

Agriculture

Key Messages:

- Elevated carbon dioxide increases the productivity and water use efficiency of nearly all plants.
- Higher levels of atmospheric CO₂ ameliorate, and sometimes fully compensate for, the negative influences of various environmental stresses on plant growth, including the stress of high temperature.
- Health promoting substances found in various food crops and medicinal plants have been shown to benefit from rising atmospheric CO₂.
- Elevated CO₂ reduces, and frequently completely overrides, the negative effects of ozone pollution on plant photosynthesis, growth and yield.
- Extreme weather events such as heavy downpours and droughts are not likely to impact future crop yields any more than they do now.
- On the whole, CO₂-enrichment does not increase the competitiveness of weeds over crops; higher atmospheric CO₂ will likely reduce crop damage from insects and pathogenic diseases.
- In addition to enhancing forage productivity, atmospheric CO₂-enrichment will likely not alter its digestibility by animals.

Agricultural productivity and yield have been increasing in the U.S. for many decades. Annual yields of the 19 crops that account for 95 percent of total U.S. food production have increased by an average of 17.4% over the period 1995-2009. Such an increase is good news for those concerned about feeding the evergrowing population of the U.S. and the world.

Food security is one of the most pressing societal issues of our time. It is presently estimated that more than one billion people, or one out of every seven people on the planet, is hungry and/or malnourished. Even more troubling is the fact that thousands die daily as a result of diseases from which they likely would have survived had they received adequate food and nutrition. Yet the problem of feeding the planet's population is presently not one of insufficient food production; for the agriculturalists of the world currently produce more than enough food to feed the globe's entire population. Rather, the problem is one of inadequate distribution, with food insecurity arising simply because the world's supply of food is not evenly dispensed among the human population, due to ineffective world markets¹.

As world population continues to grow, however, so too must our capacity to produce food continue to expand, 2,3,4 and our

Percent change in yield between 1995 and 2009 (as derived from a linear trend through the data) for the 19 crops that account for 95% of all U.S. food production. Annual crop yield data were obtained from the Food and Agricultural Organization of the United Nations, available at http://faostat.fao.org/ site/567/default.aspx#ancor.

Crop	Percent Change
Maize	32.8
Soybeans	17.3
Wheat	13.3
Sugarcane	-2.5
Sugar beet	37.3
Potatoes	22.2
Tomatoes	35.1
Sorghum	5.2
Oranges	-5.8
Seed cotton	31.5
Rice, paddy	26.3
Grapes	0.5
Barley	16.7
Apples	25.6
Lettuce and chicory	8.7
Maize, green	24.4
Onions, dry	28.9
Grapefruit	0.1
Oats	12.4
Average	17.4

ability to fulfill this task has been challenged by claims that rising air temperatures and CO₂ concentrations will adversely impact future agricultural production. The remainder of this chapter evaluates that claim.

The CO2-Temperature-Growth Interaction

The growth-enhancing effects of elevated CO₂ typically increase with rising temperature. This phenomenon is noted in experiments that exposed bigtooth aspen leaves to atmospheric CO₂ concentrations of 325 and 1935 ppm and measured their photosynthetic rates at a number of different temperatures. The figure below reproduces their results and slightly extends the two relationships defined by their data to both warmer and cooler conditions.

