Biogeochemistry 1: 219–232 (1985).

Physiological and ecological controls on carbon sequestering in terrestrial ecosystems*

BOYD R. STRAIN

Duke Phytotron, Department of Botany, Duke University,
Durham, NC 27706, USA

Key words: Carbon dioxide, carbon sequestering, biomass, net ecosystem productivity

Abstract. Carbon cycling processes in ecosystems are generally believed to be well understood. Carbon, hydrogen, oxygen and other essential elements are chemically converted from inorganic to organic compounds primarily in the process of photosynthesis. Secondary metabolic processes cycle carbon in and among organisms and carbon is ultimately released back to the environment as CO_2 by respiratory processes. Unfortunately, our understanding of this cycle was determined under the assumption that the primary inorganic form of C (CO_2 in the atmosphere) was relatively constant. With the emerging concensus that atmospheric carbon concentration is increasing, we must now reassess our understanding of the carbon cycle. How will plants, animals and decomposers respond to a doubling of carbon supply? Will biological productivity be accelerated? If plant productivity increases will a predictable percentage of the increase be accumulated as increased standing crop? Or, is it possible that doubling the availability of CO_2 will increase metabolic activity at all trophic levels resulting in no net increase in system standing crop? The purpose of this paper is to review evidence for physiological and growth responses of plants to carbon dioxide enhancement. Essentially no research has been completed on the ecological aspects of these questions. From this review, I conclude that accurate predictions of future ecosystem responses to increasing atmospheric carbon dioxide concentration are not possible without additional understanding of physiological and ecological mechanisms.

Introduction

The biota of the earth occurs in complex aggregations termed ecosystems. Ecosystems are integrated units of plants, animals, and microbes interacting through time with each other and with the physical-chemical environment. Ecosystems can be delineated by geographic, topographic, taxonomic, hydrologic, or energetic bounds. Ecosystems can be studied by quantitatively describing species relationships through time or by determining flux rates of mass and/or energy between and among ecosystem components.

In a consideration of the carbon dioxide issue, I will focus on carbon as the primary material of concern. Carbon flows within ecosystems in the

---

*Contribution from a symposium on global carbon dynamics held in May, 1984, at the annual meeting of the American Association for the Advancement of Science; Charles A. S. Hall, Convenor.

manner diagrammed in Figure 1. In the abiotic portion of ecosystems, carbon primarily occurs in the inorganic forms of $CaCO_3$ in sediments, HCO_3^- in fresh or marine waters, and CO_2 in the atmosphere. Fossilized organic matter in the form of coal and oil remained outside of the biosphere for eons but is now re-entering the biosphere through human energy consumption.

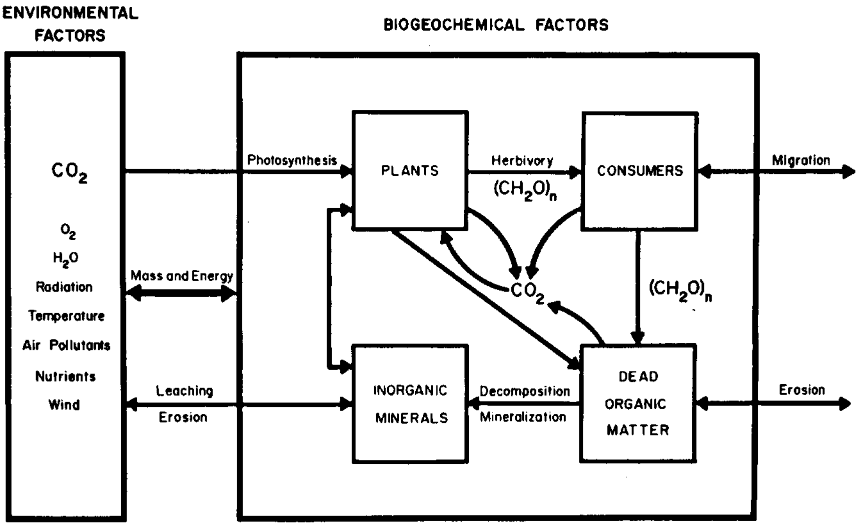

Figure 1. Carbon cycling in ecosystems. (Modified from strain, 1982).

The objective of this review is to define the components of ecosystems that are involved in the biological controls of carbon flux to and from the atmosphere and to discuss the impacts of atmospheric CO_2 enrichment on these controls. It is particularly important to identify any physiological or ecological responses that may change as atmospheric CO_2 concentration changes.

The initial response of ecosystems to atmospheric CO_2 enrichment is primarily due to direct physiological responses of plants. These primary responses lead to secondary physiological changes and finally to tertiary effects manifested as whole plant growth responses (Table 1).

Changes in plant growth differ qualitatively and quantitatively among species. These differential plant responses effect all subsequent organism interactions including the primary ones of direct organism interaction, secondary population adjustments and long term tertiary effects on evolution and ecosystem structure (Table 1).

