19

Rising Atmospheric Carbon Dioxide and Plant Biology: The Overlooked Paradigm

Lewis H. Ziska

Introduction

As human populations continue to expand, concurrent increases in energy and food will be required. Consequently, fossil-fuel burning and deforestation will continue to be human-derived sources of atmospheric carbon dioxide (CO_2). The current annual rate of CO_2 increase (~0.5%) from these sources is expected to continue with concentrations exceeding 600 parts per million (ppm) by the end of the current century (Schimel, et al. 1996).

Because carbon dioxide absorbs heat leaving the earth's atmosphere, there is widespread agreement that increasing CO_2 will result in increasing global temperatures. The extent to which temperatures increase, and the potential biological consequences—from sea-level rise, to the spread of malaria—have been discussed and debated extensively in both the scientific and popular literature.

Unfortunately, given the focus on global warming, it is seldom acknowledged that no matter what the end effect of rising temperatures, the ongoing increase in atmospheric carbon dioxide, *of and by itself*, has affected, and will continue to affect, all life on the planet.

The fact that carbon dioxide will continue to impact life directly is not derived from new science. Plants supply food, energy, and carbon to all living things. Life for us, and *for every ecosystem on the planet*, depends on the ability of plants to generate complex carbohydrates and chemical energy from just four basic resources: sunlight, nutrients (e.g., nitrogen, phosphorous), water and . . . carbon dioxide.

Imagine that, since 1960, the amount of sunlight reaching the earth had increased by 20%. Would plant biology be affected? Of course. Light is one of the four resources required by plants, and changing the amount of sunlight selects those plant species that respond positively or negatively to that resource (e.g., sun- or shade-adapted plants). Similar differential responses among plant species would be evident if water or nutrient availability had increased 20% over this same period.

Since 1960, the amount of carbon dioxide in the atmosphere has risen from 315 to 378 ppm, an increase of approximately 20%. To put this in perspective, plants evolved at a time of high atmospheric carbon dioxide (4-5 times present values), but concentrations appear to have declined to relatively low values during the last 25–30 million years (Bowes 1996). The values have been low enough, long enough, that evolution has selected for a small percentage of plants, principally tropical grasses that have maximum photosynthetic rates even at the current low CO_2 concentrations. However, these grasses (termed "C_4" plants) only comprise about 3–4% of all known plant species, the bulk (95%) of the 250,000+ plant species (termed "C_3" plants), lack optimal levels of carbon dioxide. For these plants, the recent rise and projected increase in atmospheric carbon dioxide represents an upsurge of an essential resource. There are hundreds of studies showing that both recent and projected increases in atmospheric carbon dioxide can significantly stimulate growth, development, and reproduction in a wide variety of C_3 plants (see Kimball 1983; Kimball, et al. 1993; Poorter and Navas 2003 for reviews examining the response to future CO_2 concentrations, and Sage 1995 for a review of the response to recent CO_2 increases).

So, a basic question remains: if plants are necessary for life to exist, and rising carbon dioxide is affecting how 95% of them grow and function, why aren't we discussing the global impact of rising

CO_2 on plant biology/ecology, in addition to the greenhouse effect?

CO_2 and Agricultural Systems

One obvious reason may be related to the "green is good" concept. In other words, given that carbon dioxide makes plants grow more, and plants are beneficial, isn't this is a constructive result? Why are we complaining? The impact of rising carbon dioxide on plants, particularly agronomic crops, has even been lauded by some as "a wonderful and unexpected benefit from the industrial revolution" (Robinson and Robinson 1997).

Are there really benefits to be gained in agriculture from rising carbon dioxide? Let us consider for a moment rice and wheat, two global cereals whose production supplies the calories for almost four billion of the world's six billion people. A number of studies have, in fact, demonstrated that both rice and wheat can show a positive response to increasing atmospheric carbon dioxide (Mandersheid and Weigel 1997; Horie, et al. 2000). Indeed, variation among different lines of rice and wheat in response to carbon dioxide is such that we could begin a large-scale effort to select for the most CO_2 sensitive cultivars (e.g. Ziska, et al. 1996) (Figure 19.1).

Such an effort holds significant promise, as we could, potentially, increase overall yields of these cereals at a time when the earth's population is rapidly expanding. Of course, there are challenges in such an approach; in particular, there is ubiquitous evidence indicating a decline in protein concentration for cereals as CO_2 increases (Jablonski, et al. 2002; Ziska, et al. 2004b) (Figure 19.2). Alternatively, sufficient variation may exist to make it possible to select for increased yields without sacrificing grain quality (Hall and Ziska 2000).

However, before we give in to the temptation of viewing an increase in a needed resource as being uniformly beneficial, it is important to remember that species respond differently to the same resource. Here is a simple example: in the 1950s when fertilizer (e.g., nutrients, a resource) was cheap, adding supraoptimal amounts of nitrogen was tested as a means to reduce weed competition with crops, the logic being that if there was a surplus amount of nitrogen, then competition for that resource would be reduced. Instead, scientists found that competition from weeds *increased* and crop yields were