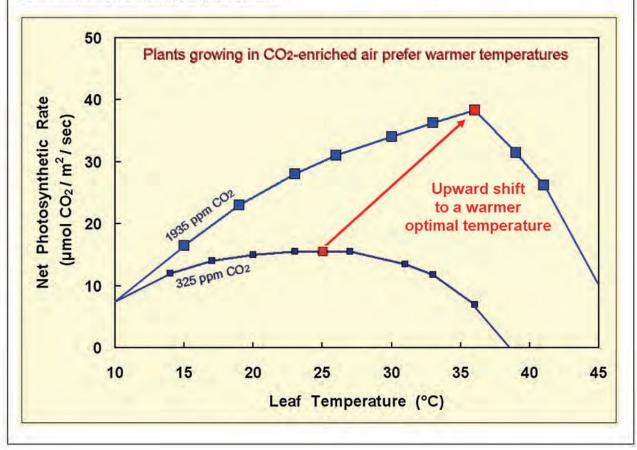
At 10° C, elevated CO_2 has essentially no effect on net photosynthesis in this particular species, as has been demonstrated is characteristic of plants in general. At 25° C, however, where the net photosynthetic rate of the leaves exposed to 325 ppm CO_2 is maximal, the extra CO_2 of this study boosts the net photosynthetic rate of the foliage by nearly 100%; and at 36° C, where the net photosynthetic rate of the leaves exposed to 1935 ppm CO_2 is maximal, the extra CO_2 boosts the net photosynthetic rate of the foliage by a whopping 450%. In addition, it is readily seen that the extra CO_2 increases the optimum temperature for net photosynthesis in this species by about 11°C: from 25° C in air of 325 ppm CO_2 to 36° C in air of 1935 ppm CO_2 .

In viewing the warm-temperature projections of the two relationships, it can also be seen that the transition from positive to negative net photosynthesis - which denotes a change from life-sustaining to life-depleting conditions - likely occurs somewhere in the vicinity of 39°C in air of 325 ppm CO₂ but somewhere in the vicinity of 50°C in air of 1935 ppm CO₂. Hence, not only was the optimum temperature for the growth of bigtooth aspen greatly increased by the extra CO₂ of this experiment, so too was the temperature above which life cannot be sustained increased, and by about the same amount, i.e., 11°C.

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Elevated carbon dioxide increases the productivity and water use efficiency of nearly all plants, providing more food to sustain the biosphere.

At a fundamental level, carbon dioxide is the basis of nearly all life on Earth, as it is the primary raw material or "food" that is utilized by plants to produce the organic matter out



of which they construct their tissues, which subsequently become the ultimate source of food for all animals, including humans. Consequently, the more CO₂ there is in the air, the better plants grow, as has been demonstrated in literally *thousands* of laboratory and field experiments.^{5,6}

Typically, a doubling of the air's CO₂ content above present-day concentrations raises the productivity of most herbaceous plants by about one-third; and this positive response occurs in plants that utilize all three of the major biochemical pathways (C₃, C₄, CAM) of photosynthesis. On average, a 300-ppm increase in atmospheric CO₂ will result in yield increases of 15% for CAM crops, 49% for C₃ cereals, 20% for C₄ cereals, 24% for fruits and melons, 44% for legumes, 48% for roots and tubers and 37% for vegetables.⁸ Thus, with more CO₂ in the air, the growth and productivity of nearly all crops will increase, providing more food to sustain the biosphere.

In addition to increasing photosynthesis and biomass, another major benefit of rising atmospheric CO₂ is the enhancement of plant water use efficiency. Studies have shown that plants exposed to elevated levels of atmospheric CO₂ generally do not open their leaf stomatal pores

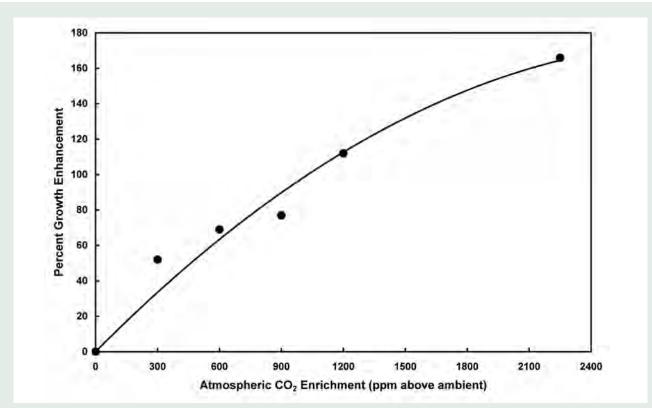


Figure 1. Percent growth enhancement as a function of atmospheric CO₂ enrichment in parts per million (ppm) above the normal or ambient atmospheric CO₂ concentration, showing that the growth benefits continue to accrue well beyond an atmospheric CO₂ concentration of 2000 ppm. These data, representing a wide mix of plant species, were derived from 1,087 individual experiments described in 342 peer-reviewed scientific journal articles written by 484 scientists residing in 28 countries and representing 142 different research institutions.⁷