Table 1. Physiological and ecological controls on carbon sequestering in carbon ecosystems

- I. Physiological controls on carbon sequestering
  - A. Primary physiological responses
    - 1. Photosynthesis
    - 2. Photorespiration
    - 3. Dark CO_2 fixation
    - 4. Stomatal aperture
  - B. Secondary physiological responses
    - 1. Photosynthate concentration
    - 2. Photosynthate composition
    - 3. Photosynthate translocation
    - 4. Plant water status
      - a. transpiration
      - b. tissue water potential
      - c. water use efficiency
      - d. leaf temperature
    - 5. Tolerance to gaseous atmospheric pollutants
  - C. Tertiary whole plant responses
    - 1. Growth rate
      - a. weight
      - b. height
      - c. leaf area
      - d. node formation
      - e. stem diameter
      - f. leaf senescence
    - 2. Growth form
      - a. height
      - b. branch number
      - c. leaf number
      - d. leaf area
      - e. root/shoot weight
      - f. stem diameter
      - g. leaf specific weight (weight/area)
      - h. cytological and anatomical changes
    - 3. 3. Reproduction
      - a. flowers produced earlier
      - b. flower size
      - c. flower number
      - d. fruits produced and mature earlier
      - e. fruit size
      - f. fruit number
      - g. seeds produced and mature earlier
      - h. seeds/plant increase
      - i. seed germination induced

- II. Ecological controls on carbon sequestering
  - A. Primary organism interactions
    - 1. Plant-plant
      - a. interference
      - b. competition
      - c. symbiosis
    - 2. Plant-animal
      - a. herbivory
      - b. pollination
      - c. shelter
    - 3. Plant-microbes
      - a. disease
      - b. decomposition
      - c. symbiosis (mycorrhizae, N-fixation)
  - B. Secondary organism interactions
    - 1. Evolutionary effects – genetic differentiation
  - C. Tertiary ecosystem responses
    - 1. Integration of all effects through time

Literature review

I. Physiological controls on carbon sequestering

A. Primary physiological responses

The direct effects of increasing atmospheric CO_2 on ecosystems are primarily exerted on carbon dioxide diffusion into plants and its assimilation in carbon metabolism (section I.A., Table 1). Net photosynthesis may be estimated if one knows the magnitude of the diffusion gradient from the CO_2 concentration of the atmospheric source (C_a) to the CO_2 concentration of the internal air spaces within the photosynthetic leaf (C_i) and the sum of all resistances (Σ r) to the diffusion of CO_2 along that concentration gradient. This relationship was defined by Gaastra (1959) and may be expressed as:

$$\text{Net photosynthesis} = \frac{C_a - C_i}{\Sigma r}$$

The resistances generally considered in this relationship are the aerodynamic nature of the air boundary layer (r_a), the variable resistance caused by the pore area of the stomata (r_s), and the sum of the gaseous, liquid, and enzymatic resistance within the leaf (r_i).

$$\Sigma r = r_a + r_s + r_i$$

Thus, it is assumed that under continuous atmospheric CO_2 enrichment, essentially all green plants should increase net photosynthesis (Tolbert and Zelitch, 1983). It has been reported, however, that increasing CO_2 will directly increase r_s (Akita and Moss, 1972), and that transpiration will decrease accordingly (Pallas, 1965). Because of the increasing diffusion gradient of CO_2, photosynthesis will remain constant or increase but transpiration will decrease (Moss et al., 1961; Bavel, 1974). The net effect is an increase in water use efficiency (Takami and Bavel, 1976; Hurt and Wright, 1976). This effect has been repeatedly confirmed (Wong, 1979; Carlson and Bazzaz, 1980; Rosenberg, 1981; Sionit et al., 1984). A recent study of the interaction between defoliation, irradiance, water stress and CO_2 enhancement clearly demonstrates the complexity of the issue (von Caemmerer and Farquhar, 1984).

In addition to direct physiological effects of CO_2 on photosynthesis and stomatal aperture, there is a well known inhibitory effect of high internal CO_2 concentration on oxygen use in photorespiration (Pearcy and Bjorkman, 1983). This reduces carbon loss in photorespiration thereby increasing net photosynthesis. There are also probable direct effects of CO_2 increase on dark CO_2 fixation in plants with crassulacean acid metabolism (CAM plants) and in heterotrophic tissues (Gates, Strain and Weber, 1983).

B. Secondary physiological responses

Beyond the primary physiological responses of the autotrophic organisms, there are many secondary physiological responses (section I.B., Table 1). The concentration of soluble sugars and starch may increase with increasing CO_2 (Madsen 1968; Cave, Tolley and Strain, 1981), and photosynthate accumulation may increase osmotic concentration and feedback to reduce photosynthesis rate (Guinn and Mauney, 1980). Accumulating starch has been shown to cause distortion of chloroplasts (Cave, Tolley and Strain, 1981; Wuff and Strain, 1982), but it has not been demonstrated that this will directly reduce photosynthesis rate (Pearcy and Bjorkman, 1983).

