



United States Department of Energy

Office of Energy Research
Office of Basic Energy Sciences
Carbon Dioxide Research Division
Washington, D.C. 20545

DOE/ER-0238
December 1985
Dist. Category UC-11

DOE/ER--0238

DE86 007397

DIRECT EFFECTS OF INCREASING CARBON DIOXIDE ON VEGETATION

Edited by:

Boyd R. Strain and
Jennifer D. Cure

Duke University
Durham, NC 27706

MASTER

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CONTRIBUTORS

BASIL ACOCK

Crop Simulation Research Unit
U.S. Department of Agriculture
Mississippi State University
Mississippi State, Mississippi

L. HARTWELL ALLEN, JR.

U.S. Department of Agriculture
University of Florida
Gainesville, Florida

FAKHRI A. BAZZAZ

Department of Organismic and
Evolutionary Biology
Harvard University
Cambridge, Massachusetts

JENNIFER D. CURE

Botany Department
Duke University
Durham, North Carolina

BERT G. DRAKE

Environmental Research Center
Smithsonian Institution
Rockville, Maryland

KEITH GARBUTT

Department of Organismic and
Evolutionary Biology
Harvard University
Cambridge, Massachusetts

DAVID M. GATES

Biological Station
University of Michigan
Ann Arbor, Michigan

BRUCE A. KIMBALL

Water Conservation Laboratory
U.S. Department of Agriculture
Phoenix, Arizona

WALTER C. OECHEL

Systems Ecology Research Group
San Diego State University
San Diego, California

JAMES F. REYNOLDS

Department of Biology
New Mexico State University
Las Cruces, New Mexico

HUGO H. ROGERS

National Tillage Machinery Laboratory
U.S. Department of Agriculture
Auburn, Alabama

BOYD R. STRAIN

Botany Department
Duke University
Durham, North Carolina

WILLIAM E. WILLIAMS

Department of Organismic and
Evolutionary Biology
Harvard University
Cambridge, Massachusetts



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FOREWORD

Over the ages, human communities have had little or no effect on the Earth's global climate. Humans have accounted for only a small part of all of the species on the planet, and their activities have been essentially benign relative to the global atmosphere. Historically, communities were small and distant from each other and transportation was slow and difficult. Very little energy was consumed, with the burden of work being carried by humans and their domesticated animals with the assistance of elementary machinery.

Science and technology paved the way for the rapid societal changes of the 20th century. With the development of transportation and communication systems plus the machinery for industrial and agricultural production, global energy consumption grew by more than 10-fold from 770 million metric tons (10^{15} grams) of coal equivalent (mmtce) in 1900 to more than 9000 mmtce in 1984. Most of this energy was produced by burning fossil fuels. The world's population increased by threefold during the same period from 1.6 billion to 4.8 billion. (The American billion, 10^9 , is the same as the British milliard, 10^9 .) Urbanization, which resulted in a major increase in demand for energy, recorded an almost 20-fold increase in 84 years, as measured by the number of urban areas with populations greater than 1 million, expanding from 13 to 247 worldwide.

This immense increase in energy use is changing the layer of gases that constitutes the Earth's atmosphere, which in turn controls global climate. So, for the first time in the planet's history, humans are truly involved in a change of their environment.

Carbon dioxide (CO_2), a naturally occurring constituent of the atmosphere, is also the product of human activities—the burning of fossil fuels for energy and the clearing of land for agriculture and urbanization. Toward the end of the 19th century, Arrhenius calculated that a doubling of the CO_2 concentration would raise the average temperature by 5° or 6°C . Chamberlain later developed a hypothesis that related causes of glacial periods and the depletion of the atmospheric CO_2 concentration. Tolman, a student of Chamberlain, described the basic roles of the ocean in absorbing atmospheric CO_2 and in moving and storing it globally.

Another important role of CO_2 was also recognized more than a century ago. Von Liebig demonstrated that plants get their carbon for photosynthesis and growth from the air. By this process, a relative atmospheric constancy is maintained where assimilation by plants is roughly balanced by CO_2 exhalation by animals. This notion of constancy became dogma until modern measurements clearly showed a change in the atmospheric concentration of CO_2 due to human intervention.

It is now known that the atmospheric CO₂ concentration in 1900 was approximately 300 parts per million by volume (ppm) (indicated by recent measurements of glacial ice cores by Oeschger). However, it wasn't until 1938 that Callendar presented the first substantive data showing that the concentration of CO₂ in the atmosphere was increasing and suggested that the increase might affect the Earth's climate. After another 20 years Keeling began to monitor the atmospheric CO₂ concentration at the Mauna Loa Observatory in Hawaii. The measurements of atmospheric CO₂ in 1958 showed the annual average concentration was 316 ppm; it was approximately 345 ppm in 1985. Platts outlined theories to explain the relationship between atmospheric CO₂ and climate in 1956, and, soon after, Revelle and Suess described the relationship between CO₂ in the atmosphere and in the oceans, and Kaplan enlarged upon the role of CO₂ in the atmosphere in terms of the global heat balance.

In 1977 leading scientists assembled in Miami Beach, Florida, to discuss the current understanding of the carbon cycle, that is, the dynamics of carbon exchanges within the Earth's atmosphere, land, and oceans that determine the atmospheric CO₂ concentration. They also reviewed possible consequences of increases in atmospheric CO₂. In addition, they identified significant gaps in the knowledge base and made recommendations for research.

Since then, significant research has been carried out by the international scientific community. The Department of Energy (DOE), the lead United States agency in the study of CO₂, and other agencies including the National Science Foundation, National Oceanic and Atmospheric Administration, National Aeronautics and Space Administration, United States Geological Survey, United States Department of Agriculture, and Environmental Protection Agency, following the recommendations of the science community, conducted and have supported research activities in universities, national laboratories, industry, and other institutions.

Looking forward to the 21st century, the DOE believed it was important to "take an accounting" to see how far this considerable effort had come in 8 years in answering the questions that were previously posed and in determining future research directions. Accordingly, the Carbon Dioxide Research Division, Office of Basic Energy Sciences, of the DOE is publishing this series of four State-of-the-Art (SOA) volumes:

- *Direct Effects of Increasing Carbon Dioxide on Vegetation* — to determine the plant response to increased atmospheric CO₂ and develop the capability to predict crop and ecosystem responses to CO₂ enrichment.
- *Atmospheric Carbon Dioxide and the Global Carbon Cycle* — to understand the mechanics of and quantify the sources, sinks, and exchanges of carbon between all elements of the global carbon system — the atmosphere, the biosphere, the oceans — including anthropogenic effects.
- *Projecting the Climatic Effects of Increasing Carbon Dioxide* — to project the magnitude and rate of the potential climate changes that could result from the increasing atmospheric CO₂ concentration.
- *Detecting the Climatic Effects of Increasing Carbon Dioxide* — to detect the changes in climate resulting from the increasing atmospheric CO₂ concentration and to isolate the climate changes from those caused by other contributing factors (natural or anthropogenic).

An index and cross-reference volume accompanies the set of volumes. Two companion reports are also being published:

- *Characterization of Information Requirements for Studies of CO₂ Effects: Water Resources, Agriculture, Fisheries, Forests, and Human Health.*
- *Glaciers, Ice Sheets, and Sea Level: Effects of a CO₂-Induced Climatic Change*, from the National Research Council's (NRC) Committee on Glaciology of the Polar Research Board.

These complementary reports aid in ensuring that "the accounting" of CO₂ research activities for the past years encompasses the entire spectrum of research.

The SOAs document what is known, unknown, and uncertain about CO₂ data, analyses, and modeling capabilities. They outline potential avenues of research for reducing critical unknowns and uncertainties. More than 70 scientists from five nations have participated in the preparation of these volumes. Each chapter and each complete SOA volume has gone through extensive peer review by the American Association for the Advancement of Science (AAAS); this review, however, does not imply that AAAS endorses the statements or recommendations presented in these volumes.

These technical reports provide the basis for a Statement-of-Findings (SOF) report. While studies over the last several years have clearly shown that increasing CO₂ concentrations have the potential for significant impacts on our physical environment, these studies have not yet provided an adequate basis for addressing questions about the fundamental relationships between the benefits and impacts of various energy systems on society's activities. The SOF will summarize what we know and do not know and the degree of certainty of our knowledge. It will also present the rationale for further studies. These studies will be needed to provide an accurate scientific basis for assessments of the potential impacts of energy-related activities.

The citizens of today's nations have the responsibility for the stewardship of all the Earth, including their actions which may affect its climate. Exercising this responsibility requires an understanding of atmospheric CO₂ and its effects. Once understood, stewardship then becomes nurturing rather than unrecognized neglect.

Scientists have created the building blocks for this understanding, and the scientific community has recognized its responsibility to more fully understand CO₂-induced effects on our global environment. Through research, as we look towards the 21st century, the application of science will ensure that the additional understanding required for nurturing our planet Earth will be developed.

Sincere thanks go to everyone who has participated in developing the SOAs and companion reports. Special thanks goes to the coordinator/editors, Jennifer D. Cure, Frederick M. Luther, Michael C. MacCracken, Boyd R. Strain, John R. Trabalka, Margaret R. White, and the NRC Committee Chairman Mark Meier; their respective chapter authors; and to the AAAS, Roger Revelle, Chairman of the Climate Committee, and David M. Burns of the AAAS staff.

We hope these definitive, scientific statements will motivate scientists to recommend explicit approaches for reducing the critical uncertainties that now exist in order to permit decision making within the next decade that is based on data, learning, understanding, and wisdom.

Frederick A. Koomanoff, Director
Carbon Dioxide Research Division
Office of Basic Energy Sciences
U.S. Department of Energy



PREFACE

Carbon dioxide (CO₂) enhancement of plant growth is one important direct effect of rising atmospheric CO₂. Through photosynthesis, plants produce food and fiber from light and carbon assimilated as CO₂ and form the foundation of the Earth's life support system. Rising atmospheric CO₂ is thus an essential input to the food-producing process, and effects of CO₂ enrichment described in this document have far-reaching implications for agricultural and ecological productivity. Establishing an empirical foundation of plant response to more CO₂ and developing the capability to predict crop and ecosystem responses to CO₂ enrichment are research goals that have been pursued in the DOE-led program. This State-of-the-Art (SOA) report on the direct effects of CO₂ on vegetation summarizes the current state of knowledge; it identifies uncertainties and suggests where more research is needed to assure understanding and delineates data and modeling requirements for future predictions. Important progress has been made over the past 5 years since the plant science community urged that more attention be given to direct effects of CO₂ enrichment. Enhanced plant growth and yield from more CO₂ is now widely recognized in different scientific and public sectors as an important element of the CO₂ problem.

While there have been gains in knowledge about a few crop plants, considerable ignorance remains about responses of native species and ecosystems to CO₂ enrichment. Only a few native species or ecosystem types have been investigated. Competition among species in relation to CO₂-induced growth differences is essentially unknown. Many interactions involving CO₂ enrichment and other physical and biological variables affecting plant growth have not been studied. Among the physiological processes directly affected by CO₂ that are not well understood are those involving net transpiration and whole-plant water use, where CO₂ reduces stomatal conductance but increases leaf size. Nutrient requirements to sustain increased photosynthesis and growth at enriched levels of CO₂ are not understood. This SOA volume examines some key responses and identifies research needed to resolve these and other key unknowns.

The great diversity of plant types and environmental situations of the Earth's vegetative cover requires that modeling be used to predict future responses to CO₂ enrichment. Whole-plant growth models have been developed, and the methodology appears useful for predicting crop yield. The job is incomplete, however, because the simulations require validation, and the models need to be extended from several to many other species. Suitable models for evaluating responses of plant communities and ecosystems to CO₂ enrichment do not now exist.

Although it is not currently possible to accurately state magnitudes of many effects of CO₂ enrichment, there are strong indications from the work that has been done for this SOA volume that rising atmospheric CO₂ represents a resource for agriculture and food production rather than a conventional air pollutant. There are potentially beneficial consequences for crop productivity, although differential plant response to CO₂ may affect weed-crop competition relationships. Likewise, differential growth effects in ecological situations are unpredictable because what often serves as a resource for one species may produce quite different responses for others.

The scientific community is just beginning to quantify and predict with confidence the direct effects of more CO₂, and the emerging knowledge can no longer be ignored in future discussions of energy, food, and water policy. The state of knowledge reported herein and new information emanating from the report's research recommendations will substantially aid balanced assessments of direct CO₂ effects and environmental benefits or impacts of a higher CO₂ world.

A special thanks goes to Boyd Strain and Jennifer Cure, Duke University, for their contributions to this document and to editors, authors, and researchers. As a leading authority on the plant effects of CO₂, Dr. Strain participated from the inception through all stages of the production. The contributions of the authors, from their critical analysis to their well-written chapters, are greatly appreciated.

Roger C. Dahlman, Program Manager
Carbon Dioxide Research Division
Office of Basic Energy Sciences
U.S. Department of Energy

EDITOR'S PREFACE

If climate is changed by an increase in global atmospheric carbon dioxide (CO_2) concentration, as discussed in two volumes of this series of State-of-the-Art (SOA) reports, plants will respond causing many changes in global carbon pools as described in another volume. This volume addresses an item of less certainty: that of the direct effects of global CO_2 enhancement on green plants and on ecosystems.

We know from decades of horticultural research in greenhouses that increasing CO_2 concentration in the atmosphere will stimulate plant growth. Ecologists and crop scientists, however, paid little attention to this knowledge, assuming that the atmosphere was well mixed and relatively stable in concentration. With the establishment of the Keeling curve of atmospheric CO_2 on Mauna Loa, however, field scientists were jolted into reality. CO_2 is not constant in the global atmosphere but is chronically increasing on a trajectory roughly paralleling annual fossil fuel consumption.

CO_2 is an essential environmental resource. It is required as a raw material for the orderly development of all green plants. As the availability of CO_2 increases, perhaps reaching two to three times the concentration prevailing in preindustrial times, plants and all other organisms dependent on them for food will be affected. Humans are releasing a gaseous fertilizer into the global atmosphere in quantities sufficient to affect all life. The purpose of this volume is to consider the direct effects of global CO_2 fertilization on plants and thus on all other life.

The preparation of this SOA volume on the direct effects of increasing CO_2 was preceded by an international conference held in Athens, Georgia, in May 1982. One hundred and thirty scientists from eight countries worked for 5 days to summarize knowledge and discuss uncertainties. The efforts were recorded in workshop reports that were molded into eight chapters and published in 1983 in a book titled *CO_2 and Plants*.¹ This book reviewed all aspects of plant response to CO_2 progressing from a chapter on biochemical aspects to chapters on aquatic and terrestrial ecosystems.

With the book *CO_2 and Plants* as an authoritative background statement, it was possible for us to concentrate on current research progress and needs in this SOA report. Principal investigators of DOE-funded research projects on vegetation response were asked to review knowns, unknowns, and uncertainties in their areas of expertise and experience. Of particular interest was a statement of the problem, a review of research progress and techniques, enumeration of the uncertainties, and listing of research needs.

¹ Lemon, E. (ed.). 1983. *CO_2 and Plants: The Response of Plants to Rising Levels of Atmospheric Carbon Dioxide*. AAAS Symposium Vol. 84. Westview Press, Boulder, Colorado.

As editors, we are extremely grateful to the chapter authors of this book. The assignment to write this SOA came at a time when most of the research projects were just moving into high gear. The principal investigators had to juggle tight research schedules with the heavy demands on their writing schedules. The chapter authors and their research teams responded in exemplary fashion, as demonstrated by the comprehensive nature of their chapters.

We also wish to thank the AAAS reviewers and the many *ad hoc* reviewers who commented on the chapters as they were being prepared. The extensive comments of many readers greatly improved the manuscripts. Although we assume final responsibility for the content of this volume, we do so with the realization that many shortcomings were eliminated following the excellent advice of the reviewers.

Across the country there are a great number of secretaries and typists breathing sighs of relief that the SOA project is at last completed. The burden was particularly heavy for Cindy Ballard and Sandra Cargas at Duke University, who processed more words in this effort than they care to recall. Their CPTs were still smoking when the completed manuscript went to the publisher. We offer all of them our sincere gratitude.

The employees of The MAXIMA Corporation in Bethesda, Maryland, contributed in many ways to the completion of this project. Editorial and graphics support are perhaps the most obvious contributions for which we are grateful. Beyond that, however, Jon Findley assisted in meetings, helped organize material, and prodded us when production schedules began to slip. Jon and Mike Madden have our gratitude. The index was prepared at Oak Ridge National Laboratory by Fred O'Hara. Lynn Alford of Duke University read every word of every chapter several times. Her assistance was of particular value to us in the final hectic days of completing the manuscript.

Boyd R. Strain
Jennifer D. Cure
Editors

AAAS REVIEW

In commissioning and publishing a summary of the state of current knowledge about the secular increase of atmospheric carbon dioxide and its effects, the Department of Energy has performed a valuable service. These volumes may prove to be the most comprehensive assembly to date of scientific results about this issue.

The Committee on Climate of the American Association for the Advancement of Science was asked to organize peer reviews of the component chapters of the books. These reviews were conducted in the traditional manner of refereeing scientific papers. We identified experts whom we knew to be well qualified, and we invited them to review anonymously an individual chapter in their field. In transmitting draft manuscripts to the reviewers, we alerted them to the ambitious nature of the "state-of-the-art" project, and particularly to the difficulties of adequately treating the many uncertainties.

The careful attention reviewers devoted to their tasks was gratifying, and indicates the importance of this issue to the world scientific community. More than 300 specialists from 23 countries gave the draft papers a careful and thorough reading and offered detailed suggestions for revision and improvement. The authors and editors thus had available a significant input from their professional colleagues as they sought to improve their drafts. But the decision as to how to use the reviewers' suggestions was the responsibility of the author(s) of the paper and the editor(s) of the books.

These volumes make clear that investigating the causes and effects of alterations to the atmosphere is an exceedingly complex undertaking, touching a wide gamut of scientific disciplines. It hardly is surprising that there were (and are) differences of interpretation.

I am grateful to the many anonymous reviewers and to my colleagues on the Committee. I hope that we have been helpful to the authors and editors in their very challenging task.

Roger Revelle, Chairman
AAAS Committee on Climate

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EXECUTIVE SUMMARY

Carbon dioxide (CO₂) is an essential compound for life on this planet. Understanding the direct effects of increasing atmospheric CO₂ concentration on vegetation is an issue independent of all other global CO₂ effects. Plants absorb CO₂ from the atmosphere and become the food supply for other organisms. Because plant growth is limited by the amount of CO₂ in the atmosphere, it is critical to understand how the world's vegetation will respond as the CO₂ concentration of the global atmosphere continues to increase. This volume addresses that issue.

At preindustrial concentrations of approximately 280 parts per million by volume (ppm), atmospheric CO₂ almost certainly was a limiting factor in agricultural productivity and ecological interrelationships. As agricultural technology has been increasing yields throughout this century, atmospheric CO₂ also has been increasing, and by 1985 was approximately 345 ppm. Although there is a considerable range of uncertainty, estimates of growth enhancement range from 0.5 to 2.0% for each 10 ppm increase in atmospheric CO₂. Thus, it is possible that some fraction of the increased agricultural yield that has occurred in this century is due to increased atmospheric CO₂ concentration.

Research has shown, however, that not all species respond to CO₂ in the same manner or magnitude. Plants with high conductance for the diffusion of CO₂ will have greater growth than plants with lower CO₂ conductance. Because many agricultural weeds have high conductance, they could have a comparatively larger growth response to increased CO₂ than some desirable crop species that have lower conductance.

It also has been observed in studies that the food quality of some plant tissues declines as atmospheric CO₂ increases. For example, soybean leaves became carbon rich and nitrogen poor as atmospheric CO₂ was increased without the addition of more soil nitrogen. An insect pest, the soybean looper, feeding on the biochemically changed leaves had to consume more leaf tissue to gain an equal amount of protein nitrogen. Thus, although agricultural productivity may increase in the future, there also may be larger increases of insect feeding rates and weed growth, and this would affect the difficulty and expense of pest control. A full understanding of the many direct and associated secondary effects of CO₂ enrichment is needed for future agricultural productivity to be engineered wisely.

In nonagricultural ecosystems, the direct effects of increasing atmospheric CO₂ are largely unknown. Most experiments to date have been conducted on agricultural species in typical monocultural conditions (with few or no other species cultivated in the same area). In addition, most experiments with non-crop species have been conducted for short periods in inadequately controlled environments. Results obtained in such studies are of little use for the prediction of ecosystem responses to long-term, increasing atmospheric CO₂ concentration. Pertinent studies of ecosystems, the functional ecological units that include both organisms and their abiotic environment, are almost nonexistent, although a few have been initiated within the last 2 years.

In contrast to agricultural systems that are managed to ensure rapid turnover of carbon, the nonmanaged terrestrial biosphere stores large amounts of carbon for long periods of time. Thus, some ecosystems have the potential to sequester a percentage of the increasing atmospheric CO₂. However, a number of secondary responses may occur in conjunction with an increased rate of CO₂ fixation. These include changing interactions among competing plants, altered population of animals, and greater incidence of disease, which may tend to reduce the net carbon content of ecosystems. Thus, the hypothetical carbon-sequestering potential of these systems may not be realized.

This volume summarizes the current knowledge of the direct effects of increasing atmospheric CO₂ on vegetation and the subsequent effects on ecosystems. The indirect effects on plants that might occur from a CO₂-induced climate change (e.g., changes in precipitation or temperature) are only considered in terms of how they modify the direct responses of plants to increasing CO₂ concentration. This executive summary provides an overview of research approaches and technical procedures, discusses our information base, and provides research recommendations where possible.

ANALYTICAL PROCEDURES

Analysis of the direct effects of CO₂ on vegetation has been underway for more than 50 years. Horticulturists realized years ago that adding CO₂ to the air in greenhouses would enhance plant growth. Many commercial greenhouses are routinely CO₂ enriched to accelerate plant development and increase economic yield, and the use of CO₂-enriched greenhouses in research on plant response is still a major technique in use worldwide. The availability of natural sunlight in greenhouses is a desirable feature, but temperature and humidity control in greenhouses is frequently inadequate for research purposes.

Beginning about 1960, environmentally controlled rooms called plant growth chambers were developed, allowing the study of the interaction between CO₂ and other factors: the control and monitoring of temperature, light intensity, relative humidity, air flow, and water and nutrient status of the soil. Although CO₂ control was sometimes employed, sufficient light intensity and routine CO₂ enrichment were not generally available for adequate CO₂ experiments until the late 1970s. Therefore, much of the early data on plant responses to CO₂ enrichment are unreliable.

Because of inadequate environmental control in standard greenhouses and inadequate light intensity of most plant growth chambers, small leaf chambers have been used to enrich part of a plant with CO₂ to determine CO₂ responses. Leaf chambers have great potential for basic research on individual plant physiology and biochemistry. The major weaknesses of this approach are that only part of the plant is CO₂ enriched and that short-term measurements do not adequately describe plant responses associated with anatomical or morphological characteristics that may be CO₂ responsive. Furthermore, it is unknown how well observations using leaf chambers describe whole-canopy processes such as photosynthesis or transpiration.

Phytotrons are large, integrated environmental control facilities that have extensive control and monitoring capabilities. Light, CO₂, water vapor, and soil conditions all can be maintained at realistic levels for long periods. Thus, plants can be germinated and maintained continuously under sufficient environmental control to allow determination of whole-plant, long-term CO₂ response. Both phytotrons and improved plant growth chambers have produced much of the dependable information now available on plant responses to long-term CO₂

enrichment. Only one of the phytotrons in the United States is being used now in CO₂ enrichment research.

Movable greenhouses and controlled environment boxes that may be erected over field crops or intact native ecosystems have been used, but rarely. An exceptional facility of 12 individual chambers with computerized control of CO₂ and other environmental factors is currently in use in permafrost tundra in Alaska. These movable facilities operate in undisturbed field environments under natural light, and provide one of the best approaches available. Large-sized plants, however, require large volume chambers, and environmental control becomes progressively more difficult and expensive as chamber volume increases.

Open top chambers have been used also in field studies of the effects of elevated CO₂ levels. They are essentially plastic enclosures placed around field crops. Air is drawn into a box by fan, enriched with CO₂, and blown through the chamber; air enters near the bottom and flows out the open top. Open top chambers have the great advantage of only partially modifying the field environment; consequently, control of CO₂, temperature, and humidity is not as good as in closed chambers.

The CO₂ enrichment of an uncontained space in a field or ecosystem may be attempted with a free-air-CO₂-enrichment (FACE) facility. In this approach, the CO₂ concentration in the air is raised to desired levels by releasing the gas from a network of pipes. Therefore, the data from these experiments would be free of chamber-induced environmental error. This system has been used for studies of toxic air pollutants (e.g., ozone, sulfur dioxide), but only few experimental attempts have been made with CO₂. Long-term open-air enrichment experiments would provide the best possible validation data for models; however, there are meteorological problems with such research, as well as uncertainties about plant physiological responses to large, short-term variations to CO₂ concentration.

In addition to the actual field experiment approaches, microcomputers and microprocessors are now available that allow more complete and better monitored environmental control than was possible when research was initiated on CO₂ effects.

Requirements for improvements in analytic procedure and, in turn, improvements in the data will necessitate the following:

Improve lighting and CO₂ control in controlled environment growth chambers to be used for CO₂ enrichment research.

Increase the use of existing phytotron facilities for CO₂ enrichment research.

Increase the number of sites where field chambers are in use, and utilize closed or open top chambers as appropriate to meet scientific objectives and practical problems of plant size.

Continue to examine technical aspects of free-air-CO₂-enrichment.

All of the systems described here need to be improved by increasing the use of state-of-the-art computerized control and monitoring systems. This will help improve both the methodology and the data for analysis.

MODELING APPROACHES

Models are needed to integrate various data about crop and ecological systems; to predict plant, crop, and ecosystem response to variable CO₂; and to evaluate interactions such as direct effects of CO₂ and impacts of climate change. It is expected that virtually all physiological processes in plants will be affected as carbohydrate levels change in response to CO₂ enrichment. Furthermore, because plants differ significantly from each other, it is not possible to empirically examine

all crops or all native species. Hence, there is a need to model what is known about plant responses and to apply these models to different crop and native species to eventually predict future responses to the changing global environment.

The models that will be the most useful will be mechanistic in nature and capable of extrapolative prediction (CEP). Models that are only capable of simple interpolative prediction (CIP) are inadequate for detailed predictions because empirical information on long-term global CO₂ enrichment is not available. However, semimechanistic CIP models may be useful for first approximations. Because no models have yet been developed completely and validated to accommodate a CO₂ increase as an environmental variable for vegetation response, extrapolative predictions are not possible at this time. The modeling approaches recommended as most effective for predicting direct effects of CO₂ on vegetation include the following:

Develop semimechanistic CIP models of ecosystems and cropping systems that contain those CO₂ responses and environmental interactions for which there is a solid data base. Avoid the development of simple, empirical CIP models that are based on limited data. These will not be able to predict the response of vegetation to increased CO₂ concentrations and other environmental variables outside the range of data on which they were based.

Develop CEP models for some of the most important agricultural and native plant species, validate them, use sensitivity analysis to decide how they may be simplified with least loss of accuracy, and aggregate these simpler models into ecosystem and cropping system models.

Explore ways of aggregating CEP single-species models where complexity can be kept at a minimum level.

Introduce stochastic elements in these models to provide a measure of uncertainty in any prediction error.

These modeling approaches require the following data:

Controlled environmental data from growth chambers and phytotrons are needed for building the CEP models. Also needed are more experiments where measurements are made on plants during field releases of CO₂. These will provide the data suitable for developing semimechanistic CIP system models or for validating comprehensive mechanistic CEP models.

In the absence of field-release data, the next best alternative is data from environmentally monitored field enclosures. Only in this way can the environment experienced by all of the plants in the enclosure be known and therefore taken into account when analyzing the data.

A detailed, quantitative description of the above- and belowground environment experienced by plants throughout their life is an essential part of any data set as well as being part of the process needed to modify and improve models for prediction purposes.

The least expensive way of validating the mechanistic models is to first validate them using field data at ambient CO₂ concentration (to elucidate their response to other environmental variables) and then to validate their response to CO₂ using controlled environment data.

AGRICULTURAL SPECIES

Because farmers want to obtain the highest product yield at the highest profit possible, they have selected crop species that can be environmentally or genetically

managed. Environmental management includes irrigation, plowing, fertilization, pest control, and planting density. CO₂, the primary source of carbon for terrestrial plants, is a fertilizer. Indiscriminate fertilization is never done by the wise or successful farmer.

However, in the case of global atmospheric CO₂ enrichment, industrialized peoples are indiscriminately fertilizing the entire world. Some crops will presumably increase in economic yield. For example, most species of the 3-carbon photosynthetic pathway show plant growth and productivity increase of 30-50% for a doubling of atmospheric CO₂. Some weed species, however, are known to be more responsive to CO₂ increases than their crop competitors. Therefore, more growth of all plant species is not desirable.

Existing information derived from an extensive survey of 10 important crop species suggests that species (and cultivars of species) differ in their response to CO₂ enrichment. To date, there is not sufficient information to predict which species will benefit most. However, what is known is that some species will respond greatly and some not at all as CO₂ continues to increase. In addition, there is insufficient information about interactions between CO₂ concentration and other environmental factors that affect plant growth. For example, as CO₂ increases in the atmosphere, stomata (variable pores in plant leaves) partially close. Net photosynthesis remains high because of increasing concentration gradient, but water loss through the closing pores declines. The ratio of CO₂ fixed to water vapor lost is termed water-use efficiency. This is one of the most important potential direct effects of increased levels of CO₂ on plants. It could greatly affect the economics of irrigation and extend dry-land agriculture into dryer regions.

Recommendations with respect to agricultural species include the following:

Experimentation in field and controlled environments is needed to elucidate the interactive mechanisms between the environmental factors of temperature, soil, water and nutrient availability, light, gaseous pollutants, soil salinity, and CO₂ concentration. Understanding these relationships is critical to further model development.

Work is needed on the extrapolation of leaf and whole-plant measurements to the prediction of whole-crop response. Plants should be grown in realistic field configurations along with measurements of whole canopy to determine if single-plant measurements can be extrapolated to whole crops.

Experiments should be planned so that crop plants are continuously exposed for their entire growth cycle to a CO₂-enriched atmosphere. Measurements of plants grown for only short periods in high CO₂ environments must be used with great caution. Measurements of CO₂ response made at one stage in a plant's development cycle are not necessarily representative of responses at other stages of growth.

Experiments should be planned and conducted with closer cooperation between experimenters and modelers. Studies should be designed to ensure that results can contribute to the development or validation of plant growth models.

It is impractical to investigate all crop species. Therefore, the following crop species, listed in order of decreasing priority, are recommended for study: wheat, corn, white potato, soybean, rice, sweet potato, sorghum, and cotton.

Mechanistic information on several organ-level responses is particularly missing. Work should be initiated on the following areas: root growth, leaf net photosynthesis rates of plants grown from seed at various CO₂ concentrations, and carbon allocation relationships between photosynthetic leaves and nonphotosynthetic growing points.

NATIVE SPECIES AND UNMANAGED ECOSYSTEMS

Whereas the biochemical and physiological processes are basically similar in agricultural and native species, these species operate in basically different environments and have been subjected to greatly different selective pressures. Agricultural cultivars have been selected for rapid growth and allocation of the maximum amount of carbon to harvestable organs. The plants are buffered from environmental stresses by irrigation, fertilization, pest control, and so forth, without regard to characteristics that ensure survival and reproduction in the wild. In contrast, native species are subjected to natural selection. Thus, the characteristics that result in desirable crop plants are quite different from those that ensure survival and reproduction of successful native plants. It is possible that native species are now responding genetically to CO₂-induced environmental change and that the adaptive change occurring will accelerate as environmental change accelerates.

Empirical information on native species is scarce. Few long-term ecological studies have been completed and these all have been in controlled environments on isolated plant individuals. More realistic field studies have been initiated but little information is available.

From the scattered information available on native species, speculations have been made about the following:

Representative ecosystems should be studied for sufficient periods of time to determine the long-term equilibrium response to CO₂ enhancement.

For native annuals, initial growth rate may increase but final weight and size may not be affected by increased CO₂. For perennial plants the increases may be accumulated from year to year and carbon may be sequestered in ultimately larger plants. However, in ecologically balanced ecosystems with animals feeding on the plants, disease organisms operating, and plants competing for light, water, and nutrients, it is uncertain whether ecosystem production will increase.

Water-use efficiency (WUE) may be more important in unmanaged ecosystems than it is in agriculture. Plants with the largest net response to the combined effects of water saving and increased growth may outcompete, and thus assume dominance over, less responsive plants. This will be particularly true in semiarid rangelands.

Increased atmospheric CO₂ may induce nutrient impoverishment in the soil of some ecosystems by accumulation of minerals in larger plant bodies. If tissue becomes nutrient poor, decomposition rates may decline, increasing the tendency for minerals to remain organically sequestered. Studies should be initiated on tissue quality, the secondary ecosystem responses or herbivory, and decomposition responses to changing tissue chemistry.

Long-term carbon sequestering has been studied in only one ecosystem: the permafrost tundra of North Slope, Alaska. Without climate change, increasing CO₂ will probably increase carbon sequestering in permafrost areas. Significant warming, however, may change precipitation and ice-melting dynamics, inducing carbon release from the peats as atmospheric CO₂ increases. This would induce a positive feedback, the net result of which has not been examined.

Long-term studies of total ecosystem dynamics are required but technical difficulties are major. This work may have to be restricted to small-stature ecosystems because of financial and technical limitations.

PLANT COMMUNITIES

Differences in response to an elevated CO₂ concentration among the members of an ecological community, interacting through time, are likely to result in changes to the species composition of the community. The composition of communities is a result of differential species response to environmental variables and the resultant competition for limited resources. As CO₂ continues to increase in the future, those species most responsive to the CO₂ increase, interacting with any climate changes that occur, will become dominant. Some species may merely decline in importance whereas others may be eliminated from the community.

From the limited number of studies on plant community responses to increasing atmospheric CO₂, the following can be stated:

Total community biomass will increase. No estimates of the magnitude of increase is possible at this time.

Community composition will change. It is not possible now, however, to predict which species will become dominant and which will become less important.

In communities in which some species have the 4-carbon pathway of photosynthesis and others have the 3-carbon pathway, the 4-carbon species will begin to decline.

Life cycles of most plant species will accelerate. Changing rates of flower, fruit, and seed production may affect coadapted animal pollinators and consumers.

Reproductive potentials will change with concomitant changes in gene frequency.

Further research in community response should be integrated with a modeling effort to help focus research on critical processes.

BIOSPHERIC RESPONSES

To understand the global biospheric response, the individual plant responses need to be evaluated in relation to biospheric processes of the landscape and the global biotic system. One element of this study is to determine if CO₂ enrichment causes detectable growth enhancement and thus increased net carbon uptake and storage by the Earth's vegetation mantle. The purpose is to extend our knowledge of individual plant response to ecosystems, and to determine the extent CO₂ enrichment might affect the Earth's global carbon budget. In this context, the effects of CO₂ enrichment may be expressed in terms of changes of net ecosystem production,

$$NEP = GPP - (R_A + R_H),$$

where the change in carbon budget (NEP) is equal to gross primary production (GPP) minus respiration of autotrophs (R_A) and heterotrophs (R_H). Although a simple concept, it is very difficult to get data for evaluating such relationships of ecosystems, and quantitative estimates of CO₂ effects on global NEP are not now possible. The following types of information are required:

The percentage of each annual increment of atmospheric carbon that can be sequestered in representative ecosystems should be determined.

Carbon pools in representative ecosystems must be better quantified and their resistance to decomposition determined.

The direct effects of increased CO₂ on autotrophic and heterotrophic respiration must be determined.

The interaction of increasing CO₂ concentration with other environmental factors that also might change must be determined.

It is a common practice for simple models of the global carbon system to employ a "biotic growth factor (β)" to represent biospheric growth enhancement from CO₂ enrichment. The " β factor" generally represents a fractional change in NEP in relation to a fractional change in atmospheric CO₂ concentration. Different " β factors" derived have been (1) assumed to be logarithmically proportional to the atmospheric CO₂ increase, (2) estimated from short-term photosynthesis, (3) based on Michaelis-Menten kinetics of plant metabolism, or (4) estimated from annual yield of crop plants. These methods all suggest a positive " β factor," usually ranging from 0.25 to 0.50, but none provides an appropriate, empirically derived expression that represents how fields and forests are responding to CO₂ enrichment. The changing amplitude of the annual atmospheric CO₂ cycle also may be related to an increasing biospheric response, and a detailed analysis of this feature in the Mauna Loa data base yields a " β factor" of 0.4 to 0.5, although the value could be as low as 0.05 if various uncertainties and different assumptions are considered.

Practically all information points to a CO₂ stimulation of the biosphere. Exactly how much cannot be stated now because of inadequate data for representative native species, ecosystems, and biomes. Exactly what happens to carbon fixed by enhanced photosynthesis is also unknown; more information is needed about autotrophic and heterotrophic respiration as well as where the fixed carbon is partitioned in ecosystems. The effects of variable water, light, and other nutrients on the CO₂ enrichment process are also unknown.

TASKS FOR THE FUTURE

In agricultural systems, humans will control adaptation by consciously deciding which cultivars and species are likely to yield the largest harvestable yield and the greatest economic return. In unmanaged ecosystems, natural selection will continue to be the mechanism of biological adaptation to increasing CO₂ levels and any associated climate changes. Adaptation of management practices is a learned behavior. Economic pressures and the rate of application of knowledge gained through research control behavioral adaptation in humans.

For the specific purpose of enhancing the capability of society to respond to the environmental changes associated with atmospheric CO₂ increase, the following recommendations are made:

Screen for overall growth and yield response under high CO₂ levels both with and without environmental stresses and both within and among plant species to identify and select genetically superior individuals. Such research is particularly important for the forest industry because of the small number of breeding cycles that will occur before the onset of the high-CO₂ world. Establish whether screening or other measurements taken on saplings are applicable to mature trees of the same species.

Identify physiological and biochemical characteristics that result in better growth and yield response (i.e., better adaptation) to higher CO₂ concentration. If, for example, specific characteristics such as better translocation into a developing seed can be identified, then breeding or genetic engineering programs could actively attempt to incorporate that characteristic into genetically superior stock.

Establish more definitively how growth responses to CO₂ may be affected by light intensity and temperature.

Determine how soil nutrient status affects CO₂ response. More information is also needed about the effects of CO₂ enrichment of nitrogen fixation for various species and conditions. Establish the extent to which greater exudation of carbohydrates and other compounds from roots with high CO₂ levels can stimulate mycorrhizal fungi and other beneficial microorganisms that, in turn, may increase the availability of phosphorus and water to various plant species.

Identify any particular crop-weed combinations that are likely to pose greater problems in the future because of differential responses to increased CO₂ and also to predicted climate changes.

Determine whether plants grown at high CO₂ levels are more vulnerable to attack by insects and diseases. In particular, what effects will a greater quantity of plant materials that have higher carbon/nitrogen ratios have on host-pest relationships?

Establish what effect more plant material, but with the high carbon/nitrogen and carbon/phosphorus ratios associated with CO₂ enrichment, will have on decomposer organisms. Similarly, how much will this plant material increase soil organic matter and reduce soil erosion?

The effects of high CO₂ on evapotranspiration and plant water requirements need considerably more attention. The extent to which there is a compensation between decrease in stomatal conductance and increase in leaf area needs investigation for many species. Establishing the effects of increased CO₂ on canopy development and leaf temperature and how these relate to evapotranspiration is also necessary.

More information is also needed about the effects of high CO₂ and partial stomatal closure on internal plant water status. To what extent can high CO₂ levels ameliorate plant water stress and maintain high productivity under dry conditions? Similarly, to what extent can high CO₂ levels counteract the effects of salinity and air pollutants?

Hydrologic modeling research also is needed to account for changes in precipitation, runoff, and evapotranspiration on streamflow in the future high-CO₂ world. The effects of decreased stomatal conductance and increased leaf area on evapotranspiration as well as the effects of increased stand density on runoff must be understood.

Systems-level models and analytical approaches need to be developed for predicting agricultural and ecological responses to both CO₂ enrichment and climate change. In particular, process-type models are needed that account for unique plant and system-level properties. The models should be generically applicable to different situations and should also be capable of analyzing alternative resource management practices.

1. BACKGROUND ON THE RESPONSE OF
VEGETATION TO ATMOSPHERIC
CARBON DIOXIDE ENRICHMENT

B. R. Strain
Duke University

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1.1 INTRODUCTION

Carbon is an element that is essential to life on Earth. The biochemical energy necessary for the continuation of life is carried in the atomic bonds of the carbon compounds of organisms. Solar radiant energy is absorbed by green plants, transformed to potential energy by photosynthesis, and stored in the chemical bonds of various organic compounds within green plants. The energy-rich compounds then pass from organ to organ within plants and from organism to organism within ecosystems. At each transfer step, carbon is returned to the atmosphere as carbon dioxide (CO_2) from respiration. The food production system of man, and indeed that of all life, absolutely depends on the availability and cycling of carbon.

Carbon is primarily available to green plants in the inorganic form of CO_2 . This gas moves from the atmosphere, where it is very diffuse (only 3 parts in 10,000), into green plants, where the carbon atoms are concentrated (up to 4 parts in 10) in organic compounds. This remarkable carbon sequestering is possible despite the relative rarity of the basic carbon supply in the atmosphere. With the knowledge that humans are increasing the carbon content of the global atmosphere, the question of plant response to CO_2 concentration becomes highly important. How will plants and other organisms respond as CO_2 continues to increase in the global atmosphere?

Tremendous gains have been made in the last 5 decades in our understanding of photosynthesis and of biological productivity. Biochemists and physiologists have carefully described the details of carbon acquisition and metabolism in plants and animals. Agriculturists and ecologists have studied intensively the qualitative and quantitative aspects of carbon accumulation and transfer in cultural and ecological systems.

Wittwer and Robb (1964) summarized knowledge of plant response to increased CO_2 concentration in greenhouses, and scientists at the 17th International Horticultural Congress (1966) focused on plant growth and yield in CO_2 -enriched greenhouses. Horticultural research in controlled environments continued to increase the understanding of plant growth in CO_2 -enriched greenhouses, and by 1978 more than 500 papers on plant response to increasing CO_2 concentration were collected (Strain 1978).

Unfortunately, before the 1970s few scientists recognized the importance of the increase that was occurring in the concentration of CO_2 in the global atmosphere. CO_2 was never identified as an environmental variable of concern during the 8 years (1968–1976) of the International Biological Programme.

A few investigators considered CO_2 as a variable along vertical gradients in field studies, but only three attempts (Kretchman 1969; Baker et al. 1970; Allen et al. 1974) were made to control atmospheric CO_2 in field experiments before 1981. Consequently, there is insufficient basic information to confidently predict how vegetation will respond as the inorganic carbon supply increases. It is possible to predict increasing photosynthesis rates and increasing efficiency of water use by some plants as CO_2 levels increase. What will happen to plants and ecosystems as they reach total adjustment to these changes, however, is uncertain. The empirical data base, although growing, is still inadequate for the prediction of agricultural or natural ecosystem response to long-term CO_2 enrichment.

This problem was recognized by 1970 and received the attention of scientific groups in the report of the study of critical environmental problems (Massachusetts Institute of Technology [MIT] 1970). Some additional concern for the response of organisms was stated in the *Study of Man's Impact on the Climate* (MIT 1971) and at the Nobel Symposium 20 (Dryssen and Jagner 1972). These three meetings, however, largely concentrated on atmospheric and oceanographic impacts of increasing CO_2 concentrations. The first major meeting to specifically address the response of the biological world to increasing global atmospheric CO_2 was the 24th Brookhaven Symposium in Biology, 1972. The results of that landmark meeting were published the following year in *Carbon and the Biosphere* (Woodwell and Pecan 1973).

After the appearance of *Carbon and the Biosphere*, there was a worldwide increase in interest in the CO_2 issue by scientists. International meetings on the CO_2 and climate issue were subsequently held in the United States in 1977 (Elliott and Machta 1979) and in Germany (Bolin et al. 1979). National meetings were also held in Australia (Pearman 1980) and in the Netherlands (Haex 1983). Although some biologists at these meetings addressed direct CO_2 responses, the meetings were focused primarily on the indirect effects of a CO_2 -induced climate change.

This shortcoming was partially rectified at the 1977 "Workshop on Anticipated Plant Responses to Global Carbon Dioxide Enrichment" (Strain 1978), at a meeting on the environmental and societal consequences of CO_2 increase held in 1979 (U.S. Department of Energy [U.S. DOE] 1980), and at an ecological meeting in 1981 (Strain and Armentano 1982). The importance of the question and the magnitude of our ignorance of the direct effects of CO_2 on biological systems, however, were not fully acknowledged until the release of the report of the 1982 International Conference on the Response of Plants to Rising Levels

Table 1.1

Chronological List of Important Meetings, Workshops, and Reports on Biological Aspects of Global CO₂ Enrichment

Report	Reference
<i>Study of Critical Environmental Problems</i> (SCEP)	MIT 1970
<i>Study of Man's Impact on the Climate</i> (SMIP)	MIT 1971
<i>Changing Chemistry of the Oceans</i> (Nobel Symposium 20)	Dryssen and Jagner (1972)
<i>Carbon and the Biosphere</i> (24th Brookhaven Symposium in Biology)	Woodwell and Pecan (1973)
CO ₂ and Climate (Boulder 1976)	Unpublished
<i>Workshop on Anticipated Plant Responses to Global Carbon Dioxide Enrichment</i> (Duke University)	Strain (1978)
<i>The Global Carbon Cycle</i> (SCOPE 13)	Bolin et al. (1979)
<i>Global Effects of Carbon Dioxide</i> (Miami 1977)	Elliott and Machta (1979)
<i>Environmental and Societal Consequences of a Possible CO₂ Induced Climate Change</i> (Annapolis)	U.S. DOE (1980)
<i>Carbon Dioxide and Climate Research</i> (Australia)	Pearman (1980)
<i>Carbon Balance in Northern Ecosystems</i> (San Diego State)	Miller (1981)
<i>Response of "Unmanaged" Ecosystems</i> (Quail Roost)	Strain and Armentano (1982)
<i>Global Dynamics of Biospheric Carbon</i> (Bloomington)	Brown (1982)
CO ₂ Review (ORAU)	Clark (1982)
International Conference on the Response of Plants to Rising Levels of Atmospheric Carbon Dioxide (Athens, Georgia 1982)	Lemon (1983)
<i>Vegetational Redistribution in Arizona and New Mexico in Response to a Doubling of the Atmospheric CO₂ Concentration</i> (Arizona State)	Idso and Quinn (1983)
Rising Atmospheric CO ₂ and Crop Productivity (Iowa State 1983)	Unpublished
<i>Part One on CO₂ Problem</i>	Haex (1983)
<i>Changing Climate</i> (National Academy of Sciences)	NAS (1983)
<i>Response of Unmanaged Forests to Climate</i> (ORNL)	Solomon et al. (1984)
Rising CO ₂ and Climate Effects of Forestry (Boulder 1984)	Unpublished
State-of-the-Art Report (DOE-SOA)	This volume

of Atmospheric Carbon Dioxide (Lemon 1983). This report clearly states that, although there is sufficient information to predict that there will be significant direct biological responses to global CO₂ enhancement, the social, economic, and ecological impacts of these responses cannot now be predicted. A chronological list of important meetings, workshops, and reports on biological aspects of global CO₂ enrichment is provided in Table 1.1.

Biological research questions and approaches were provided in most of the reports mentioned above. The purpose of this State-of-the-Art (SOA) volume is to review the progress being made in meeting the research

needs that have been identified. In the following chapters, current research activity will be summarized and recommendations for future research will be given.

1.2 JUSTIFICATION FOR THIS VOLUME

If global atmospheric CO₂ did not have direct physiological and subsequent ecological effects on organisms, no new experimental research effort would have been required to analyze the biological effects of the CO₂ question. Reconsideration of decades of agronomic and biological experiments involving other

environmental variables would be sufficient to allow us to model and predict future plant and ecological responses to changing climate. This is not the case, however. An increasing CO₂ level has direct effects on plants. Because the importance of CO₂ concentration has not always been recognized, however, there is little empirical evidence for the effects of atmospheric CO₂ concentration as an environmental variable in open air field conditions.

CO₂ as an important environmental variable for plant growth is so poorly researched because it has routinely been considered to be relatively constant in the global atmosphere. Most physiological, ecological, and agronomic studies of the decades before 1980 considered atmospheric CO₂ to be relatively constant at "ambient" or "atmospheric" levels. With a few important exceptions, most plant physiological studies prior to 1980 did not mention CO₂ concentration. If atmospheric CO₂ concentration was addressed at all, it was by ambiguous statements such as "CO₂ concentration was maintained at ambient levels," "CO₂ was normal," or "CO₂ was controlled by circulating room air through the growth chamber." Wittwer (1985) states, "Seldom has CO₂ even deserved mention in monographs or books on plant nutrition. Yet it gives the most remarkable responses of all in plant bulk, is usually in short supply, and is nearly always limiting for photosynthesis" (p. 174).

In addition, the questionable concept of single limiting factors continues to cloud the thinking of some researchers. It can still be heard in meetings and read in the literature that CO₂ enhancement will not have an effect on plant growth because some other factor is limiting. No environmental factor operates alone. All factors in the actual environment (Billings 1974) of an organism are potentially active. A change in any factor will modify the physiological behavior of an organism. The degree and nature of the modification varies with developmental stage and with genetic variability. When the ambient CO₂ level changes around a plant, the physiological response to other factors will be modified. This concept of holocoenosis (Billings 1970) is beginning to be more generally accepted by biologists, but the erroneous idea of single limiting factors still prevails.

The nature of whole plant response to any environmental change is very complex. There are first-order, whole plant responses that are primary. As temperature increases, for example, the rate of many physiological reactions will change. As light increases, the rate of photochemical reactions will change. Likewise, there are CO₂-requiring chemical reactions in plants that will change as availability of the gas changes. Photosynthesis, for example, frequently increases as atmospheric CO₂ concentration increases (Akita and

Table 1.2
Plant and Ecosystem Responses to
CO₂ Enrichment

I. First-order Effects

A. Primary Effects

1. Photosynthesis
2. Photorespiration
3. Dark CO₂ fixation
4. Stomatal aperture

B. Secondary Effects

1. Photosynthate concentration
2. Photosynthate composition
3. Photosynthate translocation
4. Growth rate
5. Growth form
6. Reproduction
7. Plant water status
8. Tolerance to gaseous atmospheric pollutants

II. Second-order Effects

A. Primary organism interaction

1. Plant-plant interaction
 - a. Interference
 - b. Competition
 - c. Symbiosis
2. Plant-animal interactions
 - a. Herbivory
 - b. Pollination
 - c. Shelter
3. Plant-microbial interactions
 - a. Disease
 - b. Decomposition
 - c. Symbiosis (mycorrhizae, N-fixation)

B. Secondary Organism Interactions

1. Evolutionary effects—genetic differentiation
2. Ecosystem responses—integration of all effects through time

Source: Strain (1985).

Tanaka 1973). Plants differ significantly in the nature and magnitude of photosynthetic response to CO₂ concentration (Percy and Bjorkman 1983). Other effects considered first-order effects in this volume are listed in Table 1.2. This concept is fully developed by Strain (1985).

In addition to primary, first-order effects of environment on whole plant behavior, there are subsequent secondary effects. These effects are unavoidable consequences of the primary effects. An increase in the rate of carbon fixation necessarily leads to an increase in the rate of photosynthate production (Madsen 1968; Harper et al. 1973). Translocation of soluble photosynthates (Ho 1977) and differential movement of soluble sugars

(Knecht and O'Leary 1974) are examples of first-order but secondary physiological responses to CO₂ increase. These effects may directly lead to changes in plant growth and reproduction.

Second-order biological effects of increasing CO₂ are ecological in nature. Each plant species responds in unique primary and secondary ways to CO₂ increase (Strain and Bazzaz 1983). In addition, varieties within species (Gardner 1966; Hartmann 1966; Heichel and Haynes 1974) differ in CO₂ response. These varietal differences have been reported in many plant species including corn (Heichel and Musgrave 1969), sorghum (Hesketh and Hellmers 1973), and barnyard grass (Potvin et al. 1984; Potvin and Strain 1985), plants that have the C₄ photosynthetic pathway.

As in all environmental effects on plant physiology and growth, the responses to CO₂ enrichment are interactive with other factors. The effects of increased CO₂ concentration when other environmental factors were also changing were recently reviewed (Gates et al. 1983). CO₂ has been shown to interact directly with high temperature (Kriedemann et al. 1976), low temperature (Sionit et al. 1981b; Potvin and Strain 1985), irradiance (Ford and Thorne 1967), nitrogen (Nevin and Loomis 1970; Wong 1979), and soil moisture (Hurt and Wright 1976). Recent research has confirmed all of these interactions (Sionit et al. 1980, 1981a, 1981b, 1981c, 1982; Sionit 1983; Patterson and Flint 1982; Paez et al. 1983, 1984; Tolley and Strain 1984). In addition, Coyne and Bingham (1977) demonstrated interaction between atmospheric CO₂ concentration and ozone (O₃), and Carlson and Bazzaz (1982) showed similar interaction between CO₂ and SO₂.

Thus, although it is not possible to adequately consider the effect of any one environmental factor without regard for other factors, it is useful to ask, "If all global environmental factors continue to affect organism physiology and growth as we now understand them to do, how will these organisms also respond to a century of continually increasing atmospheric CO₂ availability?"

The objective of this book is to consider the first-order (physiological) and second-order (ecological) effects of a chronic increase in global atmospheric CO₂ concentration on plants and on ecosystems. The indirect effects of CO₂-induced climate change will be considered only so far as the changing climatic factors will modify the CO₂ responses. The indirect climatic effects will be specifically treated in a later companion volume, *Characteristics of Prerequisites for Quantitative Research on the Indirect Effects of Carbon Dioxide: Water Resources, Agriculture, Fisheries, Forests, and Human Health*, edited by White (1985).

1.3 RELATIONSHIP OF THIS SOA VOLUME TO THE OTHERS

Research into the CO₂ issue has been divided into four major areas of concentration in the U.S. Department of Energy (DOE) program. These areas are (1) CO₂-induced climate changes, (2) global carbon distribution, (3) direct effects of CO₂ on plants and on ecosystems, and (4) indirect effects of CO₂-induced changes on humans and on human institutions.

Three of the four areas provide the focus for four volumes on the SOA reports on CO₂ research. In this section the four volumes will be briefly described to allow the reader to place this volume in the context of the overall U.S. DOE research effort. A volume analyzing indirect effects will appear later.

1.3.1 *Projecting the Climatic Effects of Increasing Carbon Dioxide*

This volume addresses considerations of the global meteorological effects of human-induced CO₂ enrichment, including the "greenhouse" effect on climate, means of studying the climate system, and interaction of CO₂ and other atmospheric trace gases on the world climate. Also explained are mathematical models that have been developed to help understand the phenomena involved in global meteorology.

1.3.2 *Detecting the Climatic Effects of Increasing Carbon Dioxide*

The determination of global climate response to atmospheric CO₂ increase is complex and difficult. The matter of how to look for the effects on the atmosphere was finally determined to warrant a separate volume. Thus, a separate volume is dedicated to the requirements for obtaining first detection of the global meteorological effects of CO₂ enhancement.

1.3.3 *Atmospheric Carbon Dioxide and the Global Carbon Cycle*

The objective of this volume is to provide an understanding of the compartmentalization of global carbon into its various storage pools. An effort is being made to improve estimates of the carbon content of the various physical and biological carbon pools and the magnitude of fluxes between and among pools. Remote and on-site measurements of the expanse and distribution of major carbon pools are described. Geographical, historical, and ecological techniques are employed to gain understanding of past and present

pool characteristics. Stable and radioactive isotopes are employed to estimate past and present atmospheric CO₂ concentrations. Compartmental models with realistic flux equations regulating carbon movement between compartments are being developed. The assumption is that empirical transfer equations that adequately simulate known or assumed fluxes can be used as predictors until first-order equations can be developed from basic knowledge.

1.3.4 *Direct Effects of Increasing Carbon Dioxide on Vegetation (this volume)*

This volume considers the first-order effects of CO₂ on plants, the second-order ecosystem response, and primary and secondary adjustments through time. The indirect effects of any CO₂-induced climate change are only treated in this volume as they interact with the direct CO₂ response. Empirical research is tightly linked with modeling to ensure basic understanding of the mechanisms involved. The information derived from this project is needed as input into the carbon cycling project. For the time being, the compartmental carbon flux projects have to rely on empirical standing crop measures of carbon content. Flux is calculated from repeated standing crop estimates. This empirical approach, of course, is inadequate for the development of mechanistic understanding.

1.3.5 *Characteristics of Prerequisites for Quantitative Research on the Indirect Effects of Carbon Dioxide: Water Resources, Agriculture, Fisheries, Forests, and Human Health (companion volume)*

The goal of this volume will be to specifically examine the possible sociological and economic impacts of weather changes associated with global CO₂ enhancement. Impacts on agricultural economy and technology will be considered here. Climate changes that will affect water resources, fisheries, and forests will be considered. Possible cultural and health effects of changing climate will be addressed.

1.4 ORGANIZATION OF THIS VOLUME

This review of knowledge of plant and ecosystem responses to atmospheric CO₂ increases will begin with a survey of the technical approaches to examine the problem. Chapter 2 examines methods of exposing plants to elevated CO₂ concentrations; the available procedures are controlled chambers and greenhouses,

open top chambers, and open air field releases. Advantages and disadvantages of these basic approaches are considered, and recommendations are given concerning the applications of the various techniques.

It is also possible to analyze possible plant responses to CO₂ increase by mathematical modeling. Chapter 3 reviews the modeling approach and presents a simplified model of plant growth. Methods for evaluating models are discussed, and a survey of existing models that might be useful is presented. Finally, research needs utilizing the modeling approach are discussed and enumerated.

Existing information on the response of crop and of native species to atmospheric CO₂ increase is reviewed in Chapters 4, 5, and 6. Chapter 4 reviews recent literature on the responses of crop plants to elevated CO₂ at the leaf and canopy levels. It also considers crop models and discusses explicitly the environmental data needed for model validation and for prediction of crop responses in the future high-CO₂ environment.

Chapter 5 addresses the question of current data availability for modeling key responses of 10 leading crop species. It tabulates and summarizes the available data in the form of predicted values for a doubling of the current ambient CO₂ concentration and considers the case for response types among these 10 species.

Chapter 6 discusses the native and the unmanaged species and their ecosystems. Interaction of CO₂ with other essential environmental factors could become critical in native ecosystems where humans do not manage them to correct possible imbalances. Empirical information is very sparse for native species, but Chapter 6 summarizes what is available and speculates on research steps to be taken in the future.

Plant community response is considered in Chapter 7. As interactive communities of different populations and plant species develop through time, it is predicted that community changes induced by differential responses of individuals to CO₂ increase will occur. The sparse evidence for this speculation is reviewed in Chapter 7, and a research approach is recommended.

While the increasing CO₂ concentration effects on plants, communities, and ecosystems occur (reviewed in Chapters 4 through 7), the global biosphere will also respond. If the changes affect net carbon sequestering, global biomass will change. Climate interactions as explained in Volume 1 will be occurring. This global-level response is considered in Chapter 8.

If changes do occur as speculated in Chapters 4 through 8, adjustments in human management activities will be required. Chapter 9 addresses the possible nature of institutional and management changes that will be required in the future as the atmospheric levels of CO₂ continue to increase.

Chapter 10 summarizes major conclusions of the volume. Recommendations are made for research at all of the various levels presented in the volume.

A companion volume entitled *Direct Effects of Atmospheric CO₂ Enhancement on Plants and Ecosystems: A Bibliography with Abstracts* is being released from the Carbon Dioxide Information Center, Oak Ridge National Laboratory. This bibliography contains over 1000 entries and is the updated version of the bibliography first released by Strain (1978).

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2. METHODS OF EXPOSING PLANTS TO ELEVATED CARBON DIOXIDE

B. G. Drake

Smithsonian Environmental Research Center

H. H. Rogers

U.S. Department of Agriculture/

Agricultural Research Service

National Tillage Machinery Laboratory

and

L. H. Allen, Jr.

U.S. Department of Agriculture/

Agricultural Research Service

University of Florida

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2.1 INTRODUCTION

The growth enhancement obtained by enriching the air with carbon dioxide (CO_2) has been recognized since the early 19th century. Studies of this effect have been conducted since that time, a period which spans most of the history of modern botany. Much of our present knowledge of this growth stimulation was obtained using crop species in controlled environments, especially greenhouses, to determine how to increase yield with "CO₂ fertilization." In the context of the recent increase in atmospheric CO₂ concentration, we want to know how crops, populations of wild, unmanaged plants, and ecosystem processes will respond. New methods and facilities have been devised to test the broader questions that are now being asked. This chapter, on the methods of exposing plants to atmospheres in which the CO₂ concentration is modified and controlled, is not intended to be exhaustive, but to illustrate the state of the art of the available technologies.

The chapter begins with a discussion of CO₂ control technology and concludes with an evaluation of the possible use of an open field release system. There are also sections describing most of the approaches that have been applied in elevated CO₂ studies, including leaf chambers, sunlit controlled environment facilities, mobile greenhouses, large greenhouses used to study crops, small greenhouses used in studies of natural vegetation, and open top chambers. The sections on open top chambers and open field release of CO₂ are relatively detailed because information on these important approaches has thus far been confined to specialized literature, and there is therefore the need to give these methods more extensive discussion than other more conventional approaches.

There are no published reports of leaf or branch chambers used to treat different leaves or plant parts with elevated CO₂ for periods longer than are needed to study the kinetic properties of photosynthesis *in vivo*. However, a chamber system that is suitable for such studies is discussed here. The available data on mechanistic changes in the photosynthetic apparatus of intact leaf tissue occurring in response to elevated CO₂ were obtained with leaf chambers and infrared gas analyzers (IRGAs).

Before about 1980, most studies on the effects of elevated CO₂ concentration were carried out in controlled environment facilities including growth chambers and greenhouses. Growth chambers are enclosed spaces in which some or all of the following parameters are controlled or monitored continuously: light quality and quantity, air and soil temperature, water vapor pressure, concentration of atmospheric gases (including water vapor and CO₂), soil nutrients, soil structure

and water content, and air movement. Photoperiods and thermoperiods may be separately controlled, and environments may be programmed to change gradually in small time increments or abruptly in larger, square-wave-type increments. For detailed descriptions of the technical aspects of controlled environments the reader is referred to the extensive literature on the subject (Went 1957; Evans 1963; Kramer et al. 1970; Downs et al. 1972; Downs and Hellmers 1975; van Bavel and McCree 1975; Langhans 1978; Tibbitts and Kozlowski 1979; and Downs 1980).

Phytotrons are integrated collections of controlled-growth facilities. The term phytotron (for plant instrument) was first applied to the Earhart Laboratory for Plant Research at the California Institute of Technology in an era when cyclotrons and betatrons were being constructed by physicists to study the behavior of small particles of matter (Downs 1980). A major advantage of the phytotron is that multiple chambers or rooms may be used to create matrices of environmental variables. A matrix of three CO₂ concentrations and three temperatures, for example, requires the use of nine growth rooms. With only two chamber replicates of each condition, this experiment would require 18 growth chambers. Within each growth room, subcells of light intensity or quality, soil nutrients or water status, or certain other environmental manipulations are possible. Separate rooms are needed for each photoperiod or thermoperiod, but if plants are grown on wheeled carts that may be moved from room to room, the number of environmental variables can be greatly increased. With the exception of phytotrons, few plant laboratories have such extensive plant growth facilities.

Carlson and Bazzaz (1980) reported competition experiments in which they used inexpensive growth chambers on wheels. These chambers were small enough for artificial lighting, but mobile so that they could be moved into the greenhouse for use with natural light. Thus they combined some of the best features of growth cabinets, namely, environmental control, with relatively high photosynthetic photon flux density as may be found in a greenhouse. The growth chambers were developed to house experiments to study the effects of various gases, including CO₂, on plants grown under several different conditions.

Naturally sunlit crop growth chambers based on "closed loop" environmental controls have proven very useful for detailed crop studies. At Clemson University, Mississippi State University, and the University of Florida, these systems have been used for short- and long-term experiments on soybean response to CO₂-enriched atmospheres. These systems, because they are closed, lend themselves to the study of water use by crop species. The chambers are divided into two parts,

an upper plant canopy chamber and a lower root zone compartment in which water use and root growth can be measured. The upper chambers are covered with clear glazing, allowing plant exposure to sunlight, and the root compartments are deep enough to allow a more field-like rooting volume than pots can provide.

Greenhouses have had a long history of contribution to agricultural research, and virtually every agricultural research organization has one or more on site. They offer at least partial control over the vagaries of the weather outside and enable an additional crop to be grown in the wintertime in climates where none would be possible in field plots. Only in greenhouses has it been economically practical to use CO₂ enrichment to increase the productivity of crops, and in cooler climates, such as the northeastern United States, it is a recommended horticultural practice (Wittwer and Honma 1969). Numerous CO₂ enrichment studies have been conducted in greenhouses over the last 64 years. Kimball (1983a, 1983b) reviewed over 140 reports and extracted more than 770 observations of the yields or biomass production with CO₂ enrichment of 56 plant species. The majority of these data were obtained from studies conducted in greenhouses. The increase of the mean weight of crop yield was 36%, which shows that CO₂ enrichment is indeed very beneficial to the greenhouse industry.

A new application of the use of greenhouses was tried by Oechel and coworkers (Prudhomme et al. 1984), who designed small greenhouses capable of tracking ambient temperature and humidity while maintaining preset CO₂ concentration to study the effect of elevated CO₂ on Arctic tundra.

The open top field chamber as described by Heagle et al. (1973, 1979) has had extensive use as the plant exposure unit in air pollution/plant effects studies in the field. The system has been used to expose both row crops and plants in pots to a variety of aerial pollutants, and it is currently in use at a number of laboratories throughout the United States. Hardy and Havelka (1975) first used an open top enclosure to expose soybeans to atmospheres enriched with CO₂ for the purpose of studying the effect of increased photosynthate production on symbiotic nitrogen fixation. Rogers et al. (1983) adapted the basic open top chamber system to generate large-scale CO₂ test atmospheres in the field.

The need to study CO₂ effects on vegetation in a natural field environment has led to the concept of artificially elevating CO₂ by release through a network of pipes. The history of this free air CO₂ enrichment (FACE) approach can be traced to studies by agronomists (Kretchman 1969; Baker et al. 1970; Allen 1973; Harper et al. 1973a, 1973b; Baker and

Lambert 1980). Field experience with this method is reported in the thesis studies of Harper (1971) and Allen (1973), and technical aspects were extensively reviewed by Allen (1979).

The FACE approach had much in common with methods developed by air pollution ecologists. DeCormis et al. (1975) described a grid release system to study air pollutant effects in vineyards for the French Ministry of Agriculture. The U.S. Environmental Protection Agency Zonal Air Pollution System (ZAPS) released air pollutants through a pipeline network in a prairie grassland (Lee and Lewis 1975; Lee et al. 1978). The U.S. Department of Energy's Argonne National Laboratory developed its own ZAPS capability (Miller et al. 1980), as did the University of British Columbia, Canada (Runeckles et al. 1981), the University of Nottingham School of Agriculture, U.K. (Greenwood et al. 1982), and the U.K. Central Electricity Research Laboratories (McLeod et al. 1983). A related open air fumigation system to provide linear gradients of exposure to a pollutant was designed by Shinn et al. (1977) and modified by Laurence et al. (1982) and by Reich et al. (1982). McLeod and Fackrell (1983) reviewed methods of open air fumigation.

2.2 CO₂ MONITORING AND CONTROL SYSTEMS

Two CO₂ control and monitoring systems are described in this section. The first was designed to be used with growth chambers, and the second utilizes open top chambers.

The CO₂ monitoring and control system for controlled environment studies reported by Norby et al. (1985) included four growth chambers, an infrared CO₂ gas analyzer (IRGA), compressed gas cylinders, a Hewlett-Packard 3497A data acquisition and control unit, and a Hewlett-Packard 9826 desktop computer with printer (Figure 2.1). The entire system was wired into a backup emergency power supply.

The system supplied two walk-in growth chambers with 3.2 m² of bench space and two reach-in chambers with 1.1 m² of bench space. The computers read CO₂ concentration from the IRGA, accumulated data, printed out statistical reports, calculated CO₂ input requirements, and actuated solenoids for controlling CO₂ sampling and injection.

The CO₂ partial pressure in the growth chambers and the ambient CO₂ outside the building were measured with an Anarad AR500RN IRGA. Gas samples were continuously delivered to the analyzer through heated stainless steel tubing (to prevent condensation). Solenoids, actuated by the HP 3497A on command from the HP 9826, routed

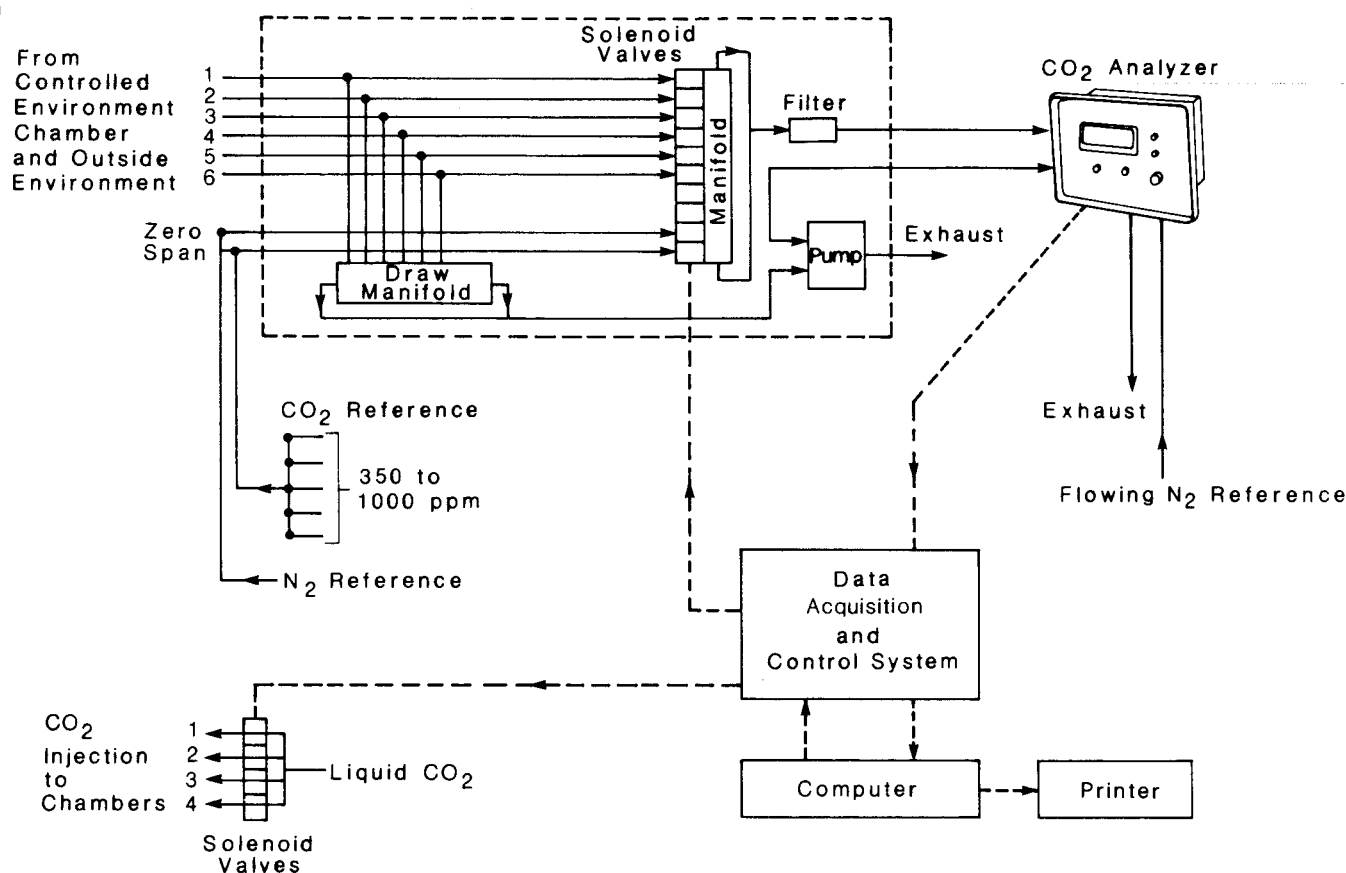


Figure 2.1. Diagram of CO₂ monitoring and control system for four controlled environment chambers. After Norby et al. (1985).

gas to the measuring cell or to a bypass to exhaust. CO₂ concentration was measured as the differential concentration of the sample gas from the reference nitrogen gas (0 parts per million by volume [ppm] CO₂). The four growth chambers and two outside ports were recorded sequentially after a 1-minute delay to allow for analyzer stabilization. Random measurement error after stabilization was approximately 0.6% of the concentration over the range 350 to 1025 ppm.

CO₂ from a cylinder of pressurized liquid CO₂ was injected into the growth chambers in pulses by opening a solenoid valve on command from the HP 3497A. Pulse duration (generally 1 to 8 s) was a function of desired CO₂ concentration and chamber size. Concentration of CO₂ in the chambers was controlled by varying pulse frequency (i.e., the time between pulses), calculated by the HP 9826. Time between pulses was adjusted during every cycle proportionate to the difference between current and desired CO₂ concentrations. The proportionality factor was chosen

to provide sufficient sensitivity to changing conditions (such as diurnal changes in ambient CO₂ or opening a growth chamber door) without overcompensating for system "noise" under relatively stable conditions.

The control strategy was satisfactory for short- and long-term experimental use. Coefficients of variation were routinely less than 10%. For example, during January 1984, coefficients of variations for the ambient-, 500-, 700-, and 950-ppm chambers were, respectively, 7.8, 6.0, 3.3, and 6.2%, based on over 10,000 measurements per chamber. During this period, 93% of the individual photoperiod and nyctoperiod means for the three elevated CO₂ chambers were within 5 ppm of the set points, and 80% were within 2 ppm of set points.

Rogers et al. (1983) described a control system for maintaining elevated CO₂ concentrations within open top chambers. A 14-ton (12.7-metric ton) liquid receiver served as a CO₂ supply reservoir. The storage receiver was equipped with an air-cooled condensing unit and a vaporizer. It was operated at between -23° and

-16°C , which gave a pressure of 243 to 307 psig (17 to 22 kg cm^{-2}). CO_2 was delivered from the receiver through 1.27-cm copper tubing to a dispensing manifold. A solenoid valve stopped flow during power failure. Regulators and manually operated flow meters dispensed CO_2 from the manifold to the chambers, where it was added to air in a plenum upstream of an axial fan to ensure thorough mixing (Figure 2.2).

The concentration of CO_2 in each of the open top chambers was monitored twice an hour. Sampling intakes were located in the center of each chamber at 1 m height above the ground. Samples were drawn

continuously from the chambers to a point near the water vapor and CO_2 analyzers. Solenoids allowed another pump to divert about 20% of the volume being sampled from the chamber into the measuring circuit.

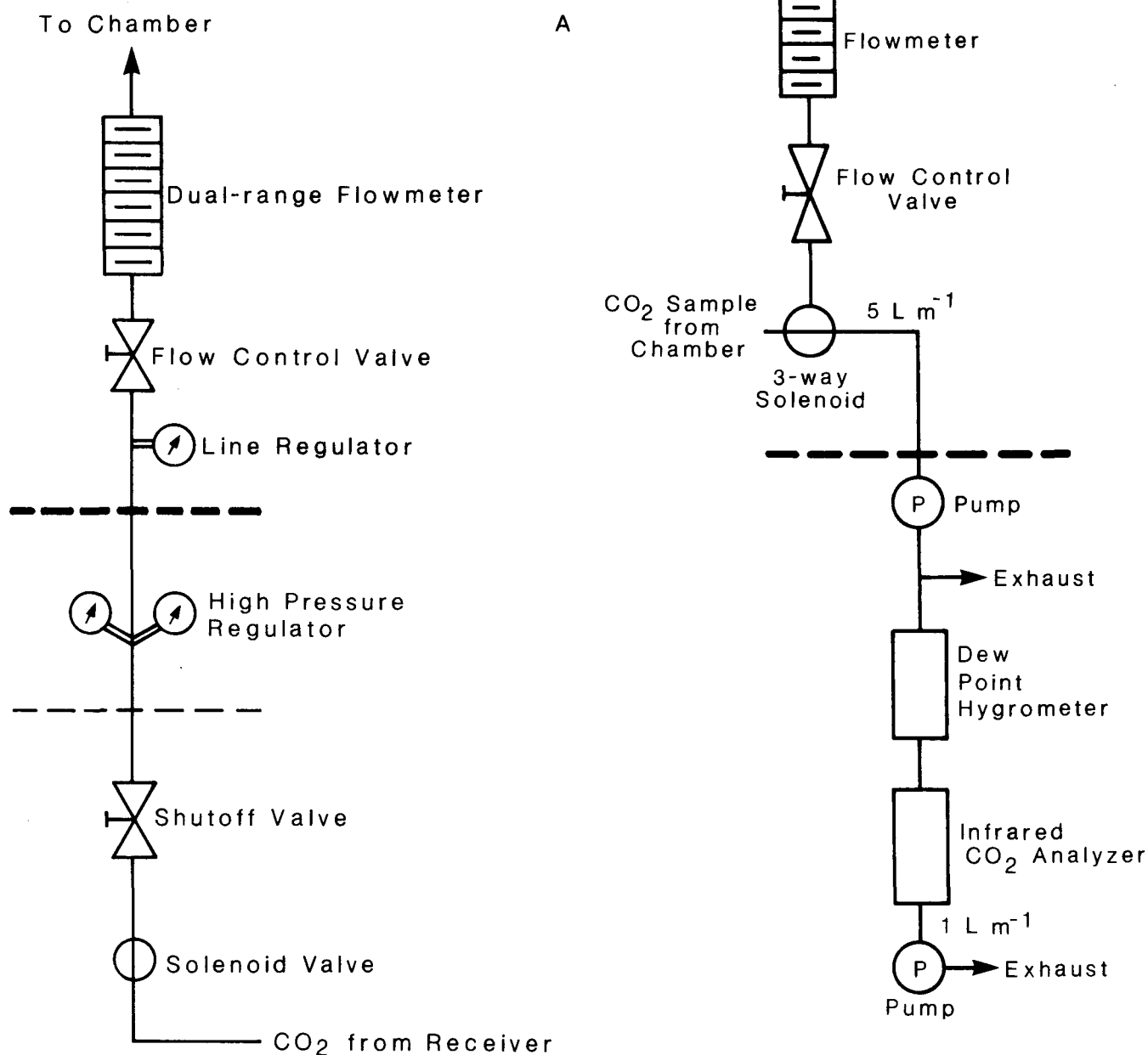


Figure 2.2. Schematic diagrams of the systems to regulate and monitor CO_2 flow. (A) System for regulation of the flow to the plant exposure chambers. (B) Monitoring system for up to 15 chambers. After Rogers et al. (1983).

Although the control of CO₂ concentration was by periodic manual adjustment of flow of CO₂ into the air supply for each chamber, the system maintained mean values for CO₂ concentration within 9% of the desired value.

2.3 LEAF CHAMBERS

There are so many chamber designs for single-leaf gas exchange measurements that an exhaustive discussion of advantages and problems of each one is beyond the scope of this chapter. Representative examples of different chamber designs developed during the past 2 decades can be found in Musgrave and Moss (1961); Mooney et al. (1971); Sestak et al. (1971); Bingham and Coyne (1977); Sinclair et al. (1979); DeJong et al. (1981); Field et al. (1982); Huck et al. (1983); and Valle et al. (1985).

The major design problem of leaf chambers is the same as for growth chambers, namely, how to control the environment around the leaf. Thus, a leaf chamber for measuring gas exchange is only one part of a system which can be subdivided into (1) control of gas composition and the environment around the leaf, (2) measurement of various physical parameters such as changes in gas concentrations, and (3) collection and evaluation of data. Bloom et al. (1980) discuss the effects of materials on water vapor and CO₂ in the gas-exchange circuit. In recently developed systems (e.g., Sinclair et al. 1979; Field et al. 1982; and Valle et al. 1985) computers have been used to integrate all subsystems as well as to manage data and provide hard copy of results.

The simplest systems have measured only CO₂ assimilation. Water vapor loss and CO₂ assimilation, however, must be measured simultaneously to make the analysis of data required to evaluate separately the effect of elevated CO₂ treatment on the supply of CO₂ through stomata to intercellular spaces and the biochemical responses of photosynthesis. von Caemmerer and Farquhar (1981) have summarized the necessary calculations, a discussion of the physical aspects of gas exchange in leaves can be found in Sestak et al. (1971), and the interpretation of gas analysis data is discussed by Sharkey (1985).

Systems for measuring gas exchange between the leaf and its environment are either open or closed. In open systems, air of known composition makes a single pass over the leaf, and the change in CO₂ and water vapor concentration brought about by the leaf is determined. In closed systems, air is continuously circulated around the leaf, and CO₂, water vapor,

and other variables of interest are controlled by compensation for exchange between the leaf and the surrounding air. Open systems may ultimately be the simplest to design and control, but they require a high degree of sensitivity in measurement of CO₂ concentration and dewpoint temperature. For example, to determine the flux of CO₂ across the epidermis, Sinclair et al. (1979) used an open system with an IRGA to measure the drop in CO₂ concentration of air as it passed over the leaf. In closed systems, a null-balance approach is used, and the change in concentration of water vapor and CO₂ in the chamber is determined from the rate of injection of water vapor and CO₂ required to maintain a set point concentration. Field et al. (1982) used a closed system and measured the change in pressure across an injection capillary required to maintain CO₂ concentration within the chamber at a set point which was measured by a gas analyzer used in absolute mode.

The leaf gas exchange system (Figure 2.3) described

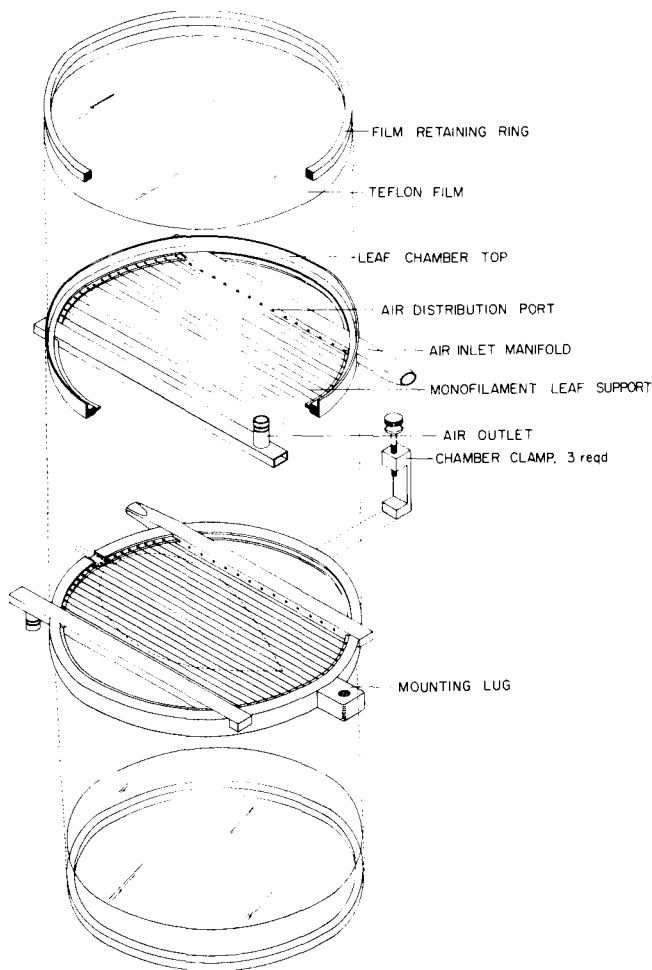


Figure 2.3. Leaf chamber for field measurement of photosynthesis. After Sinclair et al. (1979).

Table 2.1
Environmental Specifications (Minimal Requirements) for
Controlled Environments Designed for CO₂ Research

Parameter	Units
Photosynthetic Photon Flux Density	0–2000 $\mu\text{mol m}^{-2} \text{s}^{-1}$
Photoperiod	0–24 h of light continuously programmable in square or sine wave patterns
Air Temperature	5° to 40°C
Thermoperiod	0–24 h phase-separated from photoperiod but in similar wave patterns
Air Water Vapor Concentration	Controllable to give a leaf-to-air vapor pressure gradient of 0.3 – 1.5 nmol m^{-3}
Air Velocity	0–3 m s^{-1} continuously adjustable
CO ₂ Concentration	250–2500 ppm

by Sinclair et al. (1979) would be well adapted for use in studies of the effect of prolonged exposure to elevated CO₂ levels on photosynthesis, although to date it has not been used for that purpose. This system was capable of field operation and was able to track environmental temperature, humidity, and solar radiation, as well as continuous measurement of both water vapor and CO₂ exchange and control of CO₂ concentration.

The leaf chamber consisted of two disks of clear Teflon¹ separated by a pair of chrome-plated brass rings. The leaf was inserted between rows of monofilament line on each ring. Leaf temperature was controlled so as to track ambient temperature by passing the air supply line through a waterjacket in the rim of the chamber. In the study of Sinclair et al. (1979), the effect of the chamber on the plants was evaluated on leaves enclosed in the chamber for 6 weeks. There were no visually apparent effects of the chamber nor were there any effects detected in the data on the photosynthetic response when compared with data obtained on neighboring leaves that were of similar age but which had grown outside the chamber. However, leaves inside the chamber did not have insect damage, and senescence was delayed compared with other leaves in the same canopy.

A system similar to the one employed by Sinclair et al. (1979) has been used by Valle et al. (1985) for studying long-term responses of soybean (*Glycine max* [L.] Merr. 'Bragg') leaves to elevated CO₂. The chambers were used to measure photosynthesis and gas exchange in leaves that had been treated with elevated CO₂ in sunlit growth chambers.

2.4 CONTROLLED ENVIRONMENT CHAMBERS

2.4.1 Phytotrons

Integration of environmental control systems and a broad spectrum of controlled environmental variables

¹Teflon is a registered trademark.

distinguish phytotrons from greenhouses or growth chambers. Phytotrons are constructed with a redundancy of compressors, pumps, valves, and all systems required to ensure continuous and dependable operation, and warning systems help professional maintenance staff keep the systems functioning properly.

Controlled environments allow the investigator to create any environment or environmental gradient. Because each environmental factor of interest is established and varied at will, one may administer a desired environmental treatment and be assured that the results are the product of treatment alone. In addition, the experiment can be repeated with precision later. This is a decided advantage over field experiments where only selected variables are controllable. In the field, sunlight, air and soil temperatures, precipitation, insects, and diseases are different from site to site, from day to day, and from year to year. Exact duplications of experiments in the field are highly unlikely.

Specifications recommended as minimal requirements for growth chambers to be used in CO₂ research are given in Table 2.1. At the Duke University Phytotron, extensive studies of the effects of elevated CO₂ concentration on a wide range of plant processes have been carried out. Representative examples of different research projects include comparative growth of C₃ and C₄ plants (Patterson and Flint 1980) and the interaction of CO₂ with effects of temperature (Hofstra and Hesketh 1975), photosynthesis (Clough et al. 1981), drought (Paez et al. 1983), and mineral nutrition (Sionit et al. 1981).

2.4.2 Portable Growth Chambers

Portable growth chambers were designed to permit a low-budget approximation of greenhouses and to allow research on air pollutants to utilize the sunlight available inside a greenhouse, or to use a combination of artificial light with sunlight to obtain a flux density

that approximated natural sunlight (Carlson and Bazzaz 1980).

The sides and tops of the chambers described by Carlson and Bazzaz (1980) were glass and the backs and bottoms were wood. Interior wood surfaces were covered with Formica² to minimize sorption of gases including CO₂ and water vapor. They were supported on a wheeled frame of steel, which also carried the refrigeration equipment. Vents in the top of the back wall of each chamber were connected to a plenum. A fan in the plenum circulated air across heat exchangers and back into the growth chamber through a bottom vent. This vent was equipped with movable vanes so that air could be directed anywhere in the chamber to adjust circulation patterns. Air temperature in the chambers was regulated by passing the circulated air around a 600 W heating element and through expansion coils of a refrigeration system. Plants humidify the air rapidly, so humidity control was achieved by condensing moisture from the air.

Pure commercial CO₂ was metered into the chambers to elevate normal ambient CO₂ concentration to the level desired, and air was sampled from the chambers through a system of valves and flowmeters. CO₂ concentration within each chamber was controlled individually. When lamps and sunlight were used together, the plants could be supplied with 2000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ photosynthetic photon flux density.

2.4.3 Sunlit Controlled Environment Chambers

Sunlit controlled environment chambers based on "closed loop" environmental controls were developed in the late 1950s and early 1960s with Mylar³ polyester film walls. Nondispersive IRGAs allowed rapid measurement of CO₂ concentration, and these analyzers in combination with metered CO₂ allowed direct and continuous measurement of photosynthesis rates. Transpiration was measured by collecting condensate from air conditioning cooling coils. These chambers were used successfully for measuring photosynthesis and transpiration as a function of CO₂ concentration, light, temperature, and soil moisture condition (e.g., Musgrave and Moss 1961; Moss et al. 1961; Baker and Musgrave 1964; Egli et al. 1970). These systems were the predecessors to the units with controlled root zone as well as canopy zone chambers (Parsons et al. 1980; Phene et al. 1978), which have been further modified for improved systems for CO₂ studies.

Details of the design, functioning, and use of these recently improved chambers have been reported by

Jones et al. (1984a, 1984b, 1985a, 1985b). A sketch showing the overall layout of this system is shown in Figure 2.4. This system was based on the original SPAR (soil-plant-atmosphere-research) units reported by Phene et al. (1978) and Parsons et al. (1980).

These chambers were designed to provide accurate, flexible control of dry-bulb temperature, CO₂ concentration, and humidity of the canopy air. In contrast to open flow-through systems, the air mass in closed systems was continuously circulated within the chamber. Temperature, humidity, and CO₂ concentration of the ambient air were monitored and controlled. Specific methods and equipment for controlling chamber conditions varied, but were generally based on (1) sensors that measured temperature, CO₂, and humidity (e.g., dewpoint temperature) levels; (2) feedback mechanisms such as thermostats or loops in computer logic that compared sensed with desired conditions; and (3) control devices such as heaters that were regulated to produce the desired treatment conditions. Air in these systems was circulated through the canopy from top to bottom and then out through ducts, where the air was reconditioned before flowing back into the canopy chamber. Sensors and control devices were located within the ducts so that the air circulated to the top of the canopy had the experimentally prescribed temperature, CO₂ concentration, and humidity level. Measurement of plant canopy response in a closed chamber system was directly linked to the control of chamber conditions. Changes in CO₂ and humidity levels within the chamber were driven by canopy CO₂ and H₂O gas exchange processes. Thus, in the absence of excessive condensation on walls, blockage of circulation pumps, and other operational problems, successful control actions provided a mirror image of canopy net photosynthesis and transpiration, and the operation of a closed chamber system implicitly provided measurements of canopy response.

Each chamber described by Jones et al. (1984b) consisted of an acrylic plastic top 2.0 by 1.0 m in cross section by 1.5 m tall (volume, 3.0 m³) secured to a 1.0-m-deep steel lysimeter filled with fine sand. The chambers were located outside and exposed to direct natural sunlight. However, other similar systems may vary in size and in the rooting medium (e.g., Acock et al. in press).

Recent experiments using sunlit controlled environment chambers have focused on short- and long-term effects of elevated CO₂ on soybean growth and yield, photosynthesis, transpiration, and water-use efficiency (Jones et al. 1984a, 1985b), as well as on interactions between elevated CO₂ concentrations and temperature (Jones et al. 1985a) and moisture stress (Jones et al. in press). These are examples of the types of

²Formica is a registered trademark.

³Mylar is a registered trademark.

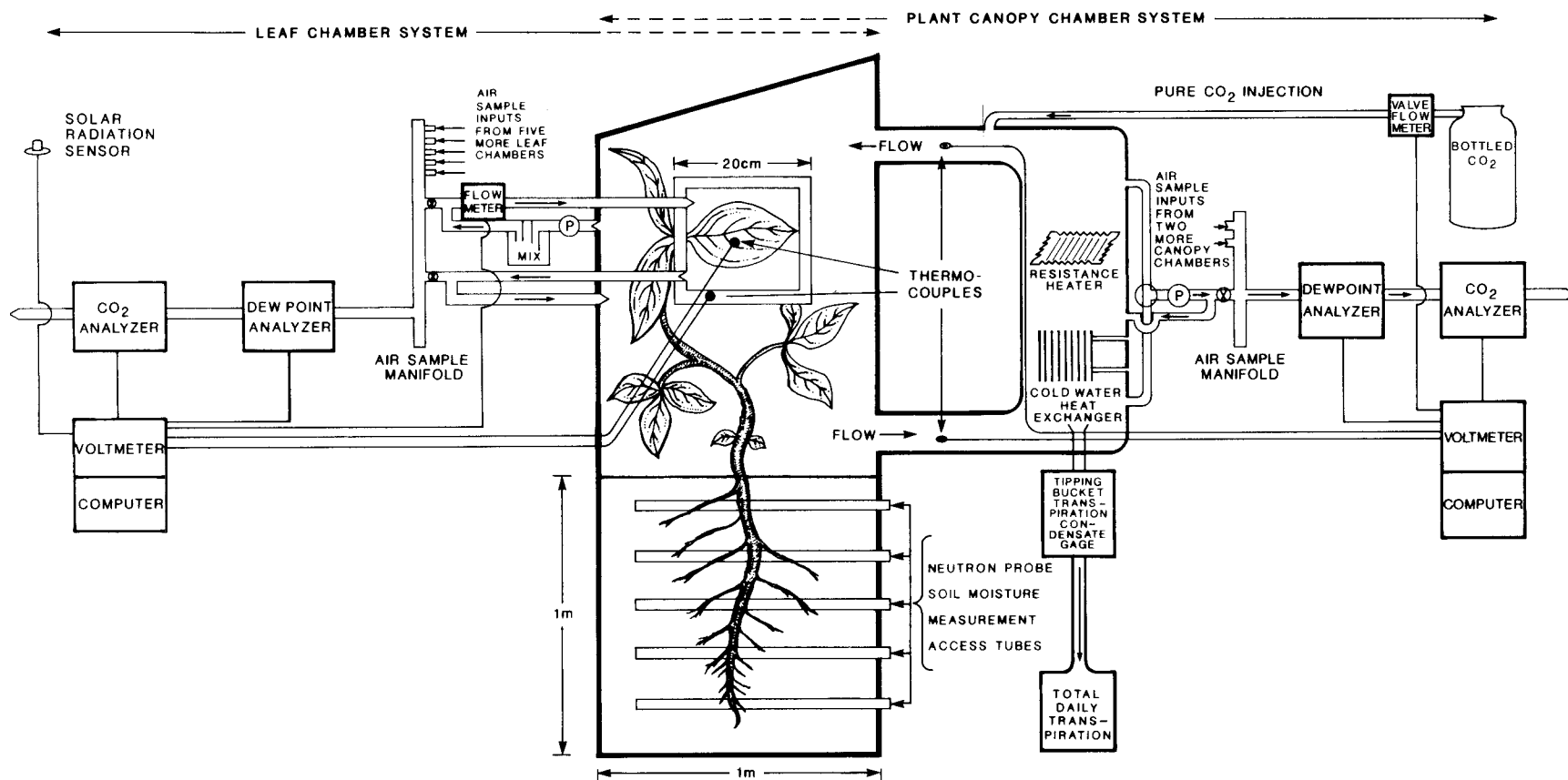


Figure 2.4. Closed system computer-controlled plant environments for CO₂ enrichment study. Plant canopy chamber system described by Jones et al. (1984a, 1984b; 1985a, 1985b). Leaf chamber system described by Valle et al. (1985).

direct CO₂ effects and coupled climate or soil-water interactions that can be obtained in sunlit controlled environment chambers. All of the studies outlined above are discussed in detail in Chapter 4 of this volume.

2.5 GREENHOUSES

Greenhouses are structural frames covered with nearly transparent skins such as glass, fiber glass, polyvinyl chloride, or polyethylene. Because they are manufactured by numerous commercial firms, they are relatively inexpensive compared with custom-built, one-of-a-kind structures. Although constant temperatures are not maintained, greenhouses are usually equipped with heaters and ventilation systems (forced or natural, evaporatively cooled or not) to prevent excessively low or high temperatures. Controls have various degrees of sophistication, but generally provide separate day and night minimum temperature set points to control the heater and a maximum temperature set point to turn on the ventilation. Humidity is usually not controlled, except possibly for some nighttime ventilation at flow rates much smaller than are used for daytime temperature control. Artificial light is generally not used except for the control of photoperiod using low-intensity incandescent light.

Kimball (1983a) has listed the ways the greenhouse environment differs from the open field, and has also reviewed (in press) the data available from the literature on the interactions of CO₂ enrichment with several environmental variables. The most obvious difference between greenhouse and open field environments is that temperatures can be controlled in the former. As in the commercial industry, this feature allows experiments to be done during seasons when it is too cold for crops to grow outside. Furthermore, CO₂ appears to stimulate plant growth by about the same amount across the range of temperatures over which plants are normally grown (Kimball in press).

Another difference between the environment inside a greenhouse and that outside is the considerably lower light intensity inside. Greenhouse coverings typically transmit two-thirds to three-fourths of the available sunlight. Also, greenhouse experiments are often done in the wintertime when the light levels are only one-third to one-tenth of the summertime open field intensities. From theoretical consideration of CO₂ effects on photosynthesis, Kimball (in press) concluded one could expect stimulation of growth by elevated CO₂ compared with growth at present ambient CO₂ concentration at very low and very high light levels with a midrange minimum. Actual observations of growth and yield of CO₂-enriched plants at a range of light intensities did not exhibit any definite

discernible pattern within experimental variability. To a first approximation, greenhouse results should apply to the field, but the available data do not support that prediction.

Greenhouses generally have higher humidity and lower windspeed than outside. Thus, greenhouse crops can generally be described as having grown under a more ideal environment with respect to water relations, and they often appear more luxuriant than their shorter, thicker leaved, field-grown counterparts. In his review, Kimball (in press) concluded that most of the previous experiments on the interaction between CO₂ and water stress showed that the stimulation of plant growth with CO₂ enrichment was as large or larger under water stress conditions than under well-watered conditions at present normal ambient CO₂ concentration. Thus, from a water relations standpoint, one could expect responses in the field to be as large as or larger than in a greenhouse. Soil moisture depletion studies can be done in a greenhouse, but the control of the development of tissue water stress is difficult. When large soil volumes are used, stress may develop more slowly than in the field. In small containers, however, stress may develop more rapidly than in the field. Because the wind flow, radiation regimen and humidity are generally different than in the field, it is particularly difficult (and the uncertainty is large) to extrapolate greenhouse water-use measurements to the field situation. Most of these comments apply to salinity stress as well (Kimball in press).

Because most of the prior CO₂-enrichment experiments in greenhouses were conducted using nonlimiting nutrient levels, conclusions based on them probably do not apply to the nutrient-limited unmanaged biosphere. Low nutrient level was the only environmental restraint that appeared to generally limit the relative response of plants to CO₂ enrichment (Kimball in press). Future farmers will need to adjust fertilizer rates to take advantage of the stimulation of yield by the increased atmospheric CO₂ (see also Chapter 9 of this volume).

The economics of doing research are not the same as those of practical horticulture. Thus, for research purposes it is justified to use refrigeration to control the temperature (and even humidity) of closed, CO₂-enriched greenhouses and growth chambers. Alternatively, injecting excessive amounts of CO₂ during ventilation of greenhouses can also be justified for research purposes. This approach uses much CO₂ but little electricity.

2.6 FIELD TRACKING CHAMBERS

The small, field tracking chamber used in studies of Arctic ecosystems (Prudhomme et al. 1984) had a 127-

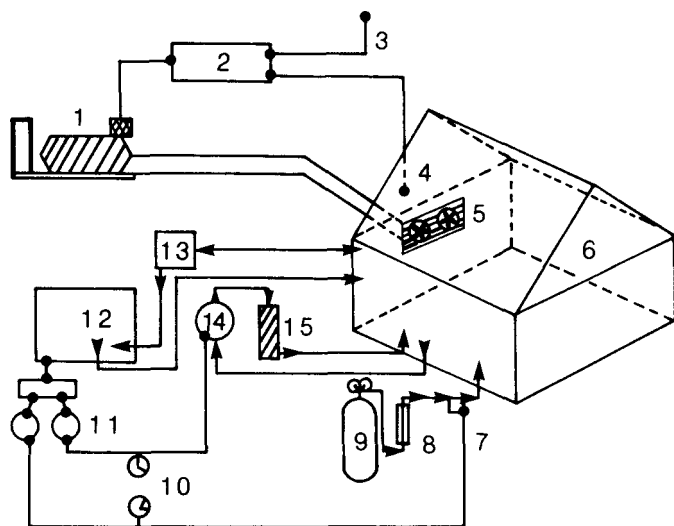


Figure 2.5. Schematic diagram of the field tracking chamber used to measure community CO_2 exchange of tussock tundra at Toolik Lake, Alaska: (1) Compressor, (2) YSI 71A controller, (3) external thermistor, (4) internal thermistor, (5) heat exchanger and fans, (6) chamber, (7) on/off solenoid, (8) flow meter, (9) carbon dioxide cylinder, (10) timers, (11) CO_2 control circuit, (12) ADC infrared gas analyzer, (13) pump, (14) scrub pump, (15) soda lime. Source: Prudhomme et al. (1984).

mm (0.5-in) polyvinyl chloride tubing frame covered with 0.8-mm clear plastic sheeting sealed to a galvanized sheet-metal frame, which was sunk 10 to 15 cm into the soil (Figure 2.5). The chamber enclosed a surface area of 1.65 m². CO_2 concentrations inside the enclosure were continuously monitored and maintained at 330 ppm CO_2 , representing ambient, or at an elevated level of 600 ppm CO_2 either by adding pure CO_2 gas or by scrubbing the greenhouse air through soda lime.

Air temperature within the chamber was maintained at the desired ambient levels. A temperature controller set to track ambient air temperature activated a compressor unit attached to a remote heat exchanger inside the chamber. The fans inside the greenhouse operated continuously to ensure adequate mixing of the air and CO_2 . The entire system was powered by a 6.5 kW generator. Temperatures of the air, moss surface, *Betula nana* leaves, and *Eriophorum vaginatum* stem base, and the soil at 2-cm and 10-cm depths both inside and outside the chamber were measured using thermocouples.

The mass of CO_2 going into the chamber was calculated from the flow rate and the time that CO_2 was injected. The mass of CO_2 removed was calculated based on volume of air removed, its CO_2 concentration, and the length of time that the chamber air was scrubbed. The difference between the mass of CO_2 injected and that removed to maintain ambient or elevated CO_2 levels in the chamber was the net carbon uptake by the community. This measure was expressed

as community production as CO_2 exchanged per square meter per day. See Chapter 6 of this volume for a detailed discussion of the results obtained with this system.