The Agricultural Debt We Already Owe to Atmospheric CO2 Enrichment

Writing as background for their study, Cunniff et al. (2008) note that "early agriculture was characterized by sets of primary domesticates or 'founder crops' that were adopted in several independent centers of origin," all at about the same time; and they say that "this synchronicity suggests the involvement of a global trigger." As they describe it, the aerial fertilization effect caused by the rise in CO₂ following the deglaciation of the last ice age, combined with its transpiration-reducing effect, led to a large increase in the water use efficiencies of the world's major C₄ founder crops; and they suggest that this development was the global trigger that launched the agricultural enterprise upon which civilizations were built.

As a test of this hypothesis, Cunniff et al. designed "a controlled environment experiment using five modern day representatives of wild C₄ crop progenitors, all 'founder crops' from a variety of independent centers." The five crops employed in their study were Setaria viridis (L.) P. Beauv, Panicum miliaceum var. ruderale (Kitag.), Pennisetum violaceum (Lam.) Rich., Sorghum arundinaceum (Desv.), and Zea mays subsp. parviglumis H.H. Iltis & Doebley. They were grown individually in 6-cm x 6-cm x 6-cm pots filled with a 1:1 mix of washed sand and vermiculite for 40-50 days in growth chambers maintained at atmospheric CO₂ concentrations of 180, 280 and 380 ppm, characteristic of glacial, post-glacial and modern times, respectively.

This work revealed that the "increase in CO₂ from glacial to postglacial levels [180 to 280 ppm] caused a significant gain in vegetative biomass of up to 40%," together with "a reduction in the transpiration rate via decreases in stomatal conductance of ~35%," which led to "a 70% increase in water use efficiency, and a much greater productivity potential in water-limited conditions."

In discussing their results, the five researchers concluded that "these key physiological changes could have greatly enhanced the productivity of wild crop progenitors after deglaciation ... improving the productivity and survival of these wild C_4 crop progenitors in early agricultural systems." And in this regard, they note that "the lowered water requirements of C_4 crop progenitors under increased CO_2 would have been particularly beneficial in the arid climatic regions where these plants were domesticated."

For comparative purposes, the researchers also included one C₃ species in their study — Hordeum spontaneum K. Koch — and they report that it "showed a near-doubling in biomass compared with [the] 40% increase in the C₄ species under growth treatments equivalent to the postglacial CO₂ rise."

In light of these several findings, it can be appreciated that the civilizations of the past, which could not have existed without agriculture, were largely made possible by the increase in the air's CO₂ content that accompanied deglaciation, and that the peoples of the Earth today are likewise indebted to this phenomenon, as well as the additional 100 ppm of CO₂ the atmosphere has subsequently acquired.

With an eye to the future, the ongoing rise in the air's CO₂ content will similarly play a pivotal role in enabling us to grow the food we will need to sustain our still-expanding global population in the year 2050 without usurping all of the planet's remaining freshwater resources and much of its untapped arable land.

Clearly, rising CO₂ has served both us and the rest of the biosphere well in the past; and it will do the same in the future.

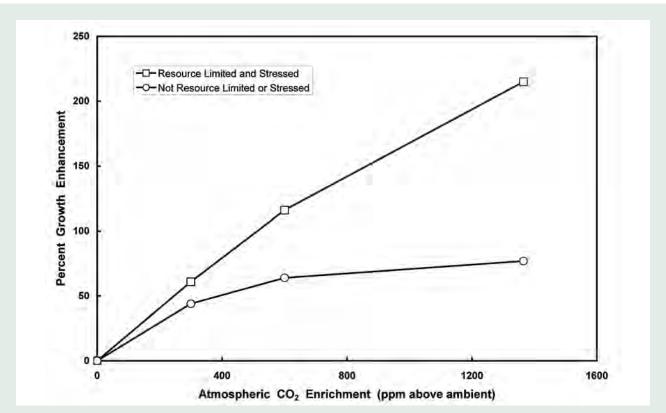
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Cunniff, J., Osborne, C.P., Ripley, B.S., Charles, M. and Jones, G. 2008. Response of wild C₄ crop progenitors to subambient CO₂ highlights a possible role in the origin of agriculture. Global Change Biology 14: 576-587.