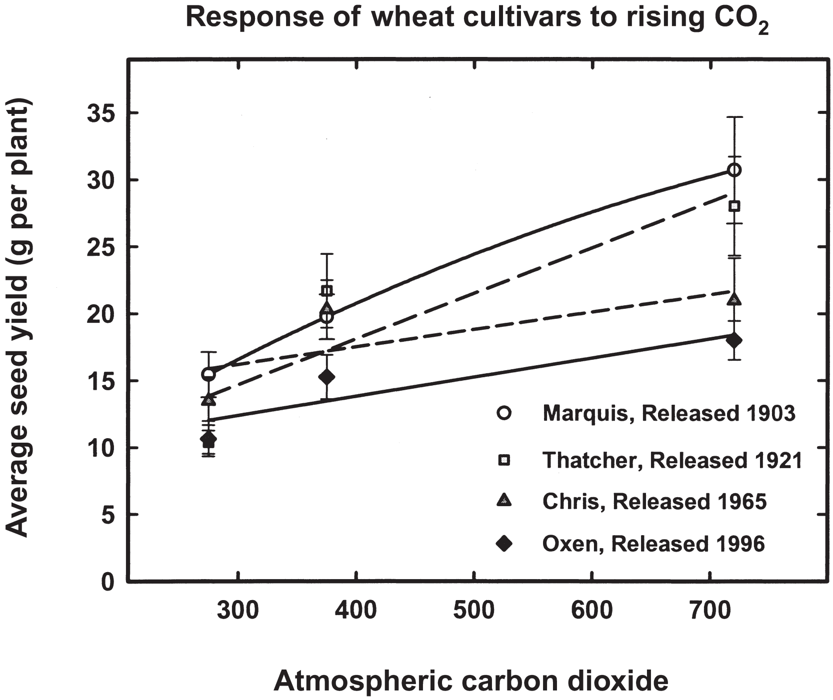

Figure 19.1 Average seed yield ± standard error of four different lines of Spring wheat in response to carbon dioxide concentrations at the beginning of the 20th century (ca. 300 ppm), the current level of carbon dioxide (ca. 400 ppm) and that projected for the end of the 21st century (ca. 720 ppm). These data suggest that sufficient variability exists among wheat lines to begin selecting for increasing seed yield in response to rising carbon dioxide.

reduced further (e.g., Vengris, et al. 1955). Why? Because weeds were able to utilize the additional resource (N) much more efficiently and less was available to the crop.

So, if we change a resource, we not only change the growth of an individual plant species, we differentially affect the growth of *all* the plant species within that community. Agriculture, in its simplest sense, represents a managed community that consists of the crop (desired plant species), and weeds (undesired plant species). Weeds, since the inception of agriculture, have limited the ability of human society to maximize crop productivity and maintain food security. In rice alone, the direct loss in production as a result of weed competition is estimated at approximately 20%, with losses climbing to 100% if weeds are not controlled (IRRI 2002).

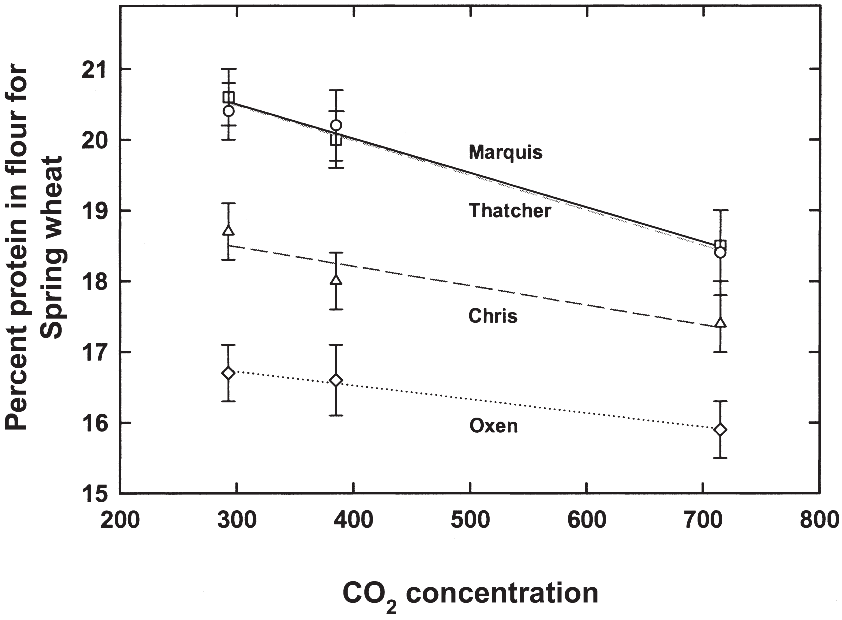

Figure 19.2 Percent protein in flour as a function of wheat variety and rising carbon dioxide concentration. Wheat varieties and carbon dioxide treatments are as described in figure 19.1. The overall trend for wheat is a decline in percent protein with increasing carbon dioxide.

Unfortunately, a number of studies indicate that among plant species in an agricultural system, weeds, rather than crops, are likely to show the strongest relative response to rising carbon dioxide (Ziska 2000; Ziska 2003b). That is, even though individual plants of rice or wheat can respond to carbon dioxide, the greater response of weedy species to CO_2 may result in increased competition and exacerbated losses in crop production (Figure 19.3). This is analogous to the supraoptimal nitrogen experiments where weeds responded more to excess nitrogen than the crop. Assuming that the studies conducted so far represent general trends, then rising carbon dioxide could actually reduce yield within agricultural systems on a global scale.