Photosynthate composition other than sugar and starch has also been shown to change as increasing CO_2 causes increasing photosynthesis rate (Madsen 1971, 1974). Tolbert and Zelitch (1983) recently reviewed carbon metabolism associated with increasing atmospheric CO_2 concentration. They speculate that increasing rates of sugar production may cause a decrease in energy available for the production of acetate, fatty acids, lipids, and isoprene polymers.

The relationship between photosynthesis rate and translocation is not a simple one. The translocation of carbohydrates is believed to be a diffusion phenomenon and so an increase in soluble sugar concentration in leaves should increase translocation rates (Ho, 1976). On the other hand, Clough, Peet, and Kramer (1981), Clough and Peet (1981) and Peet (1984) have shown that the source/sink ratio, manipulated by controlling leaf/fruit ratio, will affect photosynthesis rate in soybean. Potvin, Goeschl and Strain (1984) demonstrated that low temperature and CO_2 concentration interact to affect translocation in ecotypes of the C_4 grass *Echinocloa crus-galli* from warm and cool habitats. Translocation was drastically reduced at low temperature in genotypes from a warm habitat but high CO_2 concentration tended to ameliorate the reduction.

Plant water status is affected as CO_2 increases (section I.B.4, Table 1). The closing of stomates as described above decreases water loss rate (Palias, 1965) allowing osmotic concentration to increase sufficiently to maintain turgor above the wilting point. Sionit et al. (1981d) demonstrated that increased turgor pressure allowed greater leaf expansion and plant growth to occur at high CO_2 levels.

Transpiration will be reduced as increasing CO_2 closes stomates and the comcomitant decreases in evaporation will cause leaf temperature to increase (Pearcy and Bjorkman, 1983). Leaf heating will change photosynthesis rates and leaf vapor pressure further affecting stomatal aperture. It is difficult or impossible to predict the net result of these complicated interactions at this time.

Many gaseous air pollutants (e.g. ozone, sulfur dioxide and nitrogen oxides) detrimentally affect plants by diffusing into the leaves through the open stomates. Coyne and Bingham (1977) and Green and Wright (1977) have shown an increasing tolerance to ozone as stomates were progressively closed by increasing atmospheric CO_2 concentration. Carlson and Bazzaz (1982) clearly demonstrated the response for SO_2 and showed a differential response for plants of different metabolic pathways.

C. Tertiary whole plant responses

The secondary responses outlined above will lead to changes in plant growth and development (section I.C., Table 1). Changes will occur in the rate of growth, in the form of plants produced and in sexual reproduction of the plants.

1. Growth rate. Increase in plant weight, height, and leaf area were among the first reported responses to increased CO_2 (Cummings and Jones, 1918). Since the early studies, almost all growth responses have been shown to accelerate as CO_2 is increased in the atmosphere. Sionit and his colleagues have documented these growth responses in a large number of contemporary studies (Sionit et al., 1980, 1981a, 1981b, 1981c, 1981d, 1982, 1983, 1984, 1985). Accelerated growth rates typically accelerate the senescence of leaves in cotton (Chang, 1975), soybean, peanut, peas, and bean (Hardy and Havelka, 1977) and in whole plants of chaparral annuals (St. Omer and Horvath, 1983). However, Hardy and Havelka (1977) also reported extended physiological activity and delayed senescence in some cases.

2. Growth form. One of the important concerns over CO_2 increase comes from a great number of studies reporting changes in plant growth form (section I.C.2, Table 1). After one year of growth at high CO_2, both *Pinus taeda* and *Liquidambar styraciflua* seedlings were taller, had more branches, greater leaf number, larger leaf area, larger stem diameters, greater leaf specific weight (Sionit et al., 1985). Thus, the one year old seedlings grown at high CO_2 were more bushy than control plants grown at lower CO_2 concentration.

Cytological changes have been documented best by Madsen (1973) but electron micrographs of leaves of leguminous plants have shown important organelle effects (Cave, Tolley and Strain, 1981; Wulff and Strain, 1982). These latter studies showed that chloroplasts accumulated starch grains at high CO_2 until the grana and thylakoid membranes became contorted and compressed. Thomas and Harvey (1983) have shown anatomical effects in cell structure with more palisade cells developed in leaves of corn, soybean, sweetgum and lobolly pine at high CO_2 conditions.

3. Reproduction. Flowers are produced earlier, are normally larger and occur in greater number on plants grown at high CO_2, and the accelerated development normally results in earlier fruit and seed production (Calvert, 1972). For example, soybean yield greatly increased in number of seeds per plant

(Sionit, 1983), as did the grain production of wheat (Sionit, Strain and Hellmers, 1981c). High CO_2 has been reported to change sex ratios to more female flowers per plant in cucumber (Enoch et al., 1976). A few studies have shown that increasing CO_2 concentration induces germination in legume seeds (Ballard 1958, 1961; Grant Lipp and Ballard, 1959; Tolley, 1980).