(through which they take in carbon dioxide and give off water vapor) as wide as they do at lower CO₂ concentrations. In addition, they sometimes produce less of these pores per unit area of leaf surface. ^{9,10} Both of these changes tend to reduce most plants' rates of water loss by transpiration. As a result, the amount of carbon gained per unit of water lost per unit leaf area —or *water-use efficiency*—increases dramatically as the air's CO₂ content rises; and this phenomenon has been well documented in CO₂ enrichment experiments with agricultural crops. ^{11,12,13,14,15}

Higher levels of atmospheric CO₂ ameliorate, and sometimes fully compensate for, the negative influences of various environmental stresses on plant growth, including the stress of high temperature.

Atmospheric CO₂ enrichment has also been shown to help ameliorate the detrimental effects of several environmental stresses on plant growth and development, including high soil salinity^{16,17,18,19} high air temperature,^{20,21,22,23} low light intensity,^{24,25,26} high light intensity,^{27,28} UV-B radiation,^{29,30,31} water stress,^{32,33,34} and low levels of soil fertility.^{35,36,37,38} Elevated levels of CO₂ have additionally been demonstrated to reduce the severity of low temperature stress,³⁹ oxidative stress,^{40,41,42,43} and the stress of her-



Percent growth enhancement as a function of atmospheric CO2 enrichment in parts per million (ppm) above the normal or ambient atmospheric CO2 concentration for plants growing under stressful and resource-limited conditions and for similar plants growing under ideal conditions. Each line is the mean result obtained from 298 separate experiments.⁴⁷

bivory. 44,45,46 In fact, the percentage growth enhancement produced by an increase in the air's CO₂ concentration is generally even *greater* under stressful and resource-limited conditions than it is when growing conditions are ideal.

Among the list of environmental stresses with the potential to negatively impact agriculture, the one that elicits the most frequent concern is high air temperature. In this regard, there is a commonly-held belief that temperatures may rise so high as to significantly reduce crop yields, thereby diminishing our capacity to produce food, feed, and fuel products. It has also been suggested that warmer temperatures may cause a northward shift in the types of crops grown by latitude that could have additional adverse impacts on agricultural production. However, frequently left out of the debate on this topic is the fact that the growth-enhancing effects of elevated CO₂ typically increase with

rising temperature. For example, a 300-ppm increase in the air's CO_2 content in 42 experiments has been shown to raise the mean CO_2 -induced growth enhancement from a value of zero at 10° C to a value of 100% at 38° C.⁴⁸

This increase in CO₂-induced plant growth response with increasing air temperature arises from the negative influence of high CO₂ levels on the growth-retarding process of photorespiration, which can "cannibalize" 40 to 50% of the recently-produced photosynthetic products of C₃ plants. Since this phenomenon is more pronounced at high temperatures, and as it is ever-more-inhibited by increasingly-higher atmospheric CO₂ concentrations, there is an increasingly-greater potential for atmospheric CO₂ enrichment to benefit plants as air temperatures rise.

A major consequence of this phenomenon is that the optimum temperature for plant

growth generally rises when the air is enriched with CO₂. For a 300-ppm increase in the air's CO₂ content, in fact, several experimental studies have shown that the optimum temperature for growth in C₃ plants typically rises by 5°C or more. 49,50,51,52,53,54,55,56,57,58,59 These observations are very important; for an increase of this magnitude in optimum plant growth temperature is greater than the largest air temperature rise predicted to result from a 300-ppm increase in atmospheric CO₂ concentration. Therefore, even the most extreme global warming envisioned by the Intergovernmental Panel on Climate Change will probably not adversely affect the vast majority of Earth's plants; for fully 95% of all plant species are of the C₃ variety. In addition, the C₄ and CAM plants that make up the rest of the planet's vegetation are already adapted to Earth's warmer environments, which are expected to warm much less than the other portions of the globe; yet even some of these plants experience elevated optimum growth temperatures in the face of atmospheric CO₂ enrichment.⁶⁰ Consequently, a CO₂-induced temperature increase will likely not result in crop yield reductions, nor produce a poleward migration of plants seeking cooler weather; for the temperatures at which nearly all plants perform at their optimum is likely to rise at the same rate (or faster than) and to the same degree as (or higher than) the temperatures of their respective environments. And other research indicates that even in the absence of a concurrent increase in atmospheric CO₂, plants may still be able to boost their optimum temperature for photosynthesis as the temperature warms.⁶¹