2.7 OPEN TOP CHAMBERS

The open top chamber used by Rogers et al. (1983, 1984a, 1984b) was an open-ended cylinder roughly 3 m in diameter by 2.4 m high (Figure 2.6). A high rate of ventilation was assumed to keep the inside temperature and humidity close to those of the outside air. When air in the chamber was mixed with fresh air at normal ambient CO_2 concentration blowing over the top of the chamber, it was difficult to maintain a desired concentration near the top of the plant canopy. Accordingly, a "frustum" was added to the top of the chamber which reduced the size of the top opening to one-half of the ground area inside the chamber (Rogers et al. 1984a). The chambers consisted of a structural aluminum frame covered by panels of clear polyvinyl chloride plastic film. The bottom panel was double-walled; the inside wall was perforated by 2.5-cm holes to serve as a duct to distribute the CO_2 -air mixture uniformly into the chamber. Air to this duct was supplied from an axial fan mounted in a sheet metal plenum box with a particulate filter. Pure CO_2 was injected into the plenum box ahead of the fan to ensure thorough mixing.

The open top chamber system performed well in generating and maintaining large-scale test atmospheres in the field and presented no major difficulties once in place. Provisions for delivery of large amounts of liquid CO_2 and electrical power needs were solvable problems.

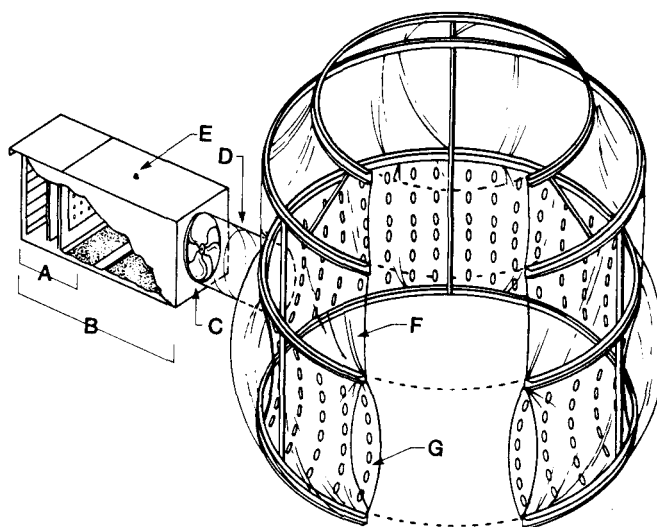


Figure 2.6. Open top field chamber. (A) filters, (B) plenum, (C) blower, (D) air duct, (E) port of injection of CO_2 , (F) single-layer wall, (G) double-layer wall with perforations for air entry. After Rogers et al. (1983).

The liquid CO₂ receiver was the best method to store and supply the large quantities of CO₂ (1×10^6 g d⁻¹) needed for a study of approximately 35 chambers. Good separation of treatment CO₂ concentration was obtained for each treatment level up to and even higher than 600 ppm above ambient. Ambient CO₂ levels and levels inside chambers with no added CO₂ were virtually the same.

There have been a number of studies that have evaluated the microenvironment within open top chambers and how it differs from that of unenclosed crop canopies (Heagle et al. 1973, 1979; Mandl et al. 1973; Kats et al. 1976; Shinn et al. 1976; Heck et al. 1979; Olszyk et al. 1980; Thompson 1981; and Winestock et al. 1982). With respect to temperature, some report that air temperature within the canopy of plants inside the chamber does not differ from air temperature in the canopy of plants not enclosed by the chambers. Kats et al. (1976) found no difference up to 38°C; Heagle et al. (1979) found less than 1°C difference; Mandl et al. (1973) found no differences greater than 1°C over the range 16° to 29°C; and Olszyk et al. (1980) found no differences greater than 2°C. Solar radiation is attenuated by the walls of the chamber: Olszyk et al. (1980) found a reduction of photosynthetically active photon flux density of 10.3%; Heagle et al. (1979) reported a reduction of total solar radiation of about 15%. Relative humidity within the chambers is higher than it is within the canopy of plants outside the chambers, which results in a reduction in daily water use of significant amounts (Olszyk et al. 1980). Shinn et al. (1976) discussed problems associated with maintaining homogeneous pollutant gradients across the chambers, desiccation of some plants, and problems with adequate irrigation.

There is only one reported study of the exchange properties of canopies enclosed within the chambers compared with canopies grown without the chambers. Unsworth et al. (1984) found the canopy boundary layer resistance to O₃ transfer of a mature soybean crop canopy inside the open top chamber to be similar to boundary layer resistance for soybean crop canopies obtained during the day using micrometeorological methods (Wesley et al. 1982).

Do differences observed between the microenvironment of plant canopies inside and outside open top chambers lead to effects on yield? Mandl et al. (1973) saw no significant differences between the rates of germination or the final dry weights of pinto beans inside or outside open top chambers compared at ambient CO₂ concentrations. Howell et al. (1979) reported that yields of plants inside the chambers were sometimes greater than and sometimes less than yields of plants grown outside the chambers. Heagle et al. (1979)

reported that the chambers often produced plants that were taller than the same species outside the chambers, but that yields were rarely different from crops in the field without chambers around them. In a later paper they reported no apparent chamber effects for 1979 but a significant effect on mean pod weight in soybean in 1980. Heggstad et al. (1980) reported that significant differences were found in approximately 25% of the 24 comparisons made between mean values of biological parameters such as height, fresh weight, pod weight, and number of pods of plants grown without chambers around them and plants within open top chambers, but there was no distinct trend in favor of either group. Olszyk et al. (1980) came to a similar conclusion, namely, that differences existed between growth statistics inside and outside the chambers, but they tended to be random rather than systematic. This led the authors to conclude that such differences were not directly attributable to the effects of the chamber on physiological or developmental processes. Winestock et al. (1982) also reported that they could find no differences between physiological processes such as stomatal resistance, transpiration, and water potential or the relationship between physiological and microclimatic parameters.

Thus, the conclusion to be drawn is that the climatological differences imposed on plants by the open top chambers do not result in great differences in growth or yield.

2.8 OPEN FIELD RELEASE

The free air CO₂ enrichment (FACE) methodology has been viewed by some as a "real-world" approach which may provide the best test for the effect of the impending CO₂ enrichment on natural ecosystems. The pros and cons of FACE methodology (Shinn and Allen, in press) are presented below at some length because FACE methodology represents a controversial possible step in the development of CO₂ vegetation effects research.

The FACE approach to CO₂ enrichment is to apply a network of pipes or plenums near the ground in such a design as to provide elevated CO₂ to the ambient air of the plants. The object is to avoid the need for an enclosure or chamber around the plants. The major differences between FACE and either outdoor controlled environment chambers or open top chambers, the closest alternatives, are that FACE eliminates the following chamber effects: (1) reduction of the solar radiation environment, and (2) unnatural wind flow, turbulence, and micrometeorological patterns.

Allen (1975, 1979) found that a single line source FACE release in a maize field required a downstream distance about 10 times the height of vegetation (H)

before horizontal gradients approximately vanished (an equilibrium was reached). Air pollution exposure systems tend to verify this. The U.S. Environmental Protection Agency Zonal Air Pollution System (ZAPS) utilized plots with dimensions of 73 m by 85 m, or about 100 H on each side, for a prairie grassland (Lee et al. 1978). The U.S. Department of Energy's Argonne National Laboratory used air pollution exposure plots with dimensions of 29 m by 27 m, about 50 H on each side, for a soybean crop (Miller et al. 1980). The U.K. Central Electricity Research Laboratories (CERL) designed a circular plot array of 27 m in diameter, or about 30 H, for a wheat crop (McLeod et al. 1983).

In computer simulations for a FACE experiment in a tropical forest, it was also found that the plot dimensions approximately scale with the vegetation height (H). Based on the combined theoretical and experimental experiences above, we would estimate that a plot would need to have a minimum area of magnitude 100 H², perhaps larger if wind direction changes are also considered. This means plots of about 100 m² for a 1-m-tall wheat field, 484 m² for a 2.2-m-tall maize field, and 48,400 m² (4.84 ha) for a 22-m-tall forest.

A large study area is an advantage when part of the sampling problem is to obtain representative plant material from populations. In natural ecosystems or forests of uneven age this is especially a problem. Ecological studies of effects of elevated CO₂ on cycles of litter production, organic matter accumulations, soil respiration, nutrient cycling, above-ground competition, and phenology require a large area of uniform exposure or treatment. A requirement of a large area with replication of experiments, however, becomes a logistics problem with large numbers of samples to process and analyze and higher associated costs, especially in natural ecosystem studies.

The concentration of CO₂ in a large area supplied through a network of pipes will depend inversely upon wind speed, directly upon the release rate (source) of CO₂ (Allen 1975; McLeod and Fackrell 1983), and inversely with vegetation height when mass consistency is taken into account (Hanna et al. 1982). To hold CO₂ concentration constant on the average, the delivery rate must be increased at higher wind speeds, and this requires a feedback mechanism to be included in the FACE design. Nevertheless, it will be very difficult to maintain constant CO₂ under all weather conditions. Uncontrollably high CO₂ levels may result during a calm in a FACE experiment. Under most conditions only the very center of a circular design will have a uniform horizontal distribution of concentration.

The dilution of gases from the network of pipes has been found to be drastically close to the release points because the major dilution mechanism is by horizontal

advection as compared with turbulent diffusion. That is, mean horizontal transport of CO₂ is much greater than vertical diffusion by eddy transport. For that reason an approximate "box budget" can be used to make first-order estimates of horizontal transport.

Use of the box budget is common in air pollution meteorology (e.g., Hanna et al. 1982). Solution of the appropriate equation for the average increase in CO₂ concentration (ΔC) across an area of dimension (ΔX) vegetation of height (H), wind speed (u), and source strength (Q) is:

$$\Delta C = Q \frac{\Delta X}{Hu} \quad (2.1)$$

and we can define the flushing time (t):

$$t = \frac{\Delta X}{u} \quad (2.2)$$

Application of such a box budget permits estimates of the source strength (Q) needed to raise ambient CO₂ concentration by any desired amount (ΔC). To elevate the CO₂ concentration (ΔC) by 100 ppm (183 mg m⁻³) for a distance (ΔX) of 54 m in a canopy wind speed of 3 m s⁻¹ and a maize crop 2.2 m tall, the value of the source Q would be 81 g m⁻² h⁻¹ or 810 kg ha⁻¹ h⁻¹. Allen (1975) computed a value of 833 kg ha⁻¹ h⁻¹ with a much better model but similar boundary conditions. The flushing time using Equation (2.2) for a 54-m plot (ΔX) would be 18 s.

Allen (1975) used a two-dimensional model to calculate the CO₂ concentration distribution from a single line source, or several line sources, perpendicular to the wind direction. It utilized observed wind speed and eddy diffusivity profiles and had a computational grid in a vertical plane parallel to the wind direction. The computed isopleths of CO₂ concentration defined a plume of CO₂ that drifted downwind. Allen found that the model agreed with observations and used it to simulate CO₂ concentrations of a Costa Rican rain forest (Allen and Lemon 1976). The model predicted that CO₂ concentration distribution in the forest would be similar to the distribution in a maize crop but that the 40-m-tall forest would require a source of CO₂ 50 to 100 times larger to achieve similar in-canopy CO₂ enrichments.

Experience has shown that in all pipeline release systems including the U.K. Central Electricity Research Laboratories (CERL), FACE, and ZAPS, there were gradients in the mean concentrations. Harper et al. (1973b) observed that to obtain net mean increase (ΔC) in CO₂ of about 100 ppm, the vertical mean gradients near the release pipe (at ground level) had to be about 20 ppm/cm. Although the observed spatial variability is a drawback, it appears that by clever design

distributed, multilayer, pipeline networks and vertical standpipe releases, coupled with a feedback system of detection and flow controls, some reasonably constant mean CO₂ concentration could be maintained. This increases the complexity of design, however, and it may also demand a custom design for each experimental site to account for local wind conditions and vegetation height and density.

An interplay of spatial and temporal variation in CO₂ concentration also would occur in FACE, not only due to turbulence, but also due to slow fluctuations in the mean wind that change the depth of the CO₂-abundant layer in the plant canopy.

Observations by air pollution ecologists have shown that air concentrations of an added gas (pollutant or CO₂) in an open release system will have a log-normal frequency distribution. McLeod and Fackrell (1983) compared the results of concentration observations by the French Ministry of Agriculture, the U.S. Environmental Protection Agency, the University of Nottingham, the U.S. Department of Energy, the U.K. Central Electricity Research Laboratories, and linear-gradient systems. All of them had a log-normal frequency distribution of concentration at a point for nearly any sample-averaging time scale (a few minutes to a few hours). The geometric standard deviation was such that 10% of the time the observed concentrations were 3 to 5 times greater than the median concentration for any given location in the grid. If the FACE design concentration calls for an added CO₂ concentration (ΔC) of 300 ppm, then about 10% of the time the concentration would exceed 900 to 1500 ppm. Most of these excursions in the CO₂ concentration would be of short duration under typical daytime turbulence conditions (Allen 1973; Desjardins et al. 1978). Furthermore, there can be large variations in average CO₂ concentration from point to point, depending on proximity to the CO₂ release lines or points and on vertical height and horizontal distance downwind in the release array (e.g., experimental data, Allen 1973; model predictions, Allen 1975 and Allen et al. 1985).

Such wide concentration variations may lead to problems of data interpretation in experiments where physiological mechanisms are the subject of investigation. Geometric fluctuations would render certain in situ physiological measurements, such as stomatal diffusion resistance, photosynthesis, and water stress, virtually impossible because they depend on quasi-steady-state conditions. However, variation in long-term average concentration with height or horizontal space may make it difficult to specify the exact CO₂ enrichment level.

The wide concentration variations might be quite acceptable, however, when large numbers of organisms

could be readily measured during FACE studies, for example in biomass determinations. There the cumulative effect is perhaps all that is important. This is an important distinction because from the agronomic point of view, as in the early days of FACE studies, yield increases were the significant end product. There may be similar needs in natural ecosystem studies.

The horizontal scale requirement for FACE is a symmetric plot with minimum area of $100 H^2$ where H is the height of the vegetation. Scaling up from a 2.2-m-tall maize field to a 22-m-tall forest requires about 100 times the plot area (48,400 m² compared with 484 m²). Using Equation (2.1) to estimate CO₂ requirements, we see that the source Q would not need to be increased to scale-up from maize to forest, when X scales with H . Using Allen's (1975) estimate for Q of 833 kg ha⁻¹ h⁻¹, to increase CO₂ by 100 ppm the maize plot of 0.0484 ha requires 40 kg h⁻¹, but the forest plot of 4.84 ha requires 100 times more, 4000 kg h⁻¹.

If the 833 kg ha⁻¹ h⁻¹ rate of CO₂ were applied to one 4.8-ha forest plot, to attain a 100 ppm increase in concentration above present ambient level the consumption of CO₂ would be about 35,000 t y⁻¹ ($t=10^6$ g). A CO₂ treatment of 300 ppm would require about 105,000 t y⁻¹. A simple experimental design with one each of the above treatments would require about 140,000 t y⁻¹. Clearly scale-up to forests would become a logistics problem, and the calculated daily consumption of 383 t would require large, liquid CO₂-holding reservoirs. About 30 CO₂ receivers, each the size of a tank truck (13 t), would be depleted each day.

As an alternative to using tank receivers, searches have been conducted for naturally occurring geosources of CO₂. Zimmerman and Perry (1979) located for the U.S. Department of Energy several naturally occurring subsurface CO₂ gas accumulations in central Mississippi, West Virginia, west Texas, Colorado, Wyoming, New Mexico, and southeast Utah. The price range used by Zimmerman and Perry (1979) for a profitable development was between \$5 and \$10 t⁻¹ at typical temperatures. Wellhead costs were estimated to be about \$20 t⁻¹.

Industrial sources of CO₂ can be found that offer prices comparable to geosources. Coal gasification plants in North Dakota, New Mexico, and Wyoming generate CO₂ at about 700 t h⁻¹ with estimated costs of \$12 t⁻¹. This production is to be used for enhanced oil recovery and will apparently not be available for other purposes.

Allen (1975) found that a maize plot (0.3 ha) FACE required 833 kg ha⁻¹ h⁻¹ to enhance CO₂ concentration of normal ambient air by 100 ppm. Adding a treatment of 300 ppm would be an additional 2500 kg ha⁻¹ h⁻¹, and the daily consumption of CO₂ for the combined

treatments, comparable to an open top chamber study reported by Surano and Shinn (1984), would be 24 t d⁻¹. At a bulk price from natural or industrial sources of between \$10 and \$30 t⁻¹, the cost for CO₂ would be \$240 to \$720 d⁻¹ for FACE. For comparison, consider the cost of open top chamber experiments in North Carolina (Rogers et al. 1983) and in California (Surano and Shinn 1984), which only consumed about 1 t d⁻¹ at a cost of between \$100 to \$150 t⁻¹ plus rent on a 13-t CO₂ receiver of \$15 to \$20 d⁻¹. Thus, FACE is currently estimated to cost about four times more than a comparable open top chamber study. However, if the cost per ton of CO₂ for the FACE study were the same as for the open top chamber studies of maize reported by Surano and Shinn (1984), that is, between \$100 to \$150 t⁻¹, then the basic cost for CO₂ used in a FACE study would be between \$2400 and \$2600 d⁻¹. The most optimistic comparison for a 120-day maize growing season would include the assumption that the CO₂ used for FACE would cost 10 to 20% of the cost of CO₂ for open top chambers. In this case the cost of CO₂ for FACE would be \$28,800 to \$86,400 whereas the cost for the same experiment for open top chambers would be \$12,000 to \$18,000.

Scale-up from crops (where FACE has been

demonstrated) to forests will require 50 to 100 times as much CO₂ per plot as for crops because of the scale dependency on the square of the vegetation height. The volume rate of CO₂ required in a perennial, FACE forest study would exceed 10⁵ t y⁻¹, which is logistically very difficult or impossible. With the cost of CO₂ from natural or industrial sources estimated to be \$10 to \$30 t⁻¹, the cost estimate for a forest study for CO₂ alone would be about \$1.4 to \$4.2 million per year.

2.9 SUMMARY

To learn how crop plants and native plants and ecosystems will respond as atmospheric CO₂ continues to increase will require additional research using all of the approaches described in this chapter. Advantages and disadvantages of the various methods discussed in the chapter are summarized in Table 2.2. The primary benefit of controlled environments in elevated CO₂ research lies with the ability to formulate, test, and improve hypotheses of organism response to environmental conditions. Environmental factors can be manipulated singly or in combinations to critically examine basic effects on organisms. In a growth

Table 2.2
Advantages and Disadvantages of the Methods Described in This Chapter

Method	Advantages	Disadvantages
Leaf Chamber	Single-leaf gas exchange kinetics obtainable.	No whole plant response such as growth; natural environment difficult to duplicate.
Phytotron	Create and control many desired environments; repeat experiments; many environmental conditions possible; biological factors controlled.	Difficult to extrapolate to natural conditions; environmental factors usually constant; plant size limitations; less than sunlight.
Portable Chambers	Small, inexpensive to build; can be used with either natural sunlight or artificial light.	Same as for most controlled environments.
Sunlit Controlled Environments (e.g., SPAR)	High light, similar to natural irradiance; variable conditions; integrated estimates of carbon and water balance; root zone similar to field; same advantages as phytotron.	Complex control; chamber effects (humidity, temperature, wind gradients); limited replication usually.
Greenhouse	Present data base on CO ₂ large; natural sunlight.	Difficult to maintain (CO ₂) under some conditions; difficult to extrapolate results to the field.
Field Tracking Chamber	Permits study of natural vegetation; track natural variation in the environment; whole ecosystem effects; integrated estimates of carbon and water balance.	Complexity of control functions in a remote setting; possible chamber effects.
Open Top Chambers	Can be used to study crops and natural vegetation in situ; natural sunlight; closely approximates natural environment ease of establishing elevated CO ₂ concentrations.	Gradients in humidity and wind produce chamber effects; growth differs inside from outside; many sample chambers needed to deal with natural variability of ecosystems.
FACE	Closest to natural environmental conditions.	Technical feasibility; strong gradients in CO ₂ in windy conditions; large sample areas needed; cost is high for large vegetation.

facility, the investigator decides on the magnitude and periodicity of each environmental factor. Results can be interpreted with confidence that the specific effects of each environmental factor are known. If a critical factor is given an inappropriate value or range, erroneous extrapolations may result. The testing of hypotheses generated from controlled environment studies by means of field validation trials is necessary before it is possible to predict field response from laboratory experimentation. van Volkenburgh and Davies (1977) discussed this problem in a report from a study conducted at the Duke University Phytotron.

In all studies of the effects of elevated CO_2 on plants that have been carried out in controlled environments, however, the growth environment differs from the natural environment of plants. Our ability to use present knowledge to predict the probable future effects of CO_2 enrichment of the atmosphere is limited by our ability to account for the differences these test environments produce on plants grown in them as compared with plants grown in the open. Thus the disadvantage of using controlled environments for studying the effects of elevated CO_2 on plant responses is the uncertainty of extrapolating results from chamber environments to field environments.

Requirements for CO_2 research in controlled environments have forced the realization that the light intensity provided in standard commercially available growth chambers is inadequate for many plants. Photosynthetic photon flux density (PPFD) available in growth chambers is typically in the range of 300 to 700 $\mu\text{mol m}^{-2} \text{s}^{-1}$, but most plants require two to three times more photosynthetic energy to respond completely to CO_2 enrichment. High-intensity discharge lamps provide the PPFD required and have been installed in many CO_2 research facilities. Although these better light sources are becoming available, they are expensive to add to existing commercial growth units that were engineered for lower energy inputs. Overheating of plants and desiccation of the air will almost certainly result unless the capacity of the refrigeration systems is also improved.

Greenhouses have a place in CO_2 enrichment research undertaken to understand the response of crops to the open field situation. To a first approximation, some environmental control is possible and the relative stimulation of vegetation by CO_2 is roughly the same over a range of light, temperature, and humidity. In addition, the light quality and intensity in greenhouses more closely approximates natural levels than those in most controlled environment facilities. However, using greenhouses for elevated CO_2 studies has the same type of disadvantage that applies to using controlled environments, namely, that the differences in

environment between the greenhouse and the natural, unobstructed environment are a source of inaccuracy that is difficult to estimate.

Sunlit controlled environment chambers and open top chambers give plants exposure to 80 to 100% of natural full sunlight, although there are some differences in the quality of light in the ultraviolet and near-infrared regions. However, the reduction of windflow and turbulence inside chambers influences water loss for both systems.

A general conclusion regarding open top chambers is that the microenvironment around the plant canopy is more humid and slightly warmer than outside the chambers. Surano and Shinn (1984) found that the seasonal rate of increase of growing degree days was higher in open top chambers than for companion plots outside the chambers. Some differences have been reported (cited above) between growth of plants within the chambers and plants not enclosed by chambers in the field when both were exposed to the same atmospheric gas composition. These differences require that control chambers (without elevated CO_2) be included in the experimental design. The chamber effect can be included in the interpretation of results by comparison between growth of the crop or ecosystem being studied in an unenclosed plot and an enclosed plot with normal ambient air supplied to the plants. In the opinion of those who have used this method, these chambers remain the best currently available technology for studying plant responses to a CO_2 -enriched atmosphere in the field.

The FACE approach has the advantages of least interference with solar radiation and natural wind flow. Its disadvantages include spatial and temporal variations in CO_2 concentrations, a larger study area than its closest alternatives, and considerably more technical difficulty. Also, at present, it appears that cost will make FACE impractical for tall vegetation, although it may be practical for short crops, forages, pastures, or grasslands (Allen et al. 1985).

2.10 CONCLUSIONS AND RESEARCH RECOMMENDATIONS

There are many technical difficulties in conducting research on CO_2 enhancement. Available facilities include greenhouses, phytotrons, growth chambers, leaf chambers, open top chambers, open air releases, and variations of these. All of these approaches have advantages and disadvantages. Environmental control allows the study of environmental factors alone and in combination. Environmental control, however, induces uncertainty in the extrapolation of results to the variable

natural environments. Controlled environments have space, size, and cost limitations.

Field chambers and open air releases allow the study of the effects of CO₂ under field conditions. Although these techniques do not ideally simulate the field, they currently offer the best available approaches to investigating plant responses to CO₂ under variable "real-world" conditions. The feasibility of FACE techniques for future validation studies of whole crop or entire ecosystem response to atmospheric CO₂ enhancement should be further investigated. Each of the other techniques discussed has an appropriate place, as follows, in CO₂ research:

1. Use controlled environments to study the effects of separate environmental factors on the CO₂ response of organisms and ecosystems.

2. Use single-leaf chambers to study basic details of CO₂ and other environmental changes on photosynthesis and other physiological properties of leaves.

3. Use controlled environment growth chambers to study long-term effects of chronic CO₂ enrichment on whole plants throughout their life cycles. Formulate hypotheses and test understanding by controlling and varying factors singly and in combinations.

4. Use phytotron chambers and refrigerated greenhouses to gain space and multiple factor controls required for larger experiments.

5. Use portable chambers for an inexpensive approach to the development of basic hypotheses.

6. Use sunlit controlled chambers and field tracking chambers to study canopy and ecosystem responses to a combination of variable and controlled-field environments.

7. Use open top chambers to study vegetation and ecosystem responses under field conditions.

8. Continue to examine the feasibility of FACE techniques for future validation studies of whole crop or entire ecosystem responses to atmospheric CO₂ enhancement.

ACKNOWLEDGMENTS

We wish to gratefully acknowledge the contributions to this chapter made by the following people: Drs. F. A. Bazzaz, P. A. Jones, B. A. Kimball, R. J. Luxmoore, W. W. Oechel, T. I. Prudhomme, J. N. Shinn, B. R. Strain, and R. D. Vallee.

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3. MODELING APPROACHES FOR EVALUATING
VEGETATION RESPONSES TO CARBON
DIOXIDE CONCENTRATION

J. F. Reynolds
New Mexico State University
and
B. Acock
*U.S. Department of Agriculture/
Agricultural Research Service
Mississippi State University*

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3.1 INTRODUCTION

3.1.1 Importance of Modeling in Assessing the Effects of Carbon Dioxide on Vegetation

When it first became obvious that global carbon dioxide (CO_2) concentration was increasing, attention was focused on the possible climatic and societal effects. The prognostications were mostly negative, for example, global warming, melting of polar ice, rise in sea level, and inundation of coastal cities. Subsequently, it was realized that, potentially, CO_2 could have beneficial effects on crop growth and might improve the chances of feeding a hungry world. Also, the effect of CO_2 on the growth of plants in natural ecosystems could alter species distributions, change the climax vegetation, and, over a number of years, sequester carbon to effectively hold down the CO_2 concentration. To examine and evaluate possible scenarios of CO_2 effects on crops and vegetation, it is necessary to develop a predictive capability. The magnitude of this challenge is placed in perspective by Strain in Chapter 1 of this volume, who discusses the multifactorial nature of plant response to environmental stimuli. Although CO_2 has a direct effect on plants, an understanding of the combined effects of CO_2 with other important environmental variables (e.g., temperature, light, nutrients, and water) is required for a more complete understanding of the potential effects of CO_2 . Thus, the key to developing a predictive capability will necessarily be a consideration of numerous interactions within the total atmosphere-plant-soil system.

The complexities involved in prediction become even more evident when extrapolation from one level of resolution to another is attempted (an example is whole plant to community) and this, in turn, is combined with projections over time (e.g., decades in the future). Because it is impossible to devise CO_2 experiments that cover the entire range of conditions of interest, as well as the time frame desired, one viable alternative is to utilize the relatively inexpensive power of the computer to develop dynamic simulation models to predict vegetation responses to CO_2 . Hence, model building is an integral component of the CO_2 research plan. This chapter introduces the different types of models and modeling approaches available, reviews some specific models being developed, and discusses future prospects of models as predictive tools in evaluating vegetation responses to CO_2 .

3.1.2 A Generalized Growth Model

Central to the U.S. Department of Energy's CO_2 research plan is the development of a generalized plant

growth model that can be used as a tool for evaluating the response of plants to CO_2 (U.S. Department of Energy 1984). Because there is a plethora of possible plant responses to CO_2 , both direct and indirect, as well as primary and secondary (see Figure 5.1 in Chapter 5 of this volume), is it necessary that this general model be able to reproduce all possible behaviors? If so, this model can be expected to be exceptionally complex. The relationship between model complexity and predictive capability or enhanced insight is not very clear, particularly for large systems models containing a mixture of empirical and mechanistic approaches. Is there some optimum level of complexity for a model commensurate with the knowledge of the real system? Can a model be aggregated (i.e., condensed and simplified) and still perform adequately? Such questions are germane to the CO_2 program. For example, because CO_2 directly affects only a few key physiological processes, like photosynthesis and leaf conductance, is it advisable to divert the majority of the modeling effort into describing these key processes in great detail (in this general growth model) while considering the remaining processes in a more superficial manner? This question will be addressed again in the critique of models. One generalization that can be made with confidence is that the imposition of complexity or simplicity, per se, into a model structure is no guarantee of its success.

In Sections 3.1.3 and 3.1.4 models are defined, several examples are given, and some modeling terminology is introduced. This material is intended for the layman, and readers with experience in this area should turn to Section 3.2.

3.1.3 What Models Are

A model is a simplified representation of a real system. Hence, there are many types of models (e.g., word models, picture models, and physical models), all of which play an important role in science. Humans, in common with all higher animals, are modelers. We observe things going on around us and try to discern some pattern that will enable us to adapt our behavior to these things to survive and even thrive. One of the most important early achievements was the development of a model of the changing seasons. Initially, the first gropings for truth were conceptual models of seasonality that existed only in the form of ideas or words. Next, considerable resources were devoted to building physical models that could predict the advent of each season; this is the most plausible explanation for the numerous circles of standing stones found worldwide, such as Stonehenge. The development of mathematics made it

possible to write seasonal models as symbols on paper, thus making them much easier to manipulate and much more portable than the physical models. Improvements in instrumentation and techniques yielded better data, which in turn made possible better seasonal models, namely the calendar. Most recently, calculation aids such as computers have made it possible to predict events to a fraction of a second with this model.

Plant growth modeling has gone through all of these stages, and even today, most growth models are developed by following this historic pattern. Everyone who works with crops or native plant species has a conceptual model of plant growth and development, and often no attempt is made to develop the model beyond this stage. The most common physical model of a field crop or natural ecosystem is an isolated plant growing in a pot. This model enabled van Helmont in the 17th century to demonstrate that plants were not primarily composed of materials taken up from the soil. Although conceptual models and physical models have had a long and honorable history in plant science, mathematical modeling, fueled by the explosion of computer technology, is increasing in its importance to the modern plant scientist.

Models cannot produce new data or facts; that is the role of experimentation. A mathematical model is a representation of someone's mental image of a system and, accordingly, is bound by certain constraints and prejudices imposed by the investigator. However, an important difference between a mental model and a mathematical model is that the latter, if good, is stated in unambiguous mathematical notation. By manipulating a mathematical model, examination of what Forrester (1971) terms the "interactions of assumptions" is possible, a feat virtually impossible to do by other means in even moderately complex systems, and one of the most powerful uses of models. As noted above, interactions are extremely critical in the study of CO₂ effects on vegetation. One common method of elucidating the "interaction of assumptions" is to explore the sensitivity of a model to changes in its structure. This is termed sensitivity analysis (Dale 1970) and encompasses a variety of techniques, some of which involve very complicated calculations if a model is itself fairly complex. One simple technique is to change the value of a parameter in a model upward and downward and to observe the resultant behavior of the system. If the system is sensitive to a parameter, a small change will have a large effect. This can provide valuable insight as to the importance of a particular parameter relative to the combined effect of other model parameters. In addition, a disparity between the behavior of a system as predicted by a mathematical model and the expected behavior based on the mental model may

result. Forrester (1971) calls this the counterintuitive behavior of systems. This behavior results from a contradiction in the mental model between assumptions concerning the structure of the system and its assumed future behavior. Consequently, mathematical models may suggest some valuable insights into the functioning of a system, although they do not provide new facts *per se*.

The following discussion is focused on mathematical models, that class of models "which can be described symbolically and discussed deductively" (Kac 1969). Hence, a mathematical model is simply an equation (or set of equations) containing variables with relationships given by the mathematical expressions. For example, the equation $P = gC_i$, where P is the rate of photosynthesis, C_i is internal CO₂ concentration of the leaf, and g is intracellular conductance, is a simple mathematical model of photosynthesis as a function of CO₂.

It is sometimes stated that there are as many models of a system as there are different views of it. An incident described by Solomon (1979) illustrates this fact. An invited seminar speaker, on concluding a presentation of a complex phenomenon to a diverse group of faculty and students from applied mathematics, statistics, and operations research, invited suggestions as to how he might model his system. Not surprisingly, mathematicians in the audience saw the phenomenon as best described by differential equations, statisticians saw it as a stochastic birth-and-death process, and the operations researchers argued that it was a perfect problem for queuing theory. Each group conceptualized the problem from the context of its own interests and skills. Although this is not necessarily bad, it should be a signal of the potential danger of treating any model of CO₂ effects on vegetation as the true or best model. Although some model may be quite effective in accomplishing an objective and, hence, be viewed as successful, it represents only one of many alternative expressions that could prove equally successful.

3.1.4 A Simplified Model of Plant Growth

This section concludes with an example of a model of plant growth. Probably the earliest mathematical model of plant growth was an empirical one proposed by Briggs et al. (1920) and used extensively in the form of a system of equations for "Growth Analysis." These equations are:

$$\text{Relative growth rate (RGR)} = \frac{1}{W} \frac{dW}{dt}, \quad (3.1)$$

$$\text{Net assimilation rate (NAR)} = \frac{1}{A} \frac{dW}{dt}, \quad (3.2)$$

$$\text{Leaf area ratio (LAR)} = \frac{A}{W}, \quad (3.3)$$

$$\text{Therefore, RGR} = (\text{NAR})(\text{LAR}), \quad (3.4)$$

where W = plant dry weight and A = plant leaf area. The equations are written in a form to solve for the parameters, but they can be rearranged to give a model capable of predictions as follows:

$$\text{Rate of dry weight gain, } \frac{dW}{dt} = A(\text{NAR}), \quad (3.5)$$

$$\text{Plant leaf area, } A = W(\text{LAR}), \quad (3.6)$$

$$\text{Therefore, } \frac{dW}{dt} = W(\text{LAR})(\text{NAR}), = W(\text{RGR}). \quad (3.7)$$

Normally, RGR is assumed to be a constant, and in that case the model predicts exponential growth. However, this is only true of the early growth of seedlings before mutual shading by leaves on the same or adjacent plants occurs. The use of the model outside of these conditions is a violation of the assumption. Figure 3.1 shows a conceptual view of the model in a Forrester diagram (named after J. W. Forrester, who first introduced these symbols in 1961). In the diagram, an irregular cloud shape represents an infinite source or sink of material, a rectangular box is a finite quantity of material, and a solid arrow is a flow of that material. A cross, or diabolo, placed over a solid arrow represents a value, and processes linked to that cross exercise control over the flow of material represented by the arrow. A dashed arrow is a flow of information. Thus, the model does not allow for the fact that CO_2 , water (H_2O), or minerals may be available in limited amounts. Leaf area is a function of plant dry weight, and the rate of accretion of CO_2 , H_2O , and minerals to make more dry weight is controlled only by leaf area. Because there is a closed control loop in the model, the rate of dry weight gain also can be expressed as a function of the current dry weight.

This model, useful though it has been, is a gross oversimplification. The model parameters should be able to vary according to the environmental conditions in which the plant is grown. Considering just the uptake

of CO_2 and its incorporation into the dry matter in the plant, a Forrester diagram can be produced like the one shown in Figure 3.2. Some of the knowledge of processes involved in carbon fixation has been used. The model in Figure 3.2 is an attempt to predict carbon fixation by simulating the mechanisms involved; it is therefore called a mechanistic model. Data on carbon fixation and some or all of the factors known to influence it could be gathered, put into the computer, and (by trial and error) the equation that explained most of the variation in the data could be found. This would have been called an empirical model. It would have summarized the results and the relationship found between factors, but it would not have improved the understanding of why the results were obtained.

The growth analysis model is a static model. Given an initial plant dry weight and a time interval, it will predict a rate of increase in dry weight and then stop. By adding an iterative loop and an equation to increment the plant dry weight, it could be made into a dynamic model. It would then calculate a rate and a new state (the current dry weight) on each iteration, with the next rate being calculated from the updated state. There is no point in actually doing this with such a simple model, because predictions can be made for any day in the future with a single set of calculations. It is merely used to illustrate the difference between static and dynamic models.

Figure 3.2 shows the processes involved in modeling the fixation of carbon, one of several materials needed in plant dry matter. Then, to continue the expansion of Figure 3.2, the processes involved in water and mineral uptake, the partitioning of dry matter, and leaf area expansion are added. When all this is done, a confusing diagram with many interconnections results. This is not surprising to the plant scientist because plants have many feedback mechanisms to maintain homeostasis.

3.2 MODEL EVALUATION CRITERIA

A large number of plant growth models for agricultural and native plant species have been published (see reviews in Wiegert 1975; Hesketh and Jones 1976; Loomis et al. 1979; Hesketh and Jones 1980; and the *Cooperative Extension Service Updated Inventory of Computer Programs* by Strain and Simmons 1984). These models run the gamut from empirical to mechanistic and from very simple to very complex, with varying degrees of validation effort. The obvious question that follows is: Do any of these models have the capability to make predictions of vegetation response to increasing CO_2 ? This chapter attempts to answer this question, but first, to aid in the evaluation of the potential usefulness of models, a hierarchical

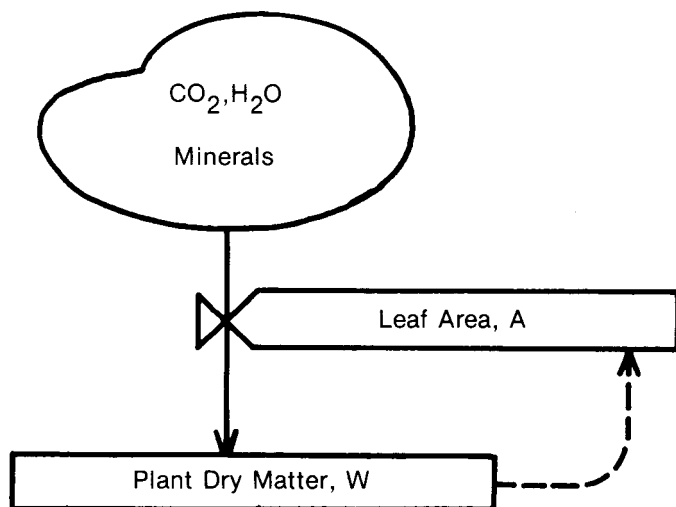


Figure 3.1. A Forrester diagram of the "growth analysis" model proposed by Briggs et al. (1920).

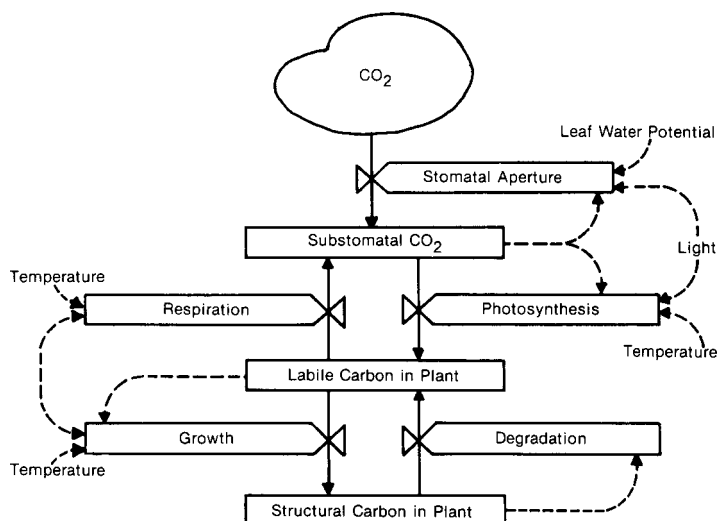
classification scheme is presented. This should help clarify the bounds of where certain models can be applied and provide a way of comparing different types of models.

3.2.1 Hierarchical Classification

Models are built at various levels in the system hierarchy: organelle, cell, organ, plant, community, ecosystem, and biome. Figure 3.3 presents a general scheme that classifies plant models with regard to hierarchy of resolution. Models of specific processes (e.g., photosynthesis, respiration, carbon partitioning, and decomposition) are termed "process" models. These tend to be mechanistic and based on data from controlled environment studies. The integration of such process submodels could form the basis for a

whole plant model that can simulate plant growth and development. The current conventional wisdom is that it is not desirable to build a model at more than one or at most two levels of hierarchy below the one at which predictions are to be made. For example, it would be possible to take one of the processes named in Figure 3.2 and write a biochemical or molecular model describing it. This is not desirable because (see Figure 3.3) (1) activities at lower levels run faster, and to simulate the variation shorter time steps in the model must be used, which increases the running time; (2) there is usually insufficient information to allow the whole model to be built at the same level of detail; and (3) with the introduction of extra detail it becomes increasingly difficult to find the source of any problems in the model. For example, to predict crop or plant community behavior, a process-level, organ-level model is appropriate. Models having a number of different processes integrated into a single system are termed "general purpose." These models are usually developed to predict over large areas (e.g., a forest or soybean field) and over a much longer time frame (e.g., months, years) than process models. They often include a number of subsystem models and tend to be a mixture of empiricism (largely) and mechanism and based on data from field studies. A wide range of diverse models exist. The model by Webb et al. (1978) (Figure 3.3) is a simple empirical relationship that predicts annual aboveground net primary production in native forest, grassland, and desert ecosystems as a function of average evapotranspiration. The model by Shugart et al. (1974) is a complex forest ecosystem model with submodels of such phenomena as meteorological events, decomposition, water and nutrient flux, and consumer dynamics. The soybean crop simulator SOYMOD, by Meyer et al. (1979) in Figure 3.3, predicts yield as a function of numerous mechanistic submodels (e.g.,

Figure 3.2. A Forrester diagram of a model for carbon fixation.



photosynthesis, respiration, growth, phloem loading, and transport) and empirical relationships (e.g., light interception and timing of flowering and fruiting events). The field bean yield model by Skjelvag (1980) is based on a simple regression model relating final yield to several meteorological and planting date variables.

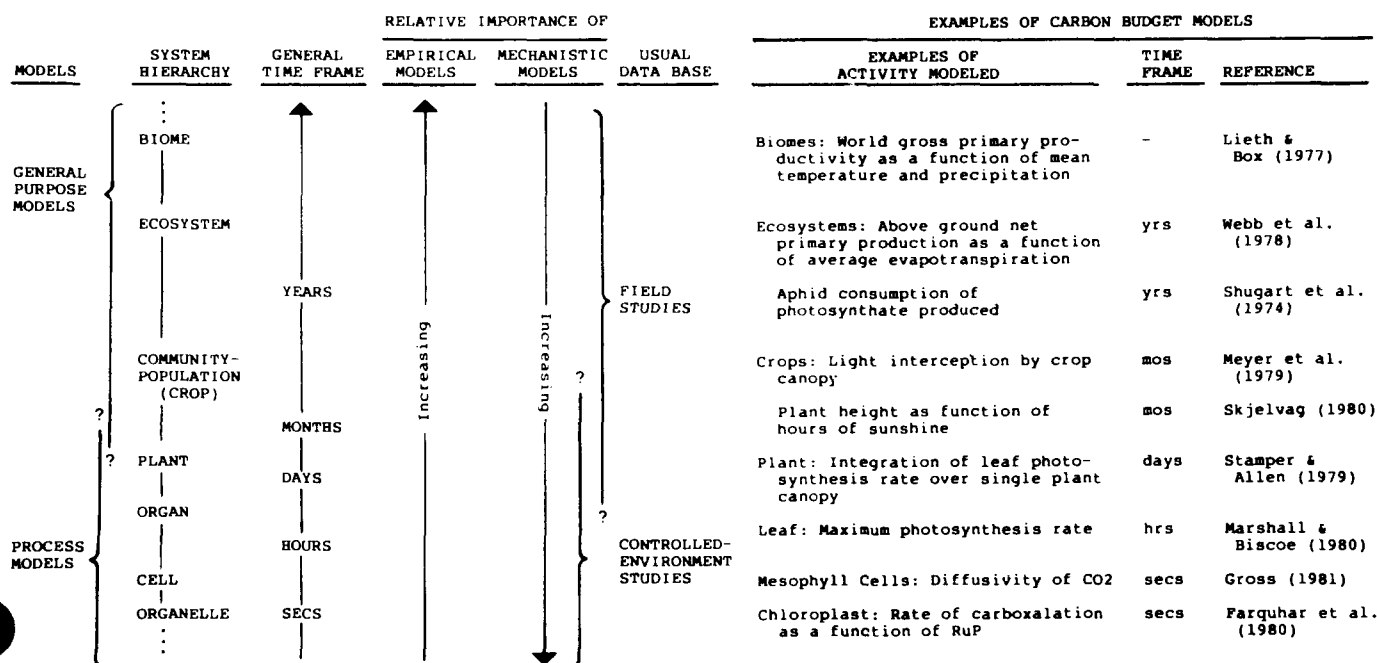
3.2.2 Utility of Various Types of Models

In comparing the models shown in Figures 3.1 and 3.2, two types of models were identified: empirical and mechanistic. Empirical models (often termed correlative models) describe relationships between variables without an implied reference to any underlying biological or physical structure that may exist between the variables; such models are merely correlative. Mechanistic models (often termed explanatory models), on the other hand, do intend to represent causality between variables. In a mechanistic model the form of the mathematical function represents what is believed to be the underlying mechanism that relates the variables and explains their observed behavior. Although the distinction between empirical and mechanistic models is useful, many plant growth models, in fact, contain a mixture of empiricism and mechanism. Furthermore, it must be admitted that all models are empirical at some level. For example, a mechanistic model of plant growth at the organ level would be considered empirical by the modeler working at the cellular level.

An empirical model of leaf photosynthesis is shown in Figure 3.4A. Gas exchange of a leaf is correlated with various CO₂ levels; mechanisms of light energy capture and leaf biochemistry are ignored. Empirical models of this sort have traditionally played an extremely important role in science. Their predictive ability is restricted to the range of the experimental conditions of the data base, and extrapolation of predictions outside this range is not recommended.

A mechanistic approach to modeling leaf photosynthesis is shown in Figure 3.4B. Only essential parts of the system are included, and mathematical equations are developed that can be viewed as analogs of the hypothesized mechanisms operating in the system (Thesen 1974). These analogs must be logically correct but, at the same time, consistent with all physical laws and the natural phenomenon being modeled (Batschelet 1966). One value of this approach is that the investigator is forced to identify explicitly all assumptions and suppositions concerning the proposed mechanistic structure of the system (Solomon 1979). Also, this approach is valuable for suggesting alternative ways of examining existing experimental data, providing a basis for deeper insight into causal mechanisms, and generating new hypotheses (Solomon 1979). In general, one would have greater confidence in making predictions outside the range of experimental data with a well-defined mechanistic model than with its empirical counterpart.

Figure 3.3. A hierarchical classification scheme for models based on levels of resolution.



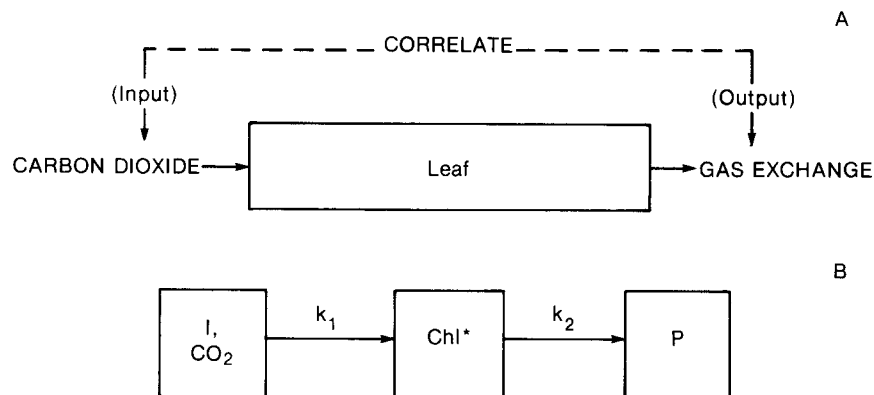
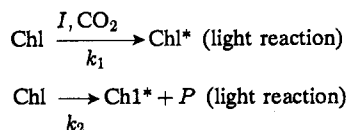


Figure 3.4. (A) An empirical approach to modeling a simple photosynthetic system. The input (CO₂) is correlated to the output (net photosynthesis) without regard to the causal factors relating the two within the system. (B) A simplified theoretical approach for modeling a photosynthesis system derived from the following relationships:



Chl and Chl* represent chlorophyll in its ground and activated states, k_1 and k_2 are the reaction coefficients, I is irradiance, CO₂ is CO₂ concentration, and P is a product of photosynthesis (e.g., O₂). A set of differential equations could be written directly which would describe the dynamics of the system utilizing such variables as chlorophyll density, cell area and thickness, oxygen production, light intensity, and CO₂ concentration.

Figure 3.5 presents a framework for further classifying models within any level of the hierarchy shown in Figure 3.3. Models that are largely empirical are placed on the left of the diagram; those that are mechanistic are placed on the right. As stated earlier, mechanistic models still contain some empiricism. "Comprehension" should perhaps be a third dimension, but, in general, the comprehension of a model increases as the amount of mechanism in it increases. The many possible uses of plant models have already been discussed, but here the uses are classified with regard to their possible roles in evaluating vegetation response to CO₂ (see Figure 3.5): (1) SM—summarizing data; (2) IP—interpolative prediction (to predict behavior within the range of the data base); (3) RM—research management (to identify the most important gaps in our knowledge base); and (4) EP—extrapolative prediction (to predict behavior outside the range of the data base); (5) IN—interpreting behavior. To summarize data, and maybe even for interpolative prediction, completely empirical models (e.g., multiple regression) may suffice. For extrapolative prediction and research management the models must be mechanistic, and for behavior interpretation they must be mechanistic and comprehensive. Models that are capable of extrapolative prediction will be referred to as CEP models, and those capable of (but limited to) interpolative prediction will be referred to as CIP models.

The simplest empirical CIP models may require little more than yield data to validate them. As the models become more mechanistic and comprehensive,

more information about processes and mechanisms is required to validate them. Not only are data less available as we go from left to right in Figure 3.5, but some of the mechanisms may not be known. As models become more mechanistic, the modelers need access to controlled environment facilities to answer questions that arise. Presently, too many models are limited by the data available to their authors. The cost of computer running time also increases with the amount of mechanism in the model, as shown in Figure 3.5, although as computers continue to get cheaper and

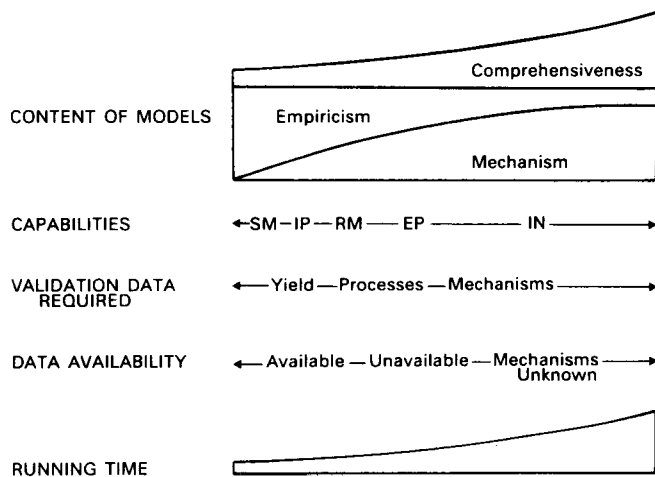


Figure 3.5. Types of plant models and some of their capabilities and requirements: SM, summarizing data; IP, interpolative prediction; RM, research management; EP, extrapolative prediction; IN, interpretation.

faster this problem will be ameliorated. However, there is always likely to be a demand for CIP models with very short running times, for instance, in large-area yield forecasting in agriculture. These models could be generated from comprehensive models by eliminating certain mechanisms with a consequent known loss of predictive ability.

3.2.3 Model Validation

As noted above, a common question asked about mathematical models concerns their validity; that is, how good are they? Thornley (1976) distinguishes model validation at two distinct levels: the level of the predictions and the level of the assumptions. To many, validation is synonymous with the comparison of model predictions to observed data (collected independently from the model-building effort); this is predictive validation. Numerous criteria are available for judging a model as a predictive tool, for example, the amount of variance in the data accounted for by the model and the magnitude of prediction errors (Draper and Smith 1966; Caswell 1976). When such criteria are satisfied, the model is said to be validated (as a predictive device).

Validation of empirical CIP models is appropriate only at the level of the predictions. Although it may appear that many criteria exist for making this assessment, in many cases (particularly for complex models involving time-series output) only a subjective evaluation can be made because of the inappropriateness of the statistical tests available (Caswell 1976). Validation of even the simplest CIP model is usually not absolute. Whereas the term "validation" implies that a model must be judged as either valid or invalid, many qualifications to these extremes exist (Mankin et al. 1975).

Validation of mechanistic CEP models may be attempted both at the level of the predictions and at the level of the assumptions. Mechanistic models may be viewed as tentative hypotheses put forth to explain observed phenomena. These models often are described as working hypotheses because they are modified each time new information becomes available. A hypothesis is tested by comparing predictions (generated under conditions specified by the hypothesis) with observed data. It is impossible to prove any hypothesis correct, because a false hypothesis may lead to correct predictions, and contradictory assumptions can sometimes lead to the same mathematical model (see Solomon [1979] for a classic example). Thus, caution should be exercised when concluding that the validation of a model at the level of the predictions constitutes a validation at the level of the assumptions. However, if a mechanistic CEP model is validated for predictive ability over a wide range of possible environmental conditions,

then confidence is gained in the assumptions employed. This confidence is not different from the confidence felt when validating predictions. In both cases a belief is developed that, as far as they have been tested, the model and its assumptions are valid. For example, the assumption that matter consists of electrons, and neutrons, and so forth, has been validated insofar as the predictions of models incorporating that assumption have been validated many times. The more assumptions there are in a given model, the harder it is to validate those assumptions (i.e., it takes many more tests to gain confidence).

Long before mechanistic CEP models even reach the stage of validation, they must pass the test of having the logic and assumptions in them examined by experimentalists at large. Indeed, experimentalists are an essential part of any modeling team, and they should present model assumptions for scientific criticism both during model development and when major changes are made.

3.2.4 Cost Classification

The more mechanistic a model, the greater its potential use but also the greater the cost of researching and writing it. Table 3.1 estimates the cost of building a CEP model such as GLYCIM at the two extremes of the spectrum shown in Figure 3.5. The soybean crop simulator GLYCIM (Acocck et al. 1985) is used as an example of a CEP model.

Consider first the cost of building a CIP model for current ambient CO₂ concentrations. It should be noted that although a single field experiment to build a CIP model is fairly inexpensive, the unsuitability of an empirical model for extrapolative prediction makes it necessary to collect data over many years, soil types, and locations. Hence, the final cost of an empirical CIP model for current ambient CO₂ concentration may not be less than that of a comprehensive, mechanistic CEP model. However, because field experiments are cheap, the temptation is to build a model with a restricted range to limit the cost. This makes sense from a local (e.g., state agriculture) point of view, but from a national (e.g., U.S. Department of Agriculture or U.S. Department of Energy) point of view, the generation of many local models is a poor use of resources. The cost of basic research in controlled environments leading to a comprehensive mechanistic CEP model is much less than that of hundreds of field experiments leading to many CIP models of restricted range. When we consider the cost of building a CIP model for higher CO₂ concentrations, using data from field releases or open top chambers, the cost advantage of CEP models is even more obvious.

Table 3.1
Estimated Costs of Developing Models
(in thousands of dollars)

Comprehensive Mechanistic CEP Model		Empirical CIP Model		
Any level of [CO ₂]		Current ambient [CO ₂]		Elevated [CO ₂]
Literature review	\$ 150	One experiment	\$ 30	\$ 100
+ Programming	150	× 5 years weather	150	500
+ 4 years growth chamber experiments	400	× 5 soil types	750	2500
+ Parameter adjustment	100	× ? locations	?	?
+ Validation	200			
+ Further development anticipated	200			
	<u>\$ 1200</u>			

Another relative view of the cost of modeling can be seen in Table 3.2, which shows the time invested in certain types of activities associated with the model-building process. This breakdown of time was estimated by Swartzman (1979) in his development (from antecedent models) of CONIFER, a large-scale coniferous forest simulation model. Table 3.2 shows that a surprisingly large amount of time is invested in such tasks as coding and debugging, fine-tuning, and documentation (Swartzman 1979). These activities can be expected to increase, of course, with increasing complexity of the model. Participants in a recent workshop on "evaluation of simulation models in agriculture and biology" concluded that anywhere from 5 to 50% of the total research effort in large-scale predictive modeling may be spent on defining and redefining objectives (Penning de Vries 1977).

3.3 MODEL EVALUATION

3.3.1 Currently Available Models of Plant Responses to CO₂

The effect of CO₂ on photosynthesis has long been of interest to plant physiologists and, as a result, many models of leaf photosynthesis include CO₂ concentration as an input variable (e.g., Charles-Edwards and Ludwig 1974; Hall and Bjorkman 1975). We already have, then, very good models of the effects of CO₂ and other environmental variables on leaf photosynthesis, but as Kramer (1981) has pointed out, we cannot extrapolate from leaf photosynthesis to crop yield. There are several intermediate steps, such as partitioning, about which we know too little. However, exercising these models of leaf photosynthesis emphasizes the importance of interactions between CO₂ and other variables. If these

Table 3.2
Days Spent on Modeling Activities in Developing CONIFER

Activity	Time Spent (Days)	Intensity of Activity Involving Model Density
<i>Conceptualization Phase</i>		
Model Development	60	High
Documentation	47	Moderate
<i>Implementation Phase</i>		
Parameter Estimation and Data Refinement	51	Variable
Coding and Debugging	75	Moderate
Parameter Fine-Tuning	72	Variable

Source: Swartzman (1979).

interactions are apparent at the leaf photosynthesis level, they are likely to be much more important at the crop level because there are so many other processes that the environmental factors can affect.

Horticulturists for a long time also have been interested in the effects of CO₂ on plants, because greenhouse atmospheres are frequently enriched to increase yield. Their data are typically for crops grown under ideal soil conditions and at optimum temperature. As a result the data give the impression that relative yield is a function of CO₂ concentration and there is little interaction with other environmental factors (Kimball 1983). Possibly because of this, many scientists involved in CO₂ research have started using extremely simple empirical models in which the plant response (e.g., growth or yield) or relative response is a function of CO₂ concentration (e.g., Bacastow and Keeling 1973; Siegenthaler and Oeschger 1978; Wong 1980). Most of these same scientists also calculate a parameter called the biotic growth factor (β factor), which is the ratio of the percent increase in response to the percent increase in CO₂ concentration. Of course, the law of limiting returns applies to CO₂ concentration as much as to other materials needed

for plant growth, so the β factor varies according to the function used to describe the data and the CO_2 concentration at which it is measured. Because the β factor is so poorly defined and because the models used to derive it ignore the possibility that some factors may limit plant response to CO_2 , the β factor and associated models have little predictive ability. Their use should be discontinued because they give an erroneous impression of simplicity in the relationship between plant response and CO_2 concentration.

Similar in their simplicity, and only slightly better in their predictive ability, are the models that relate plant response to water transpired during the season (e.g., King et al. 1985). These models generally handle transpiration semimechanistically and have in their favor the logic that both CO_2 uptake and transpiration occur primarily through the stomata. However, water-use efficiency, the ratio of CO_2 or dry matter gained to water transpired, is itself a complex function of CO_2 concentration, water vapor pressure deficit, soil water availability, and leaf area index (see Chapter 4 in this volume). Understanding how these factors affect water-use efficiency is more difficult than understanding how they affect the basic processes of dry weight gain and transpiration.

The critical deficiency of the models discussed above is that they cannot handle interactions between CO_2 concentration and other variables. These interactions occur with external variables, such as light flux density, temperature, and nutrient availability, and with internal variables, such as carbohydrate accumulation in the leaves. Only models that specifically address these processes can deal with the interactions adequately. Such models exist, but with a few exceptions they have not been built with CO_2 concentration as an input. To determine which models have the greatest potential for adapting to predict plant response to CO_2 concentration, we must first decide on a set of critical processes that should be included.

3.3.2 A Minimal Set of Critical Processes

The minimal set of critical processes that should be considered for inclusion in a generic CEP plant model for evaluating the effects of CO_2 is suggested below. The selection was based on a recent review of CO_2 effects on plants, edited by Lemon (1983). Photosynthesis and leaf conductance are directly affected by CO_2 , but they also are affected by other important factors that must be considered, for example, leaf nitrogen content, temperature, light, leaf carbohydrate levels, atmospheric humidity, and leaf water potential. The partitioning of photosynthate into different organs is a critical process. Of the numerous factors that affect

partitioning (usually by controlling organ growth rate), five are included: the amount of carbon substrate present, plant water status, temperature, nutrient status, and plant age. Many of these processes are interrelated. For example, CO_2 has been shown to affect the rate of plant senescence (Lemon 1983), and partitioning has been shown to vary in some plants with plant aging (Boote 1976). Finally, the general growth model must include information about (1) plant structure (e.g., branching patterns and plant height), which is important in plant competition; (2) senescence; (3) patterns of carbon storage; (4) the carbon:nitrogen ratio of tissue; (5) leaf expansion rate; and, for ecosystem models (6) litterfall.

3.3.3 Survey of Some Existing Plant Growth Models

Table 3.3 characterizes 46 plant growth models with regard to the criteria defined in Section 3.3.2. These models were selected from approximately 120 models examined and are intended to be representative of the wide diversity of models that exist. Some models were included because of their widespread familiarity, some because they meet most of the criteria, and others because they represent a certain agricultural or native ecosystem. Table 3.3 is divided into models of crop species (CS) and native plant species (NS). In a number of cases, the NS models are actually submodels of general-purpose ecosystem models, for example, ELM, TEEM, ARTUS.

Several conclusions can be drawn from Table 3.3:

1. The direct effect of CO_2 on photosynthesis and leaf conductance has rarely been included in plant growth models.

2. Models of leaf conductance as a function of leaf water potential are not commonly included in CS models (about one in four) or in NS models (about one in five).

3. Photosynthesis is usually modeled as a function of (listed in order of frequency): (a) light and temperature; (b) feedback inhibition from the buildup of carbon in leaves; and (c) leaf nitrogen, leaf conductance, and CO_2 concentration.

4. Regarding partitioning schemes: (a) CS models tend to include temperature effects three to one over NS models, (b) NS models tend to include nutrient status effects about two to one over CS models, (c) about 60% of the CS and NS models tend to have more than one variable affecting partitioning, and (d) only about 20% of the growth models have invariant partitioning schemes.

5. Architectural aspects of plant growth, for example, branching patterns, are rarely included in dynamic models of plant growth.

Table 3.3
Survey of Some Existing Crop and Native Species Plant Growth Models ("*" =
our acronym) Based on Selected Criteria Considered as a Minimum for Modeling
the Response of Plants to CO₂

	SYSTEM	ACRONYM	REF												
				LEAF AREA	TEMPERATURE	RADIATION	WATER	CARBON DIOXIDE	ROOT DENSITY	SOIL WATER POT.	WATER STATUS	PHOTOSYNTHESIS	CONDUCTANCE	PARTITIONING	OTHER
Crop Species Models	SOYBEAN	GLYCIM	1	•	•	•	•	•	•	•	•	•	•	•	•
		SOYMOD	2	•	•	•	•	•	•	•	•	•	•	•	•
		SOYGRO	3	•	•	•	•	•	•	•	•	•	•	•	•
		SOY*	4	•	•	•	•	•	•	•	•	•	•	•	•
	COTTON	GOSSYM	5	•	•	•	•	•	•	•	•	•	•	•	•
		COTCROP	6	•	•	•	•	•	•	•	•	•	•	•	•
	SORGHUM	SORGF	7	•	•	•	•	•	•	•	•	•	•	•	•
	SUGAR BEET	SUBGRO	8	•	•	•	•	•	•	•	•	•	•	•	•
	ALFALFA	SIMED	9	•	•	•	•	•	•	•	•	•	•	•	•
	CORN	CORNPF	10	•	•	•	•	•	•	•	•	•	•	•	•
		CORNGRO	11	•	•	•	•	•	•	•	•	•	•	•	•
	POTATO	MASHED*	12	•	•	•	•	•	•	•	•	•	•	•	•
	LETTUCE	LETTUCE*	13	•	•	•	•	•	•	•	•	•	•	•	•
	WHEAT	TAMW	14	•	•	•	•	•	•	•	•	•	•	•	•
		WHEATIES*	15	•	•	•	•	•	•	•	•	•	•	•	•
	RYE/CLOVER	RYE1*	16	•	•	•	•	•	•	•	•	•	•	•	•
		RYE2*	17	•	•	•	•	•	•	•	•	•	•	•	•
	WEED	CLOVER*	18	•	•	•	•	•	•	•	•	•	•	•	•
		SETSIM	19	•	•	•	•	•	•	•	•	•	•	•	•
Native Species Models	GENERAL	ARID CROP	20	•	•	•	•	•	•	•	•	•	•	•	•
		BACROS	21	•	•	•	•	•	•	•	•	•	•	•	•
		ELCROS	22	•	•	•	•	•	•	•	•	•	•	•	•
		GROW1	23	•	•	•	•	•	•	•	•	•	•	•	•
		CROP1*	24	•	•	•	•	•	•	•	•	•	•	•	•
		CROP2*	25	•	•	•	•	•	•	•	•	•	•	•	•
		ELM	26	•	•	•	•	•	•	•	•	•	•	•	•
		ELMAGE	27	•	•	•	•	•	•	•	•	•	•	•	•
	GRASSLAND	MATADOR	28	•	•	•	•	•	•	•	•	•	•	•	•
		BASGRAS	29	•	•	•	•	•	•	•	•	•	•	•	•
		GRASS1*	30	•	•	•	•	•	•	•	•	•	•	•	•
		GRASS2*	31	•	•	•	•	•	•	•	•	•	•	•	•
		GRASS3*	32	•	•	•	•	•	•	•	•	•	•	•	•
		GRASS4*	33	•	•	•	•	•	•	•	•	•	•	•	•
		TEEM	34	•	•	•	•	•	•	•	•	•	•	•	•
	FOREST	CERES	35	•	•	•	•	•	•	•	•	•	•	•	•
		CONIFER	36	•	•	•	•	•	•	•	•	•	•	•	•
		DOUGLA	37	•	•	•	•	•	•	•	•	•	•	•	•
		FORSIM1*	38	•	•	•	•	•	•	•	•	•	•	•	•
		FORSIM2*	39	•	•	•	•	•	•	•	•	•	•	•	•
	ARID-SYSTEM	LARREA	40	•	•	•	•	•	•	•	•	•	•	•	•
		MEDECS	41	•	•	•	•	•	•	•	•	•	•	•	•
		SHRUB*	42	•	•	•	•	•	•	•	•	•	•	•	•
	TUNDRA	NECS	43	•	•	•	•	•	•	•	•	•	•	•	•
		ARTUS	44	•	•	•	•	•	•	•	•	•	•	•	•
	SALTMARSH	ARTUS-CO ₂	45	•	•	•	•	•	•	•	•	•	•	•	•
		SPARTINA*	46	•	•	•	•	•	•	•	•	•	•	•	•

Key to references:

1=Acock et al. 1985; 2=Meyer et al. 1979; 3=Wilkerson et al. 1981; 4=Wann and Raper 1979; 5=Baker et al. 1983; 6=Jones et al. 1980; 7=Arkin et al. 1976; 8=Fick et al. 1973, 1975; 9=Holt et al. 1975; 10=Stapper and Arkin 1980; 11=Childs et al. 1977; 12=Ingram and McCloud 1984; 13=Sweeney et al. 1981; 14=Maas and Arkin 1980; 15=Hodges and Kanemasu 1977; 16=Sheehy et al. 1979; 17=Johnson et al. 1983; 18=Fukai and Silsby 1978; 19=Orwick et al. 1978; 20=Van Keulen et al. 1981; 21=de Wit 1978, Dayan et al. 1981; 22=de Wit et al. 1971; 23=Kercher 1977; 24=Huck and Hillel 1983; 25=Van Keulen et al. 1975; 26=Sauer 1978; 27=Pendleton et al. 1983; 28=Saugier et al. 1974; 29=Bachelet et al. 1983; 30=Gilmanov 1977; 31=Coughenour et al. 1984; 32=Detling et al. 1979; 33=Okubo et al. 1977; 34=Shugart et al. 1974; 35=Dixon et al. 1978; 36=Swartzman 1979, Sollins et al. 1981; 37=Mohren et al. 1984; 38=Sollins et al. 1976; 39=McMurtrie and Wolf 1983; 40=Cunningham and Reynolds 1978, Reynolds et al. 1980; 41=Miller et al. 1978; 42=Fetcher 1981; 43=Miller et al. 1983; 44=Miller et al. 1984; 45=Oechel and Blake-Jacobson^a; 46=Morris 1982.

^aW. Oechel and M. Blake-Jacobson. "Modeling Possible Responses of Arctic Tundra to Elevated Atmospheric CO₂." *Manuscript in preparation.*

In Section 3.2 the question was raised as to the availability of existing models that could predict the effect of increasing CO₂ on vegetation. Based on Table 3.3, and keeping in mind the conventional wisdom that a model built for one purpose is rarely (if ever) useful for another, we conclude the following:

1. There are a few crop and native species models (e.g., GLYCIM, SOYMOD, CERES, and ARTUS-CO₂) that include a direct effect of CO₂ on photosynthesis and, in addition, satisfy a majority of the remaining criteria discussed in Section 3.3.2. Such models are candidates for developing a generic plant growth model for CO₂ effects, although the degree of mechanism varies greatly between, for example, GLYCIM (highly mechanistic) and ARTUS-CO₂ (largely empirical, partly mechanistic).

2. For crops it appears that models for predicting yields of soybean as a function of CO₂ are available (e.g., GLYCIM and SOYMOD) and should be subjected to rigorous validation. Models for other crop species could be developed by modifying these soybean simulators, possibly incorporating some unique attributes of other general crop simulators, for example, ELCROS, BACROS, and GROW1 (Table 3.3).

3. For native species, a number of CEP models for grasslands, forests, arid-land shrubs, and tundra ecosystems exist. Very few of these include a direct CO₂ effect. However, a diversity of photosynthesis models have been developed in recent years, ranging from semimechanistic to comprehensive mechanistic (see Table 3.4), that could possibly be used. Perhaps the most serious shortcoming of ecosystem models in relation to making long-range predictions of the effects of increasing CO₂ is the absence of mechanisms for species adaptation and genetic differentiation, species interaction and competition, and successional dynamics.

A class of native species models not included in Table 3.3 is the forest successional models (e.g., JABOWA, FORET, BRIND, KIAMBRAM; see review by Shugart and West 1980, 1981; Shugart et al. 1981). These models predict long-term (centuries) forest dynamics based on empirical functions for tree regeneration, growth, and mortality. By interfacing with CERES-type forest growth models (Table 3.3), which provide a more mechanistic description of short-term growth dynamics, these forest succession models may be useful for long-term predictions. This type of modeling approach would account for species interactions (competition and successional dynamics), although mechanisms for adaptation and genetic differentiation would still be lacking.

3.3.4 Model Uncertainty

The use of models to make predictions involves varying degrees of uncertainty. This uncertainty stems from several important aspects of the model-building process: (1) abstracting a system into a select number of variables and equations, (2) the measurement errors in model parameters, (3) the assumptions of genetic and spatial homogeneity, and (4) the natural variability of systems (Gold 1977; O'Neill and Gardner 1979; O'Neill and Rust 1979; O'Neill et al. 1980).

The complexity of a generic CO₂ model must be minimized while retaining the salient features of vegetation response to atmospheric CO₂. A hypothesized relationship between model complexity and sources of uncertainty, as suggested by O'Neill (1973), is shown in Figure 3.6. O'Neill separated total error in model predictions into (1) error due to the simplification of a system into a few variables (α or systematic bias) and (2) error due to the uncertainty in the estimation of parameter values (β or measurement error). As a model increases in complexity (for example, includes more of the CO₂ interactions which are known to affect plant behavior), the α error would decline. However, as we continue to include more parameters in the model, the error associated with their measurement (the β error) can be expected to increase. Hence, if we examine the possible net result of these two sources of uncertainty (γ error), it is conceivable that there is some optimum level of model complexity for minimizing the prediction error (Figure 3.6). Recent studies by O'Neill and Gardner (1979) and O'Neill et al. (1980) suggest that the uncertainty in models because of the natural variability encountered in biotic systems (genetic, spatial) may be best accounted for by using stochastic (probabilistic) modeling approaches.

3.4 CONCLUSIONS AND RESEARCH RECOMMENDATIONS

The importance of the interactions between CO₂ concentration and other potentially limiting environmental variables was stressed earlier in this chapter. Because CO₂ affects carbon fixation rate and plant water use, there is the potential for every physiological process in the plant to be affected. It is not possible, therefore, to select a few of these processes, label them critical, and study them alone. There is a continuous gradient of processes from photosynthesis, which shows an immediate and dramatic response to CO₂, through root branching, which is enhanced in high CO₂ but may not be of very much significance. This being so, CO₂ concentration can be expected to interact with other environmental variables (see experimental

Table 3.4
Selected Examples of Photosynthesis Models that Include the Effect of CO₂
Concentration on Net Gas Exchange Rates

Photosynthesis as a Function of					References
Light	Temperature	[CO ₂]	[O ₂]	Diffusive Resistances	
X		X	X		Charles-Edwards and Ludwig 1974
X		X		X	van Bavel (1975)
X	X	X	X	X	Hall and Bjorkman (1975)
X		X			Acock et al. (1976)
X		X	X		Chartier and Prioul (1976)
X	X	X			Tenhunen et al. (1976)
X	X	X		X	Reed et al. (1976)
X	X	X			Enoch and Sacks (1978)
X		X			Watson et al. (1978)
X	X	X	X		Hall (1979)
X	X	X			Farquhar et al. (1980)
X		X		X	Marshall and Biscoe (1980)
X		X			Kaitala et al. (1982)

Note: For a complete review of photosynthesis modeling see Tenhunen et al. (1980) and Farquhar and von Caemmerer (1982). X—included in model.

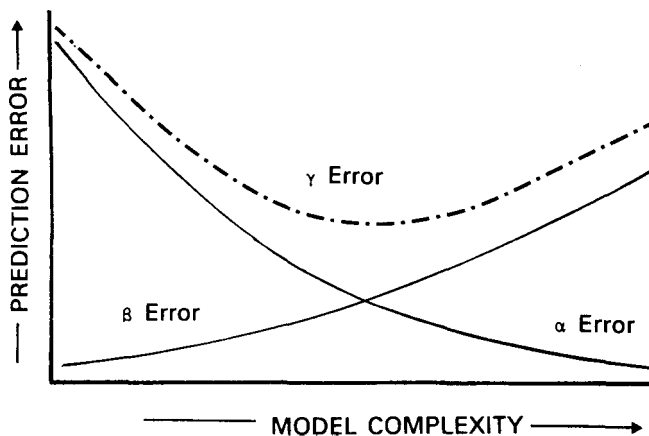


Figure 3.6. Components of error on model predictions as a function of model complexity. Systematic bias or α error is assumed to decrease as the model accounts for more of the complexities of the real system. The measurement or β error is assumed to increase as more parameters are added to the model. Hence, the resultant model inaccuracy, or gamma error ($\gamma = \alpha + \beta$), may tend to increase as model complexity increases for very complex models. Source: O'Neill (1973).

evidence presented in Chapters 4 and 5 of this volume). Very few of the possible combinations of environmental conditions have been tested, and there are not sufficient plant enclosures to test very many at one time. Hence, there is the need to model what is known about plant responses to individual environmental factors and to use such models to predict responses to the interactions. Another reason for taking this approach is that it is not yet known exactly what climatic conditions and management practices will exist in the future high-CO₂ world. Models that respond to CO₂ concentration and other environmental factors are needed to update predictions as this new information becomes available. Combining the information presented in Figures 3.3 and 3.5, two types of models can be envisioned as appropriate for modeling the response of vegetation to CO₂: (1) models that are at least semimechanistic in nature and capable of extrapolative prediction (CEP models) and (2) models that are mainly empirical and capable of (but limited to) interpolative prediction (CIP models).

Fortunately, we know how to build single-species CEP models, although relatively few have actually been constructed and they do have problems of their own. One problem is the uncertainty about some of the mechanisms and functional relationships involved.

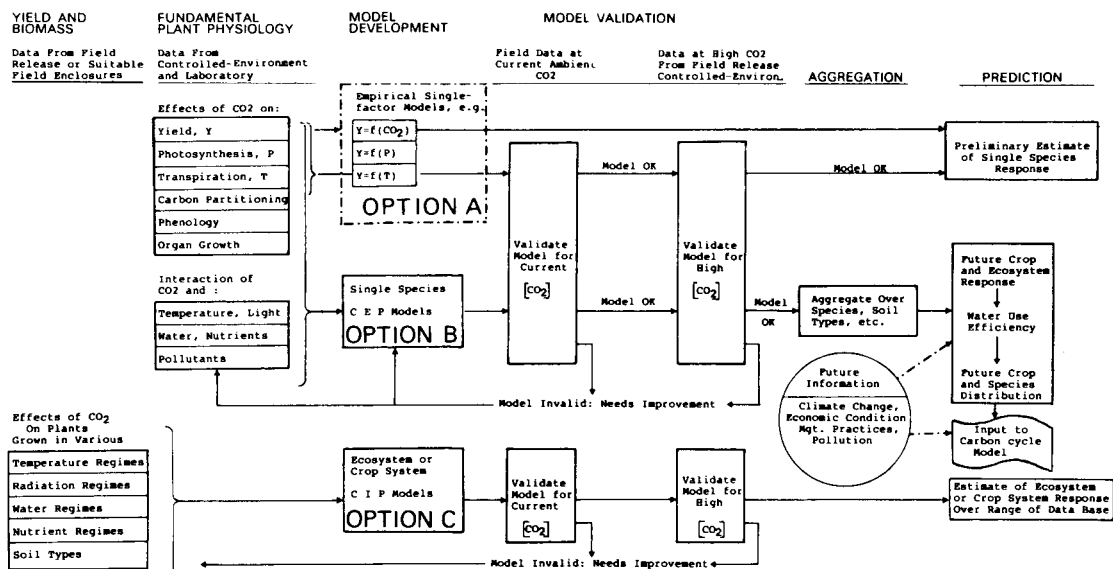


Figure 3.7. Scheme outlining plausible ways to develop modeling capability for predicting the effect of CO₂ on vegetation. Two types of models are envisioned: CIP models (capable of interpolative prediction; mainly empirical) and CEP models (capable of extrapolative prediction; mainly semimechanistic).

For instance, factors affecting stomatal aperture are known, but decades of research have failed to reveal the mechanisms involved in its regulation, and it is still not possible to predict what the degree of stomatal aperture will be in a given set of circumstances. This uncertainty can be reduced only through experimentation, but progress is unpredictable. Also, many of the processes that need to be elucidated are only indirectly affected by CO₂ concentration. Another problem is that existing CEP models have all been developed to make predictions at specific levels of hierarchy, and it is not yet known how to aggregate models of single species into ecosystem models that predict interactions between several species or into cropping system models that predict crop yields over large areas of diverse soil types and weather patterns. We know how to build CIP ecosystem and cropping system models, but they are mostly simple empirical models and do not respond to CO₂ concentration in the way required. In addition, the validity of their predictions is uncertain.

We are forced to conclude that we have not yet built any models suitable for making global-scale predictions about the response of vegetation to CO₂. One reason for the difficulty is that interactions between CO₂ and other environmental variables need to be modeled at the level of the physiological processes, but predictions must be made at the ecosystem or cropping system level. These are two to three levels apart (see Figure 3.3) and, as discussed in Section 3.2.1, this creates problems with (1) choice of the time step for the model, (2) insufficient information about mechanisms, and (3) finding the source of any problems in the model.

There are several plausible ways of meeting the objective, each having various pros and cons. A proposed scheme is outlined in Figure 3.7. One way is to start with CIP-type ecosystem and cropping system models and extend them to respond to CO₂ concentration and its interaction with other environmental variables (Option C, Figure 3.7). This method implies the existence of an adequate data base containing information about system responses to CO₂ over a wide range of other environmental conditions. As previously discussed, obtaining this data base is potentially cost prohibitive. A second plausible way of meeting the objective is to start with CEP-type models and learn how to aggregate them to some reduced level of complexity (Option B, Figure 3.7). Sensitivity analysis could show which soil characteristics or climatic variables have the least impact on the predicted responses, and this information could then be used either to aggregate the input data sets or reduce the complexity of the models. This could be done by simplifying these models step by step, evaluating the loss of accuracy at each step, and then utilizing the simplest models that still give acceptable predictions. Possibly other aggregation methods will be developed in the future (O'Neill and Rust 1979). Of course, CEP models require large amounts of precise data from controlled environment chambers, and the predictions are uncertain until the models have been validated over a wide range of conditions. Hence, a few key species, which are representatives of groups of species, should be selected for CEP modeling. Finally, empirical, single-factor CIP models (Option A, Figure 3.7) can be used to obtain

preliminary estimates of single-species response to CO₂. These models must not be used for extrapolative prediction although it is common practice to do so.

Recommendations for modeling the response of vegetation to CO₂ concentration are as follows:

1. Eschew further development of simple empirical CIP models that are based on limited data yet purport to predict the response of vegetation to CO₂ concentration and other environmental variables outside the range of available data.

2. Develop semimechanistic CIP models of ecosystems and cropping systems that contain those CO₂ responses and environmental interactions for which there is a solid data base.

3. Develop CEP models for some of the most important agricultural and native plant species, validate them, and use sensitivity analysis to aggregate them into ecosystem and cropping system models.

4. Explore other ways of aggregating CEP single-species models.

5. Introduce stochastic elements in the models described in (3) above to provide a measure of uncertainty in the prediction error.

From these recommendations on modeling there must be concomitant recommendations on data collection:

1. Measurements of plants made during field releases of CO₂ provide the only data ideally suitable for developing semimechanistic CIP system models or for validating comprehensive mechanistic CEP models. All enclosures interfere with radiation, rain, wind, and humidity, all of which affect water use (among other things). It is especially difficult to get meaningful data on transpiration rate from plants grown in controlled environment enclosures because the air-conditioning systems cause large and rapid variations in advective heating. However, field releases are expensive and there are difficulties in maintaining temporal and spatial uniformity of CO₂ concentration.

2. In the absence of field release data, the next best alternative is data from a field enclosure that has a well-defined direction and rate of airflow through it. Only in this way can the environment experienced by all the plants in the enclosure be known.

3. Controlled environment data are needed for building the comprehensive mechanistic CEP models. Data for sunlit controlled environment chambers are preferred because the light quality in artificially lit chambers produces plants that are significantly different from those grown in the field. Even so, the values of equation parameters determined from work in sunlit chambers sometimes need adjustment to match field results, especially those parameters affecting leaf expansion and stem extension.

4. A detailed, quantitative description of the life-long above- and belowground environments of plants is an essential part of any of the above data sets.

5. The least expensive way of validating the mechanistic models is first to validate them using field data at ambient CO₂ concentration (to elucidate their response to other environmental variables), and then to validate their response to CO₂, using controlled environmental data.

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1994-1995



4. CROP RESPONSES TO ELEVATED CARBON DIOXIDE CONCENTRATIONS

B. Acock

*U.S. Department of Agriculture/
Agricultural Research Service
Mississippi State University*

and

L. H. Allen, Jr.

*U.S. Department of Agriculture/
Agricultural Research Service
University of Florida*

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1.1 INTRODUCTION

Crops grown intensively in the industrialized nations typically synthesize about 470 g of dry matter per square meter of ground area per year (Penman 1971). Because it takes about 0.5 g of carbon or 1.83 g of carbon dioxide (CO_2) to produce 1.0 g of dry matter (Penning de Vries 1975), the plants must fix about $860 \text{ g m}^{-2} \text{ y}^{-1}$ of CO_2 . The present concentration of CO_2 in the air is about 340 parts per million by volume (ppm) or 0.034%, and the density of CO_2 at 25°C is 1811 g m^{-3} . This means that the plants in each square meter of cropland would have to extract all the CO_2 from about 1400 m^3 of air during the year. In fact, much greater volumes of air are processed because most crop plants remove only a few ppm of CO_2 from the air under typical daytime conditions (Lemon et al. 1971). It seems self-evident that the efficiency of this process would be improved if the concentration of CO_2 in the air were increased.

In fact there is ample evidence that under controlled conditions increasing the CO_2 concentration in which plants are growing increases their rate of net photosynthesis. This occurs primarily because the CO_2 gradient and hence the CO_2 flux into the leaf are increased. In addition, many important crops are C_3 species (some of the solar energy they capture is wasted in respiration), and for them photorespiration is suppressed under high CO_2 concentrations. Also, stomata close partially in response to an increased CO_2 concentration. This decreases the transpiration rate and can affect the leaf water potential and turgor pressure. The most immediate effect of a high CO_2 concentration is, therefore, an increase in the availability of carbon and water internally in the plants. This increased availability, in turn, usually increases the size and dry weight gain of all the plant's organs including those that are used for food, that is, the economic yield. Thus, there is no process or organ on the plant that does not have the potential to be influenced by the level of CO_2 concentration, and in our efforts to predict the response of crops to elevated CO_2 concentration no facet of the plant's physiology can be ignored.

Experiments demonstrating the practical benefits of growing crops in elevated CO_2 concentrations were first reported in France in 1902 (Demoussy). Since then many crops have been tested, and none has failed to respond to increased CO_2 concentration. Because the practice of enriching greenhouse atmospheres with CO_2 has been widespread, it might be supposed that much information would be available about crop responses to CO_2 concentration. Certainly many papers have been written on the topic, but a disappointingly high proportion of them are review papers and provide little new information. Enoch and Kimball (1986a, 1986b)

have just edited a comprehensive review of what is known about CO_2 enrichment of greenhouse crops.

Most of the papers describing original experiments deal with horticultural crops grown under favorable conditions of soil water and nutrients, and they report only the yield of the harvested plant parts. Although these crops are important to the horticultural industry, they are not major world food crops, and they have been grown under conditions that are more favorable than those encountered in the field. Another problem with many previous experiments has been that only two CO_2 concentrations were used: ambient and enriched, between 600 and 1200 ppm. Frequently, ambient was uncontrolled and was assumed to be the same as outside air, but in reality it could have been very different, depending on the leakage rate of the enclosure, crop photosynthetic rate, soil respiration rate, and so forth.

Unfortunately, the response of commercial field crops to enrichment with CO_2 is unlikely to be as favorable as the response of pampered greenhouse crops. The potential of the plants to respond may be limited by a lack of water or nutrients or by unfavorable temperatures. Because plants cannot be exposed easily to increased CO_2 concentrations under normal field conditions, an alternative way of predicting how field crops will respond to increased CO_2 concentrations under these conditions is to understand the mechanisms controlling their various physiological responses to all environmental variables including CO_2 concentration. This sort of information cannot be obtained from experiments where the precise CO_2 concentrations are not known and where the only data recorded are the yields of the harvested parts. Of course, some more detailed analytical experiments have been performed with field crop plants, but these have frequently been done in artificially lit growth cabinets under low light conditions. Furthermore, many of these experiments have been concerned only with the growth of plants during the seedling stage. Thus, despite all that has been written about plant response to CO_2 concentration, there is actually very little information on which to base a prediction of how field crops will respond to the gradually increasing CO_2 concentration in the Earth's atmosphere.

In any project on plant responses to CO_2 concentration, the experimenter is immediately faced with the problem of deciding how to expose the plants to various concentrations of the gas. All of the methods have their advantages and disadvantages; these are discussed in Chapter 2 of this volume. The experiments can also be done at various levels of aggregation (for example, organelle, organ, plant, and crop). For instance, the responses of photosynthesis to CO_2 concentrations have been investigated for single leaves and for the whole

crop canopy. The measurements made at these two levels of aggregation and the difficulties in relating those sets of measurements are discussed in Section 4.2.4.

Even though increasing the CO_2 concentration almost always increases the photosynthetic rate and decreases the transpiration rate of the crop in the short term (Section 4.2), this may not necessarily result in a yield increase. In the first place, the extra carbon available may not be partitioned to organs that further enhance the growth of the plants, and even if it is, there may be no increase in the weight of the harvested part (Section 4.3). In the second place, plant response may be limited by some other environmental variable such as light, temperature, water, nutrients, or gaseous pollutants (Section 4.4).

Chapter 5 by Cure in this volume summarizes published information about the most important responses of several crops to CO_2 . Her analysis gives numerical information about the observed direction and magnitude of these responses and the error associated with them. However, it does not advance our understanding of the mechanisms involved and, indeed, was never intended to do that. Also, the analysis presupposed an uncritical acceptance of all published observations regardless of known deficiencies in technique. In this chapter, these same published observations are utilized to develop a coherent picture of the mechanisms involved in crop response to CO_2 . This necessarily involves some judgment about the relative value of various observations and probably the suppression of some observations that seem at variance with current knowledge about crop physiology. The result is, inevitably, a somewhat personal understanding of crop response to CO_2 , but one that has endured extensive peer review.

The last part of this chapter chronicles the current state of the attempts made to predict crop response to rising CO_2 concentrations with various types of models. The advantages and disadvantages of these various types have already been discussed in Chapter 3. The models are currently imperfect, partly because the data base for building them is incomplete. However, the results indicate what level of simulation is currently possible.

4.2 PHOTOSYNTHESIS, TRANSPIRATION, AND WATER-USE EFFICIENCY

Photosynthesis is the process whereby green plants use the energy of sunlight to “fix” or incorporate CO_2 into carbohydrates. Respiration is the process whereby plants release the energy stored in carbohydrates with consequent release of CO_2 . The energy is normally used for tissue growth and maintenance. Because plants may be respiring and photosynthesizing at the same time,

the measurements of CO_2 exchange rates are usually “net photosynthetic rates” in the daytime and “dark respiration rates” at night. In this section photosynthesis will usually mean net photosynthesis unless otherwise specified.

Photosynthetic rates may be measured on a crop canopy basis, for which the reference unit is the area of ground beneath the crop canopy, or it may be measured on a leaf area basis, for which the reference unit is the leaf area itself. Although this section considers primarily the larger scale responses of leaves and crops to elevated atmospheric CO_2 concentration, it also considers briefly the effects of CO_2 concentration on some of the key biochemical reactions.

Most of the CO_2 enters the internal air space of the leaf through small pores in the epidermis called stomata, which are typically slits 7- to 38- μm long formed by two guard cells on each side of the opening (Kramer 1983; Gardner 1985). These slits can open or close depending on the internal hydrostatic pressure (turgor pressure) of the guard cells and the neighboring epidermal cells. When the guard cells are relatively turgid with respect to neighboring epidermal cells the slits widen to ellipsoid-shaped openings, and when their turgor decreases, the slits narrow and may close completely. Stomata of almost all crop plants (except crassulacean acid metabolism [CAM] plants) are typically closed at night and open in response to photosynthetic CO_2 needs of the leaf as light increases.

Stomata cannot open to admit CO_2 to the internal leaf air space without allowing water vapor to escape from the leaf. This process of evaporation and transport of water from the internal leaf cell surface to the external atmosphere is termed “transpiration.” Although several environmental factors (such as temperature, vapor pressure, radiation load, and wind) may influence transpiration rates of leaves or crop canopy systems, the stomatal apertures are the important control valves of this process. (Only a small amount of transpiration can occur through the leaf cuticle, a waxy layer covering the epidermis.) Therefore, there is a direct relationship of transpiration rates to photosynthesis for specified environmental conditions, as pointed out by Bierhuizen and Slatyer (1965), Tanner and Sinclair (1983), and Sinclair et al. (1984).

As long as crops have adequate soil water, photosynthesis can proceed at a rate unlimited by plant water stress. However, as crops run out of water, the stomata close and transpiration and photosynthesis are reduced. Because the balance of transpiration and soil water availability determine plant water status, cumulative transpiration and transpiration rate have a feedback on photosynthesis.

One result of higher CO_2 concentration is a partial

closure of stomata, thereby increasing the resistance to transpiration. This fact has been the basis for predictions that, with higher CO₂ concentrations, plant stomata will partially close, transpiration will be reduced, and higher crop yields will ensue, with less water required for transpiration. This possibility leads to the consideration of water-use efficiency (WUE) of a crop, which is defined as the ratio of some measure of biomass accumulation to some measure of water consumed. Water-use efficiency values in the literature vary widely based both on units used and on the basis of comparison. Sinclair et al. (1984) pointed out that the biomass accumulation may be expressed as assimilation of CO₂, biomass of the total crop, or grain yield of a crop, and that measures of water consumed may be expressed as transpiration, evapotranspiration, or input of total water to the system. Furthermore, useful time scales can be instantaneous rates, daily accumulations, or seasonal totals. Instantaneous leaf or crop photosynthetic WUE is simply the ratio of CO₂ uptake rate to transpiration rate. On the other end of the scale, crop yield WUE might be the ratio of seed weight produced per unit weight or volume of water used during the season by crop transpiration plus evaporation from the soil.

This introduction explains the importance of interactions among photosynthesis, stomatal response, transpiration, and WUE in response to atmospheric CO₂ concentration. The remainder of this section reviews recent progress in understanding these processes.

4.2.1 Leaf-Level Responses

4.2.1.1 *Photosynthesis*

Historically, photosynthetic rates have been measured as a function of environmental and treatment variables (e.g., light, temperature, nutrition, water, and age) as well as CO₂ concentration. Because CO₂ effects were not investigated from the standpoint of an increase in global atmospheric CO₂ concentration, enrichment levels were seldom maintained over the life of the plant. Gastra (1959) reported one of the most complete data sets of photosynthetic responses of leaves to light, CO₂, temperature, and stomatal resistance.

Work on maize (Hesketh and Musgrave 1962) and comparisons among species (Hesketh 1963) pointed out differences that were subsequently identified as the C₃ and C₄ pathways of photosynthesis. The C₃ pathway was shown to be limited by the oxygenase activity of ribulose biphosphate (RuBP) carboxylase, an effect that can be overcome by decreasing oxygen concentration or increasing CO₂ concentration (Bjorkman 1966; Moss 1966).

Recent studies have been conducted on leaves to determine direct effects of increasing CO₂ concentration on photosynthetic rates. These studies, which have generally focused on a small number of crops, such as soybean, maize, and wheat, have almost invariably shown an increase in leaf photosynthetic rates except when the sink-to-source ratio (usually seed- or fruit-to-leaf ratio) becomes imbalanced. Kramer (1981) pointed out that photosynthetic responses have been observed to decrease under high enrichment conditions over a period of days (Aoki and Yabuki 1977). Feedback inhibition due to inadequate sink and consequent buildup of starch photoassimilates in the chloroplasts may be the cause of a reversal of responses from positive to negative (reviews by Hofstra and Hesketh 1975; Guinn and Mauney 1980; Peet and Kramer 1980).

Rogers et al. (1983a, 1983c) reported that photosynthetic rates for individual soybean leaves increased linearly with CO₂ concentration at about 0.036 mg CO₂ dm⁻² h⁻¹ per each 1 ppm increase in CO₂ concentration over the range of 340 to 910 ppm in pot-grown plants. These leaves were measured at the same CO₂ concentration at which they were grown throughout their life cycles. However, subsequent data (Sionit et al. 1984) tended to show a curved response for leaves grown in pots, but a constant rate of about 50 mg dm⁻² h⁻¹ over the range of 340 to 600 ppm for leaves of plants grown in the field.

Havelka et al. (1984a) conducted experiments with "Kent" and "Ware" soybeans enriched to 1200 ppm CO₂ from day 22 onward. They found that net photosynthetic rates of uppermost fully expanded leaves on "Kent" soybeans grown and measured at 1200 ppm averaged about 30 to 40% higher than those measured at CO₂ levels near ambient. Furthermore, CO₂ enrichment did not delay the decline in photosynthetic rates associated with senescence.

Analyses by Valle et al. (1985a) show that leaves respond to higher CO₂ concentrations not only at high light but also at low light levels. However, light saturation is much higher for leaves grown at high CO₂ concentration. CO₂ concentration and irradiance interact so that as the level of one input increases, so does the response to the other. This interaction will be discussed further in Section 4.4.1.

Net photosynthetic rates of flag leaves of wheat plants enriched to about 1200 ppm from jointing to physiological maturity were measured by Havelka et al. (1984b) using a ¹⁴CO₂-pulsing apparatus similar to that of Naylor and Teare (1975). They made measurements at photosynthetic photon flux density (PPFD) greater than 1500 μmol quanta m⁻² s⁻¹ at weekly intervals from 1 week before anthesis to 5 weeks after anthesis (physiological maturity). CO₂ enrichment

(1390 ppm versus the control at 332 ppm) caused about 50% increase in flag leaf net photosynthetic rates. Higher CO₂ concentrations did not appear to delay final leaf senescence although leaves in the high CO₂ concentrations maintained relatively higher net photosynthetic rates during the decline.

Cross-switching the CO₂ concentrations resulted in a 10% reduction in net photosynthetic rates when leaves of plants grown in high CO₂ were measured at 332-ppm CO₂ compared with leaves grown at low CO₂ levels. However, the low CO₂-grown leaves, when exposed to ¹⁴CO₂ in a 1390 ppm atmosphere, gave the same net photosynthetic rates as leaves grown at high CO₂. Therefore, whereas soybean leaves appeared to adapt significantly to long-term CO₂ treatment conditions by developing higher photosynthetic capacity at all levels of CO₂, wheat flag leaves showed little or no increase in photosynthetic capacity when grown under high CO₂ levels.

4.2.1.2 *Photosynthetic Inhibition by Source-to-Sink Imbalance*

Most of the carbohydrate stored in the typical crop leaf is in the form of starch, and sugar concentrations usually are low (Hofstra and Hesketh 1975; Nafziger and Koller 1976; Ho 1977; Mauney et al. 1979; Potter and Breen 1980), but not always (Madsen 1968). The extra starch that accumulates in the chloroplasts of leaves in high CO₂ concentrations during the day is mostly exported from them at night (Ho 1977). However, if the plant is prevented from translocating and using the carbon by reason of low temperature or some other limitation to growth, starch can accumulate in leaves in amounts of up to 40% of the dry weight (West 1973; Hofstra and Hesketh 1975; Potter and Breen 1980).

Accumulation of starch under these conditions is often accompanied by a reduction in photosynthetic rate (Hofstra and Hesketh 1975; Nafziger and Koller 1976; Mauney et al. 1979; Clough et al. 1981). However, several studies have failed to find a direct correlation between starch content and photosynthetic rate (Mauney et al. 1979; Potter and Breen 1980), suggesting that some other change in the metabolism of the leaf is occurring about which we know little as yet. Kramer's review (1981) pointed out cases where CO₂ enrichment treatments introduced in the midlife of cucumber plants resulted first in a large increase in CO₂ uptake rate of leaves (Aoki and Yabuki 1977). However, a few days later, leaf CO₂ uptake rates were suppressed below the rates of the plants that were grown continuously at ambient CO₂ levels. Thus, under special circumstances, high CO₂ levels can generate end product feedback inhibition of photosynthesis. This problem appears to be negligible in most long-term

enrichment experiments when plants can adapt to utilize the additional photoassimilate. Jones et al. (1984a, 1985a, 1985c, in press) did not observe suppression of CO₂ uptake rates in soybeans that were grown continuously at elevated CO₂ levels up to 800 ppm.

End product feedback inhibition due to imbalance of "sink" relative to "source" has been invoked as a concept for regulating the photosynthetic rates of leaves, especially under CO₂ enrichment conditions (Guinn and Mauney 1980; Wittenbach 1983). Sink refers to tissues and organs that use photoassimilate, such as root tips, young expanding leaves, and reproductive structures. Source refers to tissues and organs that produce photoassimilate, such as the chloroplasts of mesophyll cells of leaves. Starch accumulation in chloroplasts has been regarded as an obvious symptom of source-to-sink imbalance (Mauney et al. 1979), and damage by large starch granules has been suggested as a cause of photosynthetic inhibition (e.g., Neales and Incoll 1968; West 1973; Nafziger and Koller 1976). In extreme cases of starch accumulation, the starch grains have been observed to disrupt the grana of the chloroplasts (Madsen 1968; West 1973; Cave et al. 1981). Fortunately, this type of anatomical response to high CO₂ concentration is rare.

Biochemical feedback on enzymes has also been proposed. One example is the inhibition of RuBP carboxylase activity by phosphorylated sugar via competition with RuBP for binding sites (Bowes and Ogren 1972). Another is some mechanism of inhibition of sucrose-phosphate synthase (SPS) which would result in photosynthetic starch formation at the expense of photosynthetic sucrose formation (Huber 1983). SPS activity generally appears to be negatively correlated with chloroplastic starch accumulation and positively correlated with total leaf sucrose (Huber 1983).

Huber et al. (1984a) postulated that the rate of sucrose formation in the cytoplasm of soybean leaf cells is limited by the activity of SPS which could be operating near maximal velocity under current atmospheric CO₂ concentrations. They found that photosynthetic rates and dry weight accumulation rates of leaves were higher under CO₂ enrichment and that SPS activities and sucrose export rates were similar when measured over the hours of 0900 to 1300 or 1500. Also, Huber et al. (1984b) studied the interaction effects of water stress and CO₂ enrichment on leaf photosynthetic rates, sucrose export rates, and SPS activity. They found that export of assimilates was less affected by water stress than was carbon exchange rate (CER). Also, water stress resulted in mobilization and release of leaf reserves (mainly starch).

These results show that daytime export rates of photoassimilate of leaves under high CO₂ concentration

may be limiting. However, the data taken between the hours 0900 and 1300 or 1500 (Huber et al. 1984a) would imply that the high-CO₂ treatment leaves should continue to accumulate photoassimilate, which was not in fact observed. Unfortunately, no export rate data were collected over the hours from 1500 to 0900 in a complete diurnal cycle, but the implication is that leaves under high CO₂ treatments (high photosynthetic responses) must have higher nocturnal exports to keep a quantitative leaf carbon balance and account for the higher biomass and seed yields observed under CO₂ enrichment conditions (Rogers 1983a, 1983c).

Recently, Hesketh et al. (1983) have speculated that the feedback control of photosynthesis by source-to-sink imbalance is mediated by the availability of phosphate at the chloroplast membrane. All of the metabolites that can cross the chloroplast membrane are phosphorylated compounds. The principal compound concerned is triose phosphate, and this is exchanged at the membrane for inorganic phosphate on a strict one-for-one basis. Normally, the triose phosphate is converted to sucrose in the cell cytoplasm, releasing inorganic phosphate, but if this fails to happen because sucrose is accumulating in the cell, the cycling of phosphate stops. When this happens, the supply of inorganic phosphate inside the chloroplast is soon used up and photosynthesis stops.

4.2.1.3 Leaf Transpiration, Stomata, and Water-Use Efficiency

The transpiration rate of leaves is essentially governed by the combination of the leaf-to-air vapor pressure difference and the diffusional and turbulent transport resistances to vapor transfer. This process has been reviewed in detail by Baker et al. (1982), based in large part on the analyses of Raschke (1956, 1958, 1960), Gates (1962), Lake (1967), Jarvis (1971), Parlange et al. (1971), Pearman et al. (1972), and Wigley and Clark (1974).