In general, the net effect of CO_2 on plant reproduction is to accelerate all events from the dates of anthesis to the date of seed maturation. Dormancy of seeds is decreased and rate of germination may be accelerated. These events will have important ecological effects if they occur in ecosystems.

II. Ecological controls on carbon sequestering

A. Primary organism interactions

1. Plant-plant. Plant-plant interactions are of three basic types: interference, competition and symbiosis. One plant may interfere with another by releasing allelopathic chemicals into the environment (Rice, 1974). Since allelochemic compounds are frequently phenolics, terpines or other secondary compounds (Tolbert and Zelitch, 1983), it is possible that production rates will increase because of increasing photosynthesis. Differential species responses in this regard would change interference potentials and perhaps cause ecological change.

Competition between plants will most certainly be affected by single organism responses to CO_2 enrichment (Patterson and Flint, 1980; Patterson, Flint and Beyers, 1984; Carter and Peterson, 1983; Bazzaz and Carlson, 1984; Zangarl and Bazzaz, 1984). Changes in plant form as outlined above may cause ecological changes (Sionit et al., 1985). There is considerable evidence that specific and sub-specific differences exist in plant communities and populations in the effects of CO_2 increase on individuals (Tolley and Strain, 1984a, b, 1985; Paez, Hellmers and Strain, 1984; Garbutt and Bazzaz, 1984.

Changes in plant height, branching and leaf area will change canopy structure and competition for light. The species or ecotype that responds the most in these aspects will gain increasing dominance over its competitors. A modification of the Lambert-Beer Extinction Law (Larcher, 1980) will demonstrate one of the mechanisms of ecological control over carbon sequesting:

$$I = I_0 \cdot e^{-k \cdot LAI}.$$

Leaf area index (LAI) changes will affect the distribution of radiation received (I_0), and the profile of light penetration (I) through the canopy. Since carbon dioxide affects all of the processes that control LAI, plant-plant competitive interactions will likely change.

Symbiotic relationships between vascular plants may be beneficial to both species (mutualism), beneficial to one species but neutral to the second (commensalism), or beneficial to one species but detrimental to the second (parasitism) (Odum, 1959). All of these relationships could be affected by differential response of individuals as outlined in the section on physiological controls. Differential growth form or phenological changes among populations of plants will definitely change the pattern of the interrelationships. I know of no specific studies on a CO_2 mediated change in a symbiotic relationship among vascular plants.

2. Plant-animal. Animals rely on plants for food and habitat and plants rely on animals for pollination and dissemination of propagules. The effects of increased CO_2 on these interactions are almost totally unknown. The only study I know of investigated the response of a herbivore to plant tissue grown at different CO_2 levels (Lincoln, Sionit and Strain, 1984). We found larvae ate more tissue as CO_2 increased with no increase in insect growth rate. The C/N of plant tissue increased with increasing CO_2 and the feeding efficiency of the larvae declined. Research is currently underway to determine if declining amino acid or protein contents are correlated with the changing C/N.

Pollination events will be affected if plant reproduction responds as described in section I.C.3. Increases in number of flowers, accelerated flower production, and the possibility that nectar volume will increase with greater carbohydrate supply should all affect pollinator activity. No specific studies of their interaction with increasing CO_2 are known.

If plants produce more tissue and if plant form changes as predicted above, animals will presumably be affected as they search for shelter and nesting sites. If plant competition results in quantitative changes in the vegetation of ecosystems, co-adapted animals will be affected. Again, no studies of this possible response have been completed.

3. Plant-microbes. Plant-microbial interactions in a CO_2 enhanced atmosphere were recently reviewed (Lamborg, Hardy and Paul, 1983). Possible responses of pathogenic fungi and bacteria to changes induced by plant responses to increased CO_2 remain speculative. If tissue quality changes, pathogenic organisms might be affected. The adaptive capabilities of microorganisms, however, are so great that gradual changes in plants and animals responding to an increase in CO_2 over decades may cause little observable difference in virulence. Fungal species differ in tolerance to atmospheric CO_2 concentration. For example, *Sclerotinia minor* and *Phytophthora infestans* are sensitive to CO_2 while *Penicillium nigricans, Cochliobolus sativus* and many species of *Fusarium* tolerate high CO_2 levels (Lamborg, Hardy and Paul, 1983). As far as I know, however, no specific studies have been attempted to examine the effects of CO_2 enhancement on pathogenic interactions.

Decomposition will almost certainly be affected by CO_2 induced changes in soils and ecosystems. Since soil atmosphere is normally well above the air in CO_2 concentration now, there is little concern that decomposers will respond directly to atmospheric CO_2 increases anticipated during the next century. If, however, increasing soil organic matter leads to increasing decomposition and this significantly decreases O_2 content in wet soils, microbial responses can be expected (Lamborg, Hardy and Paul, 1983).