Elevated CO₂ reduces, and frequently completely overrides, the negative effects of ozone pollution on plant photosynthesis, growth and yield.

Tropospheric ozone is an air pollutant created by a chemical reaction between nitrogen oxides and volatile organic compounds in the presence of sunlight. Plants exposed to elevated concentrations of this pollutant typically display reductions in photosynthesis and growth in comparison to plants grown at current ozone concentrations. Because hot weather also helps to form ozone, there are concerns that CO₂-induced global warming will further increase the concentration of this pollutant, resulting in future crop yield reductions.⁶² It is therefore important to determine how major crops respond to concomitant increases in the abundances of both of these important atmospheric trace gases, as their concentrations will likely continue to rise for many years to come; and several experiments have been conducted to determine just that - examining the interactive effects of elevated CO₂ and ozone on important agricultural commodities. These studies show that elevated CO₂ reduces, and frequently completely overrides, the negative effects of ozone pollution on plant photosynthesis, growth and yield. 63,64,65,66,67,68 When explaining the mechanisms behind such responses, most scientists suggest that atmospheric CO₂ enrichment tends to reduce stomatal conductance, which causes less indiscriminate uptake of ozone into internal plant air spaces and reduces subsequent conveyance to tissues where damage often results to photosynthetic pigments and proteins, ultimately reducing plant growth and biomass production.

Analyses of long-term ozone measurements from around the world cast further doubt on the possibility that this pollutant will cause much of a problem for future crop production.⁶⁹ In western Europe, for example, several time series show a rise in ozone into the middle to late 1990s, followed by a leveling off, or in some cases declines, in the 2000s. And in North America, surface measurements show a pattern of mostly unchanged or declining ozone concentration over the past two decades that is broadly consistent with decreases in precursor emissions. The spatial and temporal distributions of these and other observations indicate that, whereas increasing industrialization originally tends to increase the emissions of precursor substances that lead to the creation of greater tropospheric ozone pollution,

subsequent technological advances tend to ameliorate that phenomenon, as they appear to gradually lead to (1) a leveling off of the magnitude of precursor emissions and (2) an ultimately *decreasing* trend in tropospheric ozone pollution. And in light of these observations, when atmospheric ozone and CO₂ concentrations both rise together, the plant-growth-enhancing effect of atmospheric CO₂ enrichment is significantly muted by the plant-growth-retarding effect of contemporaneous increases in ozone pollution, but that as the troposphere's ozone concentration gradually levels off and declines—as it appears to be doing with the development of new and better anti-pollution technology in the planet's more economically advanced countries - the future could bring more-rapid-than-usual increases in earth's vegetative productivity, including crop yields.

Increasing atmospheric carbon dioxide will reduce agricultural sensitivity to drought.

It has been suggested that the frequency and severity of drought across much of the U.S. will increase as greenhouse gases rise, causing crops to experience more frequent and more severe water deficits, thereby reducing crop yields.¹

Recent droughts are not without historical precedent. Nonetheless, even if they were to increase in frequency and/or severity, agricultural crops become less susceptible to drought-induced water deficits as the air's CO₂ concentration rises. This is because water stress does not typically negate the CO₂-induced stimulation of plant productivity. In fact, the CO₂-induced percentage increase in plant biomass production is often greater under water-stressed conditions than it is when plants are well-watered.