Transpiration rate, TR_L , in mol H₂O m⁻² s⁻¹, given by

$$TR_L = \frac{1}{PV_m} \frac{[e^*(T_L) - e_a]}{r_a + r_s}, \quad (4.1)$$

where P is atmospheric pressure (kPa); V_m is gram-molecular volume of water vapor (m³ mol⁻¹); $e^*(T_L)$ is saturation vapor pressure at leaf temperature, T_L (kPa); e_a is air vapor pressure (kPa); r_a is boundary layer resistance for water vapor (s m⁻¹); and r_s is leaf (stomatal) resistance for water vapor (s m⁻¹). For given environmental conditions, one may expect that P , V_m , e_a , and r_a will be reasonably constant. Because r_s is largely a function of airflow past the leaf, we can assume that it is constant. Therefore, TR_L is a direct function

of vapor pressure mediated by leaf temperature and an inverse function of leaf (stomatal) resistance.

Because transpiration is a coupled mass transfer-energy transfer process, we must consider the energy balance of the leaf when considering transpiration as a function of stomatal resistance. For example, if in a specified environment stomata close, then the latent heat transfer from leaf to air will be reduced. This will tend to raise the leaf temperature, and hence raise the leaf vapor pressure, so that stomatal closure will only partly reduce transpiration compared with that which would be expected. Experiments that control leaf temperature at a set point will likely miss this aspect of transpiration.

Pallas (1965) compared transpiration rate versus CO₂ concentration from <250 to 4000 ppm based on weight loss of potted plants of five agricultural crops grown under artificial illumination in controlled environment chambers. He found transpiration reductions were greatest in corn and sorghum, followed by soybean, cotton, and tomato, as CO₂ concentration was increased. Even allowing for feedback on leaf temperature, his data showed the strong effect of stomatal control on transpiration. Baker et al. (1982) presented a leaf energy balance analysis and concluded that reduced stomatal conductance because of higher CO₂ concentration would decrease leaf transpiration and water use, increase leaf temperature, and increase WUE.

Rogers et al. (1983a, 1983c) computed stomatal conductance and WUE (defined as the ratio of net CO₂ exchange rate to transpiration rate) for maize, soybean and a seedling tree species, sweetgum, grown outdoors in 16.5-L pots. They found that stomatal conductance (reciprocal of stomatal resistance) decreased with increasing CO₂ concentration, ranging from about 0.028 to 0.013 m s⁻¹ for soybean, about 0.018 to 0.007 m s⁻¹ for maize, and about 0.019 to 0.007 m s⁻¹ for sweetgum. Water-use efficiency increased for maize mainly because of reduction in transpiration attributed to decreased stomatal conductance at increased CO₂ concentrations. For soybean and sweetgum, however, the increased WUE was due to both an increase in photosynthesis rates (see Section 4.2.2) and a decrease in transpiration rates. Havelka et al. (1984a) found the stomatal conductance of "Kent" soybean leaves enriched continuously to 1200 ppm CO₂ to be about 60% that of unenriched plants (i.e., 0.006 m s⁻¹ vs. 0.010 m s⁻¹).

Wong (1980) reported leaf photosynthetic and transpiration rates of maize, cotton, and snow gum at 330 and 660 ppm. At 660 ppm CO₂, photosynthesis rates increased 25 to 30% for maize, 50 to 70% for cotton, and, with one exception, 60 to 90% for snow

gum. However, the ratio of WUE for the two CO₂ concentrations, WUE₆₆₀/WUE₃₃₀, was about 2.0 for each case. Thus, reduction in transpiration was the most important component of increased WUE for corn, as in the experiments of Rogers et al. (1983c), and increase in photosynthetic rates was the most important component of increased WUE for cotton and snow gum.

Valle et al. (1985b) also found an increase in WUE by a factor of 2.0 for soybean leaves grown and measured at 660 ppm versus 330 ppm. Over 90% of soybean leaf WUE was due to photosynthesis increases, and less than 10% was due to transpiration decreases. Table 4.1 summarizes some of these relative contributions to WUE.

The wide ranges in the relative contributions of photosynthesis and transpiration to leaf-level WUE are probably at least partly due to characteristics of leaf chamber control and analysis systems. However, one generalization is clear: C₄ plants show little response of photosynthesis to increasing CO₂ concentrations above 340 ppm, but show considerable decrease in stomatal conductance, which results in an increase in photosynthetic WUE mainly because of a reduction in transpiration. On the other hand, C₃ plants show considerable increase in photosynthesis with a doubling of CO₂ concentration, and less decrease in stomatal conductance, which results in an increase in leaf-level WUE attributable more to the increase in photosynthesis than the reduction in transpiration.

A voluminous literature exists on leaf photosynthetic rates in response to CO₂ concentration and other variables. This overview was limited to current examples of responses after long-term exposures to different CO₂ concentrations.

4.2.2 Crop- and Canopy-Level Responses

4.2.2.1 Photosynthesis

Measurements of crop-level photosynthetic responses to CO₂ concentration began soon after techniques for leaf-level responses were developed (e.g., Thomas 1965). Some of the methods of measuring crop photosynthetic rates and an evaluation of their successes have been reviewed and analyzed by Lemon (1977), Allen (1979), and Baker et al. (1982). The CO₂ enrichment methods generally involve closed, controlled environment chambers, flow-through systems (usually open top chambers), and open air enrichment systems (see Chapter 2).

Recent research has expanded information both on C₃ crops (especially soybean, wheat, and cotton) and on C₄ crops (especially maize). Direct measurements in closed controlled environment systems have been im-

Table 4.1
Percent Contribution of Net Photosynthesis (CER) and Transpiration Rate (TR) to CO₂-Induced Increase in Leaf Photosynthetic WUE of Several Crop Species

Crop	CER (Percent)	TR (Percent)	WUE Ratio ^a
Maize ^b	27	73	~2
Cotton ^b	60	40	~2
Snow gum ^b	75	25	~2
Soybean ^c	90	10	~2

^aWUE₆₆₀/WUE₃₃₀.

^bWong (1980).

^cValle et al. (1985b).

proved considerably by refinements in control systems, by the addition of controlled soil chambers (Phene et al. 1978; Parsons et al. 1980), and by improvements in humidity control (chilled-water heat exchangers) and analysis (dewpoint analyzers) systems (e.g., Jones et al. 1984b). These systems are discussed in more detail in Chapter 2.

High-volume, open top chamber flow-through systems (e.g., Rogers et al. 1983b) have not been used successfully for measuring canopy photosynthetic rates because of the very small differences in CO₂ concentration between entry and exit flows and turbulence near the exit. However, flow-through systems with smaller exit throats have been used to measure canopy photosynthetic rates when small differences in CO₂ concentration were measured with sensitive flow-balanced and pressure-balanced CO₂ analyzers in a differential detection mode (Drake 1984). The most definitive data for whole plant or whole canopy photosynthesis come from closed controlled environment chambers.

Jones et al. (1984a) found that chambers of soybeans grown at 800 ppm CO₂ had maximum midday crop photosynthesis of 90 μmol CO₂ m⁻² s⁻¹, whereas soybeans grown at 330 ppm CO₂ had maximum values of 60 μmol CO₂ m⁻² s⁻¹. These patterns were maintained day after day under high natural irradiance conditions, and the differences were maintained across all irradiance levels. The leaf area index (LAI) of plants in 800 ppm CO₂ was 9.0, whereas that in 330 ppm was 6.9. The ratio of maximum photosynthesis in the two CO₂ concentrations (90:60 = 1.5) was reflected in the ratios for total above-ground dry weight (1457 g m⁻²:954 g m⁻² = 1.53) and for seed yield (409 g m⁻²:277 g m⁻² = 1.48).

In a later experiment (Jones et al. 1985b), total daytime CO₂ exchanges were computed for clear day conditions for fully developed soybean plants grown at 800 and 330 ppm CO₂ (Table 4.2). Daytime net canopy CO₂ uptake averaged 1.72 and 0.92 mol CO₂ m⁻² of ground area for the 800-ppm canopy and the

Table 4.2
Comparison of Daily Totals of Incident Light, CO₂ Exchange, Transpiration, and WUE of Soybean Canopies Before and After Cross-Switching CO₂ Exposure Levels

CO ₂ Acclimation Treatment (ppm)	Date	CO ₂ Exposure (ppm)	Total Daily Incident PPFD (mol quanta m ⁻²)	Total Daily CO ₂ Exchange (mol CO ₂ m ⁻²)	Total Daily Transpiration (mol H ₂ O m ⁻²)	WUE (mol CO ₂ /mol ⁻¹ H ₂ O) × 10 ⁻³
800 Canopy 1	10/20/82	800	27.5	1.64	346.4	4.73
	10/21/82	330	28.5	1.07	494.0	2.17
800 Canopy 2	10/20/82	800	27.5	1.79	380.0	4.71
	10/21/82	330	28.5	.95	495.0	1.92
330 Canopy 3	10/20/82	330	27.5	.95	363.5	2.61
	10/21/82	800	28.5	1.84	293.9	6.26
330 Canopy 4	10/20/82	330	27.5	.89	339.4	2.62
	10/21/82	800	28.5	1.72	282.0	6.10

Note: Canopies 1 and 2 were grown at 800 ppm CO₂ in controlled environment chambers from planting on August 13 until October 21. Canopies 3 and 4 were grown at 330 ppm CO₂. LAI was 6.0 for canopies 1 and 2, and 3.3 for canopies 3 and 4.

Source: Jones et al. (1985b).

330-ppm canopy, respectively. When the chamber CO₂ concentrations were cross-switched, the daytime photosynthesis averaged 0.92 and 1.78 mol CO₂ m⁻² for the 800 ppm, respectively. The LAIs of the experiment were 6.0 and 3.3 for the high CO₂ and ambient CO₂ concentration treatments, respectively. The total daytime photosynthetic response to CO₂ was essentially the same regardless of the CO₂ concentration pretreatment. This indicates that the canopy with LAI = 3.3 was intercepting most of the incident light. The cross-switched CO₂ concentrations were maintained for 4 days with similar results.

Jones et al. (1985a) maintained air temperatures at 31°C, but they found no difference in net photosynthesis across the air temperature range of 28° to 35°C, although transpiration increased with air temperature.

Moss et al. (1961) found only about a 15% increase in net photosynthetic rates of maize when CO₂ concentrations were raised from 290 to 510 ppm. However, these experiments were conducted under short-term conditions in which the crop was grown under ambient CO₂ concentrations in 1958. Carlson and Bazzaz (1980) reported a 13% increase and a 2% increase in net photosynthesis of maize measured at 600 and at 1200 ppm, respectively, compared with maize measured at 300 ppm. Plants were grown at these same CO₂ concentrations throughout their life cycles, and total weights were 24% and -7% greater for 600 and 1200 ppm, respectively, in comparison with plants grown at 300 ppm. Finally, Baker et al. (1982) showed that maize canopy net photosynthetic rates increased only 20% (or less) over the range of 330 to 600 ppm CO₂. No other studies include whole-canopy net photosynthetic rates for maize.

Baker et al. (1982) reported that field cotton canopy net photosynthetic rate responses were almost linear

with CO₂ concentration increases up to 600 ppm, so that the rate almost doubled in going from 330 to 600 ppm.

Thomas and Hill (1949) and Thomas (1965) reported linear responses in canopy photosynthetic rate for sugar beet, tomato, and alfalfa at CO₂ concentration up to 3500 ppm maintained for short durations. However, these linear responses to such high levels of CO₂ concentration do not seem to be supported by other experiments (e.g., soybean, Allen et al.¹), and they should be repeated. Other than these reports, there are no data available for whole crop photosynthetic rate as a function of CO₂ concentration.

4.2.2.2 Transpiration, Stomatal Responses, and Water-Use Efficiency

Many systems for measuring CO₂ exchange rates at the crop canopy level also have the capability of measuring transpiration. If canopy foliage-to-air vapor pressure gradients are available, then canopy resistances (stomatal plus boundary layer) to transpirational water vapor flux can be computed (Baker and Musgrave 1964). Photosynthetic WUE can be computed from the ratio of net CO₂ uptake rate to transpiration rate.

Whole canopy transpiration data have not been obtained and reported as frequently as individual leaf data. However, WUE improvement has frequently been cited as one of the expected benefits of increased CO₂ concentration (e.g., Wittwer 1980; Kimball and Idso 1983). Therefore, it is important to project CO₂ concentration effects on water use from whole canopy information under specified environmental conditions

¹Allen, L. H., Jr., Boote, K. J., Jones, J. W., Jones, P. H., Valle, R. R., Acock, B., Rogers, H. H., and Dahlman, R. C. "Response of Vegetation to Rising CO₂: Photosynthesis, Yield, and Potential for Sequestering Carbon." Manuscript in preparation.

rather than from single-leaf data. Better yet, information from real field conditions would be desirable, but water balance information may be as difficult to obtain in the field as it is to maintain CO₂ concentrations above ambient.

Soybeans. Photosynthetic rate measurements of soybeans by Jones et al. (1984a) were discussed in Section 4.2.1. In addition to net photosynthetic rates, transpiration rates were measured, and both canopy transpiration resistance and canopy WUE were computed. At high light levels (approximately 1600 $\mu\text{mol quanta m}^{-2} \text{ s}^{-1}$), the canopy transpiration resistance, defined by the ratio of the foliage-to-air vapor pressure gradient to the canopy transpiration rate, in this case was 68 s m⁻¹ for soybeans grown and measured at 800 ppm CO₂ and 56 s m⁻¹ for soybeans grown and measured at 330 ppm CO₂. Thus, the canopy transpiration resistance was roughly 1.2 times larger for the 800-ppm treatment than for the 330-ppm treatment. However, when normalized for its larger LAI, canopy resistance for the 800-ppm CO₂ treatment was 89 s m⁻¹, which is about 1.6 times larger than for the 330-ppm treatment. Alternatively, the average leaf resistance, calculated from the canopy transpiration rate divided by the leaf area, was also about 1.6 times higher at 800 ppm CO₂, which is in rough agreement with measurements of single leaves exposed to high light reported by Rogers et al. (1983a). The absolute magnitudes of the average leaf resistance calculated by this method are large because many of the leaves are heavily shaded and have partially closed stomata.

The analysis by Jones et al. (1984a) thus showed that although the whole canopy resistances (and concomitantly, the whole canopy transpiration rates) were similar, the LAI-normalized resistance and the average leaf resistance were greater at 800 ppm because the transpiration rate per unit leaf area was lower for the high CO₂ canopy. Thus, high CO₂ concentration resulted in partial stomatal closure with respect to the low CO₂ concentration canopy, but the effect of stomatal closure on canopy transpiration was considerably offset by greater LAI.

Short-term (whole day) studies of changes or cross-switching of CO₂ concentration were reported by Jones et al. (1985b). Daytime total transpiration averaged 363 mol H₂O m⁻² for 800-ppm treatments (LAI = 6.0) and 351 mol m⁻² for 330-ppm treatments (LAI = 3.3) the day before cross-switches were implemented (Table 4.2). On the day when CO₂ concentrations were cross-switched, the 800-ppm treatments, measured at 330 ppm, had a daily total transpiration of 494 mol H₂O m⁻², whereas the 330-ppm treatments, measured at 800 ppm, had a daily transpiration of 288 mol H₂O m⁻². As CO₂ concentration was increased, stomatal resistance

increased, and as CO₂ concentration was decreased, stomatal resistance decreased.

Photosynthetic WUE averaged 4.72×10^{-3} mol CO₂/mol H₂O when the 800-ppm treatment was measured at 800 ppm, and 2.04×10^{-3} mol CO₂/mol H₂O when measured at 330 ppm. Likewise, photosynthetic WUE averaged 2.62×10^{-3} mol CO₂/mol H₂O when the 330-ppm treatment was measured at 330 ppm, and 6.18×10^{-3} mol CO₂/mol H₂O when measured at 800 ppm (Table 4.2).

Figure 4.1 summarizes clearly the overall effect of CO₂ concentration exposure level and LAI on whole day, canopy-level WUE. Because photosynthesis occurs mostly in the upper canopy, and transpiration occurs throughout the canopy, larger LAI will tend to decrease photosynthetic WUE at high or low CO₂ concentrations.

Water-use efficiency calculated on other bases is also available for soybean. Rogers et al. (1984a) reported that soybean water use (transpiration) per plant decreased about 30% across the range of 340 to 910 ppm CO₂, whereas LAI increased about 45%. In another report, Rogers et al. (1984b) showed dry weight increases of about 70%. The WUE ratio

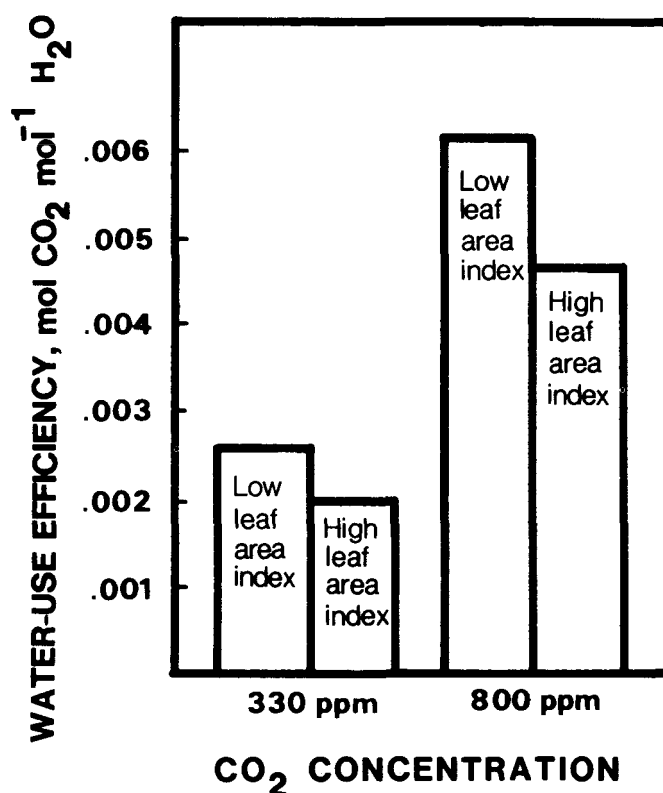


Figure 4.1. Comparison of whole-day WUE in soybean canopies with different leaf areas exposed to different CO₂ levels. The canopy grown in low CO₂ (330 ppm) had a (low) LAI of 3.3 and the canopy grown in high CO₂ (800 ppm) had a (high) LAI of 6.0. Jones et al. 1985b.

($\text{WUE}_{910}:\text{WUE}_{340}$) is calculated to be about 2.3 for these dry weight increase data collected in open top chambers with CO_2 concentrations of 910 and 340 ppm, compared with 2.31 to 2.36 for crop photosynthetic rate data collected in closed environment chambers (Jones et al. 1985b) with CO_2 concentrations of 800 and 330 ppm. This ratio is also very close to the ratio of WUE (2.4) which can be derived at 910 versus 340 ppm from leaf chamber photosynthesis rate data of Rogers et al. (1983c).

Morison and Gifford (1984a, 1984b) conducted studies on 18 agronomic and horticultural species grown from seed in spaced pots in greenhouses maintained at ambient CO_2 and at twice ambient CO_2 . Leaf areas of plants in high CO_2 varied from -8 to $+75\%$ of those of plants in ambient CO_2 , and a significant increase in leaf area was found in all but two species. High CO_2 caused a reduction in transpiration rate per unit leaf area that ranged from 4 to 39%. These two factors resulted in similar time courses of water loss per plant and thus, in general, the reduction in transpiration per unit leaf area was offset by increased leaf area per plant. Furthermore, on average, doubling the CO_2 level reduced stomatal conductance by 36% but reduced transpiration rate by only 21%. The full effect of reduced transpiration rate was partly

offset by higher leaf temperature caused by the lower stomatal conductance (Morison and Gifford 1984a). A companion paper reported an average increase of 53% in dry weight with high CO_2 , associated with a 67% increase in WUE for all species (Morison and Gifford 1984b). These data also show that the increase in WUE at elevated CO_2 is caused much more by increased photosynthetic dry matter accumulation than by water savings due to reduced transpiration.

Maize. Surano and Shinn (1984) computed WUE of maize based on the ratio of above-ground biomass at final harvest, on evapotranspiration determined from neutron-probe soil water depletion measurements, and on irrigation and rainfall inputs (water balance method) (Table 4.3). Their data show that, as CO_2 concentrations in open top chambers rose from 0 to $+300$ ppm above background, WUE rose from 5.0×10^{-3} to 6.3×10^{-3} kg biomass kg^{-1} H_2O in well-watered treatments, and from 5.4×10^{-3} to 7.6×10^{-3} kg biomass kg^{-1} H_2O in the water-stress treatments. The WUE ratio, $\text{WUE}_{650}:\text{WUE}_{350}$, was 1.26 for the well-watered treatment and 1.41 for the drought stress treatment. Stomatal conductance decreased from 0.0074 m s^{-1} at 350 ppm to 0.0049 m s^{-1} at 650 ppm in the well-watered treatment and from 0.0077 m s^{-1} at 350 ppm to 0.0051 m s^{-1} at 650 ppm in the water stress

Table 4.3
Water Use and WUE for Maize Grown in Open Top CO_2 Exposure Chambers Under Two Water Regimes

CO_2 Added to Ambient (ppm)	Aboveground Biomass (g ha^{-1})	Evapo-transpiration (kg ha^{-1})	WUE ($\text{g dry matter K}^{-1}\text{H}_2\text{O}$)	WUE/WUE _{+a}
Well-Watered				
+0	1.9×10^7	3.7×10^8	5.0	1.00
+75	2.1×10^7	3.8×10^8	5.5	1.11
+150	2.1×10^7	3.5×10^8	6.0	1.21
+300	2.2×10^7	3.5×10^8	6.3	1.26
F-Test	0.43 NS ^a	1.16 NS	1.02 NS	—
Water-Stressed				
+0	1.4×10^7	2.5×10^8	5.4	1.00
+75	1.5×10^7	2.6×10^8	5.6	1.03
+150	1.4×10^7	2.5×10^8	5.6	1.02
+300	1.7×10^7	2.2×10^8	7.6	1.40
F-Test	1.84 NS	0.65 NS	1.30 NS	
All Water				
F-Test	23.5**	106.07**	0.53 NS	
All CO_2				
F-Test	—	—	5.21*	

Note: Research performed at Lawrence Livermore National Laboratory; from Surano and Shinn (1984).

* $p < 0.05$.

** $p < 0.01$.

^aNS = nonsignificant.

Table 4.4
Physiology for Maize Grown in Open Top CO₂
Exposure Chambers Under Two Water Regimes

CO ₂ Added to Ambient (ppm)	Stomatal Conductance (cm s ⁻¹)	Predawn Water Potential (MPa)	Midday Water Potential (MPa)
<u>Well-Watered</u>			
+0	0.74 ± 0.01	0.24 ± 0.12	1.36 ± 0.21
+75	0.67 ± 0.04	0.23 ± 0.11	1.38 ± 0.26
+150	0.51 ± 0.09	0.22 ± 0.14	1.21 ± 0.17
+300	0.49 ± 0.03	0.18 ± 0.10	1.35 ± 0.29
F-Test	46.84*	0.20 NS ^a	0.55 NS
<u>Water-Stressed</u>			
+0	0.77 ± 0.01	0.30 ± 0.08	1.70 ± 0.11
+75	0.50 ± 0.03	0.38 ± 0.14	1.80 ± 0.13
+150	0.49 ± 0.03	0.39 ± 0.19	1.76 ± 0.12
+300	0.51 ± 0.03	0.31 ± 0.12	1.65 ± 0.12
F-Test	60.97*	0.44 NS	1.23 NS
<u>All Water</u>			
F-Test	—	11.04*	43.92*

Note: Research performed at Lawrence Livermore National Laboratory; from Surano and Shinn (1984).

* $p < 0.01$.

^aNS = nonsignificant.

treatments (Table 4.4). Although stomatal conductance was reduced by about one-third, evapotranspiration was reduced only about 8% in the well-watered maize, and only about 12% in the water-stressed plants. This is a clear-cut field example of a reduction in stomatal conductance giving only a fractional reduction in evapotranspiration. However, part of the difference could also be due to the same or increased evaporation directly from the soil surface in the high-CO₂ treatments. Maximum leaf area was stable across CO₂ treatments in the well-watered plants, but was increased slightly across the range of CO₂ treatments (5%) in the water-stressed plants, so this is not a big factor in transpiration from the plots.

In this experiment, even for maize, a larger portion of the increase in WUE came from increased biomass (16%) than from decreased evapotranspiration (8%) in the well-watered plants. These values were 22 and 12%, respectively, for the water-stressed plants. Therefore, about two times as much of the increase in the WUE ratio was due to increased photosynthesis in the form of biomass accumulation as was due to decreased evapotranspiration. The increased biomass at higher CO₂ may have been related to better overall plant water relations throughout the season for this maize crop (Table 4.4), whereas evaporation from the soil surface may have compensated for reduced transpiration. This is an example of the need to examine whole crop, whole season CO₂ effects rather than just short-term leaf level responses. The next two sections (4.2.3 and 4.2.4) will examine leaf- and crop-level responses in more detail.

4.2.3 Relationships Between Leaf and Crop Responses

Canopy photosynthesis can be analyzed in terms of the response of individual leaves to light and CO₂ concentration within the canopy. For single leaves, the response of net photosynthesis to light and CO₂ can be fitted by a surface that is characterized by three parameters: (1) the light use efficiency or quantum yield (i.e., the initial slope of the light response curve), (2) the conductance to CO₂ transfer (i.e., the initial slope of the CO₂ response curve), and (3) the respiration rate in darkness (see Figure 4.2 and Acock et al. 1971). Most models of canopy net photosynthesis have been based on the assumption that these single-leaf characteristics are the same for all leaves in a canopy and that the

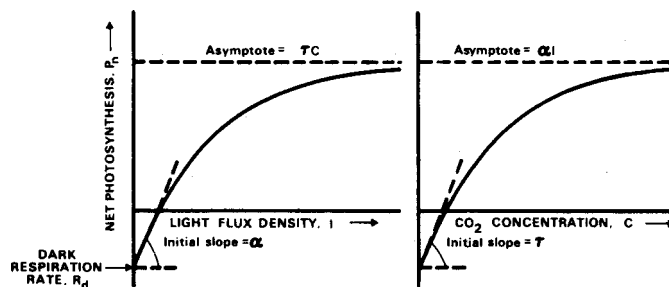


Figure 4.2. Diagram showing the significance of the parameters of dark respiration rate (R_d), light utilization efficiency (α), and conductance to CO₂ transfer (τ), when data on the net photosynthetic rate of leaves in various CO₂ concentrations and light flux densities are fitted with the equation: $P_n = [\alpha \tau C / (\alpha I + \tau C)] - R_d$.

decrease in leaf net photosynthesis with increasing depth in the canopy is caused entirely by decreasing light flux density (e.g., Duncan et al. 1967). However, we have known for some time that the photosynthetic response of a leaf depends on the light environment experienced by that leaf during its growth (El-Sharkawy et al. 1968). Because each leaf in the canopy is adapted to a different light environment, we may expect the photosynthetic characteristics (light utilization efficiency and conductance to CO_2 transfer) of these leaves to differ. In fact, leaf and canopy photosynthetic characteristics already have been successfully related in a model, the development of which is discussed below.

Measurements made by Acock et al. (1978) in a tomato crop showed that light use efficiency is virtually the same for all the leaves in the canopy but that the other photosynthetic characteristics decrease with depth. Similar results were reported by Hozumi et al. (1972) and by Kira (1975), who suggested that the leaf photosynthetic characteristics changed with depth in the canopy as a function of light flux density. By reanalyzing the results of an experiment in which tomato plants were grown in different light flux densities in controlled environments (Charles-Edwards and Ludwig 1975), Acock et al. (1978) were able to show that conductance to CO_2 transfer and dark respiration rate both increase rapidly with increasing light flux density, approaching an asymptotic value at high light. Upper, fully exposed leaves from tomato plants grown at 80 W m^{-2} photosynthetic photon flux density (PPFD) had values for both these parameters that were approximately twice the values for leaves on plants grown at 20 W m^{-2} .

Acock et al. (1978) used these data to produce a model of canopy net photosynthesis, which accounted for the variation in the photosynthetic characteristics of leaves within the canopy. The predictions of the model were then compared with measurements made on a tomato canopy that was gradually defoliated in three stages, from the ground up. The model predictions fitted the experimental observations closely.

The net photosynthetic rate of canopies is actually enhanced by their being composed of leaves that are adapted to the light levels experienced within the canopy. If a canopy were composed entirely of leaves with the photosynthetic characteristics of upper, fully exposed leaves it would have lower photosynthetic rates at low light flux densities. A model that allows leaf photosynthetic characteristics to change with depth in the canopy gives greater accuracy at the expense of introducing more parameters into the model.

Although the work by Acock et al. (1978) only looked at the relationship between leaf and canopy photosynthesis, the relationship probably is similar for

transpiration. Conductance to CO_2 is a photosynthetic parameter determined partly by stomatal conductance. Stomatal conductance affects water transfer in the same way that it affects CO_2 transfer. Thus, it seems likely that the transpiration rate of individual leaves will decrease with increasing depth in the canopy, and this will be caused by decreasing stomatal conductance as well as the leaves being less exposed to wind and solar radiation.

Although the biggest increase in net photosynthetic rate will occur in the upper two or three layers of leaves which intercept most of the light, high CO_2 concentrations will benefit all of the leaves in the canopy. This is because high CO_2 concentrations enhance leaf photosynthesis at all light levels and the changes in photosynthetic characteristics that occur in leaves deep in the canopy do not preclude their responding to CO_2 concentration.

It is not a simple matter to extrapolate from single-leaf responses to canopy responses. It can be done, but only if we know something about the position of the leaf in the canopy or its previous history of exposure to light and the relationship between the leaf photosynthetic characteristics and irradiance.

Another factor that has been observed frequently is that whole crop canopy photosynthetic rates usually exceed the rates of a horizontally displayed leaf, and the whole canopy tends to have much higher light saturation levels than do individual leaves. For instance, Valle et al. (1985a) reported that a rectangular hyperbola fit of photosynthetic rate versus light gave an asymptotic rate of $37.9 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ for leaves grown at 330 ppm and $81.8 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ for leaves grown at 660 ppm. On the other hand, Jones et al. (1985b) found that the same nonlinear equation gave asymptotic limits of about $90 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ and about $200 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ for whole-crop canopies both grown and measured at 330 and 800 ppm CO_2 , respectively.

One reason that a canopy of leaves has a greater photosynthetic response at a given light level than does an individual leaf is that within most types of crop canopies, individual leaves are displayed in a continuum of leaf elevation angles and leaf azimuth angles, so that only a small fraction of the total leaf area is displayed at perpendicular or near-perpendicular angles to the sun. This not only increases the irradiance on leaves deeper within the canopy, it also decreases the irradiance per unit leaf area of the uppermost leaves. Thus, a large part of the canopy leaf area is exposed to solar radiation on the rising part of the response curve, well below light saturation. Allen and Lemon (1975) and Allen et al. (1974) used a crop-climate model to demonstrate that leaf elements in low-radiation-load classes (but well above the light compensation point)

had higher photosynthetic efficiency (ratio of CO₂ fixed to light absorbed) than leaf elements in high-radiation-load classes. Combined with the fact that a large fraction of leaf elements are in lower radiation-load classes, this effect results in greater photosynthetic rates on a canopy basis than a single-leaf basis.

Apparently, individual leaf photosynthetic responses can be much more variable than canopy-to-canopy responses. Some of the apparent difficulty in extrapolating whole canopy responses from leaf-level responses may be related to factors such as variation in leaf responses in terms of leaf position within the canopy, time of measurement, and leaf age. Zelitch (1982) has reviewed the problem of relating crop yield to photosynthesis in detail.

4.2.4 Prospects for the Future: Water Use Versus Water-Use Efficiency

Besides increasing photosynthetic rates, the second most important direct effect of rising CO₂ concentration on plants may be on the potential for saving water through the effect of CO₂ concentration in partially closing stomata. However, there is also a tendency for plants to grow larger under CO₂ enrichment conditions. The effect of larger plants is to increase total transpiration without increasing effective light capture, so the photosynthetic rates at a specified CO₂ concentration are nearly constant (Jones et al. 1985b). The observation that the effects of high CO₂ concentration on crop water use range from a significant reduction to essentially no reduction seems to be related directly to leaf area of the crop.

When and if a climate change with warmer temperatures occurs along with the rise in global CO₂ concentration, we also may see an increase in transpiration (Rosenberg 1982), assuming other factors such as wind, humidity, and cloudiness remain unchanged, or at least do not change to compensate for increased temperature.

Two uncertainties remain from much of the data on WUE collected so far. One uncertainty is that for the most part water use has been calculated from transpiration, and therefore direct evaporation from the surface of the soil has been neglected. Although methods exist for estimating the soil evaporation component and transpiration component under field conditions, these types of measurements have not been made yet. We do not know how much of the presumed savings in transpiration under high CO₂ conditions may be lost in soil water evaporation. Any reduction in evaporation from the soil that may result from increased shading of the ground because of greater LAI is likely to be more than offset by increased transpiration. Second,

because controlled environment chambers usually have been operated under constant environmental conditions, instead of tracking actual environmental conditions that exist diurnally and seasonally, that fluctuate with variable cloudiness, and that may vary because of small microclimate changes caused by differing plant size or leaf area index, the degree of some of the crop responses may be less (or greater) than those that have been measured or calculated. Furthermore, the typical field wind, temperature, and vapor pressure profiles are modified inside plant growth chambers.

As a result, there is a great deal of uncertainty concerning what crop water use will actually be. Crop-climate models offer a mechanism to investigate the range of effects caused by CO₂ concentration, stomatal response, LAI, temperature, vapor pressure, and cloudiness, as discussed in Section 4.4. These model predictions should be tested and compared against experimental findings.

Water-use efficiency may be expected to rise with increasing global CO₂ concentration because of the photosynthetic component of the ratio, regardless of what happens to the transpiration component. Based on data presented earlier, the increase in biomass production, even for C₄ plants, may contribute much more to the WUE than the expected decreases in transpiration.

4.3 CARBON AND DRY MATTER PARTITIONING, THE INITIATION, GROWTH, AND ABSCISSION OF ORGANS, AND YIELD

4.3.1 Carbon and Dry Matter Partitioning

Unfortunately, we know very little about the mechanisms controlling carbon partitioning. However, there are two widely accepted general principles that can help us understand how plants allocate the carbon available to them. First, there is a definite order of priorities for carbon use in plants, which is suggested to be (1) survival, (2) reproduction, (3) growth of existing organs, (4) increase in the number of organs (mostly by branching), and (5) storage of excess carbon for future use. When the higher priorities for carbon use are being met, or cannot be met because of environmental limitations, the next priority will be addressed. When all possible uses for carbon are being met, some plants stop fixing carbon. The order of priorities listed is, of course, a matter for conjecture, but such an order would further the chances of survival of a species.

Second, when some material essential to plant growth is in short supply, the organs nearest the source

of that material will have proportionately more carbon partitioned to them. Physiologists talk about a plant's maintaining a functional balance in this way (e.g., Szaniawski 1983). According to this principle, if a plant growing in 340 ppm CO₂ is carbon limited, it will partition carbon preferentially to the leaves, which will have the effect of increasing its carbon fixation rate. If the same plant is grown in higher CO₂ concentrations, the carbon supply will be greater, and proportionately more of the carbon will reach the stems and roots. This second principle can also help us understand plant response to CO₂ concentration under various adverse environmental conditions (stresses). If a stress results in some material being in short supply, the organ nearest the source of that material will grow preferentially.

Under the first principle mentioned above, it was suggested that seeds, fruits, storage organs, and other plant parts associated with survival and reproduction have the highest priority for carbon. However, these plant parts often grow during the last half of the season when vegetative organs have stopped growing, especially on determinate species and cultivars. During the first half of the season, leaves, stems, and roots compete for the carbon available, and allocations made at that time greatly affect subsequent growth.

The carbon content of dry matter is rarely measured, so we actually know very little about the effect of CO₂ concentration on carbon partitioning. It is often assumed that leaf dry matter has a carbon content of 40 to 45% because there is 40% C in CH₂O. However, Ho (1976) has shown that tomato leaves have carbon-to-dry matter ratios of 26 to 40% depending on their age and position on the plant. He also found that the ratio did not differ significantly between

plants grown in CO₂ concentrations of 300 and 1000 ppm. Therefore, whatever can be said of dry matter partitioning in response to CO₂ concentration is also assumed to be true of carbon partitioning.

In high CO₂ concentrations, all organs on the plant are heavier, and changes in partitioning are detected as relative changes in the dry weights of the various organs on the plant. The ratio most frequently examined, the root-to-shoot ratio, has been reported to increase with CO₂ enrichment for barley, kale, sugar beet, radish, rice, soybean, wheat, and sweet potato (e.g., Ford and Thorne 1967; Imai and Murata 1976; Sionit et al. 1981c; Sionit et al. 1982; Bhattacharya et al. 1985). The effect of CO₂ concentration on the root-to-shoot ratio is larger with greater light CO₂ flux density and plant age (Ford and Thorne 1967; Sionit et al. 1982). This may be the reason why Hurd (1968) found no such effect on young tomato plants grown in low light. However, there seems to be a lack of responsiveness in chrysanthemum (Hughes and Cockshull 1971) and maize (Imai and Murata 1976; Sionit et al. 1982; Goudriaan and de Ruiter 1983), regardless of light flux density or plant age. Also, there are occasional experiments in which the expected increase in root-to-shoot ratio was not observed or was not statistically significant (e.g., Patterson and Flint 1982; Sionit 1983; Goudriaan and de Ruiter 1983; Morison and Gifford 1984b).

A more complete analysis of dry weight differences between the soybean and maize organs is shown in Table 4.5. The data were collected by Rogers et al. (1983a) and are for plants grown in open top field chambers at various CO₂ concentrations for 11 weeks. With high CO₂ concentration, dry weight gain was enhanced more for roots than for stems and more for stems than

Table 4.5
The Partitioning of Dry Matter to Vegetative Organs on
11-Week-Old Soybean and Maize Plants Grown in Various CO₂
Concentrations

Plant Organ	CO ₂ Concentration (ppm)			Coefficient of Variation
	520	718	910	
	(percent)			
Soybean				
Roots	96	106	151	43
Stems	69	110	115	25
Leaves	40	65	86	13
Total shoot	52	75	98	
Maize				
Roots	114	68	104	33
Stems	34	27	46	19
Leaves	15	8	18	13
Total shoot	34	34	39	

Note: The data are expressed as a percentage increase over the dry weight of organs on plants grown in 340 ppm; from Rogers et al. (1983a).

for leaves. The organs furthest from the place where the carbon was fixed benefited most from the extra carbon availability. High CO₂ concentrations do not always change dry weight partitioning; it depends on the sequence of environmental conditions previously experienced by the plant. However, in general we can state that for vegetative plants, more of the extra carbon available in high CO₂ concentrations is partitioned to roots and stems than to leaves. Now we need to ask for each organ whether this extra carbon is used to increase tissue volume or tissue density.

4.3.2 Leaf Growth

The extra carbon available to plants grown in high CO₂ concentrations usually results in a small increase in leaf area (Cooper and Brun 1967; Ford and Thorne 1967; Hofstra and Hesketh 1975; Imai and Murata 1976; Sionit et al. 1981c; Rogers et al. 1984b; Morison and Gifford 1984a; Jones et al., in press) although in one experiment leaf area increases of up to 180% were reported (Mauney et al. 1978). The increase in leaf area in response to CO₂ enrichment is proportionally less than the increase in leaf dry weight, so the leaf area to leaf dry weight ratio, the specific leaf area (SLA),

decreases (Cooper and Brun 1967; Ford and Thorne 1967; Hurd 1968; Hofstra and Hesketh 1975; Sionit et al. 1982; Rogers et al. 1984b; Morison and Gifford 1984b). Again, exceptions to this general finding have been noted in wheat and maize (Sionit et al. 1981c; Rogers et al. 1983a).

Changes in SLA over the season for soybean plants growing in various CO₂ concentrations are shown in Table 4.6. These data by Rogers et al. (1984b) show that plants in high CO₂ concentrations have a lower SLA throughout their life, even though the absolute values of SLA vary greatly during the season in all CO₂ concentrations.

Decreasing SLA is strongly correlated with increasing starch and sugar accumulation in leaves (Hofstra and Hesketh 1975; Allen et al., in press). It might be supposed, therefore, that the change in SLA is caused by the increase in carbohydrates stored in the leaves. The data in Table 4.7 show that this is not necessarily the case. In the table, the SLA for leaves of various ages grown in various CO₂ concentrations is compared with the leaf area per unit leaf residue dry matter. The latter was calculated by subtracting the amount of starch and sugar in the leaves from leaf dry weight. The data, which are taken from Allen et al. (in press), indicate that differences in structural and

Table 4.6
Specific Leaf Area (Leaf Area/Leaf Dry Weight) for Soybean Plants at Various Stages of Growth in Various CO₂ Concentrations

Week of Growth	Growth Stage	CO ₂ Concentration (ppm)						Standard Error
		332	428	534 (m ² kg ⁻¹)	623	772	910	
2	Seedling	35.4	33.2	31.0	28.8	27.4	29.4	2.9
7	Anthesis	28.1	26.4	26.1	24.0	24.0	24.1	2.0
12	Early Podfill	26.3	25.2	24.1	20.0	22.6	20.5	3.4

Source: Rogers et al. (1984b).

Table 4.7
Specific Leaf Area (Leaf Area/Leaf Dry Weight) and Leaf Area Per Unit Leaf Residue Dry Matter for Soybean Plants Grown in Various CO₂ Concentrations

CO ₂ Concentration (ppm)	Specific Leaf Area		Leaf Area/Residue Dry Matter (m ² kg ⁻¹)	
			Days After Sowing	
	48	69	48	69
330	35.4 (a)	26.7 (a)	39.7	30.0
450	32.3 (b)	22.5 (ab)	37.2	26.7
600	27.0 (c)	21.3 (b)	33.0	26.3
800	25.8 (c)	23.7 (ab)	33.9	29.9

Note: Residue dry matter is dry weight minus sugar and starch (Allen et al., in press). Within columns, means not followed by the same letter differ significantly at the 5% level.

protein dry matter per unit leaf area are at least as important as stored carbohydrates in determining SLA. In the few anatomical studies that have been reported, these differences in structure and stored carbohydrate have been observed directly on leaf sections.

In anatomical studies, the leaves of soybean, sweet potato, loblolly pine, and sweetgum (all C_3 species) became increasingly thicker as CO_2 concentrations were increased, whereas the leaf thickness of corn (a C_4 plant) remained unchanged (Hofstra and Hesketh 1975; Rogers et al. 1983c). The increments obtained in soybean and sweet potato leaves were directly attributable to significant changes in the density and number of layers of palisade mesophyll cells (Thomas and Harvey 1983). In pine and sweetgum, however, the size of the entire mesophyll area increased with CO_2 enrichment, and significant changes could not be attributed to the development of any specific cell type in preference to another. This extra leaf thickness was the result of more rapid development of leaves in high CO_2 concentration during the period of lamina differentiation and cell enlargement (Thomas 1983). Generally, epidermal cells remained constant in size across CO_2 concentrations within a species (Thomas and Harvey 1983).

In leaves grown in high CO_2 concentration, the chloroplasts of the mesophyll cells may become filled with large starch grains (e.g., Hofstra and Hesketh 1975). Thomas et al. (1983) made density determinations of starch in the palisade cells of soybean leaves at 0800, 1200, 1600, and 2000 hours. Over the day, relative starch density for plants grown in 349 ppm ranged from 4.84 to 10.16 with the peak at 2000 h, and for plants grown in 946 ppm it ranged from 10.25 to 12.66 with the peak at 1200 h. Thus, enriched plants had a higher starch density with a much smaller diurnal variation and a peak occurring only halfway through the photoperiod.

When measured in the same CO_2 concentration, leaves grown in high CO_2 concentrations have often shown almost the same photosynthetic rate per unit area as leaves grown in low CO_2 concentrations. In some instances the CO_2 concentration in which the leaves were grown had no significant effect on photosynthetic rate (Ford and Thorne 1967; Mauney et al. 1979; Acock et al. 1985b) and in other instances the leaves grown in the CO_2 concentration at which they were being tested had a higher photosynthetic rate than leaves grown in other concentrations (Frydrych 1976; Wong 1979; Valle et al. 1985a). Of course, leaves grown in high CO_2 concentrations and containing large amounts of starch often have shown low photosynthetic rates when compared in any CO_2 concentration with leaves that do not have excessive amounts of starch (Hofstra and

Hesketh 1975; Mauney et al. 1979). Obviously, complex and poorly understood adaptations are taking place.

The fact that leaves grown in high CO_2 concentrations have no clear advantage in photosynthetic efficiency over those grown in low CO_2 concentrations implies that the extra structural dry matter per unit leaf area in high CO_2 concentration is not photosynthetically active, even though, as noted above, there is often an increase in the number of mesophyll cell layers. We do not know the reason for this. Hofstra and Hesketh (1975) have suggested that there is too much resistance in the diffusion pathway for the CO_2 to allow these extra cells to be effective. Certainly they are more densely packed and there is less airspace in the leaf (although internal airspace resistance is quite small). Alternatively, Wong (1979) has suggested that the available nitrogen is being spread over more cells in the high- CO_2 leaf, that as a result each cell has a lower content of ribulose biphosphate (RuBP) carboxylase, and that this is reducing photosynthesis per unit leaf volume. However, if effective strains of nitrogen-fixing bacteria are present in the soil, soybeans and other legumes can fix enough nitrogen to maintain their tissue nitrogen content almost constant (Phillips et al. 1976; Allen et al., in press), even if this entails greatly increasing nodule number and activity in high CO_2 concentration (Hardy and Havelka 1976). If the leaves of effectively nodulated soybeans, in common with those of most other plants, have a slightly lower percentage of nitrogen in high CO_2 concentrations, it is certainly not because they lack the capacity to fix more if it were needed. Also, Boote et al. (1978) have shown that small reductions in the percentage of leaf nitrogen below the optimum have an almost negligible effect on gross photosynthetic rate. Vu et al. (1983) have further shown that for the leaves of soybean grown in high CO_2 concentration, carboxylase activity is reduced much more than protein content or chlorophyll per unit leaf area. Therefore, for soybeans and probably for other plants grown in high CO_2 concentration, the reduced nitrogen content is indicative of a change in leaf composition and anatomy induced by CO_2 enrichment, rather than of a shortage of nitrogen.

The lower specific leaf area in high CO_2 concentration, coupled with the almost constant photosynthetic efficiency per unit leaf area, means that plants grown in high CO_2 concentration use the available leaf dry matter less efficiently than plants in low CO_2 concentration. In some experiments in which growth was expressed as relative growth rate (RGR), this inefficient use of dry matter in leaves has been seen as a gradual reduction in RGR over the first few weeks of exposure until RGR in high CO_2 concentrations became equal

to (Hurd 1968; Sionit et al. 1982; Rogers et al. 1984b) or less than (Thomas et al. 1975) the RGR in low CO₂ concentrations. However, plants that have been exposed to high CO₂ concentrations have a higher absolute growth rate than those in low CO₂ concentrations, because of their increased leaf area, and they retain some of that advantage even if returned to low CO₂ concentrations for part of their growth period (Cock and Yoshida 1973; Krenzer and Moss 1975; Fischer and Aguilar 1976).

4.3.3 Stem Growth

The increased stem growth in high CO₂ concentrations often results in a moderate increase in stem height. The increase in stem height is proportionally less than the increase in dry weight, so stem dry weight per unit length increases (Ford and Thorne 1967; Sionit et al. 1981c; Rogers et al. 1983a). Either the stem diameter increases or the tissue becomes denser or both. In the few experiments where all the relevant measurements have been made, the increase in stem volume accounted for most of the increase in stem dry weight in soybean, maize, and pine seedlings (Rogers et al. 1983a; Allen et al., in press). Even so, there was a tendency for the tissue to be denser in high CO₂ concentration. Sweetgum, a broadleaf woody perennial, may be an exception because no statistically significant increase in volume accompanied the increased dry weight when the seedlings were grown in high CO₂ concentration (Rogers et al. 1983a).

4.3.4 Root Growth

Because roots are so rarely examined in detail, we have little idea of how the extra root dry weight is used by plants that are growing in high CO₂ concentrations. Of course, where the root is a storage organ that organ increases in volume (Bhattacharya et al. 1985), but the response of fibrous roots is less obvious. In one experiment, where root length and dry weight gain were measured on soybean plants, Del Castillo² found that increased root length accounted for most of the increase in root dry weight. There was also a slight tendency for the roots to get heavier per unit length as CO₂ concentration increased. However, root length was only measured at the glass face of the soil container, and the few roots thus sampled may not have been truly representative. In this experiment, the increased root length on plants in high CO₂ was not caused by an increase in the mean growth rate of individual root

axes, but by an increase in the number of active root axes presumably caused by an increased rate of root branching. If this explanation is correct, it implies that growing a plant in high CO₂ concentration will not enable it to explore a larger root volume but will enable it to explore that volume more thoroughly. A definitive experiment is clearly required. We do not know whether changes in tissue density of stem and root tissue are caused by changes in cell number and structure or are simply the result of accumulating carbohydrates.

One type of plant response that has received little or no attention in recent years, but deserves mention here, is the response to high concentrations of CO₂ in the root zone. So long as there is adequate oxygen (O₂), CO₂ concentrations between 5 and 20% in the root zone have been shown to stimulate the growth of both roots and shoots in cotton, pea, corn, and soybean (Leonard and Pinckard 1946; Geisler 1963; Grable and Danielson 1965). In most circumstances, the sum of CO₂ and O₂ concentrations in soil air is 21% by volume (Kristensen and Enoch 1964). Because O₂ concentrations can fall to 16% (Eavis et al. 1971) before root growth is affected, it follows that CO₂ concentrations of 5% can exist in soil air and there will still be adequate O₂. The actual concentrations of CO₂ and O₂ in a given soil will depend on the rate of respiration of soil micro-organisms, roots, and so on, and the rate of diffusion of O₂ down from the soil surface. An increase in decaying annual vegetation in the soil of a high-CO₂ world would shift the balance to lower O₂ concentrations, which could be beneficial or detrimental depending on the absolute concentrations of the gases. However, the direct effect of a doubling of atmospheric CO₂ concentration in increasing the soil CO₂ concentration will be negligible.

4.3.5 Initiation, Growth, Senescence, and Abscission of Organs

Plants have the potential for producing more branches, flowers and fruit than they are able to support (e.g., Hansen and Shibles 1978; Frey 1981). Depending on how much carbon and perhaps nitrogen is available, some of these organs may not be initiated, or they may be initiated and then be abscised. Thus, high CO₂ concentrations can increase the numbers of these organs by increasing initiation, retention, or both. Also, the increased carbon availability in high CO₂ concentrations sometimes enables plants to initiate and retain these organs earlier in their life cycle and thus affects the timing of events. This can be especially important for high-value seasonal crops, where high CO₂ concentrations can enable plants to set and ripen fruit a few days earlier and give a disproportionately large increase in the return on the crop (Calvert 1972). For

²Del Castillo, D., personal communication.

further discussion of the effects of CO₂ concentration on organ initiation, abscission, and timing, see Baker and Enoch (1983).

Enhanced branching and tillering in high CO₂ concentration has been reported for barley, rice, wheat, soybean, and rose (Ford and Thorne 1967; Hand and Cockshull 1975; Imai and Murata 1978; Paez et al. 1980; Sionit et al. 1981c, 1982; Sionit 1983; Rogers et al. 1984b). Sometimes the extra axes appear earlier (Imai and Murata 1976), which can lead to their being longer (Cooper and Brun 1967). The increased branching enables plants to exploit the space available to them more rapidly. They intercept more sunlight and grow even more rapidly until the crop canopy closes. Having more branches also increases the number of potential flowering and fruiting sites.

Partly as a result of the increased branching and partly because of increased initiation and retention, high CO₂ concentration increases the number of flowers on plants (Hand and Cockshull 1975). The weight and quality of blooms also can be increased (Hughes and Cockshull 1971; Kimball 1983b), and there is often a small decrease (Calvert 1972; Marc and Gifford 1984) or increase (Thomas et al. 1975) in the time to anthesis. The decreased time to anthesis can be commercially significant for tomato plants grown in heated greenhouses (Calvert 1972). However, in one experiment Hesketh and Hellmers (1973) found that floral initiation was greatly delayed in sorghum and slightly delayed in maize, sunflower, and cotton when the plants were grown in 1000 ppm CO₂. The physiology of this response has never been explained. In monoecious plants like cucumber, high CO₂ concentration increases the number of female flowers (Enoch et al. 1976) because the increased CO₂ concentration encourages branching and there are more female flowers on the branches than on the mainstem.

A high CO₂ concentration usually increases fruit and seed weight (Kimball 1983a). Where it has been measured, harvest index has been found to decrease slightly (Rogers et al. 1984b) or to increase slightly (Sionit et al. 1980; Goudriaan and de Ruiter 1983; Jones et al. in press) with increasing CO₂ concentration. Depending on the species, the extra fruit dry weight in high CO₂ concentration may result from an increase in the number of fruits, the size of fruits, or both. With tomato, wheat, and rice, both number and size are increased (Calvert 1972; Cock and Yoshida 1973; Krenzer and Moss 1975; Fischer and Aguilar 1976; Wittwer 1978; Sionit et al. 1980, 1981c). With soybean, the number is increased but the size remains nearly constant (Cooper and Brun 1967; Rogers et al. 1983a).

We do not know of any instances where the density of fruit or seed tissue changes. Analyses of seed

from soybeans and maize grown in a range of CO₂ concentrations by Rogers et al. (1983a, 1984b) showed no differences in percentages of fat, protein, or crude fiber, except that in one experiment the percentage of protein in soybean seed decreased with increasing CO₂ concentration.

Experiments in which soybeans, wheat, or rice were given high CO₂ concentrations for only part of their life cycle have shown that seed number is most responsive to enrichment before anthesis, and seed weight (size) is most responsive after anthesis (Hardman and Brun 1971; Cock and Yoshida 1973; Krenzer and Moss 1975; Fischer and Aguilar 1976). In tomato, where time to anthesis is reduced, there is also a reduction in the time taken for the first fruits to ripen (Calvert 1972).

4.3.6 Yield

Recently, Kimball (1982, 1983a, 1983b) conducted a thorough search of the literature for data on the effects of CO₂ concentration on agricultural yield. He discovered about 770 observations on the yield or biomass production of 38 agricultural crops and 18 other species, reported mostly in English-language journals before 1982. The results that he has collected suggest that increasing the CO₂ concentration from 330 to 660 ppm will probably increase agricultural yield by about 32%, with a 95% confidence range from 27 to 38% (Table 4.8). These yield increases have been substantiated by more recent reports cited in Chapter 5. Kimball pointed out that many of the reported results are for horticultural crops grown in enclosures under almost ideal conditions of temperature, water, and mineral nutrient supply. Insofar as the enclosures used in these experiments limited the amount of light available to the crops, their relative yield response may have been larger than it would have been in the

Table 4.8
Mean Predicted Marketable Yield Increases for a Doubling of CO₂ Concentration from 330 to 660 ppm and Associated 95% Confidence Intervals

Crop	Number of Observations	Percent Increase	95% Confidence Interval	
			-	+
Rice	1	9	-	-
Wheat	13	38	15	74
Barley	1	36	-	-
Corn	1	16	-	-
Sorghum	1	79	-	-
Soybean	13	17	3	37
Cotton	2	104	-	-
Clover	2	4	-	-
Tomato	6	13	0	32

Source: Kimball (1983b), Table 2.

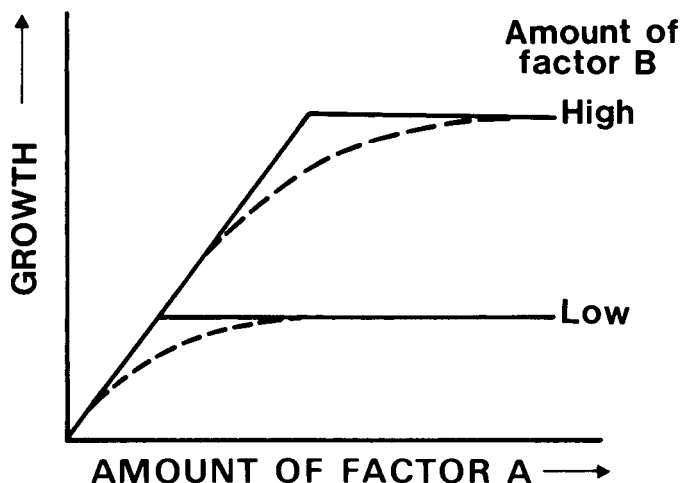


Figure 4.3. Diagram illustrating Blackman's "Principle of Limiting Factors" (Blackman 1905). The solid lines show the responses predicted by the principle, whereas the dashed lines represent observed responses.

field. However, few field-grown crops will encounter an environment that is almost ideal in every other way, as it was for most of the crops in Kimball's sample.

There is little doubt that stressful environmental conditions that limit the growth of plants in present-day concentrations of CO_2 will also limit their growth in the future higher concentrations of CO_2 . The real question is whether crop yield response to increased CO_2 concentration will be proportionately greater or less under conditions of stress than it is under ideal environmental conditions. These interactions between CO_2 concentration and other, potentially stressful, environmental factors are examined next.

4.4 INTERACTIONS BETWEEN CO_2 AND OTHER ENVIRONMENTAL FACTORS

To grow, plants need CO_2 , light, heat, water, and mineral nutrients. If one of these factors is in short supply, growth will be reduced or even stopped altogether. When this happens, the factor in short supply is said to be "limiting." The concept is embodied in the "Principle of Limiting Factors" (Blackman 1905), which is illustrated in Figure 4.3. In this figure, the slope of the response line changes abruptly when factor B becomes limiting, but we know that in fact the limit is approached asymptotically, as shown by the dashed lines and as seen in the photosynthetic response curves in Figure 4.4.

Superficially, we might expect that all plant responses to CO_2 concentration would be limited by the levels of the other growth factors in the same way. However, high CO_2 concentration increases

photosynthetic rate and decreases transpiration rate and so may partially compensate for deficiencies in light and water. High CO_2 concentration also often causes increases in root length which could conceivably alleviate mineral nutrient deficiencies. It is difficult to see how CO_2 concentration could compensate for suboptimal temperatures, although even this has been reported for okra (Sionit et al. 1981b). However, the optimum temperature for C_3 photosynthesis increases as CO_2 concentration increases (Percy and Bjorkman 1983), so that temperatures that are supraoptimal at current ambient CO_2 concentrations may become optimal at higher CO_2 concentrations. Thus, it is important to study the interactions between CO_2 concentration and other factors. We cannot just assume that a level of a factor which is limiting in ambient CO_2 concentration will prevent any response to an increase in CO_2 concentration.

4.4.1 CO_2 and Light

Considering the relationship of photosynthetic rate to light and CO_2 concentration shown in Figure 4.4, it is not surprising that plant response to CO_2 concentration in terms of absolute dry weight gain is higher in high light than in low light (Hughes and Cockshull 1971; Morgan 1971; MacDowall 1972; Gifford 1977; Kimball and Mitchell 1979; Sionit et al. 1982). Similarly,

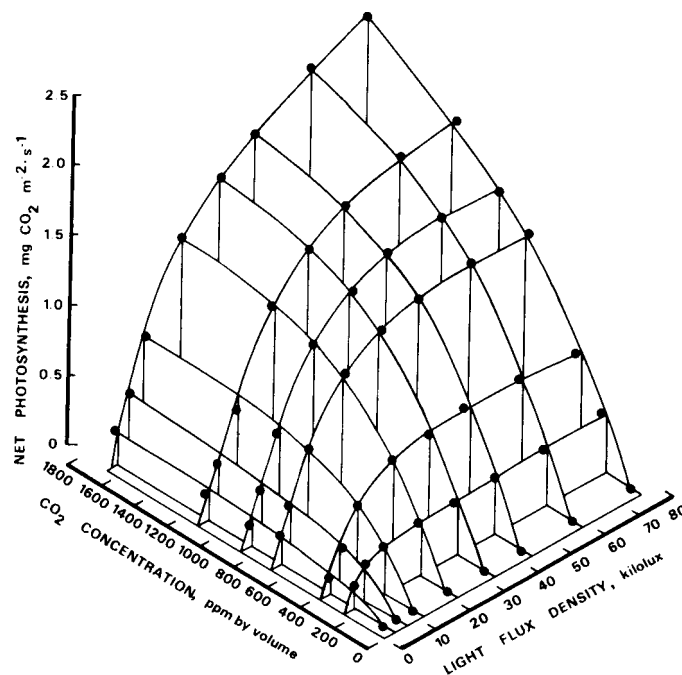


Figure 4.4. Net photosynthetic rate of single leaves of soybean cv "Hark" as a function of CO_2 concentration and light flux density. Data from Brun and Cooper (1967). 1 kilolux $\approx 39.5 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$.

the effect of CO_2 concentration on root-to-shoot ratio is more pronounced in high light (Ford and Thorne 1967). However, in two experiments using wheat, CO_2 enrichment actually gave a greater percentage increase in growth at low light flux densities than in high light (MacDowall 1972; Gifford 1977).

Because a high CO_2 concentration increases the activity of the Calvin cycle and decreases the activity of the photorespiration cycle in C_3 leaves, it effectively reduces the light compensation point. Heath and Meidner (1967) have shown that this can increase the growth of a crop such as lettuce grown in greenhouses in winter at high latitudes. They argue that leaves enclosed in the head are shaded to near the light compensation point. The reduction in the light compensation point caused by high CO_2 concentration enables such leaves to realize a net gain of carbon rather than a loss. This also probably enables the lower, more heavily shaded leaves of a normal crop canopy to show a photosynthetic gain. Percy and Bjorkman (1983) have even suggested that the relative enhancement of photosynthesis by CO_2 enrichment is greatest under light-limiting conditions. However, their contention is not supported by the data of Brun and Cooper (1967), shown in Figure 4.4, or by any similar data set known to the authors. The data we have examined all show relatively greater increases in photosynthetic rate when light is nonlimiting rather than when light is limiting.

Because CO_2 and light both act on the plant through the photosynthetic process, to some extent increased CO_2 concentration can compensate for low light (Ford and Thorne 1967; Hurd 1968).

4.4.2 CO_2 and Temperature

Net photosynthesis for C_3 leaves, as a function of temperature and CO_2 concentration, is shown in diagrammatic form in Figure 4.5. The relationship has been discussed in detail and modeled by Acock (1980) and is further supported by data from Hofstra and Hesketh (1969), Enoch and Hurd (1977), Osmond et al. (1980), and Jurik et al. (1984). As temperature increases, the chemical reactions involved in photosynthesis proceed more rapidly until a point is reached where the enzymes promoting those reactions are progressively damaged more and more by high temperature. In this way, temperature limits photosynthesis to the triangular area in Figure 4.5. Within the triangular area, photosynthesis is limited further by other factors, the chief ones being light and CO_2 concentration. Typical lines corresponding to CO_2 concentrations of 330 and 660 ppm and full summer sunlight are shown on the figure. The dashed lines are straight, except where they meet the sides of the triangle, and they slope down

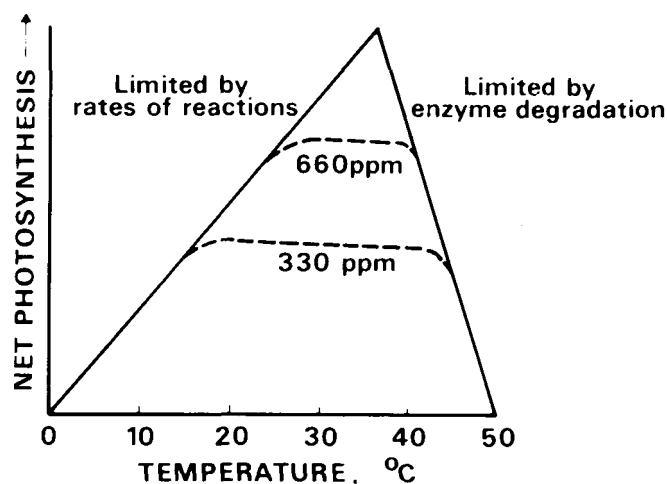


Figure 4.5. Relationship of net photosynthesis to temperature and CO_2 concentration shown in diagrammatic form for a typical C_3 leaf.

to the right because photorespiration rate increases as temperature increases. The overall effect of this is to move the temperature optimum for photosynthesis to higher temperatures as CO_2 concentration increases. This phenomenon is often discussed, but a more profound effect is usually missed. At present ambient CO_2 concentrations, temperature has little effect on net photosynthesis over a wide range of temperatures. At higher CO_2 concentrations, that range is smaller and we are more likely to see temperature limiting photosynthesis.

Given adequate substrate, the rates of appearance and expansion of organs on the plant are a function of temperature, and the relationships are similar to those for photosynthesis shown in Figure 4.5. At too low a temperature the chemical reactions involved in tissue synthesis proceed slowly, and at too high a temperature the enzymes promoting those reactions are damaged. There is, then, a temperature range over which growth proceeds at a satisfactory rate. The limits of this range vary from one species to another. When plants are grown in high CO_2 concentration, they fix more carbon. If the temperature is too low, organ growth rate may be too slow to use all of the carbon available; then the plant is said to have a low "sink strength." To take advantage of the extra carbon available in high CO_2 concentration, it may therefore be necessary to grow the plants at the correct temperature. Too low or high a temperature can markedly reduce (Hofstra and Hesketh 1975) or even completely prevent (Krenzer and Moss 1975) any yield response to CO_2 concentration, and it can cause starch accumulation and inhibition of photosynthesis in the leaves of plants in high CO_2 concentration (Section 4.2.1). As with photosynthesis, the temperature range over which the plants can take full advantage of the increased CO_2 concentration

becomes smaller as the CO₂ concentration increases. In a given CO₂ concentration, the temperature optima for net photosynthesis and organ expansion will not necessarily be the same, and because slow expansion can inhibit photosynthesis, the optimum for overall plant growth may be a third temperature (Enoch and Hurd 1977).

In complete contrast to the above, Sionit et al. (1981b) have shown that okra plants do not survive in temperature regimes of less than 26° daytime/20° nighttime at ambient CO₂ concentration but that they grow to maturity in the same temperature regimes under CO₂ enrichment. The physiology of this response has not been explained yet, but okra is a plant of tropical origin and may respond differently from most crops of temperate origin.

4.4.3 CO₂ and Soil Water Availability

As CO₂ concentration increases, the stomata gradually close and transpiration rate is reduced (Section 4.2.1). The effect is often more pronounced in C₄ plants than C₃ (Pallas 1965). This stomatal closure should reduce the rate at which water stress develops in CO₂-enriched plants. Also, such plants commonly have a root system that is relatively more enlarged than the leaf area (Section 4.3.4). However, the larger leaf area and larger root system of plants in high CO₂ concentration may cause them to use water faster and, where total water supply for the season is limited, to exhaust the available water earlier in their life cycle. Thus, the response of a plant to water stress in high CO₂ concentrations will depend on the relative importance of the CO₂-induced decrease in stomatal conductance and increase in demand for water caused by increased size (Section 4.2.4).

In an experiment where soybean plants were grown in pots at various CO₂ concentrations and irrigation was withheld for 4 days during pod fill, Rogers et al. (1984a) found that high CO₂ concentration decreased stomatal conductance so that leaf water potential was maintained at a higher (less negative) value and stress was avoided. Pot weight measurements showed a decreased daily water use by the CO₂-enriched plants despite their larger size. However, in an experiment in sunlit controlled environment chambers, Jones et al. (1985b) reported that the increased size of the CO₂-enriched plants caused them to transpire as much or more water per unit land area despite lower stomatal conductance. Avoidance of stress by decreased stomatal conductance in the experiment by Rogers et al. (1984a) did not involve any penalty in terms of decreased CO₂ assimilation rate. During the period of water stress, starch concentration

in the leaves was reduced by 34% at 330 ppm and 13% at 620 ppm but was unaffected at 910 ppm.

Sionit et al. (1980) and Gifford (1979) found that the relative yield increase with CO₂ enrichment of water-stressed wheat plants was as large as or larger than that of control plants. With the levels of CO₂ concentration and stress used in both of these experiments, the water-stressed wheat in high CO₂ concentration yielded as well as wheat without water stress in low CO₂ concentration. Sionit et al. (1980) attributed this result in part to improved osmoregulation and hence the maintenance of higher turgor pressures in the enriched plants.

4.4.4 CO₂ and Mineral Nutrients

Plants only need small amounts of mineral nutrients for growth, but these nutrients frequently are present in soil in such small amounts that they limit growth. Nitrogen is the one that is most frequently supplemented. Leaf area is highly correlated with nitrogen supply, so a shortage of nitrogen can restrict canopy development. Also, seed nitrogen concentration is almost constant, so a nitrogen deficiency can reduce the number of seeds brought to maturity. This being so, a nitrogen deficiency would be expected to reduce the response of the plants to CO₂ enrichment unless that enrichment made more nitrogen available via increased root growth (Rosenberg 1981). Similar considerations would apply to other nutrients.

There have been several experiments conducted to examine the interaction between CO₂ concentration and mineral nutrients. Sionit et al. (1981a) grew wheat under fluorescent lights at the Duke University phytotron in Hoagland solution from one to one-sixteenth normal strength. In this experiment the percentage response to CO₂ enrichment was similar in all nutrient levels through the vegetative stage of growth. However, by the final harvest the response to CO₂ concentration was much higher in the higher nutrient levels. For both CO₂ concentrations used in the experiment, the greatest total dry weight gain occurred in half-strength Hoagland solution. Dry weight gain in full-strength Hoagland solution was about 20% less than that in half-strength solution at 350 ppm CO₂ but was only about 5% less at 675 ppm CO₂. Whatever the reason for the deleterious effect of the full-strength solution (e.g., salinity), high CO₂ concentration appeared to reduce that effect. In a similar experiment with non-nodulated soybean, Sionit (1983) found that CO₂ enrichment produced almost the same percentage increase in branch number, leaf area, and pod number in plants growing in one-half and one-eighth strength Hoagland solution.

Wong (1979) grew cotton and maize plants in greenhouses in nutrient solutions that had different levels of nitrate nitrogen. He found that there was a tendency for the response of extra CO₂ to be proportionately smaller in low-nutrient treatments. The CO₂ response virtually disappeared in the very lowest nutrient treatment for maize, but not for cotton. Imai and Murata (1978), working with rice, millet, and maize exposed to treatments for 8 or 10 days, also found a strong interaction between CO₂ concentration and nitrogen. Dry weight gain and leaf area expansion both responded less to CO₂ concentration at the lower nitrogen concentration.

Goudriaan and de Ruiter (1983) grew lucerne, faba bean, ryegrass, wheat, maize, poplar, and potato inside a greenhouse in pots of sand with or without additions of nitrogen and phosphorus fertilizer. They found that doubling the CO₂ concentration increased dry matter yield in both nitrogen treatments, but the effect was greatest in the high nitrogen treatment. Except for faba bean, there was no response to CO₂ concentration in the low phosphorus treatment. The reaction of maize to extra CO₂ concentration was positive in high nitrogen and negative in low nitrogen. This last finding confirms Wong's observation (1979) that maize (a C₄ plant) may be less able than C₃ plants to take advantage of CO₂ enrichment when nitrogen is deficient.

Over the world as a whole, much of the soil in agricultural use has a nitrogen content that is well below the optimum. There is, therefore, considerable interest in the response of legumes to high CO₂ concentrations. It has been argued that the process of nitrogen fixation in legumes is limited by the amount of carbon available, and there is experimental evidence that the nitrogen fixation rate of soybeans in high CO₂ concentrations increases out of all proportion to the increase in photosynthetic rate (Hardy and Havelka 1976). However, there is considerable evidence (e.g., Bhangoo and Albritton 1976; Criswell et al. 1976) that nitrogen fixation is a demand process, that is, it is regulated by the plant's requirement for nitrogen. Soybeans appear to grow nodules and fix nitrogen only when there is insufficient mineral nitrogen in the volume of soil occupied by roots. Unless soil conditions are unfavorable, the soybean plants fix just as much nitrogen as is needed to keep the concentration in their tissues at the optimum level (Pal and Saxena 1976). Phillips et al. (1976) have shown that this simple theory is completely adequate to explain the increase in nodule development and nitrogen fixation in pea plants grown in high CO₂ concentration. There is no need to assume that high CO₂ concentrations directly promote nitrogen fixation in some way, as Hardy and Havelka (1976) and Vaggoner (1984) have done.

Soils with high phosphorus fixation capacity and low levels of plant-available phosphorus cover vast land areas of the tropics and subtropics (Sanchez and Uehara 1980). Because efficiently nodulated leguminous plants can fix atmospheric nitrogen, phosphorus is the mineral nutrient that is most likely to limit their growth and hence their response to elevated atmospheric CO₂ concentrations. Phosphorus deficiency has been shown to restrict initiation, growth, and functioning of nodules of *Stylosanthes humilis* (Gates 1974) and soybean (Ludecke 1941; Gates and Muller 1979) and, thereby, to have pronounced effects on the amount of atmospheric nitrogen fixed by these plants. As mentioned earlier, Goudriaan and de Ruiter (1983) observed that phosphorus deficiency prevented any increase in plant dry weight of lucerne, ryegrass, wheat, maize, poplar, and potato in response to a doubling of the atmospheric CO₂ concentration. However, in the same study, whole plant dry weight of faba bean (a legume), grown under phosphorus-deficient conditions, increased 67% in response to the doubling of the atmospheric CO₂ level. Evidently, legumes are less limited by phosphorus deficiency than are other species.

Because soils covering large areas of land are deficient in plant-available phosphorus and other nutrients, and because an assessment of the effect of atmospheric CO₂ enrichment on plant growth on a global scale requires an understanding of how specific nutrient deficiencies influence plant response to CO₂ enrichment, it would seem appropriate to give high priority to the study of how nutrient deficiencies affect the response of a wide range of plant species to CO₂ enrichment.

4.4.5 CO₂ and Gaseous Pollutants

As the atmospheric concentration of CO₂ increases, so does that of various gaseous pollutants that are products of fossil fuel combustion. Because most gaseous pollutants enter the leaf via the stomata and because high CO₂ concentrations reduce stomatal conductance, high CO₂ probably will decrease the damage done by pollutants. The truth of this proposition has been demonstrated for ozone damage on pinto beans and tobacco (Heck and Dunning 1967) and for sulfur dioxide damage on alfalfa and soybean (Hou et al. 1977; Carlson 1983). Also, Carlson and Bazzaz (1982) found that the presence of 0.25 ppm atmospheric sulfur dioxide (SO₂) reduced the growth of several C₃ species at 300 ppm CO₂ but not at 600 or 1200 ppm CO₂. The reverse was true for C₄ species, where the presence of SO₂ reduced growth in high CO₂ concentration but not in 300 ppm CO₂. These differences in growth were seen primarily as differences in leaf area expansion

and dry weight gain. They are thought to result from differences in photosynthetic rate brought about by SO_2 damaging the CO_2 -fixing enzymes to different extents in C_3 and C_4 species. However, the interaction between CO_2 concentrations and photosynthetic pathway was unexpected.

4.4.6 CO_2 and Salinity

In areas of the world where evaporation exceeds rainfall, salts accumulate near the surface of the soil in amounts that are toxic to plants. Because of the lack of suitable land for agriculture in many countries, these areas are farmed even though crops on them suffer from salinity stress. One effect of mild salinity stress is to increase the maintenance respiration rate (Schwarz and Gale 1984), probably because plants must expend energy to exclude (or remove) salt from their tissues. Growing plants in high CO_2 concentration would help them meet this extra demand for carbon. Also, the reduction of transpiration rate in high CO_2 concentrations would reduce the amount of saline water that the plants have to process. Thus, it has been found that a range of C_3 and C_4 species varying in their salt tolerance all gave a greater percentage increase in growth in response to high CO_2 concentrations when they were grown in high salt concentrations than when they were grown in low salt concentrations (Enoch et al. 1973; Gale 1982; Schwarz and Gale 1984; Gale and Zeroni 1985).

4.5 PREDICTING THE GROWTH AND YIELD OF CROPS IN A FUTURE HIGH- CO_2 WORLD

As discussed in Section 4.3.6, we have little difficulty in predicting the yield response to CO_2 concentration for crops that are grown with adequate heat, light, water, and nutrients. Under less favorable conditions, however, there is less information on which we can base our predictions. The discussion in Section 4.4 indicates that unfavorable environmental conditions limit crop growth and yield in all CO_2 concentrations, although in many instances the detrimental effects of stressful environmental conditions are ameliorated in high CO_2 concentrations. Thus, if we make the usual simplistic assumption that all other climatic variables will remain constant and only the CO_2 concentration will rise, in the majority of instances crop growth and yield will increase. However, other climatic variables are unlikely to remain constant, and if the increase in global CO_2 concentration produces a concomitant deterioration in the climate of a given region, then the overall effect of the high CO_2 concentration could be to reduce crop growth and yield.

On the other hand, some regions could undergo climate changes that would make them more favorable for crop production.

A change in the amount or thickness of cloud cover could produce large changes in solar radiation flux reaching the Earth and have a much more profound effect on crop performance than the change in CO_2 concentration. Changes in temperature could be of similar importance. In general, temperature controls the rate at which organs are produced, and so it can easily limit crop response to CO_2 . Changes in solar radiation, or wind speed, or vapor pressure deficit will alter the rate of water use by crops. This, coupled with any changes in rainfall, would determine the regions where various crops could be grown. However, it is not only necessary to know the effects of high global CO_2 concentrations on the annual means of these climatic factors, but it is also important to know the seasonal and, if possible, the diurnal variation. For instance, an increase in temperature during the winter will have the effect of lengthening the growing season and benefiting some crops, but a similar increase in the summer would probably do more harm than good. Similarly, an increase in night temperature would increase the respiration rate and reduce the amount of carbon available for growth. An increase in day temperature could increase photosynthetic rate if the temperature were low, but if the temperature were high already it might stress plants and cause stomata to close and photosynthetic rates to be reduced. Therefore, it will eventually be necessary to have quite detailed information about the effects of global CO_2 concentration on climate to predict accurately crop growth and yield in a future high- CO_2 world. Section 4.5.1 specifies what information will be needed and develops the rationale for this need.

4.5.1 Climatic Information Required for Predicting the Response of Vegetation to CO_2

4.5.1.1 *Light*

Light, obviously, is the primary energy driver of the photosynthesis process. Rising global CO_2 concentration could affect photosynthetic and transpiration responses of vegetation if for any reason it affected cloudiness.

4.5.1.2 *Temperature*

Annual or seasonal effects. If CO_2 concentration causes an increase in global temperatures, one might in general expect an increase in temperatures throughout the year. One effect might be the lengthening of the growing season, or at least the shortening of the frost danger

period. Increased temperatures also may lead to days or periods when plants normally adapted to a given latitude-climate band may be exposed to excessively high temperatures.

Diurnal effects. Plants do not grow and develop in a climate of constant temperatures, or even a smooth cycle of annual temperatures, but in cycles that are due to synoptic-scale weather patterns, and especially in daily cyclic patterns and fluctuations that are due to the solar forcing function, variable cloudiness, and variable wind. The aspect of the diurnal cycle perhaps has not received the attention (so far) that it should in the global (or zonal) climate.

The question of climate change effects on diurnal maximum and nocturnal minimum temperatures is an important one for plant responses. Higher midday temperatures would lead to greater evaporative demand, greater respiration, and perhaps a triggering of heat-shock protein synthesis (Vierling and Key 1985). On the other hand, lower nocturnal temperatures cause reduced respiration and cessation of leaf carbohydrate unloading and translocation at night, and can lead to excessive starch in leaves. This type of interaction would occur particularly where winter crops are grown, such as winter forages.

Clearly, one type of information that vegetation response modelers need from general circulation models (GCMs) is the annual and diurnal distribution of temperatures at each gridpoint on the globe.

4.5.1.3 Vapor Pressure and Vapor Pressure Deficit

The first-order effect of CO_2 (the stomatal effect) would be to tend to decrease the transpiration of vegetation. However, with a projected temperature increase, this would also raise the saturation vapor pressure of the atmosphere. The drying power of the air, termed the vapor pressure deficit (VPD), is the difference between the saturation vapor pressure and the actual air vapor pressure. Obviously, VPD would be variable at different GCM geoclimatological gridpoints, although overall, on a global zonal scale, VPD would be expected to be greater.

Vegetation modelers need to determine from GCMs any effects that rising global atmospheric CO_2 concentration would have on atmospheric vapor pressure and on atmospheric saturation VPD on a diurnal and annual basis to aid in predicting transpiration and plant water stress.

4.5.1.4 Precipitation Patterns

Rainfall amount, intensity, and distribution are the biggest factors of climate change that would have an impact on both agricultural and natural vegetation. This

type of information may be available in GCMs. It should be summarized on a daily basis to be useful to vegetation modelers.

4.5.1.5 Wind

Except under conditions of small vapor pressure deficit, increasing wind speed tends to increase evaporation. Also, increased wind puts more mechanical stress on plants, and may increase plant lodging, wind erosion damage, and fruit scarring under certain conditions and for certain crops. Increasing winds generally, or an increased frequency of high-wind events, would have an adverse indirect impact on crops.

4.5.1.6 Carbon Dioxide

Annual cycles of local CO_2 concentration superimposed on scenarios of CO_2 concentrations obtained from other sources of information are needed for vegetation models. This information is likely to be of secondary importance, but it is needed for simulations of photosynthesis and stomatal control.

4.5.2 Crop-Climate Models

Although several crop-climate models exist in the literature, one type of steady-state model that embodies physics and physiology will be discussed here, a soil-plant-atmosphere model (SPAM) developed by Stewart and Lemon (1969) and Stewart (1970). This model

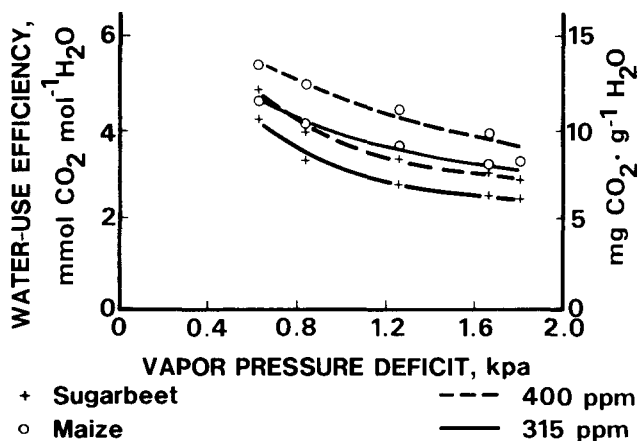


Figure 4.6. Water-use efficiency of the SPAM-simulated maize and sugarbeet crop as a function of vapor pressure deficit (VPD) as mediated by air temperature for 315 and 400 ppm CO_2 concentration. The VPDs from left to right were computed throughout the course of a day at 0800, 1000, 1200, 1400, and 1600 EST, respectively. Total solar radiation at those times was 462.5, 749.9, 890.8, 795.3, and 512.0 Wm^{-2} , respectively, and dry bulb air temperature was 14.8, 17.3, 20.0, 22.1, and 22.4°C, respectively. Other climatic variables were for Aug. 18, 1968, at Ithaca, N.Y. Adapted from data of Lister (1974).

Table 4.9
Interaction of Increased Atmospheric CO₂ and Diffuse Solar
Radiation on Net Photosynthesis as Simulated with the SPAM
Crop Model

Diffuse Radiation (percent)	CO ₂ Concentration (ppm)	Net Photosynthesis		Total Radiation (MJ m ² day ⁻¹)
		Sugar Beets (g CO ₂ m ⁻² day ⁻¹)	Maize	
10	315 (1970)	45 (1.00)	58 (1.00)	24.5 (1.0)
	400 (2090)	55 (1.21)	62 (1.04)	
30	315 (1970)	46 (1.02)	55 (0.94)	16.1 (0.76)
	400 (2090)	54 (1.20)	59 (1.00)	
60	315 (1970)	36 (0.82)	42 (0.72)	10.1 (0.41)
	400 (2090)	43 (0.94)	44 (0.75)	

Source: Lemon (1977).

predicts crop canopy responses (in 15 layers of leaves) of photosynthetic CO₂ exchange, transpiration or latent heat exchange, and sensible heat exchange based on a leaf-level photosynthetic light and CO₂ response submodel, a canopy energy exchange submodel, and a stomatal resistance function (Lemon et al. 1971). The model has been used to predict crop responses to elevated CO₂ concentrations (Allen et al. 1971; Lister 1974; Lemon 1977) and climate conditions of temperature, vapor pressure, and wind speed (Lemon et al. 1973; Shawcroft et al. 1974).

Using this model, Lister (1974) and Lemon (1977) compared simulations of net photosynthetic rates and transpiration rates of sugar beet and maize at CO₂ concentrations of 315 and 400 ppm at the hours of 0800, 1000, 1200, 1400, and 1600. When totaled over a day, the model predicted a 21% increase in photosynthesis for sugar beet, a C₃ plant, and a 4% increase for maize, a C₄ plant (Table 4.9). For sugar beet, the percent increase in photosynthesis for each percent increase in CO₂ concentration (beta factor, β) across this range was 0.87, which compares favorably with a value of 0.75 for a soybean canopy at a CO₂ concentration of 340 ppm reported by Allen et al.³ based on a rectangular hyperbola model fitted to experimental data. For maize, β was about 0.17 across the range of 315 to 340 ppm CO₂, which was somewhat lower than that reported by Wong (1979) but higher than that derivable from the data of Rogers et al. (1983a).

Lister (1974) computed WUE hourly on the hour from 0800 to 1600. Because air saturation VPD increased throughout the day, her simulated WUE data were plotted as shown in Figure 4.6. These data show C₄ versus C₃ effects (higher WUE for maize than sugarbeet), elevated CO₂ concentration effects (higher WUE at 400 ppm than at 315 ppm CO₂) and increasing VPD effects (decreasing WUE with increasing VPD).

³Allen et al., manuscript in preparation.

Lister (1974) also computed WUE by canopy layers, and her simulated data are shown in Figure 4.7. This figure shows a decreasing WUE versus depth within the canopy for the 315-ppm CO₂ case, and her data showed a similar pattern, but higher WUE, for the 400-ppm CO₂ case. These simulations imply that an increase of canopy leaf area that may be attributed to increased CO₂ concentration would tend to decrease canopy WUE. This simulation is supported by data shown in Figure 4.1.

4.5.3 Empirical Crop Models

Empirical crop models may include regression models or simple nonlinear response surfaces. Acock et al. (1971) adapted rectangular hyperbolae to represent

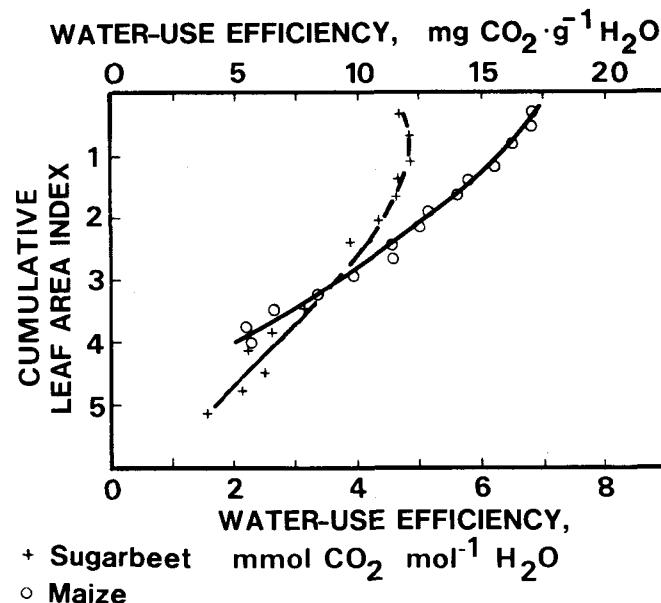


Figure 4.7. Simulated WUE distribution with downward cumulative LAI for maize and sugarbeet for the 315 ppm, 1.25 kPa, 1200 EST case of Figure 4.6. Adapted from data of Lister (1974).

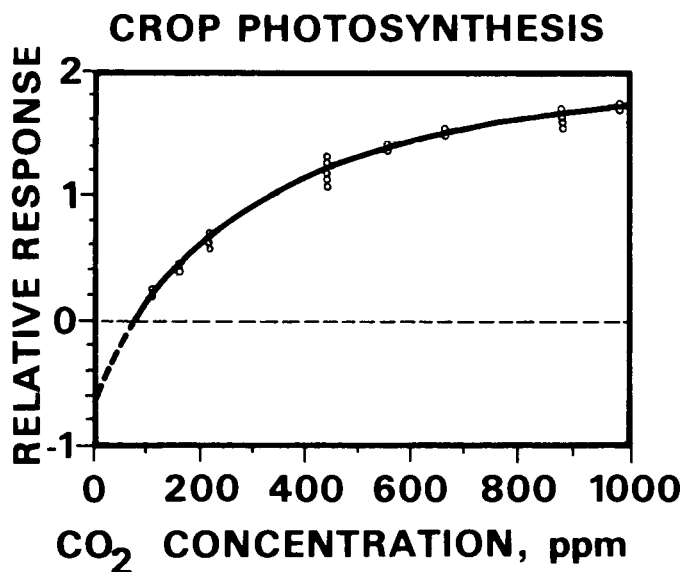


Figure 4.8. Soybean crop canopy midday net photosynthetic rate response to CO_2 concentration, normalized to 330 ppm, obtained October 23–30, 1983 (56–61 days after planting) from plants grown at 330 ppm in sunlit controlled environment chambers at Gainesville, Florida. Dots show data and the solid line shows the fitted rectangular hyperbola. Source: Allen et al.

response surfaces to both CO_2 concentration and light. Allen et al.⁴ adapted a rectangular hyperbola of a modified Michaelis-Menten equation to represent crop photosynthesis, biomass yield, and seed yield of soybean as a function of CO_2 concentration (e.g., Figures 4.8 and 4.9). These nonlinear curves provide first-order representations of overall responses to CO_2 concentration under favorable conditions when normalized to a specific level of CO_2 , such as 330 to 340 ppm. The rectangular hyperbola formulation has several advantages: (1) an analytic expression for β in terms of the fitted model parameters that can be used to predict relative responses to CO_2 concentration changes, (2) an analytic expression for CO_2 or light compensation points, and (3) asymptotic upper limits of photosynthetic or yield responses.

4.5.4 Mechanistic Crop Models

Our current concern is to predict the growth and yield of crops when global CO_2 concentration has risen and climatic changes have taken place. This necessarily implies that models will be used because (1) we do not know yet what those climate changes will be; (2) even if we did, we do not have enough experimental facilities in which plants can be exposed to the whole gamut of future climate scenarios; and (3) plants grown in chambers often behave somewhat differently from

plants grown in the field. In particular, no one has yet produced a controlled environment chamber that exposes a plant to the same energy fluxes as it experiences in the field.

In Chapter 3 of this volume, the types of models that might be used to predict plant growth in a high- CO_2 world are examined and their suitability is discussed. Simple empirical models, which do not account for the interactions of CO_2 concentration and other environmental factors, cannot react to future information about climate change, pollution, management practices, and so forth, and so can only give us preliminary estimates of plant responses. More complex empirical models, which do account for the interactions, would react to future information but would require enormous data bases because they are inherently only capable of interpolative prediction. At present, very few suitable data are being collected; they will have to come from field releases of CO_2 or from field enclosures designed in such a way that the environment experienced by the plants is known precisely. Collecting sufficient high-quality data is likely to be prohibitively expensive. A third possibility is to take what information we already have about fundamental plant physiological responses to environmental factors, including CO_2 concentration, and to use this to build crop models that are sufficiently mechanistic that they are capable of extrapolative prediction (CEP models). This method is also very

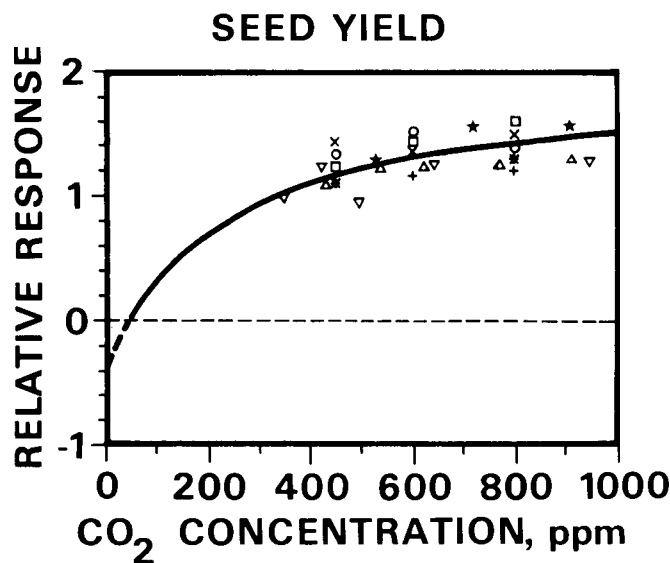


Figure 4.9. Rectangular hyperbola response of normalized soybean seed yield data for "Ransom," "Bragg," and "Forrest" cultivars. Data obtained from sunlit controlled environment chamber experiments at four locations: Gainesville, Florida, 1981 ($\square$), 1982 ($\times$); Mississippi State, Mississippi, 1981 ($\diamond$); 1982 ($+$); Clemson, South Carolina, 1982 ($*$); and from open top chamber experiments at Raleigh, North Carolina, 1980 ($*$); 1981 ($\triangle$); 1982 (∇). All data were normalized to 340 ppm = 1.0. Source: Allen et al.

⁴Ibid.

expensive, but it is at least feasible. CEP models require large amounts of precise data for development and validation, and few groups are capable of building them. We know very little about some of the mechanisms involved in plant response to CO_2 concentration (e.g., control of branching), and we have not yet learned how to aggregate these CEP models over climatic zones and soil types. Such aggregation is needed to make global-scale predictions and could probably be done by using sensitivity analyses to determine which soil characteristics or climatic variables have the least impact on predicted crop responses. This information could then be used either to aggregate the input data sets or to simplify the model with a known loss of accuracy.

The suitability of various existing crop models for predicting response to CO_2 concentration was examined in Chapter 3. One of the highest scores was obtained by GLYCIM, which is not surprising because it was specifically developed for making these predictions and its principal author was involved in selecting the test criteria. GLYCIM (Acock et al. 1985a) is a dynamic simulator of soybean crop growth which is mechanistic at the physical and physiological process level. Most of the processes and material fluxes simulated in GLYCIM are shown diagrammatically in Figure 4.10. The model is organized into routines dealing with individual processes or groups of related processes, and it runs in time steps equal to one-tenth of the photoperiod, mainly so that it can simulate diurnal variation in plant water potential.

In GLYCIM, CO_2 concentration has a direct effect on gross photosynthetic rate and on photorespiration rate. Through its effect on carbon availability, it affects the expansion and dry weight gain of all the organs on the plant. Through its effect on root growth, it influences water uptake and plant water relations. Ultimately, CO_2 concentration, both in the real plant and the model, has the potential to affect

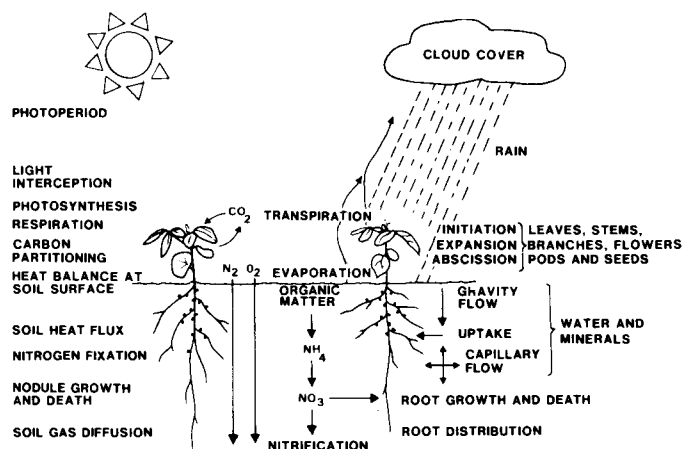


Figure 4.10. Diagram showing the influence of environmental factors on the processes and flows of materials in a soybean crop.

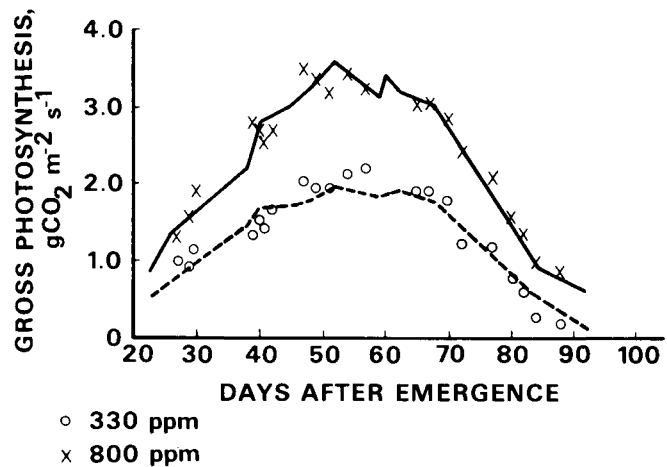


Figure 4.11. Seasonal variation in gross photosynthetic rate at a solar radiation flux density of 700 W m^{-2} for soybean plants grown in sunlit, controlled environments at two CO_2 concentrations. Continuous lines are simulations and points are observations.

every aspect of plant growth and development. For this reason, and also because the model is required to simulate interactions between CO_2 concentration and other factors, all routines in the model have a similar level of mechanistic detail. There were no processes included in the model that could be considered subcritical and therefore modeled empirically rather than mechanistically.

GLYCIM has been validated against field data from Mississippi, Florida, and North Carolina at current ambient CO_2 concentrations. Validation against data from plants grown in controlled environments at various CO_2 concentrations is in progress. An example of the progress being made is given in Figure 4.11. At present there is no adequate data set for validating the model against plants grown in the field at elevated CO_2 concentrations. In the following sections, the environmental and plant data needed to develop, run, and validate mechanistic crop models are considered.

4.5.5 Environmental Data Needed To Run Mechanistic Crop Models

In Section 4.5.1 we discussed the type of information needed from general circulation models to predict the response of vegetation to CO_2 . In this section the specific requirements of mechanistic crop models are considered. To run these models, data characterizing both the shoot and root environments are needed. The weather and soil data required are listed below, and each list is followed by a list of reasons why each variable is needed and how it is used in mechanistic models.

4.5.5.1 Weather Data

Most mechanistic models have been built to use daily weather data because it is commonly available. The variables needed are as follows:

1. Total solar radiation at the top of the crop canopy;
2. Maximum and minimum air temperature at the top of the crop canopy;
3. Rain and irrigation water reaching the soil;
4. Wind run or airflow rate over the plants; and
5. Some measurement of the water vapor content of the air.

(If this is not available and the plants are being grown in an enclosure that has outside air blown through it, then the daily minimum temperature of the outside air should be recorded.)

When plants are being grown in an enclosure with restricted airflow rate, and especially when they are exposed to high CO₂ concentrations, it is highly desirable to record the temperature of the leaves in the upper, fully exposed parts of the canopy and to attempt to relate leaf temperature to air temperature and other environmental conditions in the enclosure.

Many models also can make use of regular (say, hourly) measurements of any of the following variables: solar radiation flux density, photosynthetic photon flux density, air temperature, leaf temperature, rainfall, wind or airflow rate, and water vapor content of the air.

The reasons for needing these weather data are as follows:

Solar radiation measurements are required because solar radiation is the energy source for the photosynthetic process.

Maximum and minimum air temperature data are required, because from these the models reconstruct either the daytime and nighttime means or the complete pattern of diurnal variation. Temperature is the primary control of most plant biochemical processes including photosynthesis and respiration. It often limits the rate of organ initiation and expansion. Of course, the plant actually responds to tissue temperature rather than air temperature. However, air temperature is easier to measure and the difference between air and tissue temperature is rarely very large. In enclosures where the rate of airflow over the plants is reduced and in high CO₂ concentrations where the stomata are partially closed, the temperatures of fully exposed leaves can be several degrees higher than air temperature. For this reason it is desirable to measure these leaf temperatures and relate them to the temperature of the surrounding air and other environmental conditions.

Rain and irrigation determine the amount of water available for transpiration and for evaporation from the

soil surface, and hence they affect the water status of the plants.

Wind run or airflow rate and the water vapor content of that air are used to calculate the potential evapotranspiration rate and hence the rate at which water is extracted from the soil.

4.5.5.2 Soil Data

The variables needed are as follows:

1. Depths of the major soil horizons;
2. For each horizon: particle size analysis, bulk density, water release curve, and saturated hydraulic conductivity;
3. Residual fertilizer content at the start of the season;
4. Fertilizer applied during the season;
5. Organic matter content of the soil at planting; and
6. Deep soil temperature (1 m or deeper).

The reasons for needing soil data are as follows:

Variation in soil characteristics with depth in the profile is normally modeled as a number of layers (or layers and columns) in the model soil profile. The various layers in the model soil are given characteristics corresponding with those of the horizons at the same depths in the real soil.

Particle size analysis is used in determining thermal conductivity and hence the temperature in all parts of the soil profile.

Bulk density is primarily of interest for its effect on root growth.

The water release curve relates soil water potential to soil water content, and this determines the availability of water to plant roots in various parts of the soil profile and the gradient controlling the capillary flow of water from one part of the profile to another.

From the saturated hydraulic conductivity it is possible to calculate hydraulic conductivity at other soil water contents, which is another important variable in the calculation of capillary flow of water within soils.

Residual and applied fertilizer together indicate what nutrients are available at the start of the season. During the course of the season these may remain in the soil, be taken up by the plants, or be leached from the soil.

The amount of organic matter in the soil is another important determinant of thermal conductivity. On degradation it is also a source of nitrogen for the plants and a sink for soil oxygen.

Deep soil temperature hardly varies during the year and is used as a boundary condition, at the bottom of the soil profile, in the calculation of soil temperature. If deep soil temperature is not known, it can be estimated with little loss of accuracy.

4.5.6 Plant Data Needed To Develop and Validate Mechanistic Crop Models

The plant data needed will necessarily vary with the species under consideration, so no list can be more than a generalization.

4.5.6.1 Data for Developing Models

Essentially, information is needed about the initiation, growth, and abscission of all organs on the plant as affected by the relevant environmental variables. The exact way in which this is done depends greatly on the philosophy of the modeler. The example given below is not necessarily the only way of gathering the required information, but it has been used successfully to generate several comprehensive, mechanistic crop models.

In most models, temperature is seen as the primary driving factor. Other environmental factors are thought of as limiting the crop's response to temperature. Therefore, the plants are first grown in a range of temperatures with, as far as possible, other factors nonlimiting: summer sunlight, high CO₂ concentration, ample water and nutrients, and a deep, porous rooting medium. Under these conditions, measurements are made of the rates of initiation, expansion, and abscission for each organ on the plants and the rates of photosynthesis, respiration, and transpiration for the whole crop canopy. Sunlit, airtight, controlled environment plant growth chambers are used for these measurements. Artificially lit chambers are generally unsuitable because the quantity of light available is too low and the quality leads to abnormal plant growth and development. Xenon lamps appear to overcome these objections but pose other problems. Chambers that are airtight, or nearly so, improve the accuracy of the gas and vapor exchange measurements.