The basis for the greater response among weedy species to a resource increase is not entirely clear. In some instances, whether a crop or a weed is a C_3 or C_4 plant will determine its relative response to carbon dioxide and its competitive abilities (see Table 19.1, Ziska and Runion 2006). Many of the worst weeds for a given crop, however, are wild (uncultivated) plants of the same genus or species (e.g., rice and wild rice, oat and wild oat, sorghum and shattercane) and

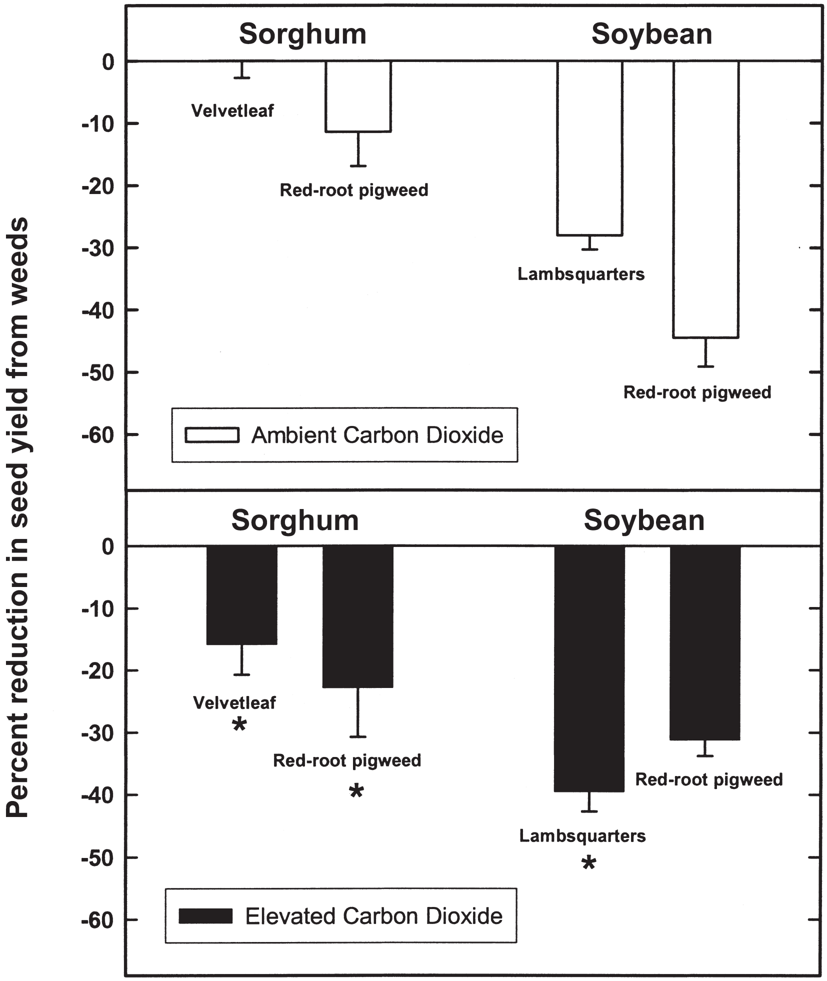

Figure 19.3 Percent reduction in seed yield for sorghum and soybean (a C4 and C3 crop respectively) as a function of competition from a C3 (velvetleaf, lambsquarters) and C4 weed (red-root pigweed) at ambient carbon dioxide and at 200 ppm above ambient. Weed spacing was two plants per meter of crop row in all cases. Increasing carbon dioxide resulted in a greater loss in crop seed yield from weedy competition (indicated by the asterisk) in all cases, except red-root pigweed in soybean. See Ziska 2000 and Ziska 2003a for additional details.

are likely to have the same photosynthetic pathway. Alternatively, it has been suggested (Treharne 1989) that the greater range of responses observed for weeds with increasing atmospheric CO_2 is related to their greater genetic diversity relative to crops; in other words, the greater the gene pool, the more likely it is for a species to respond to a resource change. In the ongoing struggle to maintain ever-increasing yields to feed a hungry world, we are relying on a narrow genetic base and increasing crop uniformity. While this has been a successful strategy in the past, we may have—inadvertently—conferred a disadvantage on current crop lines as they face increasing competition from their wild relatives for additional carbon dioxide. Whether we can recognize our strategic shortcomings and change tactics—i.e., select for genetically diverse, CO_2-responsive crop lines that can increase agricultural productivity—remains to be seen.

CO_2 and Native Systems

Unlike agricultural systems, most plant communities are complex and consist of many different plant species. Here again, it is tempting to think that rising carbon dioxide will result in increased growth of such communities. And so it may (see Rasse, et al. 2005 for marsh systems; DeLucia, et al. 1999 for loblolly pine), but, as with agricultural systems, the stimulation of growth will almost certainly be uneven (see Poorter and Navas 2003) with resulting "winners" and "losers" among plant species. Needless to say, given the complexity of such systems (e.g., forests, wetlands, prairie, desert, etc.), understanding the full implications of an increase in carbon dioxide will be difficult. Nevertheless, we can begin assessing some of the potential roles rising carbon dioxide might play by examining a simple example of invasive plant species and ecosystem function.

Invasive plants (i.e., exotic or alien species) are those plant species, nonnative to a given geographical area, whose geographic introduction within a community results in extensive economic or environmental damage. Millions of acres of productive rangelands, forests, and riparian areas have been overrun by such invaders, with a subsequent loss of native flora. E. O. Wilson, the noted ecologist, has observed that, "On a global basis, the two great destroyers of biodiversity are, first, habitat destruction and, second, invasion by exotic species" (1999). It has been estimated that more than 200 million acres of natural habitats (primarily in the western United States) have already been lost to invasive, noxious weeds, with an ongoing loss of 3000 acres a day (Westbrooks 1998). The invasive plant species that are most harmful to native biodiversity are those that significantly change ecosystem processes, to the detriment of native species.

