

Biological Consequences of Increased Concentrations of Atmospheric CO₂

SHERWOOD B. IDSO

For most of the past two millennia, the carbon-dioxide content of earth's atmosphere has been amazingly constant, hovering at a mean concentration of approximately 280 parts per million (ppm). With the dawning of the Industrial Revolution, however, this equilibrium was disturbed: the CO₂ content of the air began to rise as humanity embarked upon a course of unprecedented economic development that was fueled by the burning of massive quantities of coal, gas, and oil, which released huge amounts of carbon dioxide into the atmosphere.

The rise in the concentration of atmospheric CO₂ that has accompanied this societal transformation is currently viewed with considerable alarm, due to its purported ability to induce what many believe will be catastrophic global warming. But the

phenomenon is not without its positive aspects, among which is its ability to stimulate vegetative productivity and it is possible that this demonstrable biological consequence of increased concentrations of atmospheric CO₂ may ultimately prove to be of far greater significance than its speculative climatic consequences. Hence, it is important to review what we know about the little-publicized effects of increased concentrations of atmospheric CO₂ on the growth and development of plants; for these are the only effects of the rising CO₂ content of earth's atmosphere about which we can be truly confident.

Effects of CO₂ upon plant growth

Carbon dioxide is the basis of almost all life on earth as it is the primary raw material used by plants to produce organic matter. Rogers *et al.* (1992) have highlighted this fact by noting that carbon dioxide is the first molecular link between the atmosphere and biosphere, that it is essential for photosynthesis, which sustains plant life, the basis of the entire food chain, and that no substance is more pivotal for ecosystems, either natural or managed. The veracity of these claims is supported by literally hundreds of experiments that have convincingly demonstrated that the more CO₂ there is in the air, the better plants perform their many vital functions. In the first major review of this subject (Kimball 1983a), which was based upon 430 individual experimental results, Kimball observed that the productivity of most herbaceous plants rose by about one-third in response to a doubling of the air's CO₂ content (330 to 660 ppm); and in a subsequent analysis of 770 sets of measurements, he obtained essentially the same result (Kimball 1983b). Other reviews have revealed similar or even larger CO₂-induced growth enhancements (Lemon 1983; Cure and Acock 1986; Mortensen 1987; Lawlor and Mitchell 1991; Drake 1992a; Poorter 1993; Ceulemans and Mousseau 1994; Strain and Cure 1994; Wullschleger *et al.* 1995, 1997); while in the most comprehensive study of all, which reviewed the results of over 1000 laboratory and field experiments conducted subsequent to the time of Kimball's analyses, Idso (1992a) documented a mean productivity enhancement of 52 percent in response to a 300 ppm increase in the air's CO₂ content.

This positive response of plants to increases in the concentration of atmospheric CO₂ cuts across all botanical boundaries and is present, to a greater or lesser degree, in all types of veg-

etation (Poorter 1993). Indeed, it is now realized to be one of the verities of nature that, with more CO₂ in the air, plants generally grow larger, have more branches or tillers, more and thicker leaves, more extensive root systems, as well as more flowers and fruit (Idso 1989a); and in consequence of these well established facts, Sylvan H. Wittwer, the father of modern research in this area, stated recently that "it should be considered good fortune that we are living in a world of gradually increasing levels of atmospheric CO₂" (1997: 13). As we shall shortly see, we have already reaped immense benefits from this phenomenon and we can anticipate even greater positive consequences in the years ahead.

Effects of CO₂ upon the efficient use of water by plants

In addition to enhancing vegetative productivity, an increase in the concentration of atmospheric CO₂ tends to reduce the apertures of the small pores or stomates through which water vapor escapes from plant leaves and is lost to the atmosphere (Pallas 1965; Morison 1985). The reduction in rate of evaporation from leaves produced by this phenomenon averages about one-third for a doubling of the air's CO₂ content (Kimball and Idso 1983; Cure and Acock 1986); and combining this effect with the simultaneous CO₂-induced increase in plant productivity actually doubles the efficiency with which individual leaves utilize water to produce organic matter.

The likely consequences of this phenomenon are truly impressive. As the concentration of atmospheric carbon dioxide rises ever higher in the years ahead, plants should be able to grow where it is presently too dry for them, enabling the most drought-resistant species to reclaim great tracts of land previously lost to desertification (Idso and Quinn 1983; Idso 1989b). Greater vegetative cover should also reduce the adverse effects of soil erosion caused by the ravages of wind and rain (Idso 1991a). And, with greater plant productivity both above-ground (as noted in the previous section) and below-ground (Idso *et al.* 1988; Rogers *et al.* 1994; Jongen *et al.* 1995; Pregitzer *et al.* 1995; Tingey *et al.* 1996), there is typically an increase in soil organic matter (Lekkerkerk *et al.* 1990; Wood *et al.* 1994; Sombroek 1995; Henning *et al.* 1996; Batjes and Sombroek 1997; King *et al.* 1997; Prior *et al.* 1997), which usually produces even further benefits.

Creatures such as earthworms that live in the soil are greatly stimulated by additions of organic matter (Edwards 1988; Rogers *et al.* 1994); and an increase in their activity would likely lead to the creation of much new soil (Graham *et al.* 1988; Johnson 1988) while at the same time improving the fertility, structure, aeration, and drainage of existing soils (Edwards 1997). These improvements, in turn, would likely boost plant productivity even higher, putting still more organic matter into the soil, and so on (Idso 1991b), as the several phenomena reinforce each other to lift the whole biosphere to a new level of activity (Idso 1992b).

The challenge of inadequate resources

In spite of the impressive body of evidence that has established the reality of the many biological benefits of an atmosphere enriched with increased concentrations of CO₂, many find it difficult to believe that a gaseous effluent of our industrial society might be good for the biosphere (Gore 1992); and, from time to time, a few scientists have suggested that the limited availability of resources characteristic of unmanaged ecosystems will reduce or even totally negate the growth-enhancing effects of increased concentrations of atmospheric CO₂ upon natural (as opposed to managed, i.e. agricultural) plant communities (Kramer 1981; Oechel and Strain 1985; Bazzaz and Fajer 1992). Consequently, in an effort to resolve this issue, Idso and Idso (1994) reviewed the plant science literature of the 10-year period following the original reviews of Kimball (1983a, b) and analyzed the results of all paired sets of CO₂-enrichment experiments that were conducted simultaneously under growing conditions that were both ideal and less than ideal. Results of their several findings are summarized in the following subsections.

Low levels of light

Decreasing light intensity had no significant effect upon plants' photosynthetic response to increased concentrations of atmospheric CO₂ until the lowest light intensity of the 37 experiments studied was encountered. At that level, contrary to the contentions of those who view inadequate resources as impediments to the positive effects of increased concentrations of CO₂, there was a rise in CO₂-induced benefits: the mean percentage increase in photosynthesis due to a 300 ppm increase in atmo-

spheric CO₂ rose from 68 percent under normal light intensities to 80 percent at the lowest light intensity studied, while the mean percentage increase in photosynthesis due to a 600 ppm increase in CO₂ rose from 111 percent to 194 percent.

Studies published subsequent to the review of Idso and Idso (1994) have continued to demonstrate that low light intensities do not negate the beneficial effects of increased concentrations of atmospheric CO₂ upon plant growth and development (Maruyama and Huang 1996; Percival *et al.* 1996; Wang 1996; Kubiske and Pregitzer 1997). In fact, in a study of plants in the forest understory, Osborne *et al.* (1997) found that elevated CO₂ concentrations allowed for a positive net photosynthetic uptake of carbon on days and at locations that typically experienced light intensities so low that they were generally insufficient for positive net photosynthesis under current atmospheric CO₂ concentrations, i.e., they found that elevated CO₂ concentrations allowed the plants to live where they currently cannot due to a lack of sufficient light. Hence, they concluded that “the potential range of habitats that such species could occupy will expand considerably with rising atmospheric CO₂” (1997: 343); similar conclusions are suggested by the work of Caporn *et al.* (1994); Wang *et al.* (1995); Kubiske and Pregitzer (1996), and Liang *et al.* (1996).

Inadequate water

When lack of water posed a limitation to vegetative growth and development, the results of Idso and Idso’s (1994) analyses of 55 experiments were even more dramatic than those pertaining to low light levels. The growth enhancement caused by a 300 ppm increase in atmospheric CO₂ jumped from 31 percent when water supplies were optimal to 63 percent when they were less than optimal while, for an increase of 600 ppm in the concentration of CO₂, the CO₂-induced growth enhancement jumped from 51 percent to 219 percent when the availability of water decreased from adequate to less than adequate. Here, too, subsequent studies continue to support these general observations (Liang and Maruyama 1995; Roden and Ball 1996; Goodfellow *et al.* 1997) and, in a model-driven review of experimentally established principles derived from work on temperate forest species, Thornley and Cannell have independently concluded that the on-going rise in the air’s CO₂ content “will protect trees

from debilitating water stress" (1996: 1343). Kellomaki and Wang (1996) have come to the same conclusion as a result of their own observations and, in much the same vein, Polley *et al.* (1996) have observed that a doubling of the concentration of atmospheric CO₂ can significantly enhance the percentage of seedlings surviving when water is withheld.

Insufficient soil nutrients

In Idso and Idso's (1994) analysis of the effects of limitations of soil nutrients, the growth enhancement due to a 300 ppm rise in the air's CO₂ content exhibited a slight decline, dropping from 51 percent to 45 percent when, in a group of 70 experiments, nutrients went from a level that did not limit growth to a level that did. But when the concentration of atmospheric CO₂ increased to 600 ppm, this slight negative trend reversed itself, going from a 43 percent CO₂-induced growth stimulation when nutrients were present in abundance to a 52 percent enhancement when their supply was sub-optimal. And, with a 1200 ppm increase in atmospheric CO₂, growth enhancement jumped from 60 percent when the soil nutrient supply was adequate to 207 percent when it was less than adequate.

Examples from specific ecosystems

Detailed investigations of several managed and unmanaged ecosystems have provided striking examples of how increased concentrations of atmospheric CO₂ can endow plants with the capacities they need to overcome the restrictions upon growth that result from limited resources (Koch and Mooney 1996a). In years when the productivities of these plant communities have been unusually high, for example, the effects of elevated concentrations of CO₂ have been decidedly moderate; but when environmental factors have combined to curtail their growth and development severely, the effects of increased concentrations of atmospheric CO₂ have typically been much more dramatic (Koch and Mooney 1996b).

In the case of a Kansas tallgrass prairie, doubling the atmospheric CO₂ concentration enhanced vegetative productivity by only 5 to 10 percent in several years of high productivity but, in a year of intermediate productivity, it increased growth by approximately 40 percent and, in a year of very low productivity, it boosted production by nearly 80 percent (Owensby *et al.* 1996).

Another place where this phenomenon has been observed is in the world's most comprehensive set of Free-Air CO₂ Enrichment (FACE) experiments (Hendrey *et al.* 1993; Dugas and Pinter 1994). In a study where CO₂ was injected directly into the air over a wheat crop growing in a field devoid of any alterations to the natural environment, the imposition of a yield-reducing water stress raised the productivity enhancement created by a 180 ppm increase in atmospheric CO₂ from 10 percent to 23 percent in two different years (Pinter *et al.* 1996). Further, in a cotton crop where the wetter of two irrigation regimes reduced the yield resulting from the ambient-air treatment, it was the over-watered plants with lower yield that experienced the greater CO₂-induced stimulation to growth in two different years (Pinter *et al.* 1996).

How high CO₂ levels help plants overcome resource deficiencies

One reason that plants are able to respond positively to increased levels of atmospheric CO₂ when limited resources significantly curtail their growth is that plants grown at elevated concentrations of CO₂ typically have more extensive and active root systems than control plants growing in normal air (Curtis *et al.* 1990, 1994; Idso and Kimball 1991a, 1992b; Norby 1994; Prior *et al.* 1995; Gebauer *et al.* 1996; King *et al.* 1996; Kubiske *et al.* 1997), which allows them to explore more thoroughly larger volumes of soil in search of the things they need (Norby *et al.* 1992; Rogers *et al.* 1992; Stulen and den Hertog 1993). When more nutrients are encountered in the course of this activity, plants can also acquire them more effectively (Luxmoore *et al.* 1986; Norby *et al.* 1986) because the uptake of many essential elements requires the expenditure of metabolic energy (Pitman 1977; Jackson *et al.* 1980), and the enhanced availability of carbohydrates typically provided by the enrichment of the air with CO₂ tends to promote this process (Clement *et al.* 1978; Rufty *et al.* 1989; Rogers *et al.* 1994). A low level of nitrogen in the soil, in particular, is not an impediment to CO₂-induced growth enhancement because plants exposed to elevated concentrations of atmospheric CO₂ do not need to invest as much nitrogen in their photosynthetic apparatus (Stitt 1991) as it operates so much more efficiently at higher CO₂ levels (Nie *et al.* 1995). Hence, even in the face of severe nutrient

deficiencies, plants' photosynthetic rates may be significantly stimulated by increased concentrations of atmospheric CO₂ (Norby *et al.* 1992; Wullschleger *et al.* 1992), setting in motion still other beneficial phenomena.