In subsequent experiments other factors that can limit growth are examined by growing plants at various levels of those factors over the range of interest. Normally, water and nutrient availability are the first factors to be considered in these subsequent experiments.

Although light flux density cannot be controlled in sunlit chambers, a curve of photosynthetic rate versus light flux density can be obtained for every day of the growing season, and from this it is easy to model the limitations imposed by light.

The limitation imposed on crop growth by the current ambient CO₂ concentration is normally measured as an aside in one of the main experiments, but where CO₂ response is the primary interest, the plants are grown in a range of different CO₂ concentrations. All of these experiments involve essentially the same observations:

1. Canopy CO₂ exchange and average light flux density every few minutes;
2. Water transpired by the canopy and average air humidity every few minutes;
3. Timing of progress from one growth stage to another;
4. Rates of appearance of branches, leaves, flowers, and fruits;
5. Rates of expansion and dry weight gain of stems, leaves, fruits, and roots; and
6. Timing of senescence and abscission of leaves and fruits.

In most controlled environment experiments, sampling for dry weight is a problem because it results in loss of the canopy. Extra rows of plants can be grown during the seedling stage without affecting the more permanent plants, and dry weights can be measured at final harvest. These meager data must be supplemented with field data for intermediate stages of plant growth. Organ sizes can usually be measured nondestructively. For example, leaf area is often highly correlated with leaf length.

When soil water availability is the variable under study, soil water content is measured at several depths in the profile, and leaf water potential is measured to the extent that destruction of the canopy can be tolerated.

The above data give sufficient information to calculate the values of most parameters in the models. However, plants grown in controlled environment chambers, even sunlit chambers, do not react exactly like plants grown in the field. In particular, it is usually necessary to readjust the parameters concerned with the temperature response of stem extension and leaf expansion. These are adjusted during the early stages of validation. The reason this is necessary is not known, but it is possible that the quality of light falling on the plants in the chambers is altered by its passage through the plastic or glass enclosure. As already mentioned, light quality is a significant problem in interpreting the results from plants grown in artificially lit, controlled environment chambers.

4.5.6.2 Data Sets for Validating the Models

An essential part of any validation data set is a complete record of the soil and aerial environment in which the plants grew. The data essential to characterize this environment are listed in Section 4.5.5. Without these soil and weather data, there is no validation data set. In addition, the models require date of emergence, row spacing, plant population after emergence, and latitude of the site. Some models also use row orientation as an input. Given these essentials, almost any other data on plant performance can be useful for validation.

The most useful plant data for model validation are as follows:

1. Timing of the various stages of growth;
2. Dry weights of the major classes of organs on the plants at various times throughout the growing season;
3. Final yield and an analysis of components of yield;
4. Numbers of branches, leaves, fruits, and other organs; and
5. Mainstem and branch heights.

For water and nutrient stress experiments it is helpful to record the distribution of roots and water in the soil profile during the course of the growing season. Leaf water potential and evapotranspiration rate are also useful.

Because the models are developed using data from single-factor experiments, the validation data most likely to expose weaknesses will come from multifactor experiments. Validation experiments on the interaction of CO₂ concentration and other environmental variables have the added attraction that very few such experiments have been performed.

All plant enclosures interfere with radiation, rain, wind, and humidity, all of which influence water use (among other things). Those parts of the model dealing with water use can only be validated in the open field. To thoroughly validate model water use at high CO₂ concentrations requires an open field release of CO₂. However, the next best alternative (and a close second) is to grow plants in a field enclosure through which field air is blown in a well-defined pattern. Only in this way can the environment experienced by all plants in the enclosure be known. Controlled environment chambers are not suitable for obtaining validation data on water use because the plants in them are exposed to large and rapid variations in advected heating, that is, the oasis effect.

4.6 SUMMARY OF CURRENT INFORMATION AND STATUS OF KNOWLEDGE

4.6.1 Summary of Current Information

In summary, we can say that species and cultivars differ in their response to high CO₂ concentrations in the following ways. Plants with the C₄ pathway show modest gains in photosynthetic rate and dry weight but large reductions in transpiration rate. Plants that only have the C₃ pathway exhibit modest reductions in transpiration rate and large gains in photosynthetic rate and dry weight, resulting in a variety of changes in plant composition, anatomy, and morphology. We know too little to divide C₃ species into response groups (see Chapter 5, this volume). However, we

can describe a typical response as follows. Growing plants in CO₂-enriched environments at optimum levels of other factors will cause all organs on the plants to become heavier, with roots gaining proportionally more dry weight than stems, and stems more than leaves. The additional dry matter in the root is mainly used to increase root length or, in the case of root crops, to increase storage root volume, with very little going to increase the density of the root tissue. Additional dry matter going to the stem causes increases in its height and diameter and little increase in the density of the tissue. Additional dry matter going to the leaves causes both a small increase in leaf area and a small increase in leaf thickness. There is an increase in structural dry matter, which is probably greater than can be explained by the increase in the number of mesophyll cell layers, although no one has ever done a definitive experiment on this. Finally, there is increased starch accumulation in the leaves which, depending on the circumstances, can be very large. Branch and tiller numbers are frequently increased, as are the number of flowers. Either the weight or number of individual fruits is increased.

The consequences of these changes in composition, anatomy, and morphology are that roots can more thoroughly explore the rooting zone for water and nutrients and the tops are able, with their increased leaf area and branching, to capture more light, grow faster, and form a closed canopy sooner. Whatever plant part is harvested, the yield is increased. However, the response to CO₂ concentration depends on the level of other environmental factors, and the plant may be prevented from benefiting fully from high CO₂ concentration if sink strength is low because some other factor such as temperature or mineral nutrients limits growth. Low light flux density also limits plant response to CO₂, but in this case it acts by reducing source strength. Other environmental factors such as low soil water, salinity, and air pollutants, which are limiting in current ambient CO₂ concentrations, are less limiting when plants are grown in high CO₂ concentrations.

There appears to be luxury consumption of carbon in high CO₂ concentrations. The stems, roots, and leaves on plants grown in ambient CO₂ concentration are adequate structurally and functionally; therefore, the organs on plants grown in high CO₂ concentrations must be heavier than necessary. The dry matter, which is used to increase the weight of these organs, could possibly be diverted to harvested plant parts. Because breeding and selection for higher yields have been demonstrated to result largely in an increase in the proportion of dry matter partitioned to the harvested part (e.g., Duncan et al. 1978), it is reasonable to expect breeders to make additional gains in yield in a

high-CO₂ world by further increasing the partitioning of photosynthate to economic yield.

4.6.2 Status of Knowledge

In Table 4.10 we have listed what is "known," "uncertain," and "unknown" about the responses of crop plants to an increase in CO₂ concentration above the current ambient level. For the purposes of this section the terms are defined as follows: Known information is not subject to significant disagreement among workers in the field and is supported by substantial and internally consistent data. Uncertain information either is controversial or is supported by only a small amount of internally consistent data. Unknown is just that. The extent of our ignorance is truly humbling. The importance of doing experiments to make known each piece of information that is at present uncertain or unknown depends on which type of model we decide to use. The choice will depend on the capability required in the final model, tempered by the time and money available.

In Table 4.11 is listed what is known, uncertain, and unknown about our ability to model crop responses in a high-CO₂ world. If we can be satisfied with predicting crop response to CO₂ concentration, ignoring the interactions with other environmental factors, then we only need data on yields and photosynthetic rate, or transpiration rate, or whatever other variables are in our simple empirical models. If we decide to model interactions between CO₂ concentration and other factors, there are two courses of action open to us. One is to produce a more complex empirical model that is capable of interpolative prediction. Again, this mostly requires data on yields, but those data must cover a wide range of environmental conditions. The data would have to come from uncontrolled environments such as CO₂-enriched fields or field chambers with a well-defined airflow pattern. The other course of action possible is to develop models that are sufficiently mechanistic that they are capable of extrapolative prediction. This requires a smaller data base, but we need to know a lot more of the information that is currently uncertain or unknown. Almost all of the information in these categories in Table 4.10 would be required, except that information about leaf anatomical and biochemical adaptation to high CO₂ concentration may not be necessary if the adaptations cancel out. Some of the unknowns have proved highly resistant to experimental probing in the past (e.g., stomatal control mechanisms) and for these it may prove necessary to use empirical relationships for some time to come.

4.7 CONCLUSIONS AND RESEARCH RECOMMENDATIONS

4.7.1 Recommendations for Modeling

From Chapter 3 of this volume come the following recommendations for modeling crop responses to CO₂ concentration.

1. Eschew further development of simple empirical models that are based on limited data yet purport to predict the response of crops to CO₂ concentration and other environmental variables outside the range of the available data.
2. Develop semimechanistic models of cropping systems that contain those CO₂ responses and environmental interactions for which there is a solid data base.
3. Develop comprehensive mechanistic models for some of the most important agricultural crops, validate them, and use sensitivity analysis to aggregate them into cropping system models.

4.7.2 Recommendations for Data Collection

From these recommendations on modeling are some recommendations on data collection.

1. Measurements made on plants during field releases of CO₂ provide the only data ideally suitable for developing and validating models. All enclosures interfere with radiation, rain, wind, and humidity. However, field releases are expensive, and there are difficulties in maintaining temporal and spatial uniformity of CO₂ concentration.
2. In the absence of field release data, the next best alternative is data from a field enclosure that has a well-defined direction and rate of airflow through it. Only in this way can the environment experienced by all the plants in the enclosure be known.
3. Controlled environment data are needed for building the comprehensive mechanistic models.
4. A detailed quantitative description of the above- and below-ground environment experienced by plants throughout their life is an essential part of any of the above data sets.
5. The least expensive way of validating mechanistic models is first to validate them using field data at ambient CO₂ concentration and then to validate their response to higher CO₂ concentrations using controlled environment data.

4.7.3 Recommendations for Research Direction

Keeping in mind these recommendations about modeling and data collection, the analysis of published

Table 4.10
Response of Crop Plants to an Increase in CO₂ Concentration Above Current Ambient Level

Process	Knowns	Uncertainties	Unknowns
Leaf Photosynthetic Rate	Increases in all plants on first exposure. C ₃ respond more than C ₄ . Response follows law of diminishing returns with little further response after 1000 ppm.		Magnitude of response for some crop species.
Inhibition of Photosynthesis by Source-Sink Imbalance	Response occurs in many species.	Response is somewhat correlated with starch accumulation.	Mechanism underlying response. Magnitude of response under various conditions.
Leaf Transpiration Rate	Decreases in all plants. C ₄ plants respond more than C ₃ .	The reduction in transpiration rate reduces latent heat loss and increases temperature.	Stomatal mechanism giving response. Magnitude of response under various environmental conditions.
Leaf Anatomical and Biochemical Adaption	Leaf area, weight per unit area, thickness and number of mesophyll cell layers increase in many species.	RuBP carboxylase activity is reduced in some species. For practical purposes, counteracting responses cancel and adapted leaves have photosynthetic rates similar to unadapted. Some studies show higher carbon exchange rate for leaves adapted to high CO ₂ .	Mechanisms underlying responses.
Canopy Leaf Area	Usually increases.		Magnitude of interactions between CO ₂ and other environmental and crop variables.
Canopy Photosynthetic Rate	Similar responses as leaf photosynthetic rate.	Response can be predicted from a knowledge of how leaf photosynthetic characteristics vary with previous light exposure.	Magnitude of response for some crop species.

(Continued)

Table 4.10 *continued*
Response of Crop Plants to an Increase in CO₂ Concentration Above Current Ambient Level

Process	Knowns	Uncertainties	Unknowns
Canopy Transpiration Rate	Decreases after canopy closes. Response before canopy closure depends on counteracting effects of decreased stomatal conductance and increased canopy leaf area.		Whether response can be predicted from knowledge of how leaf characteristics vary with depth in canopy. Magnitude of response under various conditions.
Carbon Partitioning Among Organs	Proportion of carbon going to roots and stems is increased in many but not all species.		Mechanism of response. Magnitude of response under various conditions.
Stem Growth	Stem height increases in many species.	Volume and/or density of wood increases in woody species.	Magnitude of response in species where stem is harvested.
Root Growth		Number of active root axes and hence total root length increases.	Magnitude of response and whether it affects amount of soil water available to plant.
Branching, Flowering, and Fruiting	Initiation and/or retention of these organs is increased in many species.	Development of organs is generally slightly earlier.	Mechanism underlying response. Magnitude of response under various conditions.
Canopy Water-Use Efficiency	Increases in C ₃ and C ₄ plants. Increase in photosynthesis or yield contributes more than reduction in transpiration.		Magnitude of response under various conditions.
Fruit and Seed	Increases number and/or size of fruits and seeds.	No significant change in seed analysis.	Magnitude of response under various conditions.

Table 4.10 continued
Response of Crop Plants to an Increase in CO₂ Concentration Above Current Ambient Level

Process	Knowns	Uncertainties	Unknowns
Yield	Very variable, depending on harvested parts and on other environmental conditions. Increases 32% on average between 330 and 660 ppm for plants in favorable conditions.		Many of the mechanisms that determine yield.
CO ₂ × Light Interaction	Photosynthetic rate and absolute dry weight gain respond more to high CO ₂ in high light in most species, but there is still a small response in low light in C ₃ species.		Magnitude of response for some crop species.
CO ₂ Concentration × Temperature Interaction	Extremely high or low temperatures limit source or sink strength and limit response to CO ₂ .	High CO ₂ allows okra to survive low temperatures that would otherwise kill it, and allows grape to tolerate high temperatures.	Magnitude of response for most crop species.
CO ₂ Concentration × Soil Water Availability	Transpiration rate is reduced in high CO ₂ (after canopy closure) and plants need less water.	Plants maintain high turgor pressure. Relative yield response to CO ₂ is greater at low soil water availability.	Many of the mechanisms involved. Magnitude of response.
CO ₂ Concentration × Mineral Nutrients	Relative response of C ₃ species to CO ₂ is generally, but not always, less in nitrogen deficiency. In legumes, nitrogen fixation keeps pace with carbon fixation.	Potassium shortage inhibits any response to CO ₂ . Nitrogen shortage inhibits response of C ₄ species to CO ₂ .	Magnitude of response for most crop species.
CO ₂ Concentration × Salinity		Relative response to CO ₂ is higher in saline conditions.	Magnitude of response for most crop species.
CO ₂ Concentration × Gaseous Pollutants	In C ₃ species, high CO ₂ reduces the effect of pollutants because stomatal conductance is reduced.	In C ₄ species, SO ₂ damage is worse in high CO ₂ .	Mechanism in C ₄ species response. Magnitude of response for most crop species and pollutants.

Table 4.11
Our Ability to Model Crop Response in a Future High-CO₂ World

Type of Model	Knowns	Uncertainties	Unknowns
Simple, Empirical Models	Models to predict response of many crops to CO ₂ concentration if other environmental conditions remain favorable.		Parameters of the model for some crop species. Response of crops to future climate, pollution, etc.
More Complex, Empirical Models Capable of Interpolative Prediction	Method of building models.	Techniques for obtaining data.	Data base for estimating model parameters.
Models Sufficiently Mechanistic to Be Capable of Extrapolative Prediction	Method of building models and obtaining data to do so.	Predict response of soybeans to any combination of environmental conditions.	Many mechanisms needed in the models. Adequate validation data. Data and models for most crop species. Method of aggregating over soils, climate zones, etc. Information about future climate, pollution, etc.

information in Chapter 5, and the synthesis attempted in this chapter (summarized in Table 4.10), research recommendations are as follows:

1. Much is known about the response of crops to CO_2 concentration in otherwise favorable conditions. The interaction between CO_2 and light is also well understood. Further experimentation on these topics is only justifiable if it is for new crops or is being done in sunlit controlled environment chambers with the objective of developing rate equations for mechanistic models.

2. In general, there is little information about interactions between CO_2 concentration and other environmental factors that affect plant growth. Further investigations of these interactions are needed in both field enclosures and controlled environment chambers with a view to obtaining more empirical data about the interactions and also elucidating the mechanisms.

- a. The interaction of CO_2 and temperature has received very little attention. By modeling separately the effects of CO_2 concentration and temperature on plant growth it has been possible to produce mechanistic models that are capable of predicting how these factors will interact. However, there have been few empirical observations to support these predictions, and there are no data suitable for validating the model predictions. The investigation of this interaction requires the use of controlled environments.

- b. The interaction of CO_2 and soil water availability can be investigated in field enclosures and as a result has received much more attention. However, the volumes of soil occupied by plants in the different treatments must be defined so that the roots of plants in dry treatments do not grow over into wet soil areas. This precaution has not always been observed. The total water budget of the plant and soil is rarely documented. Measurements should include rain and irrigation water received at the soil surface, water evaporated from the soil surface, and water transpired by the plants. Because there is much interest in WUE, records should be kept of the growth of the canopy in terms of leaf area and architecture as it affects light interception. This is because we need to know the extent to which the increased size of plants in high CO_2 concentrations counteracts the decreased transpiration rate per unit leaf area. Finally, there have been some suggestions that plants in high CO_2 are able to osmoregulate and maintain turgor pressure better than plants in low CO_2 . Some direct measurements of plant leaf-water relations are needed to determine whether there is any substance to these conjectures.

- c. The interaction of CO_2 concentration and nutrient availability has received some attention but deserves much more. The evidence available so far indicates that nutrient availability can severely limit the response of plants to high CO_2 concentrations. Because soils over much of the Earth's surface and especially in the developing nations are deficient in nutrients, there may be little crop response to rising CO_2 concentrations unless the required fertilizer can be made available. Experiments to demonstrate the interactions of CO_2 concentration and various nutrient concentrations could be done easily in field enclosures. As far as possible these experiments should be designed to generate information about the chemistry of nutrients in the soil and the response of plants to various concentrations of nutrients in their own tissues. Because work on nutrient availability has been going on for over 100 years and our knowledge of the chemistry involved is still rather meager, it is unrealistic to believe that the mechanisms involved will be revealed during the life of this project. However, the attempt always should be made to understand the mechanism even if we ultimately have to use empirical relationships in our models.

- d. The interaction of CO_2 concentration and gaseous pollutants or CO_2 concentration and soil salinity are of interest in some parts of the world. However, the areas involved are not very large, and these interactions are of secondary importance compared with the interactions listed in a, b, and c above. Nevertheless, results obtained so far suggest that high CO_2 concentrations enable plants to overcome the deleterious effects of high soil salinity and might have the important effect of increasing the area of soils available to agriculture in desert regions. Also, the release of CO_2 from the burning of fossil fuels is accompanied by the release of pollutants so that the interaction of these two factors could become very important in a high- CO_2 world. Some further experimentation on these interactions would be worthwhile.

3. It is difficult to make crop-level predictions from observations of leaf-level responses. For example, the reduced transpiration rate of leaves on plants grown in high CO_2 concentrations leads one to expect a greatly improved WUE, but the expected improvement is not observed at the crop level because of the increase in crop leaf area. Because the purpose of this project is to predict crop responses, plants should be grown in the normal crop configuration, and measurements should be made on the whole canopy where possible. Measurements at the plant, organ, and lower levels of

aggregation are only appropriate to this project if they are designed to elucidate mechanisms involved in crop responses to CO₂.

4. It is evident from research data that plants that have been grown in normal ambient CO₂ concentrations and are then exposed to high CO₂ concentrations for part of their lives behave differently from those that have been grown all their lives in high CO₂ concentrations. It is the latter response that is of interest in this project. Experiments therefore should be planned so that plants are continuously exposed to the desired CO₂ concentration. In a similar manner, plants often respond to high CO₂ concentrations differently at various growth stages, and it is highly desirable that experiments should cover the entire life of the plant.

5. Some responses to CO₂ concentration vary greatly from one experiment to the next. For example, the effects of CO₂ concentration on root-to-shoot ratio, leaf area development, and harvest index are variable even though trends are discernible. This suggests that the responses are dynamic and depend on other environmental factors. With these and the other major interactions listed above, all affecting plant response to CO₂, the only way we will ever be able to predict that response is to understand the mechanisms. Therefore, all experiments should be designed as far as possible with a view to improving that understanding. This may be difficult in field enclosures, but it is definitely unsatisfactory just to record final yield and to have no idea how that yield was obtained.

6. Data are needed for developing and validating models. Field enclosures are less expensive and therefore more readily available than sunlit controlled environment chambers. The former are mostly used for collecting validation data although there is no reason why they should not be used to collect data that elucidate certain mechanisms and therefore can be used to develop models. However, there is a tendency for validation data to be more readily available than development data, and some effort is needed to keep a balance between these two types of data.

7. There are obvious differences among species in their responses to CO₂ concentration. It is impractical to investigate all crop species under this project. Therefore, the following crops are recommended for investigation in order of priority:

- Wheat
- Corn (maize)
- White potato
- Soybeans
- Rice
- Sweet potato
- Sorghum
- Cotton

In placing these crops into an order of priority, the following criteria were used:

- Their importance as a world food crop;
- Their ability to represent a broad class of crops;
- Their importance to the U.S. economy;
- The amount that is known about them already; and
- The ease with which further research can be performed.

Wheat was chosen to head the list rather than rice because both are C₃ grain crops, but wheat is more important in the United States. Corn, white potato, and soybeans follow as representatives, respectively, of C₄ species, root crops, and legumes. Having represented all the major crop types, we go back to pick up rice as a second representative of C₃ grains and sweet potato as another representative of root crops. Sorghum is a second representative of C₄ grains. Finally, cotton was added to the list because this is an important world fiber crop and it represents another crop type.

8. Despite the emphasis, in item 3 above, on collecting data at the crop canopy level, there is a clear need for some further work on the following organ-level responses.

Virtually nothing is known about root growth response to high CO₂ concentrations, other than that the root-to-shoot ratio generally increases. It is normally assumed that the extra root dry weight results in longer roots and a larger volume of soil being explored. This in turn would increase the availability of water and nutrients to the plants in high CO₂ concentrations. However, the results of one unpublished study cited earlier in the text suggest that the roots of plants grown in high CO₂ concentrations are more finely branched and explore a given volume of soil more thoroughly but do not explore a larger volume of soil than the roots of plants in ambient CO₂ concentrations. Clearly this is an important point to establish, and more work needs to be done on it.

Leaves of plants that have grown in various CO₂ concentrations and are then all exposed to the same CO₂ concentration have similar photosynthetic rates. If the rates were exactly the same, we could just ignore the compensating adaptations that appear to be taking place and still make accurate predictions with our models. However, there is some evidence that leaves are more photosynthetically efficient in the CO₂ concentration in which they have been grown. Some further work is needed to explain what these adaptations are, but the amount of effort expended on this problem should be small because the effect itself is small.

The mechanism for feedback inhibition of photosynthesis by source-to-sink imbalance is completely unknown, and there are not even any good empirical data on which to base a relationship. Further research

to elucidate the mechanism is highly desirable, but it could be clearly aimed at predicting when feedback inhibition occurs and not just at discovering the general biochemistry involved.

ACKNOWLEDGMENTS

The authors acknowledge with gratitude the following colleagues who drafted sections of this chapter, supplied information, or provided in-depth criticism: D. N. Baker, K. J. Boote, J. D. Cure, D. W. Israel, P. H. Jones, B. A. Kimball, J. R. Lambert, V. R. Reddy, H. H. Rogers, N. Sionit, B. R. Strain, J. D. Thomas, R. R. Valle, and C. V. Vu.

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5. CARBON DIOXIDE DOUBLING RESPONSES: A CROP SURVEY

Jennifer D. Cure
Duke University

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5.1 INTRODUCTION

The responsibility of the Department of Energy's Carbon Dioxide Vegetation Response Research Program is to develop the ability to predict crop and ecosystem responses to elevated levels of carbon dioxide (CO₂) (Dahlman et al. 1985). The approach is two-pronged: (1) the acquisition of laboratory and field data on the effects of elevated CO₂ concentration on plant physiology and growth, and (2) the simultaneous development of models to predict responses of plant species, agricultural ecosystems, and unmanaged, natural ecosystems to higher levels of CO₂ as well as to other environmental variables which themselves may change as CO₂ concentration increases. Although information is limited concerning the effects of CO₂ on crop species and agricultural ecosystems, as will be shown below, there is far more information in these areas than for native species and unmanaged ecosystems—enough to begin, at least, the exercising of some agronomic models. Although future CO₂ effects on natural ecosystems, especially those with greater carbon storage capability, are potentially more important from the viewpoint of the Earth's carbon cycle, the possibility of significantly increased agricultural yield is of distinct economic and social interest, and this has sparked a wave of activity from the agricultural research community. The purpose of the present survey is to help identify the strengths and weaknesses in this knowledge base for processes important for the modeling and prediction of crop growth in a future high-CO₂ world.

Figure 5.1 represents the logic of the Carbon Dioxide Research Program for data acquisition, model development, and eventual prediction of future CO₂ effects on agriculture. There is a good deal of similarity between the processes shown in Figure 5.1 and those considered by Reynolds and Acock to be critical to a generalized crop growth model (Table 3.3 in this volume). The central position of model development (Figure 5.1) is appropriate because it forces a quantitative definition of the assumptions about the system being modeled and because the level on which the model is written will in turn determine the data requirements. Even for a crop monoculture, for which many of the second-order effects (Figure 5.1) such as those of insects, weeds, and pathogens are theoretically controllable, there are many factors and interactions that require understanding before accurate predictions can be made about the possible effects of increased CO₂. Not only must the modelers understand first-order effects of CO₂ on plant physiology and growth and the interactions of CO₂ and other important nonbiological growth factors such as water availability and temperature, they must also deal with the biases and artifacts inherent in the data

collection methods, which range from open top field chambers to phytotrons (Chapter 2 of this volume).

5.2 THE CROP CO₂-DOUBLING RESPONSE SURVEY

This survey is (1) a tabulation of current information on selected first-order effects and interactive effects of elevated CO₂ for 10 leading crop species and (2) a tabulation of predicted values for the various response categories or variables at double the current ambient CO₂ concentration [680 parts per million by volume (ppm) CO₂], which permit direct comparison of species responses. The species selected for the survey are listed in Table 5.1. These species represent broad classes of plants as well as economically important ones and are therefore relatively well studied. The response categories or variables that were surveyed are listed in Table 5.2. No responses below the organ level (i.e., enzyme level) of organization were included because the crop modeling efforts will occur at the field or regional level of organization.

5.2.1 The Data Tables (Appendix)

These tables include summarized data, in the original units, published for 10 leading crop species (Table 5.1) and 10 response categories or variables (Table 5.2). Also included are four secondary treatments revealing interaction effects (water stress or nutrient treatment, temperature or light), important experimental conditions (exposure method and pertinent environmental conditions), the relative response values calculated from the original data, and the reference source. The relative response is usually the value of the response at elevated CO₂ divided by the value at the control CO₂ level.

5.2.2 The CO₂-Doubling Response Tables (Tables 5.3 to 5.7)

These tables present the predicted response for doubled CO₂ concentration expressed as plus or minus a percentage of the control value based on regression analysis; the 95% confidence limits around the predicted value for 680 ppm CO₂; the number of observations; and the number of studies involved in regressions (usually linear) of relative responses calculated within each species/variable class. These tables provide a comprehensive picture of the relative responses as well as the data availability within each species/variable class for the overall response and the four interaction responses. The overall response is the mean response to CO₂-doubling across any secondary treatments that

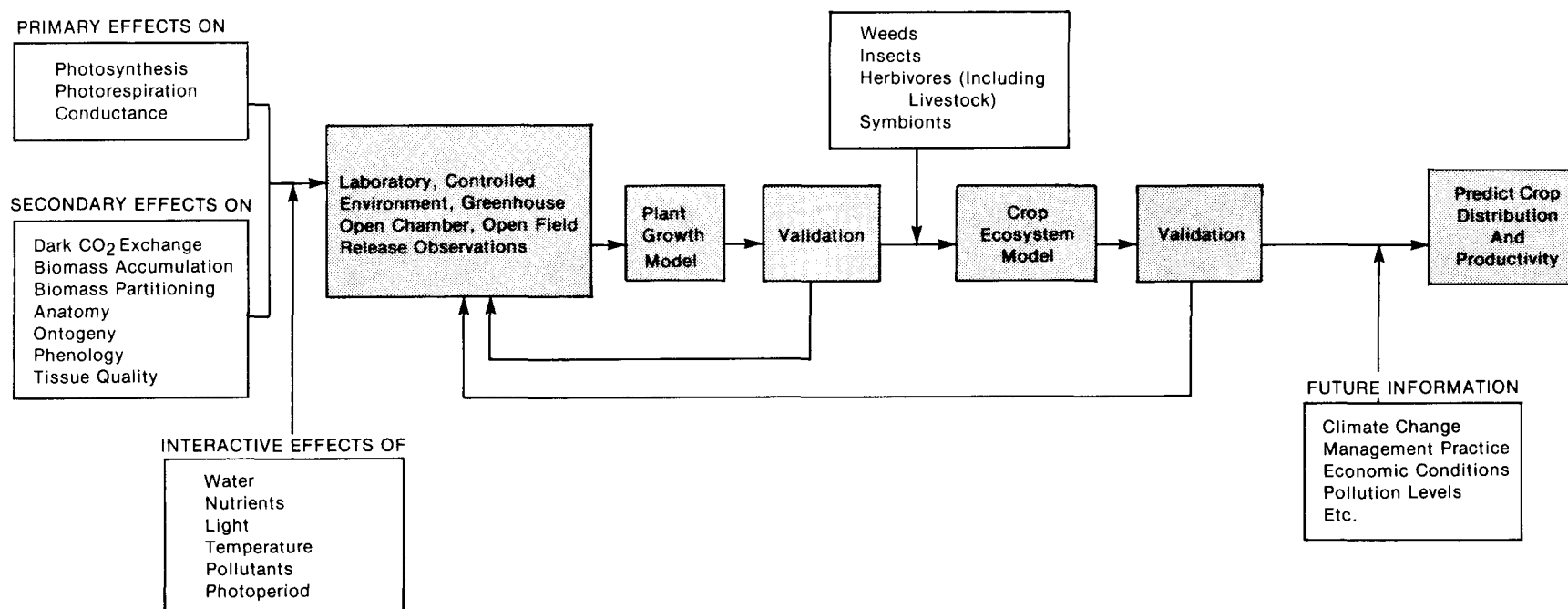


Figure 5.1. Logic diagram for data acquisition, model development, and eventual prediction of future effects of elevated CO₂ on agriculture.

Table 5.1
Botanical Character and Agronomic Significance of Crop Species Selected for Crop CO₂-Doubling Response Survey

Crop Species	Botanical Character				Use					Rank by Acreage ^a (USA) (World)	
	Metabolic Type	Grass	Broad-leaf	Legume	Grain	Forage/ Pasture	Root/ Tuber	Oil	Fiber		
Wheat <i>Triticum aestivum</i> L.	C ₃	X			X					2	1
Barley <i>Hordeum vulgare</i> L.	C ₃	X			X					6	4
Rice <i>Oryza sativa</i> L.	C ₃	X			X					10	2
Corn <i>Zea mays</i> L.	C ₄	X			X			X		1	3
Sorghum <i>Sorghum bicolor</i> (L.) Moench.	C ₄	X			X	X				5	6
Soybean <i>Glycine max</i> (L.) Merr.	C ₃		X	X	X			X		3	7
Alfalfa <i>Medicago sativa</i> L.	C ₃		X	X		X				—	—
Cotton <i>Gossypium hirsutum</i> L.	C ₃		X					X	X	7	9
Potato <i>Solanum tuberosum</i> L.	C ₃		X				X			11	12
Sweet potato <i>Ipomoea batatas</i>	C ₃		X				X			16	16

^a1984 acreages for non-forage crops were ranked according to statistics from the Food and Agricultural Organization of United Nations Monthly Report 1984.

Table 5.2
Response Variables Selected for the Crop CO₂-Doubling Response Survey

Short-term CER:	Measurements of net carbon exchange rate made on leaves of plants grown at the ambient or control level of CO ₂ and measured at elevated CO ₂ concentrations.
Acclimated CER:	Measurements of net carbon exchange rate made on leaves of plants which have been growing at the elevated CO ₂ concentration for at least a week.
Initial NAR:	Net assimilation rate of plants calculated for an interval immediately following exposure to an elevated CO ₂ concentration and not longer than (approximately) two weeks.
Long-term NAR:	Net assimilation rate of plants calculated for an interval beginning two weeks or more after initial exposure to the elevated CO ₂ concentration.
Biomass Accumulation	
Root-to-Shoot Ratio	
Harvest Index:	Seed dry weight divided by total standing top dry weight unless noted otherwise (roots excluded).
Conductance	
Transpiration	
Yield	

may have been present in the experiments. The interaction responses are responses to CO₂-doubling within contrasting levels of water, nutrient, light, and temperature secondary treatments calculated separately.

For most of the variables considered in this project, relative responses were analyzed, that is, the values at elevated CO₂ divided by the values at the control CO₂ level. This approach was taken instead of using the original units because, although differences among some units are reconcilable (e.g., g m⁻² wk⁻¹ and mg cm⁻² d⁻¹), others are not (e.g., yield per plant and yield per meter row, or kilolux and $\mu\text{E m}^{-2} \text{s}^{-1}$). Use of the relative responses permits us to compare responses of unlike variables (e.g., yield and conductance) within a species or across species, or to compare phytotron results with greenhouse or open top chamber results.

The collection of data in this form lends itself to the construction of a unified picture of "the" generic plant response to CO₂ (which is drawn for the reader in Chapter 4 of this volume), and also to the matter of species differences among growth forms or metabolic types. The C₃ and C₄ grasses, annual broadleaf species and legumes, and root crops could potentially represent categories or families of species with fundamentally different responses.

In constructing the survey tables, an attempt was made to include response categories or variables (Table 5.2) on the basis of the objective requirements for modeling growth and yield response to high CO₂ levels, rather than merely listing all the responses in the existing literature. This approach leaves blank spaces in the tables wherever information is lacking, thus highlighting our ignorance. However, because there is literally no information about second-order effects for any species or about future information (Figure 5.1), and only spotty information about first-order effects and interactions for many species, inclusion of all these response categories would result in an unreasonable number of blanks in the table. Some of these undoubtedly will be extremely important in the adaptation of agriculture to the changing environment, but they were not included because we know nothing about them.

5.3 METHODS

It was necessary to establish procedures, first, for the selection of data for inclusion in the Data Tables (Appendix) and second, for pooling these values to obtain overall CO₂-doubling responses and interaction responses (Tables 5.3 to 5.7). These procedures were developed to apply to many different kinds of experiments and were intended to minimize bias.

5.3.1 The Data Tables (Appendix)

These tables, which include the original data entries selected for inclusion in the regressions as well as other pertinent information, provide a link between the CO₂-doubling response tables (5.3 to 5.7) and the original sources.

The relative values for all variables except harvest index (HI) and root-to-shoot ratio (RSR) were calculated as the value at elevated CO₂ divided by the value at the control level of CO₂. The values for HI and RSR, being proportional variables already, were calculated as the simple difference between the value at elevated CO₂ and the value at the control level of CO₂. Most experiments included only one elevated CO₂ treatment; some included two or more elevated levels. Values for each CO₂ level were represented separately in the Data Tables. However, in cases where there were more than two elevated CO₂ treatments, or where a response was regressed against CO₂ concentration, the highest (usually less than 1300 ppm) and one intermediate value were selected for pooling. Thus, there is a maximum of three CO₂ levels represented for any given experiment: the control and two elevated levels. Most control treatments were from 300 to 350 ppm, with values occasionally as low as 290 or as high as 440 ppm. Most high CO₂ treatments ranged from 500 to 1200 ppm. If a publication showed several replications of the same experiment, one mean value was presented in the Data Tables for each CO₂ concentration.

When data (e.g., photosynthesis rates) were regressed against a secondary treatment such as light, a minimum of one point was picked at light saturation or near the highest value reported and another point at a lower light level, in order to show the direction of the interaction. When such data were tabulated in the original paper, more levels may have been included in the Data Tables (Appendix). If data greatly departed from the responses established in the other experiments in the class, or if the CO₂ level was not known with a precision of ± 100 ppm, they were listed in the Data Tables but not used in the regressions. These cases are indicated in the tables.

5.3.2 The CO₂-Doubling Response Tables (Tables 5.3 to 5.7)

All relative response values shown in the Appendix were used for calculating the CO₂-doubling response and the 95% confidence limits unless otherwise noted. The relative responses within a species/variable class were regressed against CO₂ concentration using the general linear model (GLM) procedure in SAS.¹ The slopes and

¹Statistical Analysis Systems, Cary, North Carolina.

Table 5.3
Crop CO₂-Doubling Response: Overall

Response Category	Wheat	Barley	Rice	Corn	Sorghum	Soybean	Alfalfa	Cotton	Potato	Sweet Potato
Short-term CER	+41±7 (13,6)	+50±31 (3,1)	+42±19 (8,3)	+26±9 (22,9)	-3± ^a (2,1)	+78±20 (19,8)	+139± ^a (2,1)	+60±14 (13,4)	+105±49 (3,1)	—
Acclimated CER	+27±20 (10,5)	+14± ^a (2,1)	+46± ^a (2,1)	+4±13 (9,3)	+6±16 (5,2)	+42±10 (39,16)	—	+13±19 (9,4)	—	—
Initial NAR	+11±39 (3,1)	+14± ^a (2,1)	+26±11 (8,3)	+9±4 (10,5)	—	+35±6 (15,7)	—	—	—	—
Long-term NAR	+6±31 (5,2)	+11±7 (10,4)	—	+3±9 (7,3)	+20± ^a (2,1)	+23±5 (18,9)	—	+40± ^a (2,1)	+54± ^a (2,1)	+11±25 (3,1)
Biomass Accumulation	+31±16 (23,10)	+30±17 (12,6)	+27±7 (22,11)	+9±5 (31,13)	+9±29 (6,3)	+39±5 (45,20)	+57±277 (4,2)	+84±126 (6,3)	-15± ^a (2,1)	+59±18 (3,1)
Root-to-Shoot Ratio	+1.4±3.2 ^{b,c} (8,4)	+6.4±6.9 (4,2)	-4.0± ^a (2,1)	+3.1±4.0 ^c (11,5)	-8.5± ^a (2,1)	+1.1±1.0 ^c (25,11)	-5.0±0.6 (4,2)	+3.2±8.0 (5,2)	-2.1± ^a (2,1)	+34.9±14.6 (3,1)
Harvest Index	+2.4±2.3 ^{b,c} (12,6)	+1.3± ^a (2,1)	+1.9±0.6 (6,3)	+4.3±4.6 ^c (5,2)	—	-5.0±4.4 (19,8)	—	—	+1.9± ^a (2,1)	—
Conductance	-22±29 (4,2)	-52±61 (3,1)	-33±7 (5,3)	-37±7 (13,5)	-27±45 (3,1)	-31±5 (21,7)	—	-15±32 (3,1)	-59±12 (3,1)	—
Transpiration	-17±17 (4,2)	-19±6 (7,3)	-16±9 (7,3)	-26±6 (15,6)	-27±16 (6,2)	-23±5 (19,8)	—	-18±17 (7,3)	-51±24 (3,1)	—
Yield	+35±14 ^c (17,8)	+70± ^a (2,1)	+15±3 (6,3)	+29±64 (3,1)	—	+29±8 (28,12)	—	+209± ^a (2,1)	+51±111 (6,3)	+83±12 (3,1)

Note: Data represent the percentage change at 680 ppm CO₂ compared with controls (300–350 ppm) ±95% confidence limits, as estimated by regression analysis. Exceptions are Harvest Index and Root-to-Shoot Ratio, for which absolute changes are predicted. The values in parentheses are the number of relative response values used in each regression and the number of studies supplying those values.

^aIn cases where results were based on only two data points, error degrees of freedom were 0 and confidence limits could not be calculated.

^bAll values for Root-to-Shoot Ratio and Harvest Index and their confidence limits should be multiplied by 10⁻².

^cBased on quadratic model.

Table 5.4
Crop CO₂-Doubling Response: Water Stress Interactions

Response Category	Wheat	Barley	Rice	Corn	Sorghum	Soybean	Alfalfa	Cotton	Potato	Sweet Potato
Short-term CER	—	—	—	—	—	—	—	—	—	—
Acclimated CER	—	—	—	—	—	C: +65±29 S: +38±16 (5,2)	—	—	—	—
Initial NAR	—	—	—	—	—	—	—	—	—	—
Long-term NAR	—	—	—	—	—	—	—	—	—	—
Biomass Accumulation	C: +35±34 S: +33±30 (8,4)	C: +107± ^a S: +65± ^a (2,1)	C: +51± ^a S: +52± ^a (2,1)	C: +0± ^a S: +36± ^a (2,1)	C: +26± ^a S: +31± ^a (2,1)	—	C: +130± ^a S: +78± ^a (2,1)	C: +0± ^a S: +19± ^a (2,1)	—	—
Root-to-Shoot Ratio	C: -4.1± ^{a,b} S: -3.2± ^a (2,1)	C: +1.0± ^a S: -4.0± ^a (2,1)	C: -3.0± ^a S: -5.0± ^a (2,1)	C: -26.0± ^a S: -5.0± ^a (2,1)	C: -8.0± ^a S: -9.0± ^a (2,1)	—	C: +2.0± ^a S: -12.0± ^a (2,1)	C: +10.0± ^a S: +2.0± ^a (2,1)	—	—
Harvest Index	C: +2.8±3.1 ^b S: +2.8±11.8 (4,2)	—	—	—	—	C: +1.6± ^a S: +2.7± ^a (2,1)	—	—	—	—
Conductance	—	—	—	—	—	C: -23±3 S: -32±68 (3,1)	—	—	—	—
Transpiration	—	—	—	—	—	C: -14± ^a S: -12± ^a (2,1)	—	—	—	—
Yield	C: +25±151 S: +41±250 (4,2)	—	—	—	—	C: +60± ^a S: +46± ^a (2,1)	—	—	—	—

Note: Data represent the percentage change at 680 ppm CO₂ compared with controls (300–350 ppm) ±95% confidence limits, as estimated by regression analysis. Exceptions are Harvest Index and Root-to-Shoot Ratio, for which absolute changes are predicted. The values in parentheses are the number of relative response values used in each regression and the number of studies supplying those values. C = control; S = stress.

^aIn cases where results were based on only two data points, error degrees of freedom were 0 and confidence limits could not be calculated.

^bAll values for Root-to-Shoot Ratio and Harvest Index and their confidence limits should be multiplied by 10⁻².

Table 5.5
Crop CO₂-Doubling Response: Nutrient Stress Interactions

Response Category	Wheat	Barley	Rice	Corn	Sorghum	Soybean	Alfalfa	Cotton	Potato	Sweet Potato
Short-term CER	—	—	—	—	—	—	—	C: +76± ^a S: +59± ^a (2,1)	—	—
Acclimated CER	—	—	—	C: +32±46 S: +29±43 (3,1)	—	C: +39± ^a S: +14± ^a (2,1)	—	C: +35±109 S: +23±35 (4,2)	—	—
Initial NAR	—	—	—	C: +5± ^a S: +3± ^a (2,1)	—	C: +35±73 S: +45±11 (4,2)	—	—	—	—
Long-term NAR	C: +25± ^a S: +31± ^a (2,1)	—	—	—	—	C: +19±123 S: +35±102 (4,2)	—	—	—	—
Biomass Accumulation	C: +39±15 S: +10±2 (4,2)	—	C: +32±69 S: +30±21 (4,2)	C: +14±7 S: +11±6 (6,3)	—	C: +52±73 S: +40±60 (6,3)	C: +13± ^a S: +18± ^a (2,1)	C: +146± ^a S: +133± ^a (2,1)	—	—
Root-to-Shoot Ratio	C: +1.0±0.5 ^b S: +2.5±4.4 (4,2)	—	—	C: -1.9± ^a S: +5.2± ^a (2,1)	—	C: -0.3±3.2 S: -3.2±12.5 (6,3)	C: -9.6± ^a S: -2.7± ^a (2,1)	—	—	—
Harvest Index	C: +2.7±14.7 ^b S: +1.6±15.1 (4,2)	—	—	—	—	C: -5.1± ^a S: -0.0± ^a (2,1)	—	—	—	—
Conductance	—	—	—	—	—	C: -37± ^a S: -45± ^a (2,1)	—	—	—	—
Transpiration	—	—	—	C: -47± ^a S: -49± ^a (2,1)	—	C: -28± ^a S: -36± ^a (2,1)	—	C: -33±30 S: -41±24 (4,2)	—	—
Yield	C: +43±57 S: +16±18 (4,2)	—	—	—	—	C: +126± ^a S: +102± ^a (2,1)	—	—	—	—

Note: Data represent the percentage change at 680 ppm CO₂ compared with controls (300–350 ppm) ±95% confidence limits, as estimated by regression analysis. Exceptions are Harvest Index and Root-to-Shoot Ratio, for which absolute changes are predicted. The values in parentheses are the number of relative response values used in each regression and the number of studies supplying those values. C = control; S = stress.

^aIn cases where results were based on only two data points, error degrees of freedom were 0 and confidence limits could not be calculated.

^bAll values for Root-to-Shoot Ratio, Harvest Index and their confidence limits should be multiplied by 10⁻².

Table 5.6
Crop CO₂-Doubling Response: Light Interactions

Response Category	Wheat	Barley	Rice	Corn	Sorghum	Soybean	Alfalfa	Cotton	Potato	Sweet Potato
Short-term CER	L: +37±20 H: +49±26 (3,1)	—	—	L: +21±11 H: +23±16 (7,3)	—	L: +52±51 H: +100±32 (7,3)	—	L: +67±14 H: +47±28 (6,2)	—	—
Acclimated CER	—	L: +11± ^a H: +15± ^a (2,1)	—	—	—	L: +84±23 H: +62±25 (12,6)	—	—	—	—
Initial NAR	—	L: +9± ^a H: +18± ^a (2,1)	L: +39± ^a H: +26± ^a (2,1)	L: +8± ^a H: +12± ^a (2,1)	—	L: +23± ^a H: +31± ^a (2,1)	—	—	—	—
Long-term NAR	—	L: +7±26 H: +7±7 (6,3)	—	L: -3± ^a H: +9± ^a (2,1)	—	—	—	—	—	—
Biomass Accumulation	L: +15± ^a H: +20± ^a (2,1)	L: +20±32 H: +17±14 (4,2)	L: +28± ^a H: +31± ^a (2,1)	L: +16±32 H: +19±22 (4,2)	—	L: +44±175 H: +41±73 (4,2)	—	—	—	—
Root-to-Shoot Ratio	—	—	—	L: +2.0± ^{ab} H: +1.5± ^a (2,1)	—	L: -2.0± ^a H: -1.0± ^a (2,1)	—	—	—	—
Harvest Index	—	—	—	—	—	—	—	—	—	—
Conductance	L: -31± ^a H: -25± ^a (2,1)	—	—	L: -34±23 H: -40±17 (5,2)	—	—	—	—	—	—
Transpiration	L: -27± ^a H: -11± ^a (2,1)	—	—	L: -30±19 H: -28±15 (5,2)	—	L: -7±78 H: -15±7 (4,2)	—	—	—	—
Yield	—	—	—	—	—	—	—	—	—	—

Note: Data represent the percentage change at 680 ppm CO₂ compared with controls (300–350 ppm) ±95% confidence limits, as estimated by regression analysis. Exceptions are Harvest Index and Root-to-Shoot Ratio, for which absolute changes are predicted. The values in parentheses are the number of relative response values used in each regression and the number of studies supplying those values. L = Low; H = High.

^aIn cases where results were based on only two data points, error degrees of freedom were 0 and confidence limits could not be calculated.

^bAll values for Root-to-Shoot Ratio, Harvest Index and their confidence limits should be multiplied by 10⁻².

Table 5.7
Crop CO₂-Doubling Response: Temperature Interactions

Response Category	Wheat	Barley	Rice	Corn	Sorghum	Soybean	Alfalfa	Cotton	Potato	Sweet Potato
Short-term — CER	L: +6±4 H: +52±35 (4,2)	—	—	—	—	—	— H: +177± ^a (2,1)	L: +96± ^a H: +90±27 (3,1)	L: +100±28	—
Acclimated CER	—	—	—	—	—	L: +72±95 H: +80±20 (4,2)	—	—	—	—
Initial NAR	—	—	L: +24± ^a H: +34± ^a (2,1)	L: +8± ^a H: +12± ^a (2,1)	—	L: +24± ^a H: +31± ^a (2,1)	—	—	—	—
Long-term NAR	—	—	—	—	—	—	—	—	—	—
Biomass Accumulation	—	—	L: +26± ^a H: +36± ^a (2,1)	L: +12± ^a H: +18± ^a (2,1)	—	L: +27± ^a H: +39± ^a (2,1)	—	—	—	—
Root-to-Shoot Ratio	—	—	—	—	—	—	—	—	—	—
Harvest Index	—	—	—	—	—	—	—	—	—	—
Conductance	—	—	—	—	—	—	—	—	—	—
Transpiration	—	—	—	—	—	L: -9± ^a H: -13± ^a (2,1)	—	—	—	—
Yield	—	—	—	—	—	—	—	—	—	—

Note: Data represent the percentage change at 680 ppm CO₂ compared with controls (300–350 ppm) ±95% confidence limits, as estimated by regression analysis. Exceptions are Harvest Index and Root-to-Shoot Ratio, for which absolute changes are predicted. The values in parentheses are the number of relative response values used in each regression and the number of studies supplying those values. L = Low; H = High.

^a In cases where results were based on only two data points, error degrees of freedom were 0 and confidence limits could not be calculated.

intercepts of the curves are not presented because the models, which were always linear except where noted otherwise, were constrained to pass through a relative response of unity corresponding to the control value of CO₂. This was accomplished by subtracting 1 from all the relative responses, subtracting 340 from all the elevated CO₂ values, and using the option in GLM ("NOINT") in which the intercept was not included in the model. The predicted responses were then expressed as plus or minus a percentage change. Exceptions to these procedures occurred for RSR and HI, for which the SAS regressions were based on simple differences between the values at elevated and control levels of CO₂.

As a check, regressions were run both with and without the NOINT option. Without the NOINT option the intercepts did not significantly depart from unity; consequently, forcing the regression through unity had almost no impact on the predicted CO₂-doubling response. It did cause a minor discrepancy by estimating an error term in cases where there were only two data points (nonsense). Because no estimate of variability can be meaningful in such cases, 95% confidence limits were not calculated and asterisks appear in these places on the CO₂-doubling response tables (5.3 to 5.7). Use of the NOINT option was simpler and more efficient because one degree of freedom was not used in fitting the intercept parameter, and the confidence limits were thereby narrowed somewhat.

In calculating confidence limits, effective degrees of freedom for error were less than those in the GLM output because points corresponding to control CO₂ levels were artificially generated when the data were transformed to relative units. Effective degrees of freedom for error were taken to be the degrees of freedom in the GLM output less the number of points at control CO₂, and the error mean square and confidence limits were calculated accordingly. For experiments in which the CO₂ control was outside the 300-350 ppm range, a separate regression was run, a predicted relative response for 340 ppm CO₂ was obtained, and this value was used as the control. In a few cases a quadratic model significantly improved the R², and, therefore, this model was adopted. These cases are indicated on the tables.

5.3.2.1 *The Overall CO₂ Response*

If there were no secondary treatments in a given experiment, the values for each of the one or two relative response values at high CO₂ concentrations in each experiment were pooled with those from all other experiments within the species/variable class for the purpose of the regression and obtaining the predicted CO₂-doubling response. If, however, there were other

secondary treatments, such as light, temperature, water stress, or nutrient stress, values across these other treatments were averaged together to give a single, intermediate value for a given CO₂ level in that experiment. This procedure was justified by the goal of obtaining average responses across experiments within a species/variable class: variation from experiment to experiment was often larger than variation due to secondary treatments within an experiment, and averaging across the secondary treatments ensured that the overall response for the class would not be biased toward those experiments in which there were many secondary treatments. Also, results from these secondary treatments are presented separately under interaction responses (Tables 5.4 to 5.7). This averaging procedure at each CO₂ concentration was used unless (1) the secondary treatment had a very profound effect on the response (such as the effect of nutrient deficiency on RSR) or (2) the data departed greatly from the range represented by the other experiments in the species/variable class. In such cases these data were not used in calculating the overall CO₂-doubling response and this is indicated on the tables.

5.3.2.2 *The Interaction Responses*

Interaction responses are relative responses to CO₂ enrichment at contrasting levels of the secondary treatments: water stress, nutrient stress, light, or temperature. In cases where regressions against a secondary treatment such as light or temperature appear in the source paper, only two points were picked off the regression lines for inclusion in the Data Tables (as explained above). There were sometimes, however, up to six discrete levels of the secondary treatment tabulated in the source paper and included in the Data Tables. To make treatment of tabulated data similar to that of regressed data, one level was selected as the "control" value (for water stress or nutrient stress experiments) or "low" value (for light or temperature experiments), and the others were averaged together to produce one contrasting "stress" or "high" value for that CO₂ level for that experiment. Thus, a data set with two CO₂ levels was reduced to four numbers: one at the "control" or "low" level of the secondary treatment and one at the "stress" or "high" level of the secondary treatment for each CO₂ concentration. In cases where two secondary treatments were employed, this averaging procedure was simply performed both ways. These were then pooled with similarly obtained values from other experiments in the species/variable class for the regression and prediction of the CO₂-doubling response.

It is important to bear in mind that values for all experiments dealing with the secondary treatment, even

if not very similar in approach, were nonetheless pooled. For instance, for nutrient stress interaction, results of studies using sequential dilution of Hoagland's solution were pooled with those where nitrogen or phosphorus was selectively withheld. This pooling was possible only because we have so little information on nutrient interaction with CO₂ on plant growth and physiology that differences of this kind are not yet discernible in the data. Likewise, single-episode water stress data were pooled with chronic water stress data. This crude handling of the data was necessary to construct a broad-based first approach summary of research results on interactions of CO₂ and these important environmental variables.

5.4 OBSERVATIONS

5.4.1 The Overall CO₂-Doubling Responses (Table 5.3)

The Data Tables are a tabulation of published research results on crop species responses to CO₂ enrichment. However, even as this volume is processed, this compilation of what we know about CO₂ and crop species is being expanded. Data are being processed or are about to be published in the following areas: sorghum and wheat growth in closed field chambers (E. T. Kanemasu and M. B. Kirkham); cotton growth and water use in open top field chambers (B. A. Kimball); corn growth and water use in open top field chambers (K. A. Surano and J. H. Shinn); soybean growth and water stress in open top field chambers (H. H. Rogers and J. D. Cure); and soybean nitrogen fixation in sunlit controlled environment chambers (J. R. Lambert) and open top chambers (J. D. Cure and H. H. Rogers).

Although the empty and full cells in Tables 5.3 to 5.7 are a crude measure of data availability, there is not a strict correspondence between a full cell and a well-characterized response. One begins to have some confidence in a prediction only when several independent studies have accumulated that show a similar direction and order of magnitude of response. A large number of studies is required because conditions vary so from study to study, each modifying the CO₂ response of the plants.

From Tables 5.3 to 5.7, the best-studied species is clearly soybean (C₃ broadleaf) followed by wheat (C₃ grass) and corn (C₄ grass). The root crops are the least well represented, probably because of their lesser economic importance at present (Table 5.1). However, there is some evidence that root crops may be among those which respond most strongly to CO₂ enrichment (Kimball 1983), and their relative importance as crops

may therefore increase as CO₂ concentration increases.

5.4.1.1 Carbon Assimilation

The data for the measured processes of carbon assimilation, CER (CO₂ exchange rate) and NAR (net assimilation rate), were divided into short-term and long-term categories, reflecting the importance of time for these measurements.

In general, overall responses of CER to doubled CO₂ shown in Table 5.3 were greater in the short-term studies than for acclimated plants. Soybean and cotton are the only species for which photosynthesis has been studied explicitly as a function of time of exposure to elevated CO₂. These studies (Mauney et al. 1979; Wong 1980; Clough and Peet 1981; Peet 1984; DeLucia et al., in press) support the more general observation made here and are in agreement with observations made on native species, discussed in Chapter 6 of this volume. Although for soybean the CER always fell with time, in most studies it remained high relative to CO₂ controls, whereas in a few studies it fell to about the control level or even lower. The data for cotton also support this picture. The data for wheat, barley, rice, and corn are also in general agreement, but because (unlike cotton) short-term CER data and acclimated CER data were collected by different investigators under different conditions, these do not provide the direct confirmation observed for cotton. The CER response categories include leaf as well as canopy measurements and thus could be misleading. Gifford (1977) showed in a growth chamber study that photosynthetic increases for wheat plants grown in an elevated-CO₂ atmosphere were 56% for the flag leaf, 40% for the plant canopy, and 238% on a unit ground area basis, respectively. Although the last value is in the form most appropriate for crop predictions, this kind of data has been difficult to obtain and therefore relatively rare.

Net assimilation rate is in some ways a more useful measure of net carbon input as it averages over days or weeks and is a simpler measurement to make and therefore less subject to error. To evaluate NAR data, time after the beginning of CO₂ treatment and the duration of the interval must be known, which are not always provided. Because the effects of dark respiration are by definition included in NAR, initial NAR responses were less dramatic than those for CER for all the C₃ species for which studies exist.

For soybean, NAR as well as CER fell with time at any CO₂ level, with NAR of high-CO₂ plants falling as fast or faster than that of controls (Patterson and Flint 1982; Sionit et al. 1982; Sionit 1983; Rogers et al. 1984a). The few studies directly addressing the issue have shown the requirement for high metabolic or storage "sink" (carbon utilization) activity in order

for the photosynthetic response to elevated CO_2 to be sustained (Clough and Peet 1981; Peet 1984). In a classic growth study, Neales and Nicholls (1978) clearly described this response for wheat as well, and other data for wheat and barley are also consistent (Ford and Thorne 1967; Sionit et al. 1981).

All of the data for the carbon assimilation variables for C_3 species (Table 5.3) taken together suggest that the grasses may respond somewhat less strongly to elevated CO_2 concentrations than the broadleaf species soybean and cotton. If wheat and soybean are in fact representative of the C_3 grasses and broadleaf plants, this observation may be justified. But even in this first relatively well-studied response category of carbon assimilation, we are unable to make a more concrete statement about the broader categories of grass versus broadleaf species because of sparse data and large variability.

Corn showed a surprisingly high initial CER response considering that it possesses a CO_2 -concentrating mechanism already in its leaves. Carbon assimilation responses ranged from -5% to about $+40\%$ for CO_2 -doubling, and it is not clear what other environmental factors may have caused this variability. All the carbon assimilation variables for corn and sorghum taken together, however, indicate that the C_4 crops respond very much less than the C_3 crops in this category.

5.4.1.2 Biomass Accumulation

For most of the species surveyed, the average predicted increase in biomass accumulation for 680 ppm CO_2 was greater than the increase in long-term NAR. This is probably attributable to increased leaf area of canopies or plants growing at high levels of CO_2 , which compounds the increase in NAR in producing higher biomass.

The effect of CO_2 -doubling on biomass accumulation among C_3 grasses appears to be reasonably similar at about $+28\%$, but the values for C_3 broadleaf species are sparse and erratic. If soybean may be taken to represent C_3 broadleaf crops, the effect of CO_2 -doubling on biomass accumulation appears to be higher than for the C_3 grasses, which is in keeping with their carbon assimilation responses. Biomass response to CO_2 -doubling was low for the C_4 species corn ($+9\%$) and sorghum ($+3\%$), which also agrees with the generally low response of carbon assimilation for these species.

5.4.1.3 Harvest Index and Yield

For soybean and wheat, the only species for which a number of studies exist, yield results are similar to biomass accumulation results. The relationship between biomass accumulation and yield for these two species are

consistent with their predicted changes in harvest index (HI), $+0.01$ units for wheat and -0.05 units for soybean. Soybean is the only species for which HI has consistently decreased at elevated CO_2 levels, an observation that raises questions about the efficiency of partitioning of carbohydrate in these leaves during reproductive growth.

The yield data for the C_3 grasses are few and quite variable. The value for rice is to be regarded with caution because in none of the three studies performed was there a proper chambered control treatment.

5.4.1.4 Conductance and Transpiration

The responses of conductance and transpiration are surprisingly uniform across species. The decrease in transpiration is not as large as the decrease in conductance because, as the stomata close and transpiration begins to fall, leaf temperature tends to increase, which in turn stimulates transpiration. It is important to note that these predictions are expressed on a unit leaf area basis. In terms of crop water use, the increase in canopy leaf area may compensate for the low conductance at high CO_2 concentrations (Rogers et al. 1984b; Jones et al. 1985a). The effects of CO_2 on crop water use are discussed in detail in Chapters 4 and 9.

5.4.2 The Interaction Responses (Tables 5.4 to 5.7)

5.4.2.1 Water Stress

Judging by the availability of data in the species/variable cells of Tables 5.4 to 5.7, water stress, which may be the most important of the environmental interactions with elevated CO_2 , is one of the least well studied. There are several possible ways elevated CO_2 might modify the response to low moisture availability. First, the action of high CO_2 levels on stomatal conductance lowers the rate of leaf transpiration and plant consumption of limited water supply. Some studies have shown a greater stomatal sensitivity to CO_2 for C_4 species than C_3 species (Pallas 1965; Akita and Moss 1972; Carlson and Bazzaz 1980; Rogers et al. 1983), but not all have observed this (Morison and Gifford 1983). Also, preconditioning with a water stress can sensitize stomata to CO_2 concentration, possibly through an abscisic acid mechanism (Raschke 1975). Second, high levels of CO_2 increase leaf area or leaf area index, which may or may not offset the advantage of the first effect in terms of water conservation (Rogers et al. 1984b; Jones et al. 1985b). In either case, if conditions of low water availability persist, low leaf water potentials are bound to result. Which brings us to a third possible mechanism of interaction. At least some cultivars of wheat, corn, and sorghum have demonstrated a capacity to maintain high turgor during periods of limited water supply

through the generation of osmotically active solutes, and photosynthesis is maintained at relatively low leaf water potential for these genotypes. There is evidence that for some wheat cultivars this osmotic adjustment capability is increased in the presence of elevated CO_2 concentration (Sionit et al. 1980). Soybean plants do not appear to respond osmotically to low leaf water potentials and would, therefore, benefit only from the first mechanism, the lowering of stomatal conductance and water consumption (Rogers et al. 1984b). A fourth possible mechanism of interaction of elevated CO_2 and low water availability is through plasticity in dry matter partitioning into roots and shoots. Enhanced RSRs have often been observed for crop species growing in dry conditions, and a synergistic effect of elevated CO_2 and low soil moisture might be expected, but there are very few data pertinent to the question. Sionit et al. (1980) observed that the enhancement in RSR for wheat growing in elevated CO_2 concentration was increased when the plants were water-stressed, if the calculations were based on vegetative plant weights. However, when seed yields were included in the shoot weight, the RSR decreased at high CO_2 levels because the HI was increased. We are limited not only by the few such interaction studies attempted but also by our inability to accurately measure root growth, especially under dry soil conditions.

At present the two factors that seem most important in the interaction of CO_2 and water stress are the decreased conductance and increased leaf area responses. Any net change in crop water use will be determined largely by the balance of these two opposing effects. Differences among the experiments in leaf area response to CO_2 probably account for the different relative yield responses to CO_2 with and without water stress (Table 5.4). These conflicting data underscore the need for realistic estimates of the leaf area response of crops to CO_2 enrichment under field conditions.

5.4.2.2 Nutrient Stress

In the categories of carbon assimilation, biomass accumulation, and yield, a majority of entries show that nutrient stress limits the relative effects of CO_2 enrichment (Table 5.5). For a basic understanding of the nature of this interaction, however, unlike water stress, we are not certain which processes affected by nutrient deficiencies are the critical ones.

Exposure of plants to CO_2 -enriched environments can result in increased photosynthetic leaf area, for both individual leaves (Ho 1977; Goudriaan and de Ruiter 1983) and for the whole canopy, traceable to increased branching and node number (Ford and Thorne 1967; Gifford 1977; Sionit 1983). However, when soybean and two weed species were grown at elevated CO_2 levels

with varying dilutions of Hoagland's solution, high CO_2 levels increased leaf area only at high nutrient supply (Patterson and Flint 1982; Sionit 1983). Low turgor associated with decreased hydraulic conductivity limits leaf expansion of plants growing in low nitrogen medium (Radin and Boyer 1982).

Low nutrient supply decreases leaf expansion more than assimilation per unit leaf area, with the result that carbohydrates accumulate even at current CO_2 levels (Bouma et al. 1979). Elevated CO_2 concentrations would tend to exacerbate this condition unless it made nutrients in the external medium more available to the plant, either through increased proportional carbon allocation to roots or through enhanced nutrient absorption efficiency. As with water stress, one might expect a synergistic effect of high CO_2 and low nutrient availability on RSR. Although this possibly occurs, it is not reported consistently in the literature (Table 5.5). Also, there have been no reported experiments on the effects of CO_2 concentration on nutrient uptake efficiency. Whereas an increase might be expected due to greater carbohydrate availability in the roots, the little available evidence hints at the possibility that uptake efficiency is not increased in high CO_2 plants. In cotton, a better than doubling of dry matter was accompanied by no increase in nitrogen (N) accumulation, except at the highest N level (Wong 1979). In both N-fixing and nitrate systems, Williams et al. (1981) observed that stimulation of N accumulation by high CO_2 did not keep pace with that of dry matter accumulation. The "dilution" of N is probably not fully accounted for by accumulation of carbohydrate reserves. Some may be due to greater amounts of cell wall material in the leaves at high CO_2 (Thomas and Harvey 1982). Because carbohydrate would not be limited, any remaining increment of the decreased N concentration could represent a decreased relative growth requirement for N.

If nutrient uptake does not keep pace with photosynthetic carbon fixation, the resultant imbalance will at some point inhibit further carbon assimilation. It has been suggested that the decrease in photosynthetic response to CO_2 observed with time may be due to a sequestering of P, as sugar phosphates in the chloroplast (Walker and Herold 1977; Sharkey and Badger 1984). This is an area of much uncertainty. Certainly high sucrose export rates have been associated with high phosphorus (P) import rates (Thorne and Koller 1974; Hopkinson 1964). Potassium (K), N, and P have all been observed to increase sugar efflux from mesophyll cells (Geiger 1979; Kamanina and Anisimov 1977), and increased partitioning of carbohydrate to sucrose at the expense of starch was correlated with increasing nutrient P level and increased dry matter accumulation in seeds of soybeans (Giaquinta et al. 1981).

Of the few studies demonstrating nutrient limitations on CO₂-enhanced growth, many used dilutions of Hoagland's solution instead of varying one nutrient, and very few reported tissue mineral concentrations. Documentation of the requirements for any of the major nutrients for CO₂-enhanced growth and the effects of deficiencies are almost entirely lacking for any species. These effects must be understood in the context of carbohydrate assimilation and partitioning, a critical area still very poorly understood.

5.4.2.3 *Light and Temperature Interaction*

Increases in quantum yield due to inhibition of photorespiration by high levels of CO₂ have been described for C₃ native plant species (Ehleringer and Bjorkman 1977). Such a response in a crop stand would result in enhanced photosynthesis in the lower canopy, an effect that may be great on a relative basis but overshadowed on an absolute basis by the CO₂ enhancement of photosynthesis in the upper canopy (Percy and Bjorkman 1983). However, a survey of the crop studies in which the influence of light on the CO₂ response of CER, NAR, and growth is reported shows no consistent pattern, either within or among species (Table 5.6). The absolute increase in photosynthetic rate in response to CO₂ concentration is always greater in high light than in low light. However, this is not necessarily true of the relative increase. High light intensity increased the relative response in about one-third of the studies, decreased it in another one-third, and had no effect in the remainder. In two studies, high light had a positive effect on the relative response of NAR when the plants were young, with this effect becoming neutral or negative as the plants aged (corn, Sionit et al. 1982; barley, Ford and Thorne 1967). Another influence on the light/CO₂ interaction which must be taken into account is well illustrated in a comparison of photosynthesis of potted soybeans with that of plants growing alongside them in the ground in open top field chambers (Sionit et al. 1984). The relative effect of elevated CO₂ at high light intensity was much greater for the potted plants. More importantly, CER was light saturated at 800 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ for potted plants but continued to rise with increasing light for the plants growing in the ground. The limitation on CER of the potted plants was not caused by an effect on conductance.

In all except one study, responses to CO₂ were larger at high temperature than at low temperature (Table 5.7). In most cases, the effects of temperature on CER, NAR, and biomass accumulation responses to CO₂ concentration were measured at high light intensity. Under these conditions, the relative increases due to elevated CO₂ concentration were greater at

high temperatures up to and in most cases beyond the optimum temperature (that temperature in each study at which the measured variable had the highest value). At low light intensity, however, the effect of high temperature on the CO₂ response was less positive. The interactive effects of varying light intensity, temperature, and CO₂ concentration on plant growth appear to be complex and not easily characterized. Nevertheless, accurate prediction of CO₂ responses may depend on understanding them.

5.5 CONCLUSIONS AND RESEARCH RECOMMENDATIONS

The statistical approach taken in this study requires a large number of independent data entries to arrive at a reliable estimate of a CO₂-doubling response. Table 5.3 shows that we may begin to consolidate our understanding of the overall direction of change of key physiological processes of different crop species growing under constant conditions of elevated CO₂. However, the conclusions drawn with respect to overall responses are more reliable than those for interactions. Indeed, these tables highlight the paucity and variability of data on interactions between CO₂ and other environmental variables. This review reveals that there is just too little quantitative information available to enable us to predict precise response to CO₂ concentration under well-defined environmental conditions.

Although the carbon assimilation variables for C₃ broadleaf species show stronger responses to elevated CO₂ than the C₃ grasses, the data are as yet too erratic and sparse to firmly delineate or characterize response groups based on growth form.

The C₄ plants corn and sorghum showed a smaller increase in carbon assimilation and growth than C₃ plants. In view of the presence of the CO₂-concentrating mechanism in C₄ leaves, this smaller response to an increase is not surprising. Indeed it is surprising that there was any response to high CO₂. We need to examine possible roles of increased turgor or leaf temperature in determining the final extent of C₄ canopy development.

Soybeans and wheat are relatively well represented in the tables. Further information on the growth response of the other species is required. Several independent studies are necessary to obtain reliable information about a crop because of the variability in experimental conditions.

RSRs generally increased only a small amount.

For all species except soybeans, HI increased under elevated CO₂ concentrations, thus compounding the increases in biomass accumulation in determining

increased yield. Future breeding efforts will probably correct the situation for soybean HI, thus further increasing soybean yield.

Conductance was decreased by CO₂-doubling rather uniformly across species by about 34%. Future crop water consumption, however, is difficult to predict due to uncertainty about leaf area response to high CO₂ under natural field conditions. To remove this impediment, realistic estimates of leaf area responses to elevated CO₂ under field conditions are necessary.

Many of the plants in controlled environment studies showed greater responses to CO₂ than plants grown in other systems. Whereas a fundamental understanding of CO₂ interactions with water availability, nutrition level, light, and temperature can most readily be obtained in controlled environments, only field trials of the major crops can validate model predictions with respect to all of the processes discussed above.

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6. NATIVE SPECIES RESPONSES TO INCREASED ATMOSPHERIC CARBON DIOXIDE CONCENTRATION

W. C. Oechel
San Diego State University
and
B. R. Strain
Duke University

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6.1 INTRODUCTION

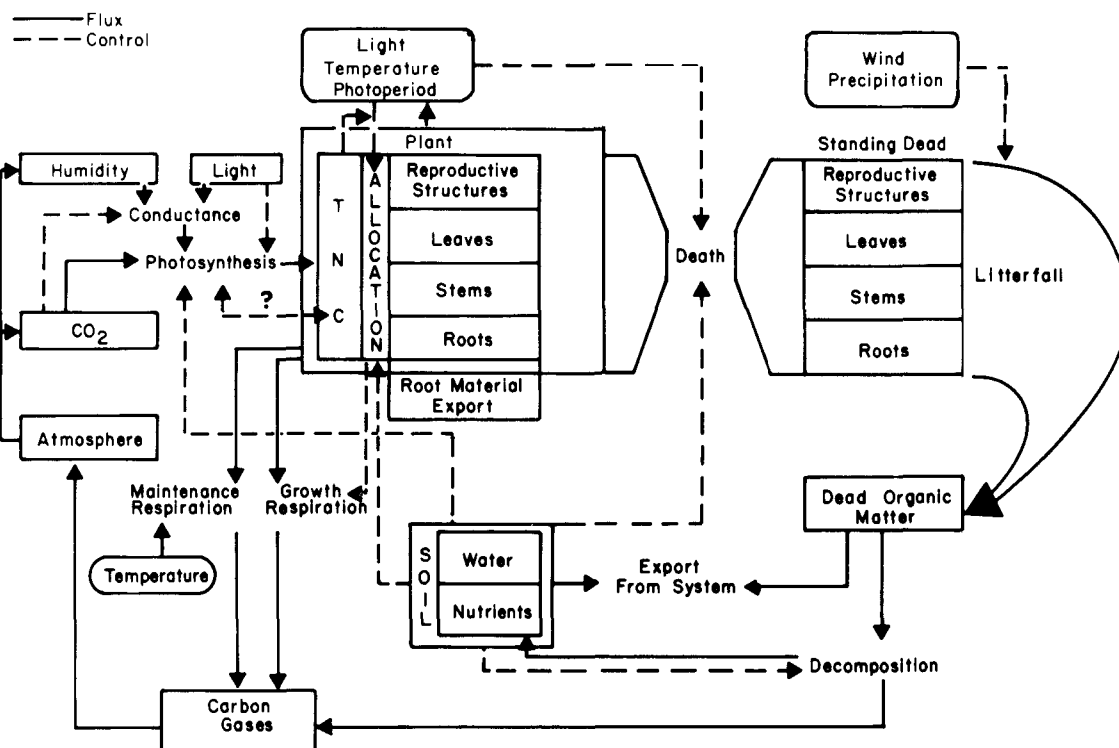
Knowledge of the responses of native plants and their ecosystems to increases in levels of atmospheric carbon dioxide (CO_2) is important. A wide range of possible effects has been hypothesized and includes changes in primary productivity, plant competition and community composition, plant-animal interactions, plant water-use efficiency and ecosystem water yield, nutrient status, and net ecosystem carbon sequestering. Chapters 4 and 5 present the responses of agricultural species. Although the biochemical and physiological processes are basically similar in agricultural and native species and in ecosystems, they operate in different environments and have been subjected to different selective pressures. Agricultural cultivars have been selected for rapid growth and allocation of the maximum amount of carbon to harvestable organs and structures in buffered and relatively favorable environments without regard to survival or competitive ability in the wild. In contrast, native species have been and will continue to be subjected to natural selection and survival defense or adaptation to a wide range of environmental stress. Thus, the characteristics that result in a successful crop plant can be quite different from those necessary for a successful native plant.

Because of the differences necessary in selection pressures and life histories, it is likely that unmanaged ecosystems will respond differently than crop systems to increasing CO_2 concentration. For example, in natural systems, water and nutrients are often limited, herbivory is less controlled, and litter quality is more important. Therefore, it is likely that there will be quantitative and qualitative differences among the responses of the two systems. Thus, predictions based on short-term measurements of photosynthesis or which reflect interactions with nutrient and water supply, growth form, and sink strength may be in error.

It is helpful to view the responses of plants to elevated CO_2 levels in a schematic model as that shown in Figure 6.1.

6.2 PHOTOSYNTHESIS

Dry matter production depends on photosynthesis for which CO_2 is the substrate. Considerations of the effects of increased atmospheric CO_2 on native plants can logically start by considering the effects of elevated CO_2 on photosynthesis. Carbon fixation can be increased directly by an increase in CO_2 concentration in the intercellular spaces of leaves and, indirectly, by an



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Figure 6.1. Major fluxes and controls important in predicting plant growth response and ecosystem response to elevated CO_2 . TNC denotes total nonstructural carbohydrates (source: Strain and Bazzaz 1983).

Table 6.1

The Effects of Long- and Short-Term Exposure to Elevated Levels of CO₂ on the Net Photosynthesis Rates of *Eriophorum vaginatum* Growing in the Arctic Tundra near Toolik Lake, Alaska

Growth CO ₂ Concentration	Measurement CO ₂ Concentration	
	340 ppm	680 ppm
340 ppm	17	28
680 ppm	8	17

Note: $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$.

Source: Tissue (1984).

increase sometimes observed in leaf area. The net dry matter production also may be increased by the decrease in photorespiration at high concentrations of CO₂. Actually the relationship between photosynthesis and CO₂ concentration is rather complex (Lister and Lemon 1976; Figure 6.1).

Short-term exposure to elevated CO₂ has been shown to result in increased photosynthetic rates at all light intensities and, therefore, a decrease in the light compensation point (Mortensen 1984). Because internal CO₂ concentration often limits the photosynthetic rate (Chapter 5 of this volume; Sharkey and Badger 1984), increased CO₂ concentration would be expected to result in higher photosynthetic rates under conditions where the CO₂ supply to the photosynthetic enzyme ribulose biphosphate (RuBP) is limiting, that is, where the RuBP carboxylase/oxygenase is not CO₂-saturated.

RuBP carboxylase/oxygenase responds to both CO₂ and O₂ levels. Photorespiration consumes 30 to 50% of CO₂ fixation by C₃ plants at ambient O₂ levels and CO₂ levels, and decreases as CO₂ increases. At 600 parts per million by volume (ppm) CO₂, photorespiration may drop to about 50% of that at current CO₂ levels. However, even at 1000 ppm there is still measurable O₂ inhibition of gross photosynthesis (Tolbert and Zelitch 1983).

6.2.1 Short-Term Responses of Photosynthesis to Elevated CO₂

Short-term studies indicate that photosynthetic rates increase at ambient CO₂ concentrations above 340 ppm for most species (Strain 1978; Kimball 1983a, 1983b; Du Cloux et al. 1984; Jurik et al. 1984; Tissue 1984). However, some researchers show C₄ species saturated at ambient CO₂ levels near 340 ppm (Osmond et al. 1980; Morison and Gifford 1983).

Short-term exposure to 600 ppm CO₂ in the arctic yields an appreciable photosynthetic response. Field photosynthetic rates of *Eriophorum vaginatum* of 17 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ at 340 ppm CO₂ are increased by 65% to 28 $\mu\text{mol m}^{-2} \text{ s}^{-1}$ at 680 ppm (Figure 6.2, Table 6.1). Other arctic species show similar increases in

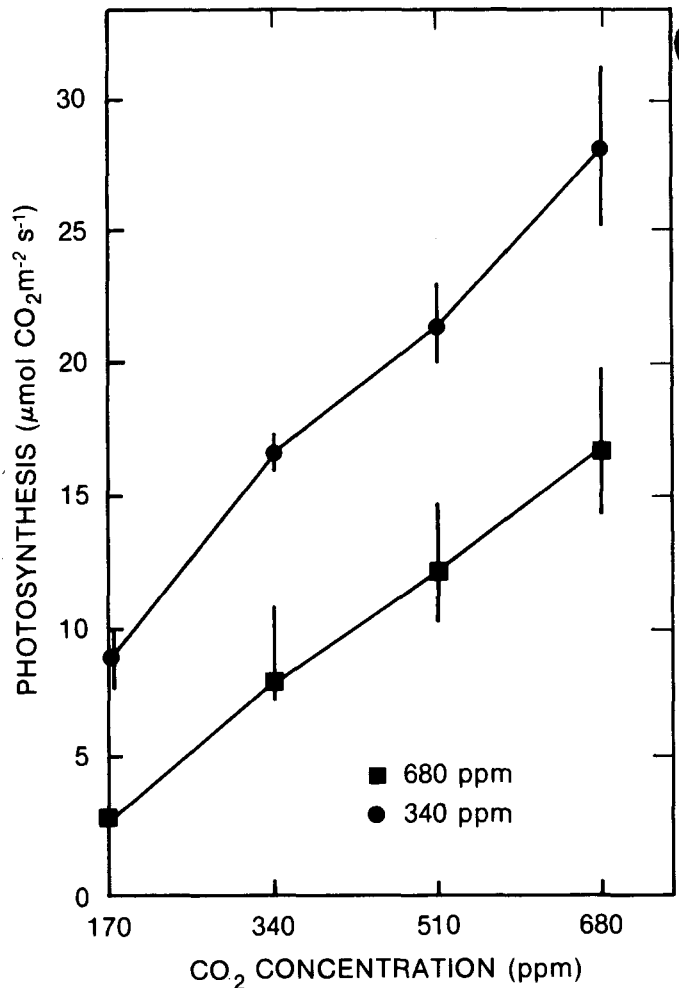


Figure 6.2. Net photosynthetic response (mean $\pm$ 1 SE, $n = 6$) of *Eriophorum vaginatum* grown at 340 and 680 ppm CO₂ when exposed to a range of CO₂ concentrations. Fumigation started during the 5–15 July sampling period.

photosynthetic rates with a short-term increase in CO₂ level (Oechel et al. 1984). Similar results were found for native plants from a cold desert (Strain and Smith 1985).

6.2.2 Long-Term Effects and Acclimation

It is critical to realize that a short-term CO₂ exposure of plants to high levels of CO₂ may overestimate the response to elevated CO₂ for plants grown continuously at the higher CO₂ levels. This may, in part, be due to the fact that other factors limit the CO₂ uptake after extended periods of exposure. Reasons for changes in the CO₂ response of photosynthesis include homeostatic mechanisms within the plant, such as acclimation and end-product inhibition (Mortensen 1984; Tissue 1985; Sasek et al. 1985).

The reasons for the reduction in net photosynthetic potential over long periods of time are not understood. Starch has been observed to accumulate in the chloroplasts of some plants in an increased CO₂ atmosphere (Madsen 1968; Cave et al. 1981; Wulff and Strain 1982; Rogers et al. 1984), indicating that translocation may not be sufficient to remove photosynthate. High starch accumulation in the chloroplasts is correlated with decreasing net photosynthesis (Sasek et al. 1985) and creates an inhibitory feedback on net photosynthesis. This possibility is implied by the dotted line with question mark in the upper portion of Figure 6.1.

The long-term response of photosynthesis to elevated CO₂ appears to depend, at least in part, on the ability of the plants to use an increased supply of photosynthate. This may be maintained when plant growth patterns, environmental conditions, and nutrient availability permit continued development of sinks sufficient to accommodate a higher photosynthetic rate. Where photosynthetic products are produced in excess, end-product inhibition or insufficient substrate availability (e.g., triose phosphate [triose-P]) will limit the potential CO₂ increases in photosynthetic rates.

End-product inhibition of photosynthesis at elevated CO₂ levels has been suggested by several authors (Strain and Bazzaz 1983; Nafziger and Koller 1976; von Caemmerer and Farquhar 1981; Goudriaan et al. 1984). At higher CO₂ there can be a switch in end-products produced, from sucrose to starch. At elevated CO₂ (600–1000 ppm), plants first accumulate sucrose. After reaching a maximum concentration, starch may be synthesized in the leaf in such large amounts that physical damage can occur to the plastids (Cave et al. 1981). According to Walker (1980), this may be due to (1) sucrose synthesis suppression by sucrose end-product inhibition inducing starch formation in the chloroplast; (2) regulation due to insufficient triose-P for the triose-P carrier because of insufficient sucrose phosphate; and (3) stimulation of chloroplast starch synthesis when the triose-P carrier is inhibited.

Goudriaan et al. (1984) assume that tissue carbohydrate levels of 20% will begin to inhibit photosynthesis, and that levels of 25% will completely inhibit photosynthesis. Thus, in their model of plant photosynthesis and growth, the photosynthetic rate decreases as photosynthetic products accumulate beyond that which can be used for growth.

This premise is consistent with data now being accumulated from long-term field experiments in the arctic (Prudhomme et al. 1984; Hilbert et al.¹; Oechel

and Blake-Jacobson²) where whole ecosystem treatment at 340, 510, and 680 ppm showed a decrease in gross primary production (GPP) after 3 weeks of 340 ppm CO₂ treatment. Maximum photosynthetic rates were similar at all CO₂ growth concentrations. Canopy CO₂ conductance decreased with increasing CO₂ treatment concentrations, indicating an adjustment of the photosynthetic machinery to yield equivalent maximum photosynthetic rates at markedly different levels of CO₂. The light utilization efficiency was unchanged by exposure to elevated CO₂, but the canopy conductance at 680 ppm CO₂ decreased to 50% of the 340 ppm value. This result is contrary to the prediction by Goudriaan et al. (1984) that elevated CO₂ treatment will result in higher light utilization efficiencies. The difference may be that Goudriaan et al. assumed no physiological changes in photosynthetic characteristics, whereas in the arctic observations, the effects of prolonged exposures to elevated CO₂ under actual conditions are included.

Tissue (1984) found that *Eriophorum vaginatum* grown in the arctic at Toolik Lake at 340 and 680 ppm CO₂ had similar photosynthetic rates when photosynthesis was measured at the growth CO₂ concentration. However, the photosynthetic sensitivity to ambient CO₂ concentration remained similar (Figure 6.2). Photosynthetic adjustments, therefore, occurred that resulted in similar photosynthetic rates despite the different ambient CO₂ concentrations.

Although higher net photosynthetic rates normally occur in leaves suddenly exposed to elevated CO₂ concentration, the photosynthetic rate often decreases back to a level not significantly different from the original equilibrium level after the tissue is completely adjusted to a new and higher CO₂ concentration. If this plant is quickly exposed to the original ambient level, net photosynthesis drops to a rate appreciably below that which originally occurred at the same CO₂ level. This response is clearly shown in the work of Wulff and Strain (1982) with *Desmodium paniculatum*, a leguminous weed native to the southeastern United States (Table 6.2). The rates of net photosynthesis are nearly equal for plants grown and measured at each of two CO₂ concentrations. Photosynthetic potential, however, was decreased in plants conditioned to 1000 ppm CO₂ as shown by a 35% reduction in photosynthesis when the plants were measured in an atmosphere of 350 ppm. This same effect has been observed in tropical tree species (Oberbauer et al., in press) and in desert grasses and shrubs (Strain and Smith 1985).

¹D. Hilbert, T. I. Prudhomme, and W. C. Oechel. "Responses of Tundra to Elevated Carbon Dioxide Regimes: Analyses of Ecosystem Carbon Dioxide Flux Through Nonlinear Modeling." Manuscript in preparation.

²W. C. Oechel and M. Blake-Jacobson. "Modeling Possible Responses of Arctic Tundra to Elevated Atmospheric Carbon Dioxide." Manuscript in preparation.

Table 6.2
The Effects of Long- and Short-Term Exposures to CO₂ Concentration Changes on the Net Photosynthesis Rates of *Desmodium paniculatum*

Growth CO ₂ Concentration	Measurement CO ₂ Concentration	
	350 ppm	1000 ppm
350 ppm	17.7	24.6
1000 ppm	10.7	16.4

Note: $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$.
Source: Wulff and Strain (1982).

Table 6.3
Effects of Temperature and Long-Term Growth CO₂ Concentration on Net Photosynthesis of Plants from Northern (Quebec) and Southern (Mississippi) Races of *Echinochloa crus-galli*

Temperature °C	CO ₂ Concentration (ppm)			
	Quebec		Mississippi	
	350	675	350	675
21	24	34	21	27
28	30	37	24	33

Note: $\mu\text{mol CO}_2 \text{ mol}^{-2} \text{ s}^{-1} \times 10^{-4}$.
Source: Simon et al. (1984).

Table 6.4
Effects of Long-Term Growth CO₂ Concentration on the ¹¹C Activity (nCi) of the Soluble Carbon Transport Pool of Plants From Northern (Quebec) and Southern (Mississippi) Races at Two Growth Temperatures

Temperature °C	CO ₂ Concentration (ppm)			
	Quebec		Mississippi	
	350	675	350	675
21	703	2139	763	699
28	1137	1622	831	1297

Source: Potvin et al. (1984).

Table 6.5
Effects of Long-Term Growth CO₂ Concentration on the ¹¹C Translocation Velocity in the Leaves of Two Populations of *Echinochloa crus-galli*

Temperature 3pt °C	CO ₂ Concentration (ppm)			
	Quebec		Mississippi	
	350	675	350	675
21	9.62	9.02	7.53	6.95
28	11.95	8.42	11.35	6.87

Note: $\text{m s}^{-1} \times 10^{-4}$.
Source: Potvin et al. (1984).

There is evidence that photosynthate pool size and translocation rates are affected by atmospheric CO₂ supply (Potvin et al. 1984). CO₂ assimilation rates and internal carbon flux dynamics were studied using the ¹¹C isotope production facility at Duke University. Increased atmospheric CO₂ concentration increased the net photosynthesis in two geographic races of *Echinochloa crus-galli*, a weedy C₄ grass, from Quebec and Mississippi (Table 6.3). There was a concomitant increase in carbon in the soluble carbon transport pool

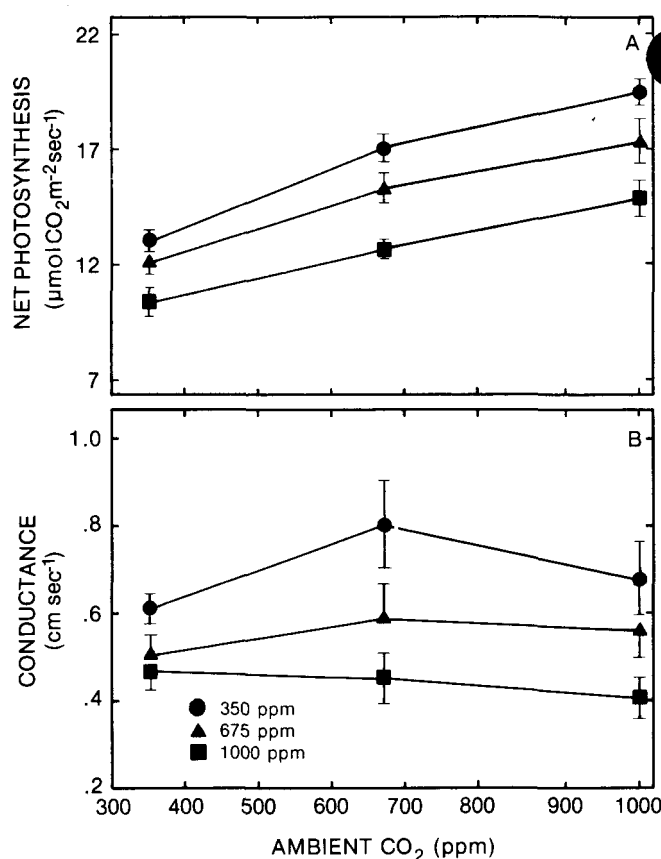


Figure 6.3. Net photosynthesis (A) and stomatal conductance (B) measured at three ambient CO₂ concentrations in plants grown at 350, 675, and 1000 ppm CO₂. Error bars are ± 2 standard errors of the mean (source: DeLucia et al., in press).

(Table 6.4) but a decrease in steady-state translocation velocity (Table 6.5).

It is clear that the reduction in net photosynthesis observed when plants are equilibrated with high CO₂ (Figure 6.3) is not strictly due to stomatal closure (DeLucia et al., in press). In cotton, internal changes occurred that reduced net photosynthesis at all internal CO₂ concentrations (Figure 6.4). One mechanism recently proposed for this reduction in photosynthesis is that it is caused by triose-P sequestering of inorganic phosphorus in the presence of high atmospheric CO₂ concentration which inhibits the triose-P carriers (Sharkey and Badger 1984; see also Chapter 4).

Tissue (1984) speculated that the loss of photosynthetic capacity on long-term exposure to elevated CO₂ might be due to a reduction in RuBP carboxylase/oxygenase levels. Although Tissue did not measure this parameter, this possibility was confirmed by Downton et al. (1980) who found that growth of *Nerium oleander*, a C₃ plant, at 660 ppm CO₂ resulted in a reduction in the amount of soluble protein allocated to carboxylase. This reduction in allocation to carboxylating enzymes has the beneficial

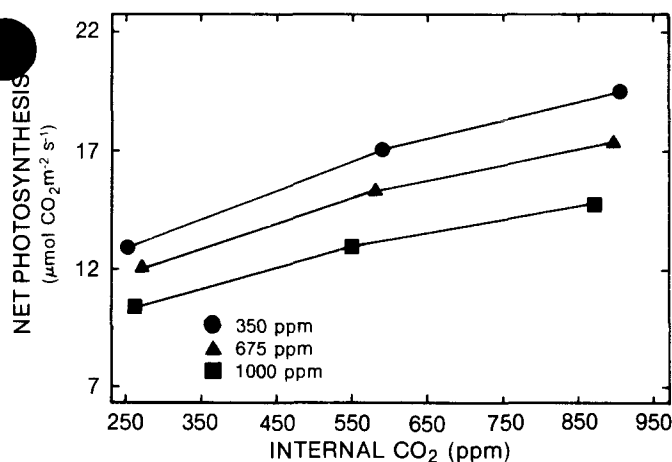


Figure 6.4. Net photosynthesis versus internal CO₂ concentration (C_i) in cotton grown at 350, 675, and 1000 ppm CO₂ (source: DeLucia et al., in press).

effect of potentially allowing a higher concentration of the enzymes used for growth and maintenance. The lower RuBP carboxylase activity has frequently been correlated with reduced photosynthetic rate of plants grown at current CO₂ levels (Hofstra and Hesketh 1975; Frydrych 1976; Imai and Murata 1978; Wong 1979; Downton et al. 1980). This lower RuBP carboxylase activity of plants grown at elevated CO₂ would tend to bring the carboxylation capacity in line with electron transport capacity at high intercellular CO₂ as long as the electron transport capability does not also change (Percy and Bjorkman 1983). Unfortunately, despite the abundant literature on RuBP carboxylase, little is known about its regulation, activation, and reaction mechanisms (Tolbert and Zelitch 1983).

In *Echinochloa crus-galli* (a naturalized C₄ grass), the activity of PEP carboxylase was higher in plants grown at 675 ppm than in plants grown at 350 ppm (Simon et al. 1984). However, Wong (1979) reported earlier that there was no effect of CO₂ enrichment on the activity of PEP carboxylase in *Zea mays* (a C₄ crop species). According to Simon et al. (1984), PEP carboxylase was present in plants from all of the CO₂ treatments in excess of amounts required to support the observed rates of CO₂ assimilation. From these results, it is not possible to conclude that there is an interaction between growth CO₂ concentrations, PEP carboxylase activity, and photosynthetic rates.

6.2.3 Time Courses of CO₂ Response

Little attention has been given to the time course of photosynthetic adjustment to elevated CO₂. Short-term response to elevated CO₂ (minutes to hours) generally

shows an increase in photosynthetic rate at elevated CO₂. As indicated in the previous section, moderate-term exposure (weeks to a few months) often shows a decrease in photosynthetic rate when the plants are returned to current ambient CO₂ levels.

Figure 6.5A shows the percent change in photosynthetic rates for six arctic species after 4 months at 675 ppm compared to control plants grown at 350 ppm CO₂. We see that 8 of the 12 species-treatment combinations showed little increase (< 10%) or an actual decrease in photosynthetic rates at elevated CO₂ compared with contemporary CO₂ levels. This leads to the conclusion that plants grown at higher CO₂ levels rapidly adjust to maintain rates of photosynthesis similar to those at ambient CO₂.

Furthermore, there were negative changes in leaf area so that the total canopy photosynthesis was generally lower at 675 ppm than at 350 ppm CO₂ (Figure 6.5B). However, this situation was changed after 22 months when plants from elevated treatment again increased in photosynthesis on a leaf area and canopy basis (Figure 6.5 [C and D]). This suggests adjustments in various processes with varying time constants: an immediate physiological response, a longer term physiological adjustment (weeks), and a long-term morphological adjustment that allows higher photosynthetic rates per plant. Few studies have been completed of the long-term responses of perennial plants in the field. We cannot predict how native species will respond at this time.

6.2.4 Species and Growth Form-Dependent Responses

Enough data now exist to show that the magnitude of the photosynthetic response to elevated CO₂ varies among native species as it does in agricultural species (Strain 1985; Chapters 4 and 5 [henceforth all chapter references will be to this volume]). However, there is insufficient information to make generalized predictions about the way that different growth forms respond to elevated CO₂. One prediction is that growth forms which are indeterminate and have a large potential sink are more likely to show stimulation of photosynthesis with elevated CO₂ than species that are determinate and have only limited potential for the expansion of carbohydrate sinks. Figure 6.5 (A and C) compares the photosynthetic response of six species from a number of growth forms of arctic plants studied for 4 to 22 months: deciduous shrubs (*Vaccinium uliginosum*, *Betula nana*), evergreen shrubs (*Vaccinium vitis-idaea*, *Ledum palustre*), and sedges (*Eriophorum vaginatum*,

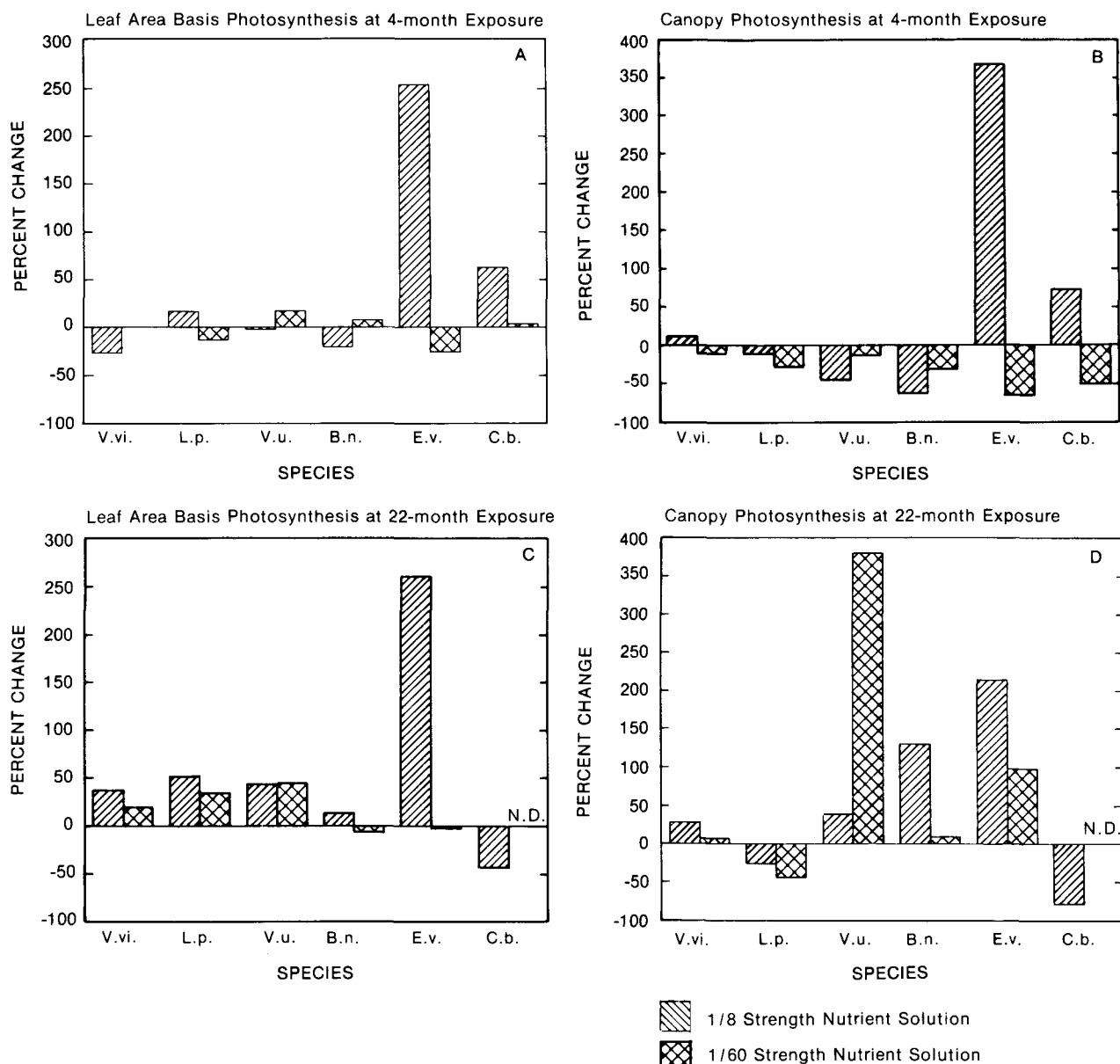


Figure 6.5. Change in photosynthetic rates on a leaf area basis (A, C) and on a canopy basis (B, D) of arctic plants grown and measured at 675 ppm CO₂ compared as a percent to those grown and measured at 350 ppm CO₂. Plants received 1/60 or 1/8 strength nutrient solution in the morning and distilled water in the afternoon. The species studied were *Vaccinium vitis-ictea* (V. vi), *Ledum palustre* (L. p.), *Vaccinium uliginosum* (Vu.), *Betula nana* (B. n.), *Eriophorum vaginatum* (E. U.) and *Carex bigelowii* (C. b.): (A, B) percentage change in photosynthetic rates for plants grown for 4 months at 675 ppm and compared with those grown and measured at 350 ppm.; (C, D) percentage change in photosynthetic rates for plants grown for 22 months and then measured at 675 ppm CO₂ and compared with plants grown and measured at 350 ppm. N.D. represents no data, since C. b. did not survive for the 22 months at 1/60 strength Hoaglands solution.

Carex bigelowii) when they are exposed to elevated CO₂ levels (Oechel et al.).³

The majority of six species increased in photosynthetic rate on a leaf area basis (Figure 6.5 [A and C]). When grown at 1/60 strength nutrient solution,

the evergreen species increased an average of 27% in photosynthetic rates at 675 ppm CO₂. The deciduous species increased an average of 31% in photosynthetic rate. While *E. vaginatum* increased 250% at 675 ppm CO₂ with moderate nutrient fertilization, photosynthesis declined 3% at 675 ppm CO₂ and 1/60 strength nutrient solution. Overall, 8 of the 11 species and treatment combinations increased photosynthesis at 675 ppm CO₂. Of all species and treatments, the average increase

³W. C. Oechel, S. Hastings, and M. Rehse. "Photosynthesis and Growth of Arctic Species Under Elevated Carbon Dioxide with Varying Nutrient Availabilities." Manuscript in preparation.

in photosynthetic rate at 675 ppm CO₂ was 41%. Even excluding *E. vaginatum*, which showed the largest observed stimulation in photosynthesis, the stimulation rate for all other species was still 23% at 675 ppm CO₂.

Leaf area is a very important variable that can affect photosynthetic uptake at elevated CO₂. Increases in leaf area at elevated CO₂ will increase plant uptake and, of course, the opposite is also true. Some arctic species responded to elevated CO₂ with an increase in leaf area, while others such as *L. palustre* decreased (Figure 6.5D). As a result, *L. palustre* showed an overall decrease in whole plant carbon uptake at 675 ppm, even though photosynthesis increased on a leaf area basis. In general, though, the stimulation of photosynthesis was greater on a whole plant basis than it was on leaf area basis (Figure 6.5C versus 5D). Overall, *V. uliginosum*, *B. nana*, and *E. vaginatum* all showed significant increases in canopy photosynthetic rates in at least one of the nutrient treatments. For these species the increase in photosynthetic rate was significant. It is important to note that *V. uliginosum* and *E. vaginatum* showed large increases in canopy photosynthetic rates at low nutrient and high CO₂ levels, conditions hypothesized to yield little photosynthetic response in arctic tundra species. So, even when under low nutrients, where photosynthetic rate increases are small or nonexistent at the leaf level, there may be an appreciable percentage effect at the whole plant level. Combining all species and nutrient treatments, the average overall increase in canopy photosynthesis was 56%. However, not all species responded positively to elevated CO₂ with canopy photosynthesis.

