown density of each plant usually increased at higher CO₂ concentrations. Although there are several published papers that state that plants produce more branches at high CO₂ concentrations, this has not always been observed. However, increased leaf size (area), which increased the apparent bushiness of the plant crowns, has been observed.

A comparative study recently was completed with determinate and indeterminate growth forms of tomato (*Lycopersicon esculentum* Mill.) and peas (Paez, 1982). Determinate, annual plants developed at faster rates when grown at high CO₂ levels but were not significantly taller or bushier by senescence. Indeterminate varieties, on the other hand, developed faster and, as long as temperature and photoperiod allowed, the plants continued to grow and accumulate more nodes, branches, leaves, and reproductive structures at high CO₂ levels. If this type of inter- and intraspecific growth form response occurs in ecosystems, important changes in community structure through time can be predicted.

PHOTOSYNTHETIC PATHWAY

Plants with the C₃ photosynthetic pathway (e.g., soybean and the weed velvetleaf) were compared with C₄ species (e.g., corn and the weed itchgrass) by Patterson and Flint (1980). Basically, they concluded that under increased atmospheric CO₂ levels, weeds with the C₃ pathway will become more competitive with C₄ crops, while weeds with the C₄ pathway will become less competitive with C₃ crops.

Riechers³ is conducting an investigation of two C₃ grass species [western wheatgrass (*Agropyron smithii* Rydb.) and green needlegrass (*Stipa viridula* Trin.)] and two C₄ grass species [little bluestem (*Andropogon scoparius* Michx.) and bluegrama (*Bouteloua gracilis* HBK. Lag.)]. These four species are dominant members of the short-grass prairie. At 1215 mg m⁻³ CO₂, the growth of all four species increased significantly. At 1800 mg m⁻³ atmospheric CO₂, however, growth response was more dependent on photosynthetic pathway; C₃ species were essentially the same height at 1215 and 1800 mg m⁻³ CO₂; C₄ species, however, declined in growth at CO₂ concentrations above 1215 mg m⁻³. The 1800 mg m⁻³ plants were not significantly different in height from the plants grown at 630 mg m⁻³ CO₂. These measurements suggest that C₄ species will become less competitive with C₃ species at some atmospheric CO₂ concentrations.

SOIL WATER STRESS

Growth, transpiration, stomatal conductance, tissue water potential, osmotic and turgor pressure, and water use efficiency have been measured against soil water depletion in the following studies: Sionit et al. (1982) {wheat (*Triticum aestivum* L.), sugarbeet (*Beta vulgaris*

³G. Riechers, 1983. Unpublished results. Department of Botany, Duke University, Durham, NC.

L.), okra [*Abelmoschus esculentus* (L.) Moench], soybean}, Tolley (1982) (sweetgum, loblolly pine), Paez (1982) (pea, tomato varieties), Wulff and Strain (1982) {beggar-lice [*Desmodium paniculatum* (L.) DC.]}, and Riechers³ (prairie grasses).

In all of these studies, it was observed that increasing CO₂ concentration decreased stomatal conductance and transpiration per leaf surface area. Water was conserved and tissue water potential remained higher in plants at a higher atmospheric CO₂ concentration than the ambient controls. Osmotic pressures were higher in plant leaves grown in a high CO₂ concentration, increasing turgor pressure and allowing growth of the high CO₂ plants to continue longer into each drought stress period. This may partially explain why all of these measurements have shown more dry weight accumulation during water stress periods in the plants grown at high CO₂ concentrations compared with plants grown at normal ambient levels. Water-use efficiency (ratio of C fixed to water consumed on a leaf-surface-area basis) also increased significantly with increasing CO₂ concentrations because of decreasing water loss with constant or increasing net photosynthesis.