One example of environmental damage related to invasive plants is the frequency and spread of natural or anthropogenic fires within native communities. For much of the western United States, cheatgrass (*Bromus tectorum*) originally introduced from central Asia, grows quickly in dry environments, colonizing open spaces between perennial, native shrubs with a fine flammable material that increases the frequency of fire events (Billings 1990, 1994). As fire events increase, native species diminish, while cheatgrass, a fire-adapted species, becomes dominant within the community. At present, cheatgrass dominates almost 17 million acres, or 17% of federally-owned lands in the western United States, with an additional 62 million acres at high risk (Jayne Belnap, US Geological Survey, personal communication). A study of three cheatgrass populations collected from different elevations within the Sierra Nevada range revealed that even small, recent changes in atmospheric carbon dioxide (approximately 50 ppm) could increase growth rate and combustibility of cheatgrass, while reducing digestibility (Ziska, et al. 2005b), all factors linked to increasing the amount of above-ground biomass, with potential effects on fire frequency and species diversity within native plant communities.

The cheatgrass observations are consistent with other data on carbon dioxide sensitivity from a range of invasive plants, suggesting that, on average, invasive species may show a stronger response to both recent and projected changes in atmospheric carbon dioxide than other plant species (Ziska and George 2004). It can be argued that such a strong response of invasive plants will be dependent on other resources, such as water and nutrients, and may not mimic experimental evaluations in situ. This is a fair criticism. Yet, it is also worthwhile to note that for invasives in managed, agricultural systems, water and nutrients may be optimal. Even in native systems such as those for cheatgrass, optimal water and nutrients may be periodically available depending on fluctuations in weather (Young, et al. 1987).

Still, actual field-based data from plant communities remains the best proof of whether rising carbon dioxide is altering the success of invasive plants (and subsequent ecosystem function). Unfortunately, field data are rare, and only a handful of studies have addressed this question with respect to projected carbon dioxide increases. A comparison of the impact of increasing CO_2 concentration on an invasive, noxious weed, yellow star thistle (*Centaurea solstitialis*), demonstrated a significant increase in biomass in monoculture, but a nonsignificant impact when yellow star thistle was grown within a grassland community (Dukes 2002), suggesting that rising carbon dioxide did not stimulate the growth of this plant species preferentially. In contrast, work with the invasive honey mesquite (*Prosopis glandulosa*) and the native species little bluestem (*Schizachyrium scoparium*) suggests that the woody invader, honey mesquite, *is* preferentially stimulated by CO_2 concentration (Polley, et al. 1994). Research on Japanese honeysuckle in a forest understory also demonstrated a strong CO_2 concentration–linked growth response and subsequent increase in percent cover (Belote, et al. 2003). Experiments with a woody invasive species in Switzerland (*Prunus laurocerasus*) showed a stronger CO_2 concentration–response relative to native trees (Hattenschwiler and Korner 2003), also suggesting preferential growth of a nonnative species. Finally, elevated CO_2 concentration increased the productivity and invasive success of a noxious invasive rangeland weed associated with fire outbreaks (*Bromus madritensis*, spp. rubens) in an arid ecosystem (Smith, et al. 2000). Overall, four of the five seminal studies suggest that rising levels of CO_2 can preferentially increase the growth of invasive plant species within a plant community. As rising CO_2 preferentially selects for a few species within a plant community, the implications with respect to basic ecological function, particularly species diversity, are troubling.

CO_2 and Human Systems

So far we have provided evidence that the rise in carbon dioxide per se, has, or will have, significant impacts on both managed (e.g., agricultural weeds) and unmanaged (e.g., invasive species) plant communities. Clearly, these impacts will have indirect effects on human society by altering the goods and services provided by these systems. Yet it is likely that there will be direct effects as well.

As with ecosystem function, the impact of rising CO_2 on human systems has not been completely elucidated. However, we are beginning to understand how rising CO_2 could interact with plant biology to affect one aspect—public health. At first glance, such an effect seems implausible. After all, plants do not carry disease. Yet, there are a number of ways in which plants directly affect human health, including allergenic reactions, contact dermatitis, and pharmacology/toxicology. All of these means, in turn, are likely to be affected by the rise in atmospheric carbon dioxide.

One of the most common plant-induced health effects is related to allergies, which are experienced by approximately 30 million people in the United States (Gergen, et al. 1987). Symptoms include sneezing, inflammation of nose and eye membranes, and wheezing. Complications such as nasal polyps or secondary infections of the ears, nose, and throat may also be common. Severe complications, such as asthma, permanent bronchial obstructions, and damage to the lungs and heart can occur in extreme cases.

Although there are over four dozen plant species that produce airborne allergens, common ragweed (*Ambrosia artemisiifolia*) causes more problems than all other plants combined (Wodehouse 1971). Initial indoor studies examining the response of ragweed to recent and projected changes in carbon dioxide demonstrated an increase in both ragweed growth and pollen production, with qualitative increases in ambient a 1, the principle protein that triggers allergic reactions (Ziska and Caulfield 2000; Wayne, et al. 2002; Singer, et al. 2005). Additional outdoor experiments that exploited an urban-rural transect that differed in carbon dioxide concentration, also showed the sensitivity of ragweed pollen production to CO_2 in situ (Ziska, et al. 2003). Overall, these data indicate a probable link between rising CO_2 (both at the local urban level, and that projected globally) and ragweed pollen production, with subsequent effects on allergic rhinitis.

Over a hundred different plant species are associated with contact dermatitis, an immune-mediated skin inflammation. Chemical irritants can be present on all plant parts, including leaves, flowers, and roots, or can appear on the plant surface when injury occurs. One well-known chemical is urushiol, a mixture of catechol derivatives. This is the compound that induces contact dermatitis in the poison ivy group (*Toxicodendron/Rhus* spp.). Currently, sensitivity to urushiol occurs in about two of every three people, and amounts as small as one nanogram (i.e., one billionth of a gram) are sufficient to induce a rash. Over two million people in the United States suffer annually from contact with members of the poison ivy group (i.e., poison ivy, oak, or sumac). The amount and concentration of these chemicals varies with a range of factors including maturity, weather, soil, and ecotype. However, recent research from the Duke Forest Free-Air CO_2 Enrichment facility also indicated that poison ivy growth and urushiol toxicity is highly sensitive to rising CO_2 levels (Mohan, et al. 2006). Overall, these data suggest a probable link between rising carbon dioxide levels and increased contact dermatitis.