If soil organic matter changes in chemical composition (e.g. nitrogen, phenol, lignin or terpine concentration) as predicted in section I, microbial decomposers will almost certainly be affected (Lamborg, Hardy and Paul, 1983). A slower rate of decay might occur if nitrogen concentration decreases (Aber and Melillo, 1980) or if secondary compounds increase (Meentemeyer, 1978; Melillo, Aber and Muratore, 1982).

Nitrogen fixation has been shown repeatedly to increase when plants are grown at increased CO_2. Both symbiotic (Hardy and Havelka, 1975; Phillips et al., 1976) and non symbiotic (Lamborg, Hardy and Paul, 1983) nitrogen fixation will increase as carbohydrates become more available. Lamborg, Hardy and Paul (1983) stated 'The activity of all rhizosphere microorganisms will be enhanced by the larger photosynthetic activity of plants at higher CO_2 which will release a greater supply of microbial substrates through the roots.'

Mycorrhizae can be expected to increase in activity and growth as increasing carbohydrates enter the roots of plants (Lamborg, Hardy and Paul, 1983). Mycorrhizae improve plant nutrition and water relations and mycorrhizal symbiosis should be enhanced for both plants and microbes as CO_2 increases (Lamborg, Hardy and Paul, 1983). As with other organism interactions, little if any, research has been done specifically on the CO_2 enhancement response.

B. Secondary organism interactions

Differential species responses to a change in environment lead to gene frequency changes in communities. Sharma and co-workers (1979) screened 33 races of *Arabidopsis thaliana* for survival and growth under decreased CO_2 levels. Differences were found among races for survival time at very low CO_2 concentration. Two races, chosen for contrasting survival time, were hybridized and the F_2 progeny compared to the parents for survival time. They reported a significant number of transgressive segregates with survival times exceeding both parents. Considerable heterosis was observed in the F_2 population giving evidence for genetic differentiation to low CO_2 concentration. No comparable studies have been completed for genetic differentiation to CO_2 enchancement. Climatic changes of the magnitude predicted by Manabe and Wetherald (1980) would definitely affect populations, and change species distribution (Idso and Quinn, 1983) and community composition (Bazzaz, 1984).

Bazzaz and co-workers (reviewed in Strain and Bazzaz, 1983) have concluded the following from their studies with CO_2 enrichment:

1) Total community production increased with CO_2 enrichment.

2) There was a change in biomass hierarchy and a shift in species dominance.
3) Mean seed biomass increased for several of the species measured.

C. Tertiary ecosystem responses

Individual organisms change in direct response to CO_2 concentration or to subsequent indirect effects of CO_2 on organisms. If the changes persist through time, gene frequencies can be expected to change and species may change in importance in ecosystems. Vegetation boundaries have been predicted by computer simulations to move in direct response to CO_2 induced changes in plant water use effeciency (Idso and Quinn, 1983). Some species may become more dominant, others less so, and perhaps some will be supressed completely. There is one study underway in Alaska (Prudhomme et al., 1984) and one in West Germany (Overdieck, 1984) examining these ecosystem responses. The studies indicate differential species responses that may lead to ecosystem changes. Several years of continuous CO_2 enrichment and observation will be required, however, to test the hypotheses involved.

Microcosm studies in the Duke Phytotron with frozen cores removed from the permafrosted tundra and taiga of Alaska, have shown that temperature, atmospheric CO_2 concentration, soil nitrogen and water level will interact to affect net ecosystem carbon cycling (Billings et al., 1982, 1983; Peterson, Billings and Reynolds, 1984). It is possible that permafrosted tundra may sequester less carbon in the future and may even become a net carbon source due to increasing decomposition in a warmer climate.

Conclusions

CO_2 will have its initial effect on ecosystem parameters involved in biomass production. Subsequent ecosystem responses are largely speculative. Net ecosystem productivity is the result of total primary productivity (PP_g) of green plants minus the respiratory loss of all plants (PP_r), animals (SP_r), and microbes (D_r) in the system, minus any losses due to fire (F), and any material harvested or otherwise removed from the system (H). The net response may be expressed as:

$$EP_n = PP_g - PP_r - SP_r - D_r - F - H$$

Since an increase in carbon sequestering can only occur if EP_n increases from year to year, it is clear that we must understand the complete impact of carbon dioxide enhancement on each of the components of the above equation. Since there has been almost no research on SP_r or D_r as affected by CO_2 increase, it is currently impossible to predict ecosystem carbon flux. Among the uncertainties are human effects on F and H. It appears that $F + H$ will continue to increase leading to increasingly negative EP_n for the globe as a whole.

Acknowledgements

Research leading to the ideas expressed in this review was supported by NSF grants DEB 80-22165, BSR 82-15533 from the Ecosystem Program and BSR 83-14925 for the Duke Phytotron from the Biological Research Resources Program and by Interagency Agreement (DEA 101-31ERG0012) between the Department of Energy, Office of Carbon Dioxide Research, and the National Science Foundation, Ecosystem Program. The bioresources Center of the Desert Research Institute, Reno, Nevada, provided support during a sabbatical leave while the manuscript was prepared.