Averaged by growth forms, the evergreen shrubs *V. vitis-idaea* and *L. palustre* showed a moderate inhibition of canopy photosynthesis of about 10%. The deciduous shrubs *B. nana* and *V. uliginosum* had stimulation of photosynthesis of 208%; in the sedges, *E. vaginatum* showed an appreciable increase in canopy photosynthesis of 155% per plant whereas *C. bigelowii* showed a decrease at moderate nutrient treatments of 78%. (Low nutrient treatment *C. bigelowii* did not survive at elevated CO₂.)

We see, in this case, that many species showed an increase in total canopy photosynthetic rate after growth for 22 months at elevated CO₂. The long-term enhancement of photosynthesis averaged 32% for the six species tested. These results indicate that possibly the range of response is varied according to species and growth form. At this time, there is insufficient information for generalization concerning the responses of various growth forms to elevated CO₂.

6.2.5 Nutrient Controls on CO₂ Responses

The photosynthetic response of plants to elevated CO₂ is controlled, at least in part, by nutrient availability. This control could be through the effect of nutrient availability on plant growth and subsequent sink activity (see Chapters 4 and 5).

In medium-term (4-month) experiments with arctic plants, there was greater increase in photosynthetic response to elevated CO₂ with greater nutrient availability. Even after 22 months, photosynthetic rates on a leaf area basis were increased on average 19% at elevated CO₂ under low nutrient treatment and 60% under high nutrient treatment (Figure 6.5C). Plants given a high nutrient treatment, therefore, had a threefold greater increase in photosynthetic rates than did the low nutrient grown plants. For total canopy photosynthesis, excluding *V. uliginosum*, moderate nutrient treatments yielded a greater increase in photosynthesis at 675 ppm CO₂. The average increase in CO₂ uptake at 675 ppm CO₂ was 50% for the moderate nutrient treatment versus 39% for the low nutrient treatment (Figure 6.5D).

There are apparent anomalies in leaf versus canopy photosynthetic rates, a very important CO₂ effect. In this case, *V. uliginosum* was largely responsible for the high average photosynthetic rate at low nutrient levels. In this study, *V. uliginosum* had a very large increase in leaf area with elevated CO₂ at low nutrients (a situation where *C. bigelowii* did not survive) yielding very large increases in canopy photosynthesis at 675 ppm CO₂. Leaf area and population effects must be considered along with CO₂ effects on long-term leaf photosynthetic rates if one is to predict long-term productivity responses to elevated CO₂ accurately.

6.3 RESPIRATION

There is little information on the effect of elevated levels of CO₂ on leaf, stem, or root dark respiration rates (Tolbert and Zelitch 1983). However, most arctic species have markedly increased leaf dark respiration rates when grown at elevated CO₂ (Figure 6.6). Because primary productivity cannot be accurately predicted without knowing carbon losses from dark respiration, this is an area which must receive more attention.

6.4 WATER USE

Increased CO₂ concentration is recognized as having a significant effect on transpiration rates, stomatal conductance, and water-use efficiency ([WUE] measured as the ratio of photosynthesis to transpiration [P:T]).

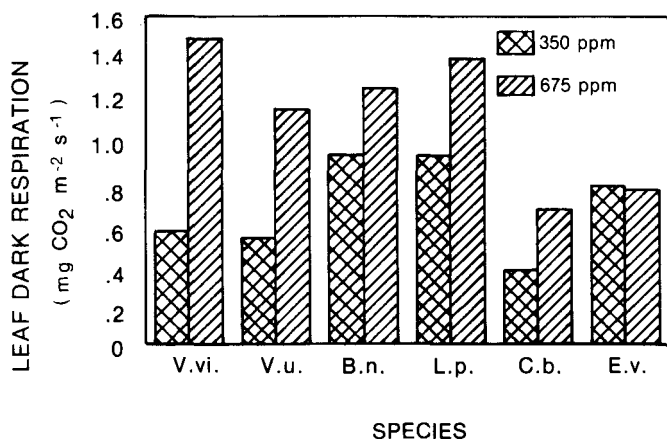


Figure 6.6. Leaf dark respiration at 15°C for six arctic species after 22 months' adjustment to CO₂ treatments of 350 ppm and 675 ppm CO₂. The species studied were *Vaccinium vitis-idaea* (V.vi.), *Ledum palustre* (L.p.), *Vaccinium uliginosum* (V.u.), *Betula nana* (B.n.), *Carex bigelowii* (C.b.), and *Eriophorum vaginatum* (E.v.).

Stomata tend to be more closed at elevated CO₂ thereby reducing conductance to water vapor and transpiration. Because stomatal conductance is a proportionally larger component of total resistance to water loss than it is to CO₂ uptake, the effect of a decrease in stomatal conductance is to decrease transpiration more than photosynthesis, and WUE is thereby increased (Farquhar and Sharkey 1982). Though no data exist, Idso and Quinn (1983) have hypothesized that this effect will result in wide-scale reduction in water use by plants in the arid southwest of the United States and that these savings in water will result in major changes in vegetation boundaries.

Whereas plants generally respond with higher WUE at higher CO₂ levels, this is not always the case. Tissue (1984) found similar WUE for *E. vaginatum* growing at 340, 510, and 680 ppm. In addition, WUE calculated as carbon fixed per water transpired, P:T per unit leaf area, will not give the total water consumed unless total leaf area and the pattern of WUE through the canopy are also known (Kimball and Idso 1983). Of eight species measured by Strain and Smith (1985), all but one species (*Eurotia ceratoides*) increased in WUE. This may be a very important observation because *E. ceratoides* is a highly desirable browse species in the Great Basin sagebrush ecosystem.

Stomata are sensitive to a number of factors including atmospheric humidity, tissue water potential, and internal CO₂ concentration (C_i) of the leaf. As atmospheric CO₂ concentration (C_a) increases, C_i will also tend to increase, possibly resulting in decreased stomatal conductance. Short-term exposure to elevated ambient CO₂ usually results in increasing C_i and a pronounced decrease in stomatal conductance

(g_s). Interestingly, the stomatal sensitivity to changing C_a or C_i decreases with decreasing vapor pressure deficit (VPD). Morison and Gifford (1983) found a single relationship between C_i and measured stomatal conductance for two C₃ grasses (rice and phalaris) and two C₄ grasses (*Paspalum* and maize); the C₃ and C₄ species maintained similar C_i to C_a ratios at low VPD (0.8 to 0.9), but these declined differentially with increasing VPD. At high VPD, C₃ plants had a much higher C_i-to-C_a ratio (0.7) than did C₄ plants (0.5) (Figure 6.7).

These data indicate that stomatal conductance will decrease in both the C₃ and C₄ species with increasing atmospheric CO₂. However, stomata of the C₄ plants are not necessarily more sensitive to CO₂ concentration than are those of C₃ plants. Only at larger VPD do C₄ plants show a significantly greater sensitivity to CO₂ than do C₃ plants. Any limitation in photosynthesis with a concomitant increase in C_i (because of factors such as end-product inhibition or triose-phosphate limitation) should result in lower stomatal conductances.

Partial stomatal closure with elevated CO₂ is common but not universal. Although many studies have shown some level of stomatal closure (Pallas 1965; Tolley and Strain 1985; DeLucia et al., in press), studies with other species have noted little if any effect (Hurd 1968; Folk et al. 1979; Tissue 1984; Tolley and Strain 1985; Potvin and Strain 1985). This implies that the magnitude of the response may be species-specific and may also be environmentally controlled. Tissue (1984) could not demonstrate long-term effects of CO₂ on

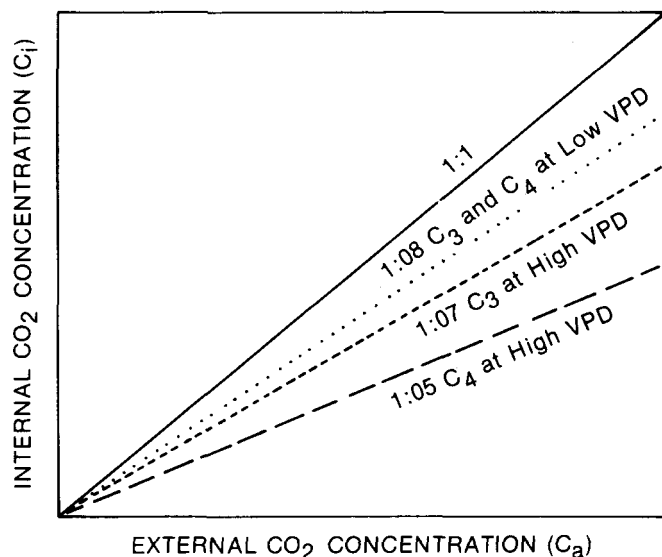


Figure 6.7. Expected change in C_i for a given change in C_a for C₃ and C₄ plant species at high and low vapor pressure deficit (VPD) (source: Morison and Gifford 1983).

transpiration rate or on stomatal aperture of an arctic edge. His conclusion was that for plants growing in an environment that is not water-limited, stomatal response to elevated CO₂ may be minimal. Potvin and Strain (1985) found no consistency in stomatal closure in two C₄ grass species from low water stress habitats of eastern North America.

Tolley and Strain (1984b) evaluated the effect of elevated CO₂ on WUE of seedlings of *Pinus taeda* and *Liquidambar styraciflua* under varied conditions of water availability and light level. They found that for both species, elevated CO₂ improved WUE at all light and moisture treatments. Under water stress and elevated CO₂, both species maintained higher tissue water potentials than plants grown under moisture stress at normal CO₂ levels. Therefore, during 14 days of water limitation, plants growing at elevated CO₂ had less water stress, higher WUE, and similar photosynthetic rates compared with those growing at current CO₂ levels. Turgor pressure of wheat was shown to remain above zero longer into a given drought cycle in plants growing in enriched CO₂ atmosphere (Sionit et al. 1981d). If this adjustment also occurs in native plants, a mechanism for partially explaining increasing drought tolerance under high CO₂ levels would be at hand.

As a result of the processes mentioned above, the transpiration rates of most plants grown at current CO₂ levels decrease after short-term exposure to elevated CO₂ (Pallas 1965; Regehr et al. 1975; Goudriaan and van Laar 1978; Morison and Gifford 1983). Transpiration rate is also decreased after long-term exposure to elevated CO₂ in some plants (Egli et al. 1970; Carlson and Bazzaz 1980), but not in all plants (Tissue 1984). Plants from mesic environments would be least likely to show a reduction in transpiration with elevated CO₂ levels.

6.5 GROWTH RATES

The ultimate fate, in terms of the final site of deposition of photosynthetically fixed carbon within a plant, is a function of the genetics of the plant involved, environmental conditions prevailing at the time, and phenological condition of the plant. Possibilities for carbon allocation into plant structure are diagrammed in Figure 4.5 in Chapter 4. Carbon fixed in photosynthesis may pass through a series of biochemical reactions that produce various metabolic or growth compounds. Whether the carbon remains in the leaf, near the site of original carboxylation, or moves out of the leaf to

Table 6.6
Effects of Atmospheric CO₂ Concentration on Flowering in First-Year *Chrysothamnus visidiflorus* Seedlings

CO ₂ Concentration During Growth (ppm)	Number of Inflorescences Per Plant	Dry Weight of Inflorescences Per Plant(g)
340	1.8	0.7
680	4.4	2.2

Source: Strain and Smith 1985.

become part of another organ system, is determined by factors mentioned above. Figure 6.8 shows the entire spectrum of possible deposition sites for a given atom of carbon. Pathways of carbon flux are indicated by solid lines in the diagram, while points where rates and direction of flow are controlled are shown by dashes.

Increased allocation of carbon to reproductive structures following elevated CO₂ may increase the reproductive potential of plants in natural ecosystems. The inflorescence number per plant and the weight of flowers produced per plant increased 2.4- and 3.1-fold, respectively, in first-year seedlings of the Great Basin shrub *Chrysothamnus visidiflorus* (Table 6.6) (Strain and Smith 1985). This response has also been observed in crop plants. Sionit et al. (1981c) observed 66% more seeds on wheat grown at 675 ppm than on plants grown at 350 ppm CO₂.

Increased photosynthetic rates that may occur in response to elevated CO₂ levels may result in greater production of carbohydrates that are then available for growth or reproduction. Where carbohydrates are limited, this increase in the pool of total nonstructural carbohydrates will result in increased growth. Relative growth rate may increase under elevated CO₂ even at low light intensities. Mortensen (1984) found that the relative growth rate of *Chrysanthemum morifolium* increased at 1600 ppm CO₂ versus 330 ppm CO₂ at all light levels between 44 and 395 $\mu\text{mol m}^{-2} \text{s}^{-1}$. The mean transient of relative growth rate was 16%. Where the ability to use carbohydrates is limited by nutrient supply, or other conditions limit growth, reserve carbohydrate levels may increase until they reach a maximum concentration at which photosynthetic rate is suppressed by end-product inhibition. At this point, photosynthesis will be inhibited (Goudriaan et al. 1984), and further increases in CO₂ would not be expected to yield increases in growth rate. When plants already have an excess of carbohydrate, little increase in photosynthetic rate might be expected.

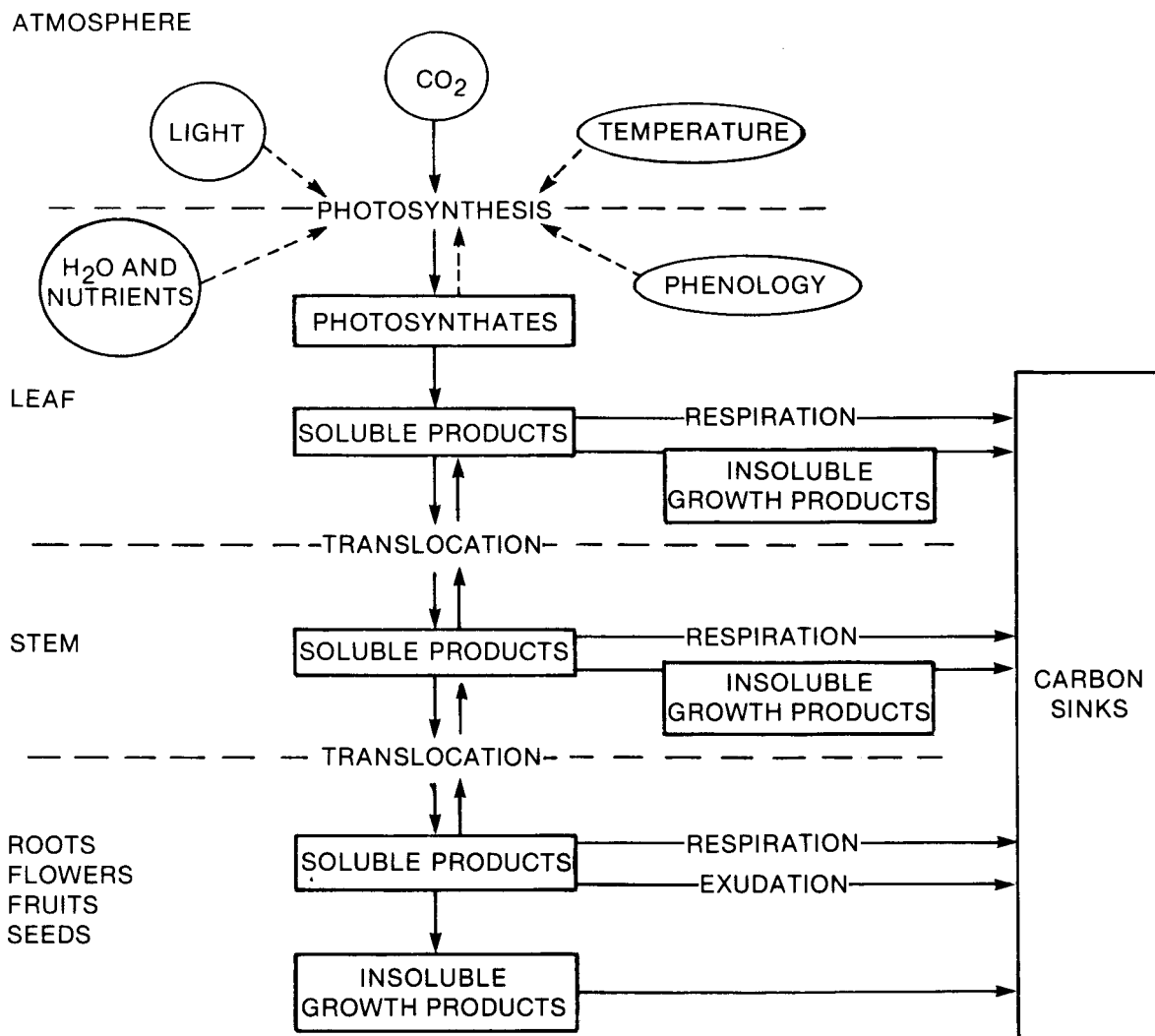


Figure 6.8. Diagram of carbon flow and utilization in plants. Of specific interest is the question of inhibitory feedback of photosynthate production on carbon assimilation and questions of carbon distribution and allocation within plants as affected by atmospheric CO_2 enhancement. Also of interest is the relationship between atmospheric CO_2 concentration and carbon losses from plants. The carbon eventually leaves the plant in respiration, seed and fruit dissemination, root exudations, herbivory, senescence, organ abscission, or death.

already have an excess of carbohydrate, little increase in photosynthetic rate might be expected.

One area of concern in ecological studies is predicting the potential growth responses for plants in an ecosystem context where nutrients may limit the potential for growth and where changes in WUE may alter patterns of moisture limitation on growth. Further, increased CO_2 does not necessarily lead to increased growth. Plant processes using assimilated CO_2 have evolved at lower CO_2 levels. With increasing levels of CO_2 , sucrose supply may increase and nutrient deficiencies may severely limit growth (Tolbert and Zelitch 1983). Native plants simply may not be adapted to using these higher levels of sucrose supply. The growth response to elevated CO_2 is a very basic and

necessary fact to determine for a number of native species from diverse habitats.

6.5.1 Leaves

The total photosynthesis of a plant is the product of (photosynthetic rate) (leaf area) (time). Therefore, the amount of leaf area on a plant and the time frame in which the leaf area is active in photosynthesis are important parameters of plant productivity. This unit is termed leaf area duration (LAD) in studies of plant structure and productivity (Kvet et al. 1971).

The major portion of photosynthesis on Earth occurs in the leaves of terrestrial vascular plants (Odum 1971; Whittaker 1975). Consequently, the carbon

compounds available for tissue formation and growth are readily available in leaves after they become photosynthetic. Initial cell divisions and growth of leaves from leaf primordia in buds of vegetative plants, however, require the translocation of carbohydrates and essential mineral nutrients from elsewhere in the plant. Initial leaf growth in an embryonic plant is from mass and energy stored in the seed and from photosynthesis of cotyledons in some species. Therefore, increased atmospheric CO₂ concentration can affect leaf growth in two primary ways: as a result of larger seeds with greater storage (Wulff and Miller-Alexander 1985) and as a result of higher photosynthetic rates in seedlings and adults.

Leaf area may also increase in rate of development and in total amount in plants developing under CO₂ enrichment (Wong 1980; Sionit 1983). Even slight gains in the rate of leaf production will significantly increase the photosynthetic area during the exponential phase of plant growth (Baker and Enoch 1983). The increased leaf area allows increased net photosynthesis, which becomes compounded into significantly more leaf area per plant in some species (Sionit 1983; Tolley and Strain 1984a) but not in others (Tolley and Strain 1984a).

Increases in leaf area might be expected both as a result of higher photosynthetic rates, and hence more photosynthate to support leaf growth, and because of higher cell turgor pressure that could result in more leaf area under a given precipitation regime.

The production of both leaf area and number of leaves is explained in detail in Chapter 4 of this volume. In consideration of the importance of accelerated leaf growth at elevated CO₂ to native plants, it must be kept in mind that some species respond by producing more leaf area per plant at faster rates in high CO₂ atmospheres than in normal atmospheric CO₂ levels, whereas other species have shown relatively little or no enhancement of leaf relative growth rate (Tolley and Strain 1984a). *E. vaginatum* growing in the arctic at Toolik Lake had similar leaf growth and total leaf area in all CO₂ treatments (Figure 6.9, Tissue 1984). Because all species do not respond equally, differential competitive potentials will likely occur and influence future community and ecosystem development (Chapter 7).

Enhanced leaf development can be a problem if the evaporative leaf area increases relatively more than the absorptive root area. In this case, water stress may occur earlier and become more extreme (Baker and Enoch 1983). This issue has not been adequately examined, but Gifford (1979a, 1979b), Sionit et al. (1980), and Sionit et al. (1981d) found that the net effect of increased leaf area but decreased stomatal conductance improved the water status of

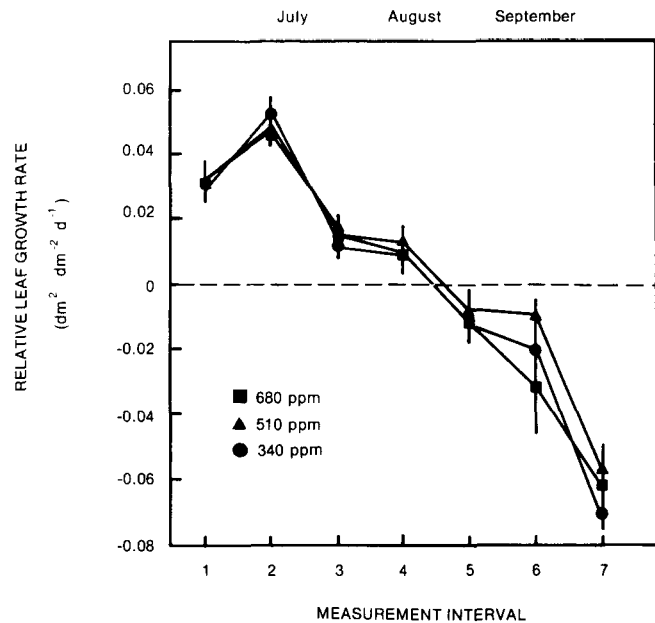


Figure 6.9. Relative leaf growth rate (RLGR) of *Eriophorum vaginatum* growing under three CO₂ conditions at Toolik Lake, Alaska (source: Tissue 1984).

wheat. Tolley and Strain (1984b, 1985) likewise found that the net effect of high CO₂ levels on 2-week-old seedlings of *Liquidambar styraciflua* and *Pinus taeda* was an improvement in water status for both species. *L. styraciflua*, however, responded relatively more, leading to the conclusion that *L. styraciflua* seedlings may gain a competitive advantage over the *P. taeda* seedlings with respect to water. Bazzaz and Carlson (1984) demonstrated differential species response to water stress at elevated CO₂ in an assemblage of old field annual plants. They concluded that *Polygonum pensylvanicum* will contribute more to community production as CO₂ levels increase, whereas *Amaranthus retroflexis* will contribute less. The greater leaf area development of *Carex bigelowii* relative to other species in the tundra at elevated CO₂ causes one to predict its increased prominence as atmospheric CO₂ rises.

6.5.2 Stem Growth

Plants grown under high CO₂ concentrations frequently show higher rates of height growth (Sionit et al. 1985). Perennial plants (Sionit et al. 1985) and annual plants with indeterminate growth (Paez et al. 1984) became taller at elevated CO₂ concentration than at normal concentrations. Determinate annuals have been shown to increase in height at a faster rate under increased CO₂, but the final height attained is not found to be affected (Paez et al. 1980, 1984). For many temperate plants, however, rates of height growth and canopy development in the spring may be more important than

final size in determining competitive success. Plants that start growing earlier and exceed their competitors in height will interfere with light penetration to the shorter, slower growing plants.

In addition to increasing plant height, growth under elevated CO₂ increases the rate of node formation (Anderson 1976; Paez et al. 1980). However, this effect varies by species. *L. styraciflua* produced more branches when grown at high CO₂, but *P. taeda* did not (Sionit et al. 1985). Thus, again we see an important growth response to elevated CO₂ where the magnitude is species specific.

6.5.3 Leaf Area and Number of Branches

Leaf area index ([LAI], the ratio of total leaf area [m²] to the total land area covered [m²]) is an important characteristic of ecosystems. Typical crops have LAI of 3 to 6, but corn may reach an LAI of 9 (Gifford 1982). Very shade-tolerant forest species (e.g., certain coniferous forests) may reach an LAI of 11, but most natural ecosystems' LAIs range from 2 to 6, under current environmental conditions (Larcher 1980).

As leaf area per shoot and the number of branches increase in response to elevated CO₂, the total number of leaves per plant increases, and the LAI may also increase. If the LAI increases and, particularly, if photosynthetic quantum efficiency is greater at high CO₂ concentration (Ehleringer and Bjorkman 1977), net photosynthesis may increase in ecosystems. CO₂-induced changes in LAI will affect light penetration into ecosystems (Strain 1985). As LAI changes, the distribution of radiation received at any given level in the canopy will change. To our knowledge, there has been no ecological study of this possible ecosystem response to CO₂ enrichment.

6.5.4 Carbon Allocation to Roots and Shoots

Plants with large carbon storage capacity in belowground tissue (e.g., white potato, sweet potato, sugar beet, radish) respond greatly with increased belowground production when CO₂ increases in the atmosphere (Chapman and Loomis 1953; Bhattacharya et al. 1985; Sionit et al. 1982; Knecht 1975). The storage organs provide active sinks for the translocation of carbohydrates away from the sites of formation in the leaves and there is no end product inhibition of photosynthesis (Clough et al. 1981). This results in a variable allocation to storage organs depending on carbohydrate supply. From greenhouse and growth chamber studies such as those cited above, we can predict that native species with bulbs, corms, rhizomes,

and tubers will respond similarly and most dramatically as CO₂ increases. Few studies have been made of native species in this regard, however, so this prediction remains speculative at this time.

Studies of root growth show that with increasing atmospheric CO₂ most plants allocate proportionally more of the extra carbon belowground, causing an increase in root-to-shoot ratios (Acock et al. 1983; Rogers et al. 1983). Several arctic plant species show a higher root-to-shoot ratio when grown at moderate or low (1/8 or 1/60 strength) nutrient solution for moderate time periods (4 months) or at moderate nutrient levels for long periods of time (22 months). Only with low nutrients for long exposures did the root-to-shoot ratio decline at elevated CO₂ (Oechel et al.⁴, Figure 6.10). This is the reverse of that which might have been predicted a priori. Other species have also been shown to produce relatively larger shoots than roots as the level of CO₂ increased, inducing a decreasing root-to-shoot ratio (Tolley and Strain 1984b). Differential allocation of carbon to various organs while atmospheric CO₂ increases will cause changes in competitive behavior that will be very important in natural ecosystems. Plants that produce relatively larger roots may gain an advantage in obtaining soil moisture and nutrients. On the other hand, an increased root-to-shoot ratio changes the balance of respiring to photosynthesizing tissue. If total plant respiration increases faster than total plant net photosynthesis, plant carbon balance will be affected negatively. No field and few laboratory studies of this problem, in the context of elevated CO₂, have been attempted; therefore, the matter remains highly speculative at this time.

6.5.5 Flower and Seed Production

Because flowers, fruits, and seeds have great economic importance, much research has been done on the response of these reproductive structures to increases in atmospheric CO₂. Agronomists and horticulturists realized long ago that increasing the CO₂ content in greenhouses caused many plant species to produce more reproductive structures and to produce these structures earlier in the growth cycle (Wittwer and Robb 1964; Calvert 1972; Kimball 1983a, 1983b).

One of the important causes of the formation of more reproductive structures is an increase in the number of branches, as described in Section 6.5.2. The production of more nodes and growing tips will give rise to more flowers if appropriate environmental and hormonal signals are present. Seed size may increase in plants growing in an enriched CO₂ atmosphere (Sionit et al. 1981c) but decreasing seed size has also been observed (Wulff and Miller-Alexander 1985). Although

⁴Ibid.

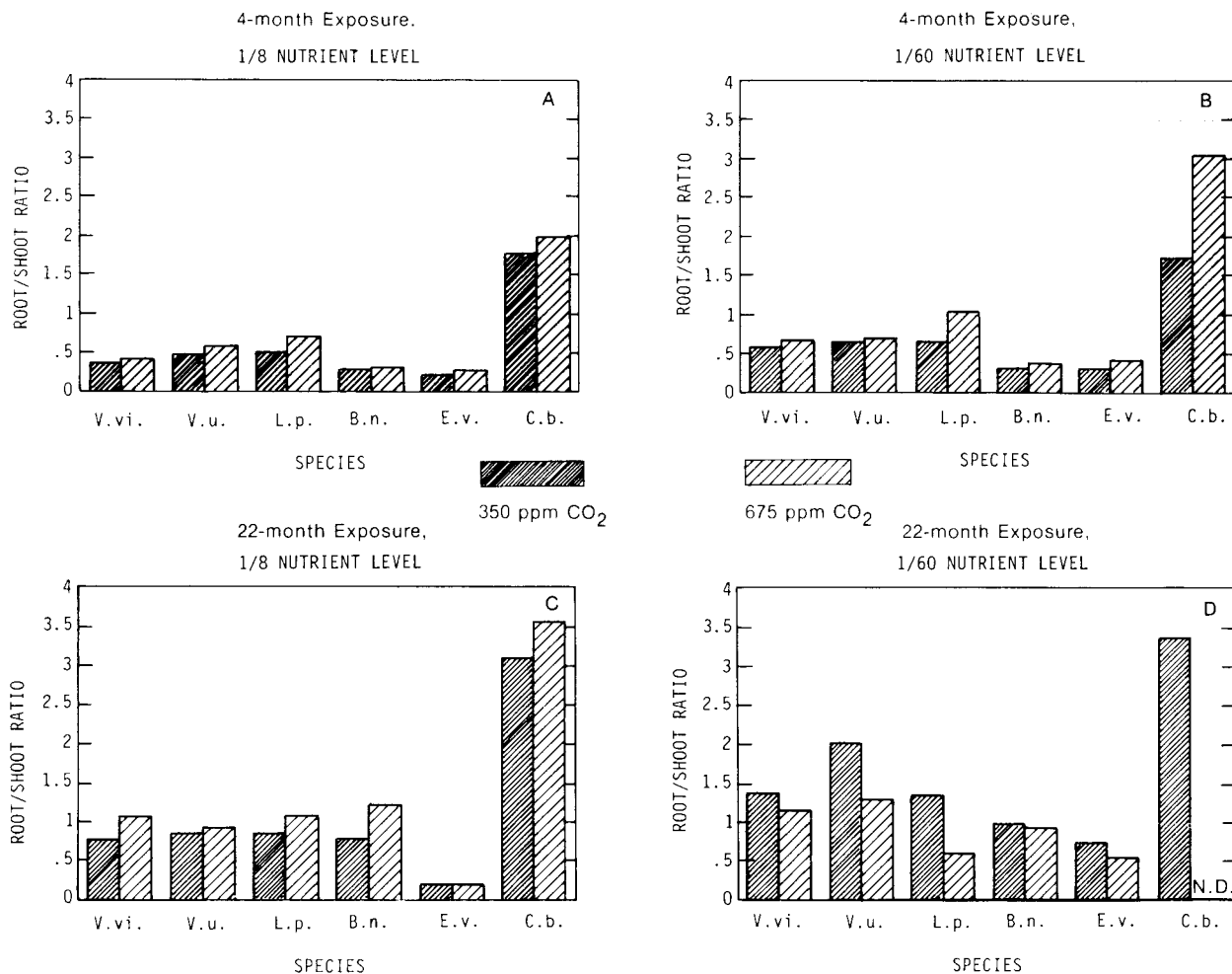


Figure 6.10. Root-to-shoot ratios of arctic plants following moderate (4 months) and long-term (22 months) exposure to elevated CO₂ at moderate (1/8 strength nutrient solution) and low (1/60 strength nutrient solution) nutrient availability. The species studied were *Vaccinium vitis-idaea* (V.vi.), *Vaccinium uliginosum* (V.u.), *Ledum palustre* (L.p.), *Betula nana* (B.n.), *Eriophorum vaginatum* (E.v.), and *Carex bigelowii* (C.b.).

larger seeds may imbibe water more slowly, thereby germinating later, larger seeds can also produce more vigorous seedlings that develop faster and produce significantly more leaf area in the first few days of development (Wulff 1982). On the other hand, large seeds may not disperse as readily. Each species responds in its own characteristic way (Rogers et al. 1980; Wulff and Miller-Alexander 1985), leading to the possibility of differential species response and possible plant community effects.

From Kimball's (1983a) summary, we can conclude that most plants will increase reproductive output as CO₂ increases. There is a great range in the specific nature of these responses, however, and we must conclude that native species will respond similarly to agronomic species. Again, differences among species will provide the potential for changing reproductive success in natural ecosystems.

In the most complete study accomplished to date, Zangerl and Bazzaz (1984) showed that reproductive potential increased in some species as CO₂ increased. The species *Polygonum pensylvanicum* produced more seed as the CO₂ increased; *Chenopodium album* did not. Four other species from an old field ecosystem (*Abutilon theophrasti*, *Ambrosia artemisiifolia*, *Setaria faberi*, and *Amaranthus retroflexus*) were intermediate, responding under some nutrient levels, but not others. Billings and Billings (1983) found that high CO₂ levels decreased seed production and delayed flowering in both arctic and alpine populations of *Saxifraga flagellaris*.

Reproductive success is essential for species survival in a natural ecosystem. Even a very strong competitor in vegetative growth and persistence will not survive over the long run without some recruitment of new individuals into the community. The production and dissemination of seeds under conditions of elevated CO₂

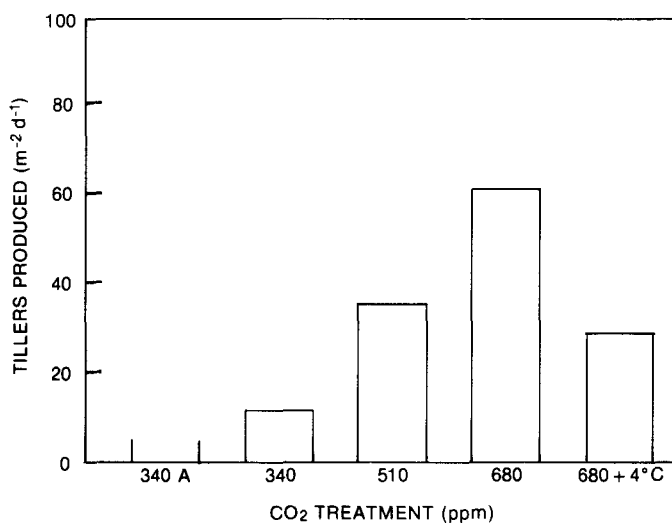


Figure 6.11. Rate of tiller production in *Eriophorum vaginatum* growing for 41 days under control (no chamber enclosure) and three CO₂ and two temperature conditions (ambient, ambient+4°C) at Toolik Lake, Alaska (source: Tissue 1984).

will be important in determining the final composition of plant communities, even when vegetative reproduction is predominant. See Chapter 7 of this volume for a more detailed discussion of this issue.

6.5.6 Asexual Reproduction and Tillering

One of the most important effects of an increase in CO₂ levels may be an increase in tillering (branching) rates. This may occur even when there is a relatively small increase in photosynthetic rates and growth rates. In *Eriophorum vaginatum*, for example, the tillering rate increased almost sixfold at 680 ppm compared with 340 ppm CO₂ (Figure 6.11) despite relatively insignificant changes in other growth parameters (Tissue 1984). Similar changes in tillering rates have been reported for agronomic species (Sionit et al. 1980). Whereas height growth of wheat is little affected by growth at elevated CO₂, the number of tillers and heads produced is greatly increased (Figure 6.12). Increasing atmospheric CO₂ concentration, higher nitrogen, and 24-hour light have been shown to generate tillers in a unicum wheat variety that was previously assumed to be genetically incapable of multiple tiller production⁵. Apparently, the lack of tillering under current CO₂ levels is due to carbohydrate limitation. Increasing the carbohydrate supply by growing plants under more elevated CO₂ concentrations and better environment apparently activates meristem production and development leading to tiller appearance. The effect of increased tillering with the consequent increase in leaf area and seed production could have profound

effects in some populations. Increased allocation to asexual reproduction is not universal, however. Where mean dry weight of stolons per plant increased in arctic populations of *Saxifraga flagellaris* at elevated CO₂ (750 ppm), stolon weight decreased in alpine populations (Billings and Billings 1983). This points out the variability of response patterns and the potential importance of ecotypic differences in response to elevated CO₂.

6.5.7 Restrictions on Growth Response

Whether or not total growth is increased by elevated CO₂ will depend in part on a number of factors including end product inhibition, size of available sinks, and nutrient availability. Mortensen (1983) found that total growth in *Chrysanthemum* was increased by 24% after 4 weeks at 1000 ppm compared with growth at 330 ppm CO₂. Significantly, intermittent short-term (45 minutes) exposure to elevated CO₂ on alternate days gave the same growth response. He did not investigate whether these results were due to growth response, to effects on the photosynthetic or translocation system, or, whether in fact, shorter periods of exposure were sufficient to saturate the plants' requirement for carbohydrates. This latter mechanism seems most likely.

6.6 EXUDATION OF CARBOHYDRATES FROM ROOTS AND OTHER ORGANS

Evidence for increasing photosynthesis and plant growth in response to atmospheric CO₂ enrichment was presented in Chapters 4 and 5 and in previous sections. In addition to increased growth associated with increased carbohydrate supply, it has been proposed (Luxmoore 1981) that some of the extra carbon might be lost from roots as soluble exudates. Root exudates are common (Rovira 1969) and are known to have chemical and biological effects in the soil (Beck and Gilmour 1983; Kepert et al. 1979; Kloss et al. 1984). Increasing atmospheric CO₂ can raise carbohydrate levels in leguminous plants and enhance symbiotic nitrogen fixation (Hardy and Havelka 1973; Finn and Brun 1982).

Luxmoore (1981) presented a hypothetical scheme for how increasing atmospheric CO₂ might affect soil processes and further enhance plant productivity (Figure 6.13). Luxmoore hypothesized that any increase in root exudation could lead to increased nonsymbiotic nitrogen fixation, increased mycorrhizal activity, increased soil microbial growth and nutrient retention, and possible increased rates of mineralization. Additionally, if mycorrhizal hyphae are produced because of extra carbon supplies to the root, and if they extend out in the soil, thereby increasing absorptive area, the water

⁵B. Buxley. Personal communication, November 12, 1985.

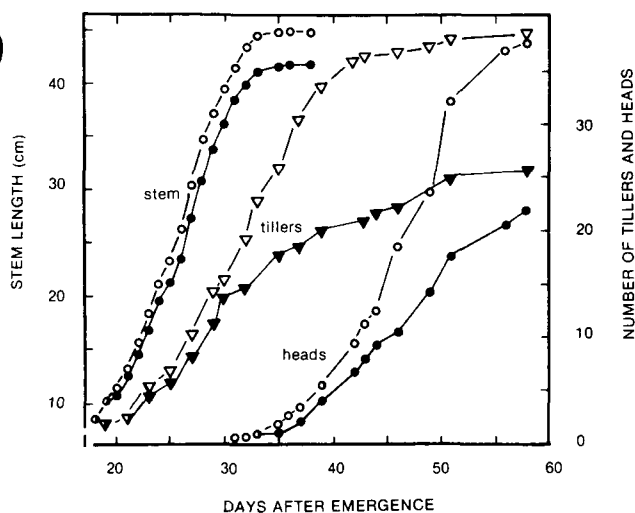


Figure 6.12. Growth of main stem and number of tillers and heads produced on wheat growing in two CO₂ concentrations (350 and 1500 ppm) under well-watered conditions in the controlled environment chambers of the phytotron (source: Sionit et al. 1980).

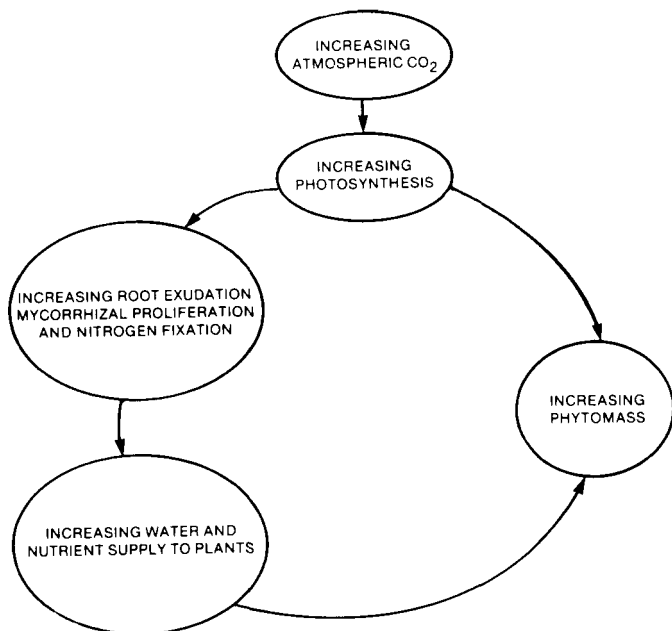


Figure 6.13. Conceptual model of vegetation response to increasing CO₂ (source: Luxmoore 1981).

and nutrient supply to the host may be enhanced. The net effect might be an increase in plant growth via the mechanism diagrammed in Figure 6.8.

Increased net photosynthesis will not necessarily lead to increased translocation of carbon to the roots. Allocation of carbon to plant organs depends on (1) the chemical partitioning of current photosynthate between sucrose and starch in the leaves; (2) the efficiency of loading carbohydrates into phloem; and (3) especially for the relative strengths of the various competing sinks (e.g., other growth points, wood, flowers, fruits, seeds), for the translocatable photosynthate.

Carbon transport velocity decreased with increased CO₂ in *Echinochloa crus-galli* (Potvin et al. 1984). On the other hand, total export of photosynthate was greater at 720 ppm than at 320 ppm CO₂ in *Lolium tremulentum* and *Sorghum sudanense* (Wardlaw 1982). Most evidence to date suggests that root growth will increase with increasing atmospheric CO₂ (Kimball 1983a). If this occurs, it will be important to understand the effect of increased root growth on plant competition, community composition, and nutrient uptake.

A wide variety of organic compounds are exuded from plant roots including carbohydrates, amino acids, organic acids, nucleotides, and enzymes (Rovira 1969). Among the organic acids, citric, fumaric, malic, oxalic, succinic, and acetic acids are important root exudates (Smith 1969 and 1976; Kloss et al. 1984).

The total amount of carbon released in root exudates ranges from small releases of 1.6–2.9% of total root carbon in *Vicia* sp. (Harmsen and Jaeger 1963) to larger values of 12–18% of all photosynthetically fixed carbon (Barber and Martin 1976). The differences among species and the environment at the time of measurement seem to be involved in creating this large range. The mechanisms of root exudation range from simple diffusion along concentration gradients (Boulter et al. 1966) to active metabolically mediated releases (Kuo et al. 1982). In addition, there is considerable material released by tissue sloughed by growing roots and by root decay. This may also be a factor in allelopathic reactions. These mechanisms respond in different ways to environmental factors, probably explaining differing observations of environmental effects.

There is no direct evidence yet available to describe the effect of atmospheric CO₂ concentration on root exudation. Other factors that increase net photosynthesis (light, temperature, and mineral nutrition) have been correlated with increasing root exudation (Rovira 1969; Hale et al. 1971), leading Luxmoore (1981) and Rosenberg (1981) to propose increased root exudation with increased atmospheric CO₂ concentration.

6.7 GROWTH AND PRODUCTIVITY

Very few experiments have been attempted that would yield information on the responses of unmanaged ecosystems to elevated CO₂ including estimates of growth and productivity. *Eriophorum vaginatum* growing in the tussock tundra of Alaska (Tissue 1984) showed no increase in relative growth rate or total production of leaf area at 510 or 680 ppm CO₂ when compared with 340 ppm. The conclusion was that the growth rate of *E. vaginatum* was limited by factors other than carbohydrate availability (probably nutrients), and therefore the lack of a growth response was predictable.

Simulation modeling and field experimentation have indicated that the growth of *E. vaginatum* is limited more by nutrient than carbohydrate availability (Miller et al. 1984; Shaver et al., in press). As mentioned above, the tillering rate did increase in *E. vaginatum* under elevated CO₂ and, in time, this might have a stimulatory effect on productivity. Of all of the arctic species examined, only *Carex bigelowii* showed an increase in growth with an increase in CO₂ concentration. Simulations indicate that this result may be due to better nutrient status of *C. bigelowii* (Oechel and Blake-Jacobson)⁶.

6.8 PHENOLOGY AND SENESCENCE

Elevated CO₂ has been shown to affect the phenology and senescence of plants. Annual plants may develop more quickly under elevated CO₂, reaching full leaf area, biomass, and flower and fruit production sooner than plants at ambient CO₂ (Paez et al. 1980, 1983, 1984). These plants may not be more productive than those at normal CO₂, but maximum biomass is reached at an earlier time (Paez et al. 1980), possibly avoiding periods when drought stress becomes severe. In a competitive situation, early leaf and seed production could shift the population dynamics and competitive relationships (Bazzaz and Carlson 1984). St. Omer and Horvath (1983) demonstrated that three species of winter annuals from the California chaparral developed faster, completed their life cycles earlier, and died earlier as atmospheric CO₂ increased.

There is, however, also evidence of delayed senescence of some species under elevated CO₂. Delayed leaf senescence has been observed in soybean (Cooper and Brun 1967; Hardy and Havelka 1975). The arctic cotton grass, *Eriophorum vaginatum*, retained maximal photosynthetic capacity later into the fall when grown at high CO₂ (Tissue 1984). Delayed leaf senescence potentially extends the growing season and increases production. However, in arctic and temperate ecosystems it may also subject plants to greater risk of tissue damage by frost before removal of organic and inorganic nutrients prior to leaf abscission.

6.9 TISSUE QUALITY AND CHEMICAL COMPOSITION

Relatively little is known of the effects of elevated CO₂ on the chemical content and tissue quality of plants in unmanaged ecosystems. More CO₂ may result in the greater production of pyruvate. This could, in turn, result in increased acetate synthesis in the mitochondria,

leading to synthesis of fatty acids and other hydrocarbon synthesis in the chloroplast (Tolbert and Zelitch 1983).

It is reasonable to expect that in nutrient-limited environments, carbon-to-nitrogen ratio may increase with an increase in CO₂, while macro- and micronutrient contents may decrease. Increases in lignin and structural carbohydrates and storage carbohydrates might be expected as has been reported along gradients of decreasing nutrient availability (Chapin 1980). The leaves of plants growing in elevated CO₂ have been shown to have higher carbohydrate levels, higher C:N ratios (Sionit et al. 1981a), and, in soybean leaves, lower leaf nitrogen content (Sionit 1983). Melillo (1983) reported an increase in C:N ratios, soluble phenolics, and structural compounds in the leaves and litter of sweetgum (*Liquidambar styraciflua* L.) plants grown at elevated CO₂. Such trends could reduce levels of litter decomposition and herbivory as explained in Sections 6.10 and 6.10.1.

6.10 ECOSYSTEM EFFECTS

A simple study of a pasture system using only two species (*Trifolium repens* L. and *Lolium perenne* L.) was initiated in Germany in 1981 (Overdieck et al. 1984). Results to date indicate that the clover (*T. repens*) may competitively exclude the grass at elevated CO₂ levels. The ongoing experiment was designed to test the long-term effects of elevated CO₂ (547–600 ppm CO₂) on production and competition in an experimental system designed to simulate fertile pastures of white clover and perennial rye grass in central Europe.

The total integrated effects of elevated CO₂ on native ecosystems are extremely complex and therefore elusive and not understood. At present there is only one study on an intact unmanaged ecosystem (Prudhomme et al. 1984). In this study, the effects of elevated CO₂ and temperature on primary production, photosynthetic rate, transpiration, and carbon sequestering in an arctic tussock tundra ecosystem are being examined. The significance of this work is that the key ecosystem parameters are being studied in the context of existing natural constraints and interactions. Because this is the only natural ecosystem-level study underway, it will be used to focus the discussion in this section. As additional studies become available the model can be modified or replaced as required to accommodate the inevitable diversity to be discovered as contrasting ecosystem types are examined.

The community and ecosystem factors of prime interest are generally those that may be affected by global increases in levels of CO₂. Primary production, carbon accumulation, plant species composition, water use, animal abundance, and animal diversity are

⁶Oechel and Blake-Jacobson. "Modeling Possible Responses..."

probable factors to be affected. However, several other types of information and relationships are necessary before these effects may be understood completely. Important effects of elevated CO₂ on nutrient cycling, herbivory, decomposition, and mineralization and the feedback effects of these responses on ecosystem structure and function are expected but are currently completely speculative.

6.10.1 Nutrient Availability

Elevated CO₂ and the concomitant increases in photosynthetic and growth potentials would be expected to deplete and sequester the limited nutrient reserves of many ecosystems. Most natural ecosystems are nutrient-limited to some extent as demonstrated by the fact that increased nutrient supply results in increased productivity. Nutrient-limited systems occur in all biomes including tundra, boreal forests, tall and short grasslands, eastern deciduous forests, tropical forests, coniferous forests, and chaparral. Within each of these biomes there may be fertile ecosystems, but the greater part of the Earth is covered by systems that are nutrient-limited. Increased carbon availability should result in even greater stress in habitats that are already limited in nutrient supply. Many of the ecosystem level changes expected, therefore, should be in the direction predicted for nutrient limitation, that is, higher C:N ratio and higher lignin content of tissue and litter. These changes might be expected to slow decomposition, nutrient turnover, and mineralization rates and to decrease nutrient supply relative to demand.

On the other hand, some responses to elevated CO₂ may act to increase nutrient availability. The circumstances of increased carbohydrate availability to decomposers and symbionts are such that symbiotic nitrogen-fixing organisms and mycorrhizal associates will act to counterbalance the tendency for decreasing nutrient availability (Lamborg et al. 1983). Root exudation, if it increases under elevated CO₂, could increase mineralization rates in the rhizosphere and the activity of asymbiotic nitrogen-fixing organisms (Luxmoore 1981). With increased mycorrhizal activity, enhanced export of carbohydrates to the roots should improve nutrient uptake rates of the host plant. Greater nonstructural carbohydrates in litterfall could also increase the rates of mineralization. Augmentation of soil sugar levels over several weeks has been shown to result in increased microbial biomass, respiration, and available nitrogen levels (Flanagan)⁷. These results differ from those obtained when sugar is added in a single addition or over a short time interval (Matson and

Waring 1984) or when sawdust is added with the sugar (Turner and Olson 1976).

It is clear that several possible effects on nutrient cycling and nutrient availability exist. Knowledge of the actual change in nutrient status and supply must await further research.

6.10.2 Productivity

Overdieck et al. (1984) found that in a white clover-perennial rye grass ecosystem, productivity was significantly increased at 547 to 600 ppm CO₂ when compared with ambient CO₂. At the second harvest in the first year, combined above- and belowground production was 50% greater under elevated CO₂ treatment. The greater production continued into the second year. Over the 2 years, the increase in production at elevated CO₂ ranged from 13 to 98%. Only *Lolium perenne* showed an enhancement of live aboveground biomass at elevated CO₂. However, *Trifolium repens* enhanced litter production at increased CO₂. Most important, *L. perenne*, normally the stronger competitor, was out-competed by *T. repens* under extended periods of elevated CO₂.

6.10.3 Carbon Sequestering

With an elevation in ambient CO₂ concentration, increased carbon sequestering by ecosystems could occur by several mechanisms. Net primary productivity (NPP) may increase with an increase in atmospheric CO₂. Soil respiration is in dynamic equilibrium with litter input and mean climatic conditions. Because soil organic matter has a mean residence time of many decades, initial increases in NPP following an atmospheric CO₂ rise should increase litterfall more than soil decomposition. Although increases in atmospheric CO₂ are gradual, many experimental studies must rely on a pulsed or step increase in ambient CO₂. Studies using such a pulsed treatment with CO₂ require careful analysis.

Following a pulsed increase in CO₂ and litterfall, soil organic content should increase until a new equilibrium is reached. In the meantime, the soil system will accumulate carbon. The time required to reach a new equilibrium between new, higher levels of litterfall and soil respiration may be several hundred years after the pulsed increase in CO₂.

Figure 6.14 illustrates hypothetical situations of a pulsed increase in atmospheric CO₂ and of a gradual increase in CO₂ of 3 to 4 ppm per year. In the first case, analogous to many experimental situations, the steep increase in CO₂ results in a marked increase in

⁷P. W. Flanagan. Personal communication, July 1985.

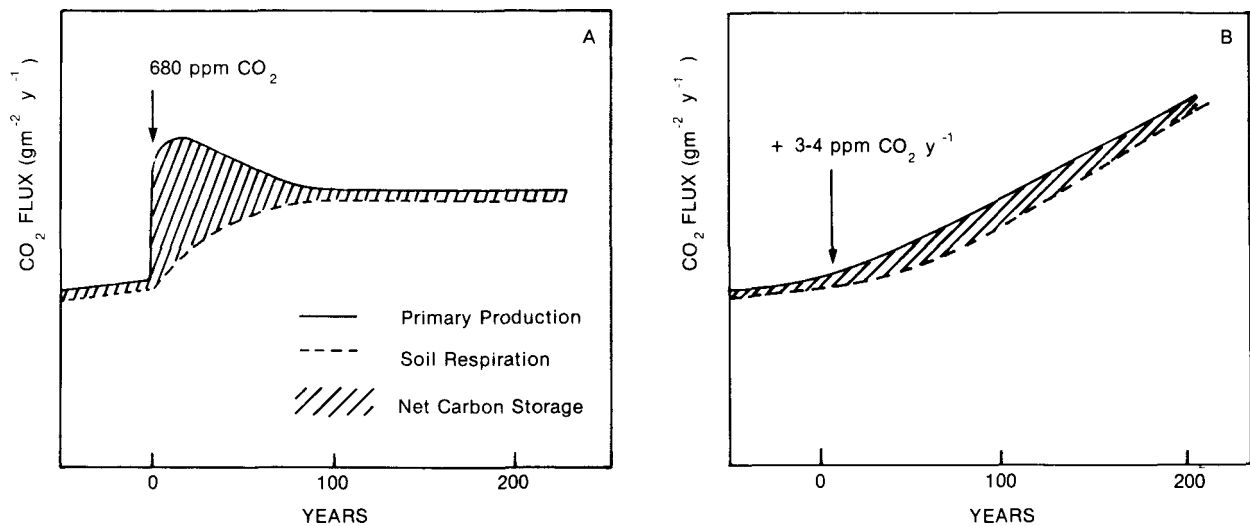


Figure 6.14. Modeled effect of (A) a pulsed (+340 ppm) and (B) a gradual (3–4 ppm CO₂ y⁻¹) increase in atmospheric CO₂ on primary production, soil respiration, and net carbon sequestering following a period where the CO₂ increase is 1–2 ppm CO₂ y⁻¹.

NPP, which greatly exceeds the rate of increase of soil respiration. This results in a situation where there is a very large initial increase in carbon sequestering in the soil system. Eventually, presumably after several hundred years, a new equilibrium is reached between litterfall and soil respiration; and carbon sequestering in the soil again falls to zero or near zero. However, in the interim, a large mass of carbon has been stored in the soil system and there is a new, larger, equilibrium soil organic pool.

This situation, although tractable in an experimental sense, gives a distorted view of carbon sequestering under current and predicted patterns of rising atmospheric CO₂ (Figure 6.14, A and B). Where atmospheric CO₂ rises at a gradual rate of 1 to 1.5% per year, rates of increase in NPP and litterfall will be more modest. In these cases, litterfall will increase by less than 1.5% annually. Again, increases in soil respiration will lag behind the increases in litter input, and carbon will be sequestered. However, the amount of sequestering will initially be much smaller, and the distribution over time will be less than with a pulse increase in CO₂. The sequestering will be smaller at first, but because litter input and decomposition continue out of phase, carbon will accumulate as long as CO₂ continues to rise.

A similar situation exists when attempting to predict carbon sequestering in plant material. Plants in mature ecosystems are nearly in energy balance between gross primary production (GPP) and plant respiration, and NPP is nearly zero. In these situations, plant growth has slowed because support of a large, respiring biomass utilizes nearly all available photosynthate. Increases in photosynthetic rates at higher atmospheric CO₂ levels allow excess carbohydrates, which can be used to

support new biomass. If the increase in CO₂ is a rapid step increase, then plants could grow quickly until maintenance respiration is again equalled by photosynthesis. Where the rise in CO₂ is more gradual, a few ppm per year as predicted over the next century, increases in plant size and carbon sequestering in plants should also be slowed. This difference in plant responses points out one cautionary note that is necessary when generalizing from experimental data with steep increases in atmospheric CO₂ level to predictions for gradual increases of several parts per million per year.

Increasing carbon storage in the soil and in plant biomass could account for considerable carbon accumulation by unmanaged ecosystems as atmospheric CO₂ increases. The increases in carbon sequestering may be much larger than anticipated. This is because current growth in ecosystem carbon is the difference between ecosystem gross production (a very large number) and ecosystem respiration (also a very large number). Yet, the difference between these two large numbers—net ecosystem carbon storage—is small, often about 0.5% of NPP or 0.25% of GPP. This leads to an apparent paradox where a doubling of CO₂ can cause a more than doubling of net ecosystem carbon storage (NECS) when one expects a much smaller effect on photosynthetic rates and on NPP. Reasons for this apparent paradox are illustrated in Figure 6.15.

In this hypothetical tundra situation, GPP is 170 g m⁻² y⁻¹ and ecosystem respiration (ER) is 152 g m⁻² y⁻¹. Net ecosystem carbon storage (NECS) is about 18 g m⁻² y⁻¹ or about 10% of GPP. If GPP increases by only 10% (a modest increase) to 187 g m⁻² y⁻¹, with a doubling of atmospheric CO₂, NECS will increase by almost 100%. A 20 or 30% increase in GPP following a doubling of

CO₂ could result in a 200 to 300% increase in NECS.

Decreases in respiration have a similar effect on NECS. Comparing bars A and C of Figure 6.15, we see that an 11% decrease in ecosystem respiration causes an 83% increase in NECS. When GPP increases and ER decreases (bar D, Figure 6.15), the net effect is a 161% increase in NECS.

Terrestrial ecosystems are major repositories of carbon containing about $2.1\text{--}2.3 \times 10^{18}$ g (Bliss et al. 1981). This comprises an amount of carbon equal to about 300% of the contemporary atmospheric carbon pool. Therefore, changes in the world's terrestrial carbon mass in biomass and dead organic matter can have profound effects on the flux to or from the atmosphere. Terrestrial ecosystems can be a major sink for CO₂ through increased steady-state biomass of perennial plants and through accumulation of dead organic matter. On the other hand, forest clearing, urbanization, agricultural practices, and changing climate could cause a net loss of CO₂ from terrestrial ecosystems (Houghton et al. 1983). These considerations are critical to accurately predicting future atmospheric CO₂ levels.

Current unknowns include the response of plant biomass to elevated CO₂ with time, maximum standing crop, and changes in dead organic matter. Major questions include whether equilibrium biomass of ecosystems (when GPP = respiration) will be larger than at present under elevated CO₂ levels. Most predictions would indicate that maximum plant biomass will increase and that some carbon storage will result (Kohlmaier et al.)⁸.

Another area of major interest concerns changes in carbon storage resulting from changes in atmospheric CO₂ and the associated climatic changes. Of particular concern are arctic and boreal ecosystems. These areas currently contain about 2.18 to 5.20×10^{17} g of carbon in living and dead total atmospheric CO₂ pool (Bliss et al. 1981; Miller et al. 1983). Because 64 to 78% of this carbon is dead organic matter, it is considered labile and easily oxidized to CO₂ should appropriate conditions arise. This organic matter is especially sensitive to release because at least 25% is currently frozen in the permafrost. Much of the rest is only slowly decomposing due to the cold, water-saturated soils. Boreal forests show an inverse relationship between forest floor depth and degree days for decomposition (Van Cleve et al. 1983). A change in temperature and drainage could have a major impact on decomposition of the stored carbon (Billings et al. 1982, 1983, 1984; Peterson et al. 1984).

⁸G. H. Kohlmaier, R. Revelle, and C. D. Keeling. "Exchange of Carbon Dioxide Between the Atmosphere and the Biosphere: Stimulation of the Terrestrial Vegetation by Fossil Fuel Carbon Dioxide in Combination with Other Man-Made Changes." Book manuscript in preparation.

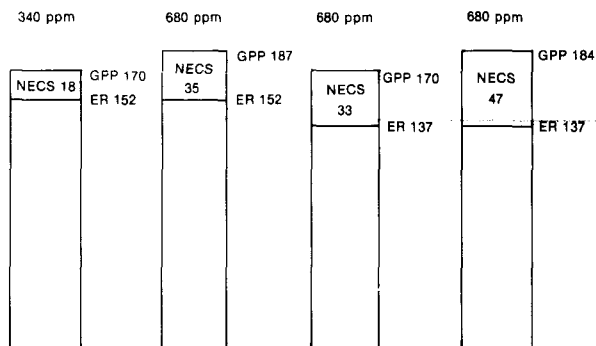


Figure 6.15. Hypothetical ecosystem carbon storage and responses to doubled CO₂ levels, showing gross primary production (GPP), ecosystem respiration (ER), and net ecosystem carbon sequestering (NECS) for: (A) ambient case, 340 ppm atmospheric CO₂, (B) double atmospheric CO₂ resulting in a 10% increase in GPP, (C) double atmospheric CO₂ resulting in a 10% decrease in ER, and (D) double atmospheric CO₂ resulting in both a 10% increase in GPP and a 10% decrease in ER. Values are in g C m⁻² y⁻¹.

Current sequestering of carbon in northern ecosystems is assumed to be about 1.9×10^{14} g C y⁻¹. This is equal to 4% of the current injection rate of CO₂ into the atmosphere or about 25% of the carbon sequestered annually by all terrestrial ecosystems (Keeling 1983; Miller 1981; Miller et al. 1983). Recent information indicates the potential for a major increase in carbon sequestering in the arctic tussock tundra and wet tundra with a doubling of atmospheric CO₂, and field studies show that carbon storage may increase severalfold with a doubling of atmospheric CO₂. This means that a substantial percentage of the contemporary CO₂ injected into the atmosphere (8–20%) may be sequestered by boreal ecosystems by the time atmospheric CO₂ reaches 680 ppm. However, there is not sufficient information to accurately predict whether boreal systems will be an increased sink for CO₂ because of the stimulatory effects of elevated CO₂ on production, or if boreal systems will be a source of CO₂ because of the stimulatory effects of an increased soil active layer (the seasonally unfrozen portion), and increased drainage that would stimulate soil decomposition (Peterson et al. 1984).

Plant growth and certain plant parameters may respond to elevated CO₂ levels in a manner similar to ecosystems. LaMarche et al. (1984) report a 100% increase in tree ring width with a 25% increase in CO₂ concentration. If the carbon available for wood production is drawn from the residual between net photosynthesis and dark plant respiration, then by an analogy to the ecosystem flux one can see how a doubling of atmospheric CO₂ might increase net photosynthesis only 10–30% while increasing the carbon available for ring production by 100% or more.

Similar arguments could be used to support the

work of Kohlmaier et al.,⁹ who are trying to explain the biological basis for the carbon storage factor in plant communities.

Ecosystems are extremely complex and subject to additional factors not yet considered in this analysis. For example, one can examine the possible response of communities in semiarid areas, such as chaparral and deserts, to increasing CO₂. In the chaparral, one would expect plants to grow larger and more quickly following increases in atmospheric CO₂, thereby producing stands of larger than average size. This seems possible when it is assumed that the growth of chaparral plants is water-limited (Miller 1981; Oechel et al. 1982; Schlesinger et al. 1982) because increased water-use efficiency following elevated CO₂ would result in greater production from the same amount of rainfall (Idso and Quinn 1983).

This process should act to increase terrestrial carbon storage and contribute to the β factor. However, the chaparral is a fire-dominated system, because of large accumulations of live and dead fuel. Because the rate of fuel accumulation is affected by the growth rate of the plants, especially where self-shading is a factor, the chaparral may burn more frequently under elevated CO₂ levels. The current 30–40 year fire cycle in San Diego County (Minnich 1983; Reid and Oechel 1984), for example, may accelerate by 5–10 years. Therefore, despite higher growth rates and larger potential plant sizes, average plant size and stand biomass may not change.

One can envision similar negative feedbacks in other ecosystems. Forest size and age may be reduced by earlier senescence under elevated CO₂. Plant senescence is often tied to developmental rates; individuals that develop more quickly may have a shorter life expectancy. Similarly, wind can be an important force in forest ecosystems. Trees that grow more quickly or taller may be subjected to being blown down earlier in their development. Similarly, wind damage may increase if top growth exceeds root growth as CO₂ increases. The net effect may be to maintain forests with biomass levels similar to the present. This process might circumvent much of the expected increase in carbon storage.

Potentially, another negative feedback is the harvesting of biomass. Most of the world's forests are utilized for fuel and fiber. Fuel wood and paper are not long-term storage products, and the carbon they contain returns to the atmosphere rather quickly after harvest. Higher growth rates may not result in a greater standing crop because trees simply may be harvested at a younger age as they become economically and commercially usable.

⁹Ibid.

Similarly, it is not clear that more carbon will be stored in the more productive, faster growing agricultural plants produced under elevated CO₂ levels. Many crops, especially annuals, mature earlier under elevated CO₂, resulting in harvesting, use, and decomposition at a younger age. Even in crops that grow to larger size with elevated CO₂, it is not clear, given the generally rapid turnover and use of agricultural products and residue, that this results in significant carbon storage.

However, given these qualifications, there appear to be ecosystems that may respond to global increases in atmospheric CO₂ with major and continued carbon storage. Ecosystems that may sequester additional carbon in the future include arctic, boreal, and bog ecosystems. These systems now accrete carbon in soil organic matter and in peat deposits.

In cold areas with anaerobic soils or permafrost, there may be a large capacity for carbon storage. These systems may continue to store carbon in the permafrost or organic layers for thousands of years. If permafrost remains after climatic warming and concomitant peat decomposition, the storage capacity seems open-ended. The upper limit of carbon storage in peat is bounded by nutrient limitations in the system as nutrients are sequestered. Also, erosion of peat can expose the sequestered carbon to oxidation (Peterson et al. 1984) as happens in the freezing and thawing cycles of small lakes in the arctic or in response to meandering rivers in the boreal forest (Viereck 1973). Despite these causes of peat exposure and oxidation, the current capacity of tundra, boreal, and bog ecosystems for long-term carbon storage is immense (Bliss et al. 1981).

Recent work has indicated a major increase in carbon sequestering with a doubling of atmospheric CO₂ in tussock tundra and wet tundra (Billings et al. 1983). The data of Billings et al. (1983) predict a 48% increase in carbon accumulation in wet tundra microcosms with a doubling of atmospheric CO₂ from 400 to 800 ppm under a simulated season at 8°C with the water table at the surface. But with the water table at –10 cm there was a significant loss of carbon from the system. Field data from the tussock tundra indicate an increase in carbon sequestering of severalfold with a doubling of CO₂.

6.10.4 Nutrient Sequestering and Interactions

Increased rates of carbon storage with elevated CO₂ will tend to result in increased nutrient storage. Dry organic matter will also contain nutrients which, as deposited, will subtract from the nutrients available to the ecosystem. This pattern, by itself, should tend to make nutrients more limiting. However, there may be a negative feedback as carbon and nutrients accumulate and nutrient impoverishment may limit the rate of

photosynthesis, growth, and future carbon sequestering. However, there are no data that demonstrate nutrient sequestering following CO₂ enhancement (Strain and Bazzaz 1983). But rates of carbon sequestering in wet tundra microcosms are greater with increased nitrogen availability (Billings et al. 1984).

Decomposition rates may fall as nutrients become more limited, as C:N ratios increase, and as litter quality falls (Meentemeyer 1978; Aber and Melillo 1980; Melillo et al. 1982). This may result in feedbacks, the nature of which can be only speculative. Other effects to be considered would be increased nitrogen fixation (Hardy and Havelka 1975) and mineralization rates (Luxmoore 1981) resulting from increased carbohydrate availability in litter and leaf and rhizosphere exudation. As pictured in Figures 6.1 and 6.8, there are a number of different and sometimes competing processes that may be stimulated by elevated atmospheric CO₂. The net effect of elevated CO₂ is likely to be a decrease in nutrient availability and in the nutrient content of tissue. However, changes in nutrient supply rates, nutrient turnover rates, and total nutrient capital will also be important. We are far from having a predictive understanding of these effects in the various ecosystems. No long-term experiments with elevated CO₂ concentrations have determined the effects on these parameters. Currently this is a major area of ignorance, and can probably only be rectified through a combination of studies of field ecosystems and controlled environments such as those that have been initiated in the tundra.

6.10.5 System Water Effects and Interactions

There is a general consensus that increased CO₂ increases water-use efficiency (WUE) at the leaf level. There is generally more carbon assimilated per mole of water expended at elevated CO₂. This effect is particularly pronounced in C₃ plants and in plants from arid and semiarid regions (Tissue 1984; Kimball and Idso 1983).

Higher WUE caused by elevated CO₂ may increase water yield in watersheds. This possibility has been used to predict changes in community distributions resulting from higher WUE. It has been predicted that higher WUE will cause sites to become more mesic and for the vegetation to change (Idso and Quinn 1983).

As with other topics covered in this chapter, conclusions and extrapolations from laboratory or leaf studies to ecosystem results may be in error. Many canopy, community, and ecosystem level processes may interact to change the expected effect of elevated CO₂ concentrations on WUE, water yield, and vegetation. Vegetation boundaries are not caused solely by available

moisture. Historical events, temperature, and nutrients all play a part.

One reasonable response of plant communities to elevated CO₂ would be an increase in leaf area index (LAI). In arid and semiarid areas, LAI may be limited by available moisture rather than light (e.g., Miller 1982). Greater WUE would result in more leaf area supported at the same precipitation. Elevated CO₂ might result in higher LAI, higher standing biomass, similar soil moisture levels, and similar water yields (Kimball et al. 1984). Increased CO₂ can increase photosynthetic rates at low light intensities (Sionit et al. 1984; Wulff and Strain 1982). Therefore, at elevated CO₂ more leaf area can be supported because (1) there will be more available moisture, and (2) leaves should tolerate a lower light level.

However, one would expect species to respond differently to these factors, and the resultant community composition at elevated CO₂ may be quite different than at present. A changing distribution of leaf area through the canopy may further affect and suppress species lower in the canopy.

Any predictions of decreased water use and increased water yield in plant communities following an increase in atmospheric CO₂ must take into account (1) the possibility of increasing leaf area with concomitant increases in water use; (2) increasing WUE with, possibly, lower overall water use; and (3) changes in vegetation boundaries and in species composition.

The result of the interaction of these factors may be much smaller increases in water yield than have recently been predicted. Decreases in water yield are also possible if a much larger leaf area index is supported.

6.10.6 Plant-Animal Interactions

The effect of elevated CO₂ on plant-animal interactions in the ecosystem context has not been determined. However, several specific effects are postulated in the following sections.

6.10.6.1 Pollination and Seed Dispersal

CO₂-induced changes in the geographic distribution of plant species have been postulated. These postulations are based on changes in environmental temperature, precipitation or water availability and water use (Idso and Quinn 1983), or in the tolerance of plants to environmental stress at elevated CO₂ (Sionit et al. 1981b; Schwarz and Gale 1984; Tolley and Strain 1985). As the range of a plant expands into new areas, the possibility exists that the proper pollinators may not or cannot move with the plants. As a result, pollinators may not exist in the new habitat. In addition, the activity patterns of the plants in the new environment

may be out of phase with the animals required for pollination or seed dispersal, and plant breeding systems may be disturbed.

6.10.6.2 Herbivory

As indicated earlier, inorganic and organic quality of plant tissue is likely to change under growth at elevated CO_2 . However, the exact nature of the change will depend on both the environment and the species involved. Likely outcomes include plant material with lower inorganic nutrient content, higher secondary chemical content, and higher usable energy levels (Strain and Bazzaz 1983). The effects of these changes are hard to predict a priori. Lower inorganic nutrient contents were, at first, proposed as a deterrent to herbivory. However, certain chewing insects may adjust to lower nitrogen contents by an increase in consumption. If this pattern is general, herbivore effects could increase as they consume more plant material in order to maintain needed nutrient levels.

When soybean looper larvae were fed soybean leaves grown at 650 ppm, they consumed 80% more leaf material than larvae consuming leaves grown at 350 ppm (Lincoln et al. 1984). The greater herbivory in 650 ppm grown plants correlated with lower leaf nitrogen content. This suggests that greater plant productivity at elevated CO_2 may be offset in part by increased herbivory. An increase in consumption by herbivores could speed nutrient turnover and increase nutrient supply. However, because herbivore feeding is not uniform, increased herbivory is expected to differentially affect plant species.

It is interesting that in the model pasture ecosystem of Overdieck et al. (1984), plant lice infestations broke out at elevated CO_2 levels. This result was also noted in the Duke University Phytotron, where plants in elevated CO_2 chambers were more heavily infested with aphids than those in the contemporary level of CO_2 (Strain)¹⁰. Most observations to date indicate that plants grown at elevated CO_2 will be more prone to insect infestation, and, once infected, the pests may consume more material than they would if the plant had been grown at ambient CO_2 . Kimball and colleagues (Butler et al.)¹¹, however, found no response of the sweet potato whitefly (*Bemisia tabaci* Genn.) developing on cotton plants grown at high CO_2 concentrations in open top chambers.

Shifts in plant growth because of direct CO_2 effects or migrations of plants in response to CO_2 -induced climate change could affect the timing of animal

herbivory relative to plant phenology. Such changes in the timing of herbivore feeding relative to plant phenology could affect productivity and competitive ability of the plants concerned. Plants may show slowed seasonal physiological senescence at elevated levels of CO_2 at the end of the season (St. Omer and Horvath 1983; Tissue 1984). Under certain circumstances, this could result in major changes in herbivory.

What is the effect of elevated CO_2 on the herbivores themselves? Plants support all higher trophic levels. If there is a general diminution of plant forage quality, what will be the impact on all animal herbivores and how will this transfer to higher trophic levels? If there is a general diminution worldwide in the quality of forage, what total impact will this have on plant and animal systems? Unfortunately, because the long-term field experiments have not been performed, the actual effects of elevated CO_2 levels on plant-animal interactions remain undetermined. Until the field studies are made, these questions cannot be answered. In this case it is not possible to extrapolate from the laboratory to the field without some field experimentation and appropriate checks on results. More laboratory and field experiments are needed with elevated CO_2 , assessing the effects on plants and their herbivores.

6.11 MODELING

Modeling the effects of CO_2 at the leaf, plant, and ecosystem levels is hindered more by the low level of our understanding of effects than by our abilities to model the specific biological processes of concern. Therefore, many models on CO_2 effects must be considered as working hypotheses and as methods of testing the implications of various assumptions about CO_2 effects. Models can also be used to assess the most critical areas of needed research. At this time, they should not be used to predict specific responses of plants from unmanaged ecosystems. Model development must go hand in hand with ecosystem research, each guiding the other. This section on modeling presents a specific example of a modeling approach. Chapter 3 covers modeling generalities and concepts; Section 6.12 presents specific applications to selected ecosystems.

6.11.1 Leaf Photosynthesis Models

No current leaf-level photosynthesis model adequately or accurately predicts the effect of slow, global increases in CO_2 on leaf photosynthesis rates. Although CO_2 concentration has been included as a variable in numerous leaf photosynthetic models (Reynolds and Acocck, in press; Chapter 3), these models only can accommodate the effects of rapid changes in CO_2 .

¹⁰B. R. Strain. Unpublished visual observation, October 1983.

¹¹G. D. Butler, B. A. Kimball, and J. R. Mauney. "Populations of *Bemisia tabaci* (Genn.) (Homoptera: Aleyrodidae) on Cotton Grown in Open-Top Field CO_2 -Enriched Chambers." Manuscript submitted.

concentration or photosynthetic rates. The models assume certain enzyme levels, mesophyll resistance to CO_2 and stomatal responses to CO_2 and H_2O vapor using data derived from studies without CO_2 enrichment as a variable. They do not allow for the effects of chronic exposure to elevated CO_2 on RuBP carboxylase oxygenase activity, or for changes in mesophyll resistance, light reaction pigments and enzymes, triose-phosphate levels, for example. The nature and direction of these changes will depend on the interactions among resource limitations, increases in growth, and patterns of photosynthate utilization. The next generation of models could work in any of several ways. First, hierarchical models could be constructed whereby a higher level model would set the state variables of the leaf model based on levels of resource availability, growth conditions, and sink strength. The leaf photosynthesis model could then operate in this domain. Alternatively, parameters for the leaf model could be based on experimental data and the model would function for those conditions.

6.11.2 Whole Plant Growth Effects (FORET and ARTUS-CO₂)

Only two models, FORET (West and Solomon 1984) and ARTUS-CO₂ (Oechel and Blake-Jacobson),¹² have been developed to deal with plant growth under prolonged exposure to elevated CO_2 in unmanaged ecosystems.

FORET is a stand growth model in which production is increased by preset amounts. FORET then predicts changes in stand composition, growth rates, and productivity. FORET is constrained, however, by the lack of field data on the response of tree species to elevated CO_2 concentrations and by the limitation that the only data available are from short-term measurements of leaves growing at current CO_2 levels and suddenly raised to higher levels (Regehr et al. 1975) or from seedlings growing in controlled environments (Tolley and Strain 1985). These seedling responses are extrapolated to adult tree responses, a tenuous extension. Also, the model assumes no concomitant changes caused by interactions, for example, in nutrient limitation, mineralization rates, or in the impact of changes in WUE on water supply and drought tolerance. Again, FORET can serve a useful role by evaluating "what if" scenarios, but the data bases are not available for definitive predictions and simulations of the effects of a doubling of atmospheric CO_2 on stand competition and productivity.

ARTUS-CO₂ appears to predict realistically the effect of elevated CO_2 on the production of arctic species. Because ARTUS-CO₂ operates in a mechanistic, process-based ecosystem mode, it incorporates known feedbacks of nutrient limitation that might operate in the field. One important response of some arctic species to elevated CO_2 is increased vegetative reproduction (Tissue 1984). ARTUS-CO₂ currently does not consider changes in vegetative reproduction, and this is a major shortcoming that should be corrected.

6.11.3 Population and Composition Models

At present, outside of FORET, no competition or population models exist that handle the effects of elevated levels of CO_2 . However, the development of population and competition models is proceeding based on the data of Bazzaz (Chapter 7).

6.11.4 Ecosystem Responses and Interactions (ARTUS-CO₂, SNECS)

The ARTUS-CO₂ model currently predicts ecosystem effects and interactions of elevated CO_2 . ARTUS-CO₂ has a structure similar to BEAM-1982 (Strain and Bazzaz 1983) (Figures 6.1 and 6.16). In ARTUS-CO₂, the maximum photosynthetic rate increases with increasing CO_2 at the rate of 0.02% per ppm increase in atmospheric CO_2 above 340 ppm. However, end-product inhibition can act to suppress photosynthetic rates as storage carbohydrates climb above a set level. Photosynthesis is completely inhibited at a storage carbohydrate concentration equal to twice that of typical early season values. Various relationships and suspected CO_2 effects have been included in the model to ascertain their possible effects on system performance. In most runs, carbohydrates are exported from the roots at rates equal to 10% of the storage carbohydrate content of the plant. This carbohydrate enters a soluble carbohydrate pool in the soil and is decomposed within a single daily time step. In some runs, doubling the atmospheric CO_2 concentration to 680 ppm has been assumed to suppress soil respiration in the fibric layer by 75% and the hemic layer by 50% (Figure 6.17) to examine the possibility of greater sensitivity to elevated CO_2 of microorganisms occurring closer to the soil surface (Flanagan)¹³ and the effect of a doubling of atmospheric CO_2 on the CO_2 concentrations of the surface soil layers in the tundra. Simulations have been run at ambient CO_2 conditions, at 680 ppm CO_2 at ambient temperatures, and at 680 ppm CO_2 with temperatures 4°C above ambient.

¹²Oechel and Blake-Jacobson. "Modeling Possible Responses..."

¹³P. W. Flanagan. Personal communication, July 1985.

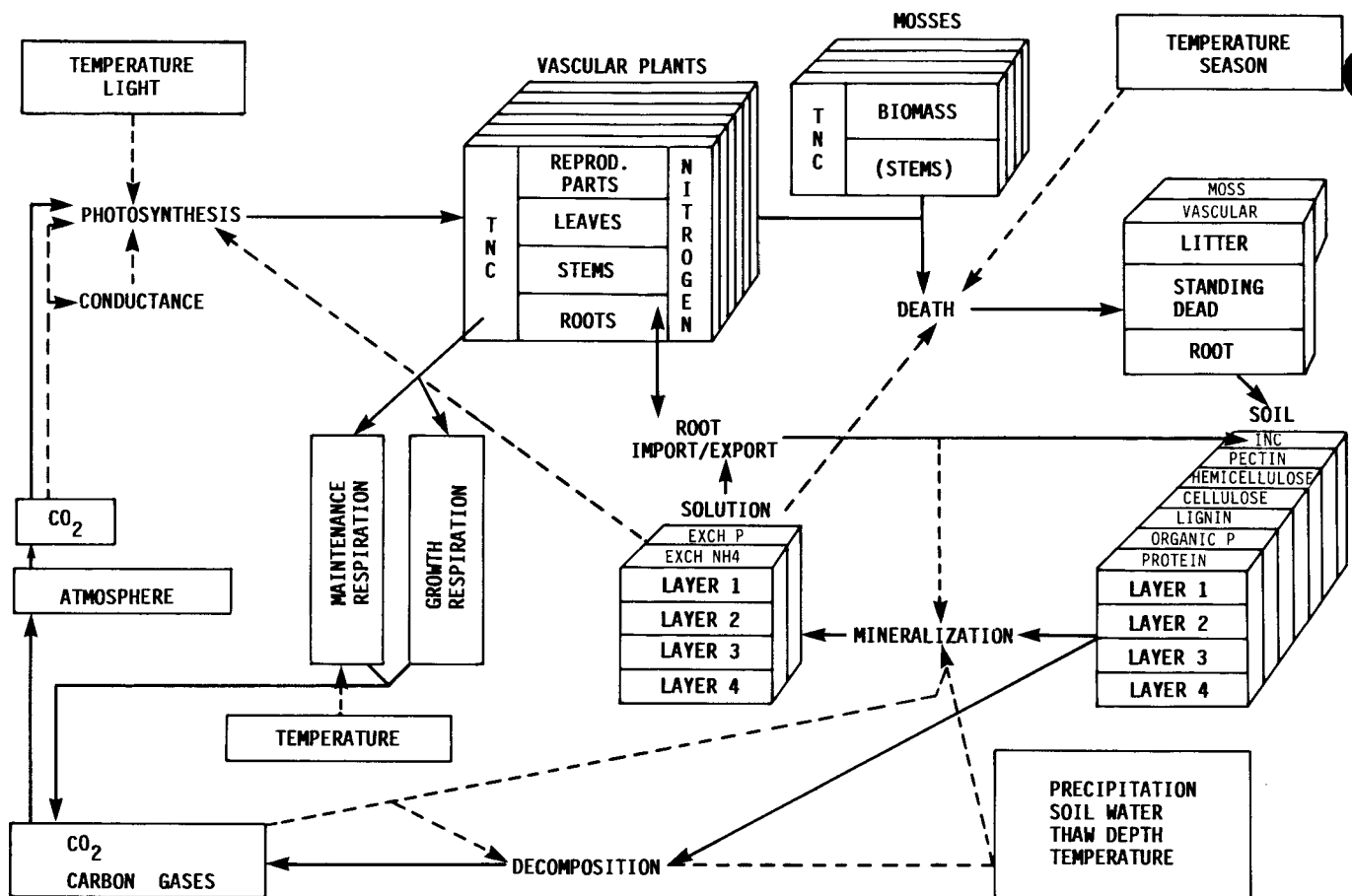


Figure 6.16. Major state variables and fluxes incorporated in the ARTUS-CO₂ model. TNC denotes total nonstructural carbohydrates. Compare with Figure 6.1.

It is important to emphasize that the model can only be viewed as a codification of our process-based understanding and hypotheses of CO₂ effects on ecosystem functions. Much more experimentation, observation, and validation of the model are needed. However, it is instructive to consider the major conclusions reached from model output for CO₂ effects:

1. If end-product inhibition does not act, a major increase in photosynthetic rate (+50%) resulting from elevated CO₂ would increase primary production only marginally in a few species. Overall, NPP of the stand would not increase.

2. Species differ in their primary productivity responses to increasing photosynthetic rates partially because of species differences in nutrient acquisition.

3. Of the various scenarios tried, only one condition significantly increased net ecosystem carbon storage with a doubling of atmospheric CO₂. This is the condition where elevated CO₂ was programmed to inhibit soil respiration. In this scenario, elevated CO₂ offset the effects of elevated temperature on soil CO₂ flux. Under ambient CO₂ conditions and +4°C, carbon storage decreased by 36%. A doubling of CO₂ returns

net ecosystem carbon sequestering to current levels and offsets this temperature effect.

The model does not account for possible changes in population dynamics nor does it simulate the effects for more than 2 years.

Another model, the simulator of northern ecosystem carbon storage (SNECS)¹⁴ (Miller et al. 1983), was constructed to incorporate changes in productivity and decomposition resulting from changes in temperature and CO₂. SNECS operates at a much higher level of resolution than ARTUS-CO₂ and operates over periods of several decades. In arctic and boreal areas SNECS predicts an increase in carbon sequestering of 2 to 8 times. This result is consistent with early experimental findings (Hilbert et al.)¹⁵. However, the time scale and resolution of SNECS renders it untestable in the short term.

¹⁴Published, and referred to elsewhere, as NECS.

¹⁵D. Hilbert, T. I. Prudhomme, and W. C. Oechel. "Responses of Tussock Tundra to Elevated Carbon Dioxide Regimes: Analysis of Ecosystem Carbon Dioxide Flux Through Nonlinear Modeling." Manuscript in preparation.

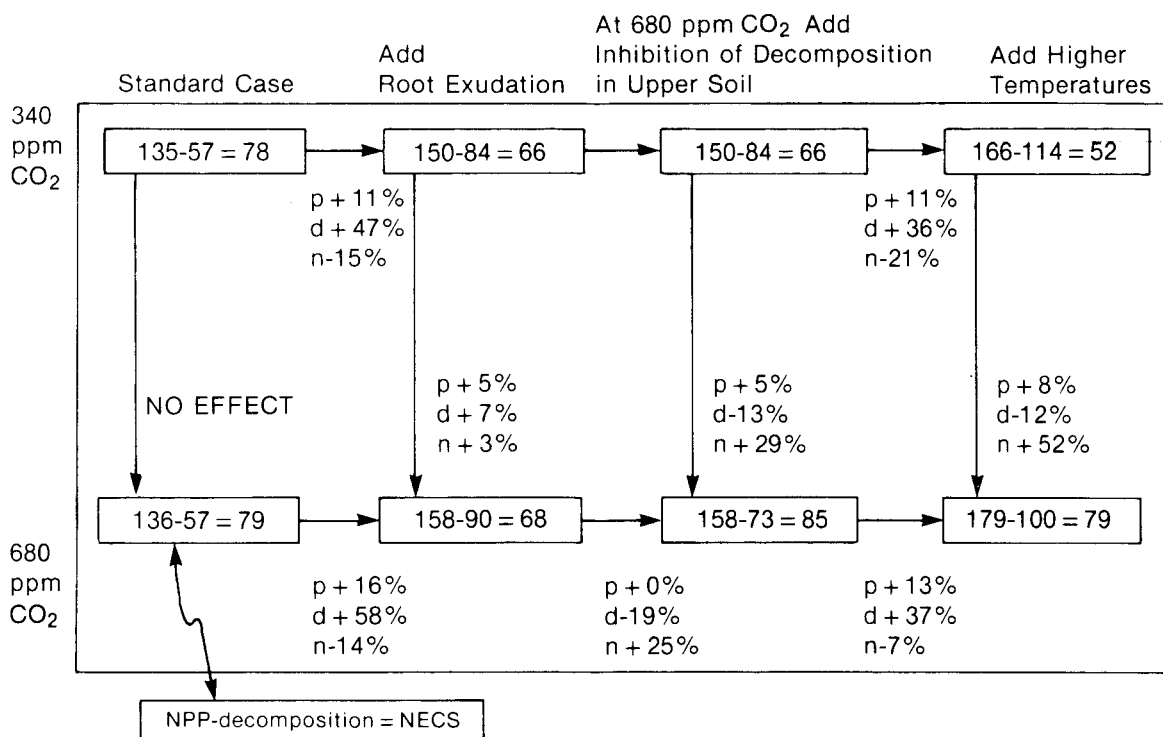


Figure 6.17. Effects of increased CO₂ levels, adding root carbohydrate exudation, and depressing soil decomposition on ARTUS-CO₂ simulations. Within each box are the values for NPP (plant growth plus any sugar exudation), soil decomposition, and net ecosystem carbon storage, respectively. Also given is the percentage change because of the effects of a change in process or treatment on (p) net primary production, (d) decomposition, and (n) net ecosystem carbon storage.

An empirical model of arctic ecosystem response has been constructed to analyze and interpret data of net ecosystem carbon flux through nonlinear regression¹⁶. Results of this exercise indicate that exposure to elevated CO₂ does not increase the light-use efficiency or the maximum photosynthetic rate. Rather, conductance of CO₂ decreases with increasing CO₂ concentration so that photosynthesis does not change significantly. Results from this empirical model are being used to parameterize and evaluate ARTUS-CO₂ and SNECS.

6.12 VERIFICATION OF DATA BASE, MODEL STRUCTURE, AND MODEL OUTPUT

As stated above, the main deficiency in model development is the lack of an adequate empirical data base or a lack of a set of defined and tested principles upon which to base model development.

The difficulty of validation of models that predict plant and ecosystem responses to elevated CO₂ varies according to the level of generality expected from the model, with the time step of the model, and with the state of knowledge with respect to the processes being

modeled. It also is dependent on whether the model being validated is intended to be heuristic or predictive. One can try to be creative in the questions asked and in experimenting and modeling, but only with a major expansion in the data base will an adequate range of models be developed and tested. Because the data base is insufficient for construction of many of the models desired, it is obvious that validation of these models will not be possible until more empirical information is available. At present there is only one field ecosystem experiment where CO₂ is being held at elevated levels throughout the active season. Therefore, development of models for other sites will require additional field research projects.

Model validation for the site of study or for the original experimental conditions may be relatively circular. Verification of model output for new situations requires major new research efforts. Only four models at present are far enough developed to consider validation. These are SNECS, ARTUS-CO₂, FORET, and the analytical model of Hilbert et al.¹⁷

6.12.1 Analytical Model

This model was developed specifically as an analytical tool to gain physiological-level information from

¹⁶Ibid.

¹⁷Ibid.

ecosystem-level CO₂ flux data. The model successfully mimics observations from the experimental site at Toolik Lake for 1983. As structured, the model gives insight into changes in respiration rates, gross photosynthetic rates, light-use efficiencies of photosynthesis, and total CO₂ conductance following increases in ambient CO₂. The utility of this approach when long time scales are considered has yet to be determined.

6.12.2 ARTUS-CO₂

ARTUS-CO₂ is a complicated ecosystem simulation model. Verification will require comparing the performance of subroutines against laboratory and field data as well as verifying important output parameters against field observations.

ARTUS-CO₂ has not yet been tested for elevated CO₂ treatments at Toolik Lake. When this is done, verification would be appropriate for other tundra sites and situations through field and laboratory experiments. Experimental field fumigation in different habitats is the definitive validation test of ARTUS-CO₂. However, this is a very time-consuming and expensive undertaking. Confidence in the predictive powers of ARTUS-CO₂ could be gained by simulating aspects of other environments in controlled environments and observing the response of key physiological and growth parameters to elevated CO₂. A simplified pattern of fumigation and observation of some key parameters could be developed. Also, natural CO₂ seeps might be used as ARTUS-CO₂ validation. Although these areas might not be ideal for primary experimental areas because of the possibility of contaminating gases or the uncertainty of homogeneity between the control area and the area receiving elevated CO₂, these areas may provide good information and perspective for validation. The important point is that even after validation we will have a process-based ecosystem model for only one vegetation type. Expansion and extrapolation to other areas will have to come with time, through a combination of experiments and the development and validation of models.

6.12.3 SNECS

Because SNECS is a comprehensive model that simulates CO₂ effects over a period of several decades for 10 vegetation zones in the arctic and boreal forest, validation in total will be very difficult. Also, there is the problem that field fumigation is only being conducted to one vegetation type and at one site, the tussock tundra, at Toolik Lake, Alaska.

However, because SNECS was built before results from this experiment were available, the predictions for

tussock tundra vegetation could be evaluated with field results currently available. Although this would give us an increased sense of the utility of SNECS, a high correspondence between field results and model output could be misleading. Our understanding of tussock tundra vegetation is better than that for many other arctic and boreal ecosystems, and reasonable agreement for tussock tundra does not necessarily mean other vegetation types will be adequately represented. Also, at this time field results are available for only 2 years of CO₂ fertilization, and initial effects of elevated CO₂ may not be maintained over the decades simulated by SNECS. Therefore, several years to decades could be required for adequate validation of the SNECS model, depending on the rates and nature of ecosystem responses to elevated levels of CO₂.

6.12.4 FORET

FORET may be even more difficult to validate than SNECS. FORET presently assumes that CO₂ effects can be entirely summarized as changes in growth rates. Interaction of CO₂ effects with water and nutrient status is ignored. CO₂ effects on growth are deduced from seedling and sapling experiments. To verify this model requires field fumigation of a forest, which is not currently available, and sufficient time to encompass the duration of the model predictions—hundreds of years.

However, some CO₂ effects can be reduced to single factor effects (e.g., change in growth rate or seed production) and the effects of changes in these factors can be validated. For example, natural areas of varying growth rate or seed production could be sought out and the effects on stand behavior verified.

6.12.5 Modeling Summary

Current models may be tested against some experimental data. However, where models are simulating perennial plants with a lifespan of decades or centuries, or simulating ecosystem processes with many complex interactions that may also take decades to change, it is clear that initial verification will be, at best, a matter of acquiring circumstantial or partial evidence of the adequacy of the predictions rather than a very tight test of the model. Even so, these models and others can help codify the existing information and give insight into important plant and ecosystem responses to elevated CO₂.

6.13 STATUS OF KNOWLEDGE AND RESEARCH NEEDS

The extreme diversity in edaphic conditions, environ-

mental conditions, growth forms, and physiology of plants from unmanaged ecosystems, and the meager data base available, make accurate generalizations concerning plants and ecosystem responses to elevated CO₂ difficult or impossible at this time. Only one experimental study has been initiated to determine the in situ effects of elevated atmospheric CO₂ on plants from unmanaged ecosystems.

Controlled environment studies are limited in scope and in the number of species studied. Less than one-tenth of 1% of the vascular plant flora has been investigated. No studies have been completed over the life cycle of trees or other long-lived perennials. Some inferential studies have been completed (LaMarche et al. 1984), but these are limited, and the absence of replication or reliable controls makes definitive conclusions impossible.

In general, much more research is needed on the effects of elevated CO₂ on the growth and physiology of plants from unmanaged ecosystems. A network of studies should be initiated that spans a sufficient diversity of growth forms or functional plant types, environments, and ecosystems to allow understanding and modeling of the major species and biomes of interest.

Such research will be time consuming and expensive, but experimental results from projects now underway are providing the information necessary to refine the questions and the hypotheses. Any carbon sequestering that occurs in the unmanaged ecosystems of the globe will reduce the need for technical mitigation or adaptation to undesirable effects of atmospheric CO₂ enrichment. Key indicators of plant response can be monitored, and processes to which ecosystem response is particularly sensitive can be studied. Also, as outlined in Chapter 1 of this volume, the main focus has been on direct effects of CO₂ and the subsequent effects on ecosystem performance. Indirect effects through the possible climate change may ultimately have greater effects on plants than do direct CO₂ effects. The interactions of these effects with elevated CO₂ concentrations need to be considered in more detail.

6.13.1 Predicting Photosynthesis and Translocation

Only a few species have been studied in detail and even fewer have been examined in the field under natural conditions. By carefully designed experiments under controlled environments, however, several major conclusions are possible. First, elevated CO₂ has a much smaller stimulatory effect on photosynthetic rates than originally thought. In most situations there is little (less than 20%) to no stimulation of photosynthetic rates following a doubling of atmospheric CO₂ (Wulff and

Strain 1982; Tissue 1984). In some situations there may even be a reduction in photosynthetic rates at the high CO₂ growth conditions (Raper and Peedin 1978; Kramer 1981; Wulff and Strain 1982; Sasek et al. 1985).

For unmanaged ecosystems, it might be safer to assume no stimulation of photosynthesis than to predict an increase because of elevated CO₂. Reasons for this effect are not completely understood, but it appears that homeostatic mechanisms adjust photosynthetic rates to maintain a given carbohydrate supply.

Plants in higher nutrient environments might be more likely to show a significant increase in photosynthesis and growth with elevated CO₂ than those in very low nutrient environments. Also, in fertile habitats, species with a strong sink for carbohydrate would be more likely to respond photosynthetically to elevated CO₂ than those with limited capacity for carbohydrate use.

More work is needed on the general patterns of photosynthetic response to elevated CO₂ and in the proximal and ultimate causes of the observed pattern of photosynthetic response to elevated CO₂. Research is needed on the interactions among sink strength, controls on translocation rates, and substrate availability (e.g., triose-phosphate). These deficits in knowledge point out that although proximal controls on photosynthetic rates are fairly well known, information on the ultimate controls on photosynthetic rates is lacking.

Research in the general areas of flexibility, homeostasis, and controls on long-term photosynthetic rates is critical to understanding responses to situations that might allow higher photosynthetic rates.

A much larger data base on the response of photosynthetic rates, translocation rates, and allocation patterns to elevated CO₂ is needed before major generalizations of response patterns are possible. This research might best be placed into a framework or matrix that includes growth form and the nutrient, moisture, and temperature status of the original habitat. This matrix would thereby allow reasonable generalizations and predictions for most plant types and environments, and would help form a rational data base for predictions and future model development (Figures 6.18 and 6.19). Only a small portion of growth forms and biomes have been studied (Figures 6.20 and 6.21). Two important aspects to be considered when trying to understand and predict plant response to elevated CO₂ are plant growth form (tree, shrub, herb) and plant lifespan. Figure 6.18 shows 19 plant forms that should be studied with respect to response to elevated CO₂. If the responses of these forms were known, we would have a good empirical data base from which to generalize to most plants. We propose that these forms should be emphasized in each ecosystem or

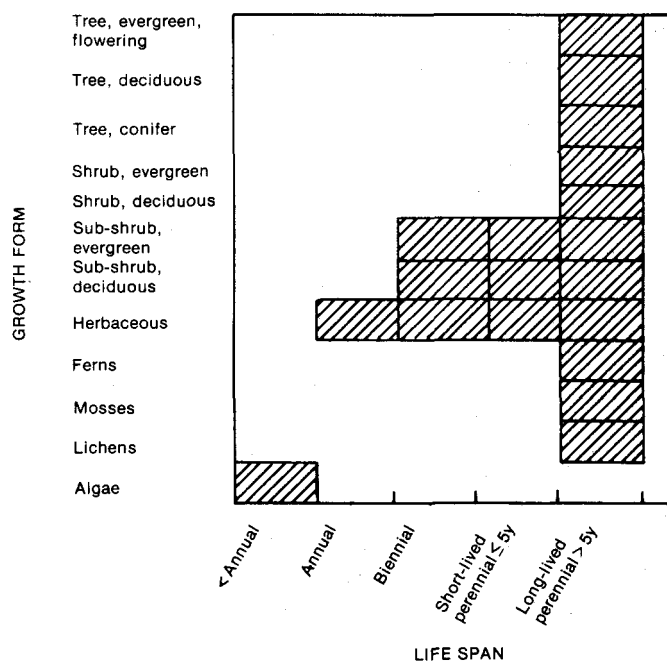


Figure 6.18. Growth forms and life spans of various plant categories. Hatched areas represent plant categories to be studied.

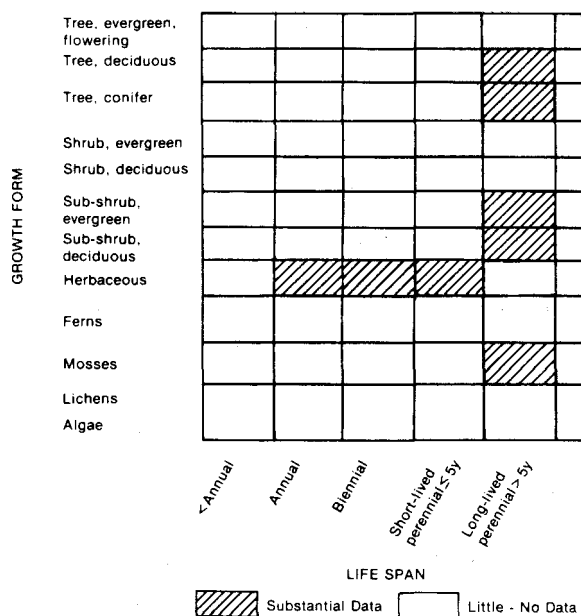


Figure 6.19. Growth forms of native species that have received some study with respect to response to elevated CO_2 .

biome studied. Of course, in any one biome not all of these forms will be important, therefore, emphasis should be placed on the functionally most important forms. To date, only about 6 of these 19 forms have received attention (Figure 6.19), illustrating the small data base existing from which to make predictions of plant response to elevated CO_2 (Figure 6.18).

Interactions among plant growth forms, moisture stress, and nutrient availability set environmental limits

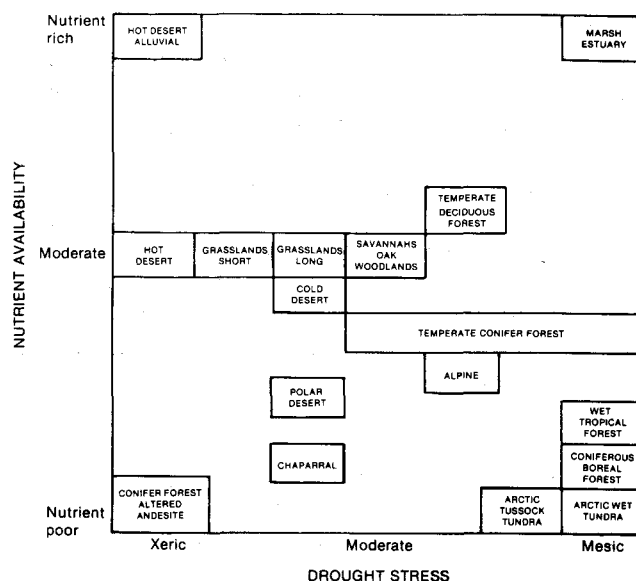


Figure 6.20. Major ecosystem types representing major biomes. These represent a range of possible response types to elevated CO_2 conditions.