One of the most important of these secondary or indirect consequences of CO₂-induced growth stimulation in situations where resources are limited is the enhancement of the activity of soil microorganisms (Lamborg *et al.* 1983; Pregitzer *et al.* 1995; Tingey *et al.* 1996) that is provided by enhanced root exudation of organic substances (Norby 1997; Hungate *et al.* 1997). This enhanced activity of microorganisms typically stimulates a multiplicity of growth-promoting effects beneath the soil surface (Zak *et al.* 1993). As the "better-fed" hyphae (filamentous structures) (Smith and Read 1996) of more numerous and robust symbiotic fungi extend outward from their CO₂-enriched hosts (Ineichen *et al.* 1995), for example, they lengthen the life of absorptive root hairs (Fogel 1983) and increase the area of root surface available for water and nutrient uptake (Tinker 1984; Clarkson 1985; Smith and Read 1996). The microscopic organisms that live in the plant's root zone or rhizosphere also secrete a number of organic acids that hasten the chemical weathering of soil minerals (Boyle and Voigt 1973; Boyle *et al.* 1974) and they are especially adept at making phosphorus available to plants by this means (Ortuno *et al.* 1978; Molla *et al.* 1984; Babenko *et al.* 1985). In addition, these microscopic organisms produce a variety of hormones that stimulate root growth (Simmons and Pope 1987, 1988), enhancing the production of lateral roots and root hairs (Umali-Garcia *et al.* 1980; Kapulnik *et al.* 1983).

Most important of all, perhaps, is the ability of elevated levels of atmospheric CO₂ to stimulate the activity of nitrogen-fixing bacteria directly (Burk 1961; Lowe and Evans 1962). The capacity of these bacteria to remove nitrogen from the atmosphere and make it available to plants appears to be limited by their host plants' rates of carbohydrate production (Sinclair and de Wit 1975; Hardy *et al.* 1976; Finn and Brun 1982). Consequently, anything that stimulates vegetative productivity, including increased concentrations of atmospheric CO₂, generally stimulates bacterial nodule growth and activity (Quebedeaux *et al.* 1975; Murphy 1986) and several-fold increases in the air's CO₂ content have indeed been found to produce several-fold increas-

es in nitrogen fixation in a number of experiments (Hardy and Havelka 1973, 1975; Havelka and Hardy 1976; Phillips *et al.* 1976; Hardy *et al.* 1978; MacDowall 1983).

Acting in concert, these phenomena typically allow the growth-enhancing effects of increased concentrations of atmospheric CO₂ to be expressed in the face of severe nutritional deficiencies, suggesting that carbon starvation (Svedang 1992; Cizkova-Koncalova *et al.* 1992; Robinson 1994) may well be a more significant impediment to the growth of the planet's vegetation than is a lack of soil nutrients. In the words of Gundersen and Wullschleger, who have reviewed the subject in depth, "hypotheses that either nutrient or water limitations would limit photosynthetic responses in natural environments have not been adequately supported by the currently available data" (1994: 384). Quite to the contrary, the data demonstrate, as noted by Gifford, that "high CO₂ increases light-use efficiency, water-use efficiency and nitrogen-use efficiency," so that "the 'law of limiting factor' concept that such vegetation cannot respond to increased CO₂ concentration does not apply to C₃ species¹" (1994: 33) which include fully 95 percent of all of earth's plants (Drake 1992b; Bowes 1993).

The challenge of environmental stresses

In addition to limited resources, there are a number of environmental stresses that are typically encountered in natural and agricultural ecosystems and it has been claimed that their debilitating influences reduce or negate the benefits that can accrue to plants from increased concentrations of atmospheric CO₂. The review of Idso and Idso (1994) demonstrates once again, however, that such effects are generally not observed in laboratory and field experiments and that, if anything, just the opposite is more likely to occur.

1 C₃ plant species are distinguished from C₄ plant species in that they use the process of photosynthesis first identified by science, a process using an enzyme that reacts with both CO₂ and O₂ and that is, thus, less efficient in the presence of relatively higher levels of O₂ than the process used by C₄ plant species, which depends upon a different enzyme that does not interact with O₂. Increased concentrations of atmospheric CO₂ are, therefore, of much greater benefit to C₃ species of plants than to C₄ species. The names come from the three-carbon (C₃) sugar that is the first product of the photosynthetic process in C₃ species and from the four-carbon (C₄) organic acid that is the first product in C₄ species.

Soil salinity and air pollution

In an analysis of 42 sets of measurements of the reponse of plant growth to increased concentrations of atmospheric CO₂ at different values of soil salinity, Idso and Idso (1994) found that the growth-promoting effects of elevated levels of CO₂ in the air were found to about the same degree in plants stressed by increased salinity of the soil as in plants in soil of normal salinity, demonstrating that, on average, soil salinity does not reduce the biological benefits of increased concentrations of atmospheric CO₂. What is more, in another 20 sets of measurements, when air pollutants were the source of stress, the percentage enhancement in growth brought about by a 300 ppm increase in atmospheric CO₂ actually rose in the face of this adversity, from 38 percent when air pollutants were absent to 54 percent when they were present in noxious quantities. And, as was the case where there were limited resources, research conducted subsequent to the review of Idso and Idso (1994) has continued to confirm their basic finding about the interaction between CO₂ and air pollution: a doubling of the air's CO₂ content was often found to compensate totally for the debilitating effects of air pollutants such as ozone (Rudorff *et al.* 1996; Volin and Reich 1996; McKee *et al.* 1997; Mulholland *et al.* 1997; Fiscus *et al.* 1997).

Global warming

The environmental stress about which certain scientists—and, therefore, the Press and the public—seem to worry most is that produced by higher air temperatures (Peters and Darling 1985; Paine 1988; Davis 1989; Woodwell 1989; Gear and Huntley 1991; Dobson 1992). They are concerned that future global warming may be so great that plants will need to migrate towards the poles in order to remain within the climatic regimes to which they are currently best suited (Overpeck *et al.* 1991; Dyer 1995) and, because the warming is predicted to be so rapid, they fear that many plants may not be able to migrate fast enough to avoid extinction (Possingham 1993; Root and Schneider 1993; Pitelka *et al.* 1997).

Although this scenario may sound reasonable, it is largely contradicted by basic research into plant physiology. In an analysis of 42 different data sets, Idso and Idso (1994), for example, found that the growth enhancement due to a 300 ppm increase in atmospheric CO₂ actually rose with increasing air temperature, climbing from nearly 0 percent at 10°C to a full 100 percent

at 38°C; for greater increases in the air's CO₂ content, the percentage of growth enhancement was greater still, something that ongoing research continues to confirm (Nijs and Impens 1996; Vu *et al.* 1997).

One reason for this counter-intuitive response is that the optimum temperature for plant growth generally rises as the air's CO₂ content rises (Berry and Bjorkman 1980; Taiz and Zeiger 1991; McMurtrie *et al.* 1992; McMurtrie and Wang 1993). Long (1991), for example, has calculated from basic principles of plant physiology that a 300 ppm increase in atmospheric CO₂ should cause the optimum temperatures of most C₃ plants to rise by about 5°C; an analysis of the results of 7 studies that have experimentally evaluated this phenomenon (Bjorkman *et al.* 1978; Nilsen *et al.* 1983; Jurik *et al.* 1984; Seemann *et al.* 1984; Harley *et al.* 1986; Stuhlfauth and Fock 1990; McMurtrie *et al.* 1992) reveals a mean optimum temperature rise of 5.9°C with a 300 ppm increase in atmospheric CO₂ (Idso and Idso 1994). And, as this rise in optimum temperature is even larger than the rise in air temperature predicted to result from the greenhouse warming caused by such a CO₂ increase (IPCC 1990, IPCC I 1996), a CO₂-induced warming would not adversely affect the vast majority of earth's plants, 95 percent of which are of the C₃ variety (Drake 1992b; Bowes 1993). In addition, the remainder of the planet's species—which may not experience quite as large a rise in optimum temperature (Chen *et al.* 1994)—are already adapted to earth's warmer environments (De Jong *et al.* 1982; Drake 1989; Johnson *et al.* 1993), which are expected to warm much less than the other portions of the globe (IPCC 1990, IPCC I 1996).

In view of these facts, it is clear that a CO₂-induced global warming would not produce massive poleward migrations of plants seeking cooler weather, for the temperatures at which nearly all plants perform at their optimum would rise at the same rate as (or faster than) and to the same degree as (or higher than) the temperatures of their respective environments. What is more, the photosynthetic rates of the 7 plants for which these evaluations have been experimentally derived were found to be nearly twice as great at their CO₂-enriched optimum temperatures as they were at their optimum temperatures under present CO₂ conditions (Idso and Idso 1994), suggesting not only that typically predicted increases in atmospheric CO₂ and

global air temperatures would not hurt earth's vegetation, but also that they might actually help it, as subsequent investigations have revealed as well (Wang 1996).

Finally, at the highest air temperatures encountered by plants, increased concentrations of atmospheric CO₂ have been demonstrated to be especially valuable for they often mean the difference between life and death (Rowland-Bamford *et al.* 1996; Idso 1997), as they typically enable plants to maintain positive carbon exchange rates in situations where plants growing under present CO₂ concentrations exhibit negative rates that ultimately lead to their demise (Idso *et al.* 1989, 1995). Faria *et al.* (1996) have studied this phenomenon in detail in seedling oak trees and believe that the life-sustaining function of increased concentrations of atmospheric CO₂ at high air temperatures may also be partly due to a stabilization of enzymes susceptible to heat through the increased concentration of sugars generally found in CO₂-enriched leaves.

Long-term exposure to increased concentrations of CO₂

Most studies of plants' responses to increased concentrations of atmospheric CO₂ have been of rather short duration, ranging from hours to days to weeks. Some agricultural investigations have lasted longer, encompassing entire growing seasons; even in the case of long-lived plants, such as trees, however, few experiments have had their durations measured in years. Consequently, there has always been a concern that results derived from short-term experiments may not apply to plants over the longer term; and, in fact, there is an experimental basis for this worry.

Acclimation to high CO₂

According to a concept variously referred to as "acclimation" or "down regulation," it is believed by some biologists that long-term exposure to elevated levels of carbon dioxide will result in a reduction of the photosynthetic capacity of plants. This contention is based on the results of a number of experiments that have indeed revealed such behaviour in several plants (Kramer 1981; Pearcy and Bjorkman 1983; Delucia *et al.* 1985; Cure and Acock 1986; Tissue and Oechel 1987) and, although it is possible that such a phenomenon may regularly occur in certain species (Sicher and Bunce 1997), and that it may occur

more generally under certain circumstances (Lewis *et al.* 1994; Luo *et al.* 1994; Reining 1994; Ziska *et al.* 1995; Marek and Kalina 1996; Micallef *et al.* 1996), there are reasons to believe that it is not expressed—or not as consistently expressed (Sicher and Kremer 1994; Van Oosten and Besford 1996)—in the majority of plants growing in natural situations.

Many of the experiments that have exhibited long-term declines in CO₂-induced benefits to plants, for example, have been conducted in controlled environments or greenhouses (Drake and Leadley 1991), where the plants that were studied were grown in pots or some other type of root-restricting container. As a number of studies have demonstrated (Masle *et al.* 1990; Arp 1991; Hogan *et al.* 1991; Thomas and Strain 1991; Samuelson and Seiler 1992), root restrictions may sometimes prevent the full expression of the effects of increased concentrations of atmospheric CO₂, particularly when the plants grow larger, a natural consequence of longer experiments.