References

Aber J.D. and J.M. Melillo. 1980. Litter decomposition: measuring state of decay and percent transfer into forest soils. Canadian Journal of Botany, 58:416–421.

Akita, S. and D.N. Moss. 1972. Differential stomatal response between C_3 and C_4 species to atmospheric CO_2 concentration and light. Crop Science 12:789–793.

Ballard, L.A.T. 1958. Studies of dormancy in the seeds of subterranean clover (*Trifolium subterraneum* L.). I. Breaking of dormancy by carbon dioxide and by activated carbon. Australian Journal of Biological Sciences 11:246–260.

Ballard, L.A.T. 1961. Studies of dormancy in the seeds of subterranean clover (*Trifolium subterraneum* L.). II. The interaction of time, temperature, and carbon dioxide during passage out of dormancy. Australian Journal of Biological Sciences 14:173–186.

van Bavel, C.H.M. 1974. Antitranspirant action of carbon dioxide on intact sorghum plants. Crop Science 4:208–212.

Bazzaz, F.A. and R.W. Carlson, 1984. The response of plants to elevated CO_2. I. Competition among an assemblage of annuals at different levels of soil moisture. Oecologia 62:196–198.

Billings, W.D., J.O. Luken, D.A. Mortensen and K.M. Peterson. 1982. Arctic tundra: A source or sink for atmospheric carbon dioxide in a changing environment? Oecologia 57:7–11.

Billings, W.D., J.O. Luken, D.A. Mortensen and K.M. Peterson. 1983. Increasing atmospheric carbon dioxide: Possible effects on arctic tundra. Oecologia 58:286–289.

von Caemmerer, S. and G.D. Farquhar. 1984. Effects of partial defoliation, changes of irradiance during growth, short term water stress and growth at enhanced $p(CO_2)$ on the photosynthetic capacity of leaves of *Phaseolus vulgaris* L. Planta 160:320–329.

Calvert, A. 1972. Effects of day and night temperatures and carbon dioxide enrichment on yield of glasshouse tomatoes. Journal of Horticultural Science 47:231–247.

Carlson, R.W. and F.A. Bazzaz. 1980. The effects of elevated CO_2 concentrations on growth, photosynthesis, transpiration and water use efficiency of plants. In: J.J. Singh and D. Deepak (eds.) Environmental and Climatic Impact of Coal Utilization. Academic Press, New York.

Carlson, R.W. and F.A. Bazzaz. 1982. Photosynthetic and growth response to fumigation with SO_2 at elevated CO_2 for C_3 and C_4 plants. Oecologia 54:50–54.

Carter, D.R. and K.M. Peterson. 1983. Effects of a CO_2-enriched atmosphere on the growth and competitive interaction of a C_3 and C_4 grass. Oecologia 58:188–193.

Cave, G., L.C. Tolley and B.R. Strain. 1981. The effect of carbon dioxide enrichment on chlorophyll content, starch content and starch grain structure in *Trifolium* subterraneum leaves. Physiologia Plantarum 51:171–174.

Chang, C.W. 1975. Carbon dioxide and senescence in cotton plants. Plant Physiology 55:515–519.

Clough, J.M. and M.M. Peet. 1981. Effects of intermittent exposure to high atmospheric CO_2 on vegetative growth in soybean. Physiologia Plantarum 53:565–569.

Clough, J.M., M.M. Peet, and P.J. Kramer. 1981. Effects of high atmospheric CO_2 and sink size on rates of photosynthesis of soybean cultivar. Plant Physiology 67:1007–1010.

Coyne, P.I. and G.E. Bingham. 1977. Carbon dioxide correlation with oxidant air pollution in the San Bernardino Mountains of California. Journal of the Air Pollution Control Association 27:782–784.

Cummings, M.B. and C.H. Jones. 1981. The aerial fertilization of plants with carbon dioxide. Vermont Station Bulletin 211.

Enoch, H.Z., I. Rylski and M. Spigelman. 1976. CO_2 enrichment of strawberry and cucumber plants grown in unheated greenhouses in Israel. Scientia Horticulturae 5:33–41.

Garbutt, K. and F.A. Bazzaz. 1984. The effects of elevated CO_2 on plants. III. Flowers, fruit and seed production and abortion. New Phytologist 98:433–446.

Gates, D.M., B.R. Strain and J.A. Weber. 1983. Ecophysiological effects of changing atmospheric CO_2 concentration. In: O.L. Lange, P.S. Nobel, C.B. Osmond and H. Ziegler. (eds.) Physiological Plant Ecology IV. Encyclopedia of Plant Physiology, N. S. 12 D. Springer Verlag, N.Y. 644 pp.