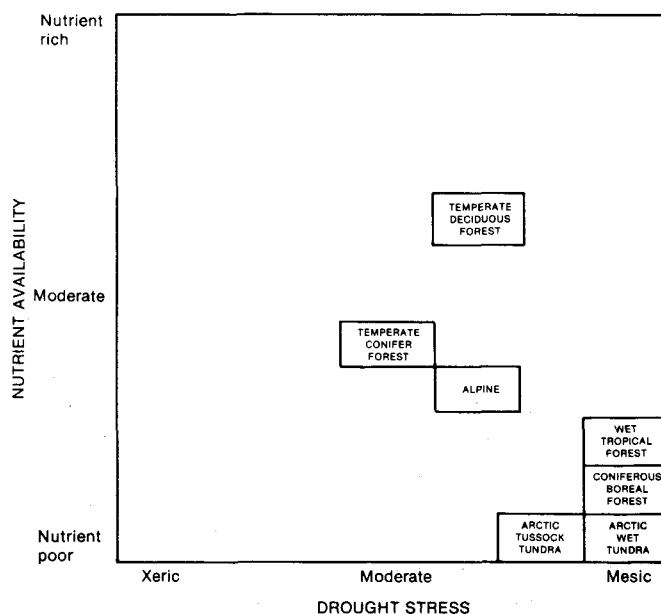


Figure 6.21. Major ecosystem types for which some information on plant response to elevated CO_2 is known. Species studied may be successional, minor, or for trees, seedling or sapling, elements of the biome.

on plant response to elevated CO_2 concentrations. By studying ecosystems selected to represent a range of moisture and nutrient conditions (both at the extremes and in moderate ranges) and by emphasizing the more important ecosystems, a scheme can be developed that will allow interpolation to most ecosystems. Seventeen ecosystem types are proposed for study (Figure 6.21). Perhaps a few of these types could be deferred from study (e.g., the polar desert) or other types

substituted for them. However, the point is that a set of ecosystems can be studied that will yield direct information on important ecosystem response patterns as well as a framework for interpolating to other important ecosystem types. Of the 17 ecosystems proposed for study, we have some information on only about 7 and much of this is very limited in extent. Furthermore, the sites studied to date are primarily from moderate to mesic moisture status and of moderate to poor nutrient status. These seven sites are, therefore, not representative of areas of nutrient rich sites or those with considerable moisture stress.

Furthermore, the scheme presented in Figure 6.20 does not consider a third axis to include the level of ecosystem disturbance and the successional state. Because this can clearly influence ecosystem response to elevated CO_2 , it should be considered in future planning.

It is clear that only a very small percentage of the ecosystems and growth forms that should be studied are currently under investigation (Figure 6.20). We know that plant response to elevated levels of CO_2 varies by species, ecotypes, growth form, and environment. There is insufficient empirical information to generalize or even hypothesize with confidence about likely response categories and patterns.

6.13.2 Predicting Growth and Productivity

In ecosystems, growth and productivity are limited by a myriad of factors in addition to CO_2 . These include light, temperature, nutrient supply, and water supply all interacting with plant physiology. Greater potential photosynthetic rates will not necessarily translate to higher growth and productivity if other factors such as nutrient supply are limited. However, interactions among all of these factors are possible and likely. For example, elevated CO_2 may induce higher water-use efficiency extending the water resource, delaying drought, and increasing stand productivity.

The effects of CO_2 on growth and productivity have been insufficiently studied to predict the response of unmanaged ecosystems to atmospheric enrichment; only a few laboratory or field studies have been initiated. Results from Toolik Lake, Alaska, indicate little increase in productivity in most species in the community, and modeling exercises yield similar predictions. These results seem to be due to the fact that most species are limited more by nutrient supply than by carbohydrate supply. However, these are relatively short-term field studies and the longer term effects are not known. For example, the effect of increased tillering rates on *Eriophorum vaginatum* may eventually have a stimulatory effect on photosynthesis even though

the growth rates of individual tillers remain unchanged (Tissue 1984). So far, the effects of elevated CO_2 on growth and photosynthesis of mosses and lichens in the tundra have not been investigated.

We have limited data on only a couple of ecosystems. One would expect evidence of increases in production where availability of carbon, rather than other factors, is limiting. However, field fumigation of a diversity of ecosystems is necessary before reasonable predictions of the response of production in different ecosystem types to elevated CO_2 will be possible.

Further research should include the growth and productivity response of several ecosystems that span the range of nutrient, moisture, temperature, and growth forms indicated in Figure 6.16. Depending on the ecosystem, CO_2 fumigation could be in greenhouse units, open top chambers, or by open air fumigation. These field approaches are only feasible if technology can be scaled to the stature of the ecosystem in question and if it can be applied at a reasonable cost.

6.13.3 Predicting Growth Rates

Several generalizations concerning the effect of elevated CO_2 levels on growth rates seem possible. For annual plants and those with determinant growth patterns, initial growth rate may be increased, but final weight and size may be similar. This means that the maturation processes are faster, but total growth is unchanged (Paez et al. 1980). For perennial plants and those of indeterminant growth pattern, growth rates and total biomass may increase. This effect is dependent on sufficient resources to support these higher growth rates (Tissue 1984; Paez et al. 1980; Bermudez 1982; Sionit et al. 1985).

However, more species and growth forms must be examined before a predictive understanding of growth response is possible for all major growth forms. Plant growth forms for which few or no data are available include: sapling and adult evergreen and deciduous trees; large shrubs such as those from semiarid and arid areas; mosses, lichens, and algae including blue-green (nitrogen-fixing) algae.

6.13.4 Predicting Ecosystem Responses

Few of the potentially important effects of elevated CO_2 on ecosystem function have been studied in any ecosystem. These effects include nutrient impoverishment because of increased nutrient demand; rhizosphere effects resulting from increased export of carbon to the roots and root exudation (possibly resulting in increased mycorrhizal activity, mineralization rates, and symbiotic nitrogen fixation); decreased litter quality (decreased

mineralization rates); decreased forage quality for herbivores (resulting in increased or decreased herbivory); increased water-use efficiency (resulting in increased soil moisture, leaf area, and production in arid and semiarid areas); changing patterns of competition; and changing community composition. Most of these effects must, at this time, be considered possible outcomes of global increases in atmospheric CO₂ concentrations. Most likely, all of these effects will be observed in at least some ecosystems and biomes. Unfortunately, most effects have been examined in only one, or a few, ecosystems. Therefore, no paradigm exists for the prediction of what effects will occur and in which system they will be important. This lack of knowledge is critical because it is at the system level that increases in CO₂ are most uncertain.

The likely ecosystem level responses need to be identified for selected ecosystems representing a range of growth forms, nutritional levels, and moisture regimes (Figures 6.18 and 6.19). The effect of elevated CO₂ on these processes should then be observed through a series of controlled laboratory and field experiments. Results could be used to parameterize a family of generic models based on a process-based ecosystem model like ELM (Sauer 1978), ARTUS-CO₂, or the Mediterranean Ecosystem Simulator (MEDECS) (Jacobson et al. 1981). These models, being similar in structure, would allow comparison of ecosystem responses to elevated CO₂ for the various ecosystems studied.

6.13.5 Carbon Sequestering

In only one region, the arctic tundra, is there experimental data on the effect of elevated CO₂ on carbon sequestering (Billings et al. 1983, 1984; Prudhomme et al. 1984; Miller et al. 1983). For wet tundra and tussock tundra, a doubling of CO₂ is expected to cause substantial increases in carbon accumulation of a few percentage points (Billings et al. 1982, 1983, 1984) to 800% (Miller et al. 1983).

Major uncertainties regarding responses in the arctic include the effect of elevated CO₂ on soil respiration and plant respiration. At present, large increases in net ecosystem carbon accumulation are measured, but the contributing elements in the ecosystem are not fully understood.

It is worth mentioning that associated changes in the environment, for example, water level, nitrogen availability, depth of thaw, and temperature, may have as large or larger an effect on net ecosystem carbon flux than does elevated CO₂ (Billings et al. 1982, 1983, 1984).

There are no experimental data for the effects of elevated CO₂ on carbon sequestering in other arctic

ecosystems, in the boreal forest, in bogs, or in other ecosystems. In areas where carbon sequestering may be important, these data will need to be obtained, preferably in the context of ecosystem experiments.

6.14 CONCLUSIONS

Global increases in atmospheric CO₂ will increase photosynthetic rates, growth rates, productivity, and water-use efficiency in some instances but not others. In general: (1) Photosynthetic rates will increase where nutrients are abundant and where plants with high growth potential exist. However, this pattern of response is not universal. (2) Productivity will most likely increase where parent materials contain abundant elements and where nitrogen fixation rates, mineralization rates, and water availability increase as atmospheric CO₂ increases. (3) CO₂-induced increases in water-use efficiency will be important where water is limited.

Unfortunately, accurate predictions concerning the responses of most ecosystems to these factors are not possible because of the small data base.

Other ecosystem responses are even more uncertain. In nutrient-limited environments, decreasing forage quality and litter quality have been hypothesized. However, these predictions have not been thoroughly validated. Laboratory studies are available showing decreasing litter quality (Melillo 1983) and forage quality (Lincoln et al. 1984) for plants grown at elevated CO₂. A decrease in litter quality should reduce decomposition rates and mineralization rates. A decrease in forage quality, on the other hand, may increase herbivory if animals must eat more material to obtain needed nutrients.

The knowledge of the likely responses of unmanaged ecosystems to elevated CO₂ is of critical importance. Future rates of carbon sequestering, stand productivity, nutrient status, stand composition, herbivory, behavior of weeds, species composition, and species diversity are areas of considerable concern for unmanaged ecosystems. Only through a comprehensive and organized program of experimentation will reasonable predictions for the major ecosystems be possible.

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7. EFFECT OF INCREASED ATMOSPHERIC
CARBON DIOXIDE CONCENTRATION
ON PLANT COMMUNITIES

F. A. Bazzaz,
K. Garbutt,
and
W. E. Williams
Harvard University

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7.1 INTRODUCTION

Most of the basic research on the long-term effect of carbon dioxide (CO₂) enrichment has been directed at understanding the physiology of CO₂ responses. This research, recently reviewed by Bjorkman and Pearcy (1983), suggests that the primary effect of an increasing CO₂ concentration is on the photosynthetic rate and stomatal aperture: photosynthesis is increased and stomatal conductance is decreased. Increases in photosynthetic rate cause more carbohydrates to become available for growth and respiration, whereas decreases in stomatal conductance reduce water loss and can improve the water status of the plant, especially under conditions of water stress. Past studies have generally concluded that secondary effects, such as changes in plant morphology, were small, even insignificant, but more recent research is beginning to challenge this view. Overdieck et al. (1984) have reported increases of up to 36% in specific leaf weight in 600 parts per million by volume (ppm) over that in 340 ppm CO₂ in white clover after 1 year, Hesketh and Hellmers (1973) have shown changes in floral phenology, and Tolley and Strain (1984a) have shown a significant interaction between irradiance and the CO₂ concentration affecting the root-to-shoot ratio in loblolly pine and sweetgum.

Extensive studies have been made of crop growth under elevated CO₂ concentrations (reviewed by Wittwer 1983; Kimball 1983). Results of this research indicate that productivity and yield almost always increase with elevated CO₂ levels, but there is also large variability among species in the amount of response. Crop plants with the three-carbon (C₃) pathway, for example, always show greater photosynthetic enhancement than do the four-carbon (C₄) plants, and this effect has a clearly understood physiological basis. There also are many differences among C₃ species and even among genotypes of the same species, but the physiology of these differences has not yet been investigated.

Differences in response to elevated CO₂ levels among the members of an ecological community are likely to result in changes to the species composition of the community. The composition of the communities depends on the interactions of the community members with their physical and biotic environments. An elevated CO₂ level is likely to have different effects on different species, causing the species in turn to exert different effects on each other. The result is a very complex set of interactions that will affect communities in complex ways.

7.2 STUDIES OF COMMUNITIES

Two types of studies have been done on the effects

of elevated CO₂ levels on plant communities. Most studies involve the growing of several species of plants individually and focusing on the differences observed in final biomass, growth rates, seed or fruit weight, or some other measure of potential competitive success. There have been relatively few examples of the other type of study, in which natural or artificial communities of plants are exposed to different levels of CO₂ and competitive outcomes are directly observed. Efforts are being made to bring these two approaches together by mathematical modeling techniques.

7.2.1 Individual Species Experiments

Carlson and Bazzaz (1980) compiled a list of 14 plant species that they studied, showing a wide variety of changes in plant weight and photosynthetic rate for two CO₂ concentrations (Table 7.1). Total biomass changes were significantly different among species, and results ranged from a weight gain of 96% for *Datura stramonium* L. to a weight loss of 7% for *Zea mays* L., both at a CO₂ concentration of 1200 ppm when compared with growth at 300 ppm.

Rogers et al. (1983) have compared the stimulation of growth of four economically important species under four CO₂ concentrations, using open top chambers. Effects of CO₂ enrichment on growth of crop and forest species were studied at daytime mean CO₂ concentrations of 340, 520, 718, and 910 ppm, as well as in ambient control plots. Increased growth of the plant parts of corn (*Zea mays* L. 'Golden Bantam'), soybean (*Glycine max* L. [Merr.] 'Ramson'), loblolly pine (*Pinus taeda* L.), and sweetgum (*Liquidambar styraciflua* L.) was recorded (Table 7.2). Growth increases for soybean as well as sweetgum in atmospheres with elevated concentrations of CO₂ were caused by increases in leaf area and photosynthesis per unit leaf area along with decreases in conductance and therefore water use. For corn, however, photosynthesis was unaffected by CO₂ enhancement, and growth stimulation was probably caused by lowered conductance and increased water-use efficiency alone.

As a prelude to the weed-crop competition experiments described below, Patterson and Flint (1980) studied the growth of several weed and crop species as individuals. They used mathematical growth analysis techniques to evaluate the effects of CO₂ concentrations of 350, 600, and 1000 ppm on growth and biomass partitioning in corn (*Zea mays* L. 'Dekalb XL 395'), itchgrass (*Rottboellia exaltata* L. f), soybean (*Glycine max* [L.] Merr. 'Tracy'), and velvetleaf (*Abutilon theophrasti* Medic.) grown in individual pots. Controlled environment chambers with day and night temperatures of 28° and 22°C, respectively, and

Table 7.1
Percent Increase in Total Biomass and in Mean Single-Leaf
Photosynthesis for Growth 28 Days After Planting at Different CO₂
Concentrations Relative to the Values at 300 ppm

Species	Percent Increase ^a			
	Photosynthesis		Biomass	
	600 ppm	1200 ppm	600 ppm	1200 ppm
C₃ Plants				
<i>Datura stramonium</i> (1)	74	96	74	115
(2)	67	83	60	107
<i>Chenopodium album</i>	57	79	76	140
<i>Polygonum pensylvanicum</i>	51	64	48	100
<i>Abutilon theophrasti</i>	44	75	38	65
<i>Ambrosia artemisiifolia</i>	10	24	68	112
<i>Acer saccharinum</i>	61	89	32	63
<i>Populus deltoides</i>	65	74	29	20
<i>Platanus occidentalis</i>	13	30	33	33
<i>Glycine max</i>	58	75	47	100
<i>Helianthus annuus</i>	20	38	40	55
C₄ Plants				
<i>Setaria faberii</i>	13	37	42	106
<i>Setaria lutescens</i>	40	20	70	45
<i>Amaranthus retroflexus</i> (1)	41	21	36	59
(2)	27	33	29	48
<i>Zea mays</i>	24	-7	21	10

^aPercent increase over values at 300 ppm.
Source: Carlson and Bazzaz (1980).

Table 7.2
Final Dry Weights of Four Economic Species as Percentages
of Control Weights

Species	Percent Increase CO ₂ Concentration (ppm)			
	340	520	718	910
Corn	100	158	148	160
Soybean	100	157	179	186
Pine	100			157
Sweetgum	100			160

Note: For corn, pine, and sweetgum, N = 18, for soybean, N = 6.
Source: Rogers et al. (1983).

photosynthetic photon flux densities of 650 $\mu\text{mol m}^{-2} \text{s}^{-1}$ photosynthetically active radiation were used. Dry matter production of the two C₃ species (soybean and velvetleaf) was increased significantly by raising the CO₂ concentration above 350 ppm. In corn (a C₄ species) dry matter production was lowest at 1000 ppm CO₂ and did not differ between the 350- and 600-ppm treatments. For itchgrass (also a C₄ species), dry matter production was greatest at 600 ppm CO₂ and did not differ between the 350- and 1000-ppm treatments (Table 7.3). An increase in the CO₂ concentration caused an increase in the rate of dry matter production per unit leaf area (net assimilation rate [NAR]) in soybean and velvetleaf, but either decreased or did not alter NAR in corn or itchgrass. At 45 days after planting, the weed-to-crop ratios for total dry matter production for velvetleaf to

corn and itchgrass to corn were significantly greater at both 600 and 1000 ppm than at 350 or 600 ppm CO₂. Compared with the value at 350 ppm, the weed-to-crop ratio for velvetleaf to soybean was greater at 600 ppm and less at 1000 ppm CO₂. Patterson and Flint (1980) concluded that atmospheric CO₂ enrichment probably would make weeds with the C₃ photosynthetic pathway more competitive with crops that have the C₄ pathway. Weeds with the C₄ pathway may become less competitive with crops that have the C₃ pathway.

To test the interactive effects of CO₂ with nutrient status, Patterson and Flint (1982) grew soybean (*Glycine max* [L.] Merr. 'Tracy') and two associated weeds, sicklepod (*Cassia obtusifolia* L.) and showy croton (*Crotalaria spectabilis* Roth), in separate pots in controlled enrichment chambers with CO₂ concentrations of 350 or 675 ppm and one-eighth or one-half strength Hoagland nutrient solution applied three times daily. Leaf areas and dry weights of plant parts were determined at 1, 3, and 5 weeks. Stomatal resistances, transpiration rates, leaf water potentials, and leaf chlorophyll contents were measured, and NAR and leaf area durations (LAD) were calculated. In all species, growth in 675 ppm CO₂ enhanced dry matter production through increases in both NAR and LAD. The increased dry matter production with one-half strength compared with one-eighth strength Hoagland solution was, however, caused by increased LAD alone. Stomatal conductances and transpiration rates decreased

Table 7.3
Effects of CO₂ Concentration on Dry Weights of Corn, Itchgrass,
Soybean, and Velvetleaf Harvested at 12, 24, and 45 Days
After Planting

Species	Days After Planting	Dry Weight CO ₂ Concentrations (ppm)		
		300	600	1000
		(g)		
Corn	12	0.626b	0.732a	0.759a
	24	6.963a	6.235a	6.628a
	45	91.290a	89.490ab	80.080b
Itchgrass	12	0.077b	0.158a	0.151a
	24	2.103b	3.824a	3.502a
	45	39.245b	47.470a	38.619b
Soybean	12	0.341c	0.523b	0.613a
	24	3.596c	4.682b	6.382a
	45	50.554c	62.186b	87.086a
Velvetleaf	12	0.083c	0.272a	0.205b
	24	1.940b	3.727a	3.647a
	45	35.335c	47.963b	54.339a

Note: Within each species at each harvest, values sharing the same letter are not significantly different at the 0.05 level, according to the Duncan multiple range test.

Source: Patterson and Flint (1980).

Table 7.4
Effects of CO₂ and Nutrient Concentration on Vegetative Growth of Soybean,
Sicklepod, and Showy Crotalaria 35 Days After Planting

Species	CO ₂ Concentration (ppm)	Nutrient	Dry Weight (g)	Leaf Area (dm ²)	Leaves (no.)	Plant Height (cm)
Soybean	350	1/8	16d	22c	27c	100c
	350	1/2	30b	52b	37b	121b
	675	1/8	21c	18c	16d	105c
	675	1/2	45a	65a	44a	131a
Sicklepod	350	1/8	10d	13c	25c	30d
	350	1/2	25b	44b	65b	64b
	675	1/8	15c	15c	30a	36c
	675	1/2	40a	59a	96a	72a
Showy Crotalaria	350	1/8	10c	16c	56c	42d
	350	1/2	12b	26b	93b	52b
	675	1/8	14b	17c	57c	47c
	675	1/2	20a	40a	121a	56a

Note: Within each column, values for the same species sharing the same letter are not significantly different at the 0.05 level, according to the Duncan multiple range test.

Source: Patterson and Flint (1982).

in 675 ppm CO₂ but were not affected by nutrient level. High CO₂ concentrations or low nutrient levels generally decreased the leaf chlorophyll content per unit area. Growth enhancement by CO₂ was greater with one-half strength than with one-eighth strength Hoagland solution (Table 7.4).

In a highly detailed study, Tolley and Strain (1984a) examined the growth and development of sweetgum (*Liquidambar styraciflua*) and loblolly pine (*Pinus taeda*) during the early phase of their development in response to elevated levels of CO₂. In addition, these authors investigated the effects of the interaction

between CO₂ and the light environment (Tolley and Strain 1985) and CO₂ and the moisture environment (Tolley and Strain 1984b) on growth and development. In both species, the response to CO₂ was strongly influenced by light and water status. The response was species dependent, with loblolly pine responding substantially less than sweetgum at all light and water status.

Tolley and Strain drew the following conclusions:

1. Biomass partitioning in these two species, particularly sweetgum, changes with the CO₂ con-

centration. Elevated CO₂ concentrations compensate for a reduction in the root-to-shoot ratio of sweetgum and loblolly pine grown under low light levels. The increased root-to-shoot ratio suggests that both these species would be better competitors with understory hardwood plants in an environment with high CO₂ concentrations because low root-to-shoot ratios often hinder establishment in low-light environments. This statement should be treated with caution until the effects of elevated CO₂ concentrations on the other components of the community and on community interactions are understood.

2. In abandoned old fields of the piedmont, loblolly pine predominates in the drier areas and sweetgum assumes dominance in moister patches under the present CO₂ regime. The physiological data presented strongly suggest that if the CO₂ concentration were to increase, the distribution of the species would alter, with the drier sites being invaded by sweetgum, which could displace loblolly pine.
3. The effects of elevated CO₂ concentrations described above appear to decline with time (also reported by Aoki and Yabuki 1977; Patterson and Flint 1980; Wulff and Strain 1982). Thus, long-term experiments, particularly with woody perennials, are needed to evaluate the true long-term effects of elevated CO₂ concentrations.

Sionit et al. (1985) have investigated the growth and development of sweetgum and loblolly pine grown for an entire growing season, mimicking field temperatures throughout the season, under three CO₂ levels. Their results support those of Tolley and Strain. At the end of the growing season, both species had responded to elevated CO₂ levels, but sweetgum grew taller and produced more branches and thicker stems than did

loblolly pine (Table 7.5). These differences again suggest that changes in seedling growth patterns may alter the competitive relationship between the two species.

Without a better understanding of plant-plant competition, it is difficult to draw any broad conclusions about competition from these experiments on individual plants. They do, however, add evidence to the hypothesis that the performance of several plant species relative to each other will change as the concentration of CO₂ increases.

A unique pair of experiments was performed by Garbutt and Bazzaz (1984), who studied the effects of CO₂ concentration on flowering and fruiting with particular attention given to the timing of flowering. An alteration of the flowering time could disrupt pollination relationships in insect-pollinated flowers, but even plants that are totally self-pollinating appear to have a close correlation between flowering time and amount of seed set (Schmitt 1983). Figure 7.1 shows that increased levels of CO₂ advance the flowering time for several populations of *Phlox drummondii* Hook., but that the differences in timing among the populations were preserved. Increased CO₂ levels enhanced all floral characters measured, that is, maximum display, flower production rate, longevity, and the total number of flowers produced. Figure 7.2 shows the results of a study of CO₂ effects on the reproductive biomass of *Datura stramonium* and *Abutilon theophrasti*. As CO₂ concentration increased, seed number did not significantly increase in *D. stramonium* and actually decreased in *A. theophrasti*, but this decrease was offset by increases in individual seed weight. Fruit weight increased significantly in *D. stramonium*. *A. theophrasti* grew more quickly, but final biomass was not significantly affected by the CO₂ concentrations. Taken together, these studies illustrate the danger of assuming that increased biomass translates into increased seed

Table 7.5
Effects of Atmospheric CO₂ Enrichment on Growth of *Liquidambar styraciflua* and *Pinus taeda* at 32 Weeks After Planting in Controlled Greenhouses With Natural Photoperiod and Simulation of Outside Temperature

Species	CO ₂ Concentration	No. of Branches	Stem Weight (g)	Leaf Weight (g)	Root Weight (g)	R:S Ratio	Total Weight (g)
	(ppm)						
<i>Liquidambar styraciflua</i>	350	1.8a	2.1b	1.5a	6.3a	1.7ab	9.9a
	500	1.7a	3.4b	1.6ab	9.2b	1.8b	14.1b
	650	4.0b	3.7b	2.0b	8.6ab	1.5a	14.3b
<i>Pinus taeda</i>	350	2.0a	0.4a	1.4a	2.1a	1.2a	3.9a
	500	2.7a	1.0b	2.3b	2.9b	0.9a	6.2b
	650	2.3a	0.8b	2.1b	3.2b	1.1a	6.1b

Note: Within each column, values for the same species sharing the same letter are not significantly different at the 0.05 level, according to the Duncan multiple range test ($N = 15$).

Source: Sionit et al. (1985).

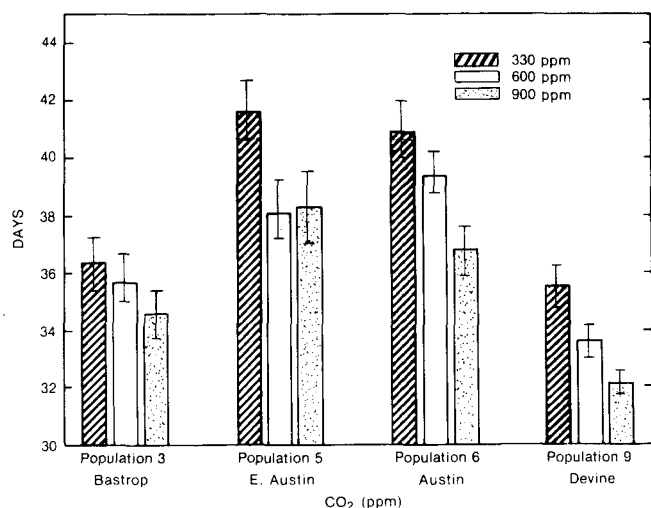


Figure 7.1. The flowering responses of four populations of *Phlox drummondii* to three levels of CO₂. Bars indicate two standard errors. Source: Garbutt and Bazzaz (1984).

output, especially if this increased biomass is measured at any time before reproductive maturity.

Table 7.6 summarizes what is known about individually grown natural species.

7.2.2 Multispecies Competition Experiments

Direct competition experiments have examined weed versus crop interactions, as well as communities consisting of old field annuals, deciduous tree seedlings, and herbs of a California serpentine grassland.

A recurrent theme in competition research is the pairing of C₃ and C₄ species, presumably because prediction of the outcome based on physiology is so clear: as the CO₂ concentration increases, the C₃ plant should do progressively better with respect to the C₄ plant, unless there is water stress. If there is water stress, the competitive relationship probably would not change significantly with the level of CO₂ (Bjorkman and Pearcy 1983).

Carter and Peterson (1983) grew *Festuca elatior* L. (C₃) and *Sorghum halepense* (L.) Persoon (C₄) in mixed and unmixed cultures under 350 and 600 ppm CO₂ for 112 days. High CO₂ levels stimulated increases of total dry weight and leaf surface area in *F. elatior* despite unfavorably high temperatures (precise temperature data were not presented). In *S. halepense* delay of leaf senescence and of floral initiation was attributed to high CO₂ concentrations. Growth of unmixed cultures of *S. halepense* under 600 ppm CO₂ was relatively poor because of an apparent interaction of high concentrations of CO₂ with self-shading. Growth analysis results support the hypothesis that elevated CO₂ levels will affect the competitive interaction of C₃ and C₄ species (Figure 7.3). Peak net assimilation rates of C₃ and C₄ plants were seasonally separated at 350 ppm CO₂

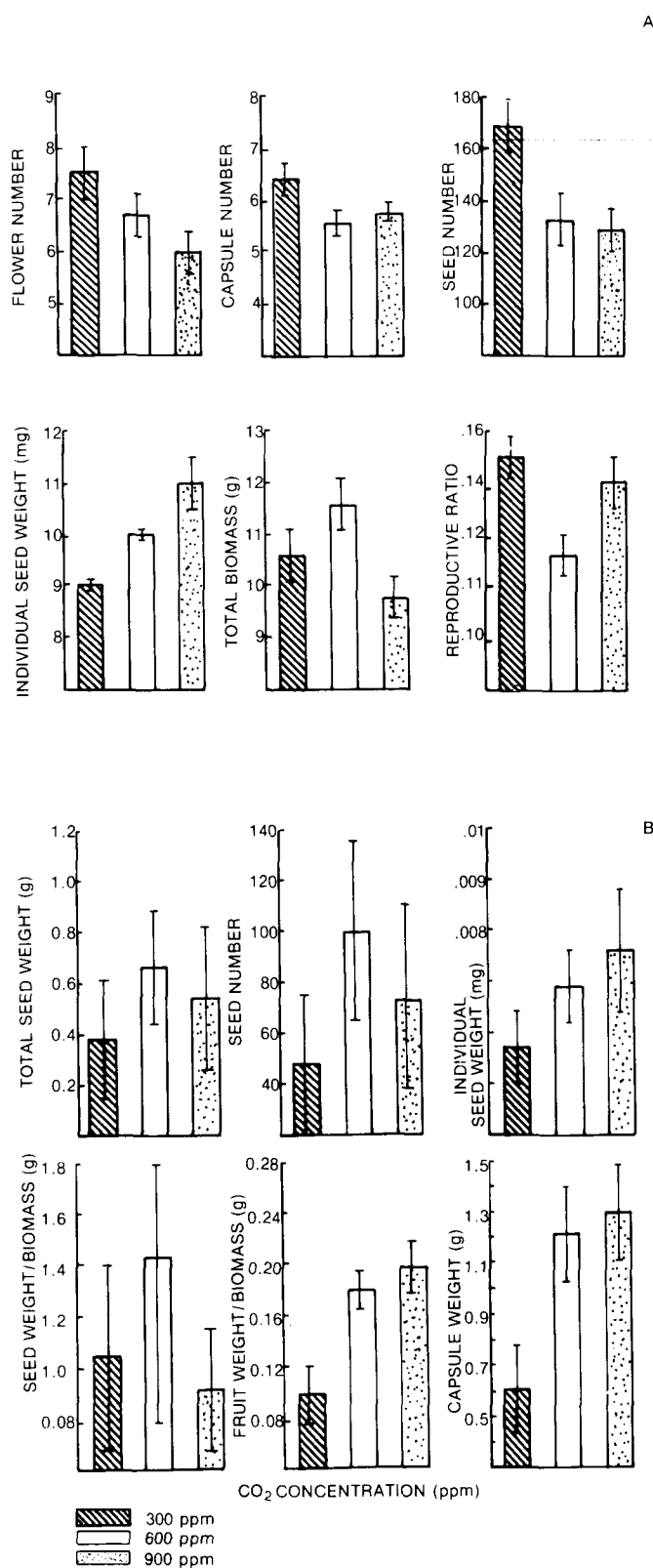


Figure 7.2. The reproductive response of two old-field annuals to concentrations of CO₂. (A) *Abutilon theophrasti*. (B) *Datura stramonium*. All data are on a per plant basis, all weights are grams. Source: Garbutt and Bazzaz (1984).

Table 7.6
Characteristics of Natural Species Grown Individually at Elevated Concentrations of CO₂

Genus, Species	P _s	ψ	WUE	RGR	Phenology	Reproductive Biomass	Vegetative Biomass	Source
<i>Abutilon</i>	I	I	I		U	UC	U	Carlson & Bazzaz (1980, 1982)
<i>Amaranthus</i>	I	I	I		E	I	U	Bazzaz & Carlson (1984)
<i>Chenopodium</i>	I	U	I				I	Garbutt & Bazzaz (1984)
<i>Ambrosia</i>	I	I	I				I	
<i>Setaria faberii</i>	I	I	I				I	
<i>Datura</i>	I		I		E	IC ^a	I	
<i>Phlox</i>					E	I	IC	
<i>Setaria lutescens</i>	I		I				IC	
<i>Acer</i>	I		I				I	Carlson & Bazzaz (1980)
<i>Populus</i>	I		I				I	Tolley & Strain (1984a,b;
<i>Platanus</i>	I		I				I	1985) Sionit et al. (1985)
<i>Liquidambar</i>	U		I	U			I	Bazzaz et al. (1985)
<i>Pinus</i>	UC		U	DC			I	
<i>Quercus</i>	I		I					
<i>Liriodendron</i>	I		I					
<i>Fraxinus</i>	I		I					
<i>Carya</i>	I		I					
<i>Crotalaria</i>							I	Patterson & Flint (1982)
<i>Cassia</i>							I	Patterson et al. (1984)
<i>Sorghum</i>				D	L	I	I	Carter & Peterson (1983)

Note: Abbreviations: P_s, photosynthesis; ψ, water potential; WUE, water-use efficiency; RGR, relative growth rate. Symbols: E, earlier; I, increased; U, unchanged; L, later; D, decreased; C, complex changes.

^aTrend only.

but coincided at 600 ppm. Based on these observations of *F. elatior* and *S. halepense*, Carter and Peterson (1983) projected that global CO₂ enrichment might alter the competitive balance between C₃ and C₄ plants and subsequently affect seasonal niche separation, species distribution patterns, and net primary production (NPP) within mixed communities.

A C₄ weed, *Sorghum halepense* (L.) Pers. #3 SORHA (johnsongrass), and the C₃ crop, *Glycine max* (L.) Merr. 'Ransom' (soybean), were grown separately and in inter- and intraspecific competition at 350 and 675 ppm CO₂ (Patterson et al. 1984) (Table 7.7). In the absence of competition the higher CO₂ concentration stimulated dry matter accumulation, leaf area expansion, NAR, and LAD of soybeans more than that of johnsongrass. The plant relative yield (yield in mixture divided by yield in pure culture) of soybean in competition with johnsongrass increased, and that of johnsongrass in competition with soybean decreased, as the CO₂ concentration was increased from 350 to 675 ppm. Therefore, the competitiveness of the C₃ crop with the C₄ weed increased with an increase in the CO₂ concentration. Relative yield totals were not significantly different from 1.0, indicating that the two species were competing for the same resources. From these data it was predicted that the competitiveness of C₃ crops with C₄ weeds could be increased with an increase in the CO₂ level.

Bazzaz and Carlson (1984) have studied the competition among four species, three C₃ and one C₄, at two levels of moisture (Figure 7.4). The

effects of moisture and CO₂ amplified each other, so that *Polygonum pensylvanicum*, a wet-soil C₃ species, gradually displaced *Amaranthus retroflexus*, a C₄ species, as the CO₂ and moisture levels increased. The total biomass of the community increased with an increase in the CO₂ concentration, but the interactions of the other two species, *Abutilon theophrasti* and *Ambrosia artemisiifolia*, did not change with a change in the CO₂ concentration.

The results of these studies are in general agreement with physiological predictions, but they must be considered preliminary. All competitive studies used only one chamber for each CO₂ treatment, making it impossible to be sure that some property of the chambers not related to CO₂ concentration did not influence the results, although the investigators did take care to control temperature, relative humidity, and light. The studies of Patterson et al. (1984) and Bazzaz and Carlson (1984) were only run for about one-fourth to one-half of the life cycle of the plant. This can produce seriously misleading results because life cycles of most C₃ species are speeded up at higher CO₂ concentrations (St. Omer and Horvath 1983), and the life cycles of *Sorghum halepense* and *Sorghum bicolor*, both C₄ species, are apparently slowed down (Hesketh and Hellmers 1973; Carter and Peterson 1983). Similarly, biomass differences seen between CO₂ levels early in the life cycle of annual plants do not always translate into significant biomass or reproductive output differences at the end of the life cycle or growing season (Garbutt and Bazzaz 1984).

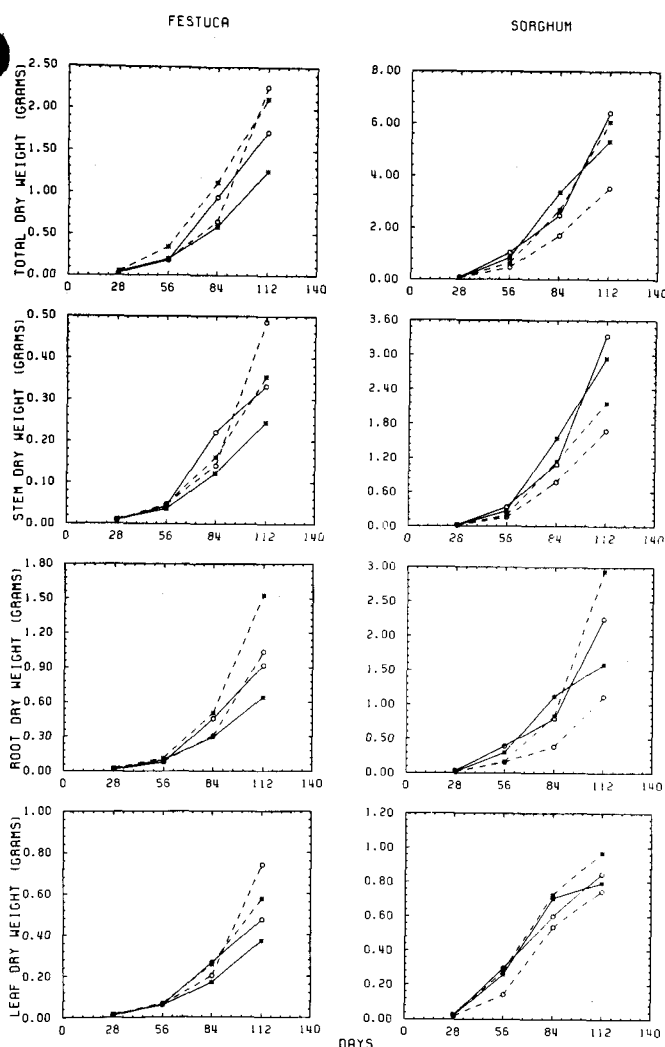


Figure 7.3. Total and partitioned biomass dry weights for *Festuca* and *Sorghum* grown in mixed cultures (*) or unmixed cultures (o) at 350 μL (---) or 600 μL (---) CO_2 . Source: Carter and Peterson (1983).

Zangerl and Bazzaz (1984) exposed six members of an annual community to combinations of CO_2 and nutrient concentrations, and CO_2 concentrations and light intensities. In the CO_2 -nutrient study, plants were collected at reproductive maturity, and seeds were sorted out and weighed separately from the rest of the plant (Figure 7.5). Under low light levels, total community production was not highest at the highest CO_2 concentration (Figure 7.6). This suggests that some environmental conditions may cause the production of at least some members of the community to decrease with elevated CO_2 concentrations. Once again, however, only one chamber per treatment was used, so a chamber-specific effect cannot be ruled out. Anecdotal observations and some experiments currently under way, however, suggest that a production peak in mixed communities between 500 and 600 ppm CO_2 may be real, and further research is indicated.

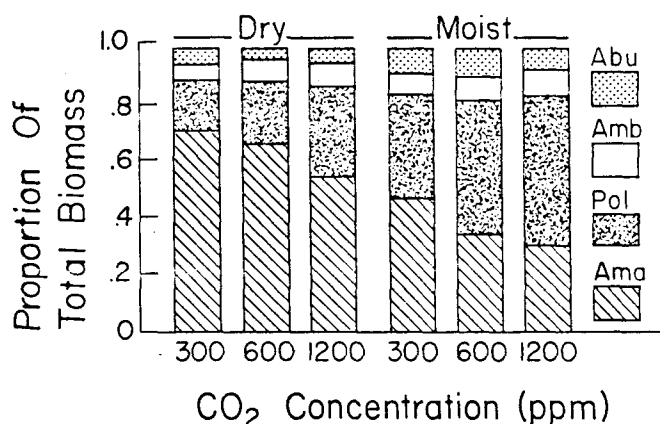


Figure 7.4. Proportion of total aboveground biomass for assemblages of *Abutilon theophrasti* (Abu), *Ambrosia artemisiifolia* (Amb), *Polygonum pennsylvanicum* (Pol), and *Amaranthus retroflexus* (Ama) grown at 300, 600, and 1200 μL CO_2 and 15% (dry) or 30% (moist) soil moisture. Source: Bazzaz and Carlson (1984).

Table 7.7
Effects of Competition and CO_2 Concentrations on Total Dry Weight, Leaf Area, and Height of Soybean and Johnsongrass After 24 Days

Species	Competitor	Dry Weight		Leaf Area		Height	
		CO ₂ Concentration (ppm)		CO ₂ Concentration (ppm)		CO ₂ Concentration (ppm)	
		350	675	350	675	350	675
		(g)		(dm ²)		(cm)	
Soybean	None	6.92c	10.43a	14.68b	16.20a	53.6a	53.9a
	Soybean	5.00d	6.80c	10.23d	10.50d	51.5a	53.4a
	Johnsongrass	5.40d	8.15b	11.69c	12.74c	51.2a	52.8a
Johnsongrass	None	5.62ab	6.19a	10.39a	10.68a	90.6d	106.4a
	Soybean	3.72c	3.70c	7.43b	5.75c	88.3d	98.6c
	Johnsongrass	4.23c	5.20b	8.00b	7.82b	94.2cd	102.5ab

Note: For each measured variable, within each species, values sharing the same letter are not significantly different at the 0.05 level, according to the Duncan multiple range test.

Source: Patterson et al. (1984).

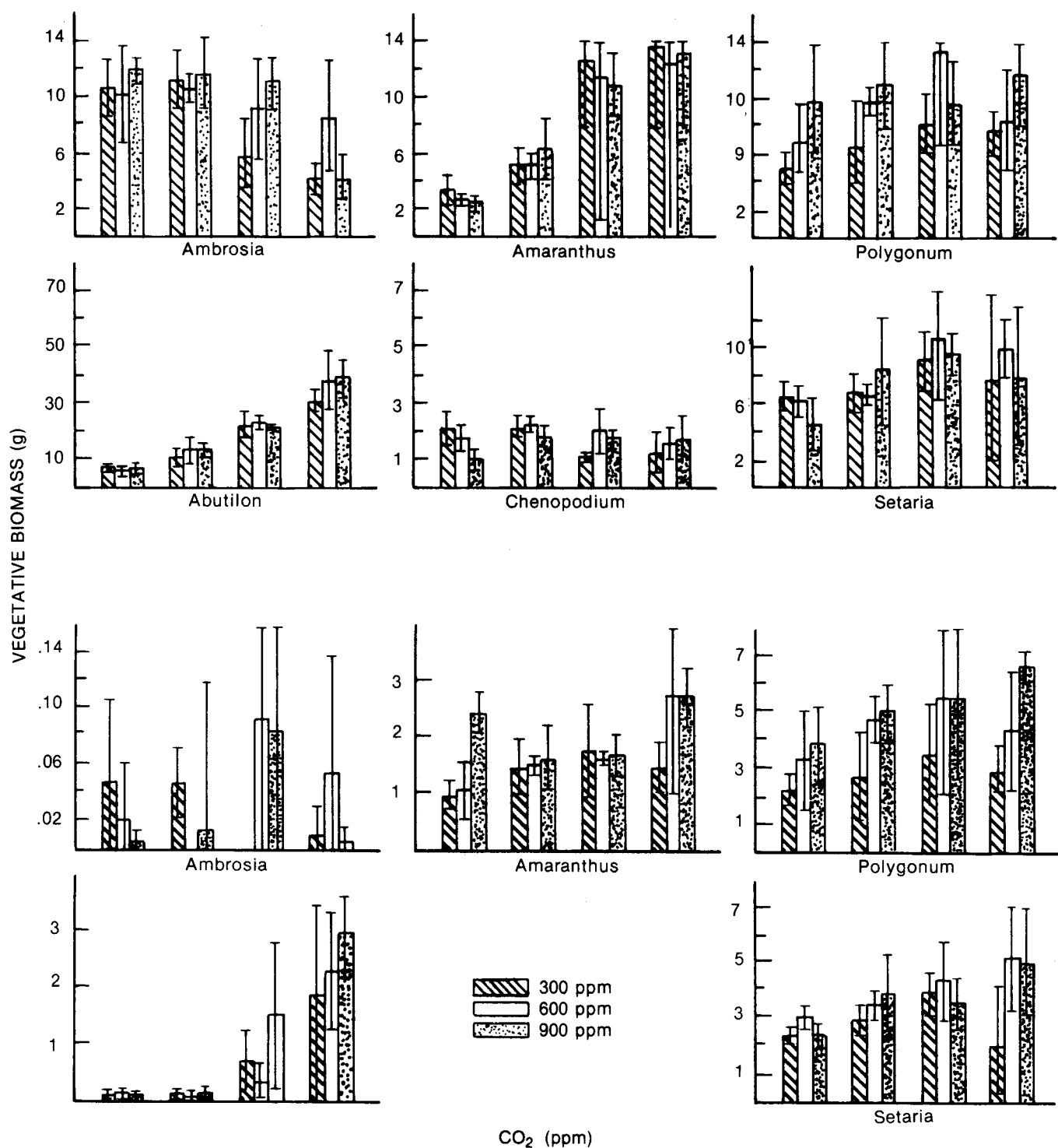


Figure 7.5. Individual species responses to CO₂ enrichment and nutrient availability (*Setaria* and *Amaranthus* are C₄ plants, the others are C₃): (A) vegetative biomass, (B) seed biomass. Nutrient level increases from left to right; 95% confidence limit is indicated for each mean. Source: Zangerl and Bazzaz (1984).

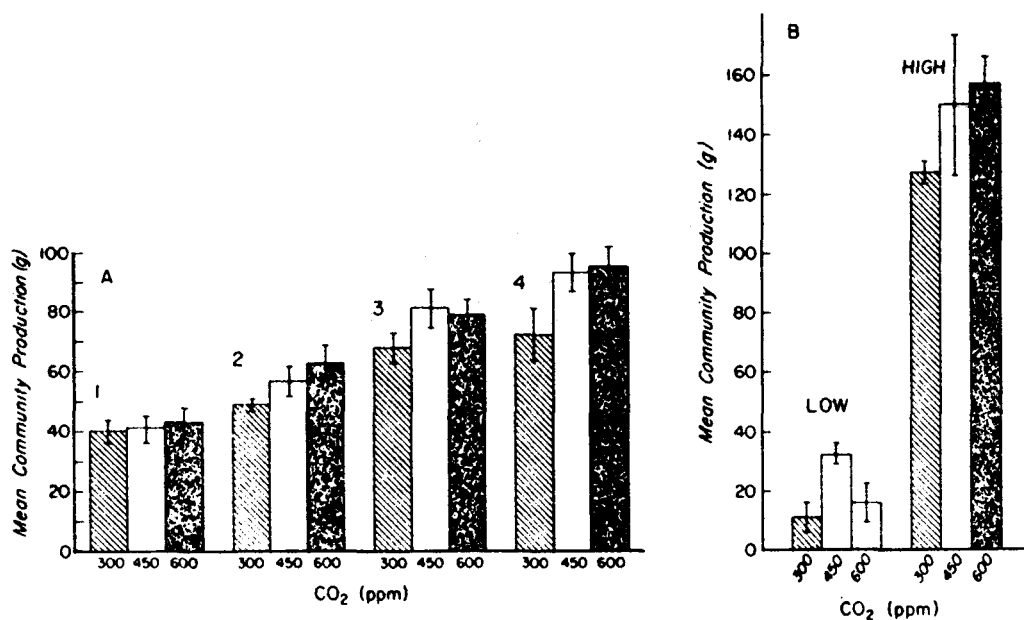


Figure 7.6. Mean total production of an annual community at three CO₂ concentrations. (A) Responses to CO₂ at four levels of soil nutrients (the lowest is 1, the highest is 4). (B) Response to CO₂ at two light intensities, 30% full sun (low) and 100% full sun (high). A 95% confidence limit is indicated for each mean. Source: Zangerl and Bazzaz (1984).

Overdieck (in press) studied 1:1 mixtures of perennial ryegrass (*Lolium perenne* L.) and white clover (*Trifolium repens* L.) at 600 and 340 ppm CO₂ for 13 months in open top chambers in the Federal Republic of Germany; this is the longest continuous CO₂ experiment with mixed species that we know of. At the time of maximum growth, the clover had 30% greater leaf area and 19% greater specific leaf weight at elevated CO₂, whereas the ryegrass had 18% greater leaf area and 29% greater specific leaf weight in 600 ppm compared with 300 ppm. The clover showed much longer petioles (67%) in environments with elevated concentrations of CO₂ at the beginning of the experiment. This difference between treatments temporarily declined during the maximum growth period, but finally increased such that petioles were 100% longer in the high CO₂ concentration at the end of the experiment. After 13 months, the blades of ryegrass were 19% longer at 600 ppm than at 340 ppm, but seed production was significantly decreased. Seed production was significantly increased, however, in the clover (Table 7.8). In the long run, additional CO₂ seems to enhance seed production in *Trifolium* and vegetative propagation in both species.

Richmond et al. (1982), studying techniques to eliminate blue-green algal contaminants from green algae cultures, grew *Chlorella vulgaris* and *Spirulina platensis* together in the presence of varying concentrations of dissolved CO₂ and bicarbonate (HCO₃). *C.*

vulgaris did better under high levels of CO₂ and low HCO₃ conditions, whereas *S. platensis* dominated when the CO₂ concentration was low and the HCO₃ concentration was high. Although the concentration of dissolved CO₂ in bodies of water is determined by many factors other than the atmospheric CO₂ concentration, this result nevertheless indicates the possibility that even aquatic systems may be directly affected by increasing atmospheric CO₂ concentrations (Wetzel and Grace 1983).

Two final experiments still under analysis deal with deciduous forest trees and with forbs from a serpentine grassland at Jasper Ridge, California (Bazzaz et al., 1985). The trees showed significant changes in relative biomass among the species, depending on CO₂ treatment (Figure 7.7). Variation within the treatment

Table 7.8
Effects of Elevated CO₂ concentration on Seed Production in Competitive Arrays of *Trifolium repens* and *Lolium perenne*

Species	Weight 1000 Seeds CO ₂ Concentrations (ppm)			P
	340	600		
	(g)			
<i>Trifolium repens</i>	0.547 ± 0.052	0.702 ± 0.040		<0.001
<i>Lolium perenne</i>	2.084 ± 0.174	1.992 ± 0.195		<0.05

Note: N = 25.
Source: Overdieck et al. (1984).

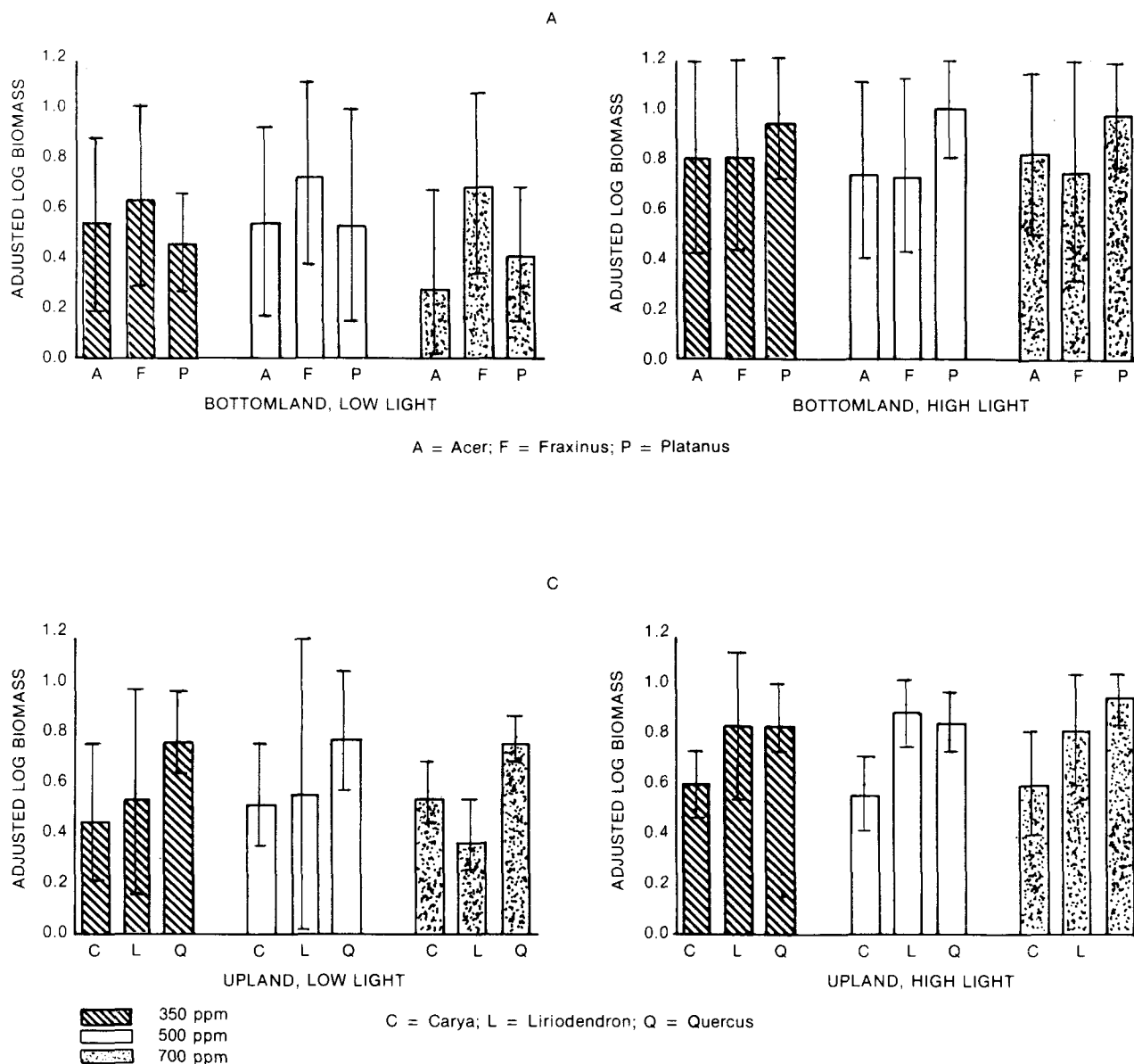


Figure 7.7. Response of two tree communities to CO₂ in shade and sun. Means are adjusted to compensate for sapling initial biomass. Bars represent standard errors. Source: Bazzaz et al. (1985).

group was quite large, however, and the experiment is being repeated to include more than one growing season. The carbon:nitrogen (C:N) ratio of leaf litter will also be measured. The short grass forbs from the California grassland, all C₃ species (Figure 7.8), showed a very large increase in total biomass, but an analysis of variance showed that the order of dominance was not significantly changed by the CO₂ concentration. Unlike the other community experiments we have seen, in this community elevated CO₂ levels apparently have no effect on competition. This may be related to adaptations in these plants to the impoverished and unbalanced nutrient supply in the California serpentine grassland, and the experiment is being repeated to

investigate this possibility.

Table 7.9 summarizes the state of knowledge about pairwise interactions, and Table 7.10 shows similar data for larger assemblages.

7.3. CONCLUSIONS AND RESEARCH RECOMMENDATIONS

All of the studies reviewed in this paper were carried out in some type of growth chamber, and in general all factors except those specifically under study were maintained at levels as optimal as practical for plant growth. Herbivores and pathogens were excluded,

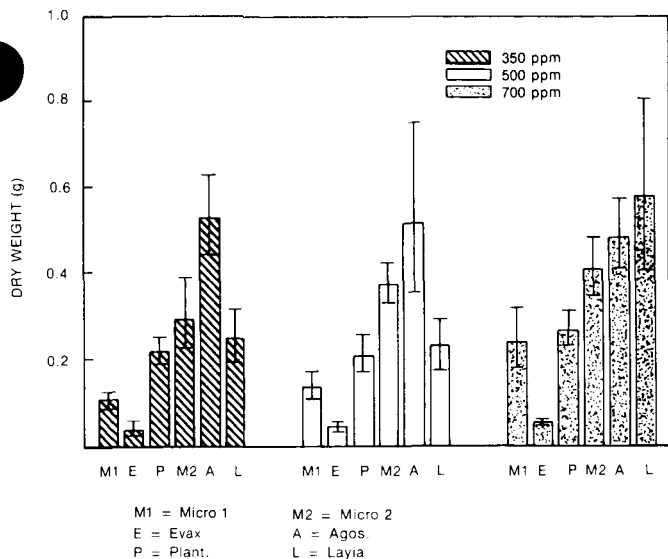


Figure 7.8. Response of six serpentine grassland species to CO₂. Source: Bazzaz et al. (1985).

extremes of temperature and light were avoided, and water was available without limit except in moisture stress experiments. In short, only a fraction of the ordinary stresses experienced by most plants over even short time periods were included in these experiments, because they were designed to test specific aspects of the effects of elevated atmospheric CO₂. The effects of the current worldwide CO₂ increase will, by contrast, be felt against the enormously multifaceted background of the global environment, and so these effects are likely to be much more complex than the ones reviewed here. The conclusions found in Table 7.11 should be viewed with this caution in mind.

Future research on the effects of elevated CO₂ concentration at the community level should be guided by a coordinated plan; such a plan is presented in this section. Also presented are suggestions for specific research projects and the techniques that should be used in these projects.

Table 7.9
Effects of Elevated CO₂ Concentrations on Pairs of Species

Genus, Species		RGR ^a Phenology	Reproductive Biomass		Vegetative Biomass		Other Variables	Source
Target	Competitor		Target	Mix	Target	Mix		
<i>Abutilon</i>	<i>Glycine</i>				I	I	Nutrients	Carlson and Bazzaz (1980)
<i>Amaranthus</i>	<i>Glycine</i>				I	I	Nutrients	Carlson and Bazzaz (1980)
<i>Festuca</i>	<i>Sorghum halepense</i>	C	I ^b			U		Carter and Peterson (1983)
<i>Sorghum halepense</i>	<i>Festuca</i>	C	D ^b			U		Patterson et al. (1984)
<i>Sorghum halepense</i>	<i>Glycine</i>		U			I		Patterson et al. (1984)
<i>Trifolium</i>	<i>Lolium</i>		I	I ^b				Overdieck et al. (1984)
<i>Lolium</i>	<i>Trifolium</i>		D ^b	I ^b				Overdieck et al. (1984)

Note: Symbols: I, increase; D, decrease; U, unchanged; C, complex changes.

^aRGR, relative growth rate.

^bTrend only.

Table 7.10
The Effects of Elevated CO₂ on Groups of Species

Species Group	Total Biomass	Composition Biomass	Change Seeds	Other Variables	Source
<i>Acer</i> <i>Franixus</i> <i>Platanus</i>	I	X	-	Light	Bazzaz et al. (1985)
<i>Liriodendron</i> <i>Carya</i> <i>Quercus</i>	I	X	-	Light	Bazzaz et al. (1985)
<i>Amaranthus</i> <i>Polygonum</i> <i>Ambrosia</i> <i>Abutilon</i>	I	X	-	Moisture	Bazzaz & Carlson (1984)
<i>Abutilon</i> <i>Amaranthus</i> <i>Ambrosia</i> <i>Chenopodium</i> <i>Polygonum</i> <i>Setaria</i>	I I	X X	X X	Light Nutrient	Zangerl & Bazzaz (1984)
Serpentine Annuals	I	U	-	-	Bazzaz et al. (1985)

Note: Symbols: I, increased; X, changed; U, unchanged.

Table 7.11
Summary of Effects of Increased CO₂ Concentrations on Plant Communities

Effect	Uncertainty	Comments
Total community biomass will increase in essentially all communities	Extremely low	Virtually all data sets agree
Community composition will change	Low for the general principle, high for exactly what changes will occur	So far, there is no clear way to predict "winners"
C ₄ species will compete less well against C ₃ species	Low	Preliminary data on <i>Setaria</i> and <i>Amaranthus</i> , both C ₄ , show substantial growth stimulation
Life cycles of most plants will speed up	Moderate	C ₃ speeds up, <i>Sorghum</i> C ₄ slows down, corn C ₄ speeds up
Vegetation growth enhancement will result in reproductive enhancement	Low	An entire spectrum of changes in seed output can be seen
Crop-weed interactions may increasingly favor C ₃ weeds	Low	<i>Amaranthus</i> (C ₄) may increase in importance, undermining this conclusion

7.3.1 Recommendations for Modeling

Modeling is an essential step in order to avoid running growth chamber experiments for all communities of interest. However, a mathematical model is only as good as the data on which it is based, so an extremely close coordination of modeling and experimentation is essential.

Figure 7.9 shows a plan for modeling, validation, and model refining for a community of early successional annuals. The plan calls for a gradual buildup, from a detailed understanding of the physiological response of two species to elevated CO₂ concentrations, to a predictive model that will describe the response of a multispecies community. At each step, the model is extended and validated and then refined to take into account any discrepancy between the prediction made by the model and the empirical data.

7.3.2 Recommendations for Experimental Approach

7.3.2.1 Experiment Duration

Carbon dioxide fumigation experiments must be carried to reproductive maturity whenever possible. Evidence cited in this report indicates that life-cycle times can

be altered by elevated concentrations of CO₂. Such alterations in growth period can lead to the conclusion that CO₂ has caused an increase in biomass, when the correct conclusion is that the same final biomass is reached at all CO₂ levels, but it is reached more quickly at higher CO₂ levels. Garbutt and Bazzaz (1984) showed no significant difference in final biomass of reproductively mature *Abutilon* grown at different CO₂ concentrations while Bazzaz and Carlson (1984) reported a significant increase in biomass at elevated CO₂ concentrations of plants harvested at 45 days. Although these data are drawn from different experiments, current experiments are confirming this effect.

The effect of the CO₂ concentration on seed number and quality is the single most important index of its effect on evolutionary potential in the community, and seed set can only be evaluated at reproductive maturity.

7.3.2.2 Growth Analysis

Growth analysis as well as simple final yields, seed set, and biomass should be used. It is essentially impossible to construct models of CO₂-induced effects without the dynamic picture provided by growth analysis.

7.3.2.3 Long-Term Effects

Physiological understanding of the long-term effects

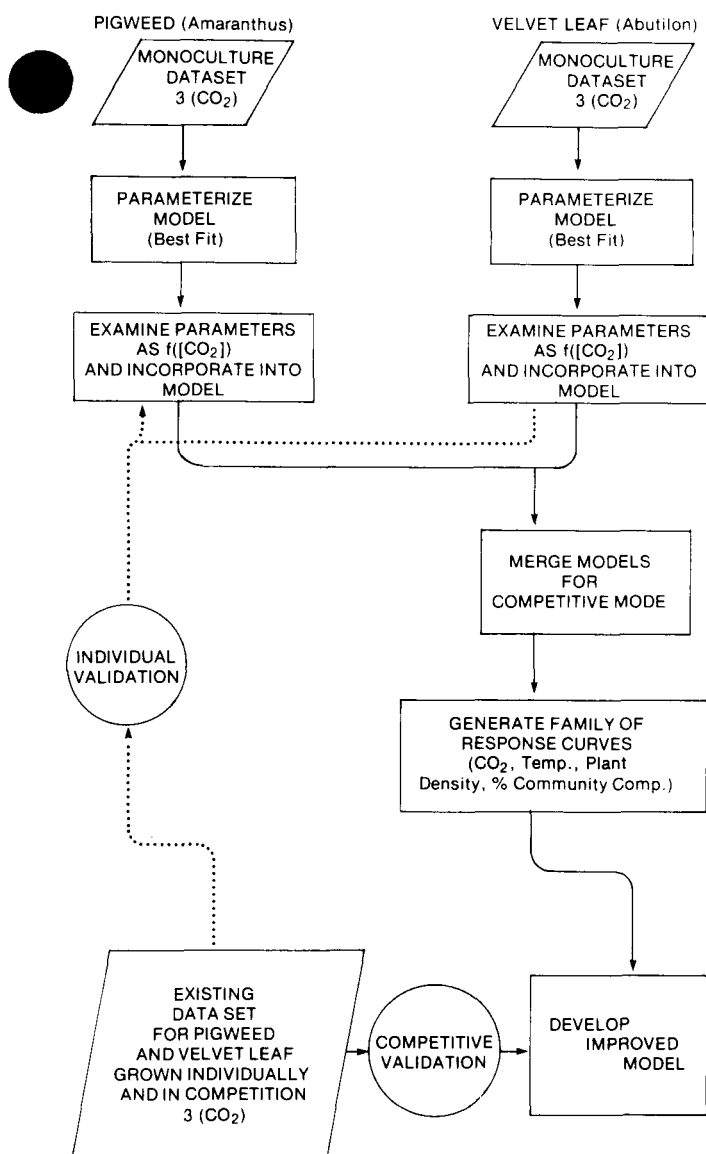


Figure 7.9. Plan for model definition, validation, and refinement.

of CO₂ must be extended. Single-point data on photosynthesis and water use are not sufficient for modeling. Measurements should be made of the daily course of stomatal conductance, photosynthesis, and water relations of several species under several CO₂ conditions so that the physiological predictions from leaf chamber studies can be validated and refined. Very few data are available about the interaction of high CO₂ concentrations and stresses, especially water stress, but many predictions have been based on these few data.

7.3.2.4 Weed-Crop Interactions

Weed-crop interactions must be studied more extensively. Previous studies usually have not been carried to reproductive maturity, for either weeds or crops,

and so more research is needed. The data on seed production from Zangerl and Bazzaz (1984) suggest that *Amaranthus retroflexus*, a C₄ weed that has developed a strain that is immune to triazine herbicides, shows a much greater stimulation by CO₂ than would ordinarily be expected for a C₄ plant, so the economic importance of research in this area could be substantial.

7.3.2.5 Plant-Animal Interactions

Plant-animal interactions should be included in the CO₂ research program. There is ample evidence from the general plant-animal literature that C:N ratios of plant tissue are important in determining herbivore preferences, and from studies carried out with varying concentrations of CO₂ it is clear that C:N ratios change, usually increasing with an increase in the atmospheric CO₂ concentration. No plant-herbivore population studies have yet been performed. However, in the only study of its kind, changes in feeding behavior and subsequent growth of individual soybean looper larvae were related to changes in C:N ratio of soybean leaves grown in elevated CO₂ concentration (Lincoln et al. 1984). Increasing atmospheric CO₂ may well have effects on population levels, feeding preferences, and life cycles of herbivores, especially insects, which may then alter the structure of plant communities. This area has not been studied.

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8. GLOBAL BIOSPHERIC RESPONSE
TO INCREASING ATMOSPHERIC
CARBON DIOXIDE CONCENTRATION

D. M. Gates
University of Michigan

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8.1 INTRODUCTION

An understanding of the response of the biosphere to increasing levels of atmospheric carbon dioxide (CO_2) concentration is of great importance for our understanding of the global carbon cycle. The biosphere is made up of many ecosystems, small and large, terrestrial and aquatic, and managed and unmanaged. The biosphere may be a source or a sink of CO_2 to or from the atmosphere because of the following activities occurring simultaneously: clearing of land for agriculture and pasture, harvest and regrowth of forests, abandonment of agricultural land, and the stimulated growth of vegetation resulting from a CO_2 fertilization. The sum of the fluxes from all of these activities produces a net flux of CO_2 between the biosphere and the atmosphere.

The title of this chapter suggests a concern with the direct response of the biosphere to increasing levels of atmospheric CO_2 . Direct human disturbances to the biosphere, such as land clearing, deforestation, or burning, which contribute CO_2 to the atmosphere, are not addressed in this chapter. Increasing levels of atmospheric CO_2 may affect primary productivity and in turn affect autotrophic respiration. Heterotrophic respiration may also be affected. Climate change accompanying an increase in atmospheric CO_2 will be highly significant to the biosphere, but this topic is not to be addressed here.

Primary productivity by vegetation fixes large quantities of CO_2 annually and respiration by all organisms, both plants and animals, including fungi and microbes, releases CO_2 to the atmosphere. Whether fixation exceeds respiration, or vice versa, determines whether the biosphere is a net sink or source of atmospheric CO_2 . Two properties of plant communities or biomes that are of significance to the global carbon budget and to the future atmospheric CO_2 concentration are the amount of standing biomass and net primary productivity (NPP). Temperature and moisture are the principal environmental variables determining the productivity of biomes, but radiation, CO_2 concentration, and nutrient availability are also important.

8.2 NET ECOSYSTEM PRODUCTION

The main fluxes of carbon between the atmosphere and the biosphere are gross primary production (GPP), autotrophic respiration, heterotrophic respiration, and human induced fluxes. The fixation of CO_2 into carbohydrates by green plants is referred to as GPP. Plants respire CO_2 in a process known as autotrophic respiration (R_A) that results from maintenance respira-

tion and growth respiration. NPP is given by the following equation:

$$\text{NPP} = \text{GPP} - R_A. \quad (8.1)$$

This represents the accumulation of biomass that would occur if there were neither harvesting and grazing nor decaying of any plant material. However, animals use plant materials for food and pass some of the biomass along the food chain to various omnivores and carnivores. The living animals respire some of this material and excrete some of it. All plants and animals eventually die and are decomposed by microorganisms. During all of these processes CO_2 is released through heterotrophic respiration, R_H . Within any community of plants and animals, net ecosystem production (NEP) is given as follows:

$$\text{NEP} = \text{NPP} - R_H = \text{GPP} - R_A - R_H \quad (8.2)$$

For an ecosystem to accumulate biomass it must have an NEP greater than zero. However, as an ecosystem matures toward a climax stage, the NEP rate may be less than it was for intermediate stages of development and indeed it may even approach zero. It is often assumed that 50% of the global GPP is used by plants for respiration. However, the amount going into autotrophic respiration may vary from 20 to 80% according to Whittaker and Likens (1973). In the special case of $\text{NEP} = 0$, if $R_A = 0.50 \text{ GPP}$ then $R_A = \text{NPP} = R_H$. If $\text{GPP} = R_A + R_H$ for an ecosystem, then there would result neither a gain nor a loss of biomass over time. If $\text{GPP} > R_A + R_H$, an ecosystem will accumulate biomass or carbon over time. If an ecosystem has $R_A + R_H > \text{GPP}$, then it is a decomposing system that is losing biomass, and the net result is a release of CO_2 to the atmosphere.

One of the most important questions concerned with the carbon cycle of the global ecosystem is whether NEP is positive, zero, or negative over time and how it will respond to an increasing concentration of atmospheric CO_2 .

8.3 CO_2 STIMULATION OF PRIMARY PRODUCTIVITY

It is well known that an increase of the atmospheric concentration of CO_2 will produce an increase in the assimilation rate of whole plant leaves. Lemon (1983) and Chapters 4 through 6 in this volume present a full discussion of the photosynthesis response to increasing levels of CO_2 . In terms of the global carbon budget it

is necessary to understand how an increase in the whole leaf photosynthetic rate may translate into an increase of the NPP rate and from this to a possible increase of the net ecosystem production rate.

Although we have a good deal of information concerning the direct response of plant leaves to increased CO₂ concentration, there is very little information to guide us concerning the response of plants grown throughout their life cycle in an enriched CO₂ atmosphere, especially those grown with the limiting factors of nitrogen, water, and temperature. There is no information as to what will happen to plant responses when the plants are grown in slowly increasing enriched CO₂ atmospheres for many generations, similar to the conditions that are expected to occur in nature over the next 100 years or more.

If it is difficult to predict how whole plant communities respond to increasing atmospheric CO₂ levels, it is even more difficult to predict how whole ecosystems will respond. This is particularly so because of heterotrophic respiration and its response to CO₂ levels.

8.4 BIOTIC GROWTH FACTOR

In order to model the response of the land biota to increasing levels of atmospheric CO₂ when formulating a global carbon cycle model, Bacastow and Keeling (1973) defined a parameter, β , called the "biotic growth factor." It is defined as a fractional change in the NPP productivity with a fractional change in the atmospheric CO₂ concentration and may be written as:

$$\beta = \frac{\Delta \text{NPP}}{\text{NPP}_0} \div \frac{\Delta C_a}{C_{a0}}, \quad (8.3)$$

where NPP₀ is the initial value of the net primary productivity for an initial value of the atmospheric CO₂ concentration C_{a0}.

An assumption made by Bacastow and Keeling was that plant photosynthesis and growth is proportional to the logarithm of the amount of CO₂ in the atmosphere. Actually, plant photosynthesis, and ultimately growth, does not follow a logarithmic response to CO₂. The response curve always approaches a maximum value asymptotically, something a logarithmic curve does not do. It is more correct to use Michaelis-Menten kinetics to describe the photosynthetic response or growth response to increasing CO₂ concentration, even though the chemical reactions of photosynthesis are much more complex than single enzyme kinetics.

The Michaelis-Menten expression for the photosynthetic rate as a function of the atmospheric CO₂

concentration is given by the following rectangular hyperbola:

$$P = \frac{P_{\max} + R_0}{1 + \frac{K_m}{C_a}}, \quad (8.4)$$

where P_{max} is the maximum photosynthetic capacity of the plant, K_m is the Michaelis coefficient and has the value of the atmospheric CO₂ concentration when P = P_{max}/2, and R₀ is the residual respiration at zero CO₂ concentration. See Lommen et al. (1971) and Edwards and Walker (1983) for a discussion of the application of enzyme kinetics to whole leaf photosynthesis.

When the Michaelis-Menten response function is used to determine the biotic growth factor, one gets

$$\beta' = \frac{K_m}{K_m + C_a} \frac{P_{\max} C_a}{P_{\max} C_a + R_0 [C_a + K_m]}, \quad (8.5)$$

which reduces to the following approximation for small values of R₀:

$$\beta' = \frac{K_m}{K_m + C_a} \quad (8.6)$$

Values of the biotic growth factor may be calculated whenever one has the measured response to CO₂ concentration of photosynthesis, growth, or even yield for a plant. The absolute values of β or β' differ depending on whether Equation 8.3, 8.5, or 8.6 is used for the calculation; however, general trends and relative changes will be similar among the formulations. It is clear from Equation 8.5 or 8.6 the value of β' will increase with increasing K_m.

8.4.1 Values of β' for Field-Grown Soybeans

Soybeans were grown at four locations in the southeastern United States in outdoor controlled environment chambers or open-top chambers exposed to natural sunlight. Photosynthesis, biomass yield, and seed yield were measured at concentrations ranging from 120 to 990 parts per million by volume (ppm). Allen et al. (in press) have calculated β' from these data and some of their values are given in Table 8.1 for atmospheric concentrations of 340 and 680 ppm. The β' factor decreased as the physiological process went from net photosynthesis to biomass yield to seed yield. The authors explain that part of the reason for the decrease in β' may lie with the fact that CO₂ exchange rates for photosynthesis were measured near midday rather than integrated over the whole day and season. However,

Table 8.1
Biotic Growth Factor β' for Several Plant Species

Plant	Carbon Dioxide Concentration		Source
	340 ppm	680 ppm	
<i>Glycine max</i>			Allen et al. (in press)
Photosynthesis	0.75	0.42	
Biomass Yield	0.64	0.34	
Seed Yield	0.49	0.28	
<i>Populus deltoides</i>			Regehr et al. (1975)
Photosynthesis	0.49	0.29	
<i>Populus grandidentata</i>			Jurik et al. (1985)
Photosynthesis			
Canopy, 30°C	0.61	0.44	
Canopy, 20°C	0.50	0.33	
<i>Quercus rubra</i>			Jurik et al. (1985)
Photosynthesis			
Canopy	0.69	0.53	
Understory	0.60	0.43	
<i>Acer saccharum</i>			Jurik et al. (1985)
Photosynthesis			
Understory	0.56	0.39	
Understory	0.50	0.33	
Understory	0.50	0.33	

they also point out that there is a drop in the ratio of seed yield to biomass yield, a ratio called the harvest index, with increasing CO₂ concentration. They suggest that this trend of proportionately less partitioning of photoassimilate to seed growth might be corrected with improved plant breeding and selection.

Allen et al. (in press) also determined values of β' when levels of atmospheric CO₂ were as low as 260 ppm. They conclude that we might have had an 11% increase in seed yield from about 1700 to 1958 because of increased CO₂ concentration if the preindustrial value of CO₂ was 260 ppm. From 1958 to 1982, when the CO₂ concentration was increasing from 315 to 340 ppm, the analysis predicts that soybean seed yield may have increased by 4%.

If the atmospheric concentration of CO₂ increases from 340 to 680 ppm, Allen et al. (in press) predict a further soybean seed yield increase of 30%, all other factors being equal. Kimball (1983) and Cure (Chapter 5, in this volume) have predicted 33 and 29% increases in soybean yield, respectively, with a doubling of CO₂. Waggoner (1984) has estimated soybean and other grain legume yield improvement of 0.1% for each ppm increase of CO₂ or 34% increase for a doubling of the CO₂ concentration. This is equivalent to a $\beta' = 0.34$ at an initial CO₂ concentration of 340 ppm.

8.4.2 Values of β' for Tree Leaves

Kramer and Sionit (in press) have discussed the effects of increasing CO₂ concentration on the physiology and growth of forest trees. The growth of trees is often limited by drought, shade, mineral deficiency, and lack of nitrogen, as well as by low CO₂ concentrations in a forest stand. Unfortunately, the information available concerning these factors and their combined effect on forest trees is very scarce. For the present discussion we shall assume that forests will respond to increasing levels of atmospheric CO₂ in a manner proportionate to their photosynthetic response. There is evidence for increased photosynthetic response of forest conifers *Pinus attenuata*, *P. coulteri*, and *P. ponderosa* to increased CO₂ levels according to Hurt and Wright (1976) and Green and Wright (1977).

Measurements of the photosynthetic response to concentrations of CO₂ by the leaves of deciduous forest trees in situ in northern Michigan have been made by Jurik et al. (1985). From the data for Aspen, *Populus grandidentata*, the values for β' are given in Table 8.1. Aspen leaves are shade intolerant and therefore these measurements were made on leaves near the top of the canopy. Regehr et al. (1975) made measurements of the photosynthetic rate of seedlings of cottonwood, *P. deltoides*, and the values derived from their data are also given in Table 8.1. *Quercus rubra* leaves exhibited the

highest β' value measured, a value of 0.69 as given in Table 8.1. The leaves of this tree were in the overstory near the top of the canopy. *Acer saccharum* leaves in the understory were measured to have the β' values shown in Table 8.1.

Most of the understory leaves have smaller β' values than do the leaves making up the canopy of the forest. Therefore, the understory plants are going to be less responsive to increasing levels of CO_2 than the overstory trees will be.

8.4.3 Effect of Limiting Environmental Factors on β

Much of the data available for the photosynthetic response to increasing CO_2 levels are for plants well supplied with nutrients and water, and for saturating light and optimum temperature conditions. However, there is now some information in the literature concerning the CO_2 response of photosynthesis when plants are growing under limited amounts of water, nutrients, and light, or growing at various temperatures.

A number of investigators of the response of plants to increasing levels of atmospheric CO_2 have felt that the NPP would be strongly limited by nitrogen, other nutrients, light, water, or temperature. If CO_2 enrichment of a plant stimulates growth or yield, then the plant will require more nutrients to build the additional plant material. It is then logical to suggest that a lack of nutrients will limit growth and that additional CO_2 will not produce more growth. It is also logical to assume that if light or water are limiting to growth that little response to increased CO_2 will occur.

Botkin (1977) felt that where limitations of temperature, moisture, and soil nutrients are severe, CO_2 enrichment would have a negligible effect on plant productivity. This idea has been reiterated by Hobbie et al. (1984) and Lugo (1983). Many modelers of the global carbon cycle have assumed that β values would be substantially smaller for the biospheric response to increasing CO_2 levels than for the response of single leaves or of crops because of limiting environmental factors. Limitations imposed by soil nitrogen availability are widespread and water stress limitations are commonplace for many ecosystems (see Goudriaan and Ajtay 1979). It is conceivable that water stress may be of particular significance in limiting a plant's response to increasing CO_2 levels, because it usually occurs when temperature and light are optimal. It is also possible, as pointed out by Gifford (1980), that CO_2 enrichment may improve the use efficiency by plants of water, light, or nutrients. There is also an increase of K_m and hence of β or β' for photosynthesis with

increasing oxygen concentration (see Tenhunen et al. 1980; Charles-Edwards 1981).

8.4.3.1 Nitrogen Effect

In the case of nitrogen supply, Wong (1980) gives the photosynthetic response to CO_2 for plants with various levels of nitrogen nutrition (24, 12, 4, and 0.6 mM NO_3). Wong calculated β values according to Equation 8.3 at ambient CO_2 and at 660 ppm. In most instances the value β decreased with increasing nitrogen deficiency, but the change was very small except at the lowest level of nitrogen. For cotton plants there was a slight increase in β with increasing nitrogen deficiency except at the lowest level of nitrogen. Gifford (1980) reported that for wheat plants grown in abundant nitrogen and for those grown in limited amounts of soil nitrogen the response to CO_2 enrichment was greater in low nitrogen levels than it was in high nitrogen levels. Kimball (1985) has placed the results of many different crop growth or yield response experiments to CO_2 fertilization with various nitrogen concentrations into a single figure. The general trend of all the data is for a greater percentage increase in growth with a CO_2 enrichment as a function of the increasing availability of nitrogen. Kimball uses this observation to say that as the ambient levels of CO_2 increase farmers will need to increase the fertilizer amounts in order to gain the yields commensurate with the CO_2 increase. Although we do not have the evidence from natural ecosystems, it is most probable that nitrogen limitations in natural environments will reduce the responsiveness of these plants to increasing levels of CO_2 .

8.4.3.2 Water

It is well known that an increase in the ambient partial pressure of CO_2 reduces the transpiration rate of a plant, other environmental conditions being the same. Raschke (1975) showed that this is the result of a closing response of stomata to increasing concentrations of CO_2 . A useful concept is the term water-use efficiency, defined as the ratio of the quantity of CO_2 fixed to the quantity of water transpired. Water-use efficiency always increases with increasing CO_2 concentration for two reasons, as further discussed in Chapter 4 of this volume. The first reason is that with increasing ambient CO_2 concentration there is an increase in the concentration gradient for the diffusion of CO_2 into the plant and therefore an increase in photosynthesis. Secondly, the stomatal conductance decreases with increasing ambient CO_2 and produces a greater percentage change in the total conductance to water vapor diffusion than it does to CO_2 diffusion. Water-use efficiency increases at a greater rate for C_4 plants than it does for C_3 plants with increasing ambient CO_2 concentration (see Wong 1980). However, one can expect that plants growing

in environments with higher CO₂ levels will develop larger leaves, greater canopies, and more extensive root systems, each of which will enhance the use of water and partially offset the improved water-use efficiency just described. Although C₄ plants will have better water-use efficiencies than C₃ plants, the C₃ plants will have greater photosynthetic responses than C₄ plants to higher CO₂ levels.

I have analyzed the data by Mooney (1980) who obtained from four Death Valley species responses of CO₂ assimilation rate with CO₂ concentration at different levels of leaf water potential. The values for K_m and β are given in Table 8.2 for the various leaf water potentials. Water stress was induced by withholding soil water. All of these plants grow where water stress can be encountered at any time of the year. The values of K_m and β increase with increasing water stress for *Atriplex hymenelytra* and *Tidestromia oblongifolia*, the two C₄ species, remain unchanged for *Larrea divaricata*, and decrease somewhat for *Camissonia brevipes*, the two C₃ species. One cannot assume that these well-adapted desert plants respond to water stress in a manner typical of plants from other habitats. However, they happen to be plants for which useful data are available. Also, Hurt and Wright (1976) and Green and Wright (1977) report that three species of pines were more responsive to an incremental increase of CO₂ when under water stress than they were when they were well watered.

Regehr et al. (1975) measured the photosynthetic and transpiration response of *Populus deltoides* to increasing CO₂ levels under conditions of drought and flooding. From their photosynthetic response curve to CO₂ I have calculated the value of β' as given in Table

8.1. Values of 0.49 and 0.29 at 340 and 680 ppm of CO₂, respectively, were obtained for well-watered plants. The photosynthetic rate decreased with increasing water stress only when the leaf water potential was below -8 bar (10⁴ Pa) and became zero at -10 to -11 bar. There is not sufficient data given to calculate β' as a function of the water stress, except to indicate that it would increase with increasing water stress.

Gifford (1979a, 1979b) reported gas exchange experiments in which wheat (*Triticum aestivum* L.) plants were grown in controlled environments at normal (340 ppm) CO₂ concentration and elevated (590 ppm) CO₂ concentration under water-limited and light-limited conditions. Gifford calculated a β factor based on the logarithmic response function used originally by Bacastow and Keeling (1973). The published data are not sufficient to calculate a β' according to Equation 8.3, so the values of β given by Gifford are reported. The values of β for the growth of wheat plants grown under increasing levels of moisture stress were as follows: 0.49 for wet, 0.76 for moist, 0.74 for dry, and 0.84 for very dry soil.

Kimball (1985) and Cure (Chapter 5 of this volume) give tabulations of the growth or yield responses of several crop plants to a doubling of atmospheric CO₂ concentration under well-watered and drought-stressed conditions. They conclude that a greater relative CO₂ stimulation of growth or yield occurs under drought-stress conditions than under well-watered conditions.

Under water stress the rate of plant growth is determined more by the photosynthetic supply than by the strength of the sinks for photosynthates going into new plant material. Therefore, it may be expected that

Table 8.2
Calculated Values of K_m and β for Four Species of Plants
Native to Death Valley, California at Various Levels of Water Stress

<i>Atriplex hymenelytra</i> , C ₄				
Leaf Water Potential (bars)	-10	-20	-31	
K_m	18	45	45	
β^a	0.05	0.12	0.12	
<i>Tidestromia oblongifolia</i> , C ₄				
Leaf Water Potential (bars)	-9	-11	-14	-15
K_m	28	48	70	110
β	0.08	0.12	0.17	0.24
<i>Larrea divaricata</i> , C ₃				
Leaf Water Potential (bars)	-10	-27	-30	-36
K_m	175	220	180	200
β	0.34	0.39	0.35	0.37
<i>Camissonia brevipes</i> , C ₃				
Leaf Water Potential (bars)	-1.5	-6.9	-14.3	
K_m	125	120	85	
β	0.27	0.26	0.20	

Note: CO₂ response curves from Mooney (1980).

^aCalculated at 340 ppm.

the growth of plants will generally be more favorably enhanced by an increase of CO₂ for plants under water stress than for well-watered plants. However, there are probably exceptions to this and one should not count on a great deal of enhancement of β with water stress as a general rule. For β under drier conditions one may expect C₄ plants to respond better than C₃ plants because of a greater increase in water-use efficiency.

8.4.3.3 Light

Plants adapted to a low light regime have quite different photosynthetic responses to light than do plants grown in a high light climate. Gifford (1980) shows that for cotton (*Gossypium hirsutum*) leaf photosynthesis is relatively more responsive to CO₂ enrichment at low light levels than it is at higher light levels. He also reports the same trend for *Pinus attenuata*. Gifford (1979a, 1979b) calculated β for the growth of wheat (*Triticum aestivum*) plants the following values of: 0.23 for high light (640 $\mu\text{mol m}^{-2}\text{s}^{-1}$) and 0.45 for low light (220 $\mu\text{mol m}^{-2}\text{s}^{-1}$). Since the plants grown under high light conditions developed larger leaf surfaces than those grown under low light, Gifford then calculated β values when the growth rate was normalized to a leaf area index of 3.5. He then obtained values of 0.11 and 0.62 for high and low light levels, respectively, at a CO₂ concentration of 340 ppm. One can argue physiologically that higher CO₂ levels are more effective in suppressing photorespiration rates at low light than at high light levels. This effect has been discussed by Bjorkman (1971). However, as described in the following paragraphs, not all plant species seem to behave in this anticipated manner.

Kimball (1985) shows growth response data for C₃ plants with CO₂ enrichment at several light intensities. The author comments on the high amount of scatter in the data, but concludes “. . . that by the time a plant has integrated its varying photosynthetic response into a final growth response, the stimulation of C₃ crops by CO₂ enrichment is roughly the same over a very wide range of light regimes.” In the figure there is a slight suggestion that C₃ plants are relatively more responsive to CO₂ stimulation at low light compared with higher light intensity, but it is not a strong effect. Cure (Chapter 5) observed no consistent pattern either within or among crop species in relative response to elevated CO₂ concentration at different light levels.

Referring to the β' factors given in Table 8.1 for some forest tree species from the research of Jurik et al. (1985), it is clear that there is not a significant difference between the responsiveness of the understory and the canopy plants. Comparing bigtooth aspen (*P. grandidentata*), a canopy plant, with sugar maple (*A. saccharum*), an understory plant, the β' value is almost unchanged. But when the β' factor for red oak leaves

in the canopy is compared with that for red oak leaves in the understory, the β' value went down.

Wong (1980) reported that the growth of snow gum (*Eucalyptus pauciflora*) to increasing levels of CO₂ yielded a β factor that increased with an increase in light intensity.

8.4.3.4 Temperature

Kimball (1985) summarized the results of several CO₂ enrichment experiments for the growth of plants at several temperatures. The scatter of the data is large, but the conclusion is that there is not a significant temperature effect. However, there seems to be a trend toward a greater responsiveness toward temperature optimum. Calculations by Gates et al. (1983) concerning the photosynthetic response of laboratory-grown soybeans to increasing levels of CO₂ show that the β factor is slightly reduced at suboptimal temperatures. Gifford (1980) also indicates this to be his experience. Jurik et al. (1985) found a lower β' factor at 20°C compared with 30°C for bigtooth aspen in the forest canopy as shown in Table 8.1. Similarly, Cure (Chapter 5) found responses to CO₂ were larger at high temperature than at low temperature in all except one of the studies on crop species examined.

8.4.3.5 Probable β Value

The actual effective β value for annual ecosystem net carbon fixation would be modified by the way the ecosystem partitioned incremental growth between the rapid turnover components made up of leaves and roots, and the long-term storage parts made up of wood and soil organic matter. Without having definitive measurements of ecosystem response to increasing levels of atmospheric CO₂ concentration, it is inferred from the response of single plants and of single plant leaves that the β factor is expected to be positive and most likely between 0.25 and 0.50.

8.4.4 Values of β from Global Carbon Models

Bacastow and Keeling (1973) formulated a nonlinear six-reservoir geochemical model of the interaction of the atmospheric CO₂ concentration with the oceans and land biota. Then they adjusted the parameters of the model until the model predictions agreed as closely as possible with the following observations: the observed CO₂ increase in the atmosphere from 1959 to 1969, the measured decrease in atmospheric ¹⁴C/C ratio, and the observed ¹⁴C/C ratios of surface and deep ocean water. Here, C refers to the inactive carbon in the system. The adjusted parameters included the biotic growth factor, some transfer times for the ocean and

atmosphere, and the carbon content ratio of the surface layer to the atmosphere. They obtained an inferred β in the range 0.4 to 0.5. However, by changing certain assumptions in the model, based on uncertainties in the airborne fraction of fossil fuel CO_2 released to the atmosphere and other assumptions, they found that β could have been as low as 0.05. It is evident now that they had chosen a value for the carbon content of the land biota (1720 Gt) ($1 \text{ Gt} = 10^{15} \text{ g}$) that was at least three times the currently accepted value (562 Gt). This change would have placed their minimum value of β at 0.15.

Björkström (1979) used a mathematical model of the global carbon cycle to calculate carbon exchange among the atmosphere, oceans, and land biota. His ocean model was divided into 12 compartments. At first he used a preindustrial atmospheric CO_2 level of 285 ppm and obtained $\beta = 0.25$ to account for the apparent increase in the atmospheric CO_2 concentration up to 1970 when the measured value was 350 ppm. He then questioned the use of 285 ppm as the preindustrial value used and suggested that it might have been less than 285 ppm. He ran his model keeping all parameters constant except the preindustrial atmospheric concentration of CO_2 and β . If $\beta = 0$, the preindustrial level of CO_2 had to be 250 ppm in order that the 1970 value would be at 320 ppm. He then tested the sensitivity of the model to a large (1090 Gt) biota with a slow (39 Gt y^{-1}) turnover time of carbon and a small (560 Gt) biota with a fast (86 Gt y^{-1}) turnover time. He found that if the preindustrial value was 270 ppm, $\beta = 0.04$ for the small and fast biota, and $\beta = 0.08$ for the large and slow biota. The higher the preindustrial level of atmospheric CO_2 is assumed to be, the larger the β factor must be to account for the rise in atmospheric CO_2 .

It is also possible that these earlier modelers had underestimated the total amount of CO_2 being emitted to the atmosphere because of an underestimate of the amount released from forest destruction during the latter 19th and early 20th centuries. Björkström (1979) would have obtained a larger β value if he had used for the integrated release of carbon of biological origin for the period 1860 to 1975 a value greater than the 60 Gt of carbon (C) that he used. Bolin (1970) estimated the value to between 40 and 100 Gt C. Stuiver (1978) estimated 100 Gt C released for the period up to 1950. Therefore, the total amount released up until 1975 may have been as much as $150 \pm 25 \text{ Gt C}$. Hampicke (1979) concluded that the annual release of biological carbon in 1970 was between 1.5 and 4.5 Gt y^{-1} .

8.4.5 Values of β from CO_2 Amplitude

The seasonal amplitude of the atmospheric CO_2 concentration at various stations throughout the world varies with latitude, and all stations appear to have a slowly increasing amplitude with time. The seasonal amplitude is largest, about 12 ppm, at Weathership P located at 50°N latitude. The amplitude is less at low latitude stations, such as Mauna Loa, Hawaii, at 19.5°N latitude where it is 6 ppm and at Fanning Island at 3.9°N latitude, where it is 2 to 3 ppm. South of the equator the seasonal amplitude is 1 to 2 ppm. Bacastow and Keeling (1973), Bacastow et al. (1981), Fung et al. (1982), Pearman and Hyson (1980, 1981), and Wong and Pettit (1981) have discussed the seasonal amplitude and its possible causes.

Kohlmaier et al.¹ have made calculations of the possible amount of carbon stored in ecosystems in response to increasing levels of atmospheric CO_2 that will account for some of the increase in the seasonal amplitude as recorded at Mauna Loa over the period 1958 to 1982. They analyzed data from plant growth experiments in the field obtained by Rogers et al. (1983) at North Carolina State University, involving soybeans, corn, loblolly pine, and sweetgum. They also used Hartwell Allen's data for soybeans. Although there was a lot of variability in the values derived, they came to the conclusion that β should be between 0.25 and 0.50 and that the most appropriate value to use in their model would be 0.37.

Kohlmaier et al.² conclude that the change in the annual CO_2 amplitude must be larger than the relative increase in primary productivity. There is an amplification factor produced by respiration. If 20% of the stimulated NPP is stored in the biosphere and 80% of NPP is respired, using $\beta = 0.37$ they find an amplification factor of 1.6 for the amplitude at Mauna Loa, Hawaii. Since the mean value of $\Delta C_a/C_{a0}$ over the Mauna Loa record (1958 to 1982) is $0.33\% \text{ y}^{-1}$, they get $\Delta A/A_0 = 0.37 \times 0.33 \times 1.6 = 0.20\% \text{ y}^{-1}$. The more recent Mauna Loa amplitude change is about $0.66\% \text{ y}^{-1}$. It appears that the CO_2 fertilization effect on the biota will account for about 30% ($0.20/0.66 \times 100 = 30\%$) of the observed amplitude increase. Kohlmaier et al.³ give an uncertainty for this number from 23 to 42%.

Other processes must be contributing to the annual change in seasonal amplitude. An important contribution must come from the increase in use of fossil fuels during

¹ G. H. Kohlmaier, R. Revelle, and C. D. Keeling, "Exchange of CO_2 Between the Atmosphere and the Biosphere: Stimulation of the Terrestrial Vegetation by Fossil Fuel CO_2 in Combination With Other Man-made Changes." Manuscript in preparation.

² Ibid.

³ Ibid.

the last 24 years. Also there are disturbances of the biosphere that may be making a contribution to the changing amplitude. Such disturbances would include an increase in world food production, tropical forest clearing and afforestation in many other parts of the world, and maybe a small increase in the biological productivity of the oceans. These contributions to the increase in the CO₂ amplitude at Mauna Loa are estimated as follows: CO₂ stimulation (0.15 to 0.27% y⁻¹), world food production (0.11 to 0.17% y⁻¹), seasonal atmospheric circulation (0.07 to 0.26% y⁻¹), afforestation and deforestation (0.13 to 0.35% y⁻¹), seasonal fossil fuel use (0.02 to 0.08% y⁻¹), and an increase of ocean productivity (0.01 to 0.04% y⁻¹). The total contribution to the increasing CO₂ amplitude of the seasonal cycle at Mauna Loa would be from a minimum of 0.49 to a maximum of 1.18% y⁻¹. It is clear that if the maximum value is chosen for each component the change in amplitude could be accounted for entirely without any CO₂ stimulation of plant growth. If the minimum values are chosen for all except the growth stimulation, then the stimulation effect should have been about 0.30% y⁻¹.

Cleveland et al. (1983) have analyzed the time trends of the seasonal amplitudes of the atmospheric CO₂ at Mauna Loa and at the South Pole. They considered four possible causes of the changes in the seasonal amplitudes to be (1) changes in the seasonal use of fossil fuels, (2) increasing amounts of vegetation, (3) global photosynthetic activity, and (4) changes in ocean temperatures. They concluded that it was most likely that the CO₂ seasonal behavior reflects an increase in global photosynthetic activity.

8.5 EVIDENCE OF GROWTH ENHANCEMENT FROM TREE RINGS

Workers at the Laboratory of Tree-Ring Research, University of Arizona, have found a systematic trend of enhanced growth in subalpine conifers as revealed by annual growth rings. LaMarche et al. (1984) report greatly increased growth rates in the annual rings of subalpine conifers in the western United States since the mid-19th century. These growth rates are shown to be consistent in magnitude with global trends in the atmospheric CO₂ concentration.

Tree-ring measurements on subalpine bristlecone pines (*Pinus longaeva* D. K. Bailey and *P. aristata* Engelm.) at high-altitude sites from New Mexico and Colorado to California revealed large increases in growth rates from about 1840 to 1970. This positive growth trend correlated very well with warm season temperatures

for the years 1901 through 1960. However, when temperatures began to decrease during the 1960s, the growth rates of the trees continued to increase. A more recent sampling of the growth rates for limber pine (*P. flexilis* James) in central Nevada showed growth to accelerate during the 1970s. Then a study was made of the bristlecone pines growing at high altitude (3400 to 3500 m above sea level) in the White Mountains of eastern California, where nearby two high-altitude meteorological observatories were operated. These stations showed no significant climate trends during the years 1950 to 1980, while the growth rates of the trees remained at very high levels during the 1970s and into the 1980s.

LaMarche et al. (1984) believe "that subalpine vegetation generally, and upper tree-line conifers in particular, could now be exhibiting enhanced growth as a direct response to increasing concentrations of atmospheric CO₂." In fact, they show that the increase in the average growth rate of high-altitude bristlecone pine and limber pine is consistent with a 26% increase in the atmospheric CO₂ concentration from 1850 to 1983 (270 to 340 ppm). Furthermore, they believe that rising CO₂ levels have important long-term effects on the number of needle primordia and the rate of needle elongation leading to large long-term gains in photosynthetic biomass that in turn could reinforce the direct effects of CO₂.

However, Stockton⁴ has presented a very plausible alternative hypothesis for the cause of the observed increase in tree growth during the period 1850 to 1980 in central Nevada. His hypothesis is that climate, and particularly an increase in the annual September through August total precipitation, is likely to be the cause of the observed increased tree growth. Stockton writes that "this increase occurs over the elevation ranges 6000–11,000 ft. and is synchronous with trends in the records of nearby climatic stations as well as regional climate records." From careful spectral and cross-spectral analysis of both high and low elevation tree-ring sites he finds that both are responding positively to the September through August total precipitation, while only the high-elevation sites respond to summer precipitation. The September through August temperatures seem to be important, but in a negative sense. Higher temperatures result in smaller growth rings. This paper indicates that we cannot conclude that a growth enhancement produced by an atmospheric CO₂ fertilization effect has been demonstrated.

⁴"An Alternative Hypothesis to Direct CO₂ Fertilization as a Cause of Increased Tree Growth During 1850–1980 in Central Nevada." Manuscript in preparation.

8.6 ACCUMULATION OF CARBON BY THE BIOSPHERE

In the previous sections the responses of single leaves and of whole plants to increasing levels of atmospheric CO_2 have been discussed. As suggested earlier, the net ecosystem response to increasing CO_2 , to climate change, and to human disturbance is of great importance to the global carbon budget. However, this chapter is concerned explicitly with the biospheric response to increasing levels of CO_2 . For this purpose it is necessary to know the NPP of the major vegetation types in the world and then to understand how each type partitions the carbon assimilated into various storage pools, some of which are short-lived and some long-lived. A recent attempt to estimate the biospheric response to increasing CO_2 was made by Gifford (1980). He used nine major vegetation types in the world and based his NPP values on Ajtay et al. (1979). More recently Olson et al. (1983) have revised earlier estimates of the carbon content and NPP estimates for the major ecosystems of the world. Olson's group and Ajtay's group agree that the total plant carbon in the world is about 559 Gt, not counting the oceans which contribute only about 3 Gt. The NPP of the world's terrestrial ecosystems is about 60 Gt y^{-1} and they agree as to this number. It is difficult to compare their distribution of these numbers among the various ecosystems because they classify them somewhat differently.

Gifford (1980) calculated the annual increment of carbon stored in wood and soil organic matter in 1979 by the biosphere above what it would have been with a 1958 atmosphere (316 ppm) to be 1.65 Gt y^{-1} . Of this, 65% is stored as wood and 35% as soil organic matter. The total soil organic pool of carbon in the world was estimated by Schlesinger (1977, 1984) at about 1500 Gt. Therefore, any increased storage as estimated above as soil carbon is much too small a change to be detectable. Of the total carbon estimated to be stored in 1979, the greatest amount of storage is probably by the tropical savannas and grasslands (0.43 Gt y^{-1}), the next greatest by tropical forests (0.32 Gt y^{-1}) followed by temperate forests (0.20 Gt y^{-1}) and temperate grasslands (0.16 Gt y^{-1}). Lakes, bogs, and streams are estimated to store about 0.21 Gt y^{-1} of carbon. This would suggest that tropical forests, for example, are storing only about 19% ($0.32/1.65 \times 100\%$) of the total. Tropical grasslands would appear to be storing about 26% of the total. The calculations by Gifford are based on $\beta = 0.60$, and this was applied to all ecosystems. The amount of carbon stored in wood, 1.07 Gt y^{-1} , is a temporary storage because eventually this wood will decompose. The due course wood decay will equal or exceed the rate of sequestering, perhaps inside of 100 years. If

Gifford had used $\beta = 0.37$ instead of 0.60, he would have found that about 1.0 Gt y^{-1} of carbon would now be stored by the biosphere.

The primary productivity of the oceans and all contiguous waters amounts to about 46 Gt y^{-1} according to deVooy (1979). Considering the low total biomass of the oceans, between 2 and 3 Gt of carbon, this is a high productivity. However, the expected stimulation effect of the oceanic primary productivity by increasing atmospheric CO_2 concentration is for all practical purposes zero. The reason is that CO_2 in the oceans is not limiting primary productivity; in fact it is available in large excess. Furthermore, because of the chemical composition of seawater there is a buffering action such that for a given increase of the atmospheric CO_2 concentration there results a much smaller increase in the total CO_2 concentration of the ocean.