MINERAL NUTRITION INTERACTIONS

Growth, total C and N content, and C/N ratios as affected by the general fertility level of the soil and atmospheric CO₂ level have been measured in wheat (Sionit et al., 1981). As the supply of soil nutrients decreased and atmospheric CO₂ content increased, plant tissue became relatively poor in total N content. This caused the C/N ratio to increase significantly. Melillo of the Ecosystems Center, Marine Biology Laboratory (MBL) at Woods Hole, MA has taken some of the plant tissue from the aforementioned experiment to use in controlled experiments on decomposition. It is his hypothesis that the C/N ratio affects the metabolic activity of some decomposers (Melillo et al., 1982). If N-poor tissue does decompose more slowly, nutrient cycling rates would be affected in ecosystems. In addition, where would be an increased amount of C, N, and P stored in duff and litter (Vitousek et al., 1982), which might lead to decreased system productivity.

PHOTOSYNTHETIC PHOTON FLUX DENSITY EFFECTS

Irradiance and CO₂ concentration are known to be interactive as they affect net photosynthesis (Reynolds et al., 1980). Because of the effects observed in one long-term study (Wulff & Strain, 1982), however, it is not clear whether instantaneous irradiance level or irradiance integrated through time is most critical.

For sweetgum grown at 600 and 1200 $\mu\text{mol m}^{-2} \text{s}^{-1}$ photosynthetic photon flux density (PPFD) for 14 h (30.2 $\text{mol m}^{-2} \text{d}^{-1}$ and 60.5 $\text{mol m}^{-2} \text{d}^{-1}$, respectively) considerable chlorosis and anthocyanin pigmentation occurred at the higher irradiance level (Tolley, 1982). At 1800 mg m^{-3} CO₂ and 60.5 $\text{mol m}^{-2}/14 \text{ h}$ total PPFD, plants were even more chlorotic and higher in anthocyanin. Hypothetically, the pigmentation changes were caused by excessive carbohydrate production and accumulation. In the vegetative phase, there were insufficient growth sites for utilization of photosynthates

(Clough et al., 1981). Work with subterranean clover (*Trifolium subterraneum* 'Dinninup') (Cave et al., 1981) and beggar-lice (Wulff & Strain, 1982) suggests that carbohydrates accumulated in the leaves and the developing starch grains damaged the chloroplasts.

Research (Sionit et al., 1982) with four species at three CO₂ concentrations (630, 1215, and 1800 mg m^{-3}) and two PPFD levels (600 and 1200 $\mu\text{mol m}^{-2} \text{s}^{-1}$) showed that CO₂ enrichment at both light levels significantly enhanced tiller and branch formation in three C₃ species (e.g., wheat, soybean, and bean). Significant increases in the number of seeds produced per plant were also correlated with increasing CO₂ concentration and irradiance. In contrast, corn, a C₄ species, responded less to CO₂ increases than the C₃ crops at a given PPFD. These comparative analyses show that plant responses to CO₂ increase are species specific and are predictable within a growth form.

In summary, the primary objective of the detailed studies in the Duke Phytotron has been to determine basic differences or similarities in CO₂-related patterns of C allocation in plants representative of major growth forms. It seems clear that some species will produce more dry matter than others at high CO₂ concentrations. Thus, questions of the responses of neighboring plants and associated animals and microbes come to the forefront.

SUMMARY AND CONCLUSIONS

Logic, objectives, and approaches are summarized for the government's research plan for investigating responses of plants to increased atmospheric CO₂. The plan addresses (i) crop yield in relation to different levels of atmospheric CO₂, (ii) effects on plant physiology and growth from long-term exposure to elevated CO₂, and (iii) responses of ecosystems (in terms of productivity, altered plant communities, and C change) from CO₂ enhancement of growth. This information will provide an improved understanding of plant responses to CO₂ and will be used in balanced assessments related to future energy, environmental, and food production policies. New results related to the research plan concerning responses of crop and noncrop species to elevated atmospheric CO₂ are also summarized. Using the open-top chamber approach, new *field* data confirm increased growth and productivity of plants at CO₂ levels above ambient, but less than 1800 mg m^{-3} . Experiments using controlled environments have provided data on detailed physiological responses (photosynthesis, water use, stomatal conductance); these data are improving scientific understanding of the interaction of CO₂-growth response and other environmental variables. Coupled with other DOE/USDA/NSF-supported research on CO₂, the results of this study are contributing to an improved knowledge base for estimating how vegetation will respond to higher atmospheric CO₂ levels in the future.

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