Grant Lipp, A.E. and L.A.T. Ballard. 1959. The breaking of seed dormancy of some legumes by carbon dioxide. Australian Journal of Agricultural Research 10:495–499.

Green, K. and R. Wright. 1977. Field response of photosynthesis to CO_2 enhancement in ponderosa pine. Ecology 58:687–692.

Guinn, G. and J. Mauney. 1980. Analysis of CO_2 exchange assumptions: feedback control. In: J.D. Hesketh and James W. Jones (eds.), Predicting photosynthesis for ecosystem models Vol. 2. pp. 1–16. CRC Press, Inc., Boca Raton, Florida.

Hardy, R.W.F. and U.D. Havelka. 1977. Possible routes to increase the conversion of solar energy to food and feed by grain legumes and cereal grains (crop production): CO_2 and N_2 fixation, foliar fertilization, and assimilate partitioning. In: A. Mitsui, S. Miyachi, A. San Pietro and S. Tamura (eds.), Biological Solar Energy Conversion. pp 299–322. Academic Press.

Ho, L.C. 1976. The relationship between the rates of carbon transport and photosynthesis in tomato leaves. Journal of Experimental Botany 27:87–97.

Hurt, P. and R.D. Wright. 1976. CO_2 compensation point for photosynthesis: Effect of variable CO_2 and soil moisture levels. American Midlands Naturalist 95:450–453.

Idso, S.B. and J.A. Quinn. 1983. Vegetational redistribution in Arizona and New Mexico in response to a doubling of the atmospheric CO_2 concentration. Chimatological Publ. Sci. Paper. 16.7. Laboratory of Chimatology, Arizona State University, Tempe, AZ 85287. 52 pp.

Lamborg, M.R., R.W. Hardy and E.A. Paul. 1983. Microbial effects. In: E. Lemon (ed.) CO_2 and Plants. American Association for the Advancement of Science Select Symposium 84. Westview Press, Boulder, CO, 280 p.

Larcher, W. 1980. Physiological plant ecology. Second edition. Springer Verlag, N.Y. 303 pp.

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

Madsen, E. 1968. Effect of CO_2-concentration on the accumulation of starch and sugar in tomato leaves. Physiologa Plantarum 21:168–175.

Madsen, E. 1971. The influence of CO_2-concentration on the content of ascorbic acid in tomato leaves. (English summary). Ugeskrift for Agronomer 116:592–594.

Madsen, E. 1973. Effect of CO_2-concentration on the morphological, histological and cytological changes in tomato plants. Acta Agriculturae Scandinarica 23:241–246.

Madsen, E. 1974. The effect of CO_2-concentration on the occurrence of a number of acids from the citric acid cycle in tomato leaves. Physiologia Plantarum 32:10–13.

Manabe, S. and R.T. Wetherald. 1980. On the distribution of climatic changes resulting from an increase in CO_2 content of the atmosphere. Journal of Atmospheric Science 37:99–118.

Meentemeyer, V. 1978. Macroclimate and lignin control of decomposition rates. Ecology 59:465–472.

Melillo, J.M., J.D. Aber and J.F. Muratore. 1982. Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. Ecology 63:621–633.

Moss, D.N., R.B. Musgrave and E.R. Lemon. 1961. Photosynthesis under field conditions. III. Some effects of light, carbon dioxide, temperature, and soil moisture on photosynthesis, respiration, and transpiration of corn. Crop Science 1:83–87.

Odum, E.P. 1959. Fundamentals of ecology. Second edition. W.B. Saunders Company, Philadelphia, 226 pp.

Overdieck, D. 1984. Longterm effects of an increased CO_2 concentration level on terrestrial plants in model ecosystems. I. Phytomass production and competition of *Trifolium repens* L. and *Lolium perenne* L. Progress in Biometeorology 3:344–352.

Paez, A., H. Hellmers and B.R. Strain. 1984. CO_2 enrichment and water stress interaction on growth of two tomato cultivars. Journal of Agricultural Science 102:687–693.

Pallas, J.E., Jr. 1965. Transpiration and stomatal opening with changes in carbon dioxide content of the air. Science 147:171–173.

Patterson, D.T. and E.P. Flint. 1980. Potential effects of global atmospheric CO_2 enrichment on the growth and competitiveness of C_3 and C_4 weed and crop plants. Weed Science 28:71–75.

Patterson, D.T., E.P. Flint and J.L. Beyers. 1984. Effects of CO_2 enrichment on competition between a C_4 and C_3 crop. Weed Science 32:101–105.

Pearcy, R.W. and O. Bjorkman. 1983. Physiological Effects. In: E.R. Lemon (ed.), CO_2 and Plants. American Association for the Advancement of Science Select Symposium 84, Westview Press, Boulder CO, 280 pp.

Peet, M.M. 1984. CO_2 enrichment of soybeans. Effects of leaf/pod ratio. Physiologia Plantarum 60:38–42.