In contrast to the results of studies in controlled environments, long-term field experiments often show no reductions in the photosynthetic capacities of plants exposed to elevated concentrations of CO₂ (Radin *et al.* 1987; Sage *et al.* 1989; Idso and Kimball 1991b; Norby and O'Neill 1991; Gunderson *et al.* 1993; Dufrene *et al.* 1993; Jones *et al.* 1995; Teskey 1995, 1997; Wang and Kellomaki 1997), or they show an actual increase or “up regulation” in photosynthesis and growth over extended periods of time (Campbell *et al.* 1988; Conroy 1989; Chen and Sung 1990; Ziska *et al.* 1990; Arp and Drake 1991; Long and Drake 1991; Drake 1992c; Barton *et al.* 1993; Vogel and Curtis 1995; Liu and Teskey 1995; Jacob *et al.* 1995). There has been one field experiment that produced a contrary result (Oechel and Strain 1985; Tissue and Oechel 1987; Grulke *et al.* 1990) but the Arctic tussock tundra of that study was growing close to the temperature (10°C) at which its response to increased concentrations of atmospheric CO₂ truly should have been near zero, according to the analysis of temperature effects in the review of Idso and Idso (1994) and in harmony with the published opinions of several scientists who have analyzed this particular experiment in some detail (Drake and Leadley 1991; Long 1991; Drake 1992c; Kirschbaum 1994; Webber *et al.* 1994). What is more, in a subsequent three-year study of this same ecosystem, an artificially imposed warming of only 4°C totally eliminated the down regulation

observed at current air temperatures (Field 1994; Oechel *et al.* 1994). Consequently, although not to be ruled out in all instances, down regulation of photosynthesis and growth does not appear to be a major impediment to the long-term effectiveness of the aerial fertilization effect of increased concentrations of atmospheric CO₂ in stimulating the productivity of earth's vegetation for, as Woodrow has concluded after reviewing the subject in considerable depth, "C₃ plants probably possess the genetic feedback mechanisms required to efficiently 'smooth out' any imbalance within the photosynthetic system caused by a rise in atmospheric CO₂" (1994: 401) so that, in the words of Amthor, "acclimation . . . of photosynthesis to increasing CO₂ concentration is unlikely to be complete" (1995: 243).

*The world's longest experiment studying
increased concentration of CO₂*

In the longest study of its kind ever to be conducted—and where down-regulation would be expected to appear if it were a truly ubiquitous consequence of long-term exposure to increased concentrations of CO₂—my colleagues and I planted 8 seedling sour-orange trees directly into the ground at Phoenix, Arizona, in July of 1987 and enclosed them in pairs within 4 open-topped chambers made of clear polyethylene film. Then, in November of that year, we began to pump air with a CO₂ concentration of 700 ppm continuously into two of the enclosures through perforated plastic tubes that lay upon the ground while we pumped ambient air with a CO₂ concentration of 400 ppm into the other two enclosures (Idso *et al.* 1991). This protocol we have faithfully maintained to the present day, documenting the course of the effects of increased concentrations of atmospheric CO₂ upon the trees as they have progressed from tiny seedlings through the juvenile stage of development and into full maturity, which they appear to have reached about two years ago.

The results of this decade-long experiment have been truly remarkable. Over the entire course of the study, the CO₂-enriched trees, which receive 75 percent more CO₂ than the control trees—have continually produced over twice as much biomass as the trees growing in normal air (Idso and Kimball 1997); at our last harvest, we picked over three times as much fruit from the trees exposed to the extra CO₂. Hence, although we intend to continue the experiment for several more years

and do not yet have the final word on the subject, we feel confident that the beneficial effects of increased concentrations of atmospheric CO₂ observed to date will likely persist over the entire life span of the trees.

Historical trends in forest productivity

In addition to the experiments of scientists, the biosphere itself is providing evidence for the reality and long-term sustainability of the aerial-fertilization effects of increased concentrations of atmospheric CO₂. In the southwestern United States, for example, there is considerable evidence that the woody plants that were present in pre-industrial times, when the air's CO₂ content was much lower than now, were somewhat stunted compared to their present-day descendants (Johnston 1963; Scifres 1980). This phenomenon was not fully appreciated, however, until LaMarche *et al.* published a paper (1984) describing an analysis of annual growth rings obtained from pine trees growing near the timberline in California, Colorado, Nevada, and New Mexico. All of the trees that they studied exhibited large increases in growth rate between 1859 and 1983 and some of them doubled their productivity during this time. The researchers noted that the increased growth rates exceeded those expected from climatic trends but were consistent in magnitude with what would be expected from the historical trend of increasing concentrations of atmospheric CO₂, a trend particularly pronounced in recent decades.

Reports of a similar nature followed in quick succession. Along the western coast of North America, conifers growing in the high altitudes of the Cascade Mountains of Washington were found to have increased their growth rates by approximately 60 percent since 1890 (Graumlich *et al.* 1989). In British Columbia, ring-width measurements of Douglas firs also revealed a marked increase in growth in recent decades and Parker noted that "environmental influences other than increased CO₂ have not been found that would explain [the phenomenon]" (1987: 511).

In New England, a study of a 320-year-old *Pinus rigida* rock-outcrop community showed its trees to have experienced a dramatic increase in growth since 1970 (Abrams and Orwig 1995). Another study of 10 tree species revealed a mean growth enhancement of 24 percent from 1950 to 1980 (Hornbeck *et al.* 1988). In Georgia, annual growth increments of long-leaf pines began to rise

dramatically about 1920, increasing by approximately 30 percent by the mid-1980s (West 1988). In this study, too, it was reported that the increased growth could not be explained by trends in either precipitation or temperature, leaving the rising CO₂ content of the air as the most likely cause of the increase in productivity.

In between these regions, the growth rates of several hardwoods in the Great Smokey Mountains also increased over the last half-century (Busing 1989), as did those of other conifers in other regions of both the United States (Jacoby 1986; Graybill 1987; Hornbeck 1987; Kienast and Luxmoore 1988) and Canada (Jozsa and Powell 1987). In one such study, a colleague and I analyzed data collected from long-lived bristlecone, foxtail, and limber pines at high-altitude sites in Arizona, California, Colorado, and Nevada (Graybill and Idso 1993). In almost all of the chronologies we developed, a sharp upward growth trend began about the middle of the 1850s and has continued to the present. No comparable variations were observed anywhere else in the records, which continued back in time almost two millennia, suggesting that the accelerating growth observed in the last century-and-a-half of the several chronologies were truly unique and the result of some major regional or global factor. Furthermore, comparisons of the chronologies with records of changes in temperature and precipitation ruled out the possibility that either of these climatic variables played a significant role in enhancing the trees' growth rates, strongly implicating the rise in the air's CO₂ content as the factor responsible for the trees' increasing productivities over the past 150 years.

In Europe, a number of field studies have told much the same story. In forests of silver firs in the mountains of northeastern France, radial growth measurements have revealed a productivity increase of nearly 70 percent from 1830 to 1935 (Becker 1989) and the last decades of the century have seen significant increases in the growth of beech and spruce stands in southern Sweden (Bjorkdahl and Eriksson 1989; Falkengren-Grerup and Eriksson 1990). Similarly, stands of Scots pine in northern Finland have experienced growth increases ranging from 15 to 43 percent between 1950 and 1983 (Hari *et al.* 1984; Hari and Arovaara 1988). Since CO₂ is the only environmental factor that has changed systematically during this century in the remote area of this study, it was thus to this factor that Hari and Arovaara attributed the increased growth of the trees.

Germany presents an even more intriguing situation. In the late 1970s and early 1980s, reports of a large-scale decline in forest productivity were commonplace. When detailed studies based on extensive measurements finally appeared, however, just the opposite proved to be true (Eichkorn 1986; Glatzel *et al.* 1987; Spelsberg 1987). From the middle of the 1950s at the latest, Norway spruce, silver fir, and beech have all showed remarkable increases in growth rate (Kenk 1989; Spieker 1990), not following the normal age trend (Kenk and Fischer 1988); the growth of pine likewise increased (Pretzsch 1985a, 1985b). By the end of the 1980s, yields of most European forests were clearly above normal (Innes and Cook 1989). In early 1992, for example, scientists from the Finnish Forest Research Institute reported a general increase in forest growth in Austria, Finland, France, Germany, Sweden, and Switzerland (Kauppi *et al.* 1992) and Weidenbach (1992) reported that annual growth increments in the German state of Baden-Württemberg had risen approximately 20 percent in just the past 20 years.

Possibly the most revealing observations of all are those that come from tropical forests. Noting that the turnover rates of mature tropical woodlands correlate well with measures of their net productivity (Weaver and Murphy 1990), Phillips and Gentry (1994) assessed the turnover rates of forty tropical forests from around the world in order to test the hypothesis that forest productivity is increasing globally. Not surprisingly in view of the material just reviewed, they found that the turnover rates of these highly productive tropical woodlands have indeed been rising ever higher since 1960, if not earlier, and that there seems to have been a worldwide acceleration of this trend since about 1980. They also noted that “the accelerating increase in turnover coincides with an accelerating buildup of CO₂” (Phillips and Gentry 1994: 957). And as Pimm and Sugden stated in a companion article, it was “the consistency and simultaneity of the changes on several continents that [led] Phillips and Gentry to their conclusion that enhanced productivity induced by increased CO₂ is the most plausible candidate for the cause of the increased turnover” (1994: 933–34).

The breath of the biosphere

Compelling evidence for increasing stimulation of earth's plant life by the ongoing rise in the atmosphere's CO₂ concentration

is to be found in the air itself. Each spring, when the northern hemisphere's thin veneer of vegetation awakens from the dormancy of winter and begins a new season of growth, it draws enough carbon dioxide out of the air to reduce the concentration of atmospheric CO₂ by several parts per million. In the fall, when much of this vegetation dies, it releases huge quantities of carbon dioxide back to the air, causing the CO₂ content of the atmosphere to rise by a small amount. Meticulous measurements obtained over the past four decades have clearly demonstrated that the difference between the high and low points of this seasonal oscillation—this “breath of the biosphere” (Idso 1995)—is growing ever larger. Several groups of scientists have studied the phenomenon in detail and nearly all of them have concluded that it implies that the photosynthetic activity of the earth's plant life is growing greater and greater each year; many suggest that the ever-increasing aerial fertilization effect of the steadily rising CO₂ content of the atmosphere is its primary cause.

Working with data for atmospheric CO₂ from Mauna Loa Observatory in Hawaii, Point Barrow in Alaska, and Weather Station P in the North Pacific Ocean, Pearman and Hyson (1981) concluded that “it is most probable that there has been an increase in the summer net ecosystem production of the Northern Hemisphere of 8.6 percent over the period 1958–1978,” stating that “the results are consistent with the concept of enhanced activity due to increased levels of CO₂” (1981: 9842). Two years later, Cleveland *et al.* (1983) confirmed this finding with additional data from Mauna Loa and a companion record from the South Pole, stating: “we believe it most likely that the CO₂ seasonal behaviour reflects an increase in either the seasonally varying biomass or in global photosynthetic activity resulting from the increasing concentration of atmospheric carbon dioxide” (1983: 10,945). Two years later, Keeling *et al.* (1985) confirmed the earlier results for Ocean Weather Station P, stating that the increase in the amplitude of its annual CO₂ cycle “reflects an increase in activity of terrestrial plants” (1985: 10,522). Contemporaneously, after two more years of data were obtained from Mauna Loa, Bacastow *et al.* (1985) reported that the increase in the seasonal amplitude since 1958 was “approximately 1 ppm, a sizeable fraction of the average amplitude of 6 ppm,” adding that “it seems likely that the increase mainly reflects en-

hanced metabolic activity of the land biota” and that “one obvious factor that might produce this enhancement is the CO₂ concentration itself” (1985: 10,529).

Reaffirmations of the reality of this CO₂-induced phenomenon continue to appear as more and more data are collected and analyzed. Keeling (1994), for example, observed that the amplitude of the seasonal CO₂ cycle increased by as much as 20 percent at high latitudes in both hemispheres between 1988 and 1993, noting that “a preliminary investigation suggests that an increase in the net primary production of plants . . . caused the amplitude increase” (1994: 110). Fourteen months later, Keeling *et al.* (1995) reported that the amplitude of the seasonal CO₂ cycle at Mauna Loa had also risen significantly over this time period, while Okamoto *et al.* (1995), after analyzing seasonal CO₂ amplitude trends at 17 stations stretching from the south pole to Alaska, concluded that “CO₂ fertilization exists on the global scale” (1995: 206).