Plants display a wide range of chemical diversity. Many of these chemicals are historically acknowledged as having pharmaceutical value (Table 19.1). Even in developed countries, where synthetic drugs dominate, 25% of all prescriptions dispensed from community pharmacies from 1959 through 1980 contained plant extracts or active principles prepared from higher plants (e.g., codeine, Farnsworth, et al. 1985). For developing countries, however, the World Health Organization (WHO) reported that more than 3.5 billion people rely on plants as components of their primary health care (WHO 2002). Furthermore, for both developed and developing countries, there are a number of economically important pharmaceuticals derived solely from plants (e.g., tobacco), whose economic value is considerable (see Table 2 in Raskin, et al. 2002).

Table 19.1 Plant-Derived Pharmaceutical Drugs and Their Clinical Usage Although many of these drugs are synthesized in developing countries, the World Health Organization estimates that as many as 3.5 billion people still rely on botanical sources for medicines (WHO 2002). Recent work on atropine and scopolamine indicates that increasing carbon dioxide and/or temperature will alter the concentration and or production of these plant-derived compounds (Ziska, et al. 2005b).

Drug	Action/Clinical Use	Species
Acetyldigoxin	Cardiotonic	*Digitalis lanata*
Allyl isothiocyanate	Rubefacient	*Brassica nigra*
Atropine	Anticholinergic	*Atropa belladonna*
Berberine	Bacillary dysentery	*Berberis vulgaris*
Codeine	Analgesic, antitussive	*Papaver somniferum*
Danthron	Laxative	*Cassia spp.*
L-Dopa	Anti-Parkinson's	*Mucuna spp.*
Digitoxin	Cardiotonic	*Digitalis purpurea*
Ephedrine	Antihistamine	*Ephedra sinica*
Galanthamine	Cholinesterase inhibitor	*Lycoris squamigera*
Kawain	Tranquilizer	*Piper methysticum*
Lapachol	Anticancer, antitumor	*Tabebuia spp.*
Ouabain	Cardiotonic	*Strophantus gratus*
Quinine	Antimalarial	*Cinchona ledgeriana*
Salicin	Analgesic	*Salix alba*
Taxol	Antitumor	*Podophyllum peltatum*
Vasicine	Cerebral stimulant	*Vinca minor*
Vincristine	Antileukemic agent	*Catharanthus roseus*

There are an increasing number of studies that are beginning to address how rising carbon dioxide affects the production or concentration of these pharmaceuticals. For example, growth of wooly foxglove (*Digitalis lanata* Ehrh.) and production of digoxin (a cardiotonic used in heart surgery) were increased at 1,000 ppm CO_2 relative to ambient conditions (Stuhlfauth and Fock 1990). Similarly, production and concentration of atropine and scopolamine (strong anticholinergics—chemicals that block the transmission of nerve impulses) was stimulated with both recent and projected carbon dioxide increases (Ziska, et al. 2005a).

The effect of CO_2 on such chemicals, however, is a two-edged sword. Given the subtle distinctions that exist between toxicity and pharmacology, CO_2-induced changes in their production or ratio will almost certainly influence their efficacy and use in human systems, particularly in developing countries (Uzun, et al. 2004). In addition, there are chemicals that are known poisons, with no pharmaceutical benefit. Poison hemlock (*Conium maculatum*), oleander (*Nerium aleander*), and castor bean (*Ricinus communis*) are so poisonous that tiny amounts can be fatal if ingested (e.g., ricin in castor beans has a greater potency than cyanide). Unfortunately, the impact of carbon dioxide on the concentration or production of such poisons is almost completely unknown. This is unfortunate, given that in 2001 alone, 73,000 cases of accidental plant ingestion were reported for children under the age of six in the United States (Dr. Rose Anne Soloway, American Association of Poison Control Centers, personal communication).

Rising CO_2 and Human Control Efforts

But even if rising carbon dioxide stimulates the growth of undesirable plants, won't we still be able to limit where and when such species grow? Can't we control the establishment and success of unwanted plant species either by mechanical, chemical, or biological means? Wouldn't this limit or negate any adverse effects (direct or indirect) associated with rising carbon dioxide?

Control of undesirable plant species is a difficult task. One only need consider the spread of an invasive weed like kudzu (*Pueraria lobata*) in the southeastern United States to appreciate the fact that no matter the amount of human effort, kudzu is here to stay. In fact, human control of selected species within an ecosystem requires a tremendous amount of effort and financial commitment, and is often unsuccessful.

But what about highly managed systems, such as agriculture? For the United States and many developed countries, chemical methodologies allow for cheap, effective control in agronomic production. Actually, a single herbicide, glyphosate (commercially sold as "Round-Up"), is so effective in controlling weeds that more than three-quarters of the US soybean crop, and over a third of the US corn crop have been genetically modified to be glyphosate resistant (e.g., Gaskell et al. 1999).