8.7 CARBON BUDGET INFERENCES FOR THE BIOSPHERE

The Health Council of the Netherlands issued a report on the CO_2 problem, referred to here as Haex (1984). This report contains an analysis of the global carbon cycle and in particular of the carbon flow through the biosphere. The contributors to this report used the values for surface areas, standing biomass, and net primary productivity from Ajtay et al. (1979) as a basis for their model. It was found that the net uptake of carbon by the entire terrestrial biosphere is now equal to 0.34 Gt y^{-1} . This represents the difference between two large numbers. They calculated a total net ecosystem production for the world of 7.25 Gt y^{-1} , a figure that results from considerable regrowth of areas following human disturbance. The group included in their model for growth enhancement from an increase of the CO_2 concentration a $\beta = 0.50$. Then the sum of fluxes resulting from human activities such as burning, deforestation, and shifting cultivation was calculated. All of these disturbances added up to a net flux of 6.91 Gt y^{-1} of carbon to the atmosphere. The researchers conclude that the terrestrial biosphere is now a net sink for carbon, although only a small one. Their model calculations show that in the past the biosphere was a net source of carbon because deforestation rates exceeded the net ecosystem production rates so that the CO_2 content of the atmosphere grew faster than if the biosphere were inert. The reversal from source to sink occurred about 1967 according to their model. Because of the biosphere being a net source over most of the last 100 years, the average oceanic uptake of carbon was a larger fraction (44%) of the fossil fuel release than the present oceanic absorption value (35%) according to their model.

Hobbie et al. (1984) compare the global carbon models of the geochemists with those of the ecologists. According to the ecologists, the geochemists have not properly accounted for deforestation nor for land-use changes. The ecological model developed by Houghton et al. (1983), sometimes referred to as a "bookkeeping" model, computes year-by-year changes in the carbon of vegetation and soils as a result of land clearing, deforestation, and regrowth for about 60 ecosystems in the world. They have run their model using several different input assumptions and obtained quite different results. For example, they found the biosphere in 1980 giving a net release of carbon to the atmosphere of 1.8 Gt y^{-1} based on an expansion of agriculture according to FAO data, 2.6 Gt y^{-1} based on a population increase and per capita use of agricultural land, and 4.7 Gt y^{-1} based on a survey of deforestation rates. In every case they get the biosphere to be a net source of carbon. They do not include a CO_2 stimulation factor for enhanced primary productivity.

8.8 CONCLUSIONS AND RESEARCH RECOMMENDATIONS

It is clear that our knowledge concerning the response of the biosphere to increasing levels of atmospheric CO_2 is very poor. Relatively few measurements exist to show the growth response of the dominant plants of major biomes to increasing CO_2 . The measurements we do have available are most often for a few crop species and only rarely for perennials. There is no information available concerning long-term growth response for major plant species, whether trees or grasses, to slowly increasing levels of CO_2 , and in particular, there is no information covering several plant generations.

Our understanding as to how a plant partitions its incremental increase of photosynthate production with an incremental increase of CO_2 is not adequate. Information is greatly needed concerning the source-sink relationships for carbon within the major plant species. We need to know where the carbon assimilated by a plant goes and its residence time in leaves, twigs, branches, boles, roots, or litter. Although some information is available concerning the biotic growth factor for a few plant species, it is essential that we understand the biotic growth factor for the major ecosystems of the world. Our lack of understanding of respiration rates within ecosystems, particularly of heterotrophic respiration, and their response to increasing CO_2 concentration is a significant impediment to adequate ecological modeling of the global carbon budget.

To understand better the response of the biosphere to increasing atmospheric CO_2 concentration it is necessary to make a better assessment of the following:

1. The biotic growth factor β must be determined for the most representative forest trees and shrubs characteristic of the major biomes of the world. A few grass species characteristic of the major grasslands must be assessed as well. The relationship between the value of β determined from the photosynthetic response curve to CO_2 and the growth response to CO_2 for selected species must be established.

2. The partitioning of carbon assimilated by forest trees into short-lived and long-lived pools must be established. In particular it must be determined to what extent assimilated carbon becomes inactive carbon in soil not susceptible to decomposition and decay.

3. More accurate assessments of both autotrophic and heterotrophic respiration rates in the major ecosystems of the world need to be established. Especially needed will be an understanding of any changes in these rates to be expected from increasing CO_2 levels. If biomass production increases with increasing CO_2 , will respiration rates increase in a commensurate manner or will carbon accumulate in the biosphere?

4. One of the important questions not fully answered by available data is whether the growth response of plants subjected to higher CO_2 levels is greater or less when under different amounts of water, light, or nutrient limitation. Further experiments along this line are much needed.

5. It is expected that increasing levels of atmospheric CO_2 will change the relative species composition of a plant community as shown by Shinn and Daley (1984) and Bazzaz and Carlson (1984). Plant species, especially those that possess the C_3 photosynthetic pathway versus those with the C_4 pathway, will respond differentially to increased CO_2 and to various amounts of water stress. Many carefully managed experiments are needed with a community of selected plant species in competition with one another exposed to several levels of CO_2 and under a variety of water and nutrient limitations.

6. The interaction of pathogens and insects with the plants of an ecosystem will change with increasing levels of CO_2 . Research is needed on this topic to ensure that a better understanding of the response of the biosphere to increasing CO_2 is achieved.

7. Finally, almost all of the research recommendations made in the other chapters of this volume have direct bearing on our ability to understand better the response of the biosphere to an increasing concentration of atmospheric CO_2 .

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9. ADAPTATION OF VEGETATION AND MANAGEMENT PRACTICES TO A HIGHER CARBON DIOXIDE WORLD

B. A. Kimball
*U.S. Department of Agriculture/
Agricultural Research Service
U.S. Water Conservation Laboratory*

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9.1 INTRODUCTION

The carbon dioxide (CO_2) content of the atmosphere is increasing and will probably double sometime during the middle of the next century (Edmonds et al. 1984). The increased CO_2 concentration will affect the growth of plants directly, as discussed at length in previous chapters. In addition, the increased CO_2 has been predicted to increase temperatures and alter precipitation patterns worldwide (National Research Council 1983). Whether such climate changes will actually occur is a hotly debated subject (Idso 1984). Nevertheless, if the increased atmospheric CO_2 levels do affect the climate, then the additional CO_2 will undoubtedly also indirectly affect the vegetation because of the altered temperature and moisture availability. These indirect effects of a CO_2 -induced climate change are discussed by Decker et al. (1985) in *Determination of Prerequisites for Quantitative Research on the Indirect Effects of Carbon Dioxide*, a companion volume to this series. I will concentrate on how managed and unmanaged vegetation may adapt to living in a higher CO_2 world, both with and without a possible accompanying climate change.

The term "adaptation" varies somewhat in meaning among plant scientists and has been the topic of scientific papers (Stern 1970; Kramer 1980; Reed 1984). In this chapter, an adaptation to a higher CO_2 world refers to those heritable characteristics of plants that enable them and their progeny to survive (or even thrive) and reproduce better than other plants which lack those characteristics (or express them to a lesser degree). Some plants change their characteristics in response to changes in the environment, such as partially closing their stomata with an increased CO_2 concentration. The next generation will not automatically also have narrow stomata unless they too grow in higher CO_2 environments. Such a nonheritable modification should properly be called an "acclimation" to the new environment (Kramer 1980). If, on the other hand, succeeding generations have a greater degree of closing at the same high CO_2 concentrations, and if this attribute causes them to have greater growth and higher survival, then the trend toward greater stomatal closing is an "adaptation" to the higher CO_2 world. Considering the prediction that a doubling of CO_2 will occur in about 70 years (Edmonds et al. 1984), annual species will have many generations to adapt, whereas individuals of long-lived perennial tree species will probably only be able to acclimate to the new conditions. The population of such long-lived species, however, will also adapt through time.

In the unmanaged biosphere, natural selection will determine which plants are best adapted or most

fitted for the future high- CO_2 world. The plants with characteristics that ensure greater survival and reproductive advantages in competition with all other plants will be selected. In the managed agricultural biosphere, on the other hand, growers and plant breeders will select the plants whose characteristics enable growers to obtain the most profit in the future high- CO_2 world. Those plants or crops will be grown that produce the greatest and most valuable yield response with the least expense relative to other crops. Therefore, the plants that possess the largest yield response to CO_2 will likely be selected, and such a yield response can be regarded as an adaptation to a higher CO_2 world.

Changes in agricultural and forestry management practices will probably be made to obtain the most profitable yields under the conditions of the future higher CO_2 world. These adjustments in the behavior of managers are learned rather than inherited, and they will be made concurrently with adaptations of the vegetation. However, for simplicity the term adaptation will be used in this chapter to refer to these managerial adjustments which are made together with adaptations of the vegetation. Such adjustments in management practices together with adaptations of domesticated vegetation have enabled agriculture and forestry to adapt to a huge range of climates from the Equator to the Arctic Circle. Such adaptation will continue into the future, stimulated by the results of agronomic research and by environmental and economic pressures.

9.2 KNOWN RESPONSES OF INDIVIDUAL PLANTS TO HIGHER LEVELS OF CO_2

Before trying to predict how a broad expanse of agricultural and natural vegetation will adapt to a higher CO_2 world, it is necessary to review the known effects of CO_2 on individual plants. This has been the topic of previous chapters of this volume, particularly Chapters 4 through 6. The major responses have been summarized nicely in Table 4.10 of Chapter 4. This section shall reiterate the more important responses from that table which will likely govern trends in the adaptation of vegetation as we know them today. It should be kept in mind that the plants measured today are not necessarily the same plants that will be growing tomorrow (with the important exception of long-lived species of trees and other perennials). First and foremost, leaf and canopy photosynthetic rates will increase with increases in CO_2 concentration to at least 1000 parts per million by volume (ppm). As a consequence, plants in general are simply going to be bigger. There are likely to be differences among species. In particular, photosynthesis of C_3 species has a qualitatively greater photosynthetic

response to CO₂ than that of C₄ species. There probably will also be increases in leaf area, weight per unit area, leaf thickness, stem height, branching, and seed and fruit number and size. There will be some likely changes in relative organ size within individual plants; root-to-shoot ratios are likely to increase. The proportion of carbon going to the roots and stems may increase in many but not all species. The composition of plant tissues is likely to change somewhat also; in particular, the carbon-to-nitrogen (C:N) and carbon-to-phosphorus (C:P) ratios will increase (Strain and Bazzaz 1983). Most important for humankind, agricultural yields are likely to increase with a doubling of the current ambient CO₂ concentration, probably by an average of 32% (Kimball 1983a, 1983b) but with large variability among species (Chapter 5, this volume).

Another important direct effect of increasing CO₂ concentrations on individual plants is that the leaf stomata tend to close partly. This increases the resistance to evaporative water loss with resultant decreases in leaf transpiration rates (Chapters 4 and 5; Kimball and Idso 1983) and increases in daytime leaf temperatures. The C₄ species respond somewhat more in this respect than C₃.

Because many of the previous CO₂ studies have been conducted in greenhouses or growth chambers with environmental conditions unlike those in an open field, and also because there may be climate changes in the future, it is important to ascertain whether the vegetation response to CO₂ changes with differing environmental conditions. Table 4.10 of Chapter 4 and Tables 5.4-5.7 of Chapter 5 list known interactions of CO₂ with other variables, and Kimball (in press) has also tabulated the available data on the CO₂ stimulation of growth and yield under environmental restraints. Summarizing from these reports, it appears that at low light intensity, decreases in the light compensation point with increasing CO₂ concentration can cause huge relative increases in photosynthesis of C₃ plants, and large relative and absolute increases could also occur at high light intensities because of saturation effects. However, actual observations of growth and yield with CO₂ enrichment at various light intensities exhibit much scatter, so to a first approximation it appears that relative CO₂ growth stimulation is rather constant with light intensity (Table 5.6). Similarly, it appears that relative growth stimulation is rather constant with temperature over the temperature range at which plants normally grow (Kimball, in press) although some experiments show limited response to CO₂ concentration at low temperatures (Table 5.7), one experiment with okra has indicated that CO₂ can greatly stimulate growth at lower than normal temperatures (Sionit et al. 1981a). The partial closure

of stomata with increasing CO₂ concentration may somewhat compensate for water and salinity stress, and the leaf tissue damage from air pollutants may be somewhat less (Kimball, in press). Thus, the stimulation of plant growth from increasing CO₂ concentration would be likely to ameliorate the negative effects of water, salinity, or air pollutant stress. When nutrients are limiting, however, the relative growth response to CO₂ enrichment appears to be less (Table 5.5 of Chapter 5; Kimball, in press). There is an exception in the case of legumes; in these plants nitrogen fixation increases with increasing CO₂ concentration, but shortages of phosphorus or the other essential elements could still reduce the CO₂ response. However, preliminary results reported by Norby et al. (1984) indicate that increased levels of CO₂ stimulate growth of tree species even in infertile soils, probably because of greater root exploration and possible stimulation of mycorrhizal fungi, which make phosphorus and water more available to the plant.

To summarize the known effects of higher CO₂ levels on individual plants, the most important effect is probably the overall stimulation of growth, and those species and individuals within species that are most stimulated probably will be best adapted. To a first approximation, the growth stimulation is relatively constant over a wide range of light intensities and temperatures at which plants normally grow, but it also seems likely that individual differences in response may be important in determining adaptation. The increased growth of roots relative to shoots may increase nutrient and water absorption from the soil, but harvest indices may decline slightly for nonroot crops. Carbon-to-nitrogen and carbon-to-phosphorus ratios will increase. The partial stomatal closure at high CO₂ levels may improve water relations as well as somewhat ameliorating the stress of salinity and air pollutants. All of these known responses will probably affect how crops will be managed in the future, as well as affecting the relative fitness and competition among plants growing in the wild.

9.3 ADAPTATION OF AGRICULTURE

9.3.1 Plant Selection and Breeding

Since the dawn of agriculture, humans have selected plants for higher yield and other desirable traits. Within the last couple of centuries, plant breeders have accelerated the development of desirable plant varieties with selection and breeding programs. Frey (1983) described the program used by Pioneer Hybrid International and pointed out that breeding, evalua-

tion, and selection of plant varieties are continuous processes that occur while the climate is changing. For their annual crops, a complete breeding cycle takes approximately 10 years from the time inbred development begins until a final product is marketed. Evaluation of new varieties is conducted at several experimental sites over a fairly wide climate range. The new hybrids that are selected are those best adapted to the environmental conditions, as shown by high, stable yields across several test sites representative of a geographical area during the last 3 years of testing. Thus, the breeding programs currently in use are already automatically incorporating the responses to increasing CO₂ concentration and changing climate in each area where a particular crop is being tested. Indeed, Allen et al.¹ estimated that 15% of the soybean yield increase that has occurred from about the year 1700 to the present can be attributed to the increasing atmospheric CO₂ concentration.

Frey (1983) said that the entire history of hybrid corn breeding has included only about five breeding cycles, and major improvements in productivity over a wide range of climatic conditions have occurred within this time. For annual crops there should be enough time for roughly six more cycles before the atmospheric CO₂ concentration doubles (Edmonds et al. 1984). Therefore, plant breeders probably have plenty of time to develop new varieties of annual crops that will be adapted to the future high-CO₂ world. For tree and other perennial crops, however, the number of breeding cycles that can be conducted in the available time is much smaller.

At least one deliberate attempt has been made to select specifically for a yield response to increased CO₂ concentration. During the 1960s, Maxon Smith (1977) initiated a greenhouse lettuce pedigree breeding program. Parent lettuce hybrids were grown at approximately threefold CO₂ enrichment, and their offspring in the F₂ through F₈ generations were selected for large leaves, good heart, and broad base, as well as rapid maturity. Progeny from selections made under one treatment were always grown under the same treatment the next year. The experiment showed that the lettuce in the CO₂-enriched greenhouse yielded 35% more than the controls on the average for 8 generations. Then in 1969 and 1970 sister progenies of the F₇ and F₈ generations, respectively, were grown in ambient and CO₂-enriched environments. The coefficients of variation were only 5.2 and 4.6% for the 2 years,

yet no significant differences in yield response to CO₂ enrichment were detected between the selections made in the ambient or the enriched cropping system. Thus, it appeared that there was no significant adaptation to higher CO₂ concentration per se.

Maxon Smith's experiment (1977) was a failure in the sense that no heritable increase in lettuce yield under CO₂ enrichment was obtained. On the other hand, it indicates that, at least for a 10-year breeding cycle, the CO₂ response of present day cultivars is probably similar to that of cultivars that will be developed in the future. However, this was one experiment with only one crop, so there is a need for additional experiments of this type before definite conclusions can be drawn. Considering the variability in yield response reported among CO₂-enrichment experiments by Kimball (1983a, 1983b), it seems only logical that genetic variability exists among individuals and that selections could be made for desirable CO₂ responses, despite the result found by Maxon Smith.

Recently, there has been speculation about using genetic engineering to produce qualitative changes in plants, such as to reduce the photorespiration of C₃ plants and make them more like C₄ plants or to incorporate nitrogen-fixing capability into nonlegume plants (Hannah 1982; Heichel 1984; Randall 1984). Such engineered adaptations have the potential to produce profound effects in the future with or without higher levels of CO₂. However, Heichel (1984) predicted that increases in crop productivity by 2030 from such technology will be likely to be less than half of the productivity increase that will be achieved by traditional plant breeding. Thus, the proven breeding programs of the past (Frey 1983) should continue to automatically achieve adaptations to the coming high-CO₂ world, at least for short-life-cycle plants. Even though productivity adaptations to the higher CO₂ world probably will be achieved by following this traditional passive approach with respect to CO₂ concentration, it would seem prudent for plant breeders and other plant scientists to be conscious of CO₂ effects on plants. Then, for example, some intermediary traits such as greater stomatal response to increased CO₂ possibly could be incorporated into plant breeding or genetic engineering programs to achieve greater drought tolerance.

Regardless of whether genetic engineering will have a significant impact on future crop productivity, there is another relatively new technology that probably will influence production of at least several horticultural crops. That technology is tissue culture, which permits the production of many genetically identical plants from a single individual (Hannah 1982). If genetically superior individuals can be identified through selection, traditional plant breeding, or genetic engineering, then

¹L. H. Allen, Jr., K. J. Boote, J. W. Jones, P. H. Jones, R. R. Valle, B. Acock, H. H. Rogers, and R. C. Dahlman, "Responses of Vegetation to Rising CO₂: Soybean Photosynthesis and Yield." Manuscript in preparation.

tissue culture may provide the means to multiply that genetic potential into the large numbers of plants needed for commercial crop production. As the CO₂ content of the atmosphere increases, selection for desirable productivity responses to the high CO₂ will undoubtedly be made, whether automatically in field plots exposed to the higher atmospheric concentration or consciously in growth chambers with controlled CO₂ concentrations.

9.3.2 Changes in Cultural Practices

9.3.2.1 Fertilizer

Experiments to test the interaction between nutrient concentration and atmospheric CO₂ concentration as it affects plant yield and growth have fairly consistently shown that the relative CO₂ stimulation is smaller when nutrients are in short supply (Kimball, in press; Table 5.5 in Chapter 5). Therefore, if farmers are to obtain maximum benefit from the future higher atmospheric CO₂ concentration, soil nutrient levels must not be depleted. Fertilization will probably become even more important, therefore, because the plant yield response will reflect a greater relative increase from CO₂ as well as the normal absolute increase from the fertilizer.

As mentioned previously, yields are likely to increase by a third, on the average, for a doubling of atmospheric CO₂ concentration. Therefore, if a third more nutrient is removed from the soil each year, it is only logical that soil nutrient levels will more rapidly become depleted if they are not replenished. There is some uncertainty, however, whether the increased fertilizer needs will bear a 1:1 relationship to increased yields (see Chapter 5 for discussion). Randall and Engelstad (1983) predict that increased amounts of fertilizers will be needed to exploit the higher future yield potential from improved plant varieties and production systems. They did not explicitly consider the effects of elevated levels of CO₂, but certainly it will be one of the factors in the improved future production system.

Phosphorus and potassium. Phosphorus (P) and potassium (K) will be considered first because their inorganic transformations are better understood. Soils naturally vary considerably in P and K contents and in the rates at which weathering processes break down minerals to make the P and K available to plants. If a crop now obtains 50% of its P and K from the soil and 50% from applied fertilizers, and if CO₂-induced growth requires 33% more P and K to sustain yields and avoid depletion, then the fertilizer application might have to be increased as much as 66%. However, Randall and Engelstad (1983) predict that improvements will be

forthcoming in the efficiency of fertilizer use, which will tend to decrease this figure.

The increased atmospheric CO₂ concentration may improve the efficiency of nutrient uptake and fertilizer use. One reason is that there may be an increased extent of soil exploration due to increased root-to-shoot ratios. Another possibility is that the high-CO₂ plants may exude greater amounts of carbohydrates and other organic compounds from their roots, thereby stimulating the growth of mycorrhizal fungi. These fungi form symbiotic associations with roots of some plant species and are known to help plants obtain P. If they have a greater supply of carbohydrates, it is plausible that they will in turn make more P available to the plants (Lamborg et al. 1983). Preliminary results for trees, reported by Norby et al. (1984), support the hypothesis that stimulation of tree-root and rhizosphere processes by elevated CO₂ increases nutrient availability.

As already mentioned, soils vary greatly in their natural fertility, and crops vary in their requirements for P and K and in their response to CO₂. Localized testing of soil nutrient levels and of the various crop responses to applied fertilizer will have to continue into the future for farmers to adapt to the higher CO₂ world.

Nitrogen. Nitrogen (N) is not an abundant element in soil-forming minerals, so the supply of this most important nutrient must come from external or fertilizer sources for sustained production. Many fertile soils such as the midwestern mollisols have high levels of organic matter from the remains of decaying plant and animal material from previous years and centuries. As this organic material decays, some N becomes available for plant growth, analogous to the release of available P and K from weathering of soil-forming minerals just discussed. Because plants will be larger in the higher CO₂ world, there probably will be a greater quantity of plant material available for decomposition each year, which in turn is likely to increase the organic matter content of the soil (Larson et al. 1984), and more soil nitrogen will become available each year. Although quantities of plant material will be larger, the quality of the material may be lower in the sense that its higher C:N and C:P ratios may somewhat inhibit decomposer organisms (Strain and Bazzaz 1983). For sustained agricultural production, therefore, most N will have to come from external sources.

The primary source of N is from N₂ in the atmosphere. Nitrogen-fixing bacteria live in the soil and in symbiotic association with legumes and a few other plants. These bacteria obtain energy for metabolism from decaying organic material, or directly from their hosts in the case of symbionts, and they have the ability to reduce atmospheric nitrogen and transform it into other forms that can be metabolized by themselves and

their host plants.

CO₂ enrichment has increased the amount of N₂ fixed by leguminous crops rather dramatically, with a doubling of CO₂ concentration producing a doubling of N fixation in several experiments (Hardy and Havelka 1977). More recent studies have shown substantial, although more modest, increases (Williams et al. 1981). Thus, we can surmise that leguminous crops will probably not be limited by a lack of N in the future high-CO₂ world, or at least not any more than they are now.

Leguminous crops are often grown in crop rotations because their residue contains high levels of N that remain in the soil for the succeeding crop. In CO₂-enrichment experiments, the yield and growth of legumes on the average have been increased by the same 32% as other crops (Kimball 1983b; Table 5.3 in Chapter 5). Therefore, legume rotation should be at least as good a method for obtaining N for the nonlegume crops in the future high-CO₂ world as it is now. However, Randall and Engelstad (1983), without considering CO₂ enrichment, predict that biological nitrogen fixation will have little effect on fertilizer needs by 2030.

Most nonleguminous crops in developed countries are grown with additions of N from commercial fertilizer. To sustain yields that are 32% higher in the future, it seems logical that applications of N will have to be increased by roughly the same average percentage, remembering of course that crops vary in their requirements, that soils vary in their organic matter content, and that adjustments will have to be made for residual N from previous legume crops. Currently the efficiency of nitrogen fertilizer use is only about 50% (the proportion of applied fertilizer taken up by the crop), at least for corn (Randall and Engelstad 1983). Improvements in the efficiency of nitrogen use are forecast for the future, so this increase in efficiency could possibly provide some of the extra nitrogen needed to sustain higher yields in the future higher CO₂ world. As with P and K, the increased CO₂ concentrations may cause some increase in efficiency through increases in root exploration and through stimulation of microbial activity.

Supply and demand. The amounts of fertilizers that will be applied in the future per unit area will be determined by the marginal product value/fertilizer cost ratio that brings the most profit. Although yields are likely to increase about 32% on the average with a doubling of CO₂ levels, as discussed previously, the price of the agricultural product cannot be predicted with any certainty.

Population increase was predicted to outpace food production increase even before the days of

Malthus (Heady 1984). Instead, however, increases in agricultural production have led to food surpluses in the United States and other developed countries, and the world hunger problem has in fact been a distribution and economic problem, albeit severe and deadly to some, rather than a shortage of production. Heady (1984) predicts that a slower rate of population growth will cause the demand for agricultural products to grow very slowly until about the year 2000, and after that time demand will be close to production, so increased food prices and increased profitability of fertilizer application will result.

The fertilizer cost part of the ratio is also influenced by population pressures and the size of available reserves. Engelstad (1984) said that ample supplies of potash exist in Canada. However, the supply of high-grade phosphate ore is limited, so progressively lower grades of phosphate rock will have to be mined. On the other hand, there are ample reserves of the lower grade rock, so costs for P and K should not drastically change. Nitrogen fertilizer production requires large amounts of fossil fuel energy and a hydrocarbon feedstock, so in recent years the price of nitrogen fertilizer has been tied to the price of natural gas (Engelstad 1984). Coal may substitute for natural gas in the future, but nitrogen fertilizer from coal will be more than twice as expensive as that from natural gas. Increasing population brings increasing demand for energy, and industrial development in Third World countries also increases energy demand. Thus, for the short term it certainly appears that the optimal rates of N application will be lower, but they are likely to increase in the distant future as food prices increase more rapidly than energy prices.

9.3.2.2 *Pest Control*

Weeds. Increasing CO₂ concentration has increased growth, on the average, of all species of plants that have been studied. The growth increase of the 770 observations analyzed by Kimball (1983b) averaged 36%, but the range of individual responses was from about -40 to +700%. Obviously there is a huge amount of variability, so those plants that can gain a larger relative advantage from the higher CO₂ level will have a competitive edge over their neighbors. If the plants that gain the most from the CO₂ happen to be weeds, then greater weed control problems loom ahead in the future.

However, as noted by Wittwer (in press), of the 20 most important food crops, 16 have the C₃ photosynthetic pathway. On the other hand, of the world's 18 most noxious weeds, 14 have the C₄ photosynthetic pathway. As already noted, C₃ plants generally have a greater growth response to CO₂ than

do C_4 plants, so C_3 plants can be expected to benefit relatively more from higher CO_2 . Such has been the case in competition tests between C_3 and C_4 species (reviewed in Chapter 7 in this volume). Thus for the 16 C_3 food crops, weeds are likely to be less of a problem than they are now. On the other hand, the four major C_4 crops (corn, sorghum, sugarcane, and millet) are likely to face stiffer competition from C_3 weeds in the future.

In addition to the direct effects of CO_2 levels on growth that are likely to influence plant competition, interactions of CO_2 with other climatic variables probably will also affect weed problems. If increased CO_2 concentration causes climate changes, then there will probably be shifts in the geographical areas most suited for each species. However, to a first approximation such shifts are likely to be similar for present crops and the weeds now normally associated with them and adapted to the same conditions. Even in the absence of climate changes, the elevated levels of CO_2 may in some instances affect the range of certain plants, as suggested by the experiment of Sionit et al. (1981a), which indicated that CO_2 enrichment enabled okra to survive at abnormally cool temperatures.

Although the patterns of weed competition probably will change in a future high- CO_2 world, advances in herbicide development and integrated pest management systems may produce an overall improvement in weed control (Frisbie and Leeper 1983). Commercial application of allelopathic chemicals, which are compounds produced by plants that have herbicidal effects on other plants, are likely to receive greater attention and may similarly improve future crop productivity (Putnam et al. 1983).

Insects and diseases. A doubling of CO_2 concentration is not likely to have any direct effects on insect or disease organisms. Because the CO_2 will affect their host plants, however, some interactive effects undoubtedly will occur. Evolutionary patterns of host-pest relationships have evolved over many millennia, and as plants evolve and adapt to the higher CO_2 world, insects and diseases will simultaneously evolve and adapt to the future plants. Therefore, if more nectar is produced in flowers because of increased carbohydrate supply with high CO_2 , then bees and other pollinators will probably respond with increasing populations and pollinating activity.

Only a few studies have been published to determine whether plants grown with CO_2 enrichment are likely to be more or less vulnerable to insect attacks. Lincoln et al. (1984) fed leaves from soybeans grown at various CO_2 concentrations to soybean looper larvae, and they found that the larvae fed more on the leaves from the higher CO_2 concentrations. They attributed the

propensity for greater feeding on the high CO_2 leaves to the fact that they had greater C:N ratios, so the larvae had to eat more to obtain the same amount of needed nutrition. Thus, this study suggests that the impact of herbivorous insects may increase. On the other hand, Butler et al. (1985) found no differences among population numbers of white flies (a sucking insect) trapped and counted in open top field enrichment chambers in which cotton was exposed to various CO_2 concentrations. Another study (Mauney et al. 1979) has indicated that CO_2 enrichment does not change the soluble sugar content of cotton. Therefore, these studies suggest that sucking insect problems might not change significantly. Overall, the only conclusion that can be drawn is that some plants probably will become more or less vulnerable to particular insects, whereas other host-pest relationships will not change significantly.

No studies of elevated CO_2 effects on disease resistance or susceptibility of plants have been published. As with insects, it is logical to expect continued mutual host-pest adaptations, with some particular diseases becoming more of a problem while some current problem diseases become less so. Schroth and Hancock (1982) have recently proposed the use of disease-suppressive soil- and root-colonizing bacteria as a new technology for improving crop productivity. If the preliminary results by Norby et al. (1984) are correct, that higher CO_2 causes tree roots to exude greater amounts of carbohydrates, then the future high- CO_2 world may enhance the practicability of this technology. The greater amount of root exudate may stimulate the growth of the disease-suppressive bacteria, which in turn should protect the plant. Such a concept is highly speculative, but clearly, the impact of higher CO_2 concentrations on the relationship between plants and disease-causing as well as beneficial microorganisms needs attention. Entomologists and pathologists will have to work continually to keep beneficial crop adaptations a step ahead of undesirable pest adaptations. However, improvements are continually being made in pest control methods. Frisbie and Leeper (1983) predict that integrated pest management (IPM) systems will increase crop yields 5 to 10% by about 2030.

Some indirect effects of increasing CO_2 concentration on insects and disease are possible if the increasing CO_2 causes a climate change. As discussed by Decker et al. (1985), temperature and humidity affect both host and pest in complex ways by altering their rates of development, distribution, migration, and adaptation. The possible warming associated with the increased CO_2 concentration would move the regions suited for development of pests poleward, but without reducing the populations in areas now affected. Thus, it may be more difficult to achieve the 5 to 10% yield

improvement previously forecast for integrated pest management systems by Frisbie and Leeper (1983).

9.3.2.3 Plant Residue Management

The most striking effect of higher CO₂ concentrations on plants is that they grow larger, about 32% on the average for a doubling of CO₂ concentrations, as already discussed. Because harvest index is not likely to increase by nearly this amount, there probably will be about a third more plant residue to manage with a doubling of the CO₂ level.

Larson et al. (1984) state that soil erosion is a serious threat to continued high crop productivity on many soils. As a solution, they promote conservation tillage, which relies on crop residues on the soil surface to reduce the energy available for particulate detachment at the soil surface from rainfall or wind. They regard plant residues as a natural resource for preventing erosion as well as for maintaining or increasing the organic matter content of the soil. Soil organic matter improves several soil chemical and physical properties such as improved nutrient cycling and plant availability, water-holding capacity, tilth, and erodibility. Thus, the future higher atmospheric CO₂ concentrations should increase the abundance of this resource for reducing soil erosion and for increasing soil organic matter content.

9.3.2.4 Plant Growth Regulators

Wittwer (1983) states that one of the most promising new technologies for improving agricultural productivity is the use of plant growth regulators. He has tabulated several effects of these regulators ranging from enhancement of overall productivity to improved storage life. The more general effect, however, is to change the way plants partition their carbohydrate and other resources in the direction of producing greater amounts of marketable product, that is, improving the harvest index.

One of the effects observed frequently in CO₂ enrichment experiments is a slight increase in harvest index for most crops except soybeans (Chapter 5, this volume). It seems likely, therefore, that plant varieties developed in the future will have higher harvest indices than those of the cultivars being tested today. Plant growth regulators might provide a means for converting an even greater portion of the increase in photosynthate production from higher CO₂ levels into marketable products.

9.3.3 Plant Water Relations and Interactions with CO₂-Induced Climate Change

As CO₂ concentration increases in the atmosphere, climate patterns are predicted to change in many

regions of the Earth (reviewed briefly below and more thoroughly in a companion volume, *Projecting the Climatic Effects of Increasing Carbon Dioxide*). Thus, the physiological responses of different crop species to increased CO₂ levels under various environmental conditions will determine which crop will yield the greatest return on the farmer's investment and, thus, future crop production areas. From this point of view, the most important physiological responses are probably those involved in plant water relations and water consumption.

9.3.3.1 Reduction of Consumptive Water Use

An important direct effect of increasing CO₂ concentration on plants is the tendency to cause partial closure of the stomata, as discussed in Chapters 4 through 6 of this volume. This closure reduces stomatal conductance and hence the rate of transpirational water loss from the leaves. Kimball and Idso (1983) calculated a 34% reduction in transpiration with a doubling of CO₂ concentration when they averaged the results of 46 observations from 18 different species taken by 10 workers in short-term growth chamber experiments. Such a reduction in transpiration represents an upper limit (on the average) to the amount that evapotranspiration may be reduced in future fields by a doubling of atmospheric CO₂ concentration.

Consumptive use is defined as the amount of water required for transpiration, plus that for evaporation from adjacent soil, to produce a crop whose growth and yield are not significantly reduced by drought stress (Erie et al. 1982). Several climatic and farm management factors influence plant growth and thereby the amount of water used. Nevertheless, for maximum production at a specific location, a specific crop requires a fairly definite amount of water during the growing season, as tabulated, for example, by Erie et al. (1982) for 33 crops in the Southwest United States for present-day climate conditions. However, plants are probably going to be larger and have a greater leaf area in the future high-CO₂ world, thus tending to increase transpiration. They probably will also have a larger, more vigorous root system and be able to extract more water from the soil. Any decreases in transpiration will make more thermal energy available for soil evaporation. Therefore, the amount by which consumptive water use (and irrigation requirements) will be reduced by a doubling of CO₂ concentration is going to be less than the potential average 34% reduction in leaf transpiration rate.

Only a few measurements of the influence of CO₂ concentration on actual water consumption have been made. In one study Rogers et al. (1984) measured the water use for a few days from well-watered, mature

soybeans grown in pots in open top chambers at several CO₂ concentrations. They found that a doubling of the CO₂ level caused a 40% reduction in the rate of water loss expressed either as per leaf area or per pot. In this study there was a 67% reduction in stomatal conductance and a 26% increase in leaf area, so the change in conductance dominated the change in leaf area, resulting in a significant water savings. Over the entire season, however, the savings in water use was probably less than 40% because early in the season the leaf area differences probably were larger.

In a growth chamber study with 16 different species grown in pots, Morison and Gifford (1984) observed that the rates of water loss per pot were not significantly different between ambient and doubled CO₂ treatments. Leaf areas were increased 20 to 75%, so, apparently, decreases in stomatal conductance and increases in leaf temperature altered leaf transpiration rates to almost exact compensation.

In other studies, Jones et al. (1984, 1985, in press) have measured whole canopy transpiration (soil evaporation was prevented by barriers) over entire seasons in sunlit chambers with well-watered soybeans. In two experiments, Jones et al. (1984, 1985) found that the water use was very similar at four levels of CO₂ ranging from 330 to 800 ppm. The plants in the higher CO₂ chambers had lower leaf transpiration rates, but they also had greater leaf areas, which provided almost exact compensation. In another experiment, however, Jones et al. (in press) found that the plants in a 660-ppm chamber did transpire 10% less water than the plants in the 330-ppm control chamber. Kimball et al. (1983) used weighing lysimeters and neutron soil-moisture probes to determine the water use of field-grown cotton in open top CO₂ enrichment chambers. They found that there was no detectable difference in water use between chambers with differing CO₂ concentrations when water use was determined from soil moisture depletion using the neutron data. On the other hand, the lysimeter data showed that plants in 500- and 650-ppm chambers used 9 and 4% less water, respectively, than the control plants at ambient CO₂ concentration.

These data indicate that the consumptive use of water may not be greatly affected by the future high CO₂ concentrations, although reductions of up to 10% or so can be expected. Those plants whose relative stomatal closure in high CO₂ is more than their leaf area increase are considerably more likely to have a reduction in water use. As discussed in Chapters 4 and 5, the stomata of C₄ plants are responsive to CO₂ concentration, yet their photosynthesis is relatively unaffected by higher CO₂ concentration, so it is likely that C₄ crops will have a larger decrease in consumptive use than C₃ plants

such as soybeans and cotton. Clearly, the relationship between stomatal closure, leaf canopy development, and evapotranspiration at ambient and elevated CO₂ concentration needs further study.

9.3.3.2 *Internal Plant Water Status and Growth*

The partial closing of leaf stomata also has the potential to affect the internal water status of plants and consequently also to affect their growth and yield. After irrigation or rainfall, plants growing in a CO₂-enriched atmosphere transpire at a lower rate (at least on a leaf area basis), thereby depleting soil moisture more slowly and lagging behind their counterparts growing in ambient CO₂ in experiencing plant water stress. Sionit et al. (1980), Paez et al. (1983, 1984), Rogers et al. (1984), and Tolley and Strain (1984, 1985) observed that CO₂-enriched plants lag behind ambient control plants in developing low leaf water potential. This improvement in plant water relations has resulted in several observations of a greater relative CO₂ stimulation of growth or yield under drought-stress conditions than under well-watered conditions. As listed in Table 9.1, the average growth increase due to a doubling of CO₂ concentration was 76% for drought-stressed compared to 43% for the well-watered treatments. Of 18 observations, only 3 did not follow this trend. Thus, there are strong indications that the relative increase in growth due to future higher atmospheric CO₂ concentrations will be larger under drought stress than under well-watered conditions.

The foregoing results suggest that the greater growth with CO₂ enrichment may compensate for the loss of growth from drought stress. The extent to which this compensation is a 1:1 equality is indicated by the fourth column in Table 9.1, which lists the growth or yield from CO₂-enriched, drought-stressed plants as a percentage of the growth or yield from ambient-CO₂, well-watered plants. Except for the 232- and 150-mm values of Gifford (1979a, 1979b), the data in Table 9.1 indicate that a doubling of CO₂ does almost exactly compensate on the average for mild water stress. The 232- and 150-mm data, however, show that the compensation is far from exact for severe water stress. Thus, plants appear to possess the capability to acclimate (and probably to adapt) to a somewhat drier climate in a future high-CO₂ world without much loss of productivity. However, in the absence of such a climate change, productivity is likely to increase much more from the higher CO₂.

9.3.3.3 *Interaction with Possible CO₂-Induced Climate Change*

Although all crops respond to increases in CO₂ concentration, there is considerable interspecies variation, as mentioned previously. Those crops that produce

Table 9.1
Growth or Yield Response to a Doubling (Approximate) of Atmospheric CO₂ Concentration
Under Well-Watered and Drought-Stressed Conditions

No.	Growth Increase ^a		CO ₂ -DS AMB-WW ^b	Species	Researchers	Comments
	Well-Watered	Drought-Stressed				
1	27	46	89	Wheat	Gifford (1979a,b)	Cv. "WW15," 232 mm transpiration vs. 379 for control (grain yield)
2	27	60	53	"	"	Cv. "WW15," 150 mm
3	27	264	27	"	"	Cv. "WW15," 132 mm
4	52	63	92	"	"	Cv. "Gabo," 232 mm
5	52	120	62	"	"	Cv. "Gabo," 150 mm
6	52	120	14	"	"	Cv. "Gabo," 132 mm
7	62	89	109	"	Sionit et al. (1980)	One stress cycle (grain yield)
8	62	49	100	"	"	Two stress cycles
9	80	71	153	"	Sionit et al. (1981b)	One stress cycle (grain yield)
10	80	93	151	"	"	Two stress cycles
11	33	50	101	Pea	Paez et al. (1983)	Dry weight in 30 days with one stress cycle
12	23	23	88	Tomato	Paez et al. (1984)	Dry weight in 18 days with one stress cycle, cv. "New Yorker"
13	14	49	101	"	"	Same conditions, cv. "Better Boy"
14	46	22	103	Soybean	Jones et al. (in press)	Stress from 70th to 83rd day (seed yield)
15	46	49	122	"	"	Stress from 52th to 66th day
16	19	15	64	Mixture	Bazzaz and Carlson (1984)	Dry weight of mixture of 1 C ₄ and 3 C ₃ species
17	67	148	137	Sweetgum	Tolley and Strain (1984)	Dry weight increment for 10-day drought stress period plus following 2-week recovery period
18	-2	32	69	Loblolly pine	"	As above except stress cycle was 14 days
Avg.	43	76	91 (106 when Gifford's 150- and 132-mm data are not included)			

Note: Stress imposed by soil moisture depletion.

^a [(Treatment - Control) × 100/control] where treatment is the growth or yield in a CO₂-enriched atmosphere and control is the growth or yield in a more normal atmosphere of about 330 ppm CO₂.

^b Growth or yield from high-CO₂, drought-stressed (CO₂-DS) condition × 100 divided by growth or yield from ambient-CO₂, well-watered (AMB-WW) condition.

the greatest increase in yield, relative to concurrent increasing costs, are going to become more profitable for the farmers to grow, and therefore, shifts are likely to occur among the cropped areas and market shares of the various commodities. Off-farm factors such as consumer preferences, export policies, government price supports, labor union interests, grower cooperatives, and so forth, complicate the whole issue. Nevertheless, we can speculate, for example, that C₃ crops such as wheat and barley are likely to become more profitable relative to a C₄ crop such as corn, so C₃ crops probably will have a larger share of the feed grain market in the future. Similarly, C₃ sugar beets may become a

more profitable sugar producer relative to C₄ sugarcane. Cotton may respond more to CO₂ enrichment than other C₃ crops (Kimball 1983b; Kimball et al. 1983; Chapter 5, this volume). Therefore, even in the absence of any climate changes, there are likely to be shifts in the geographical distribution of major crop-producing areas. Wheat production may increase in present midwest corn-producing areas to the detriment of present wheat-producing areas. Farmers in the present wheat areas may in turn find it more profitable to grow sugar beets to the detriment of Hawaiian sugarcane plantations, and so on.

It appears difficult and even futile to try to predict the details of such shifts now. However, in the

industrialized countries, the long-term demand for food is likely to keep pace with population growth, so it seems likely that any current production area will be able to find something profitable to grow. Indeed, it seems more likely that even more marginal land will be brought into production. An increased atmospheric CO₂ concentration appears to ameliorate water and salinity stress, so marginal semiarid lands may even become more productive.

Predictions from climate models indicate that there may be a general warming with the poles heating more than the equator. Considering that production worldwide is limited more by temperatures that are too cold rather than too warm, such a warming, with consequently longer growing seasons, should be good news. However, production areas may move poleward, thus entering different soil types and competing with present production areas.

Along with a warming of the Earth, climate models generally also predict greater evaporation from tropical oceans in the future high-CO₂ world, and consequently, precipitation also is predicted to increase on the average worldwide. However, the water content of an air mass is dependent on where it has been as well as where it is. Therefore, the greatest concern is focused on whether the higher CO₂ world with the possible higher temperatures will affect the patterns of atmospheric circulation and consequent patterns of temperature and precipitation distribution. Manabe and Wetherald (1980) and Rind and Lebedeff (1984), for example, have used general circulation models and predicted that some areas of the Earth might indeed become drier while others become wetter. The scale of these models is very coarse, and they do not accurately predict present-day precipitation patterns, so their reliability for any particular location is questionable. Probably, in the future, cloud behavior, ocean dynamics, sea ice, direct vegetation effects, and other admitted model deficiencies can be simulated on a smaller grid size so that realistic models can be developed.

Palutikof et al. (1985) have recently used another approach to predict the effects of the increasing atmospheric CO₂ concentration on weather patterns. They extracted data from the historical record for cold versus warm years, particularly when there was a warming trend during the early 20th century, and have used these data to draw detailed predictive maps showing possible future temperature and precipitation distributions for Europe and North America. Temperatures are depicted as generally higher, consistent with a predicted increase in mean Earth air temperature, although European winters may become colder and more variable. They predict less variability in temperatures for most of North America most of the year, but with some of the Western States experiencing greater fluctuations in some seasons

and less in others. They also predict rainfall will decrease in spring and summer and increase in winter in both Europe and North America, but that large areas will show the opposite pattern. Autumn is predicted to be wetter in Europe, but drier in North America. However, the absolute magnitudes of the temperature differences used by Palutikof et al. (1985) were generally less than a quarter of the change predicted by the climate modelers from a CO₂-concentration doubling.

Thus, the future weather patterns have not been predicted with any certainty, and considering that the temperature of the Earth is decreasing most where the climate models predict the largest increase, doubt exists that any significant changes in temperature and precipitation will occur because of the increasing atmospheric CO₂ concentration (Idso 1984).

Nevertheless, if changes in weather patterns do occur, then these shifts will indirectly affect plants, as discussed in detail by Decker et al. (1985), Rosenberg (1982), Wittwer (1980), and Kimball and Idso (1983). Neglecting any of the direct effects of CO₂ on plants, these studies conclude generally that shifts in production areas may occur, but that vegetation and agriculture in particular have already demonstrated a resiliency and a capability to adapt to temperature and precipitation changes as large as those predicted for the future. Yet such shifts may be detrimental if, for instance, the region most favorable climatically for corn production shifts northeastward to less fertile soils (Decker et al. 1985).

Wittwer (1980) presented some examples of adaptations and adjustments to climate change. He noted that during the past century, American farmers have coped with year-to-year variations of 30 mm in rainfall in eastern Kansas and with 2-week changes in the growing season in Minnesota. From 1915 to 1945 Indiana agriculture adapted to a +0.1°C per year trend and a total change of +2°C during the past century. Rosenberg (1982) presented another example of adaptation to climate change. Between 1920 and 1980 red winter wheat production spread northward from Nebraska across Montana to the Canadian border by development of cultivars adapted to an 88-mm decrease in mean annual precipitation, a 4.2°C decrease in mean annual temperature, and a 10-day decrease in growing season. The crop has also adapted to a 100-mm decrease in precipitation, a 0.7°C decrease in temperature, and a 10-day increase in growing seasons while spreading southward from Oklahoma to central Texas. Thus, wheat and other crop species probably have sufficient genetic variability to allow development of cultivars adapted to climate changes of the size predicted.

Even if agriculture can adapt to climate changes, the specter arises that such changes may limit production to levels below the average potential yield increase of about 32% that appears possible with a doubling of CO₂

concentration. Waggoner (1983, 1984) used statistical regression methods to evaluate the effects of a 10% decrease in precipitation and a 1°C warming on the yield of several crops in the American grain belt. Such a climate change would probably cause yield decreases of 2 to 12%. Another approach using a mechanistic computer model led to roughly the same conclusion.

In a similar study, Rosenzweig (in press) used the Rind and Lebedeff (1984) model to predict potential CO₂ climate effects on North American wheat-producing regions. She tried to circumvent the model's inability to predict present-day absolute precipitation by only using the precipitation changes it predicted between now and a future doubled CO₂ concentration. These precipitation changes were then superimposed on the known measured absolute precipitation values of today. Her results predict that production will increase in northern areas, particularly Canada, because of increased growing degree units with doubled CO₂ concentration. Major wheat regions in the United States are expected to remain nearly the same, whereas the wheat-growing region of Mexico is identified as vulnerable to high temperature stress.

However, all of these predictions are pessimistic because they do not account for any amelioration of drought stress directly by the CO₂ nor for future development of improved, more drought-adapted varieties. Nevertheless, if the increased atmospheric CO₂ concentration does cause drier (and warmer) weather, indirect CO₂ effects probably will modestly but significantly reduce the productivity increase that would otherwise be caused by the increased CO₂.

9.3.3.4 *Implications for Water Resources*

The increasing atmospheric CO₂ concentration decreases leaf transpiration, and consequently, it also could affect hydrologic processes and streamflow. Certainly the predictions of climate modelers that there will be changes in precipitation also forecast the possibility of future changes in water supplies to which irrigated agriculture, urban societies, and wildlife must adapt.

A few attempts have been made to predict changes in streamflow and water resources. One recent study was done by Aston (1984), who used a hydrologic model to predict streamflow increases of 40 to 90% for a doubling of CO₂ concentration. Unfortunately, the result generally appears too optimistic because he assumed an unrealistically high value for the decrease in transpiration per unit of leaf area, and he also failed to account for probable increases in leaf area. He did not consider possible climate changes.

Another attempt to predict changes in streamflow because of increased atmospheric CO₂ concentration,

was done by Revelle and Waggoner (1983). Using an empirical relationship to calculate annual runoff from annual precipitation and weighted mean annual temperatures from many drainage basins in the Western United States, they came to some very ominous conclusions. A 2°C increase in temperature and a 10% reduction in precipitation such as predicted by the climate modelers could reduce Western U.S. streamflows by 40 to 76%. In their analysis, however, they only considered these climate changes, and they completely ignored any direct effects of CO₂ on vegetation and consequent changes in evapotranspiration.

Recognizing the deficiency of the Revelle and Waggoner (1983) study, Idso and Brazel (1984) incorporated a reduction in leaf transpiration into the Revelle and Waggoner approach to predict the vegetation effects of the increasing atmospheric CO₂ concentration on water resources in Arizona. They predicted an average increase in Arizona streamflow of 87% for the case of no change in climate. When climate was assumed to change by a 2°C increase in temperature and a 10% decrease in precipitation, streamflows were still predicted to increase an average of 42% when the vegetation response was included. Ignoring the vegetation response but changing the climate drastically decreased many of the streamflows in accord with the work of Revelle and Waggoner (1983). Like Aston (1984), however, Idso and Brazel (1984) appear to have overestimated the evapotranspiration change likely caused by a doubling of CO₂ concentration because they ignored the probable increase in leaf area and only considered the decrease in transpiration per unit of leaf area.

A more recent study was done by Wigley and Jones (in press) who used a simple hydrologic model incorporating leaf transpiration and vegetation area effects. Their calculations show that arid region river basins that currently have a low percentage of runoff are most sensitive to vegetation effects. Wigley and Jones' results are consistent with those of Aston, Revelle and Waggoner, and Idso and Brazel when the corresponding assumptions are made. Their equations also indicate how an increase in streamflow due to stomatal effects could be counterbalanced by an increase in vegetation area in a high-CO₂ world.

Revelle and Waggoner, Idso and Brazel, and Wigley and Jones all assumed that runoff was the difference between precipitation and evapotranspiration. Actually, after a precipitation event, a high proportion of the water runs off quickly by overland flow, and relatively little runs off by infiltration to the groundwater and subsequent lateral flow to the stream (70 and 30%, respectively, for the United States as a whole [Jensen 1984]). The greater amount of vegetation

growing in the future higher CO₂ world would probably slow the rate of overland flow, thus retaining more water on the landscape to be lost by subsequent evapotranspiration. Thus, probably, evapotranspiration should be considered to be the difference between precipitation and runoff, rather than the other way around. This possible additional direct effect of CO₂ was not considered in any of the studies of streamflow just discussed.

At this juncture it seems almost futile to try to predict what will happen to streamflow. First, streamflow is a relatively small difference between larger quantities of precipitation and evapotranspiration. Second, the degree and nature of any possible climate changes are not known with any certainty. Third, the magnitude of the decrease in leaf transpiration relative to the increase in leaf area appears crucial to determining the effects of CO₂ on evapotranspiration, and little data exist. Fourth, the effect of increased densities of vegetation on overland flow has not yet been adequately considered. Contrasting the results of Revelle and Waggoner (1983) with those of Idso and Brazel (1984), it is apparent that changes in the assumptions about the CO₂ effects on both climate and vegetation produce widely disparate predictions of streamflow. Certainly, this is an area where much further research is needed. The cycle is complicated, so a sophisticated model is needed, perhaps one like that of Aston (1984) but with much more accurate simulation of vegetation effects.

If streamflows do decrease in the Western United States as suggested by Revelle and Waggoner (1983), western irrigated agriculture certainly will have much difficulty in adapting, and it seems likely that irrigated acreages would have to be reduced. In the humid East, relatively little irrigation is now practiced, and streamflows far exceed demand. In a possibly drier future climate, it seems logical that eastern agriculture would adapt by utilizing more irrigation, as also suggested by Decker et al. (1985).

9.4 ADAPTATION OF FORESTRY

The greater portion of this paper has focused on the adaptation of agronomic plants and management practices to a future high-CO₂ world. This emphasis is not intended to detract from the importance of nonagricultural vegetation and the likely changes that will occur in the biosphere. Rather it reflects the experience of the author and the fact that most CO₂ research has been conducted on monocultures of agricultural species. The separation of forestry is rather arbitrary because forests are becoming more and more like agricultural lands as management levels intensify.

However, forestry is concerned with the culture of long-lived species, which places it in a special category for concern. Nut and fruit tree crops, considered agricultural, are also in this category. The reason for concern is that individuals of these long-lived perennial species will not have many generations to adapt to the higher concentrations of CO₂ and any possible accompanying climate changes. Rather, they may only have time to acclimate physiologically as discussed in the introduction.

No controlled CO₂-enrichment experiments have been conducted for the entire life cycle of any perennial tree species. Interestingly enough, however, it is an increase in growth rate of bristlecone pine trees during the last century and a half that may be the first detected response to the increasing atmospheric CO₂ concentration (LaMarche et al. 1984; Chapter 8, this volume). Kramer and Sionit (in press), Sionit and Kramer (in press), and Kimball (1983b) have reviewed the literature on the reaction of woody plants to CO₂ enrichment. They concluded that woody plants behave like C₃ herbaceous plants in that dry weight, stem diameter, height, branching, leaf area, and stomatal resistance increase with CO₂ concentration to at least 700 ppm. However, there is considerable interspecies variation in response to elevated levels of CO₂, so it is necessary to study each species individually. Wright (1974) reported considerable variation in photosynthetic rate among tree species and predicted that the rising atmospheric CO₂ concentration may, in general, place gymnosperms at a relative disadvantage. However, if the climate does become drier, their superior drought tolerance might compensate for this. The increasing CO₂ concentration will partly compensate for water stress and possibly even mineral deficiencies (Norby et al. 1984), but droughts and low levels of soil nutrients will still limit forest productivity (Kramer and Sionit, in press).

The need to be concerned about the adaptation of forests to increasing CO₂ has been discussed in detail by Layser (1980), Hoffman et al. (1982), and Hoffman (1984). A recent conference was devoted to this topic (see reference for Kramer and Sionit, in press). Trees being planted today will be entering their period of greatest growth when the CO₂ concentration and possibly climate will already have changed. Layser (1980) and Hoffman and co-workers (1982) recommend that the forest industry begin developing plans now to adapt to CO₂-altered conditions. If some areas do become drier, forest fires will become more of a problem, so strategies and technologies for controlling fire losses as well as pest losses need to be continually researched, revised, and re-evaluated. Breeding and possibly genetic engineering

programs need to be accelerated to select and breed for high responsiveness to CO₂ levels coupled with environmental stress resistance. If genetically superior individuals can be identified, tissue cultures possibly could be used to replicate them in large numbers, as discussed previously.

Because of the long life span of trees, it is difficult to compress the amount of elapsed time before results can be obtained. Each year of delay before starting means an additional year lost before the results are obtained. The situation is urgent because the information will be more valuable if it can be obtained in time to be used in management decisions on how to adapt to the changes anticipated in the future higher CO₂ world.

9.5 ADAPTATION OF THE UNMANAGED TERRESTRIAL BIOSPHERE

It is entirely possible that the complexion of natural plant stands, with their numerous competing species, will change even more in the future higher CO₂ world than will cultivated fields with only a few domesticated species. Chapter 6 (this volume) discusses the responses of native plant species to enrichment, which are similar to those for the agricultural species already discussed (Chapters 4 and 5). Also, Chapter 7 summarizes the existing literature regarding the effects of enrichment on plant communities. The number of studies is fairly small, but Bazzaz et al. (Chapter 7) have made a few generalizations. First, because of differences in the response to increasing concentration, dominant relationships among species in a community are likely to change. In warm, high-light environments, C₄ plants now have a competitive advantage, which may become much smaller or be eliminated as C₃ plants respond positively to the higher CO₂. They also say that the life cycle of C₃ plants is shortened under higher CO₂ and note that the dry weight increase at elevated levels of CO₂ will not necessarily be translated into reproductive output. Thus, it is likely that the dominant species in most areas will change as natural selection favors those individuals best adapted to take advantage of the higher CO₂ concentrations.

Not only will plant-to-plant relationships be changed with an increased CO₂ concentration, but the ecological relationships among all organisms will probably be affected (Strain and Bazzaz 1983). The plants are the primary producers whose growth will be directly stimulated, as discussed before. Herbivores in turn will be stimulated by a larger food supply, as will decomposers when the plants die. Pathogenic and carnivorous organisms in turn are likely to respond to the adaptations of the primary producers, herbivores, and decomposers. Because the quality of the plant

material grown in higher CO₂ concentrations may be poorer with respect to C:N and C:P ratios, the degree of stimulation of the other organisms may be somewhat less than the magnitude of stimulation of the plants (Strain and Bazzaz 1983).

If the predicted climate changes accompany the increase in CO₂ concentration, then plant communities will be altered also in response to temperature and precipitation changes. In the absence of direct CO₂ effects, the direction of plant community changes can be predicted with more reliability than the suggested climate changes. Anyone who has traveled from south to north and from tropics to desert is aware of the huge range of plant adaptation that already exists. As the Earth's temperature increases, warm-adapted species will be able to spread poleward. Similarly, if changes in precipitation patterns occur, then there will also be shifts in drought-adapted species.

Another ecological factor that may change as a result of higher CO₂ concentrations is fire. Fires rapidly convert organic matter back into oxides of carbon, sulfur, and nitrogen, thereby shortening the usual lag time that characterizes decomposition (Strain and Bazzaz 1983). Burning also improves the availability of most nutrients, particularly phosphorus and nitrogen. Besides these stimulatory effects for grasses and other plants whose roots survive below the soil surface, the fires are, of course, often deadly for many organisms at the time of occurrence. In a future high-CO₂ world with higher primary productivity, greater amounts of accumulating biomass and standing dead material may contribute to increases in fire frequency in some ecological systems. Chaparral is an example of a system where such a scenario is more likely to occur (see Chapter 6, this volume). Possible CO₂-induced shifts in precipitation patterns would also tend to increase fire frequency in presently humid areas that become drier and vice versa.

As with agricultural species, interactions between the direct response to CO₂ and the possible indirect climatic effects are also likely to occur. As already discussed (Table 9.1), CO₂ enrichment stimulates growth relatively more under drought stress and compensates to some extent for the decrease in growth from lack of water. Also, because of the increase in stomatal resistance with increased CO₂ concentration, leaf transpiration (and possibly evapotranspiration per unit of land area) is decreased. Therefore, water-use efficiency is greatly enhanced, and those species with the larger increase in efficiency will be better adapted for a drier climate.

A case study of the above phenomena was performed by Idso and Quinn (1983), who considered how vegetation might be redistributed in Arizona and New

Mexico in response to a doubling of CO₂ concentration. Their basic premise was that if the water-use efficiency of a plant is doubled, it can survive and reproduce with half the amount of precipitation. Starting with maps of present vegetation types, they calculated and drew new maps showing where the vegetation types could grow with a doubling of water-use efficiency. The general pattern was for each vegetation type to move somewhat down the mountain slopes from the moist summits to the desert valleys. Although a doubling of water-use efficiency is probably an overestimate for a doubling of CO₂, and although factors other than water availability influence where the plants are able to survive, the study of Idso and Quinn nevertheless provides an interesting illustration of the shifts in plant communities that may occur with the coming of the future high-CO₂ world.

9.6 CONCLUSIONS AND RESEARCH RECOMMENDATIONS

As the CO₂ concentration of the atmosphere increases, those plants possessing characteristics that make them more fit for survival through natural selection (or deliberate agronomic selection) will pass those characteristics to their progeny in a continuing evolutionary process of adaptation. The managers of agricultural and forested lands must also adjust their plant selection, technology, and cultural practices to adapt similarly to the future high-CO₂ world.

Agricultural species will probably undergo many adaptations, especially new varieties that are higher yielding and more environmentally stress-resistant. In a continuous development process, plant breeders now test new varieties at experimental sites over a wide climate range. Therefore, their traditional selection process should automatically select those varieties possessing the best agronomic response to the future conditions. The new technology of genetic engineering may or may not have an impact, but tissue culture techniques might prove useful in the future for multiplying individuals that are identified as genetically superior under high-CO₂ conditions. Plant growth regulators that increase harvest index under the high-CO₂ conditions might also be developed.

Although wide variability exists, a doubling of CO₂ concentration is likely to increase yields, on the average, by about one-third. A one-third increase in fertilizer use may be required, therefore, to avoid depletion of soil nutrient levels. Because plant growth is expected to increase, greater quantities of plant residue will remain after each crop. If used in a program of conservation tillage, the residue should reduce soil erosion, while at the same time increasing soil organic matter content and tilth. The higher C:N and C:P ratios of the residue may

retard decomposition by microorganisms, however.

Weed and other pest problems are also likely to change. The C₄ crops (corn, sorghum, sugarcane) will face greater competition from C₃ weeds, whereas many C₃ crops will probably gain a competitive edge over several noxious C₄ weeds. Continuing development of selective herbicides should help. As they have in the past, insects and diseases will continue to evolve and adapt to the new plants as the plants adapt to the new CO₂ concentrations. The higher C:N ratio of plants grown in high CO₂ might result in herbivorous insects becoming more of a problem; other insects may continue to cause about the same level of damage, and some possibly less. Breeders of resistant varieties will have to work continually to keep the adaptations of the resistant plants ahead of the adaptations of the pests in order to overcome the resistance. Possible CO₂-induced climate change might also complicate the situation as it affects development and migration. Weed scientists, entomologists, and pathologists face a continuing struggle to improve pest management systems.

Even as C₄ species face stiffer direct weed competition, so will they face greater competition from C₃ crops for a share of the market. There probably will be shifts in the most profitable production areas for many crops as a result of differences in CO₂ response. If accompanying climate changes occur, additional shifts in crop production areas are likely, but agriculture probably has the resiliency to adapt.

The water relations of future plants will also be affected by the higher CO₂ concentration because of the partial closing of leaf stomata. Leaf transpiration will be reduced an average of about one-third for a doubling of CO₂ levels, but growth and leaf area will probably increase about one-third, so consumptive water use may not be greatly affected. The internal water status of plants will be improved, however, enabling them to sustain even greater relative growth under drought as compared with well-watered conditions. The latter response should help to mitigate the effects of predicted adverse climate changes, but if such changes occur, the resultant yield increase from a doubling of CO₂ will be less than the potential increase of about one-third.

Streamflow may be greatly affected by higher atmospheric CO₂ concentrations. However, predictions of future flows are very sensitive to the relative change in leaf transpiration and leaf area, and predictions of climate changes are very uncertain, so neither the direction nor the magnitude of future streamflows can now be predicted. If streamflow does decline, it will be very difficult for western irrigated agriculture to adapt because demand already exceeds supply, whereas eastern agriculture might adapt by using more irrigation.

As with agricultural crops, there will be shifts in the complexion of forests and unmanaged plant communities in a higher CO₂ world. Variations in growth and transpirational responses to increasing CO₂ will enable some plants to gain relative to others. Ecological relationships among all organisms will probably be affected, with the stimulation of plants, the primary producers, in turn stimulating the herbivores and decomposers, who then stimulate the carnivores; when they all die, the decomposers will be stimulated, which recycles nutrients back to the plants, and so on. Interactions with a possible CO₂-induced climate change complicate any predictions. The general trends will be toward bigger and more drought-resistant plants, yet deficiencies of soil nutrients and soil moisture will continue to limit productivity. There probably will be a downward shift in the elevation at which various plants can survive in arid regions. If the predicted climate changes occur, there are likely to be shifts poleward and upward shifts on mountains of warm-adapted species with superimposed lateral shifts of drought-adapted species because of altered precipitation patterns. The frequency of fires may increase in some ecosystems because of increases in standing plant biomass and possible changes in precipitation patterns. To make the best adaptations to the new conditions, foresters especially must act expeditiously. The life span of the trees they tend is sufficiently long that those planted now may be actively growing when the concentration of CO₂ has doubled.

The following are some recommendations to be considered for future research in the adaptation of vegetation to increasing levels of atmospheric CO₂.

1. Screen for overall growth and yield response under high concentrations of CO₂ both with and without environmental stresses and both within and among species to identify and select genetically superior individuals. Such research is particularly important for the forest industry because of the small number of breeding cycles available before the high-CO₂ world arrives.

2. Establish whether screening or other measurements taken on saplings are applicable to mature trees of the same species.

3. Identify physiological and biochemical characteristics that result in better growth and yield response (i.e., better adaptation) to higher CO₂ concentration. If specific characteristics, such as better translocation into a developing seed can be identified, then breeding or genetic engineering programs could actively attempt to incorporate that characteristic into genetically superior stock.

4. Establish definitively how growth responses to CO₂ may be affected by light intensity and temperature.

5. Determine how soil nutrient status affects CO₂ response. More information is also needed about the effects of CO₂ enrichment on nitrogen fixation for various species and conditions. Establish the extent to which greater exudation of carbohydrates and other compounds from roots with high CO₂ concentrations can stimulate mycorrhizal fungi and other beneficial microorganisms, which in turn may increase phosphorus and water availability to various plant species.

6. Identify any particular crop-weed combinations that are likely to pose greater problems in the future because of differential responses to increased CO₂ and also to predicted climate changes.

7. Determine whether plants grown at high CO₂ are more vulnerable to attack by insects and diseases. In particular, what effects will a greater quantity of plant material that has higher C:N and C:P ratios have on host-pest relationships?

8. Establish what effect more plant material, but with the high C:N and C:P ratios associated with CO₂ enrichment, will have on decomposer organisms. Similarly, how much will this plant material increase soil organic matter and reduce soil erosion?

9. In the future there probably will be a need for economic-social research. If trends for CO₂-induced shifts in geographical crop production areas are recognized, then the economic and social consequences for the old and new areas need to be evaluated so that appropriate agency actions can be taken.

10. More accurate climate models are needed so that future trends of temperature and precipitation can be predicted more reliably.

11. The effect of high CO₂ levels on evapotranspiration and plant water requirements needs considerably more attention. The extent to which there is a compensation between decrease in stomatal conductance and increase in leaf area needs investigation for many species. Establishing the effects of CO₂ on canopy development and leaf temperature and how these relate to evapotranspiration is also necessary.

12. More information is also needed about the effects of high CO₂ levels and partial stomatal closure on internal plant water status. To what extent can high CO₂ ameliorate plant water stress and maintain high productivity under dry conditions? Similarly, to what extent can high CO₂ counteract the effects of salinity and air pollutants?

13. Hydrologic modeling research is also needed to account for changes in precipitation, runoff, and evapotranspiration on streamflow in the future high-CO₂ world. We must account for the effects of decreased stomatal conductance and increased leaf area on evapotranspiration as well as the effects of increased stand density on runoff.

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10. STATUS OF KNOWLEDGE
AND RECOMMENDATIONS
FOR FUTURE WORK

B. R. Strain
and
J. D. Cure
Duke University

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10.1. STATUS OF KNOWLEDGE

The objective of this chapter is to give a concise overview of the current understanding of the effects of CO₂ on plants, on communities of plants, and on ecosystems. In addition, research needs and some recommended research projects are presented.

10.1.1 Plant-Level Responses

10.1.1.1 *Photosynthesis*

Photosynthesis begins with a diffusion phenomenon in which carbon dioxide diffuses from an area of higher concentration in the air to an area of lower concentration at the site of fixation inside of plant leaves. It has been shown many times that a doubling of CO₂ in the atmosphere will cause a short-term increase in photosynthesis. When the plant comes to a new steady state in equilibrium with the increased CO₂ concentration, however, the increase in photosynthesis has usually been reduced to some rate less than the observed short-term values. Stomatal aperture, leaf cell structure, and internal biochemical changes all have been shown to contribute to the reduced level of photosynthesis.

The actual level of photosynthesis to be expected in future crop and native plants will vary with plant species and variety, with other environmental conditions, and with management techniques. Too few empirical data exist to allow adequate predictions of photosynthesis rates to be expected.

10.1.1.2 *Acclimation*

Physiological changes will occur in plants as atmospheric CO₂ increases. For the purposes of this book these changes are termed acclimation. On the average, plants will photosynthesize more as atmospheric CO₂ continues to increase, at least up to the doubling concentration of 680 ppm. In managed crop, range, and forested ecosystems, desirable product species will be selected by humans, and the economic productivity of these systems may increase. In unmanaged ecosystems natural selection will occur and those plants species most successful under the new environments will increase in dominance. No long-term CO₂ enrichment experiments under realistic field conditions have been completed, and the net effect of physiological change and ecological adjustment cannot be predicted with confidence at this time. The mechanisms of plant acclimation to increased atmospheric CO₂ and the major factors controlling the new steady states are not known.

10.1.1.3 *Conductance*

Stomatal conductance is sensitive to CO₂ concentration as well as to light, leaf water potential, temperature, and

atmospheric humidity. As CO₂ concentration increases, conductance decreases. Some plants have been shown to be more sensitive than others in stomatal conductance response to CO₂ increase. The fundamental mechanisms of stomatal response to CO₂ concentration are still unknown. Quantitative evaluations of the responses of important species have not been made.

10.1.1.4 *Biomass Accumulation*

High-CO₂ experiments for C₃ crop species conducted under favorable environmental conditions almost always show a substantial enhancement of biomass accumulation. Also, lesser but still positive effects of CO₂ on growth have been observed for C₄ species. This effect of elevated CO₂ is very species-dependent and sensitive to other environmental factors, however (see below), and few generalizations can be made about growth responses of native species growing in their natural habitats.

10.1.1.5 *Respiration*

Photorespiration of C₃ species is greatly decreased in elevated CO₂ conditions. However, the few published data indicate an increase in dark respiration rate on a per unit dry weight or leaf area basis. These increases are probably associated with increased growth rates. Also, on the ecosystem level, autotrophic dark respiration will be proportional to total biomass as well as to temperature. Quantitative estimates of these changes have not been made.

10.1.1.6 *Dry Matter Partitioning*

Growing plants in CO₂-enriched environments at optimum levels of other factors causes all plant organs to become heavier, with roots often gaining proportionally more dry weight than stems, and stems more than leaves. The additional dry matter in the root comes from increasing root length and volume of storage roots with little increase observed in tissue density. Stem height and diameter also increase with little increase in stem tissue density. There is a small increase in leaf area as well as in leaf thickness, and an increase in structural dry matter in leaves. Few definitive experiments have been done on structural responses, however, and there is no consistent pattern among species. There is increased starch accumulation in leaves grown at high CO₂ which, depending on the circumstances, can be very large. Branch and tiller numbers are frequently increased, as is the number of flowers. Either the weight or number of individual fruits is increased and harvest index is usually increased.

The ways in which other environmental factors will interact with CO₂ to determine dry matter partitioning

to roots, shoots, and reproductive structures of various species are largely unknown.

10.1.1.7 *Water Use and Water-Use Efficiency*

Instantaneous measurements show that water-use efficiency of leaves is always increased in elevated CO₂ even though the proportional contribution of photosynthesis and transpiration may vary with species and environment. However, the net effects of increased CO₂ concentration on actual water use in the field are much less certain because the increases in leaf area and root extension observed in high-CO₂ plants tend to increase water use and may counteract the effect of low transpiration rate per unit leaf area. Because methodology for actually measuring water use in the field is poorly developed, there are almost no data and there is much speculation surrounding this complex issue.

10.1.1.8 *Senescence*

Elevated CO₂ has been shown to affect phenology and senescence of some, but by no means all, of the plants studied. Determinate species may reach full leaf area, biomass, and flower and fruit production earlier with little or no effect on final yield. From the sparse data available it appears that CO₂ may either accelerate or delay flowering and senescence. Rates seem to depend on the species and on environmental conditions as well. These interactions may profoundly affect seasonal duration of growth and interspecific competition.

10.1.1.9 *C₃ and C₄ Responses*

The responses to elevated CO₂ of C₃ plants in terms of photosynthesis and growth are comparatively greater than those of C₄ species. In some studies, the reverse pattern has been shown for conductance and resultant changes in water balance. The physiology of the C₄ growth response to CO₂ enhancement has not been adequately studied.

10.1.1.10 *Tissue Quality*

Higher carbohydrate levels, lower nitrogen and other nutrient concentrations, and greater levels of soluble phenolics and structural compounds have been observed in leaves and litter of plants grown in CO₂-enriched atmospheres. These changes in tissue quality could have far-reaching effects on herbivory, host-pathogen relationships, nutrient sequestering, decomposition, and mineralization processes. At this time, however, tissue quality changes and their ecological significance are purely speculative.

10.1.1.11 *Response Types by Growth Form*

Although research to date with plant responses to

CO₂ enrichment has focused on agriculturally important species, we still cannot say with certainty that among crops there are response types based on growth form. Because of the great number of native plant species, selection of representative ones by growth form and habitat should be attempted and tested to lay a foundation for extrapolation to other species.

10.1.2 *Interactions with Other Environmental Factors*

Plant responses to increased CO₂ are entirely conditioned by the other environmental factors at work in the system under study, and to understand plant responses to CO₂ concentration we must understand these interactions.

10.1.2.1 *Light*

Elevated CO₂ increases photosynthesis at low light intensities and decreases the light compensation point, thus increasing the potential for a positive carbon balance deep in a plant canopy. It seems reasonable to assume, however, that a full response to CO₂ concentration can occur only where light is not limited. There is at this time no consensus among investigators as to the nature of the interaction between CO₂ and light intensity on photosynthesis and growth. Possible confounding factors which have been mentioned are plant or leaf age, rooting volume, sink activity, and temperature. This interaction is important for modeling responses of crop plants in the event of future changes in cloud cover as well as variable species responses to CO₂ in complex ecosystems with a range of light intensities.

10.1.2.2 *Temperature*

Photosynthesis and growth responses to temperature and CO₂ concentration are highly species dependent. The optimum temperature for net photosynthesis of most C₃ species increases in elevated CO₂ due to differential responses of photosynthesis and photorespiration. At low temperatures, the rate of organ growth is limited and reduced sink activity can cause starch accumulation and feedback inhibition of photosynthesis. At high temperature, enzyme degradation limits both photosynthesis and growth. Photosynthesis and growth are limited by temperature proportionally more at high CO₂ concentration than at current ambient levels.

10.1.2.3 *Water*

The decreased conductance observed in leaves of plants growing at high CO₂ limits transpiration per unit leaf area and serves to conserve soil water. This leads to high leaf water potential and turgor, thus increasing leaf expansion rate and photosynthesis for plants

growing in high CO₂ but in limited water environments. Counteracting these trends, however, are the greater conducting surfaces (leaf area) and root systems of these plants, which tend to increase water consumption. The resulting total effect on water use by different crops in different environments is unknown. Also, because water is so often limiting in unmanaged ecosystems, the differential responses of various species to CO₂ in terms of conductance and increased leaf and root growth should profoundly affect species competition and distribution. These responses have yet to be assessed for the vast majority of important native plant species.

10.1.2.4 *Nutrition*

The growth response to CO₂ is limited by insufficient nutrient availability, probably through complex mechanisms poorly understood but similarly at work at current CO₂ concentrations. At high CO₂ levels, nitrogen concentrations of plant tissues have been shown to decrease in both nonlimiting nitrate and N₂-fixing systems, but to what extent this represents a dilution of N by carbohydrate and to what extent a reduced N requirement for growth of different species is unknown. The minimum requirements of various nutrients for maximum growth in higher CO₂ has never been addressed for any species. Also unknown are effects of CO₂ concentration on nutrient uptake capacity and changes in root-to-shoot ratio in conditions of low nutrient supply, effects by which increased CO₂ concentration could help compensate for nutrient-poor soil. Species differences in these responses should greatly affect species competition in infertile habitats.

10.1.2.5 *Pollutants*

As the atmospheric CO₂ concentration increases so do the levels of pollutants that are by-products of the burning of fossil fuels. The small amount of evidence available supports the intuitive prediction that CO₂-induced decrease in leaf conductance serves to mitigate the effects of toxic gaseous pollutants such as ozone. The reverse of this interaction, i.e., the possible limitation of the CO₂ growth response by the negative effects of pollutants, has received even less attention. No information is available on air quality for any of the CO₂ enrichment experiments reviewed herein, except those few explicitly designed to elucidate the interaction. Therefore, even if future pollutant levels are controlled, we do not know to what extent studies performed to date have been confounded. For these reasons, evaluating CO₂/pollutant interactions on photosynthesis and growth is just as important for construction of models as other environmental interactions.

10.1.2.6 *Salinity*

Salinity stress, like water stress, increases the relative growth response to elevated CO₂ by at least two mechanisms: first, the carbohydrate required to maintain exclusion of salts from the roots is supplied by higher photosynthesis rates; and second, lower leaf conductance results in lower water consumption to maintain turgor and, therefore, a lower activity of salt exclusion and lower cell respiration. The impact of this interaction on the extension of arable land surface or on different native species competing in saline environments is unknown.

10.1.3 Further Ecosystem-Level Observations

10.1.3.1 *Competition*

Because of differential photosynthetic and growth responses to elevated CO₂ among plant species, competitive relationships are subject to shifts in both managed and unmanaged ecosystems. Work with a limited number of weed/crop combinations under favorable environmental conditions confirms the expected competitive advantage of C₃ species. However, because C₄ plants often display greater decrease in transpiration than C₃ plants at elevated CO₂, the competitive outcome is far less predictable in the presence of limited soil moisture or other environmental stresses present in field situations. Differential species responses in flowering and seed production with increasing CO₂ will change reproductive potentials and therefore will affect competition among crop, weed, and native species.

10.1.3.2 *Water Balance, Water-Use Efficiency, and Streamflow*

As mentioned above, the differential CO₂ responses of plants to factors that affect the water balance of the plant, such as changes in conductance, root extension, and leaf area, are important in determining the competitive relationships of plants within ecosystems. In addition, geographical changes in vegetative patterns would be expected in a future high-CO₂ world. Direct CO₂ effects will cause vegetation distribution changes even if CO₂-induced changes in climate do not occur. Because of increased water-use efficiency, areas currently marginally unproductive may support more growth, causing shifts in both profitable crop production areas and populations of native species. Predictions of streamflow are very sensitive to the relative changes in leaf transpiration and leaf area (i.e., total water use). Until realistic field estimates of these parameters can be made, however, changes in streamflow cannot be anticipated.

10.1.3.3 *Herbivory and Host-Pathogen Relationships*

A number of experiments have shown an increase in the carbon-to-nitrogen ratio of plant tissues grown in elevated CO₂, and one controlled environment study has shown that insect consumption of such tissue increased in comparison with control tissue. Beyond this, nothing is known about this type of interaction or of how changes in tissue quality might affect host-pathogen relationships.

10.1.3.4 *N₂-Fixation, Soil Microbial Activity, and Mycorrhizal Associations*

Early findings of tremendous increases in N₂-fixation of soybeans in response to elevated CO₂ have not been repeated. More recent data show the response of N₂-fixation may fall slightly short of the response of carbon fixation but that this does not constitute a limitation on growth. There is currently speculation that increased carbon availability may lead to increased carbohydrate exudation by roots which may in turn stimulate nonsymbiotic N₂-fixation, microbial growth, and mycorrhizal associations with an accompanying increase in nutrient and water mining of soil. No work has been published on this interesting hypothesis.

10.1.3.5 *Productivity*

The little fieldwork accomplished to date indicates that field-related stresses decrease the stimulation of productivity because of CO₂ relative to that observed in more controlled environments. Soybean, the most thoroughly studied species, has been grown in the field only 2 years, and most important agricultural species have not been evaluated at all in the field.

Although biomass accumulation has been shown to increase for many native species, technical limitations have prevented evaluation of ecosystem productivity in situ. In unmanaged systems, productivity is more sensitive to possible interactions of CO₂ with processes of herbivory, nutrient sequestering, litter decomposition, pollination, and seed dispersal. Data are completely lacking for CO₂ effects on these processes, and the technical limitations to undertaking such studies for some ecosystems are formidable. Nevertheless, estimates of productivity responses of critical ecosystems are important for an understanding of the broad effects of CO₂ on vegetation. We must understand the role of ecosystems as sources or sinks in the global carbon cycle.

10.2 DEVELOPING THE PREDICTIVE CAPABILITY

10.2.1 *Coordination of Modeling and Research for Ecosystems*

As discussed above, CO₂ concentration can be expected to interact with a vast number of other environmental

influences which together control plant growth and development. Because only a fraction of all combinations of these environmental variables have been tested or are testable, and since future climatic conditions are also unknown, there is a need to model plant responses to individual environmental factors and to use these models to predict the interactions. Only models which are at least semimechanistic and extrapolative in nature have the flexibility to respond to a broad range of interacting factors.

The basis of ecosystem and cropping system models is the single-species, mechanistic extrapolative model. Problems encountered in developing these models may be associated with the data base (for instance, uncertainty with respect to some of the mechanisms and functional relationships on which the model is built), or they may be associated with the modeling process per se (for instance, the necessity to model CO₂ interactions at the level of physiological processes), whereas predictions must be made at the ecosystem or cropping system level. These kinds of problems exist to differing degrees for crop modelers and natural ecosystem modelers.

Agricultural ecosystems are simpler than unmanaged natural ecosystems. A crop model is largely an extension of a single species plant growth model, in contrast to the multiple plant species present in natural ecosystems. Consequently, although the plant responses to CO₂ described above are exceedingly complex, similar responses are encountered over broad cropping areas. Also, in advanced agricultural systems, the amount of soil water is sufficient or is at least known, reasonable nutrient levels are maintained, and interactions with animals, insects, and diseases are controllable. All of these factors greatly complicate modeling of unmanaged systems. In addition, most crop species are annuals. Annual species are far more easily evaluated for CO₂ responses than perennial shrubs and trees, which may exhibit unknown long-term CO₂ effects. Finally, the obvious economic importance of crops has facilitated the funding of modeling efforts, so that flexible mechanistic models capable of responding to CO₂ concentration exist or are being constructed for several crop species. However, the aggregation of single-species models into cropping system models that predict crop yields over large areas with diverse soil types and weather patterns cannot be done yet. Also, it is still unknown whether crops fall into response groups, or to what extent the data base must be developed. Plant response options are known to exist, and often the direction of the response is known, but the actual magnitude of the critical responses under various field environments remains to be estimated for most species. To achieve a reasonably accurate predictive capability

for the most important crops, close coordination of modeling and experimentation is essential. Response profiles for each major crop species are required. A fundamental understanding of how other environmental factors influence the CO₂ response is essential.

The critical importance of quantifying the role of natural ecosystems in the present and future global carbon balance has only recently been recognized. For instance, particularly important from the point of view of global carbon cycling are the arctic, boreal, and bog ecosystems. However, there is not sufficient information to predict whether these will be net sinks for carbon because of increased biomass production or net sources of carbon because of temperature and drainage effects on oxidation of organic matter. Other ecosystems critical to an understanding of the contribution of world vegetation to the global carbon cycle must be identified, and their current and future behavior as sources or sinks of carbon estimated through ecosystems-level models.

Like models for agricultural ecosystems, the basis of the unmanaged or natural ecosystem model is the plant growth model. However, the natural ecosystem model must also be extended to account for long-term CO₂ effects of perennial species as well as species competition over long time periods. As complex a challenge as this represents, the current limitations are ones of understanding of biological effects and lack of data. At this time, CO₂ models should be considered working hypotheses with which to test the implications of assumed CO₂ responses and to assess critical areas of needed research. Therefore, model development and ecosystem research must each guide the other.

To achieve a predictive capability with respect to long-term adaptation of major world ecosystems to chronically increasing CO₂, research efforts will have to be highly coordinated and focused, first, on technically achievable as well as ecologically important systems. Only one unmanaged ecosystem, albeit a critical one, is being studied with respect to CO₂ effects, and here study of the higher level of effects of CO₂ on ecosystem function and nutrient turnover are not yet a part of the objectives. With expansion of the data base for this and other systems, model development and validation will follow.

Meanwhile, a network of controlled environment autecological studies should be initiated which spans a sufficient diversity of growth forms or functional plant types, environments, and ecosystems to allow understanding and modeling of the responses of major species, and subsequently, the responses of major biomes of interest. The scheme presented in Chapter 6 represents one example of possible research coordination tactics.

10.2.2 Specific Research Recommendations

Work on the following list of specific recommendations would go far to close the gaps in our knowledge and reduce the current uncertainties with respect to CO₂ responses of vegetation.

10.2.2.1 *Photosynthesis and Acclimation*

High priority should be given to work on the mechanism involved in photosynthetic acclimation. Feedback inhibition, if not elucidated biochemically, should become empirically predictable for each species selected for in-depth model development. Rate equations must be developed and quantitative evaluation of light and temperature limitations on photosynthesis and organ development for these species must be obtained.

10.2.2.2 *Water Consumption*

The effects of high CO₂ on total plant (or crop) water consumption should be assessed under field conditions as well as in carefully controlled environments. The extent to which increased leaf area and root growth may counteract the water-conserving effects of CO₂ on leaf conductance should be established for major crop species, as well as for appropriate native species in critical ecosystems for which population dynamics are determined by relative plant water consumption patterns.

10.2.2.3 *Nutrient Interaction*

Work should proceed on the nature of plant responses to elevated CO₂ under various conditions of nutrient availability. Minimum tissue concentrations of the most critical nutrients for maximum growth of agricultural species should be obtained. Assuming that crop plants, selected by humans for maximum growth in fertile habitats, may differ in their nutritional behavior from native plants evolved in unfavorable environments, the mechanism of nutrient limitations of carbon assimilation and growth should be assessed for both. Likewise, possibly compensating effects of high CO₂ on nutrient uptake capacity or root-to-shoot ratios should be investigated for various plant types.

10.2.2.4 *Light and Temperature*

Interactions of light and temperature with CO₂ concentration on photosynthesis and growth are not well documented. Empirical data are needed to validate predictions which result when these factors are modeled separately.

10.2.2.5 *Carbon (Dry Matter) Partitioning*

Quantitative estimates of dry matter partitioning to organs are required for accurate growth predictions of any species selected for in-depth modeling, including the interactions of CO₂ with the major environmental influences, namely water availability, nutrient availability, light, and temperature. Of particular importance are the differential allocation of dry matter to leaf thickness versus leaf area or to root length (and number) versus root diameter.

10.2.2.6 *Insect/Pathogen Interactions*

Much more work is required to determine to what extent possible changes in C:N (or C:P) ratio of tissues developing in elevated CO₂ will affect associated insect and pathogen activity, which will in turn affect total ecosystem productivity. Other aspects of the effects of tissue quality (as affected by high CO₂) on herbivores and pathogens should be studied.

10.2.2.7 *Soil Microbial Activity*

The importance of possible CO₂-induced increases in root carbohydrate exudation should be assessed in both short- and long-term experiments. Specifically, changes in mycorrhizal activity, nonsymbiotic N₂-fixation, general microbial activity, mineralization, and nutrient sequestering should be investigated.

10.2.2.8 *Respiration*

Photorespiratory reductions anticipated in high-CO₂ environments should greatly affect carbon balance, but should be automatically included in measurements of net photosynthesis. On the other hand, on the basis of very little data, dark respiration supporting both growth and maintenance of existing tissues is expected to increase, and quantitative estimates of these changes are necessary for productivity and carbon balance projections. The response of net ecosystem respiration to the overall carbohydrate status of the system must be studied.

10.2.2.9 *Carbon Sequestering*

The partitioning of carbon assimilated by ecosystems into short-lived and long-lived pools must be established. In particular it must be determined to what extent assimilated carbon becomes inactive carbon in products that are slowly decomposed. The factors that will reverse carbon sequestering, causing the release of previously stored carbon, must also be studied.

10.2.2.10 *Responses of Plant Types by Growth Form and Habitat*

The documentation of CO₂ responses of a broad range

of plant growth forms and habitats will permit testing of the hypothesis that plants fall into response types. Because of the variability in experimental conditions, several experiments are required to establish a response range for a species. Perhaps insight of this sort may result more readily from experiments in which different species are evaluated under similar environmental conditions.

10.2.2.11 *Mechanism of the C₄ Response*

In view of the presence of the CO₂-concentrating mechanism in leaves of C₄ species, alternative mechanisms for the often observed growth responses to elevated CO₂ should be investigated. Possible causes to be studied are more rapid canopy development due to either improved leaf water status or increased leaf temperature resulting from lower transpiration.

10.2.2.12 *Salinity*

The reported enhancement of growth of some species under conditions of salinity stress have not been tested under field conditions. The potential for extending agriculture into currently marginal areas will depend on how much otherwise suitable land falls into the range of salinity over which CO₂ enrichment can increase productivity to the point of profitability. The impact of this CO₂/salinity interaction on world agricultural productivity should be analyzed. Natural saline systems should be studied to determine if changes will occur in the vegetation.

10.2.2.13 *Pollutants*

Systematic studies should be undertaken to determine the interactive effects of CO₂ with O₃, SO₂, and NO₂. Because the causes of variability among species with respect to pollution sensitivity are largely unknown, the interactions with CO₂ cannot be anticipated and should be investigated over a range of species.

10.2.2.14 *Productivity and Higher Order Ecosystem Interactions*

Total ecosystem productivity is the sum of a great many complex, interacting forces. While the growth responses of plants grown in favorable environments bear a certain relation to the photosynthetic responses, in the field higher order interactions (such as competition, herbivory, nutrient sequestering, etc.) will modify this relationship. This is perhaps most obvious for unmanaged ecosystems, but is also true for agricultural ecosystems to the extent that the environment is not completely controlled. Therefore, to understand these higher order interactions and to determine the direction and magnitude of their responses to elevated

CO₂, ecosystems themselves must be studied. Not all important ecosystems are amenable to long-term CO₂ exposure studies, but knowledge gathered from those that are technically feasible should help us to understand the dynamics of possible system-level responses.

10.2.3 Technical Considerations

Each of the exposure methods discussed in Chapter 2 of this volume has important advantages to offer the CO₂ research community. Indoor and outdoor controlled environment chambers are particularly well suited for experiments to elucidate basic CO₂ responses or physiological response mechanisms, or to supply empirical data as input to mechanistic models. Experiments in open top chambers or tracking chambers are ideal for model validation but also to investigate community-level processes as they too respond to elevated CO₂. Of course, for these systems, adjustments must be made for differences in microenvironments between the chamber interior and the outside. The open field release is considered to be the most realistic condition possible for the study of a future high-CO₂ environment.

10.2.4 Specific Modeling Recommendations

It is important to eschew the development of simple empirical interpolative models that are based on limited data yet purport to predict the response of vegetation to CO₂ concentration and other environmental variables outside the range of available data.

Researchers should develop semimechanistic interpolative models of ecosystems and cropping systems that contain those CO₂ responses and environmental interactions for which there is a solid data base. These serve very valuable research and heuristic functions with regard to CO₂ response mechanisms for the short term. Measurements made on plants during field releases of CO₂ would provide data ideally suited for developing these models.

The long-term objective is to develop comprehensive, mechanistic extrapolative models for the most important agricultural and native plant species. Controlled environment data are required to parameterize these models.

These models must be validated. Measurements made on plants during field release of CO₂ would provide the ideal data for validation. An alternative, however, would be to validate them using field data at ambient CO₂ concentration (to elucidate their response to other environmental variables), and then to validate their response to CO₂ using controlled environment data.

Sensitivity analysis should be used to decide how models may be simplified with least loss of accuracy.

Exploring ways of extending crop models over large geographical areas with diverse soil types and weather patterns and of aggregating models for different species into ecosystem models is important.

Stochastic elements should be introduced into the models in order to provide a measure of uncertainty in the predictions.



APPENDIX: DATA TABLES FOR CARBON DIOXIDE-DOUBLING RESPONSE SURVEY

This appendix is a tabulation of all the data available in the open literature on 10 selected responses to elevated CO₂ for 10 leading annual crop species. The data form the basis of predicted relative (percent) responses to a doubling (to 680 ppm) of current ambient CO₂ concentration, which will probably occur during the 21st century, based on regression analysis. Details of data selection and pooling procedures for the regressions as well as the resulting predicted responses are found in Chapter 5.