Shortly thereafter, Keeling *et al.* (1996), working with an ever-expanding data base, reported that the annual amplitude of the seasonal CO₂ cycle had increased by fully 20 percent in the latitudinal vicinity of Hawaii and by 40 percent in the Arctic since the early 1960s, noting that “the amplitude increases reflect increasing assimilation of CO₂ by land plants” (1996: 146). They also observed shifts in the time of occurrence of different portions of the seasonal CO₂ cycle, which suggested that the vegetative growing season had lengthened by about a week during the latter part of the same time period. Then, in an analysis of reflectance data obtained from satellites deployed to monitor various processes on the earth’s surface, Myneni *et al.* (1997) found that terrestrial vegetation between 45°N and 70°N latitudes had grown steadily more productive from 1981 to 1991 and that, simultaneously, the region’s active growing season had lengthened by approximately 12 days, a development that Fung has called “the first direct observation of the biosphere that photosynthesis has increased on such a broad scale for such a long time” (1997: 659).

Productivity of plants and biodiversity in the earth’s ecosystems

The evidence for an ongoing CO₂-induced rejuvenation of the biosphere that has been reviewed in the preceding pages is irrefutable: the totality of earth’s plant life is growing ever more

vigorously as we flood the air with ever more carbon dioxide. This development is fortunate indeed, for many of man's activities have consequences that are not nearly so benevolent and that truly do degrade earth's ecosystems, leading to massive reductions in biodiversity (Pimm *et al.* 1995; Vitousek *et al.* 1997). This one beneficent side-effect of our industrial activities, however, tends to mitigate the adverse consequences of many facets of industrialization. In some cases, the increase in the concentration of atmospheric CO₂ more than compensates: it has clearly resulted in a net increase in the planet's vegetative biomass over the past several decades, as is readily evident from long-term measurements of the air's CO₂ concentration and contemporary measurements of the planet's surface reflectance. Even measurements of atmospheric oxygen support this scenario (Keeling and Shertz 1992; Bender *et al.* 1996; Keeling *et al.* 1996) for, as Bender (1996) has noted, they suggest "the existence of a large oxygen source, which can only be from photosynthesis associated with the net growth of the land biosphere" (1996: 195).

This CO₂-induced increase in vegetative productivity may well be one of the best allies we will ever have in our battle to preserve the planet's biodiversity; in a landmark study of the vascular plant components of 94 terrestrial ecosystems from every continent of the globe except Antarctica, it was found that biodiversity in an ecosystem is more positively correlated with its productivity than it is with anything else (Scheiner and Rey-Benayas 1994). What is more, a major review of interactions between plants and animals in 51 terrestrial ecosystems found that the biomass of plant-eating animals or herbivores was also an increasing function of above-ground primary production (McNaughton *et al.* 1989). A review of 22 aquatic ecosystems found that the herbivore biomass of watery habitats increased in response to a rise in underwater vegetative productivity (Cyr and Pace 1993) and a number of experiments have demonstrated that the growth of aquatic plants is also enhanced as the air's CO₂ content rises (Titus *et al.* 1990; Raven 1991, 1993; Sand-Jensen *et al.* 1992; Titus 1992; Madsen 1993; Riebesell *et al.* 1993; Madsen and Sand-Jensen 1994; Hein and Sand-Jensen 1997; Shapiro 1997). Consequently, it is abundantly clear that earth's animal life—both terrestrial and aquatic—will respond to rising levels of atmospheric CO₂ with increases

in population that will parallel the increases in the plant kingdom, for “the greater the food base, the greater the superstructure of life that can be supported” (Idso 1995a: 13). Greater populations of individual organisms are clearly required for greater biodiversity, as all species must maintain a certain “critical biomass” to sustain their identities and ensure their long-term viability.

Conclusions

An increase in the concentration of atmospheric CO₂ significantly stimulates the growth and development of plants while dramatically enhancing their efficient use of water. These desirable manifestations of carbon dioxide’s aerial fertilization effect are rooted in fundamental properties of plants that express themselves almost universally, even in the face of significant resource deficiencies and environmental stresses. Consequently, as the carbon dioxide content of the atmosphere has risen because of the large-scale utilization of fossil fuels, so too has the productivity of the planet’s vegetation risen because of the magnitude of mankind’s CO₂ emissions.

The striking consequences of this mutually beneficial phenomenon are evident in numerous tree-ring records, historical trends in global forest productivity, and the increasing amplitude of the atmosphere’s seasonal CO₂ cycle. Indeed, the ongoing rise in the air’s CO₂ content is enhancing agricultural productivity the world over (Wittwer 1995) at the same time as it helps to sustain the biodiversity of the planet’s natural ecosystems. Thus, Wittwer has written truly of this exceptional consequence of humanity’s industrial activity that, “the rising level of atmospheric CO₂ is a universally free premium, gaining in magnitude with time, on which we can all reckon for the future” (1997: 13).

References

- Abrams, M.D., and D.A. Orwig (1995). Structure, radial growth dynamics and recent climatic variations of a 320-year-old *Pinus rigida* rock outcrop community. *Oecologia* 101: 353–360.

- Amthor, J.S. (1995). Terrestrial higher-plant response to increasing atmospheric $[\text{CO}_2]$ in relation to the global carbon cycle. *Global Change Biol* 1: 243–274.
- Arp, W.J. (1991). Effects of source-sink relations on photosynthetic acclimation to elevated CO_2 . *Plant Cell Environ* 14: 869–75.
- Arp, W.J., and B.G. Drake (1991). Increased photosynthetic capacity of *Scirpus olneyi* after 4 years of exposure to elevated CO_2 . *Plant Cell Environ* 14: 1003–06.
- Babenko, Y.S., G.I. Tyrugina, E.F. Origoreev, L.M. Dalgikh, and T.I. Borisova (1985). Biological activity and physiological biochemical properties of phosphate dissolving bacteria. *Microbiol* 53: 427–33.
- Bacastow, R.B., C.D. Keeling, and T.P. Whorf (1985). Seasonal amplitude increase in atmospheric CO_2 concentration at Mauna Loa, Hawaii, 1959–1982. *J Geophys Res* 90: 10,529–40.
- Barton, C.V.M., H.S.J. Lee, and P.J. Jarvis (1993). A branch bag and CO_2 control system for long-term CO_2 enrichment of mature Sitka spruce (*Picea sitchensis* (Bong. Carr.)). *Plant Cell Environ* 16: 1139–48.
- Batjes, N.H., and W.G. Sombroek (1997). Possibilities for carbon sequestration in tropical and subtropical soils. *Global Change Biol* 3: 161–73.
- Bazzaz, F.A., and E.D. Fajer (1992). Plant life in a CO_2 -rich world. *Sci Amer* (Jan): 68–74.
- Becker, M. (1989). The role of climate on present and past vitality of silver fir forests in the Vosges mountains of northeastern France. *Can J For Res* 19: 1110–17.
- Bender, M. (1996). A quickening on the uptake? *Nature* 381: 195–96.
- Bender, M., T. Ellis, P. Tans, R. Francey, and D. Lowe (1996). Variability in the O_2/N_2 ratio of southern hemispheric air, 1991–1994: implications for the carbon cycle. *Global Biogeochem Cycles* 10: 9–21.
- Berry, J., and O. Bjorkman (1980). Photosynthetic response and adaptation to temperature in higher plants. *Ann Rev Plant Physiol* 31: 491–543.
- Bjorkdahl, G., and H. Eriksson (1989). Effects of forest decline on increment in Norway spruce (*Picea abies* (L.) Karst) in southern Sweden. In K. Bjor and B. Halvorsen (eds), Air pollution as stress factor in Nordic forests. *Medd Norsk Inst Skogforsk* 42: 19–36.
- Bjorkman O., M. Badger, and P.A. Armond (1978). Thermal acclimation of photosynthesis: Effect of growth temperature on photosynthetic characteristics and components of the photosynthetic apparatus in *Nerium oleander*. *Carnegie Inst Wash Yearbook* 77: 262–76.
- Bowes, G. (1993). Facing the inevitable: Plants and increasing atmospheric CO_2 . *Ann Rev Plant Physiol Plant Mol Biol* 44: 309–32.
- Boyle, J.R., and G.K. Voigt (1973). Biological weathering of silicate minerals: implications for tree nutrition and soil genesis. *Plant Soil* 38: 191–201.

- Boyle, J.R., G.K. Voigt, and B.L. Sawhney (1974). Chemical weathering of biotite by organic acids. *Soil Sci* 117: 42–45.
- Burk, D. (1961). On the use of carbonic anhydrase in carbonate and amine buffers for CO₂ exchange in manometric vessels, atomic submarines, and industrial CO₂ scrubbers. *Ann New York Acad Sci* 92: 372–400.
- Busing, R.T. (1989). A half century of change in a Great Smokey Mountain cove forest. *Bull Torrey Bot Club* 116: 282–88.
- Campbell, W.J., L.H. Allen Jr., and G. Bowes (1988). Effects of CO₂ concentration on rubisco activity, amount, and photosynthesis in soybean leaves. *Plant Physiol* 88: 1310–16.
- Caporn, S.J.M., D.W. Hand, T.A. Mansfield, and A.R. Wellburn (1994). Canopy photosynthesis of CO₂-enriched lettuce (*Lactuca sativa* L.). Response to short-term changes in CO₂, temperature and oxides of nitrogen. *New Phytol* 126: 45–52.
- Ceulemans, R., and M. Mousseau (1994). Effects of elevated atmospheric CO₂ on woody plants. *New Phytol* 127: 425–46.
- Chen, D.-X., M.B. Coughenour, A.K. Knapp, C.E. Owensby (1994). Mathematical simulation of C₄ grass photosynthesis in ambient and elevated CO₂. *Ecol Modelling* 73: 63–80.
- Chen, J.J., and J.M. Sung (1990). Gas exchange rate and yield responses of Virginia-type peanut to carbon dioxide enrichment. *Crop Sci* 30: 1085–89.
- Cizkova-Koncalova, H., J. Kvet, and K. Thompson (1992). Carbon starvation: a key to reed decline in eutrophic lakes. *Aquatic Bot* 43: 105–13.
- Clarkson, D.T. (1985). Factors affecting mineral nutrient acquisition by plants. *Ann Rev Plant Physiol* 36: 77–115.
- Clement, C.R., M.J. Hopper, L.H.P. Jones, and E.L. Leafe (1978). The uptake of nitrate by *Lolium perenne* from flowering nutrient solution. II. Effect of light, defoliation, and relationship to CO₂ flux. *J Exp Bot* 29: 1173–83.
- Cleveland, W.S., A.E. Frenny, and T.E. Graedel (1983). The seasonal component of atmospheric CO₂: information from new approaches to the decomposition of seasonal time-series. *J Geophys Res* 88: 10,934–40.
- Conroy, J. (1989). Influence of high CO₂ on *Pinus radiata*. PhD thesis, Macquarie University, Australia.
- Cure, J.D., and B. Acock (1986). Crop responses to carbon dioxide doubling: a literature survey. *Agric For Meteorol* 8: 127–45.
- Curtis, P.S., L.M. Balduman, B.G. Drake, and D.F. Whigham (1990). Elevated atmospheric CO₂ effects on below ground processes in C₃ and C₄ estuarine marsh communities. *Ecology* 71: 2001–06.
- Curtis, P.S., D.R. Zak, K.S. Pregitzer, and J.A. Terri (1994). Above- and below-ground response of *Populus grandidentata* to elevated atmospheric CO₂ and soil N availability. *Plant Soil* 165: 45–51.