So is the solution to simply spray to control any undesirable plant pests? Unfortunately, there is an increasing number of studies (Ziska, et al. 1999; Ziska and Teasdale 2000) that demonstrate a decline in pesticide efficacy with rising CO_2 levels (Figure 19.4). The basis for the observed decline in efficacy is unclear. In theory, rising CO_2 levels could hamper absorption of pesticides into leaves by reducing the number or aperture of stomata (pores in the leaf that control exchange of gases and liquids) or by altering leaf thickness or size. In addition, CO_2-induced changes in transpiration could limit uptake of soil-applied pesticides. For weed control, timing of application may need to be adjusted if elevated CO_2 decreases the time the weed spends in the seedling stage (i.e., the time of greatest chemical susceptibility). Overall, it is likely that weeds could still be controlled chemically, either through additional sprayings, or increased herbicide concentrations, but this would almost certainly alter the environmental and economic costs of pesticide usage.

What about other means of control? In the developing world, mechanical control is still the predominant means to prevent weed-induced crop losses. Tillage, a common form of weed control, cuts and discs roots. But one response to rising CO_2 levels is an increase in below-ground root growth relative to above-ground shoot growth (Ziska 2003). For some invasive weeds, asexual propagation from small root segments is commonly observed. For Canada thistle, an invasive North American weed, rising CO_2 can double root growth relative to shoot growth in the field (Ziska, et al. 2004). As a consequence, increasing tillage as a control measure would lead to additional plant propagation for this species in a higher CO_2 environment.

Biological control of pest plants by natural or manipulated means is also likely to be affected by increasing atmospheric carbon dioxide

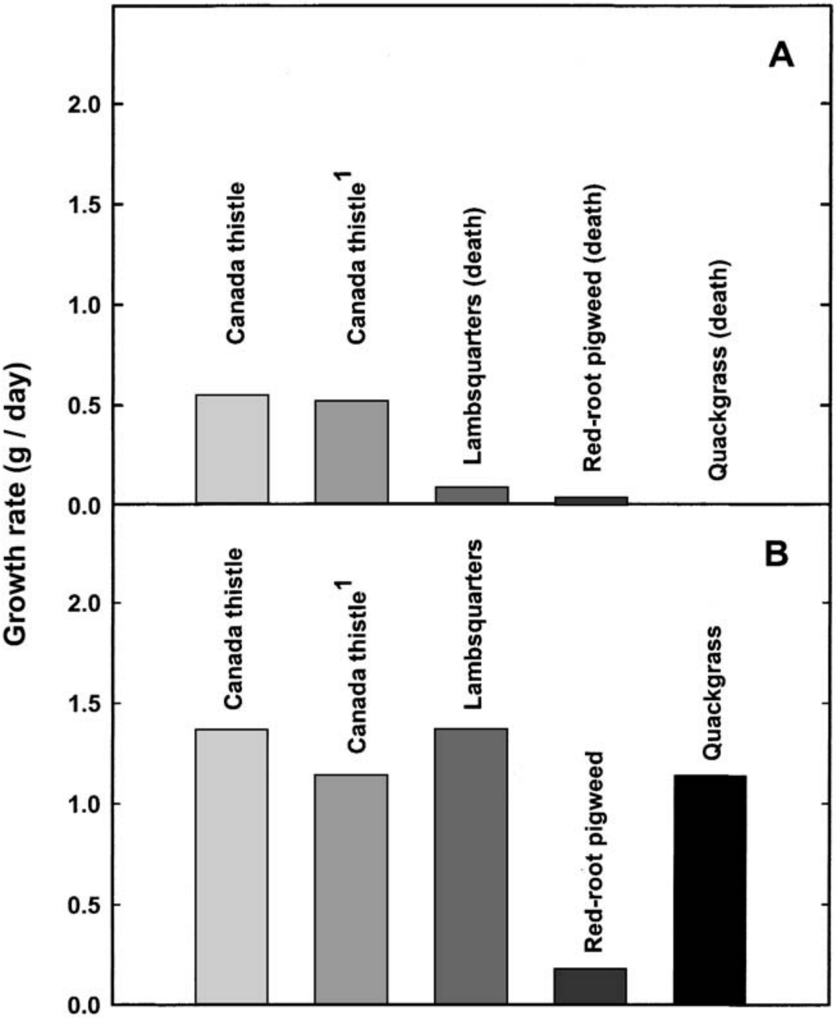

Figure 19.4 Change in growth rate (gram dry matter per day) for agronomic and invasive weeds when sprayed at recommended rates of herbicide at either: (A) current CO_2 or (B) future CO_2 levels (600-800 ppm). All growth rates less than 0.1 resulted in plant death. Herbicide was glyphosate in all cases except Canada thistle[1], which was sprayed with glufosinate. Overall, these data indicate a greater resistance to chemical control in weedy species as a function of rising atmospheric carbon dioxide.

(Norris 1982; Froud-Williams 1996). Since rising carbon dioxide can affect the development, growth, and reproduction of any given plant, such changes would alter any pest-plant synchrony with subsequent changes in control. In addition, rising CO_2 levels are likely to reduce the concentration of leaf nitrogen (Jablonski, et al. 2002). If insects are used as a biocontrol agent, this is likely to affect feeding patterns and the degree of induced damage. Overall, however, direct experiments to determine CO_2-induced changes in biocontrol of unwanted species have not been explicitly conducted.

CO_2 and Plant Biology, Revisited

Although the title of this book is *Controversies in science and technology*, there is no question that rising carbon dioxide levels will differentially stimulate the growth and function of plant species on a global basis, thereby affecting the flow of energy and carbon through ecosystems. Indeed, it seems fair to anticipate that, as carbon dioxide increases, ecosystem composition itself will change (e.g., cheatgrass and fires). In any event, increasing atmospheric carbon dioxide per se will have a number of consequences for both managed and unmanaged plant communities, and, hence, for all living things. It is imperative then, that we begin, in earnest, to assess the positive and negative aspects of these consequences in regard to both the natural environment and human society. It is regrettable that in the debate regarding rising CO_2 levels and global warming, that the direct impact of increased carbon dioxide on plant biology, and the role of plants in sustaining life, remains underappreciated by all sides.