During times of water stress, atmospheric CO₂ enrichment often stimulates plants to develop larger-than-usual and more robust root systems that invade greater volumes of soil for scarce and much-needed moisture. Elevated

levels of atmospheric CO₂ also tend to reduce the openness of stomatal pores on leaves, thus decreasing plant stomatal conductance. This phenomenon, in turn, reduces the amount of water lost to the atmosphere by transpiration and, consequently, lowers overall plant water use. Atmospheric CO₂ enrichment thus increases plant water acquisition, by stimulating root growth, while it reduces plant water loss, by constricting stomatal apertures; and these dual effects typically enhance plant water-use efficiency, even under conditions of less-thanoptimal soil water content. These phenomena contribute to the maintenance of a more favorable plant water status during times of drought, as has been demonstrated in several studies.2,3,4,5

On the whole, CO₂-enrichment does not increase the competitiveness of weeds over crops; higher atmospheric CO₂ will likely reduce crop damage from insects and pathogenic diseases.

Elevated CO₂ typically stimulates the growth of nearly all plant species in monoculture, including those deemed undesirable by humans, i.e., weeds, and concerns have been expressed that CO₂ enrichment may help weeds outcompete crops in the future. However, such worries are likely overstated. Out of the 18 weeds considered most harmful in the world, 14 are of the C₄ species type. ⁸⁴ In contrast, of the 86 plant species that provide most all of the world's food supply, only 14 are C₄ (the remainder are C₃ species),85 and studies conducted on C₃ crops with C₄ weeds—the most common arrangement of all crop/weed mixed-species stands—typically demonstrate that elevated CO₂ favors the growth and development of C₃ over C₄ species. 86,87,88,89,90,91,92,93 Therefore, the ongoing rise in the air's CO₂ content should, on the whole, provide crops with greater protection against weed-induced decreases in their productivity and growth.

With respect to crop damage from insects, the majority of studies to date indicate that the

fraction of plant production that is consumed by herbivores in a CO₂-enriched world will likely remain about the same as it is now or slightly decrease. 94,95,96,97,98,99 In one study, for example, offspring numbers of the destructive agricultural mite Tetranychus urticae, feeding on bean plants growing in 700-ppm CO₂ air, were 34% lower in the first generation and 49% lower in the second generation than the offspring produced in bean plants growing in air of 350-ppm CO₂.¹⁰⁰ This CO₂-induced reduction in the reproductive success of this invasive insect, which negatively affects more than 150 crop species worldwide, bodes well for society's ability to grow the food we will need to feed the population of the planet in the future.

In a somewhat different experiment, researchers fed foliage derived from plots of calcareous grasslands in Switzerland (maintained experimentally at 350 and 650 ppm CO₂) to terrestrial slugs, and found they exhibited no preference with respect to the CO₂ treatment from which the foliage was derived. 101 And, in a study that targeted no specific insect pest, it was observed that a doubling of the air's CO₂ content enhanced the total phenolic concentrations of two Mediterranean perennial grasses (Dactylis glomerata and Bromus erectus) by 15% and 87%, respectively. These compounds tend to enhance plant defensive and resistance mechanisms to attacks by both herbivores and pathogens. 102

Notwithstanding such findings, another herbivore-related claim is that insects will increase their feeding damage on C₃ plants to a greater extent than on C₄ plants because increases in the air's CO₂ content sometimes lead to greater decreases in the concentrations of nitrogen and, therefore, protein in the foliage of C₃ plants as compared to C₄ plants. To make up for this lack of protein, it has been assumed that insects would consume a greater amount of vegetation from plants growing under higher CO₂ levels as opposed to lower CO₂ levels. However, contrary to such assertions, observations show little to no evidence in this regard.

It has been suggested that the lack of increased consumption rates at higher CO₂ levels may be explained by post-ingestive mechanisms that provide a sufficient means of compensation for the lower nutritional quality of C3 plants grown under elevated CO₂. ^{103,104}