- Cyr, H., and M.L. Pace (1993). Magnitude and patterns of herbivory in aquatic and terrestrial ecosystems. *361*: 148–50.
- Davis, M.B. (1989). Lags in vegetation response to greenhouse warming. *Climatic Change* 15: 75–82.
- De Jong, T.M., B.G. Drake, and R.W. Pearcy (1982). Gas exchange responses of Chesapeake Bay tidal marsh species under field and laboratory conditions. *Oecologia* 52: 5–11.
- Delucia, E.H., T.W. Sasek, and B.R. Strain (1985). Photosynthetic inhibition after long-term exposure to elevated levels of atmospheric carbon dioxide. *Photosyn Res* 7: 175–84.
- Dobson, A. (1992). Withering heats: global warming will exact heavy toll on earth's biodiversity. *Nat Hist* 101, 9: 2–8.
- Drake, B.G. (1989). Photosynthesis of salt marsh species. *Aquatic Bot* 34: 167–80.
- (1992a). The impact of rising CO₂ on ecosystem production. *Water Air Soil Poll* 64: 25–44.
- (1992b). Global warming: the positive impact of rising carbon dioxide levels. *Eco-Logic* 1, 3: 20–22.
- (1992c). A field study of the effects of elevated CO₂ on ecosystem processes in a Chesapeake Bay wetland. *Aust J Bot* 40: 579–95.
- Drake B.G., and P.W. Leadley (1991). Canopy photosynthesis of crops and native plant communities exposed to long-term elevated CO₂. *Plant Cell Environ* 14: 853–60.
- Dufrene, E., J.-Y. Pontalier, and B. Saugier (1993). A branch bag technique for simultaneous CO₂ enrichment and assimilation measurements on beech (*Fagus sylvatica* L.). *Plant Cell Environ* 16: 1131–38.
- Dugas, W.A., and P.J. Pinter, Jr. (1994). The free-air carbon dioxide enrichment (FACE) cotton project: a new field approach to assess the biological consequences of global change. *Agric For Meteorol* 70: 1–342.
- Dyer, J.M. (1995). Assessment of climatic warming using a model of forest species migration. *Ecol Modelling* 79: 199–219.
- Edwards, C.A. (1988). Earthworms and agriculture. *Agron Abstr* 80: 274.
- (1997). *Earthworm Ecology*. Boca Raton, FL: St. Lucie Press.
- Eichkorn, T. (1986). Wachstumanalysen an Fichten in Sudwestdeutschland. *Allg Forst Jagdztg* 157: 125–39.
- Falkengren-Grerup, U., and H. Eriksson (1990). Changes in soil, vegetation and forest yield between 1947 and 1988 in beech and oak sites of southern Sweden. *For Ecol Manage* 38: 37–53.
- Field, C.B. (1994). Arctic chill for CO₂ uptake. *Nature* 371: 472–73.
- Fiscus, E.L., C.D. Reid, J.E. Miller, and A.S. Heagle (1997). Elevated CO₂ reduces O₃ flux and O₃-induced yield losses in soybeans: possible implications for elevated CO₂ studies. *J Exp Bot* 48: 307–13.

- Faria, T., D. Wilkins, R.T. Besford, M. Vaz, J.S. Pereira, and M.M. Chaves (1996). Growth at elevated CO₂ leads to down-regulation of photosynthesis and altered response to high temperature in *Quercus suber* L. seedlings. *J Exp Bot* 47: 1755–61.
- Finn, G.A., and W.A. Brun (1982). Effect of atmospheric CO₂ enrichment on growth, nonstructural carbohydrate content, and root nodule activity in soybean. *Plant Physiol* 69: 327–31.
- Fogel, R. (1983). Root turnover and productivity of forests. *Plant Soil* 71: 75–85.
- Fung, I. (1997). A greener north. *Nature* 386: 659–60.
- Gear, A.J., and B. Huntley (1991). Rapid changes in the range limits of Scots pine 4000 years ago. *Science* 251: 544–47.
- Gebauer, R.L.E., J.F. Reynolds, B.R. Strain (1996). Allometric relations and growth in *Pinus taeda*: the effect of elevated CO₂ and changing N availability. *New Phytol* 134: 85–93.
- Gifford, R.M. (1992). Interaction of carbon dioxide with growth-limiting environmental factors in vegetative productivity: implications for the global carbon cycle. *Adv Bioclim* 1: 24–58.
- Glatzel, G., M. Kazda, D. Grill, G. Halbwachs, and K. Katzensteiner (1987). Ernährungsstörungen bei Fichte als Komplexwirkung von Nadelschaden und erhöhter Stickstoffdeposition—ein Wirkungsmechanismus des Waldsterbens? *Allg Forst Jagdztg* 158: 91–97.
- Goodfellow, J., D. Eamus, and G. Duff (1997). Diurnal and seasonal changes in the impact of CO₂ enrichment on assimilation, stomatal conductance and growth in a long-term study of *Mangifera indica* in the wet-dry tropics of Australia. *Tree Physiol* 17: 291–99.
- Gore, A. (1992). *Earth in the balance: ecology and the human spirit*. Boston: Houghton Mifflin.
- Graham, R.C., H.B. Wood, and M.A. Lueking (1988). Soil morphologic development in a 40-year-old chaparral biosequence. *Agron Abstr* 80: 258.
- Graumlich, L.J., L.B. Brubaker, and C.C. Grier (1989). Long-term trends in forest net primary productivity: Cascade Mountains, Washington. *Ecology* 70: 405–10.
- Graybill, D.A. (1987). A network of high elevation conifers in the western US for detection of tree-ring growth response to increasing atmospheric carbon dioxide. In G.C. Jacoby Jr., and J. W. Hornbeck (eds), *Proceedings of the international symposium on ecological aspects of tree-ring analysis* (Washington, DC: US Dept. of Energy): 463–74.
- Graybill, D.A., and S.B. Idso (1993). Detecting the aerial fertilization effect of atmospheric CO₂ enrichment in tree-ring chronologies. *Global Biogeochem Cycles* 7: 81–95.
- Grulke, N.E., G.H. Riechers, W.C. Oechel, U. Hjelm, and C. Jaeger (1990). Carbon balance in tussock tundra under ambient and elevated atmospheric CO₂. *Oecologia* 83: 485–94.

- Gunderson, C.A., R.J. Norby, and S.D. Wullschleger (1993). Foliar gas exchange responses of two deciduous hardwoods during three years of growth in elevated CO₂: no loss of photosynthetic enhancement. *Plant Cell Environ* 16: 797–807.
- Gunderson, C.A., and S.D. Wullschleger (1994). Photosynthetic acclimation in trees to rising atmospheric CO₂: a broader perspective. *Photosyn Res* 39: 369–88.
- Hardy, R.W.F., and U.D. Havelka (1973). Symbiotic N₂ fixation: multi-fold enhancement by CO₂-enrichment of field-grown soybeans. *Plant Physiol Supplement* 48: 35.
- (1975). Photosynthate as a major factor limiting nitrogen fixation by field-grown legumes with emphasis on soybeans. In P.S. Nutman (ed), *Symbiotic Nitrogen Fixation in Plants* (Cambridge: Cambridge University Press: 421–39.
- Hardy, R.W.F., U.D. Havelka, and B. Quebedeaux (1976). Opportunities for improved seed yield and protein production: N₂ fixation, CO₂ fixation, and O₂ control of reproductive growth. In National Research Council (eds), *Genetic Improvement of Seed Protein* (Washington, DC: National Academy Press): 196–228.
- (1978). The opportunity for and significance of alteration of ribulose 1,5-bisphosphate carboxylase activities in crop production. In H.W. Siegelman and G. Hind (eds), *Photosynthetic Carbon Assimilation* (New York: Plenum): 165–78.
- Hari, P., and H. Arovaara (1988). Detecting CO₂ induced enhancement in the radial increment of trees. Evidence from the northern timberline. *Scand J For Res* 3: 67–74.
- Hari, P., H. Arovaara, T. Raunemaa, and A. Hautajarvi (1984). Forest growth and the effects of energy production: a method for detecting trends in the growth potential of trees. *Can J For Res* 14: 437–40.
- Harley, P.C., J.D. Tenhunen, O.L. Lange (1986). Use of an analytical model to study the limitations on net photosynthesis in *Arbutus unedo* under field conditions. *Oecologia* 70: 393–401.
- Havelka, U.D., R.W.F. Hardy (1976). Legume N₂ fixation as a problem in carbon nutrition. In W.E. Newton and C.J. Nyman (eds), *Proceedings of the 1st Symposium on Nitrogen Fixation, Vol. 2.* (Pullman, WA: Washington State University Press): 456–75.
- Hein, M., and S. Sand-Jensen (1997). CO₂ increases oceanic primary production. *Nature* 388: 526–27.
- Hendrey, G.R., K.F. Lewin, and J. Nagy (1993). Free air carbon dioxide enrichment: Development, progress, results. *Vegetatio* 104/105: 17–31.
- Henning, F.P., C.W. Wood, H.H. Rogers, G.B. Runion, and S.A. Prior (1996). Composition and decomposition of soybean and sorghum tissues grown under elevated atmospheric carbon dioxide. *J Environ Qual* 25: 822–27.

- Hogan, K.P., A.P. Smith, L.H. Ziska (1991). Potential effects of elevated CO₂ and changes in temperature on tropical plants. *Plant Cell Environ* 14: 763–78.
- Hornbeck, J.W. (1987). Growth patterns of red oak and red and sugar maple relative to atmospheric decomposition. In *Proceedings of the 16th Central Hardwood Forest Conference* (Knoxville, TN: University of Tennessee): 277–82.
- Hornbeck, J.W., R.B. Smith, and C.A. Federer (1988). Growth trends in 10 species of trees in New England, 1950–1980. *Can J For Res* 18: 1337–40.
- Hungate, B.A., E.A. Holland, R.B. Jackson, F.S. Chapin III, H.A. Mooney, and C.B. Field (1997). The fate of carbon in grasslands under carbon dioxide enrichment. *Nature* 388: 576–79.
- Intergovernmental Panel on Climate Change (IPCC) (1990). *Climate Change: The IPCC Scientific Assessment*. Report prepared for IPCC by Working Group I. John T. Houghton *et al.* (eds). Cambridge: Cambridge University Press.
- Intergovernmental Panel on Climate Change, Working Group I (IPCC I) (1996). *Climate Change 1995: The Science of Climate Change*. Contribution of Working Group I to the Second Assessment Report of the Intergovernmental Panel on Climate Change. John T. Houghton *et al.* (eds). Cambridge: Cambridge University Press.
- Idso, K.E. (1992a). *Plant responses to rising levels of atmospheric carbon dioxide: A compilation and analysis of the results of a decade of international research into the direct biological effects of atmospheric CO₂ enrichment*. Tempe, AZ: Office of Climatology, Arizona State University.
- (1995a). Rising CO₂: a breath of new life for the biosphere. *World Climate Rev* 3(3): 8–15.
- Idso, K.E., and S.B. Idso (1994). Plant responses to atmospheric CO₂ enrichment in the face of environmental constraints: A review of the past 10 years' research. *Agric For Meteorol* 69: 153–203.
- Idso, S.B. (1989a). *Carbon Dioxide: Friend or Foe?* Tempe, AZ: IBR Press.
- (1989b). Carbon dioxide, soil moisture, and future crop production. *Soil Sci* 147: 305–07.
- (1991a). Cooling the global greenhouse? *The World and I* 6, 3: 276–83.
- (1991b). Carbon dioxide and the fate of Earth. *Global Environ Change* 1: 178–82.
- (1992b). Carbon dioxide and global change: end of nature or rebirth of the biosphere? In J.H. Lehr (ed), *Rational Readings on Environmental Concerns* (New York: Van Nostrand Reinhold): 414–33.
- (1995b). *CO₂ and the Biosphere: The Incredible Legacy of the Industrial Revolution*. St. Paul, MN: Department of Soil, Water and Climate, University of Minnesota.

- (1997). The poor man's biosphere, including simple techniques for conducting CO₂ enrichment and depletion experiments on aquatic and terrestrial plants. *Environ Exp Bot*: in press
- Idso, S.B., S.G. Allen, M.G. Anderson, and B.A. Kimball (1989). Atmospheric CO₂ enrichment enhances survival of *Azolla* at high temperatures. *Environ Exp Bot* 29: 337–41.
- Idso, S.B., K.E. Idso, R.L. Garcia, B.A. Kimball, and J.K. Hooper (1995). Effects of atmospheric CO₂ enrichment and foliar methanol application on net photosynthesis of sour orange tree (*Citrus aurantium*; Rutacea) leaves. *Amer J Bot* 82: 26–30.
- Idso, S.B., and B.A. Kimball (1991a). Effects of two and a half years of atmospheric CO₂ enrichment on the root density distribution of three-year-old sour orange trees. *Agric For Meteorol* 55: 345–49.
- (1991b). Downward regulation of photosynthesis and growth at high CO₂ levels: no evidence for either phenomenon in three-year study of sour orange trees. *Plant Physiol* 96: 990–92.
- (1992b). Seasonal fine-root biomass development of sour orange trees grown in atmospheres of ambient and elevated CO₂ concentration. *Plant Cell Environ* 15: 337–41.
- (1997). Effects of long-term atmospheric CO₂ enrichment on the growth and fruit production of sour orange trees. *Global Change Biol* 3: 89–96.
- Idso, S.B., B.A. Kimball, and S.G. Allen (1991). CO₂ enrichment of sour orange trees: two-and-a-half years into a long-term experiment. *Plant Cell Environ* 14: 351–53.
- Idso, S.B., B.A. Kimball, and J.R. Mauney (1988). Effects of atmospheric CO₂ enrichment on root:shoot ratios of carrot, radish, cotton and soybean. *Agric Ecosys Environ* 22: 293–99.
- Idso, S.B., and J.A. Quinn (1983). *Vegetational Redistribution in Arizona and New Mexico in Response to a Doubling of the Atmospheric CO₂ Concentration*. Tempe, AZ: Climatology Laboratory, Arizona State University.
- Ineichen, K., V. Wiemken, and A. Wiemken (1995). Shoots, roots, and ectomycorrhiza of pine seedlings at elevated atmospheric carbon dioxide. *Plant Cell Environ* 18: 703–07.
- Innes, J.L., and E.R. Cook (1989). Tree-ring analysis as an aid to evaluating the effects of pollution on tree growth. *Can J For Res* 19: 1174–89.
- Jackson, W.A., R.J. Volk, and D.W. Israel (1980). Energy supply and nitrate assimilation in root systems. In A. Tanaka (ed), *Carbon-nitrogen Interaction in Crop Production* (Tokyo: Japanese Society for Promotion of Science): 25–40.
- Jacob, J., C. Greitner, and B.G. Drake (1995). Acclimation of photosynthesis in relation to Rubisco and non-structural carbohydrate contents and *in situ* carboxylase activity in *Scirpus olneyi* grown at elevated CO₂ in the field. *Plant Cell Environ* 18: 875–84.