Ultimately, one of the fundamental challenges we face in the 21st century is the unprecedented level of human-induced change. In addition to the rapid rise in atmospheric carbon dioxide, humans are significantly altering rates of nitrogen deposition (Wedin and Tilman 1996), the extent of tropospheric ozone (Krupa and Manning 1988), and land-use patterns (Pielke, et al. 2002). These induced changes will also, in time, transform life on a panoptic scale. It isn't just about warming anymore.

References

Belote, R. T. et al. 2003. Response of an understory plant community to elevated [CO_2] depends on differential responses of dominant invasive species and is mediated by soil water availability. *New Phytologist* 161:827–835.

Billings, W. D. 1990. Bromus tectorum, a biotic cause of ecosystem impoverishment in the Great Basin. In *The Earth in transition: Patterns and* *processes of biotic impoverishment,* ed. G. M. Woodwell, 310–322. Cambridge, UK: Cambridge University Press.

Billings, W. D. 1994. Ecological impacts of cheatgrass and resultant fire on ecosystems in the western Great Basin. In *Ecology and management of annual rangelands: US Forest Service general technical report,* ed. S. B. Monsen and S. G. Kitchen, 22–30. Ogden, UT: Intermountain Research Station.

Bowes, G. 1996. Photosynthetic responses to changing atmospheric carbon dioxide concentration. In *Photosynthesis and the environment,* ed. N. R. Baker, 387–407. Dordrecht, Netherlands: Kluwer Publishing.

DeLucia, E. H. et al. 1999. Net primary production of a forest ecosystem with experimental CO_2 enrichment. *Science* 284:1177–1179.

Dukes, J. S. 2002. Comparison of the effect of elevated CO_2 on an invasive species (*Centaurea solstitialis*) in monoculture and community settings. *Plant Ecology* 160:225–234.

Farnsworth, N. R. et al. 1985. Medicinal plants in therapy. *Bulletin of the WHO* 63:965–981.

Froud-Williams, R. J. 1996. Weeds and climate change: Implications for their ecology and control. *Aspects of Applied Biology* 45:187–196.

Gaskell, G. et al. 1999. Worlds apart? The reception of genetically modified foods in Europe and the U.S. *Science* 285:384–387.

Gergen, P. J. et al. 1987. The prevalence of allergic skin-test reactivity to eight common aeroallergens in the US population: Results from the second National Health and Nutrition Examination survey. *Journal of Allergy and Clinical Immunology* 80:669–679.

Hall, A. E., and L. H. Ziska. 2000. Crop breeding strategies for the 21st century. In *Climate change and global crop productivity,* ed. K. R. Reddy and H. F. Hodges, 407–419. New York: CAB International Press.

Hattenschwiler, S., and C. Korner. 2003. Does elevated CO_2 facilitate naturalization of the nonindigenous *Prunus laurocerasus* in Swiss temperate forests? *Functional Ecology* 17:778–785.

Horie, T. et al. 2000. Crop ecosystem responses to climate change: rice. In *Climate change and global crop productivity,* ed. K. R. Reddy and H. F. Hodges, 81–101. New York: CABI Publishing.

IRRI. 2002. Pests, diseases and weeds of rice. http://www.riceweb.org/research.

Jablonski, L. M. et al. 2002. Plant reproduction under elevated CO_2 conditions: A meta-analysis of reports on 79 crop and wild species. *New Phytologist* 156:9–26.

Kimball, B. A. 1983. Carbon dioxide and agricultural yield: An assemblage and analysis of 430 prior observations. *Agronomy Journal* 75:779–788.

Kimball, B. A. et al. 1993. Effects of increasing atmospheric CO_2 on vegetation. *Vegetation* 104/105:65–75.

Krupa, S.V., and W.J. Manning. 1988. Atmospheric ozone: Formation and effects on vegetation. *Environ. Pollut.* 50:101–137.

Mandersheid, R., and H. J. Weigel. 1997. Photosynthetic and growth responses of old and modern spring wheat cultivars to atmospheric CO_2 enrichment. *Agriculture, Ecosystems and the Environment* 64:65–71.

Mohan, J. E. et al. 2006. Biomass and toxicity responses of poison ivy (Toxicodendron radicans) to elevated atmospheric CO_2. *Proceedings of the National Academy of Sciences* 103:9086–9089.

Norris, R. F. 1982. Interactions between weeds and other pests in the agroecosystem. In *Biometeorology in integrated pest management,* ed. J. L. Hatfield and I. J. Thomason, 343–406. New York: Academic Press.

Pielke, R.A. et al. 2002. The influence of land-use change and landscape dynamics on the climate system: Relevance to climate-change policy beyond the radiative effect of greenhouse gases. *Philos. Trans. R. Soc. Lond.* 360:1705–1719.

Polley, H. W. et al. 1994. Increasing CO_2: Comparative responses of the C_4 grass *Schizachyrium* and grassland invader *Prosopis*. *Ecology* 75:976–988.

Poorter, H., and M-L. Navas. 2003. Plant growth and competition at elevated CO_2: On winners, losers and functional groups. *New Phytologist* 157:175–198.

Raskin, I. et al. 2002. Plants and human health in the twenty-first century. *TRENDS in Biotechnology* 20:522–531.

Rasse, D. P. et al. 2005. Seventeen years of elevated CO_2 exposure in a Chesapeake Bay Wetland: Sustained but contrasting responses of plant growth and CO_2 uptake. *Global Change Biology* 11:369–377.

Robinson, A., and Z. Robinson. 1997. Science has spoken, global warming is a myth. *The Wall Street Journal*, December 4.