Peterson, K.M., W.D. Billings and D.N. Reynolds. 1984. Influence of water table and atmospheric CO_2 concentration on the carbon balance of arctic tundra. Arctic and Alpine Research 16:331–335.

Potvin, C., J.D. Goeschl and B.R. Strain. 1984. Effects of temperature and CO_2 enrichment on carbon translocation of plants of the C_4 grass species *Echinocloa crus-galli* L. Beauv. from Cool and Warm Environments. Plant Physiology 75:1054–1057.

Prudhomme, T.I., W.C. Oechel, S.J. Hastings and W.T. Lawrence. 1984. Net ecosystem gas exchange at ambient and elevated carbon dioxide concentration in tussock tundra at Toolik Lake, Alaska: An evaluation of methods and initial results. In: J.H. McBeath et al. (eds.). The Potential effect of carbon dioxide induced climate changes in Alaska. Miscellaneous Publication 83-1. School of Agriculture and Land Resources Management, University of Alaska, Fairbanks. 208 pp.

Rice, E.L. 1974. Allelopathy. Academic Press, N.Y. 352 pp.

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

Sharma, R.K., B. Griffing and R.L. Scholl. 1979. Variations among races of *Arabidopsis thaliana* (L.) Heynh for survival in limited carbon dioxide. Theoretical Applied Genetics 54:11–15.

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

Sionit, N., H. Hellmers, and B.R. Strian. 1980. Growth and yield of wheat under CO_2 enrichment and water stress. Crop Science 20:687–690.

Sionit, N., D.A. Mortensen, B.R. Strain and H. Hellmers. 1981. Growth response of wheat to CO_2 enrichment and different levels of mineral nutrition. Agronomy Journal 73:1023–1027.

Sionit, N., B.R. Strain and H.A. Beckford. 1981b. Environmental controls on the growth and yield of okra. I. Efffects of temperature and of CO_2 enrichment at cool temperature. Crop Science 21:885–888.

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

Sionit, N., B.R. Strain, H. Hellmers and P.J. Kramer. 1981d. Effects of atmospheric CO_2 concentration and water stress on water relations of wheat. Botanical Gazette 142: 191–196.

Sionit, N., H. Hellmers and B.R. Strain. 1982. Interaction of atmospheric CO_2 enrichment and irradiance on plant growth. Agronomy Journal 74:721–725.

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

Sionit, N., B.R. Strain, H. Hellmers, G.H. Riechers and C.H. Jaeger. 1985. Long term atmospheric CO_2 enrichment affects the growth and development of *Liquidambar styraciflua* L. and *Pinus taeda* L. seedlings. Canadian Journal Forest Research (in press).

St. Omer, L. and S.M. Horvath. 1983. Elevated carbon dioxide concentration and whole plant senescence. Ecology 64:1311–1314.

Strain, B.R. 1982. Ecological aspects of plant responses to carbon dioxide enrichment. In: S. Brown (ed.), Global dynamics of biospheric carbon. United States Department of Energy CONF-8108131. 194 pp.

Strain, B.R. and F.A. Bazzaz. 1983. Terrestrial plant communities. In: E.R. Lemon (Ed.), CO_2 and Plants. American Association for the Advancement of Science Select Symposium 84. Westview Press, Boulder, CO, 280 pp.

Takami, S. and C.H.N. van Bavel. 1976. Numerical experiments on influence of CO_2 release at ground level on crop assimilation and water use. Agricultural Meteorology 15:193–203.

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

Tolbert, N. and I. Zelitch. 1983. Carbon metabolism. In: E. Lemon (ed.) CO_2 and Plants. American Association for the Advancement of Science Select Symposium 84. Westview Press, Boulder, CO, 280 pp.

Tolley, L.C. 1980. Effects of CO_2 enrichment on seed germination. M.S. Thesis. Department of Botany, Duke University, Durham, N.C. 27706, 89 pp.

Tolley, L.C. and B.R. Strain. 1984a. Effects of CO_2 enrichment on growth of *Liquidambar styraciflua* and *Pinus taeda* seedlings under different irradiance levels. Canadian Journal Forest Research 14:343–350.

Tolley, L.C. and B.R. Strain. 1984b. Effects of atmospheric CO_2 enrichment and water stress on growth of *Liquidambar styraciflua* L. seedlings. Canadian Journal of Botany 62:2135–2139.

Tolley, L.C. and B.R. Strain. 1985. Effects of CO_2 enrichment and water stress on gas exchange of *Liquidambar styraciflua* and *Pinus taeda* seedlings. Oecologia 65:166–172.

Wong, S.C. 1979. Elevated atmospheric partial pressure of carbon dioxide and plant growth. I: Interactions of nitrogen nutrition and photosynthetic capacity in C_3 and C_4 plants. Oecologia 44:68–74.

Wulff, R. and B.R. Strain. 1982. Effects of carbon dioxide enrichment on growth and photosynthesis in *Desmodium paniculatum*. Canadian Journal of Botany 60:1084–1091.

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