- Jacoby, G.C. (1986). Long-term temperature trends and a positive departure from the climate-growth response since the 1950s in high elevation lodgepole pine from California. In C. Rosenzweig and R. Dickinson (eds), *Proceedings of the NASA Conference on Climate-Vegetation Interactions* (Boulder, CO: University Corporation for Atmospheric Research): 81–83.
- Johnson, D.L. (1988). Biomantle evolution and the redistribution of earth materials and artifacts. *Agron Abstr* 80: 259.
- Johnson, H.B., H.W. Polley, and H.S. Mayeux (1993). Increasing CO₂ and plant-plant interactions: effects on natural vegetation. *Vegetatio* 104/105: 157–70.
- Johnston, M.C. (1963). Past and present grasslands of southern Texas and northeastern Mexico. *Ecology* 44: 456–66.
- Jones, M.B., J.C. Brown, A. Raschi, and F. Miglietta (1995). The effects on *Arbutus unedo* L. of long-term exposure to elevated CO₂. *Global Change Biol* 1: 295–302.
- Jongen, M., M.B. Jones, T. Hebeisen, H. Blum, and G. Hendrey (1995). The effects of elevated CO₂ concentrations on the root growth of *Lolium perenne* and *Trifolium repens* grown in a FACE system. *Global Change Biol* 1: 361–71.
- Jozsa, L.A., and J. M. Powell (1987). Some climatic aspects of biomass productivity of white spruce stem wood. *Can J For Res* 17: 1075–79.
- Jurik, T.W., J.A. Weber, and D.M. Gates (1984). Short-term effects of CO₂ on gas exchange of leaves of bigtooth aspen (*Populus grandidentata*) in the field. *Plant Physiol* 75: 1022–26.
- Kapulnik, Y., R. Gafny, and Y. Okon (1983). Effect of *Azospirillum* spp. inoculation development and NO₃⁻ uptake in wheat (*Triticum aestivum* cv. Miriam) in hydroponic system. *Can J Bot* 63: 627–31.
- Kauppi, P.E., K. Mielikainen, K. Kuusela (1992). Biomass and carbon budget of European forests, 1971–1990. *Science* 256: 70–74.
- Keeling, C.D. (1994). A study of the abundance and ¹³C/¹²C ratio of atmospheric carbon dioxide and oceanic carbon in relation to the global carbon cycle. In M.R. Riches (ed), *Global Change Research: Summaries of Research in FY 1994*. (Washington, DC: US Department of Energy): 109–10.
- Keeling, C.D., J.F.S. Chin, and T.P. Whorf (1996). Increased activity of northern hemispheric vegetation inferred from atmospheric CO₂ measurements. *Nature* 382: 146–49.
- Keeling, C.D., T.P. Whorf, M. Wahlen, and J. van der Plicht (1995). Interannual extremes in the rate of rise of atmospheric carbon dioxide since 1980. *Nature* 375: 666–70.
- Keeling, C.D., T.P. Whorf, C.S. Wong, R.D. Bellagay (1985). The concentration of carbon dioxide at ocean weather station P from 1969–1981. *J Geophys Res* 90: 10,511–28

- Keeling, R., S.C. Piper, M. Heimann (1996). Global and hemispheric CO₂ sinks deduced from changes in atmospheric O₂ concentration. *Nature* 381: 218–21.
- Keeling, R., and S. Shertz (1992). Seasonal and interannual variations in atmospheric oxygen and implications for the global carbon cycle. *Nature* 358: 723–27.
- Kellomaki, S., and K.-Y. Wang (1996). Photosynthetic responses to needle water potentials in Scots pine after a four-year exposure to elevated CO₂ and temperature. *Tree Physiol* 16: 765–72.
- Kenk, G. (1989). Zuwachsuntersuchungen im Zusammenhang mit den gegenwartigen waldschaden in Baden-Württemberg. In J.B. Bucher and W.I. Bucher (eds), *Air pollution and forest decline* (Brimensdorf, Switzerland: Eidgenossische Anstalt für das forstliche Versuchswesen): 263–69.
- Kenk, G. and H. Fischer (1988). Evidence from nitrogen fertilization in the forests of Germany. *Environ Poll* 54: 199–218.
- Kienast, F., and R.J. Luxmoore (1988). Tree-ring analysis and conifer growth responses to increased atmospheric CO₂ levels. *Oecologia* 76: 487–95.
- Kimball, B.A. (1983a). Carbon dioxide and agricultural yield: an assemblage and analysis of 430 prior observations. *Agron J* 75: 779–88.
- (1983b). *Carbon Dioxide and Agricultural Yield: An Assemblage and Analysis of 770 Prior Observations*. Phoenix, AZ: US Water Conservation Laboratory.
- Kimball, B.A., and S.B. Idso (1983). Increasing atmospheric CO₂: effects on crop yield, water use and climate. *Agric Water Management* 7: 55–72.
- King, A.W., W.M. Post, and S.D. Wullschleger (1997). The potential response of terrestrial carbon storage to changes in climate and atmospheric CO₂. *Climatic Change* 35: 199–227.
- King, J.S., R.B. Thomas, and B.R. Strain (1996). Growth and carbon accumulation in root systems of *Pinus taeda* and *Pinus ponderosa* seedlings as affected by varying CO₂, temperature and nitrogen. *Tree Physiol* 16: 635–42.
- Kirschbaum, M.U.F. (1994). The sensitivity of C₃ photosynthesis to increasing CO₂ concentration: a theoretical analysis of its dependence on temperature and background CO₂ concentration. *Plant Cell Environ* 17: 747–54.
- Koch, G.W., and H.A. Mooney (1996a). *Carbon Dioxide and Terrestrial Ecosystems*. San Diego, CA: Academic Press.
- (1996b). Response of terrestrial ecosystems to elevated CO₂: a synthesis and summary. In Koch and Mooney 1996a: 415–29.
- Kramer, P.J. (1981). Carbon dioxide concentration, photosynthesis and dry matter production. *BioSci* 31: 29–34.

- Kubiske, M.E., and K.S. Pregitzer (1996). Effects of elevated CO₂ and light availability on the photosynthetic light response of trees of contrasting shade tolerance. *Tree Physiol* 16: 351–58.
- Kubiske, M.E., and K.S. Pregitzer (1997). Ecophysiological responses to simulated canopy gaps of two tree species of contrasting shade tolerance in elevated CO₂. *Functional Ecol* 11: 24–32.
- Kubiske, M.E., K.S. Pregitzer, C.J. Mikan, D.R. Zak, J.L. Maziasz, and J.A. Teeri (1997). *Populus tremuloides* photosynthesis and crown architecture in response to elevated CO₂ and soil N availability. *Oecologia* 110: 328–36.
- LaMarche, V.C., Jr., D.A. Graybill, H.C. Fritts, and M.R. Rose (1984). Increasing atmospheric carbon dioxide: tree ring evidence for growth enhancement in natural vegetation. *Science* 223: 1019–21.
- Lamborg, M.R., R.W. Hardy, and E.A. Paul (1983). Microbial effects. In E.R. Lemon (ed). *CO₂ and Plants: The Response of Plants to Rising Levels of Atmospheric Carbon Dioxide* (Boulder, CO: Westview Press): 131–76.
- Lawlor, D.W., R.A.C. Mitchell (1991). The effects of increasing CO₂ on crop photosynthesis and productivity: a review of field studies. *Plant Cell Environ* 14: 807–18.
- Lekkerkerk, L.J.A., J.A. Van Veen, S.C. Van de Geijn (1990). Influence of climatic change on soil quality; consequences of increased atmospheric CO₂-concentration on carbon input and turnover in agro-ecosystems. In J. Goudriaan, H. Van Keulen, and H.H. Van Laar (eds). *The Greenhouse Effect and Primary Productivity in European Agro-ecosystems* (Wageningen, NL: Pudoc): 46–47.
- Lemon, E.R. (1983). *CO₂ and Plants: The Response of Plants to Rising Levels of Atmospheric Carbon Dioxide*. Boulder, CO: Westview Press.
- Lewis, J.D., K.L. Griffin, R.B. Thomas, and B.R. Strain (1994). Phosphorus supply affects the photosynthetic capacity of loblolly pine grown in elevated carbon dioxide. *Tree Physiol* 14: 1229–44.
- Liang, N., and K. Maruyama (1995). Interactive effects of CO₂ enrichment and drought stress on gas exchange and water-use efficiency in *Alnus firma*. *Environ Exp Bot* 35: 353–61.
- Liang, N., K. Maruyama, and Y. Huang (1996). Effects of CO₂ concentration on the photosynthetic and carboxylation efficiencies of *Fagus crenata* and *Quercus crispula*. *Photosynthetica* 32: 355–65.
- Liu, S., and R.O. Teskey (1995). Responses of foliar gas exchange to long-term elevated CO₂ concentrations in mature loblolly pine trees. *Tree Physiol* 15: 351–59.
- Long, S.P. (1991). Modification of the response of photosynthetic productivity to rising temperature by atmospheric CO₂ concentrations: has its importance been underestimated? *Plant Cell Environ* 14: 729–39.

- Long, S.P., B.G. Drake (1991). Effect of the long-term elevation of CO₂ concentration in the field on the quantum yield of photosynthesis of the C₃ sedge, *Scirpus olneyi*. *Plant Physiol* 96: 221–26.
- Lowe, R.H., and H.J. Evans (1962). Carbon dioxide requirement for growth of legume nodule bacteria. *Soil Sci* 94: 351–56.
- Luo, Y., C.B. Field, and H.A. Mooney (1994). Predicting responses of photosynthesis and root fraction to elevated [CO₂]_a: interactions among carbon, nitrogen, and growth. *Plant Cell Environ* 17: 1195–204.
- Luxmoore, R.J., E.G. O'Neill, J.M. Eells, H.H. Rogers (1986). Nutrient-uptake and growth responses of Virginia pine to elevated atmospheric CO₂. *J Environ Qual* 15: 244–51.
- MacDowall, F.D.H. (1983). Effects of light intensity and CO₂ concentration on the kinetics of 1st month growth and nitrogen fixation of alfalfa. *Can J Bot* 61: 731–40.
- Madsen, T.V. (1993). Growth and photosynthetic acclimation by *Ranunculus aquatilis* L. in response to inorganic carbon availability. *New Phytol* 125: 707–15.
- Madsen, T.V., and K. Sand-Jensen (1994). The interactive effects of light and inorganic carbon on aquatic plant growth. *Plant Cell Environ* 17: 955–62.
- Marek, M.V., and J. Kalina (1996). Comparison of two experimental approaches used in the investigations of the long-term effects of elevated CO₂ concentration. *Photosynthetica* 32: 129–33.
- Maruyama, L.K., and Y. Huang (1966). Effects of CO₂ concentration on the photosynthetic and carboxylation efficiencies of *Fagus crenata* and *Quercus crispula*. *Photosynthetica* 32: 355–65.
- Masle, J., G.D. Farquhar, and R.M. Gifford (1990). Growth and carbon economy of wheat seedlings as affected by soil resistance to penetration and ambient partial pressure of CO₂. *Aust J Plant Physiol* 17: 465–87.
- McKee, I.F., J.F. Bullimore, and S.P. Long (1997). Will elevated CO₂ concentrations protect the yield of wheat from O₃ damage? *Plant Cell Environ* 20: 77–84.
- McMurtrie, R.E., H.N. Comins, M.U.F. Kirschbaum, and Y.-P. Wang (1992). Modifying existing forest growth models to take account of effects of elevated CO₂. *Aust J Bot* 40: 657–77.
- McMurtrie, R.E., and Y.-P. Wang (1993). Mathematical models of the photosynthetic response of tree stands to rising CO₂ concentrations and temperatures. *Plant Cell Environ* 16: 1–13.
- McNaughton, S.J., M. Oesterheld, D.A. Frank, and K.J. Williams (1989). Ecosystem-level patterns of primary productivity and herbivory in terrestrial habitats. *Nature* 341: 142–44.
- Micallef, B.J., P.J. Vanderveer, and T.D. Sharkey (1996). Responses to elevated CO₂ of *Flaveria linearis* plants having a reduced activity