Sage, R. F. 1995. Was low atmospheric CO_2 during the Pleistocene a limiting factor for the origin of agriculture? *Global Change Biology* 1:93–106.

Schimel, D. et al. 1996. Radiative forcing of climate change. In *Climate change 1995: The science of climate change,* ed. J. T. Houghton et al., 22–46. Cambridge, UK: Cambridge University Press.

Singer, B. D. et al. 2005. Increasing Amba1 content in common ragweed (*Ambrosia artemisiifolia*) pollen as a function of rising atmospheric CO_2 concentration. *Functional Plant Biology* 32:667–670.

Smith, S. D. et al. 2000. Elevated CO_2 increases productivity and invasive species success in an arid ecosystem. *Nature* 408:79–82.

Stuhlfauth, T., and H. P. Fock. 1990. Effect of whole season CO_2 enrichment on the cultivation of a medicinal plant, *Digitalis lanata*. *Journal of Agronomy and Crop Science* 164:168–173.

Treharne, K. 1989. The implications of the 'greenhouse effect' for fertilizers and agrochemicals. In *The greenhouse effect and UK agriculture,* ed. R. C. Bennet, 67–78. Ministry of Agriculture, Fisheries and Food, UK.

Uzun, E. et al. 2004. Traditional medicine in Sakarya province (Turkey) and antimicrobial activities of selected species. *Journal of Ethno-Pharmacology* 95:287–296.

Vengris, J. et al. 1955. Plant nutrient competition between weeds and corn. *Agronomy Journal* 47:213–216.

Wayne, P. et al. 2002. Production of allergenic pollen by ragweed (*Ambrosia artemisiifolia* L.) is increased in CO_2-enriched atmospheres. *Annals of Allergy, Asthma and Immunology* 80:669–679.

Wedin, D.A., and D. Tilman. 1996. Influence of nitrogen loading and species composition on the carbon balance of grasslands. *Science* 274:1720–1723.

Westbrooks, R. 1998. *Invasive plants, changing the landscape of America: Fact book*. Washington, DC: Federal Interagency Committee for the Management of Noxious and Exotic Weeds (FICMNEW).

Wilson, E. O. 1999. *The diversity of life*. New York: W. W. Norton Press.

Wodehouse, R. P. 1971. *Hayfever plants*, 2nd Edition. New York: Hafner Publishing.

World Health Organization. 2002. Traditional medicine: Growing needs and potential. *WHO Policy Perspectives on Medicines* 2:1–6.

Young, J. A. et al. 1987. Cheatgrass. *Rangelands* 9:266–270.

Ziska, L. H. 2000. The impact of elevated CO_2 on yield loss from a C_3 and C_4 weed in field-grown soybean. *Global Change Biology* 6:899–905.

Ziska, L. H. 2003a. Evaluation of the growth response of six invasive species to past, present, and future carbon dioxide concentrations. *Journal of Experimental Botany* 54:395–404.

Ziska, L. H. 2003b. Evaluation of yield loss in field sorghum from a C_3 and C_4 weed with increasing CO_2. *Weed Science* 51:914–918.

Ziska, L. H., and F. A. Caulfield. 2000. Rising carbon dioxide and pollen production of common ragweed, a known allergy-inducing species: Implications for public health. *Australian Journal of Plant Physiology* 27:893–898.

Ziska, L. H., and G. B. Runion. 2006. Rising atmospheric carbon dioxide and global climate change: Assessing the potential impact on agroecosystems by weeds, insects, and diseases. In *Agroecosystems in a changing climate,* ed. P. C. D. Newton et al., Boca Raton, FL: CRC Press, Taylor & Francis Group, pages 261–290.

Ziska, L. H., and J. R. Teasdale. 2000. Sustained growth and increased tolerance to glyphosate observed in a C_3 perennial weed, quackgrass (*Elytrigia repens*), grown at elevated carbon dioxide. *Australian Journal of Plant Physiology* 27:159–164.

Ziska, L. H., and K. George. 2004. Rising carbon dioxide and invasive, noxious plants: Potential threats and consequences. *World Resource Review* 16:427–447.

Ziska, L. H. et al. 1996. Intraspecific variation in the response of rice (*Oryza sativa* L.) to increased CO_2 and temperature: growth and yield response of 17 cultivars. *Journal of Experimental Botany* 47:1353–1359.

Ziska, L. H. et al. 1999. Future atmospheric carbon dioxide may increase tolerance to glyphosate. *Weed Science* 47:608–615.

Ziska, L. H. et al. 2003. Cities as harbingers of climate change: Common ragweed, urbanization and public health. *Journal of Allergy and Clinical Immunology* 111:290–295.

Ziska, L. H. et al. 2004a. Changes in biomass and root:shoot ratio of field-grown Canada thistle (*Cirsium arvense*), a noxious, invasive weed, with elevated CO_2: Implications for control with glyphosate. *Weed Science* 52:584–588.

Ziska, L. H. et al. 2004b. Quantitative and qualitative evaluation of selected wheat varieties released since 1903 to increasing atmospheric carbon dioxide: Can yield sensitivity to carbon dioxide be a factor in wheat performance? *Global Change Biology* 10:1810–1819.

Ziska, L. H. et al. 2005a. Alterations in the production and concentration of selected alkaloids as a function of rising atmospheric carbon dioxide and air temperature: Implications for ethnopharmacology. *Global Change Biology* 11:1798–1807.

Ziska, L. H et al. 2005b. The impact of recent increases in atmospheric CO_2 on biomass production and vegetative retention of Cheatgrass (Bromus tectorum): Implications for fire disturbance. *Global Change Biology* 11:1325–1332.