Data Tables

MEASUREMENTS	OTHER CONDITIONS		OBSERVATIONS		RELATIVE RESPONSES	REFERENCES
ALFALFA CARBON ASSIMILATION						
Short-term CER	Greenhouse; 32/18°C; 7000 ft-c; variable RH.	15°C 25°C 35°C	[300] 15.6 28.9 31.6	[480] 22.3 44.3 56.5	[480] 1.43 1.53 1.79	Wright 1974
ALFALFA BIOMASS ACCUMULATION						
Biomass (rel. units)	Greenhouse; CO ₂ and nutrient trts began after 4 wks; C = balanced nutrient; -N = replace 60% of NO ₃ ⁻ with Cl ⁻ ; -P = replace 90% H ₂ PO ₄ ⁻ with Cl ⁻ .	C -N -P	[350] 74.0 69.5 34.0	[700] 84.5 90.0 33.0	[700] 1.14 1.29 0.97	Goudriaan and de Ruiter 1983
Biomass (rel. units)	Greenhouse; 19/14°C MJm ⁻² d ⁻¹ ; 8h photosynthetic period; 16h php; 0.66/0.48 kPa VPD; "first" period were watered; "whole" period extended into water stress.	Period first whole	[340] 1.00 1.00	[680] 2.30 1.78	[680] 2.30 1.78	Morison and Gifford 1984b
ALFALFA ROOT:SHOOT RATIO						
Root:shoot ratio	Greenhouse; CO ₂ and nutrient trts began after 4 wks; C = balanced nutrient; -N = replace 60% of NO ₃ ⁻ with Cl ⁻ ; -P = replace 90% of H ₂ PO ₄ ⁻ with Cl ⁻ .	C -N P	[350] 0.276 0.219 0.308	[700] 0.174 0.200 0.269	[700] -0.102 -0.019 -0.038	Goudriaan and de Ruiter 1983
Root:shoot ratio	Greenhouse; 19/14°C 10.2 MJm ⁻² d ⁻¹ ; 8h photosynthetic period; 16h php; 0.66/0.48 kPa VPD; "first" period well watered; "whole" period extended into water stress.	Period first whole	[340] 0.30 0.81	[680] 0.32 0.69	[680] +0.02 -0.12	Morison and Gifford 1984b

MEASUREMENTS

OTHER CONDITIONS

OBSERVATIONS

RELATIVE RESPONSES

REFERENCES

ALFALFA HARVEST INDEX

--No Data--

ALFALFA CONDUCTANCE

--No Data--

ALFALFA TRANSPIRATION

--No Data--

ALFALFA YIELD

--No Data--

ALFALFA COMPONENTS OF YIELD

--No Data--

MEASUREMENTS	OTHER CONDITIONS	OBSERVATIONS				RELATIVE RESPONSES		REFERENCES
BARLEY CARBON ASSIMILATION								
Short-term CER (mg m ⁻² s ⁻¹)	Short-term measurements on field grown plants; 80 x 80 cm canopy chambers; air T = 20.7-21.0°C; 730-760 W m ⁻² ; VPD = 1000-1200 Pa.	[330] 1.34	[600] 1.94	[800] 2.20		[600] 1.45	[800] 1.64	Louwerse 1980
Acclimated CER (mg CO ₂ dm ⁻² h ⁻¹)	Growth chambers; 20/15°C; 16h php; 74/92% RH. Mean of Experiments 2 and 3.	cal dm ⁻² min ⁻¹ ---3.7--- ---7.7--- [300] [1000] [300] [1000] 9.6 11.7 14.0 18.2				cal dm ⁻² min ⁻¹ -3.7-- --7.7-- [1000] [1000] 1.22 1.30		Ford and Thorne 1967
Initial NAR (g m ⁻² wk ⁻¹)	Growth chambers; 20/15°C; 16h php; 74/92% RH; trt began 25 d after planting. Exp 2 wk 0-2	cal dm ⁻² min ⁻¹ ----3.7---- ----7.7---- [300] [1000] [300] [1000] 23 27 31 42				cal dm ⁻² min ⁻¹ -3.7-- --7.7-- [1000] [1000] 1.2 1.3		
Long-term NAR (g m ⁻² wk ⁻¹)	Growth chambers; 20/15°C; 11.6 cal dm ⁻² min ⁻¹ ; 16h php; 74/92% RH; trt began 26 d after planting. Exp 1 wk 3 wk 6	[300] [1000] 39 53 23 26				[1000] 1.4 1.1		Ford and Thorne 1967
Long-term NAR (g m ⁻² wk ⁻¹)	Growth chambers; 20/15°C; 16h php; 74/92% RH; trt began 25 d after planting. Exp 2 wk 2-4 wk 4-6	cal dm ⁻² min ⁻¹ ----3.7---- ----7.7---- [300] [1000] [300] [1000] 15 12 20 22 10 14 13 14				cal dm ⁻² min ⁻¹ --3.7-- --7.7-- [1000] [1000] 0.8 1.1 1.4 1.1		Ford and Thorne 1967
Long-term NAR (g m ⁻² wk ⁻¹)	Growth chambers; 20/15°C; 16h php; 74/92% RH; trt began at planting. Exp 3 days 17-39	cal dm ⁻² min ⁻¹ ----3.7---- ----7.7---- [300] [1000] [300] [1000] 27 32 36 44				cal dm ⁻² min ⁻¹ --3.7-- --7.7-- [1000] [1000] 1.2 1.2		Ford and Thorne 1967
Long-term NAR (mg cm ⁻² d ⁻¹)	Small outdoor chambers; over 15 d trt.	[350] 3.5	[1050] 4.8			[1050] 1.4		Imai and Murata 1976

MEASUREMENTS

OTHER CONDITIONS

OBSERVATIONS

RELATIVE RESPONSES

REFERENCES

BARLEY BIOMASS ACCUMULATION

Biomass (mg plant ⁻¹)	Small growth chambers; growth over 15 days.		[350] 175	[1050] 317	[1050] 1.81	Imai and Murata 1976
Biomass (g pot ⁻¹)	Growth chambers; 20/15°C; 11.6 cal dm ⁻² min ⁻¹ ; 16h php; 74/92% RH; trt began 26 d after planting.	Exp 1 wk 3 wk 6	[300] 18 49	[1000] 26 63	[1000] 1.4 1.3	Ford and Thorne 1967
Biomass (g pot ⁻¹)	Growth chambers; 20/15°C; 16h php; 74/92% RH; trt began 25 d after planting.	Exp 2	cal dm ⁻² min ⁻¹ -----3.6-----8.3----- [300] [1000] [300] [1000] 31 40 49 63		cal dm ⁻² min ⁻¹ --3.6-- --8.3-- [1000] [1000] 1.3 1.3	
Biomass (g m ⁻²)	Growth chambers; 20/15°C; 16h php; 74/92% RH; trt began at planting.	Exp 3 17d 39d	cal dm ⁻² min ⁻¹ ---3.6--- ---8.3--- [300] [1000] [300] [1000] 0.7* 0.8* 1.0* 1.2* 11.7* 17.7* 20.4* 28.1*		cal dm ⁻² min ⁻¹ --3.6-- --8.3-- [1000] [1000] 1.14* 1.20* 1.51* 1.38*	
Biomass (g m ⁻²)	1 m ⁻² exposure chambers in field; avg. max/min T = 24/13°C; well irrigated; daily rad. mean = 620 and 470 cal m ⁻² before and after anthesis.		[305] 852	[706] 1438	[706] 1.69	Gifford et al. 1973
Biomass (rel. units)	Greenhouse; 19/14°C 10.2 MJm ⁻² d ⁻¹ ; 8h photosynthetic period; 16h php; 0.66/0.48 kPa VPD; "first" period well watered; "whole" period extended into water stress.	Period first whole	[340] 1.00 1.00	[680] 2.07 1.64	[680] 2.07 1.64	Morison and Gifford 1984b

* Not used in calculation of overall response

MEASUREMENTS	OTHER CONDITIONS	OBSERVATIONS			RELATIVE RESPONSES		REFERENCES	
BARLEY ROOT:SHOOT RATIO								
Root:shoot ratio	Growth chambers; 20/15°C; 11.6 cal dm ⁻² min ⁻¹ ; 16h php; 74/92% RH; trt began 26 d after planting.	Exp 2 wk 2 wk 4	[300] 0.333 0.256	[1000] 0.333 0.303	[1000] +0.000 +0.047		Ford and Thorne 967	
Root:shoot ratio	Greenhouse; 19/14°C 10.2 MJm ⁻² d ⁻¹ ; 8h photosynthetic period; 16h php; 0.66/0.48 kPa VPD; "first" period well watered; "whole" period extended into water stress.	Period first whole	[340] 0.36 0.23	[680] 0.37 0.19	[680] +0.01 -0.04		Morison and Gifford 1984b	
BARLEY HARVEST INDEX								
Harvest index	1 m ² exposure chambers in field. average max/min T = 24/13°C; irrigated; daily radiation mean = 620 and 470 cal m ⁻² before & after anthesis.		[305] 0.314	[706] 0.328	[706] +0.014		Gifford et al. 1973	
BARLEY CONDUCTANCE								
Conductance (mm s ⁻¹)	Short-term measurements on field grown plants; 80 x 80 cm chamber; air T = 20.7-21.0°C; 730-760 W m ⁻² ; VPD = 1000-1200 Pa.		[330] 45.5	[600] 21.5	[800] 16.8	[600] 0.472	[800] 0.369	Louwerse 1980

MEASUREMENTS	OTHER CONDITIONS	OBSERVATIONS			RELATIVE RESPONSES	REFERENCES	
BARLEY TRANSPIRATION							
Transpiration (rel. units)	Small growth chambers. 1-5 days 6-10 days 11-15 days	[350] 100 100 100	[1050] 57 55 67		[1050] 0.57 0.55 0.67	Imai and Murata 1976	
Transpiration (mg m ⁻² s ⁻¹)	Short-term measurements on field grown plants; 80 x 80 cm chamber; air T = 20.7-21.0°C; 730-760 W m ⁻² ; VPD = 1000-1200 Pa.	[330] 225	[600] 184	[800] 154	[600] 0.818	[800] 0.684	Louwerse 1980
Transpiration (rel. units)	Short-term measurements on green- house plants with leaf chamber; leaf T = 30.5°C; 0.4 cal cm ⁻² min ⁻¹ PAR; VPD = 2-3 g cm ⁻³ .	[300] 98.5	[800] 83.0		[800] 0.84		Akita and Moss 1972
BARLEY YIELD							
Grain yield (g m ⁻²)	1 m ² exposure chambers in field. average max/min T = 24/13°C; irrigated; daily radiation mean = 620 and 470 cal m ⁻² before & after anthesis.	[305] 268	[706] 471		[706] 1.76		Gifford et al. 1973
BARLEY COMPONENTS OF YIELD							
Grain wt (mg grain ⁻¹) Grain no ear ⁻¹ Ear m ⁻²	1 m ² exposure chambers in field. average max/min T = 24/13°C; irrigated; daily radiation mean = 620 and 470 cal m ⁻² before & after anthesis. wt grain ⁻¹ grain no ear ⁻¹ ears m ⁻²	[305] 36.0 11.5 647	[706] 40.9 11.8 973		[706] 1.14 1.03 1.50		Gifford et al. 1973

MEASUREMENTS	OTHER CONDITIONS		OBSERVATIONS		RELATIVE RESPONSES		REFERENCES	
CORN CARBON ASSIMILATION								
Short-term leaf CER (rel. units)	Greenhouse.		[350] 47	[800] 56		[800] 1.2	Akita and Moss 1973	
Short-term leaf CER (mg CO ₂ dm ⁻² h ⁻¹)	Outdoor in pots; in summer.		[300] 32.0	[1000] 39.0		[1000] 1.22	Akita and Tanaka 1973	
Short-term leaf CER (μmol m ⁻² s ⁻¹)	Growth chambers (or field grown) 23/29°C; 20h php; 70/80% RH.	growth chamber field grown	[300] 13.3 28.9	[500] 14.0 30.0		[500] 1.05 1.04	Farquhar et al. 1978	
Short-term leaf CER (mg dm ⁻² h ⁻¹)	Greenhouse; in pots; excised leaves.		[350] 58	[600] 75	[1000] 92	[600] 1.3	[1000] 1.6	Hesketh 1963
Short-term leaf CER (mg dm ⁻² h ⁻¹)	Field grown, in summer.	0.4 ly min ⁻¹ 1.2 ly min ⁻¹	[325] 28 60	[500] 32 80		[500] 1.1 1.3		Hesketh and Moss 1963
Short-term leaf CER (10 ⁻⁸ g cm ⁻² s ⁻¹)	Field grown, mean of upper and lower leaves for Pa83.		[360] 4.2	[720] 6.5	[1080] 8.6	[720] 1.5	[1080] 2.0	Gifford and Musgrave 1970
Short-term leaf CER (10 ⁻⁶ kg CO ₂ m ⁻² s ⁻¹)	Growth chamber; 20°C; 60 W m ⁻² ; after 4 weeks trt.	J m ⁻² s ⁻¹ 150 300	[300] 0.77 0.95	[500] 0.95 1.10	[1000] 1.05 1.30	[500] 1.2 1.2	[1000] 1.4 1.4	Goudriaan and van Laar 1978
Short-term CER (μmol m ⁻² s ⁻¹)	Growth chambers; 25/20°C; 630 μE m ⁻² s ⁻¹ ; 16h php; 70% RH.		[340] 32.0	[600] 32.0	[800] 31.3	[600] 1.0	[800] .978	Morison and Gifford 1983

MEASUREMENTS

OTHER CONDITIONS

OBSERVATIONS

RELATIVE RESPONSES

REFERENCES

CORN CARBON ASSIMILATION (CONTINUED)

Short-term crop CER (mg CO ₂ dm ⁻² h ⁻¹)	Field grown.	3000 ft-c 6000 ft-c	[270] 14.0 24.5	[510] 16.3 28.7	[510] 1.16 1.17	Moss et al. 1961		
Acclimated leaf CER (mg CO ₂ dm ⁻² h ⁻¹)	Greenhouse, then growth chambers; 27/18°C; 800 to 2000 μE m ⁻² s ⁻¹ ; 75% RH; after 14 or 28 days trt.		[300] 34	[600] 38	[1200] 34	[600] 1.1	[1200] 1.0	Carlson and Bazzaz 1980
Acclimated CER (mg m ⁻² s ⁻¹)	Open top chambers; in pots.		[340] 1.35	[520] 1.30	[910] 1.25	[520] 0.963	[910] 0.926	Rogers et al. 1983
Acclimated CER (μmol m ⁻² s ⁻¹)	Greenhouse; 32/20°C; 2000 μmol quanta m ⁻² s ⁻¹ ; 50-70% RH.	mM NO ₃ 0.6 4 12 24	[300] 26 38 41 50	[480] 30 46 50 61	[780] 34 52 57 68	[480] 1.2 1.2 1.2 1.2	[780] 1.3 1.4 1.4 1.4	Wong 1980
Initial NAR (mg cm ⁻² d ⁻¹)	Small growth chambers out- doors; for 15 d trt.		[350] 4.4	[1000] 5.0	[1000] 1.1	Imai and Murata 1976		
Initial NAR (rel. units)	Small growth chambers out- doors; after 8-10 d trt.	N low high	[350] 100 100	[1000] 105 110	[1000] 1.05 1.10	Imai and Murata 1978a		
Initial NAR (rel. units)	Greenhouse then growth chambers; 3/pot; 12h php; after 5 d trt.	27 klx; 28/23°C 48 klx; 23/20°C 48 klx; 28/23°C	[350] 100 100 100	[1000] 115 116 132	[1000] 1.15 1.16 1.32	Imai and Murata 1979b		
Initial NAR (rel. units)	Growth chambers; 28/23°C; 48 klux; 12h php; 40-70% RH; after 5 d trt.		[300] 100	[1000] 127	[1000] 1.27	Imai and Murata 1979a		

MEASUREMENTS	OTHER CONDITIONS		OBSERVATIONS		RELATIVE RESPONSES		REFERENCES	
CORN CARBON ASSIMILATION (CONTINUED)								
Long-term NAR (g m ⁻² wk ⁻¹)	Greenhouse, then growth chamber; 20/15°C; 16h php, 74-92% RH; after 6 wks. trt.		[300] 54	[1000] 64		[1000] 1.2	Ford and Thorne 1967	
Long-term NAR (g dm ⁻² d ⁻¹)	Growth chambers; 28/22°C; 650 μE m ⁻² s ⁻¹ ; 14h php; 70% RH.	d 12-24 d 24-25	[350] 0.114 0.124	[600] 0.111 0.119	[1000] 0.109 0.110	[600] 0.974 0.960	[1000] 0.956 0.887	Patterson and Flint 1980
Long-term NAR (g dm ⁻² d ⁻¹)	Growth chamber; 26/20°C; 14h php; 70% RH.		μE m ⁻² s ⁻¹ -----600-----1200----- [350] [675] [350] [675] 0.095 0.093 0.170 0.200 0.054 0.053 0.152 0.151			μE m ⁻² s ⁻¹ -600- -1200- [675] [675] 0.979 1.176 0.981 0.993	Sionit et al. 1982	
		d 26-33 d 33-40						
CORN BIOMASS ACCUMULATION								
Biomass (g plant ⁻¹)	Small growth chamber; 23.5°C; 266 cal cm ⁻² s ⁻¹ ; after 20 d trt.		[300] 2.851	[1000] 2.401		[1000] 0.8422	Akita and Tanaka 1973	
Biomass (rel. units)	Greenhouse then growth chamber; 27/18°C; 800-2000 μE m ⁻² s ⁻¹ ; 75% RH; trt after 20 d.		[300] 1.00	[600] 1.24	[1200] 0.93	[600] 1.24	[1200] 0.93	Carlson and Bazzaz 1980
Biomass (g pot ⁻¹)	Growth chambers; 20/15°C; 11.6 cal dm ⁻² min ⁻¹ ; 16h php; 74/92% RH; trt after 26 d.	week 3 6	[300] 7.9 37.0	[1000] 8.0 45.0		[1000] 1.0 1.2	Ford and Thorne 1967	
Biomass (g pot ⁻¹)	Greenhouse compartments; 21/13°C; 12h php; 65/95% RH, C = balanced nutrient; -N = replace 60% NO ₃ ⁻ with Cl ⁻ ; -P = replace 90% H ₂ PO ₄ ⁻ with Cl ⁻ .	C -N -P	[350] 167 81 44	[700] 191 98 38		[700] 1.14 1.21 0.86	Goudriaan and de Ruiter 1983	
							Imai and Murata	
Biomass (mg)	Small growth chambers; after 15 d trt.		[350] 1513	[1050] 1645		[1050] 1.087	Imai and Murata 1976	

CORN BIOMASS ACCUMULATION (CONTINUED)

Biomass (mg)	Small growth chambers; after 8 d trt.	N low high	[350] 1171 1457	[1000] 1415 1817	[1000] 1.208 1.247	Imai and Murata 1978a		
Biomass (mg)	Small growth chambers; 28/23°C; 48 klux; 12h php; 40-70% RH; after 5 d trt.		[300] 466	[1000] 621	[1000] 1.33	Imai and Murata 1979a		
Biomass (mg)	Small growth chambers; after 5 d trt.	°C 28/23 23/20	klux ---27--- [300] [1000] [300] [1000] 372 480 432 612 385 474 334 418		klux --27-- -48-- [1000] [1000] 1.29 1.42 1.23 1.25		Imai and Murata 1979b	
Biomass (g plant ⁻¹)	Growth chambers; 28/22°C; 650 μE m ⁻² s ⁻¹ ; 14h php; 70% RH.	Day 12 24 45	[350] 0.63 6.96 91.3	[600] 0.73 6.24 89.5	[1000] 0.76 6.63 80.1	[600] 1.160 0.897 0.980	[1000] 1.210 0.953 0.877	Patterson and Flint 1980
Biomass (g plant ⁻¹)	Open top chambers; in pots; after 11 wks trt.		[340] 85.3	[718] 116.5	[910] 123.2	[718] 1.37	[910] 1.44	Rogers et al. 1983
Biomass (g plant ⁻¹)	Growth chambers; 26/20°C; 14h php; 70% RH; after 40 d trt.	μE m ⁻² s ⁻¹ 550 1200	[350] 86 155	[675] 108 195	[675] 1.26 1.26			Sionit et al. 1982
Biomass (g plant ⁻¹)	Greenhouses; 32/20°C; 2 μE m ⁻² s ⁻¹ ; natural php; 60% RH.	mM NO ₃ 24.0 12.0 4.0 0.6	[330] 32 25 18 11	[640] 37 30 22 12	[640] 1.2 1.2 1.2 1.1			Wong 1979
Biomass (rel. units)	Greenhouse; 28/23°C; 9.5 MJm ⁻² d ⁻¹ ; 8h photosynthetic period; 16h php; 1.51/1.12 kPa VPD; "first" period. well-watered; "whole" period extended into water stress.	Period first whole	[340] 1.00 1.00	[680] 1.00 1.36	[680] 1.00 1.36			Morison and Gifford 1984b

MEASUREMENTS	OTHER CONDITIONS		OBSERVATIONS			RELATIVE RESPONSES		REFERENCES
CORN ROOT:SHOOT RATIO								
Root:shoot ratio	Greenhouse compartments; 21/13°C; 12h php; 65/95% RH; C = balanced nutrient; -N = replace 60% NO ₃ ⁻ with Cl ⁻ ; -P = replace 90% H ₂ PO ₄ ⁻ with Cl ⁻ .	C -N -P	[350] 0.14 0.23 0.22	[700] 0.12 0.37 0.19	[700] -0.02 +0.14 -0.03			Goudriaan and de Ruiter 1983
Root:shoot ratio	Growth chambers; 28/22°C; 650 μE m ⁻² s ⁻¹ 14h php; 70% RH.		[350] 0.25	[600] 0.28	[1000] 0.23	[600] +0.03	[1000] -0.02	Patterson and Flint 1980
Root:shoot ratio	Open top chambers in pots; after 11 wks. trt.		[340] 0.09	[718] 0.12	[910] 0.14	[718] +0.03	[910] +0.05	Rogers et al. 1983
Root:shoot ratio	Growth chambers; 26/20°C; 14h php; 70% RH.	μE m ⁻² s ⁻¹ 550 1200	[350] 0.115 0.225	[675] 0.135 0.240	[675] +0.020 +0.015			Sionit et al. 1982
Root:shoot ratio	Small growth chambers; after 15 d trt.		[350] 0.75*	[1050] 0.59*	[1050] -0.16*			Imai and Murata 1976
Root:shoot ratio	Greenhouse; 28/23°C; 9.5 MJm ⁻² d ⁻¹ ; 8h photosynthetic period; 16h php; 1.51/1.12 kPa VPD; "first" period well watered; "whole" period extended into water stress.	Period first whole	[340] 0.52 0.38	[680] 0.26 0.33	[680] -0.26 -0.05			Morison and Gifford 1984b
*Not used in calculation of overall response								

MEASUREMENTS

OTHER CONDITIONS

OBSERVATIONS

RELATIVE RESPONSES

REFERENCES

CORN HARVEST INDEX

Harvest index (seed wt/ total top wt)	Greenhouse compartments; 21/13°C; 12h php; 65/95% RH; C = balanced nutrient; -N = replace 60% NO ₃ ⁻ with Cl ⁻ ; -P = replace 90% H ₂ PO ₄ ⁻ with Cl ⁻ .	C -N -P	[350] 0.46 0.25* 0*	[700] 0.49 0* 0*	[700] +0.03 -0.25* +0*	Goudriaan and de Ruiter 1983		
Harvest index (ear wt/ total top wt)	Open top chambers; in pots.		[340] 0.42	[718] 0.47	[910] 0.41	[718] +0.05	[910] -0.01	Rogers et al. 1983
* Not used in calculation of overall response								

CORN CONDUCTANCE

Conductance (cm s ⁻¹)	Greenhouse; grown at amb. CO ₂ ; measurement conditions = 30.5°C leaf temp; 0.4 and 0.05 cal cm ⁻² min ⁻¹ light intensity.	$\frac{\text{cal cm}^{-2} \text{ min}^{-1}}{0.05}$ 0.40	[300] 0.44 0.36	[800] 0.29 0.14	[800] 0.66 0.39	Akita and Moss 1973		
Conductance (mol m ⁻² s ⁻¹)	Growth chambers or field.	Field Growth chamber	[300] 0.23 0.14	[500] 0.15 0.07	[500] 0.65 0.50	Farquhar et al. 1978		
Conductance (10 ⁻³ m s ⁻¹)	Growth chamber; 20°C; 60 W m ⁻² ; Attached leaves; 4 wk old plant; 25°C.	$\frac{\text{J m}^{-2} \text{ s}^{-1}}{150}$ 300	[300] 2.15 2.65	[500] 1.30 1.75	[1000] 0.64 0.80	[500] 0.605 0.660	[1000] 0.30 0.30	Goudriaan and van Laar 1978
Conductance (10 ⁻⁸ g cm ⁻² s ⁻¹)	Growth chamber; 630 μE m ⁻² s ⁻¹ ; 25/20°C; 16h php; 70% RH; mean of 4 VPD.		[340] 0.548	[600] 0.360	[800] 0.285	[600] 0.657	[800] 0.520	Morison and Gifford 1983
Conductance (cm s ⁻¹)	Open top chambers; n pots; leaf chamber.		[340] 0.0165	[718] 0.0088	[910] 0.0080	[718] 0.53	[910] 0.50	Rogers et al. 1983

MEASUREMENTS	OTHER CONDITIONS	OBSERVATIONS			RELATIVE RESPONSES		REFERENCES	
CORN TRANSPIRATION								
Leaf transpiration (g dm ⁻² hr ⁻¹)	Greenhouse grown at amb. CO ₂ ; 30.5°C leaf temp; 0.4 and 0.05 cal cm ⁻² min ⁻¹ .	$\frac{\text{cal cm}^{-2} \text{ min}^{-1}}{0.05}$ 0.40	[300] 2.0 2.9	[800] 0.9 1.9	[800] 0.45 0.66		Akita and Moss 1973	
Leaf transpiration (g H ₂ O dm ⁻² hr ⁻¹)	Greenhouse then growth chamber at d 20; 27/18°C; 75% RH; measurement after 2 and 4 wk trt at 25°C; 2200 μE m ⁻² s ⁻¹ ; 50% RH.		[300] 2.0	[600] 1.1	[1200] 0.7	[600] 0.55	[1200] 0.4	Carlson and Bazzaz 1980
Leaf transpiration (rel. units)	Small growth chambers.	Days 5 10 15	[350] 100 100 100	[1050] 63 65 80	[1050] 0.63 0.65 0.80			Imai and Murata 1976
Crop transpiration (mg m ⁻² s ⁻¹)	Field grown; crop enclosed; soil covered.	W m ⁻² 300 600	[335] 94 158	[540] 67 106	[1008] 51 77	[540] 0.71 0.67	[1008] 0.54 0.49	Louwerse 1980
Plant transpiration (g dm ⁻² 2 hr ⁻¹)	Growth chambers; 25/20°C; 0.6 cal cm ⁻² min ⁻¹ ; 14h php; 60/90% RH; mean of 4 varieties.		[300] 2.75	[600] 1.65	[1000] 1.00	[600] 0.60	[1000] 0.36	Pallas 1965
Transpiration (mmol m ⁻² s ⁻¹)	Greenhouse plants; 32/20°C; 2000 μmol quanta m ⁻² s ⁻¹ ; 50-70% RH; measurements at leaf T ⁰ = 30°; 2000 μmol quanta m ⁻² s ⁻¹ ; 20 mbar VPD; a, short term, b, long term.	mM NO ₃ 0.6 4.0 12.0 24.0	[310] 4.60 6.70 7.20 7.85	[620 ^a] 2.60 3.90 4.40 5.30	[620 ^b] 2.05 3.20 4.40 5.60	[620 ^a] 0.565 0.582 0.611 0.675	[620 ^b] 0.446 0.478 0.611 0.713	Wong 1980

CORN YIELD

Seed dry wt.	Greenhouse; 21/13°C; 65/95% RH; trt after 4 wks; C = balanced nutrient; -N = replace 60% NO ₃ ⁻ with Cl ⁻ ; -P = replace 90% H ₂ PO ₄ ⁻ with Cl ⁻ .		[Amb]	[700]	[700]		Goudriaan and de Ruiter 1983	
		C	68*	83*	1.2*			
		-N	20*	--	--			
		-P	--	--	--			
Ear dry wt.	Open top chamber; in pots.		[340]	[718]	[910]	[718]	[910]	Rogers et al. 1983
			32.5	48.6	44.8	1.49	1.38	

CORN COMPONENTS OF YIELD

Ears plants ⁻¹ g ear ⁻¹	Open top chambers; in pots.	ear plant ⁻¹ g ear ⁻¹	[340] 1.5 26.8	[718] 1.7 31.1	[910] 1.5 33.3	[718] 1.13 1.16	[910] 1.00 1.24	Rogers et al. 1983
Core of cob Seed yield	Greenhouse; 21/13°C; 65/95% RH; trt after 4 wks; C = balanced nutrient; -N = replace 60% NO ₃ ⁻ with Cl ⁻ ; -P = replace 90% H ₂ PO ₄ ⁻ wit Cl ⁻ .	C -N -P	----cob---- [Amb] 15 4 --	----seed---- [700] 17 4 --	----cob---- [Amb] 68 20 --	----seed---- [700] 83 -- --	--cob-- --seed-- [700] [700] 1.1 1.2 1.0 -- -- --	Goudriaan and de Ruiter 1983
* Not used in calculation of overall response								

MEASUREMENTS	OTHER CONDITIONS		OBSERVATIONS			RELATIVE RESPONSES		REFERENCES
COTTON CARBON ASSIMILATION								
Short-term CER (mg CO ₂ dm ⁻² ground area min ⁻¹)	Field grown plants in a semi-closed chamber system.	ly min ⁻¹	[350]	[475]	[600]	[475]	[600]	Baker 1965
		0.4	0.54	0.78	1.00	1.44	1.85	
		25°C	0.9	0.78	1.06	1.36	1.74	
		1.3	1.13	1.56	2.02	1.38	1.79	
		0.4	0.32	0.38	0.45	1.19	1.41	
		35°C	0.9	0.75	1.02	1.33	1.36	
		1.3	0.92	1.23	1.58	1.34	1.72	
Short-term CER (mm ³ cm ⁻² h ⁻¹)	Greenhouse grown; 35-40/25°C; 14-15h php; attached leaves at 6 wks.	ft-c	[350]	[750]	[1000]	[750]	[1000]	Bierhuizen and Slatyer 1964
		1000	52	98	113	1.88	2.17	
		2000	88	177	181	2.01	2.06	
		4000	120	197	207	1.64	1.73	
		6000	128	212	213	1.66	1.66	
Short-term CER (mg CO ₂ dm ⁻² h ⁻¹)	Greenhouse grown; excised leaves.		[300]	[500]	[1000]	[500]	[1000]	Mortimer 1959
			9*	32*	52*	4*	6*	
Short-term CER (mol m ⁻² s ⁻¹)	Greenhouse plants; 32/20°C; 2000 μmol quanta m ⁻² s ⁻¹ midday; 50-70% RH; measurements at leaf T = 30°; 2000 μmol quanta m ⁻² s ⁻¹ ; 20 mbar VPD.	mM NO ₃	[310]	[620]		[620]	Wong 1980	
		0.6	19.5	24.5		1.26		
		4.0	25.8	42.0		1.63		
		12.0	29.5	48.3		1.64		
		24.0	33.7	51.5		1.53		
Short-term CER (nmol cm ⁻² s ⁻¹)	Greenhouse plants max/min T = 35/21°C; natural summer light and php; mean of 2 y.		[330]	[630]		[630]	Mauney et al. 1979	
			2.52	3.90		1.55		
Acclimated CER (nmol cm ⁻² s ⁻¹)	Greenhouse plants max/min T = 35/21°C; natural summer light and php; mean of 2 y.		[330]	[630]		[630]	Mauney et al. 1979	
			2.52	2.87		1.14		

COTTON CARBON ASSIMILATION (CONTINUED)

Acclimated CER ($\mu\text{mol m}^{-2} \text{ s}^{-1}$)	Greenhouse plants; 32/20°C; 2000 $\mu\text{mol quanta m}^{-2} \text{ s}^{-1}$ midday; 50-70% RH; measurements at leaf T = 30°C; 2000 $\mu\text{mol quanta m}^{-2} \text{ s}^{-1}$; 20 mbar VPD.	mM NO_3 0.6 4.0 12.0 24.0	[320] 20.0 27.5 29.0 34.5	[640] 20.5 31.0 42.0 51.0	[640] 1.03 1.13 1.45 1.48	Wong 1979		
Acclimated CER ($\mu\text{mol m}^{-2} \text{ s}^{-1}$)	Greenhouse plants; 32/20°C; 2000 $\mu\text{mol quanta m}^{-2} \text{ s}^{-1}$ midday; 50-70% RH; measurements at leaf T = 30°C; 2000 $\mu\text{mol quanta m}^{-2} \text{ s}^{-1}$; 20 mbar VPD.	mM NO_3 0.6 4.0 12.0 24.0	[310] 19.5 25.8 29.5 33.7	[620] 15.8 25.0 33.5 50.0	[620] 0.810 0.969 1.140 1.480	Wong 1980		
Acclimated CER ($\mu\text{mol m}^{-2} \text{ s}^{-1}$)	Growth chamber; 26/20°C; 600 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$; 12h php; 70% RH; measurements made at saturating irradiance; 26°C; 1 kPa VPD.		[350] 13.0	[675] 15.2	[1000] 14.7	[675] 1.17	[1000] 1.13	DeLucia et al. 1985
Long-term NAR ($\text{mg dm}^{-2} \text{ d}^{-1}$)	Greenhouse plants. max/min T = 35/21°C; natural summer light and photoperiod; mean of 2 y.	juvenile reproductive mature	[330] 187 88 48	[630] 280 100 52	[630] 1.5 1.1 1.1		Mauney et al. 1978	
* Not used in calculation of overall response								

MEASUREMENTS	OTHER CONDITIONS	OBSERVATIONS	RELATIVE RESPONSES	REFERENCES	
COTTON BIOMASS ACCUMULATION					
Biomass (g plant ⁻¹)	Greenhouse plants; max/min T = 35/21°C; natural summer light and php; mean of 2 y.	juvenile reproductive mature	[330] [630] 11 29 200 480 550 1100	[630] 2.6 2.4 2.0	Mauney et al. 1978
Biomass (g plant ⁻¹)	Greenhouse; 32/20°C; 2000 μmol quanta m ⁻² s ⁻¹ at midday; 50-70% RH; natural php; whole season.	mM NO ₃ 0.6 4.0 12.0 24.0	[330] [640] 8.0 17.5 12.5 27.0 17.0 39.0 22.0 48.0	[640] 2.19 2.16 2.29 2.18	Wong 1979
Biomass (rel. units)	Greenhouse; 28/23°C; 9.5 MJm ⁻² s ⁻¹ ; 8h photosynthetic period; 16h php; 1.51/1.12 kPa VPD; "first" period were watered; "whole" period extended into water stress.	Period first whole	[340] [680] 1.00 1.00 1.00 1.19	[680] 1.00 1.19	Morison and Gifford 1984b
COTTON ROOT:SHOOT RATIO					
Root:shoot ratio	Greenhouse; 28/23°C; 9.5 MJm ⁻² s ⁻¹ ; 8h photosynthetic period; 16h php; 1.51/1.12 kPa VPD; "first" period well watered; "whole" period extended into water stress.	Period first whole	[340] [680] 0.24 0.34 0.25 0.23	[680] +0.10 -0.02	Morison and Gifford 1984b
Root:shoot ratio	Growth chamber; 26/20°C; 600 μmol photons m ⁻² s ⁻¹ ; 12h php; 70% RH; measurements made at saturating irradiance; 26°C; 1 kPa VPD.		[350] [675] [1000] 0.24 0.15 0.17	[675] [1000] -0.09 -0.07	DeLucia et al. 1985
COTTON HARVEST INDEX					
	--No Data--				

COTTON CONDUCTANCE

Conductance (cm s^{-1})	Growth chamber; 26/20°C; 600 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$; 12h php; 70% RH; measurements made at saturating irradiance; 26°C; 1kPa VPD.	[350] 0.61	[675] 0.58	[1000] 0.40	[675] 0.95	[1000] 0.66	DeLucia et al. 1985

COTTON TRANSPIRATION

Transpiration (g dm ⁻² 2h ⁻¹)	Growth chambers; 25/20°C; 0.6 cal cm ⁻² min ⁻¹ ; 14h php; 60/90% RH; mean of 4 varieties.		[300] 3.08	[600] 2.59	[1000] 2.52	[600] 0.84	[1000] 0.82	Pallas 1965
Evaporation rate (mmol m ⁻² s ⁻¹)	Greenhouse plants; 32/20°C; 2000 μmol quanta m ⁻² s ⁻¹ at midday; 50-70% RH; measure- ments at leaf T = 30°C; 2000 μmol quanta m ⁻² s ⁻¹ ; 20 mbar VPD.	mM NO ₃ 0.6 4.0 12.0 24.0	[330] 7.4 9.3 9.3 9.9	[640] 3.5 5.0 6.9 7.9		[640] 0.47 0.54 0.74 0.80		Wong 1979
Transpiration (μmol m ⁻² s ⁻¹)	Greenhouse plants; 32/20°C; 2000 μmol quanta m ⁻² s ⁻¹ at midday; 50-70% RH; measure- ments at leaf T = 30°C; 2000 μmol quanta m ⁻² s ⁻¹ ; 20 mbar VPD. a, short term; b, long term.	mM NO ₃ 0.6 4.0 12.0 24.0	[310] 6.9 8.4 9.8 11.0	[620 ^a] 4.6 7.3 8.3 9.1	[620 ^b] 2.5 3.8 5.4 8.1	[620 ^a] 0.67 0.87 0.84 0.83	[620 ^b] 0.36 0.45 0.55 0.74	Wong 1980

MEASUREMENTS	OTHER CONDITIONS	OBSERVATIONS		RELATIVE RESPONSES	REFERENCES	
COTTON YIELD						
Lint wt. (g plant ⁻¹)	Greenhouse plants; max/min T = 35/21°C; natural summer light and php; mean of 2 y.	[330] 61	[630] 170	[630] 2.8	Mauney et al. 1978	
COTTON COMPONENTS OF YIELD						
No. blooms plant ⁻¹ % retention Lint boll ⁻¹	Greenhouse plants; max/min T = 35/21°C; natural summer light and php.	Blooms plant ⁻¹ % retention lint boll ⁻¹	[330] 69 54 1.65	[630] 110 74 2.12	[630] 1.59 1.37 1.28	Mauney et al. 1978
* Not used in calculation of overall response						

POTATO CARBON ASSIMILATION

Short-term CER ($\mu\text{g CO}_2 \text{ cm}^{-2} \text{ s}^{-1}$)	Growth chambers; 20/15°C; 40 neinsteins $\text{cm}^{-2} \text{ s}^{-1}$; 16/8 php; 50-60% RH; measured at 25°C, 150 neinsteins $\text{cm}^{-2} \text{ s}^{-1}$; 11-15 mb VPD.	[330] 47.0	[470] 68.5	[610] 85.0	[470] 1.46	[610] 1.81	Ku et al. 1977
Long-term NAR ($\text{g m}^{-2} \text{ wk}^{-1}$)	Greenhouse; 22/16.5°C; natural light; 15h php; a, trt before flowering 55 d (55 d); b, trt after flowering. 110 d	[335] 30.0 13.4	[650 ^a] 40.2 12.4*	[650 ^b] 31.9* 24.4	[650 ^a] 1.34 0.92*	[650 ^b] 1.06* 1.82	Collins 1976
* Not used in calculation of overall response							

POTATO BIOMASS ACCUMULATION

Biomass (g pot ⁻¹)	Greenhouse; 21/13°C; natural light and php; 65/95% RH; exposed after 4 wks growth.	[350] 1394	[700] 1174	[700] 0.8422	Goudriaan and de Ruiter 1983

POTATO ROOT:SHOOT RATIO

Root:shoot ratio	Greenhouse; 21/13°C; natural light and php; 65/95% RH; exposed after 4 wks growth. Root:shoot ratio apart from tuber	[350] 0.131*	[700] 0.109*	[700] -0.022*	Goudriaan and de Ruiter 1983

POTATO HARVEST INDEX

Harvest index (tuber dry wt) (total dry wt)	Greenhouse; 21/13°C; natural light and php; 65/95% RH; exposed after 4 wks growth.	[350] 0.81*	[700] 0.83*	[700] +0.02*	Goudriaan and de Ruiter 1983
* Not used in calculation of overall response					

* Not used in calculation of overall response

MEASUREMENTS

OTHER CONDITIONS

OBSERVATIONS

RELATIVE RESPONSES

REFERENCES

RICE CARBON ASSIMILATION

Short-term CER (mg CO ₂ dm ⁻² h ⁻¹)	Potted plants grown outdoors and measured in leaf chamber; leaf T = 29-30°C; 50 klux.	[300] 25	[800] 38	[1000] 39	[800] 1.5	[1000] 1.6	Akita and Tanaka 1973
Short-term CER (μmol m ⁻² s ⁻¹)	Growth chambers; 25/20°C; 630 μE m ⁻² s ⁻¹ ; 16h php; 70% RH.	[340] 14.0	[600] 18.0	[800] 19.0	[600] 1.3	[800] 1.4	Morison and Gifford 1983
Short-term CER (mg CO ₂ dm ⁻² h ⁻¹)	Potted plants in small growth chambers outdoors at 350 and 1000 ppm CO ₂ ; measured with a leaf chamber; leaf T = 28°C; 55 klux; 70-85% RH.	[350] 30.4	[925] 67.5		[925] 1.79		Imai and Murata 1978b
Acclimated CER (mg CO ₂ dm ⁻² h ⁻¹)	Potted plants in small growth chambers outdoors at 350 and 1000 ppm CO ₂ ; measured with a leaf chamber; leaf T = 28°C; 55 klux; 70-85% RH.	[350] 30.4	[925] 54.3		[925] 2.22		Imai and Murata 1978b
Initial NAR (mg cm ⁻² d ⁻¹)	Small outdoor growth chambers; for 15 d trt.	[350] 0.73	[1050] 0.91		[1050] 1.2		Imai and Murata 1976
Initial NAR (rel. units)	Growth chambers; 28/23°C; 48 klux; 12h php; 40-70% RH; after 5 d trt.	[300] 100	[1000] 159		[1000] 1.59		Imai and Murata 1979a
Initial NAR (rel. units)	Greenhouse, then growth chambers; 3/pot; 12h php; 27 klux; 28/23°C after 5 d trt. 48 klux; 28/23°C 48 klux; 23/20°C	[300] 100 100 100	[1000] 182 158 150		[1000] 1.82 1.58 1.50		Imai and Murata 1979b

MEASUREMENTS	OTHER CONDITIONS	OBSERVATIONS			RELATIVE RESPONSES		REFERENCES
RICE BIOMASS ACCUMULATION							
Biomass (g plant ⁻¹)	Daytime exposure in outdoor chambers for 30 d; 23.5°C; 266 cal cm ⁻² d ⁻¹ ; mean of 2 cultivars.	[300] 1.06	[1000] 2.10		[1000] 1.98		Akita and Tanaka 1973
Biomass (mg plant ⁻¹)	Small outdoor growth chambers; 15 d trt.	[350] 178	[1050] 234		[1050] 1.31		Imai and Murata 1976
Biomass (mg plant ⁻¹)	Conditions uncertain (in Japanese); after 10 d trt.	[350] 37.5	[1000] 54.0		[1000] 1.44		Imai and Murata 1978a
	water culture	20 62.0	87.0		1.40		
	water culture	40 53.5	96.0		1.79		
		ppm N					
		5					
		[350] 700	[1000] 1064		[1000] 1.52		
		30 946	1727		1.83		
		mg N plant ⁻¹					
	soil culture	120					
Biomass (mg)	Growth chambers; 28/23°C; 48 klux; 12h php; 40-70% RH; after 5 d trt.	[300] 73	[1000] 118		[1000] 1.6		Imai and Murata 1979a
Biomass (mg)	Greenhouse, then growth chambers; 3 plants pot ⁻¹ ;	[300] 35	[1000] 53		[1000] 1.5		Imai and Murata 1979b
	27 klux; 23/20°C	32 56	65		1.8		
	12h php; after 5 d trt.	41 50	88		1.6		
	48 klux; 23/20°C				1.8		
	48 klux; 28/23°C						
Biomass (t ha ⁻¹)	Open top chambers in field; daytime exposures; dry season. a, control (no chamber); b, trt 30 d before heading; c, trt 28 d after heading.	[amb ^a] 18.4	[900 ^b] 22.7	[900 ^c] 20.2	[900 ^b] 1.23	[900 ^c] 1.10	Cock and Yoshida 1973
Biomass (t ha ⁻¹)	Open top chambers in field; daytime exposures; wet season. a, control (no chamber); b, trt 30 d before heading; c, trt 29 d after heading.	[amb ^a] 12.7	[900 ^b] 15.7	[900 ^c] 14.4	[900 ^b] 1.24	[900 ^c] 1.13	Cock and Yoshida 1973

RICE BIOMASS ACCUMULATION (CONTINUED)

Biomass (kg m ⁻²)	Open top chamber in field; daytime exposures. a, control (no chamber); b. trt 33 d before flowering; c, trt 30 d after flowering.	[amb ^a] 2.00	[900 ^b] 2.42	[900 ^c] 2.21	[900 ^b] 1.21	[900 ^c] 1.10	Yoshida 1973
Biomass (rel. units)	Greenhouse; 28/23°C; 9.5 MJm ⁻² d ⁻¹ ; 8h photosynthetic period; 16h php; 1.51/1.12 kPa VPD, "first" period well watered; "whole" period extended into water stress.	Period first whole	[340] 1.00 1.00	[680] 1.51 1.52	[680] 1.51 1.52		Morison and Gifford 1984b

RICE ROOT:SHOOT RATIO

Root:shoot ratio	Small outdoor growth chambers, for 15 d treatment.		[350] 1.62*	[1050] 2.33*	[1050] +0.71*		Imai and Murata 1976
Root:shoot ratio	Greenhouse; 28/23°C; 9.5 MJm ⁻² d ⁻¹ ; 8h photosynthetic period; 16h php; 1.51/1.12 kPa VPD; "first" period well watered; "whole" period extended into water stress.	Period first whole	[340] 0.35 0.37	[680] 0.32 0.32	[680] -0.03 -0.05		Morison and Gifford 1984b

MEASUREMENTS	OTHER CONDITIONS	OBSERVATIONS			RELATIVE RESPONSES		REFERENCES
RICE HARVEST INDEX							
Harvest index	Open top chambers in field; day-time exposures. a, control (no chamber); b, trt 33 d before flowering; c, trt 30 d after flowering.	[Amb ^a 0.51	[900 ^b 0.55	[900 ^c 0.52	[900 ^b +0.04	[900 ^c +0.01	Yoshida 1973
Harvest index	Open top chambers in field; day-time exposures; dry season. a, control (no chamber); b, trt 30 d before heading; c, trt 28 d after heading.	[Amb ^a 0.49	[900 ^b 0.51	[900 ^c 0.54	[900 ^b +0.02	[900 ^c +0.05	Cock and Yoshida 1973
Harvest index	Open top chambers in field; day-time exposure; wet season. a, control (no chamber); b, trt 30 d before headings; c, trt 29 d after heading.	[Amb ^a 0.45	[900 ^b 0.49	[900 ^c 0.48	[900 ^b +0.04	[900 ^c +0.03	Cock and Yoshida 1973
* Not used in calculation of overall response							
RICE CONDUCTANCE							
Conductance (cm s ⁻¹)	Potted plants in small growth chambers outdoors; measured with leaf chamber; leaf T = 28°C; 55 klux; 70-85% RH. a, acclimated to 350 ppm; b, acclimated to 1000 ppm.	[350] 0.303	[1000 ^a] 0.139	[1000 ^b] 0.095	[1000 ^a] 0.459	[1000 ^b] 0.310	Imai and Murata 1978b
Conductance (mol m ⁻² s ⁻¹)	Growth chambers; 25/20°C; 630 μE m ⁻² s ⁻¹ ; 16h php; 70% RH; mean of 4 VPD.	[340] 0.373	[600] 0.248	[800] 0.215	[600] 0.665	[800] 0.576	Morison and Gifford 1983

MEASUREMENTS	OTHER CONDITIONS		OBSERVATIONS			RELATIVE RESPONSES		REFERENCES
RICE TRANSPIRATION								
Transpiration (g dm ⁻² h ⁻¹)	Potted plants grown outdoors, measured in leaf chambers; leaf T = 29-30°C; 50 klux.		[300] 3.00	[800] 2.45	[1000] 2.22	[800] 0.817	[1000] 0.740	Akita and Tanaka 1973
Transpiration per unit leaf area (relative units)	Small outdoor growth chambers. 15 d trt.	d 1-5 d 6-10 d 11-15	[350] 100 100 100		[1050] 83 77 73		[1050] 0.83 0.77 0.73	Imai and Murata 1976
Transpiration (g H ₂ O dm ⁻² h ⁻¹)	Potted plants in small growth chambers outdoors; measured with leaf chamber; leaf T = 28°C; 55 klux; 70-85% RH. a, accli- mated to 350 ppm; b, acclimated to 1000 ppm.		[350] 1.52	[925 ^a] 0.98	[925 ^b] 0.55	[925 ^a] 0.64	[925 ^b] 0.36	Imai and Murata 1978b
RICE YIELD								
Seed yield (kg m ⁻²)	Open top chamber in field; day- time exposures. a, control (no chamber); b, trt 33 d before flowering; c, trt 30 d after flowering.		[Amb ^a] 1.02	[900 ^b] 1.33	[900 ^c] 1.15	[900 ^b] 1.30	[900 ^c] 1.13	Yoshida 1973
Seed yield (t ha ⁻¹)	Open top chambers in field; day- time exposures; dry season. a, control (no chamber); b, trt 30 d before heading; c, trt 28 d after heading.		[Amb ^a] 9.0	[900 ^b] 11.6	[900 ^c] 10.9	[900 ^b] 1.3	[900 ^c] 1.2	Cock and Yoshida 1973
Seed yield (t ha ⁻¹)	Open top chambers in field; day- time exposures; wet season. a, control (no chamber); b, trt 30 d before heading; c, trt 29 d after heading.		[Amb ^a] 5.7	[900 ^b] 7.7	[900 ^c] 6.9	[900 ^b] 1.4	[900 ^c] 1.2	Cock and Yoshida 1973

MEASUREMENTS	OTHER CONDITIONS		OBSERVATIONS			RELATIVE RESPONSES		REFERENCES
RICE COMPONENTS OF YIELD								
Panicle no. (no. m ⁻²)	Open top chamber in field; day-time exposures. a, control (no chamber); b, trt 33 d before flowering; c, trt 30 d after flowering.	panicle no.	[Amb ^a]	[900 ^b]	[900 ^c]	[900 ^b]	[900 ^c]	Yoshida 1973
Grain no. (10 ³ m ⁻²)		grain no.	365	363	360	0.994	0.986	
Filled grain %		filled grain	40.4	48.2	38.9	1.19	0.963	
		grain wt.	85.4	87.6	92.4	1.03	1.08	
			23.7	25.7	26.0	1.08	1.10	
Grain no. (10 ³ m ⁻²)	Open top chambers in field; day-time exposures; dry season. a, control (no chamber); b, trt 30 d before heading; c, trt 28 d after heading.	grain no.	[Amb ^a]	[900 ^b]	[900 ^c]	[900 ^b]	[900 ^c]	Cock and Yoshida 1973
Filled grain %		filled grain	45.7	50.9	44.6	1.11	0.976	
Grain wt. (mg)		grain wt.	74	77	86	1.04	1.16	
			23.1	25.9	25.1	1.12	1.09	
Grain no. (10 ³ m ⁻²)	Open top chambers in field; day-time exposures; wet season. a, control (no chamber); b, trt 30 d before heading; c, trt 29 d after heading.	grain no.	[Amb ^a]	[900 ^b]	[900 ^c]	[900 ^b]	[900 ^c]	Cock and Yoshida 1973
Filled grain %		filled grain	28.8	34.1	29.5	1.18	1.02	
Grain wt. (mg)		grain wt.	78	81	85	1.04	1.09	
			24.3	26.2	26.1	1.08	1.07	

MEASUREMENTS

OTHER CONDITIONS

OBSERVATIONS

RELATIVE RESPONSES

REFERENCES

SORGHUM CARBON ASSIMILATION

Short-term CER (nmol cm ⁻² s ⁻¹)	Greenhouse; 35/21°C max/min; 2000 μE m ⁻² s ⁻¹ at noon; 14h php; 40% average RH.	[330] 4.05	[630] 3.95	[630] 0.975	Mauney et al. 1979		
Acclimated CER (g m ⁻² h ⁻¹)	Growth chambers; 30°C; 2120 μE m ⁻² s ⁻¹ ; 16h php; 80% RH.	[300] 5.24	[600] 6.52	[1200] 5.97	[600] 1.24	[1200] 1.14	van Bavel 1974
Acclimated CER (nmol cm ⁻² s ⁻¹)	Greenhouse; 35/21°C max/min; 2000 μE m ⁻² s ⁻¹ at noon; 14h php; 40% average RH.	[330] 4.05	[630] 3.85	[630] 0.951	Mauney et al. 1979		
Long-term NAR (mg dm ⁻² d ⁻¹)	Greenhouse; 35/21°C max/min; 2000 μE m ⁻² s ⁻¹ at noon; 14h php; 40% average RH.	[330] 190 129	[630] 270 103	[630] 1.420 0.798	Mauney et al. 1978		

SORGHUM BIOMASS ACCUMULATION

Biomass (g plant ⁻¹)	Greenhouse; 35/21°C max/min; 2000 μE m ⁻² s ⁻¹ at noon; 14h php; 40% average RH.	[330] 85	[630] 100	[630] 1.2	Mauney et al. 1978	
Biomass (g shoot ⁻¹)	Growth chamber; 24/21°C; 12h php; 600-650 μmol m ⁻² s ⁻¹ ; 70% RH; mean of last 4 harvests.	[370] 22.8	[870] 21.9	[870] 0.960	Marc and Gifford 1984	
Biomass (rel. units)	Greenhouse; 28/23°C; 9.5 MJm ⁻² d ⁻¹ ; 8h photosynthetic period; 16h php; 1.51/1.12 kPa VPD; "first" period well watered; "whole" period extended into water stress.	<u>Period</u> first whole	[340] 1.00 1.00	[680] 1.26 1.31	[680] 1.26 1.31	Morison and Gifford 1984b

MEASUREMENTS	OTHER CONDITIONS		OBSERVATIONS			RELATIVE RESPONSES		REFERENCES
SOYBEAN CARBON ASSIMILATION								
Short-term leaf CER (mg CO ₂ dm ⁻² h ⁻¹)	Growth chambers; 27/21°C; 16h php; after 3 wks trt.	75 Klux 11 Klux	[300] 14.4 18.0	[700] 23.7 47.2	[1200] 25.3 64.6	[700] 1.65 2.62	[1200] 1.76 3.59	Brun and Cooper 1967
Short-term leaf CER (mg CO ₂ leaf ⁻¹ h ⁻¹)	Growth chambers; 26/20°C; 600 μE m ⁻² s ⁻¹ ; 12h php; trt after 40 d.	low sink (5:1 pod:leaf) high sink (15:1 pod:leaf)	[350] 32 45	week 1 [1000] 117 155	[1000] 3.7 3.4			Peet 1984
Short-term canopy CER (g CO ₂ m ⁻² ground 15 min ⁻¹)	Field grown; 20-30°C; natural light and php; mean of three varieties.		[300] 1.12	[450] 1.55	[600] 1.93	[450] 1.38	[600] 1.72	Egli et al. 1970
Short-term whole plant CER (mg CO ₂ dm ⁻² h ⁻¹)	Greenhouse assimilation chambers; 30°C; 1400 μE m ⁻² s ⁻¹ ; 60% RH; trt after 3-4 wks.		[350] 19.0	[600] 29.8	[1200] 34.3	[600] 1.57	[1200] 1.80	Carlson 1983
Short-term plant CER (mg CO ₂ plant ⁻¹ h ⁻¹)	Growth chamber; 26/20°C; 600 μE m ⁻² s ⁻¹ ; 12h php; trt after 44 d; CER after 4 d trt.	low sink (2:1 pod:leaf) high sink (7:1 pod:leaf)	[350] 20 32	[1000] 60 100	[1000] 3.0 3.1			Clough et. al. 1981
Short-term canopy CER (μmol CO ₂ m ⁻² s ⁻¹)	SPAR units; variable light; 25/25°C; VPD 2.4 kPa.	μE m ⁻² s ⁻¹ 300 900 1500	[320] 10 27 38	[640] 25 58 69	[640] 2.5 2.1 1.8			Jones et. al. 1985c

MEASUREMENTS

OTHER CONDITIONS

OBSERVATIONS

RELATIVE RESPONSES

REFERENCES

SORGHUM ROOT:SHOOT RATIO

Root:shoot ratio	Greenhouse; 28/23°C; 9.5 MJm ⁻² d ⁻¹ ; 8h photosynthetic period; 16h php; 1.51/1.12 kPa VPD; "first" period well watered; "whole" period extended into water stress.	Period first whole	[340] 0.32 0.50	[680] 0.24 0.41	[680] -0.08 -0.09	Morison and Gifford 1984b

SORGHUM HARVEST INDEX

	--No Data--					

SORGHUM CONDUCTANCE

Conductance (m s ⁻¹)	Growth chamber; 30°C; 2120 μE m ⁻² s ⁻¹ ; 16h php; 80% RH.	[300] 5.0	[600] 3.1	[1200] 1.9	[600] 0.62	[1200] 0.38	van Bavel 1974

SORGHUM TRANSPIRATION

Transpiration (g dm ⁻² 2h ⁻¹)	Growth chamber; 0.5 - 0.6 cal m ⁻² min ⁻¹ ; 25/20°C; 14h php; 50-70/85-95% RH.	[300] 3.9	[600] 1.8	[1000] 1.4	[600] 0.46	[1000] 0.36	Pallas 1965
Transpiration (g m ⁻¹ h ⁻¹)	Growth chamber; 30°C; 2120 μE m ⁻² s ⁻¹ ; 16h php; 80% RH.	[300] 204	[600] 175	[1200] 96	[600] 0.858	[1200] 0.47	van Bavel 1974

SORGHUM YIELD

	--No Data--					

SORGHUM COMPONENTS OF YIELD

	--No Data--					

MEASUREMENTS	OTHER CONDITIONS		OBSERVATIONS		RELATIVE RESPONSES		REFERENCES	
SOYBEAN CARBON ASSIMILATION (CONTINUED)								
Short-term leaf CER (nmol cm ⁻² s ⁻¹)	Greenhouse; 21-35°C; 2000 μE m ⁻² s ⁻¹ ; 14h php; 40% RH.		[330] 1.3	[630] 1.7		[630] 1.3	Mauney et al. 1979	
Short-term canopy CER (μmol CO ₂ m ⁻² s ⁻¹)	SPAR units; 31/23°C; variable light; dew point 21°C.	μE m ⁻² s ⁻¹ 250 750 1250	[330] 8 25 36	[800] 16 50 68		[800] 2.0 2.0 1.9	Jones et al. 1985b	
Acclimated leaf CER (mg CO ₂ dm ⁻² h ⁻¹)	Growth chambers; 26/20°C, 700 μE m ⁻² s ⁻¹ ; 9h php with 3h interruption of night; after 2 wks trt.		[400] 26.7	[1000] 24.9		[1000] 0.933	Rufty et al. 1981	
Acclimated leaf CER (mg CO ₂ leaf ⁻² h ⁻¹)	Growth chambers; 26/20°C; 600 μE m ⁻² s ⁻¹ ; 12h php; trt after 40 d; week 4.	low sink (5:1 pod:leaf) high sink (15:1 pod:leaf)	[350] 8 18	[1000] 8 22		[1000] 1.0 1.2	Peet 1984	
Acclimated leaf CER (mg CO ₂ dm ⁻² h ⁻¹)	Greenhouse, then growth chamber; 27/18°C; natural light; 75% RH; trt after 28 d.		[300] 23	[600] 33	[1200] 41	[600] 1.4	[1200] 1.8	Carlson and Bazzaz 1980
Acclimated leaf CER (μmol cm ⁻² s ⁻¹)	Greenhouse; 21 to 35°C; 2000 μE m ⁻² s ⁻¹ ; 14h php; 40% RH; trt after 6 wks; 250 measurements on mature leaves over 10 weeks.		[330] 1.3	[630] 2.0		[630] 1.5	Mauney et al. 1979	

SOYBEAN CARBON ASSIMILATION (CONTINUED)

Acclimated leaf CER	Open top chambers; natural light, temperature and php; R3-R5 stage.	pots, well watered pots, water stress field grown, irrigated	[332] 26 29 49	[623] 46 42 50	[910] 50 45 -	[623] 1.8 1.4 1.0	[910] 1.9 1.6 -	Sionit et al. 1984
Acclimated leaf CER (mg dm ⁻² h ⁻¹)	Open top chambers; pot or field grown, R3-R5 stage.	in pots field-grown	$\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ -----300----- -----1400----- [332] [623] [332] [623] 8 22 22 32 13 18 44 48				$\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ -300- -1400- [623] [623] 2.8 1.4 1.4 1.1	Sionit et al. 1984
Acclimated leaf CER (mg dm ⁻² h ⁻¹)	Open top chambers; pot or field grown; R3-R5 stage.	in pots field-grown	$^{\circ}\text{C}$ -----20----- -----35----- [332] [623] [332] [623] 18 27 16 25 22 29 23 38				$^{\circ}\text{C}$ --20--- --35--- [623] [623] 1.5 1.6 1.3 1.6	Sionit et al. 1984
Acclimated leaf CER (mg CH ₂ O dm ⁻² h ⁻¹)	Open top chambers; natural light, temp and php; during pod filling.		[350] 23.5	[425] 26.0	[500] 27.5	[425] 1.11	[500] 1.17	Huber et al. 1984
Acclimated leaf CER ($\mu\text{mol m}^{-2}$ s ⁻¹)	SPAR units; variable light; 330 ppm, 28.4°C; 660 ppm, 29.6°C; during pod filling.	$\mu\text{E m}^{-2} \text{ s}^{-1}$ 300 1100	[330] 9 21	[660] 18 41		[660] 2.0 1.9		Valle et al. 1985
Acclimated plant CER (mg CO ₂ plant ⁻¹ h ⁻¹)	Growth chamber; 26/20°C; 600 $\mu\text{E m}^{-2} \text{ s}^{-1}$; 12 h php; trt after 44 d; CER after 4 wks trt.	low sink (2:1 pod:leaf) high sink (7:1 pod:leaf)	[350] 8 12	[1000] 17 30		[1000] 2.1 2.5		Clough et al. 1981

MEASUREMENTS	OTHER CONDITIONS	OBSERVATIONS	RELATIVE RESPONSES	REFERENCES
SOYBEAN CARBON ASSIMILATION (CONTINUED)				
Acclimated whole plant CER (mg CO ₂ plant ⁻¹ h ⁻¹)	Growth chamber; 28/25°C; 700 μ E m ⁻² s ⁻¹ ; 14h php; 70% RH; after 22 d trt.	<u>mm NH₄NO₃</u> 0.0 1.0 8.0	[320] 17 31 40	[1000] 26 35 70
				[1000] 1.5 1.1 1.7
Acclimated canopy CER (μ mol CO ₂ m ⁻² s ⁻¹)	SPAR units; variable light.	<u>°C</u> <u>μE m⁻²s⁻¹</u> 28 300 28 900 28 1500 33 300 33 900 33 1500	[330] 12.5 27.5 37.5 12.5 27.5 37.5	[800] 25.0 58.0 80.0 25.0 58.0 80.0
				[800] 2.00 2.11 2.13 2.00 2.11 2.13
Cumulative canopy CER (mol CO ₂ season ⁻¹)	SPAR units; variable light; 31/23°C; dew point 16°C. Values are long term, cumulative, day plus night.	well watered stressed d 52-66 stressed d 70-83	[330] 38.1 34.3 35.3	[660] 65.0 47.0 48.8
				[660] 1.71 1.37 1.38
Acclimated canopy CER (μ mol CO ₂ m ⁻² s ⁻¹)	SPAR units; variable light; 31/23°C; dew point 21°C; CER not adjusted for greater leaf area for high CO ₂ plants.	<u>μE m⁻²s⁻¹</u> 250 750 1250	[330] 8 25 36	[800] 20 50 70
				[800] 2.5 2.0 1.9
Acclimated canopy CER (μ mol CO ₂ m ⁻² s ⁻¹)	SPAR units; variable light; 25/25°C; VPD 2.4 kPa. CER not adjusted for greater leaf area for high CO ₂ plants.	<u>μE m⁻²s⁻¹</u> 300 900 1500	[320] 10 27 38	[640] 17 47 63
				[660] 1.7 1.7 1.7
Acclimated canopy CER (μ mol CO ₂ m ⁻² s ⁻¹)	SPAR units; 35/21°C max/min; natural light and php; 70 d after planting.	<u>μE m⁻²s⁻¹</u> 300 800 1300 1800	[330] 12 29 43 60	[800] 20 49 67 80
				[800] 1.7 1.7 1.6 1.3
				Williams et al. 1981
				Jones et al. 1985a
				Jones et al. in press
				Jones et al. 1985b
				Jones et al. 1985c
				Jones et al. 1984

SOYBEAN CARBON ASSIMILATION (CONTINUED)

Initial NAR (g dm ⁻² d ⁻¹)	Growth chambers; 29/23°C; 600 μE m ⁻² s ⁻¹ ; 12h php; trt d 7-35.	d 7-21	Hoagland's				Hoagland's		Patterson and Flint 1982
			---1/2---	---	1/8---		-1/2-	-1/8-	
			350	675	350	675	[675]	[675]	
			0.13	0.16	0.14	0.20	1.2	1.4	
Initial NAR (g dm ⁻² d ⁻¹)	Growth chambers; 26/20°C; 550/1200 μE m ⁻² s ⁻¹ ; 14h php; 70% RH; high light data inconclusive.	low light day 8-17	[350]	[675]			[675]		Sionit et al. 1982
			0.075	0.115			1.5		
Initial NAR (g dm ⁻² d ⁻¹)	Open top chambers; in pots; d5-14.		[332]	[623]	[910]		[623]	[910]	Rogers et al. 1984a
			17.5	25.2	29.0		1.44	1.66	
Initial NAR (rel. units)	Growth chambers; 2/pot; 28/23°C; 48 klux; 12h php; 40-70% RH; after 5 d trt.		[300]	[1000]			[1000]		Imai and Murata 1979a
			100	175			1.75		
Initial NAR (rel. units)	Growth chambers; 2/pot; 12h php; after 5 d trt.	27 klux; 28/23°C 48 klux; 28/23°C 48 klux; 23/20°C	[300]	[1000]			[1000]		Imai and Murata 1979b
			100	145			1.45		
			100	175			1.75		
			100	147			1.47		
Initial NAR (g dm ⁻² d ⁻¹)	Growth chambers; 26/20°C; 550 μE m ⁻² s ⁻¹ ; 12h php; 70% RH; d 8.		Hoagland's				Hoagland's		Sionit 1983
			----1/2----	----	1/8----		--1/2--	--1/8--	
			[350]	[675]	[350]	[675]	[675]	[675]	
			0.081	0.118	0.082	0.119	1.5	1.4	
Long-term NAR (g dm ⁻² d ⁻¹)	Growth chambers; 28/22°C; 650 μE m ⁻² s ⁻¹ ; 14h php; 70% RH.	d 12-24 d 24-45	[350]	[600]	[1000]		[600]	[1000]	Patterson and Flint 1980
			0.119	0.145	0.154		1.22	1.29	
			0.079	0.096	0.106		1.22	1.34	

MEASUREMENTS	OTHER CONDITIONS	OBSERVATIONS	RELATIVE RESPONSES	REFERENCES
SOYBEAN CARBON ASSIMILATION (CONTINUED)				
Long-term NAR (g dm ⁻² d ⁻¹)	Growth chambers; 29/23°C; 600 μE m ⁻² s ⁻¹ ; 12h php; after 7-35 d trt.	Hoagland's ---1/2--- ---1/8--- [350] [675] [350] [675] 0.08 0.08 0.08 0.12	Hoagland's --1/2-- --1/8-- [675] [675] 1.0 1.5	Patterson and Flint 1982
Long-term NAR (g dm ⁻² d ⁻¹)	Growth chambers; 29/23°C; 950 μE m ⁻² s ⁻¹ ; 14h php; 70% RH; After 17-24 d trt.	Competition [350] [675] none 0.084 0.121 soybean 0.075 0.096 johnsongrass 0.073 0.098	[675] 1.4 1.3 1.3	Patterson et al. 1984
Long-term NAR (g dm ⁻² d ⁻¹)	Growth chambers; 26/20°C; 550/1200 μE m ⁻² s ⁻¹ ; 14h php; 70% RH; high light data inconclusive; mean of d 17-66.	low light [350] [675] 0.036 0.042	[675] 1.2	Sionit et al. 1982
Long-term NAR (g dm ⁻² d ⁻¹)	Open top chambers; in pots.	d 14-49 [332] [623] [910] 8.0 9.9 9.4 d 49-84 3.5 5.0 4.5	[623] 1.4 [910] 1.3 1.2 1.2	Rogers et al. 1984a
Long-term NAR (g dm ⁻² d ⁻¹)	Growth chambers; 26/20°C; 600 μE m ⁻² s ⁻¹ ; 12h php; trt d 10-35.	[350] [1000] 0.10 0.16	[1000] 1.6	Clough and Peet 1981
Long-term NAR (g dm ⁻² d ⁻¹)	Growth chambers; 26/20°C; 550 μE m ⁻² s ⁻¹ ; 12h php; 70% RH; d 17.	Hoagland's -----1/2----- -----1/8----- [350] [675] [350] [675] 0.047 0.065 0.044 0.052	Hoagland's ---1/2--- ---1/8--- [675] [675] 1.4 1.2	Sionit 1983
Long-term NAR (mg dm ⁻² d ⁻¹)	Greenhouse; 35-21°C; 2000 μE m ⁻² s ⁻¹ at noon; natural php.	[330] [630] 130 192 54 60 24 8	[630] 1.48 1.1 0.3	Mauney et al. 1978

SOYBEAN BIOMASS ACCUMULATION

Biomass (g plant ⁻¹)	Outdoor growth chambers; seeded rows; in pots; trt for 20 d.		[300] 1.181	[1000] 1.950		[1000] 1.651	Akita and Tanaka 1973	
Biomass (rel. units)	Greenhouse then growth chambers; 27/18°C; 800-2000 $\mu\text{E m}^{-2}\text{s}^{-1}$; 75% RH; trt after 20 days.		[300] 100	[600] 58	[1200] 75	[600] 0.58	[1200] 0.75	Carlson and Bazzaz 1980
Biomass (g)	Growth chambers; 26/20°C; 640 $\mu\text{E m}^{-2}\text{s}^{-1}$; 12h php; trt d 10-35.		[350] 19.0	[1000] 34.9		[1000] 1.84		Clough and Peet 1981
Biomass (g)	Growth chambers in greenhouse; 30-32°C; natural light plus 1500 ft-c; 14-12h php; after 38 d trt.	Hark Chippewa	[350] 9.6 10.2	[1350] 15.5 18.0		[1350] 1.61 1.76		Cooper and Brun 1967
Biomass (g plant ⁻¹)	Open top chambers; field grown, spaced.		[425] 349	[1200] 573		[1200] 1.64		Hardman and Brun 1971
Biomass (g plant ⁻¹)	Open top chambers; seeded rows; trt d 38 to maturity.		[Amb] 20.6	[1000] 30.7		[1000] 1.49		Hardy and Havelka 1975
Biomass (g plant ⁻¹)	Growth chambers; 28/22°C; 650 $\mu\text{E m}^{-2}\text{s}^{-1}$; 14h php; 70% RH.		[350] 50.6	[600] 62.2	[1000] 87.1	[600] 1.23	[1000] 1.72	Patterson and Flint 1980
Biomass (g plant ⁻¹)	Growth chambers; 29/23°C; 600 $\mu\text{E m}^{-2}\text{s}^{-1}$; 12h php.	Hoagland's 1/2 1/8	[350] 30 16	[675] 45 21		[675] 1.5 1.3		Patterson and Flint 1982
Biomass (g plant ⁻¹)	Growth chambers; 29/23°C; 950 $\mu\text{E m}^{-2}\text{s}^{-1}$; 14h php; 70% RH, after 24 d trt.	Competition none soybean johnsongrass	[340] 6.92 5.00 5.40	[675] 10.43 6.80 8.15		[675] 1.51 1.36 1.51		Patterson et al. 1984

MEASUREMENTS	OTHER CONDITIONS		OBSERVATIONS		RELATIVE RESPONSES		REFERENCES	
SOYBEAN BIOMASS ACCUMULATION (CONTINUED)								
Biomass (g plant ⁻¹)	Growth chambers; 29/18°C; 6000 ft-c; 12h php; 75% RH; trt d 18-83.		[300] 18.8	[1200] 48.6		[1200] 2.58	Quebedeaux et al. 1975	
Biomass (g plant ⁻¹)	Open top chambers; in pots; after 12 wks trt; vegetative growth only.		[332] 82.0	[623] 133.5	[910] 140.2	[623] 1.63	[910] 1.71	Rogers et al. 1984a
Biomass (g plant ⁻¹)	Open top chambers; in pots; after 11 wks trt.		[340] 41.4	[718] 74.0	[910] 77.3	[718] 1.79	[910] 1.87	Rogers et al. 1983
Biomass (g plant ⁻¹)	Growth chambers; 26/20°C; 550 μE m ⁻² s ⁻¹ ; 12h php; 70% RH; after 66 d trt.	Hoagland's 1/2 1/8	[350] 91.4 58.9	[675] 206.9 119.3		[675] 2.26 2.02		Sionit 1983
Biomass (g plant ⁻¹)	Growth chambers; 26/20°C; 14h php; 70% RH; after 51 d trt.	μE m ⁻² s ⁻¹ 550 1200	[350] 35 51	[675] 69 83		[675] 2.0 1.6		Sionit et al. 1982
Biomass (g plant ⁻¹)	Growth chambers; 28/25°C; 700 μE m ⁻² s ⁻¹ ; 14h php; 70% RH; after 22 d trt.	mM NH ₄ NO ₃ 0.0 1.0 8.0	[320] 785 1384 2766	[1000] 1183 2068 4526		[1000] 1.507 1.494 1.636		Williams et al. 1981
Biomass (mg)	Greenhouse then growth chambers.		klux			klux		Imai and Murata 1979b
			----27----			--27-- --48--		
		°C	[300]	[1000]	[300]	[1000]	[1000]	
		28/23	214	359	266	484	1.68 1.82	
		23/20	220	328	221	342	1.49 1.55	

SOYBEAN BIOMASS ACCUMULATION (CONTINUED)

Biomass (mg)	Greenhouse then growth chambers; 28/23°C; 48 klux; 12h php.	[300] 313	[1000] 614	[1000] 1.96	Imai and Murata 1979a		
Biomass (g m ⁻²)	SPAR unit; 35/21°C max/min.	[330] 954	[600] 1294	[800] 1457	[600] 1.36	[800] 1.53	Jones et al. 1984
Biomass (g m ⁻²)	SPAR units, variable light; 31/23°C; dew point 16°C.	[330] 773	[660] 1083	[600] 1.40	Jones et al. in press		
	well watered	685	875	1.28			
	stressed d 52-66	686	856	1.25			
	stressed d 70-83						

SOYBEAN ROOT:SHOOT RATIO

Root:shoot ratio	Open top chambers; seeded rows; d 38 to maturity.	[Amb] 0.10	[1000] 0.09	[1000] -0.01	Hardy and Havelka 1975	
Root:shoot ratio	Growth chambers; 26/20°C; 640 $\mu\text{E m}^{-2}\text{s}^{-1}$; 12h php; trt d 10-35.	[350] 0.23	[1000] 0.23	[1000] +0.00	Clough and Peet 1981	
Root:shoot ratio	Growth chambers; 29/23°C; 600 $\mu\text{E m}^{-2}\text{s}^{-1}$; 12h php.	Hoagland's <u>1/2</u> 1/8	[350] 0.16 0.45	[675] 0.19 0.45	[675] +0.03 +0.00	Patterson and Flint 1982
Root:shoot ratio	Growth chambers; 29/23°C; 950 $\mu\text{E m}^{-2}\text{s}^{-1}$; 14h php; 70%; no competition.	[350] 0.23	[675] 0.29	[675] +0.06	Patterson et al. 1984	

MEASUREMENTS	OTHER CONDITIONS		OBSERVATIONS			RELATIVE RESPONSES		REFERENCES
SOYBEAN ROOT:SHOOT RATIO (CONTINUED)								
Root:shoot ratio	Growth chambers; 29/18°C; 6000 ft-c; 12h php; 75% RH; trt d 18-83.		[300] 0.08	[1200] 0.07		[1200] -0.01		Quebedeaux et al. 1975
Root:shoot ratio	Growth chambers; 26/20°C; 550 $\mu\text{E m}^{-2}\text{s}^{-1}$; 12h php; 70% RH.	Hoagland's 1/2 1/8	[350] 0.04 0.06	[675] 0.03 0.05		[675] -0.01 -0.01		Sionit 1983
Root:shoot ratio	Growth chambers; 26/20°C; 14h php; 70% RH.	$\mu\text{E m}^{-2}\text{s}^{-1}$ 550 1200	[350] 0.11 0.07	[675] 0.09 0.06		[675] -0.02 -0.01		Sionit et al. 1982
Root:shoot ratio	Growth chambers; 28/25°C; 700 $\mu\text{E m}^{-2}\text{s}^{-1}$; 14h php; 70% RH.	mM NH_4NO_3 0.0 1.0 8.0	[320] 0.48 0.49 0.33	[1000] 0.36 0.43 0.31		[1000] -0.12 -0.06 -0.02		Williams et al. 1981
Root:shoot ratio	Open top chambers; in pots; after 11 wks trt.		[340] 0.14	[718] 0.17	[910] 0.20	[718] -0.03	[910] -0.06	Rogers et al. 1983
Root:shoot ratio	Open top chambers; in pots; after 16 wks trt.		[332] 0.07	[623] 0.08	[910] 0.08	[623] +0.01	[910] +0.01	Rogers et al. 1984a
Root:shoot ratio	SPAR units; 35/21°C; seeded rows.		[330] 0.021	[600] 0.024	[800] 0.023	[600] +0.003	[800] +0.002	Jones et al. 1984

MEASUREMENTS

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SOYBEAN HARVEST INDEX

Harvest index	Growth chambers in greenhouse; 30-32°C; natural light +1500 ft-c; 14-12h php.	Hark Chippewa	[350] 0.61 0.59	[1350] 0.57 0.55	[1350] -0.04 -0.04	Cooper and Brun 1967		
Harvest index	Open top chambers; field grown, spaced.		[425] 0.32	[1200] 0.26	[1200] -0.06	Hardman and Brun 1971		
Pod harvest index	Open top chambers; seeded rows; trt d 38 to maturity.		[Amb] 0.47*	[1000] 0.56*	[1000] +0.09*	Hardy and Havelka 1975		
Harvest index	Growth chambers; 29/18°C; 6000 ft-c; 12h php; 75% RH; trt d 18-83.		[300] 0.48	[1200] 0.48	[1200] 0.00	Quebedeaux et al. 1975		
Harvest index	Open top chambers; in pots; after 16 wks trt.		[332] 0.52	[623] 0.47	[910] 0.45	[623] -0.05	[910] -0.07	Rogers et al. 1984a
Harvest index	Growth chamber; 26/20°C; 550 $\mu\text{E m}^{-2}\text{s}^{-1}$; 12h php; 70% RH.	Hoagland's 1/2 1/8	[350] 0.73 0.73	[675] 0.68 0.73	[675] -0.05 +0.00	Sionit 1983		
Harvest index	Open top chambers; in pots; after 18 wks trt.		[340] 0.59	[718] 0.52	[910] 0.50	[718] -0.07	[910] -0.09	Rogers et al. 1983
Harvest index	SPAR units; 35/21°C; seeded rows.		[330] 0.42	[600] 0.42	[800] 0.40	[600] +0.00	[800] -0.02	Jones et al. 1984
Harvest index	SPAR units; variable light; 31/23°C; dew point 16°C.	well watered stressed d 52-66 stressed d 70-83	[330] 0.365 0.348 0.337	[660] 0.380 0.340 0.395	[660] +0.015 -0.008 +0.058	Jones et al. in press		

* Not used in calculation of overall response

* Not used in calculation of overall response

MEASUREMENTS	OTHER CONDITIONS	OBSERVATIONS			RELATIVE RESPONSES		REFERENCES	
SOYBEAN CONDUCTANCE								
Conductance (cm s ⁻¹)	Growth chambers; 25 klux; 32/26/23°C.	[300] 0.71	[1000] 0.40		[1000] 0.56		Hofstra and Hesketh 1975	
Conductance (cm s ⁻¹)	Greenhouse then growth chamber; 30°C; 1400 μE m ⁻² s ⁻¹ ; 60% RH; CO ₂ conductance.	[300] 0.91	[600] 0.72	[1200] 0.35	[600] 0.79	[1200] 0.38	Carlson 1983	
Canopy conductance (m s ⁻¹)	Greenhouse then growth chamber; 30°C; 1400 μE m ⁻² s ⁻¹ ; 60% RH; CO ₂ conductance. Not adjusted for differences in LAI.	-31 31 31 μE m⁻²s⁻¹ 250 750 1250	[330] 0.0038* 0.0083* 0.0100*	[800] 0.0036* 0.0079* 0.0095*	[800] 0.95* 0.95* 0.95*		Jones et al. 1985a	
		35 35 35	250 750 1250	0.0038* 0.0083* 0.0100*	0.0036* 0.0079* 0.0095*	0.95* 0.95* 0.95*		
Conductance (cm s ⁻¹)	Growth chambers; 29/23°C; 600 μE m ⁻² s ⁻¹ ; 12h php; after 34 d trt; H ₂ O conductance.	Hoagland's 1/2 1/8	[350] 2.44 2.33	[675] 1.54 1.28	[675] 0.631 0.549		Patterson and Flint 1982	
Conductance (cm s ⁻¹)	Open top chambers; in pots; H ₂ O conductance.		[332] 1.0	[623] 0.38	[910] 0.28	[623] 0.38	[910] 0.28	Rogers et al. 1984b
Conductance (cm s ⁻¹)	Open top chambers; in pots or field grown; H ₂ O conductance.	field grown in pots, control in pots, water stress	[332] 0.75 0.59 0.69	[629] 0.49 0.48 0.38	[910] 0.40 0.36 0.38	[629] 0.65 0.81 0.55	[910] 0.53 0.61 0.55	Sionit et al. 1984
Conductance (cm s ⁻¹)	SPAR units, plants in ground.		[330] 0.0333	[800] 0.0159	[800] 0.48		Jones et al. 1985b	
Conductance (m s ⁻¹)	Open top chambers; in pots.		[340] 0.028	[718] 0.018	[910] 0.014	[718] 0.64	[910] 0.50	Rogers et al. 1983

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SOYBEAN TRANSPIRATION

Transpiration (g dm ⁻² 2h ⁻¹)	Growth chambers; 25 ^o /20 ^o C; 0.6 cal cm ⁻² min ⁻¹ ; 14h php; 75% RH.		[300] 2.6	[600] 2.0	[1000] 1.2	[600] 0.77	[1000] 0.46	Pallas 1965
Transpiration (g H ₂ O dm ⁻² hr ⁻¹)	Greenhouse then growth chambers; 27/18 ^o C; 800-2000 μ E m ⁻² s ⁻¹ ; 75% RH; trt after 20 d.		[300] 2.8	[600] 2.2	[1200] 1.3	[600] 0.79	[1200] 0.46	Carlson and Bazzaz 1980
Transpiration (g dm ⁻² h ⁻¹)	Growth chambers; 29/23 ^o C; 600 μ E m ⁻² s ⁻¹ ; 12h php; after 34 d trt.	Hoagland's 1/2 1/8	[350] 5.0 4.8	[675] 3.6 3.1		[675] 0.72 0.65		Patterson and Flint 1982
Transpiration (mg dm ⁻² min ⁻¹)	Open top chambers; in pots.		[332] 14.4	[623] 8.6	[910] 6.4	[623] 0.60	[910] 0.44	Rogers et al. 1984b
Canopy transpiration (μ mol H ₂ O m ⁻² s ⁻¹)	SPAR units; 31/23 ^o C, dew point, 21 ^o C.	μ E m ⁻² s ⁻¹ 250 750 1250	[330] 6800 11900 16800	[800] 5000 10500 13600		[800] 0.735 0.882 0.809		Jones, et al. 1985b
Cumulative canopy transpiration (mol H ₂ O season ⁻¹)	SPAR units; variable light; 31/23 ^o C; dew point 16 ^o C.	well watered stressed d 52-65 stressed d 70-83	[330] 400 297 290	[660] 346 279 244		[660] 0.865 0.939 0.841		Jones et al. in press
* Not used in calculation of overall response								

MEASUREMENTS	OTHER CONDITIONS		OBSERVATIONS		RELATIVE RESPONSES		REFERENCES	
SOYBEAN TRANSPIRATION (CONTINUED)								
Canopy transpiration ($\mu\text{mol H}_2\text{O m}^{-2} \text{ s}^{-1}$)	SPAR units; 31/23°C; dew point 21°C.	$\frac{0^\circ\text{C}}{28}$	$\frac{\mu\text{E m}^{-2}\text{s}^{-1}}{250}$	[330] 2900	[800] 3000	[800] 1.03	Jones et al. 1985a	
		28	750	8000	6700	0.84		
		28	1250	11200	9700	0.87		
		33	250	4200	4600	1.10		
		33	750	10400	9000	0.86		
		33	1250	13700	9700	0.71		
SOYBEAN YIELD								
Seed wt. (g plant ⁻¹)	Small growth chambers; 32°C; natural light + 1500 ft-c; 14h php; 3/pot; after 92 d trt.	Hark Chippewa	[350] 24.7 25.4	[1350] 38.9 35.7	[1350] 1.57 1.41	Cooper and Brun 1967		
Seed wt. (g plant ⁻¹)	Open top chambers; spaced plants in ground.		[<425] 110	[1200] 151	[1200] 1.37	Hardman and Brun 1971		
Pod wt. (g plant ⁻¹)	Open top chambers; field grown; trt from d 38.		[Amb] 8.8	[1000] 15.7	[1000] 1.8	Hardy and Havelka 1976		
Seed wt. (g plant ⁻¹)	Growth chambers; 29/18°C; 6000 ft-c; 12h php; 75% RH; trt d 18-83.		[300] 8.4	[1200] 21.7	[1200] 2.6	Quebedeaux et al. 1975		
Pod wt. (g plant ⁻¹)	Open top chambers; in pots; after 16 wks trt.		[332] 73.2	[623] 95.0	[910] 96.7	[623] 1.30	[910] 1.32	Rogers et al. 1984a

SOYBEAN YIELD (CONTINUED)

Seed wt. (kg ha ⁻¹)	Open top chambers; seeded rows; after 46 d trt.	Straw 0 2t/ha 4t/ha	[Amb] 1244 2315 2688	[1000] 2652 2985 3370	[1000] 2.132 1.289 1.254	Shivashankar and Vlassak 1978		
Seed wt. (g)	Small chambers in greenhouse; in pots; for 32 d trt.	Straw 0 3t/ha 6t/ha	[Amb] 0.871 0.925 1.022	[1000] 0.914 0.960 1.062	[1000] 1.05 1.04 1.04	Shivashankar et al. 1976		
Seed wt. (g plant ⁻¹)	Growth chambers; 26/20°C; 550 μE m ⁻² s ⁻¹ ; 12h php; 70% RH; after 66 d trt.	Hoagland's 1/2 1/8	[350] 45.6 28.6	[675] 102.3 57.5	[675] 2.24 2.01	Sionit 1983		
Seed wt. (g plant ⁻¹)	Open top chambers; in pots; after 18 wks trt.		[350] 131.0	[718] 191.4	[910] 193.4	[718] 1.461	[910] 1.476	Rogers et al. 1983
Seed wt. (g plant ⁻¹)	Open top chambers; in pots.		[332] 47.7	[623] 59.3	[910] 61.7	[623] 1.24	[910] 1.29	Rogers et al. 1981
Seed yield (g m ⁻²)	SPAR unit; 35/21°C; natural light.		[330] 276.5	[600] 377.1	[800] 408.7	[600] 1.364	[800] 1.478	Jones et al. 1984
Seed wt. (g m ⁻²)	SPAR units; variable light; 31/23°C; dew point 16°C.	well watered stressed d 52-66 stressed d 70-83	[330] 282 231 239	[660] 411 345 291	[660] 1.46 1.49 1.22			Jones et al. in press

MEASUREMENTS	OTHER CONDITIONS	OBSERVATIONS				RELATIVE RESPONSES	REFERENCES
SOYBEAN COMPONENTS OF YIELD							
Pod no. Seeds pod ⁻¹ Seed no. g 100 seed ⁻¹	Small growth chambers; 32°C; natural light + 1500 ft-c; 14h php; 3/pot; after 92 d trt.	pod no. seeds pod ⁻¹ seed no. g/100 seed ⁻¹	----Hark---- [350] [1350] 63.0 100.5 2.3 2.5 142.0 246.8 17.4 15.8	----Chippewa- [350] [1350] 67.5 89.5 2.2 2.3 151.0 206.5 17.1 17.5	-Hark-- --Chippewa- [1350] [1350] 1.59 1.33 1.09 1.00 1.738 1.367 0.908 1.02	Cooper and Brun 1967	
Filled pod no. g 100 seed ⁻¹	Open top chamber; spaced plants in ground.	filled pod no. g/100 seed ⁻¹	[<425] 334 32.30	[1200] 552 26.30	[1200] 1.653 0.814	Hardman and Brun 1971	
			Hoagland's		Hoagland's	Sionit 1983	
Seeds pod ⁻¹ Seeds plant ⁻¹ Wt. seed ⁻¹ Pods plant ⁻¹	Growth chamber; 26/20°C; 550 μE m ⁻² s ⁻¹ ; 12h php; 70% RH; after 66 d trt.	seed pod ⁻¹ seed plant ⁻¹ wt. seed ⁻¹ pods plant ⁻¹	---1/2-- [350] [675] 1.79 1.92 219 455 205 226 122 236	--1/8--- [350] [675] 2.18 1.95 155 287 185 201 71 147	--1/2-- --1/8-- [675] [675] 1.07 0.894 2.08 1.85 1.10 1.09 1.93 2.07		
Seed plant ⁻¹ Dry wt. seed ⁻¹	Open top chambers; in pots; after 16 wks trt.	seed plant ⁻¹ dry wt. seed ⁻¹	[350] 131.0 163	[718] 191.4 174	[910] 193.4 168 [718] [910] 1.461 1.476 1.067 1.031	Rogers et al. 1983	

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SWEET POTATO CARBON ASSIMILATION

NAR (g dm ⁻² d ⁻¹)	Growth chambers 28/20°C; 550 μE m ⁻² s ⁻¹ ; 14h php; VPD 10.5 mb.		[350]	[675]	[1000]	[675]	[1000]	Bhattacharya et al. in press
		d 20-35	0.060	0.074	0.090	1.2	1.5	
		d 35-50	0.065	0.057	0.053	0.88	0.81	
		d 50-65	0.050	0.050	0.075	1.0	1.5	

SWEET POTATO BIOMASS ACCUMULATION

Biomass (g plant ⁻¹)	Growth chambers 28/20°C; 550 μE m ⁻² s ⁻¹ ; 14h php; VPD 10.5 mb.		[350]	[675]	[1000]	[675]	[1000]	Bhattacharya et al. in press
			79.4	129.9	168.2	1.64	2.12	

SWEET POTATO ROOT:SHOOT RATIO

Root:shoot ratio	Growth chambers 28/20°C; 550 μE m ⁻² s ⁻¹ ; 14h php; VPD 10.5 mb; R:S ratio at 65 d.		[350]	[675]	[1000]	[675]	[1000]	Bhattacharya et al. in press
			1.1	1.4	1.8	+0.3	+0.7	

SWEET POTATO HARVEST INDEX

	--No Data--							

SWEET POTATO CONDUCTANCE

	--No Data--							

SWEET POTATO TRANSPIRATION

	--No Data--							

MEASUREMENTS	OTHER CONDITIONS	OBSERVATIONS	RELATIVE RESPONSES	REFERENCES
SWEET POTATO YIELD				
Tuber wt. (g plant ⁻¹)	Growth chambers 28/20°C; 550 μE m ⁻² s ⁻¹ ; 14h php; VPD 10.5 mb; tuber wt. = 0.95 x root wt at d 65.	[350] 39.3 [675] 72.5 [1000] 101.7	[675] 1.84 [1000] 2.59	Bhattacharya et al. in press
	SWEET POTATO COMPONENTS OF YIELD			
	--No Data--			

WHEAT CARBON ASSIMILATION

Short-term leaf CER (relative units)	Greenhouse; attached leaves of ambient CO ₂ -grown plants; leaf chamber.		[350] 68	[800] 100		[800] 1.5	Akita and Moss 1973	
Short-term CER (mg CO ₂ dm ⁻² h ⁻¹)	Natural conditions, summer.		[300] 30	[800] 51		[800] 1.7	Chmora et al. 1976	
Short-term canopy CER (relative units)	Small growth chambers; 20/15°C; 610 μE m ⁻² s ⁻¹ .		[330] 100	[600] 125		[600] 1.25	Gerbaud and Andre 1980	
Short-term CO ₂ assimilated (cm ³ plant min ⁻¹)	Growth chamber; in nutrient solution; 19°C; 74% RH.	W cm ⁻² 0.044 0.070	[340] 5.58 7.38	[410] 6.25 8.55	[820] 8.45 12.45	[410] 1.12 1.16	[820] 1.51 1.69	Hoover et al. 1933
Short-term CER (mg h ⁻¹ g fr. wt.)	Growth chamber; 26/18°C; 2000 ft-c; 16h php; after 10-14 days trt; excised shoots.	°C -13 20 26 34	[350] 33.0 37.3 38.0 33.0	[500] 34.0 39.5 41.5 40.0		[500] 1.03 1.06 1.09 1.21	Joliffe and Tregunna 1968	
Short-term CER (mg CO ₂ dm ⁻² h ⁻¹)	Growth chamber; 26/18°C; 2000 ft-c; 16h php; after 9-11 d trt; excised shoots.	°C -13 20 25 30 35 40	[350] 11.0 15.5 18.5 25.5 25.5 17.8	[570] 11.4 15.0 21.0 30.5 33.0 24.5		[570] 1.04 0.97 1.13 1.20 1.29 1.38	Joliffe and Tregunna 1973	

MEASUREMENTS	OTHER CONDITIONS	OBSERVATIONS		RELATIVE RESPONSES	REFERENCES
WHEAT CARBON ASSIMILATION (CONTINUED)					
Acclimated CER of flag leaf (mg cm ⁻² s ⁻¹)	Growth chamber; 21/26°C; natural light in winter; 16h php; 75% RH.	[290] 64	[490] 100	[490] 1.56	Gifford 1977
Acclimated canopy CER (mg cm ⁻² leaf area s ⁻¹)	Growth chamber; 21/26°C; natural light in winter; 16h php; 75% RH.	[290] 1.9	[490] 2.6	[490] 1.4	Gifford 1977
Acclimated canopy CER (mg cm ⁻² ground area s ⁻¹)	Growth chamber; 21/26°C; natural light in winter; 16h php; 75% RH.	[290] 14.5	[490] 34.5	[490] 2.38	Gifford 1977
Acclimated canopy CER per plant (mg CO ₂ h ⁻¹ plant ⁻¹)	Growth chamber; 24/18°C; 600 mol m ⁻² s ⁻¹ ; 14h php; 50/85% RH; after 35 d trt.	[330] 8.2	[660] 11.2	[660] 1.4	du Cloux et al. 1984
Acclimated flag leaf CER (μmol CO ₂ m ⁻² s ⁻¹)	Open top chambers; natural temperature, light and php; mean of 2 years; exposure from jointing to physiological maturity.	[340] 529	[1200] 633	[1200] 1.20	Havelka et al. 1984
Long-term NAR (g dm ⁻² d ⁻¹)	Growth chambers; 26/20°C; 550 μE m ⁻² s ⁻¹ ; 12h php; 70% RH.	Hoagland's	[350]	[675]	Sionit et al. 1981a
		1/16	0.11	0.17	
		1/8	0.12	0.16	
		1/2	0.12	0.15	
		1/1	0.13	0.14	
		Means over 4 nutrient levels	[350]	[675]	
	d 9-16	0.145*	0.158*	1.09*	
	d 23-30	0.108*	0.160*	1.48*	
	d 30-37	0.110*	0.140*	1.27*	

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WHEAT CARBON ASSIMILATION (CONTINUED)

Long-term NAR (mg cm ⁻² d ⁻¹)	Growth chamber; 22/20°C; 90 W m ⁻² ; 20h php; after 3-14 d trt.	days	[300]	[600]	[800]	[600]	[800]	Neales and Nicholls 1978
		10	2.00	2.33	2.20	1.16	1.10	
		17	1.72	1.97	1.90	1.14	1.10	
		24	1.65	1.23	1.33	0.74	0.81	
		* Not used in calculation of overall response						

WHEAT BIOMASS ACCUMULATION

Total above-ground biomass (g m ⁻²)	Field grown; 3 yrs; exposed to high CO ₂ in chamber only during certain stages of growth. Control data are for plants without chambers.	1971	[Amb]	[750]	[750]	Fischer & Aguilar 1976
		1972	1677	1895	1.230	
		1973	1392	1489	1.070	
			1457	1515	1.040	
Total crop biomass (kg m ⁻²)	Growth chambers; 21/18°C; 8h php; 75% RH.		[290]	[490]	[490]	Gifford 1977
			2.28	3.0	1.3	
Total crop biomass (g)	Growth chambers; 26/20°C; 600 μE m ⁻² s ⁻¹ ; 12h php 70% RH.		[350]	[675]	[1000]	Sionit et al. 1981b
			9.44	18.22	25.37	
Total crop biomass (kg m ⁻²)	Growth chambers; 19°C; 640 μE m ⁻² s ⁻¹ ; 16h php. control water stress		[340]	[590]	[590]	Gifford 1979a
			1.92	2.43	1.27	
			0.79	1.13	1.43	
Total crop biomass (g plant ⁻¹)	Growth chambers; 26/20°C; 600 μE m ⁻² s ⁻¹ ; 12h php; 10.5 mb VPD; trt after 18d. control 1 stress cycle 2 stress cycles		[350]	[1000]	[1000]	Sionit et al. 1980
			25.9	32.9	1.27	
			17.2	24.6	1.43	
			20.4	22.2	1.09	

MEASUREMENTS	OTHER CONDITIONS		OBSERVATIONS		RELATIVE RESPONSES		REFERENCES
WHEAT BIOMASS ACCUMULATION (CONTINUED)							
Total crop biomass (g pot ⁻¹)	Chambers in greenhouse; 21/13°C; 12h php; 65/95% RH; C = balanced nutrient; -N = replace 70% NO ₃ ⁻ with Cl ⁻ ; -P = replace 90% H ₂ PO ₄ ⁻ with Cl ⁻ .		C -N -P	[Amb] 60 31 41	[700] 86 38 42	[700] 1.4 1.2 1.0	Goudriaan & de Ruiter 1983
Total crop biomass (g plant ⁻¹)	Growth chambers; 26/20°C; 550 µE m ⁻² s ⁻¹ ; 12h php; 70% RH.		1/2 Hoagland's 1/16 Hoagland's	[350] 63.0 27.5	[650] 83.9 30.0	[650] 1.33 1.09	Sionit et al. 1981a
Biomass (g plant ⁻¹)	Growth chambers; 25°C; 16 h php.			ft-c -----300----- ---3600----- [350] [1300] [350] [1300] 0.063 0.089 1.59 2.47		ft-c --300- -3600- [1300] [1300] 1.4 1.55	MacDowall 1972
Biomass (g plant ⁻¹)	Growth chambers; 26/20°C; 600 µE m ⁻² s ⁻¹ ; 12h php; 10.5 mbar VPD, trt after 18 d.		control water stress	[350] 41.5 34.0	[1000] 73.1 57.8	[1000] 1.76 1.70	Sionit et al. 1981c
Biomass (kg m ⁻²)	Open top chambers; natural temperature, light and php; mean of 2 years; exposure from jointing to physiological maturity.			[340] 529	[1200] 633	[1200] 1.20	Havelka et al. 1984
Biomass (rel. units)	Greenhouse; 19/14°C 10.2 MJm ⁻² d ⁻¹ ; 8h photosynthetic period; 16h php; 0.66/0.48 kPa VPD; "first" period well watered; "whole" period extended into water stress.		Period first whole	[350] 1.00 1.00	[680] 1.97 1.83	[680] 1.97 1.83	Morison and Gifford 1984b

WHEAT ROOT:SHOOT RATIO

Root:shoot ratio	Growth chambers; 21/18°C; 8h php; 75% RH.		[290] 0.03	[490] 0.02	[490] -0.01	Gifford 1977
Root:shoot ratio	Growth chambers; 19°C; 640 $\mu\text{mol m}^{-2}\text{s}^{-1}$; 16h php; A to D = highest to lowest watering trt.	A B C D	[340] 0.07 0.06 0.08 0.20	[590] 0.04 0.05 0.06 0.16	[590] -0.03 -0.01 -0.02 -0.04	Gifford 1979b
Root:shoot ratio	Growth chambers; 26/20°C; 600 $\mu\text{E m}^{-2}\text{s}^{-1}$; 12h php; 10.5 mb VPD; trt after 18d.	well watered 1 stress cycle 2 stress cycles	[350] 0.079 0.114 0.095	[1000] 0.072 0.077 0.088	[1000] -0.007 -0.037 -0.022	Sionit et al. 1980
Root:shoot ratio	Growth chambers; 26/20°C; 550 $\mu\text{E m}^{-2}\text{s}^{-1}$; 12h php; 70% RH.	Hoagland's 1/1 1/2 1/8 1/16	[350] 0.09 0.12 0.13 0.16	[650] 0.10 0.1 0.15 0.22	[650] +0.01 +0.01 +0.02 +0.06	Sionit et al. 1981a
Root:shoot ratio	Growth chambers in green- house; 21/13°C; 12h php; 65/95% RH; C = balanced nutrient; -N = replace 60% NO_3^- with Cl^- ; -P = replace 90% H_2PO_4^- with Cl^- .	C -N -P	[350] 0.20 0.16 0.24	[700] 0.21 0.17 0.27	[700] +0.01 +0.01 +0.03	Goudriaan and de Ruiter 1983
Root:shoot ratio	Greenhouse; 19/14°C; 10.2 $\text{MJm}^{-2}\text{d}^{-1}$; 8h photosynthetic period; 16h php; 0.66/0.48 kPa VPD; "first" period was well watered; "whole" period extended into water stress.	Period first whole	[340] 0.42 0.31	[680] 0.36 0.28	[680] -0.06 -0.03	Morison and Gifford 1984b

MEASUREMENTS	OTHER CONDITIONS	OBSERVATIONS		RELATIVE RESPONSES	REFERENCES
WHEAT HARVEST INDEX					
Harvest index	Growth chamber in green-house; 21/16°C; 16h php; 75% RH; summer crop.	[290] 0.42	[490] 0.46	[490] +0.04	Gifford 1977
Harvest index	Growth chambers; 19°C; 640 $\mu\text{E m}^{-2}\text{s}^{-1}$; 16h php; A to D = highest to lowest watering trts.	A 0.40 B 0.36 C 0.27 D 0.06	[340] [590] 0.43 0.43 0.39 0.32 0.15	[590] +0.03 +0.03 +0.05 +0.09	Gifford 1979b
Harvest index	Growth chambers; 26/20°C; 600 $\mu\text{E m}^{-2}\text{s}^{-1}$; 12h php; 10.5 mb VPD; trt after 18 d.	well watered 1 stress cycle 2 stress cycles	[350] 0.42 0.40 0.41	[1000] +0.05 +0.04 +0.04	Sionit et al. 1980
Harvest index	Growth chambers; 26/20°C; 550 $\mu\text{E m}^{-2}\text{s}^{-1}$; 12h php; 70% RH.	Hoagland's 1/1 1/2 1/8 1/16	[350] 0.47 0.48 0.48 0.54	[650] +0.49 0.48 0.47 0.41	Sionit et al. 1981a
Harvest Index	Growth chambers in green-house; 21/13°C; 12h php; 65/95% RH; C = balanced nutrient; -N = replace 60% NO_3^- with Cl^- ; -P = replace 90% H_2PO_4^- with Cl^- .	C -N -P	[350] 0.44 0.47 0.39	[700] +0.49 0.48 0.39	Goudriaan and de Ruiter 1983
Harvest Index	Open top chambers; natural temperature, light and php; mean of 2 years; exposure from jointing to physiological maturity.		[340] 0.36	[1200] 0.36 +0.00	Havelka et al. 1984

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WHEAT CONDUCTANCE

Conductance (cm s ⁻¹)	Growth chambers; 26/20°C; 600 μ E m ⁻² s ⁻¹ . 12h php; 10.5 mbar VPD; trt after 18d.	well watered -1.5 MPa	[350] 5.98 0.03*	[1000] 3.82 0.05*	[1000] 0.639 1.67*	Sionit et al. 1981c
Conductance (cm s ⁻¹)	Greenhouse; attached leaves of ambient CO ₂ grown plants; leaf chamber.	$\frac{\text{cal m}^{-2} \text{ min}^{-1}}{0.05}$ 0.40	[300] 0.345 0.435	[800] 0.198 0.286	[800] 0.574 0.657	Akita and Moss 1973

WHEAT TRANSPIRATION

Transpiration (g dm ⁻² h ⁻¹)	Greenhouse; attached leaves of ambient CO ₂ grown plants; leaf chamber.	$\frac{\text{cal m}^{-2} \text{ min}^{-1}}{0.05}$ 0.40	[300] 3.65 3.85	[800] 2.30 3.25	[800] 0.630 0.844	Akita and Moss 1973
Transpiration (g dm ⁻² h ⁻¹)	Greenhouse; 20-30°C; 0.40 Ly min ⁻¹ ; attached leaves of ambient CO ₂ grown plants; leaf chamber.		[300] 3.25	[800] 2.6	[800] 0.80	Akita and Moss 1972
Transpiration (kg m ⁻² d ⁻¹)	Greenhouse; 19/14°C; 10.2 MJ m ⁻² d ⁻¹ ; 8h photosynthetic period; 16h php; 0.66/0.48 kPa VPD; d15 = early, well-watered; d24 = max transpiration; d33 = water- stressed.	d 15 d 24 d 33	[340] 2.45 2.22 0.77	[680] 1.56 1.40 0.34	[680] 0.64 0.63 0.44	Morison and Gifford 1984a
* Not used in calculation of overall mean						

MEASUREMENTS	OTHER CONDITIONS	OBSERVATIONS		RELATIVE RESPONSES	REFERENCES
WHEAT YIELD					
Seed wt. (mg plant ⁻¹)	Growth chambers; 27/16°C; 600 μE m ⁻² s ⁻¹ ; 16h php; 75% RH.	[350] 41.7	[1500] 37.4	[1500] 0.897	Apel 1976
Seed wt. (kg m ⁻²)	Growth chambers in greenhouse; 21/16°C; 16h php; 75% RH; summer crop.	[290] 0.97	[490] 1.40	[490] 1.40	Gifford 1977
Seed wt. (g plant ⁻¹)	Growth chambers; 26/20°C; 600 μE m ⁻² s ⁻¹ ; 12h php; 70% RH; after 92 d trt.	[350] 23.5	[675] [1000] 37.5 38.1	[675] [1000] 1.60 1.62	Sionit et al. 1981b
Seed wt. (kg m ⁻²)	Growth chambers; 19°C; 640 μE m ⁻² s ⁻¹ ; 16h php. A A to D = highest to lowest B watering trt. C 				

WHEAT YIELD (CONTINUED)

Seed wt. (g plant ⁻¹)	Greenhouse compartments; 21/13°C; 12h php; 65/95% RH; C = balanced nutrient; -N = replace 60% NO ₃ ⁻ with Cl ⁻ ; -P = replace 90% H ₂ PO ₄ ⁻ with Cl ⁻ .	[350] [700] 22 34 23 28 13 13	[700] 1.5 1.2 1.0	Goudriaan and de Ruiter 1983
Seed yield (g m ⁻²)	Open top chambers; natural temperature, light, and php; mean of 2 years; exposure from jointing to physiological maturity.	[340] [1200] 529 633	[1200] 1.20	Havelka et al. 1984
* Not used in calculation of overall response				

MEASUREMENTS	OTHER CONDITIONS	OBSERVATIONS				RELATIVE RESPONSES			REFERENCES
WHEAT COMPONENTS OF YIELD									
ears m ⁻² spikelet ear kernels spikelet ⁻¹ kernel wt. (mg)	Growth chambers in greenhouse; 21/16°C; 16h php; 75% RH; summer crop.	ears m ⁻² spikelet ear ⁻¹ kernels spikelet ⁻¹ kernel wt. (mg)	[290] 1316 18.4 1.16 34.9	[490] 1787 17.1 1.32 36.5	[490] 1.36 0.93 1.14 1.05				Gifford 1977
spikelet ear kernels plant ⁻¹ kernel wt. (g)	Growth chambers; 26/20°C; 600 µE m ⁻² s ⁻¹ ; 12h php; 70% RH; after 92 d trt.	spikelet ear ⁻¹ kernels plant ⁻¹ kernel wt. (g)	[350] 10.8 828.4 28.2	[675] 12.4 1379.3 27.2	[1000] 13.3 1174.4 32.8	[675] 1.148 1.665 0.964	[1000] 1.231 1.148 1.163	Sionit 1981b	
ears m ⁻² spikelet ear kernels spikelet ⁻¹ kernel wt. (mg) kernels m ⁻²	Growth chamber; 19°C; 640 µE m ⁻² s ⁻¹ ; 16h php; "stress" = mean of 3 suboptimal watering trts.	ears m ⁻² spikelet ear ⁻¹ kernels spikelet ⁻¹ kernel wt. (mg) kernels m ⁻²	---control--- [340] [590] 570 780 13.5 15.5 2.05 2.05 46 40 25 16	-water stress- [340] [590] 300 426.7 8.2 9.7 2.0 2.35 39.7 40.7 10.2 5.8	control water stress [590] [590] 1.37 1.42 1.15 1.18 1.00 1.18 0.87 1.03 0.64 0.57	Gifford 1979b			
ears plant ⁻¹ spikelet ear kernels spikelet ⁻¹ kernel wt. (mg)	Growth chambers; 26/20°C; 600 µE m ⁻² s ⁻¹ ; 12h php.	ears plant ⁻¹ spikelet ear ⁻¹ kernels spikelet ⁻¹ kernel wt. (mg)	---control--- [350] [1000] 32.0 38.0 10.8 12.8 2.4 2.4 28.3 32.9	-water stress- [350] [1000] 22 30.8 11.85 12.9 2.2 2.05 26.1 30.25	control water stress [1000] [1000] 1.19 1.40 1.18 1.09 1.00 0.93 1.16 1.16	Sionit et al. 1980			
ears plant ⁻¹ kernels plant ⁻¹ kernel wt. (mg)	Growth chambers; 26/20°C; 550 µE m ⁻² s ⁻¹ ; 12h php; 70% RH.	ears plant ⁻¹ kernels plant ⁻¹ kernel wt. (mg)	Hoagland's ----1/2----1/16---- [350] [675] [350] [675] 37.5 51.6 17.8 20.0 1143.2 1379.3 523.3 350.0 24.9 27.1 26.4 31.5		Hoagland's -1/2- -1/16- [675] [675] 1.376 1.124 1.207 0.669 1.088 1.193		Sionit et al. 1981a		
ears pot ⁻¹ kernels ear ⁻¹ kernel wt. (mg)	Growth chambers in green- house 21/13°C; 65/95% RH; C = balanced nutrient; -N = replace 60% NO ₃ ⁻ with Cl ⁻ ; -P = replace 90% H ₂ PO ₄ ⁻ with Cl ⁻ .	ears pot ⁻¹ kernels ear ⁻¹ kernel wt. (mg)	---- C ---- -N ---- -P ---- [350] [700] [350] [700] [350] [700] 22.6 25.2 21.3 33.2 16.7 18.2 27.8 36.2 32.6 24.4 25.8 23.9 36.1 39.2 34.1 31.4 27.2 27.5	--C-- -N-- -P-- [700] [700] [700] 1.11 1.56 1.09 1.30 0.75 0.93 1.09 0.92 1.01		Goudriaan and de Ruiter 1983			

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GLOSSARY

AMB	Ambient
CAM	Crassulacean acid metabolism
CEP	Capable of extrapolative prediction
CER	Carbon exchange rate
CERL	Central Electricity Research Laboratories (U.K.)
CIP	Capable of interpolative prediction
CS	Crop species
DOE	Department of Energy
DS	Drought stressed
ER	Ecosystem respiration
FACE	Free air carbon dioxide enrichment
GCM	General circulation model
GLM	General linear models
GPP	Gross primary production
HI	Harvest index
IPM	Integrated pest management
IRGA	Infrared gas analyzer
LAD	Leaf area duration
LAI	Leaf area index
LAR	Leaf area ratio
MIT	Massachusetts Institute of Technology
NAR	Net assimilation rate
NECS	Net ecosystem carbon storage
NPP	Net primary production
NS	Native plant species
PEP	Phosphoenolpyruvate
PPFD	Photosynthetic photon flux density
R_A	Autotrophic respiration
RGR	Relative growth rate
R_H	Heterotrophic respiration
RLGR	Relative leaf growth rate
RSR	Root-to-shoot ratio
RuBP	Ribulose biphosphate
SAS	Statistical Analysis Systems
SLA	Specific leaf area
SOA	State of the art (report)
SPAR	Soil-plant-atmosphere research
SPS	Sucrose phosphate synthase
TR	Transpiration rate
VPD	Vapor pressure deficit
WUE	Water use efficiency
WW	Well watered
ZAPS	Zonal Air Pollution System

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