- of cytosolic fructose-1,6-bisphosphatase. *Plant Cell Environ* 19: 10–16.
- Molla, M.A.Z., A.A. Chowdhary, and A.H. Islam (1984). Microbial mineralization of organic phosphate in soil. *Plant Soil* 78: 393–99.
- Morison, J.I.L. (1985). Sensitivity of stomata and water use efficiency to high CO₂. *Plant Cell Environ* 8: 467–74.
- Mortensen, L.M. (1987). Review: CO₂ enrichment in greenhouses. Crop responses. *Sci Hort* 33: 1–25.
- Mulholland, B.J., J. Craigon, C.R. Black, J.J. Colls, J. Atherton, and G. Landon (1997). Effects of elevated carbon dioxide and ozone on the growth and yield of spring wheat (*Triticum aestivum* L.) *J Exp Bot* 48: 113–22.
- Murphy, P.M. (1986). Effect of light and atmospheric carbon dioxide concentration on nitrogen fixation by herbage legumes. *Plant Soil* 95: 399–409.
- Myneni, R.B., C.D. Keeling, C.J. Tucker, G. Asrar, and R.R. Nemani (1997). Increased plant growth in the northern high latitudes from 1981 to 1991. *Nature* 386: 698–702.
- Nie, G.Y., S.P. Long, R.L. Garcia, B.A. Kimball, R.L. LaMorte, P.J. Pinter, Jr., G.W. Wall, and A.N. Weber (1995). Effects of free-air CO₂ enrichment on the development of the photosynthetic apparatus in wheat, as indicated by changes in leaf proteins. *Plant Cell Environ* 18: 855–64.
- Nijs, I., I. Impens (1996). Effects of elevated CO₂ concentration and climate-warming on photosynthesis during winter in *Lolium perenne*. *J Exp Bot* 47: 915–24.
- Nilsen, S., K. Hovland, C. Dons, and S.P. Sletten (1983). Effect of CO₂ enrichment on photosynthesis, growth and yield of tomato. *Sci Hort* 20: 1–14.
- Norby, R.J. (1994). Issues and perspectives for investigating root responses to elevated atmospheric carbon dioxide. *Plant Soil* 165: 9–20.
- Norby, R.J. (1997). Inside the black box. *Nature* 388: 522–23.
- Norby, R.J., C.A. Gunderson, S.D. Wullschleger, E.G. O'Neill, and M.K. McCracken (1992). Productivity and compensatory responses of yellow-poplar trees in elevated CO₂. *Nature* 357: 322–24.
- Norby, R.J., and E.G. O'Neill (1991). Leaf area compensation and nutrient interactions in CO₂-enriched seedlings of yellow-poplar (*Liriodendron tulipifera* L.). *New Phytol* 117: 515–28.
- Norby, R.J., E.G. O'Neill, and R.J. Luxmoore (1986). Effects of atmospheric CO₂ enrichment on the growth and mineral nutrition of *Quercus alba* seedlings in nutrient-poor soil. *Plant Physiol* 82: 83–89.
- Oechel, W.C., S. Cowles, N. Grulke, S.J. Hastings, B. Lawrence, T. Prudhomme, G. Riechers, B. Strain, D. Tissue, and G. Vourlitis (1994). Transient nature of CO₂ fertilization in Arctic tundra. *Nature* 371: 500–03.

- Oechel, W.C., and B.R. Strain (1985). Native species responses to increased atmospheric carbon dioxide concentration. In B.R. Strain, and J.D. Cure (eds), *Direct Effects of Increasing Carbon Dioxide on Vegetation* (Washington, DC: US Department of Energy): 117–54.
- Okamoto, K., S. Tanimoto, and K. Okano (1995). Statistical analysis of the increase in atmospheric CO₂ concentrations and its relation to the possible existence of CO₂ fertilization of a global scale. *Tellus* 47B: 206–11.
- Ortuno, A., A. Hermansarz, J. Noguera, V. Morales, and T. Armero (1978). Phosphorus solubilizing effect of *A. niger* and *Pseudomonas fluorescens*. *Microbiol Esp* 30: 113–20.
- Osborne, C.P., B.G. Drake, J. LaRoche, S.P. Long (1997). Does long-term elevation of CO₂ concentration increase photosynthesis in forest floor vegetation? *Plant Physiol* 114: 337–44.
- Overpeck, J.T., P.J. Bartlein, and T. Webb III (1991). Potential magnitude of future vegetation change in eastern North America: comparisons with the past. *Science* 254: 692–95.
- Owensby, C.E., J.M. Ham, A.K. Knapp, C.W. Rice, P.I. Coyne, and L.M. Auen (1996). Ecosystem-level responses of tallgrass prairie to elevated CO₂. In G.W. Koch and H.A. Mooney (eds), *Carbon Dioxide and Terrestrial Ecosystems* (San Diego, CA: Academic Press): 175–93.
- Paine, S. (1988). No escape from the global greenhouse. *New Sci* 1638: 38–43.
- Pallas, J.E. (1965). Transpiration and stomatal opening with changes in carbon dioxide content of the air. *Science* 147: 171–73.
- Parker, M.L. (1987). Recent abnormal increase in tree-ring widths: a possible effect of elevated atmospheric carbon dioxide. In G.C. Jacoby, Jr. and J.W. Hornbeck (eds), *Proceedings of the International Symposium on Ecological Aspects of Tree-ring Analysis* (Washington, DC: US Department of Energy): 511–21.
- Pearcy, R.W., and O. Bjorkman (1983). Physiological effects. In E.R. Lemon (ed), *CO₂ and Plants: The Response of Plants to Rising Levels of Atmospheric Carbon Dioxide* (Boulder, CO: Westview Press): 65–105.
- Pearman, G.I., and P. Hyson (1981). The annual variation of atmospheric CO₂ concentration observed in the northern hemisphere. *J Geophys Res* 86: 9839–43.
- Percival, D.C., J.T.A. Proctor, and M.J. Tsujita (1996). Whole-plant net CO₂ exchange of raspberry as influenced by air and root-zone temperature, CO₂ concentration, irradiation, and humidity. *J Amer Soc Hort Sci* 121: 838–45.
- Peters, R.L., and J.D.S. Darling (1985). The greenhouse effect and nature reserves. *BioSci* 35: 707–17.
- Phillips, D.A., K.D. Newell, S.A. Hassel, and C.E. Felling (1976). The effect of CO₂ enrichment on root nodule development and symbiotic N₂ reduction in *Pisum sativum* L. *Amer J Bot* 63: 356–62.

- Phillips, O.L., and A.H. Gentry (1994). Increasing turnover through time in tropical forests. *Science* 263: 954–58.
- Pimm, S.L., G.J. Russell, J.L. Gittleman, and T.M. Brooks (1995). The future of biodiversity. *Science* 269: 347–50.
- Pimm, S.L., and A.M. Sugden (1994). Tropical diversity and global change. *Science* 263: 933–34.
- Pinter, P.J. Jr., B.A. Kimball, R.L. Garcia, G.W. Wall, D.J. Hunsaker, and R.L. LaMorte (1996). Free-air CO₂ enrichment: responses of cotton and wheat crops. In G.W. Koch, and H.A. Mooney (eds), *Carbon Dioxide and Terrestrial Ecosystems* (San Diego, CA: Academic Press): 215–49.
- Pitelka, L.F., R.H. Gardner, J. Ash, S. Berry, H. Gitay, I.R. Noble, A. Saunders, R.H.W. Bradshaw, L. Brubaker, J.S. Clark, M.B. Davis, S. Sugita, J.M. Dyer, R. Hengeveld, G. Hope, B. Huntley, G.A. King, S. Lavorel, R.N. Mack, G.P. Malanson, M. McGlone, I.C. Prentice, and M. Rejmanek (1997). Plant migration and climate change. *Amer Sci* 85: 464–73.
- Pitman, M. (1977). Ion transport into the xylem. *Ann Rev Plant Physiol* 28: 71–88.
- Polley, H.W., H.B. Johnson, H.S. Mayeux, C.R. Tischler, and D.A. Brown (1996). Carbon dioxide enrichment improves growth, water relations and survival of droughted honey mesquite (*Prosopis glandulosa*) seedlings. *Tree Physiol* 16: 817–23.
- Poorter, H. (1993). Interspecific variation in the growth response of plants to an elevated ambient CO₂ concentration. *Vegetatio* 104/105: 77–97.
- Possingham, H.P. (1993). Impact of elevated atmospheric CO₂ on biodiversity: mechanistic population-dynamic perspective. *Aust J Bot* 41: 11–21.
- Pregitzer, K.S., D.R. Zak, P.S. Curtis, M.E. Kubiske, J.A. Teeri, C.S. Vogel (1995). Atmospheric CO₂, soil nitrogen and turnover of fine roots. *New Phytol* 129: 579–85.
- Pretzsch, H. (1985a). Wachstumsmerkmale suddeutscher Kiefernbestände in den letzten 25 Jahren. *Forschungsbericht der Forstlichen Forschungs-Anstalt Munchen* 65.
- (1985b). Wachstumsmerkmale oberpfälzischer Kiefernbestände in den letzten 30 Jahren. Vitalitätszustand-Strukturverhältnisse-Zuwachsgang. *Allg Forstzeitschr* 42: 1122–26.
- Prior, S.A., H.H. Rogers, G.B. Runion, B.A. Kimball, J.R. Mauney, K.F. Lewin, J. Nagy, and G.R. Hendrey (1995). Free-air carbon dioxide enrichment of cotton: Root morphological characteristics. *J Environ Qual* 24: 678–83.
- Prior, S.A., H.A. Torbert, G.B. Runion, H.H. Rogers, C.W. Wood, B.A. Kimball, R.L. LaMorte, P.J. Pinter, and G.W. Wall (1997). Free-air carbon dioxide enrichment of wheat: soil carbon and nitrogen dynamics. *J Environ Qual* 26: 1161–66.

- Quebedeaux, B., U.D. Havelka, K.L. Livak, R.W.F. Hardy (1975). Effect of altered pO_2 on the aerial part of soybean on symbiotic N_2 fixation. *Plant Physiol* 56: 761–64.
- Radin, J.W., B.A. Kimball, D.L. Hendrix, and J.R. Mauney (1987). Photosynthesis of cotton plants exposed to elevated levels of carbon dioxide in the field. *Photosyn Res* 12: 191–203.
- Raven, J.A. (1991). Physiology of inorganic C acquisition and implications for resource use efficiency by marine phytoplankton: relation to increased CO_2 and temperature. *Plant Cell Environ* 14: 779–94.
- (1993). Phytoplankton: limits on growth rates. *Nature* 361: 209–10.
- Reining, E. (1994). Acclimation of C_3 photosynthesis to elevated CO_2 : hypotheses and experimental evidence. *Photosynthetica* 30: 519–25.
- Riebesell, U., D.A. Wolf-Gladrow, and V. Smetacek (1993). Carbon dioxide limitation of marine phytoplankton growth rates. *Nature* 361: 249–51.
- Robinson, J.M. (1994). Speculations on carbon dioxide starvation, Late Tertiary evolution of stomatal regulation and floristic modernization. *Plant Cell Environ* 17: 345–54.
- Roden, J.S., and M.C. Ball (1996). The effect of elevated $[CO_2]$ on growth and photosynthesis of two eucalyptus species exposed to high temperatures and water deficits. *Plant Physiol* 111: 909–19.
- Rogers, H.H., L.H. Allen, Jr, B.A. Kimball, S.B. Idso, J.E. Miller, S.L. Rawlins, and R.C. Dahlman (1992). Potential impacts of climate change on agricultural production. Testimony before public hearing of the Committee of Enquiry on Protecting the Earth's Environment (17–18 February). Enquete Kommission, Deutcher Bundestag, Bundeshaus, Bonn, D.
- Rogers, H.H., C.M. Peterson, J.N. McCrimmon, and J.D. Cure (1992). Response of plant roots to elevated atmospheric carbon dioxide. *Plant Cell Environ* 15: 749–52.
- Rogers, H.H., G.B. Runion, and S.V. Krupa (1994). Plant responses to atmospheric CO_2 enrichment with emphasis on roots and the rhizosphere. *Environ Poll* 83: 155–89.
- Root, T.L., and S.H. Schneider (1993). Can large-scale climatic models be linked with multiscale ecological studies? *Conserv Biol* 7: 256–70.
- Rowland, A.J., J.T. Baker, L.H. Allen, Jr., and G. Bowes (1996). Interactions of CO_2 enrichment and temperature on carbohydrate accumulation and partitioning in rice. *Environ Exp Bot* 36: 111–24.
- Rudorff, B.F.T., C.L. Mulchi, E. Lee, R. Rowland, and R. Pausch (1996). Photosynthetic characteristics in wheat exposed to elevated O_3 and CO_2 . *Crop Sci* 36: 1247–51.
- Rufty, T.W., Jr., C.T. MacKown, and R.M. Volk (1989). Effects of altered carbohydrate availability on whole-plant assimilation of $^{15}NO_3^-$. *Plant Physiol* 89: 457–63.