When it comes to pathogenic diseases, researchers have noted a number of CO₂-induced changes in plant physiology, anatomy and morphology that have been implicated in increased plant resistance to disease and that can enhance host resistance at elevated CO₂, among which are (1) increased net photosynthesis that allows the mobilization of resources into host resistance, 105,106 (2) a reduction in stomatal density and conductance, 107 3) greater accumulation of carbohydrates in leaves, (4) an increase of waxes, extra layers of epidermal cells, and increased fiber content, 108 (5) production of papillae and accumulation of silicon at penetration sites, 109 (6) more mesophyll cells, 110 (7) increased biosynthesis of phenolics, 111 (8) increased root biomass and functionality, 112,113 (9) higher condensed tannin concentrations, 114,115 (10) increased root colonization by arbuscular mycorrhizal fungi,116 (11) increased production of glyceollins, 117,118 (12) increased plant carbon gain,119 and (13) changes in the allometric relation between below-ground and above-ground biomass. 120 Whatever the mechanism, the vast bulk of the available data suggests that elevated CO₂ has the ability to significantly ameliorate the deleterious effects of various stresses imposed upon plants by numerous pathogenic invaders. Consequently, as the atmosphere's CO₂ concentration continues its upward climb, earth's vegetation should be increasingly better equipped to successfully deal with pathogenic organisms and the damage they have traditionally done to society's crops, as well as to the plants that sustain the rest of the planet's animal life.

It is a well-established fact that atmospheric CO₂ enrichment not only boosts the productivity of both crops and natural vegetation, but it also enhances the *quality* of many important

substances found within them by increasing the concentration of many important vitamins^{121,122,123,124,125} antioxidants, ^{126,127,128} and other phytonutrients 129,130,131,132,133,134 that are well-known for their nutritional and medicinal value. Experiments with bean sprouts, for example, have shown that a doubling of atmospheric CO₂ doubled the plant's vitamin C content.¹³⁵ Likewise, antioxidant concentrations have been found to increase by as much as 171% in a CO₂-enriched strawberry experiment. 136 Other studies show elevated atmospheric CO₂ increased the concentration of the heart-helping drug digoxin in woolly foxglove (Digitalis lanata) by 11 to 15%. 137,138 And in the tropical spider lily (Hymenocallis littoralis), in addition to increasing plant biomass by 56%, a 75% increase in the air's CO₂ content was shown to increase the concentrations of five different substances proven effective in treating a number of human cancers (melanoma, brain, colon, lung and renal) and viral diseases (Japanese encephalitis and yellow, dengue, Punta Tora and Rift Valley fevers) by 6 to 28%.139

Enhanced atmospheric CO₂ and food and forage quality.

One concern that is frequently expressed with respect to the quality of CO₂-enriched food, however, is that large increases in the air's CO₂ content sometimes lead to small reductions in the protein concentrations of animal-sustaining forage and human-sustaining cereal grains when soil nitrogen concentrations are sub-optimal. Many crops, in contrast, do not show such reductions, or do so only in an ever so slight manner. 140 Nevertheless, for those that do, when they are supplied with adequate nitrogen, as is typical of modern farming techniques, no such protein reductions are observed. 141,142,143,144 It should also be noted that the rate of rise of the atmosphere's CO₂ concentration is only a couple parts per million per year, which is fully two orders of magnitude less than the CO₂ increases employed in most experiments that show small reductions

in plant protein contents when soil nitrogen concentrations are less than adequate; and there are many ways in which the tiny amount of extra nitrogen needed to maintain current crop protein concentrations in the face of such a small yearly increase in the air's CO₂ concentration may be readily acquired.

Crops experiencing rising levels of atmospheric CO₂ produce larger and more-branching root systems (as they typically do in experiments when exposed to elevated CO₂ concentrations), which should allow them to more effectively explore ever larger volumes of soil for the extra nitrogen and other nutrients the larger CO₂-enriched crops will need as the air's CO₂ content continues to rise. Also, tiny bacteria and algae that remove nitrogen from the air and make it directly available to plants are found nearly everywhere; and elevated atmospheric CO₂ concentrations typically enhance their ability to perform this vital function.¹⁴⁵ As these phenomena are gradually enhanced by the slowly rising CO₂ content of the air, the slowly rising nutrient requirements of both crops and natural vegetation should be easily satisfied; and plant protein concentrations should therefore be maintained, at the very least, at their current levels.

Interrelated with the concern about CO₂induced decreases in plant nutritive value is a hypothesis that lowered plant nitrogen will significantly reduce the nutritive value of grassland herbage and, therefore, affect the digestibility, forage intake and productivity of ruminants. In fact, there are a number of observational studies that indications in atmospheric CO₂ enrichment will not have a negative impact on total herbage nitrogen concentration¹⁴⁶ or digestibility; ^{147,148,149} and even if it did, the impact would likely not be large enough to negatively impact the growth and wellbeing of ruminants feeding upon the forage150,151,152 as the nutritive value of grassland plants is often above the minimum range of crude protein necessary for efficient digestion by ruminants.¹⁵³

Atmospheric CO₂ Enrichment of a Pair of Medicinal Plants

According to Stutte et al. (2008), "many Scutellaria species are rich in physiologically active flavonoids that have a wide spectrum of pharmacological activity." Leaf extracts of Scutellaria barbata, as they describe it, "have been used in traditional Chinese medicine to treat liver and digestive disorders and cancers (Molony and Molony, 1998)," and they say that "recent research has shown extracts of S. barbata to be limiting to the growth of cell lines associated with lung, liver, prostate and brain tumors (Yin et al., 2004)."

In an attempt to understand how these phytonutrients might respond under elevated CO₂ growing conditions, the three researchers studied both *S. barbata* and *S. lateriflora*, measuring effects of elevated atmospheric CO₂ concentrations (1200 and 3000 ppm vs. a control value of 400 ppm) on total plant biomass production and plant concentrations of six bioactive flavonoids — apigenin, baicalin, baicalein, chrysin, scutellarein and wogonin — all of which substances, in their words, "have been reported to have anticancer and antiviral properties," as described in the review papers of Joshee *et al.* (2002) and Cole *et al.* (2007). These experiments were conducted in a large step-in controlled-environment chamber that provided a consistent light quality, intensity and photoperiod to six smaller plant growth chambers that had "high-fidelity control of relative humidity, temperature, and CO₂ concentration." Each chamber also monitored nutrient solution uptake by plants that they grew from seed for a period of 49 days.

With respect to plant productivity, in the case of *S. barbata*, increasing the air's CO₂ concentration from 400 to 1200 ppm resulted in a 36% increase in shoot fresh weight and a 54% increase in shoot dry matter, with no further increases between 1200 and 3000 ppm CO₂. In the case of *S. lateriflora*, on the other hand, the corresponding increases in going from 400 to 1200 ppm CO₂ were 62% and 44%, while in going all the way to 3000 ppm CO₂, the total increases were 122% and 70%, respectively.

With respect to flavonoid concentrations in the plants' vegetative tissues, Stutte et al. report that in the case of S. barbata, "the combined concentration of the six flavonoids measured increased by 48% at 1200 and 81% at 3000 ppm CO₂," while in S. lateriflora they say "the total flavonoid content increased by over 2.4 times at 1200 and 4.9 times at 3000 ppm CO₂." Thus, in consequence of the compounding effect of increases in both plant biomass and flavonoid concentration, the total flavonoid content in S. barbata rose by 72% in going from 400 to 1200 ppm CO₂, and by 128% in going all the way to 3000 ppm CO₂, while in S. lateriflora the corresponding increases were 320% and 1,270%.

In the concluding sentence of their paper's abstract, Stutte et al. say their results indicate that "the yield and pharmaceutical quality of Scutellaria species can be enhanced with controlled environment production and CO₂ enrichment," and massively so. In addition, since they indicate that over 200 substances — of which over 80% are flavonoids — have been found in a total of 65 Scutellaria species, it would appear that the "increased concentration of flavonoids through CO₂ enrichment," as they describe it, "has the potential to enhance the production and quality of [many] medicinal plants."

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Given the considerations noted above, it is likely that the ongoing rise in the air's CO₂ content will continue to increase food production around the world, while maintaining the digestibility and nutritive quality of that food and enhancing the production of cer-

tain disease-inhibiting plant compounds. The increase atmospheric CO₂ concentration is not only helping to meet the caloric requirements of the planet's burgeoning human and animal populations; it is also helping to meet their nutritional and medicinal requirements as well.