- Sage, R.F., T.D. Sharkey, and J.R. Seemann (1989). Acclimation of photosynthesis to elevated CO₂ in five C₃ species. *Plant Physiol* 89: 590–96.
- Scheiner, S.M., and J.M. Rey-Benayas (1994). Global patterns of plant diversity. *Evol Ecol* 8: 331–47.
- Samuelson, L.J., and J.R. Seiler (1992). Fraser fir seedling gas exchange and growth in response to elevated CO₂. *Environ Exp Bot* 32: 351–56.
- Sand-Jensen, K., M.F. Pedersen, and S. Laurentius (1992). Photosynthetic use of inorganic carbon among primary and secondary water plants in streams. *Freshwater Biol* 27: 283–93.
- Scifres, C.J. (1980). *Brush Management: Principles and Practices for Texas and the Southwest*. College Station, TX: Texas A and M University Press.
- Seemann, J.R., J.A. Berry, and J.S. Downton (1984). Photosynthetic response and adaptation to high temperature in desert plants. A comparison of gas exchange and fluorescence methods for studies of thermal tolerance. *Plant Physiol* 75: 364–68.
- Shapiro, J. (1997). The role of carbon dioxide in the initiation and maintenance of blue-green dominance in lakes. *Freshwater Biol* 37: 307–23.
- Sicher, R.C., and J.A. Bunce (1997). Relationship of photosynthetic acclimation to changes of Rubisco activity in field-grown winter wheat and barley during growth in elevated carbon dioxide. *Photosyn Res* 52: 27–38.
- Sicher, R.C., and D.F. Kremer (1994). Responses of *Nicotiana tabacum* to CO₂ enrichment at low-photon flux density. *Physiol Plant* 92: 383–88.
- Simmons, G.L., and P.E. Pope (1987). Influence of soil compaction and vesicular-arbuscular mycorrhizae on root growth of yellow poplar and sweet gum seedlings. *Can J For Res* 17: 970–75.
- (1988). Influence of soil water potential and mycorrhizal colonization on root growth of yellow-poplar and sweet gum seedlings grown in compacted soil. *Can J For Res* 18: 1392–96.
- Sinclair, T.R., C.T. deWit (1975). Photosynthate and nitrogen requirements for seed productivity by various crops. *Science* 189: 565–67.
- Smith, S.E., and D.J. Read (1996). *Mycorrhizal symbiosis*. London: Academic Press.
- Sombroek, W.G. (1995). Aspects of soil organic matter and nutrient cycling in relation to climate change and agricultural sustainability. In International Symposium on Nuclear and Related Techniques in Soil-Plant Studies on Sustainable Agriculture and Environmental Preservation, *Nuclear Techniques in Soil-Plant Studies for Sustainable Agriculture and Environmental Preservation* (Vienna, AT: International Atomic Energy Agency): 15–26.

- Spelsberg, G. (1987). Zum Problem der Beurteilung des Zuwachses in geschädigten Beständen. *Allg Forst Jagdztg* 158: 205–10.
- Spieker, M. (1990). Growth variation and environmental stresses: long-term observations on permanent research plots in south-western Germany. *Water Air Soil Poll* 54: 247–56.
- Stitt, M. (1991). Rising CO₂ levels and their potential significance for carbon flow in photosynthetic cells. *Plant Cell Environ* 14: 741–62.
- Strain, B.R., and J.D. Cure (1994). Direct effects of atmospheric CO₂ enrichment on plants and ecosystems: an updated bibliographic data base. Oak Ridge, TN: Oak Ridge National Laboratory.
- Stuhlfauth, T., and H.P. Fock (1990). Effect of whole season CO₂ enrichment on the cultivation of a medicinal plant, *Digitalis lanata*. *J Agron Crop Sci* 164: 168–73.
- Stulen, I., and J. den Hertog (1993). Root growth and functioning under atmospheric CO₂ enrichment. *Vegetatio* 104/105: 99–115.
- Svedang, M.U. (1992). Carbon dioxide as a factor regulating the growth dynamics of *Juncus bulbosus*. *Aquatic Bot* 42: 231–40.
- Taiz, L., and E. Zeiger (1991). *Plant Physiology*. Redwood City, CA: Benjamin-Cummings.
- Teskey, R.O. (1995). A field study of the effects of elevated CO₂ on carbon assimilation, stomatal conductance and leaf and branch growth of *Pinus taeda* trees. *Plant Cell Environ* 18: 565–73.
- (1997). Combined effects of elevated CO₂ and air temperature on carbon assimilation of *Pinus taeda* trees. *Plant Cell Environ* 20: 373–80.
- Thomas, R.B., and B.R. Strain (1991). Root restriction as a factor in photosynthetic acclimation of cotton seedlings grown in elevated carbon dioxide. *Plant Physiol* 96: 627–34.
- Thornley, J.H.M., and M.G.R. Cannell (1996). Temperate forest responses to carbon dioxide, temperature and nitrogen: a model analysis. *Plant Cell Environ* 19: 1331–48.
- Tingey, D.T., M.G. Johnson, D.L. Phillips, D.W. Johnson, and J.T. Ball (1996). Effects of elevated CO₂ and nitrogen on the synchrony of shoot and root growth in ponderosa pine. *Tree Physiol* 16: 905–14.
- Tinker, P.B. (1984). The role of microorganisms in mediating and facilitating the uptake of plant nutrients from the soil. *Plant Soil* 76: 77–91.
- Tissue, D.T., and W.C. Oechel (1987). Response of *Eriophorum vaginatum* to elevated CO₂ and temperature in the Alaskan tussock tundra. *Ecology* 68: 401–10.
- Titus, J.E. (1992). Submersed macrophyte growth at low pH. II. CO₂ sediment interactions. *Oecologia* 92: 391–98.
- Titus, J.E., R.S. Feldman, and D. Grise (1990). Submersed macrophyte growth at low pH. I. CO₂ enrichment effects with fertile sediment. *Oecologia* 84: 307–313

- Umali-Garcia, M., D.H. Hubbel, M.H. Gaskin, F.B. Dazzo (1980). Association of *Azospirillum* with grass roots. *Appl Environ Microbiol* 39: 219–26.
- Van Oosten, J.-J., and R.T. Besford (1996). Acclimation of photosynthesis to elevated CO₂ through feedback regulation of gene expression: climate of opinion. *Photosyn Res* 48: 353–65.
- Vitousek, P.M., H.A. Mooney, J. Lubchenco, and J.M. Melillo (1997). Human domination of Earth's ecosystems. *Science* 277: 494–99.
- Vogel, C.S., and P.S. Curtis (1995). Leaf gas exchange and nitrogen dynamics of N₂-fixing, field-grown *Alnus glutinosa* under elevated atmospheric CO₂. *Global Change Biol* 1: 55–61.
- Volin, J.C., P.B. Reich (1996). Interaction of elevated CO₂ and O₃ on growth, photosynthesis and respiration of three perennial species grown in low and high nitrogen. *Physiol Plant* 97: 674–84.
- Vu, J.C.V., L.H. Allen Jr., K.J. Boote, and G. Bowes (1997). Effects of elevated CO₂ and temperature on photosynthesis and Rubisco in rice and soybean. *Plant Cell Environ* 20: 68–76.
- Wang, K.-Y. (1996a). Apparent quantum yield in Scots pine after four years of exposure to elevated temperature and CO₂. *Photosynthetica* 32: 339–53.
- (1996b). Canopy CO₂ exchange of Scots pine and its seasonal variation after four-year exposure to elevated CO₂ and temperature. *Agric For Meteorol* 82: 1–27.
- Wang K.-Y., and S. Kellomaki (1997). Effects of elevated CO₂ and soil-nitrogen supply on chlorophyll fluorescence and gas exchange in Scots pine, based on a branch-in-bag experiment. *New Phytol* 136: 277–86.
- Wang, K.-Y., S. Kellomaki, and K. Laitinen (1995). Effects of needle age, long-term temperature and CO₂ treatments on the photosynthesis of Scots pine. *Tree Physiol* 15: 211–18.
- Weaver, P.L., and P.G. Murphy (1990). Forest structure and productivity in Puerto Rico's Luquillo Mountains. *Biotropica* 22: 69–82.
- Webber, A.N., G.-Y. Nie, S.P. Long (1994). Acclimation of photosynthetic proteins to rising atmospheric CO₂. *Photosyn Res* 39: 413–25.
- Weidenbach, P. (1992). Waldbauliche ziele und ergebnisse. *Allg Forstzeitschr* 13: 711–17.
- West, D.C. (1988). Detection of forest response to increased atmospheric carbon dioxide. In F.A. Koormanoff (ed), *Carbon Dioxide and Climate: Summaries of Research in FY 1988* (Washington, DC: US Department of Energy): 57.
- Wittwer SH (1995). *Food, Climate, and Carbon Dioxide: The Global Environment and World Food Production*. Boca Raton, FL: CRC Press/Lewis Publishers.
- (1997). The global environment: it's good for food production. In P.J. Michaels (ed), *State of the Climate Report: Essays on Global Climate Change* (New Hope, VA: New Hope Environmental Services): 8–13.

- Wood, C.W., H.A. Torbert, H.H. Rogers, G.B. Runion, and S.A. Prior (1994). Free-air CO₂ enrichment effects on soil carbon and nitrogen. *Agric For Meteorol* 70: 103–16.
- Woodrow, I.E. (1994). Optimal acclimation of the C₃ photosynthetic system under enhanced CO₂. *Photosyn Res* 39: 401–12.
- Woodwell, G.M. (1989). The warming of the industrialized middle latitudes 1985-2050: causes and consequences. *Climatic Change* 15: 31–50.
- Wullschleger, S.D., R.J. Norby, and C.A. Gunderson (1997). Forest trees and their response to atmospheric CO₂ enrichment: a compilation of results. In L.H. Allen Jr., M.B. Kirkham, D.M. Olszyk, and C.E. Whitman (eds.), *Advances in Carbon Dioxide Effects Research* (Madison, WI: American Society of Agronomy): 79–100.
- Wullschleger, S.D., R.J. Norby, and D.L. Hendrix (1992). Carbon exchange rates, chlorophyll content, and carbohydrate status of two forest tree species exposed to carbon dioxide enrichment. *Tree Physiol* 10: 21–31.
- Wullschleger, S.D., W.M. Post, and A.W. King (1995). On the potential for a CO₂ fertilization effect in forests: estimates of the biotic growth factor based on 58 controlled-exposure studies. In G.M. Woodwell, and F.T. Mackenzie (eds), *Biotic Feedbacks in the Global Climatic System* (Oxford: Oxford University Press): 85–107.
- Zak, D.R., K.S. Pregitzer, P.S. Curtis, J.A. Teeri, R. Fogel, D.L. Randlett (1993). Elevated atmospheric CO₂ and feedback between carbon and nitrogen cycles. *Plant Soil* 151: 105–17.
- Ziska, L.H., B.G. Drake, and S. Chamberlain (1990). Long-term photosynthetic response in single leaves of a C₃ and C₄ salt marsh species grown at elevated atmospheric CO₂ *in situ*. *Oecologia* 83: 469–72.
- Ziska, L.H., R.C. Sicher, and D.F. Kremer (1995). Reversibility of photosynthetic acclimation of swiss chard and sugarbeet grown at elevated concentrations of CO₂. *Physiol Plant* 95: 355–64.