WEEDS IN A CHANGING CLIMATE

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ABSTRACT

Of the several aspects of global environmental change, some, such as an increase in atmospheric carbon dioxide concentration, are almost certain to continue and would have a large impact on weed biology, while others, such as increased nitrogen deposition, are not likely to affect weeds in agronomic situations. It is important to identify changing environmental factors and plant responses to them which are likely to affect the impact of weeds on crops, in order to modify management strategies accordingly. This paper reviews several ways in which weeds are pre-adapted to benefit greatly from increases in temperature and atmospheric carbon dioxide, and reviews the few recent field studies of weed-crop interactions under global change conditions, which often indicate the potential of larger crop losses due to weeds. Information is presented which indicates that weeds may be adapted to the current atmospheric concentration of carbon dioxide and may also evolve more rapidly than crops to take advantage of increases in atmospheric carbon dioxide. This suggests that current experiments may underestimate the impact of global change factors on crop losses due to weeds.

INTRODUCTION

Man's activities are causing global changes in several environmental factors, including an increase in atmospheric carbon dioxide concentration, a decrease in stratospheric and an increase in tropospheric ozone concentrations, deposition of nitrogenous compounds from the atmosphere into ecosystems, and global warming (Reddy & Hodges, 2000). Some of these factors, such as increased tropospheric ozone pollution (Chameides *et al.*, 1994), could have a significant impact on agriculture, while others, like nitrogen deposition (Vitousek *et al.*, 1997), are probably more important in natural ecosystems than in agriculture. Still others, such as increased ultraviolet-b radiation caused by loss of ozone in the statosphere, are probably most important for their impact on human health. Two global environmental change factors which we have good reason to believe would strongly affect weeds in agriculture are the increasing concentration of carbon dioxide in the atmosphere, and global warming. This paper discusses how these two factors may affect crop losses due to weeds and our ability to control weeds.

The concentration of carbon dioxide in the Earth's atmosphere has increased approximately exponentially from about 280 μmol/mol^{-1} before the Industrial Revolution in Europe to about 370 μmol/mol^{-1} currently, mostly due to deforestation and the burning of fossil fuels. A further doubling of the concentration by the end of the next century seems likely (Mearns, 2000), especially given the current lack of political will to reduce carbon dioxide emissions worldwide. Several plant physiological processes and the growth rates of many plants are responsive to concentrations of carbon dioxide in the range of the current concentration to double the current concentration. In addition to direct effects of carbon dioxide concentration on plant processes, increased concentrations of carbon dioxide increase the tolerance of plants to stresses such as drought, and high and low temperatures, which influence the distribution and competitiveness of weeds.

Global warming seems increasingly likely to result from the increase of "greenhouse gases," of which carbon dioxide is a major component (Mearns, 2000). Because temperature is one of the primary factors influencing the distribution of weeds, we can anticipate poleward shifts in weed distributions. This could potentially expose temperate zone agriculture to new, aggressive weed species currently limited by low temperatures. However, it should be kept in mind that global warming is only likely to occur if atmospheric carbon dioxide concentration increases, so it is the response of plants to the combination of elevated carbon dioxide and warmer temperatures that is of primary interest.

Just as plants are not uniform in their responses to temperature or any other environmental variable, they are also not uniform in their response to carbon dioxide concentration. In fact, much of the literature on responses of weed species to rising atmospheric carbon dioxide concentration has focused on the contrasting responses of plants with C_3 and C_4 carbon metabolism, combined with the well-known over representation of C_4 metabolism among weeds of agronomic importance. This narrow focus has produced an optimistic forecast of weeds becoming less competitive than crops as atmospheric carbon dioxide concentration rises. For reasons to be discussed, I think this view is overly optimistic, and that control of weeds in agriculture may become more difficult as the environment changes.

ADAPTATION OF WEEDS TO ELEVATED CARBON DIOXIDE AND TEMPERATURE

Several features of weed biology have pre adapted them to respond very positively to increases in atmospheric carbon dioxide concentration and global warming.

An increased rate of photosynthesis is the primary means by which elevated concentrations of carbon dioxide stimulate the growth rate of plants. In theory, this leads to a clear distinction between plants with C_3 and C_4 photosynthetic metabolism. Plants with C_3 photosynthesis should be responsive to increases in carbon dioxide concentration above the current ambient concentration of about 370 μmol/mol^{-1}, while plants with C_4 photosynthesis theoretically should be saturated for carbon dioxide even below the current atmospheric concentration (e.g. Tissue *et al.,* 1995). Indeed, all studies to date which have examined competition between C_3 and C_4 species as a function of carbon dioxide concentration have found that higher carbon dioxide concentrations favor the C_3 species (Table 1). This is, perhaps, the one bit of good news with respect to weed/crop interactions in the face of climate change. Of course, it is not good news for those trying to grow C_4 crops in competition with C_3 weeds, nor for the management of C_4 grasslands.

Table 1. Studies in which competition between C_4 and C_3 species has been examined at elevated carbon dioxide.

C_4 species (weed)	C_3 species (crop)	Environment	Elevated CO_2 favors	Reference
Amaranthus retroflexus	soybean	field	C_3	1
Sorghum halepense	meadow fescue	glasshouse	C_3	2
Sorghum halepense	soybean	chamber	C_3	3
Paspalum dilatatum	various grasses	chamber	C_3	4
Echinochloa glabrescens	rice	glasshouse	C_3	5
various grasses	alfalfa	field	C_3	6

References: Ziska, 2001; Carter & Peterson, 1983; Patterson *et al.*, 1984; Newton *et al.*, 1996; Alberto *et al.*, 1996; Bunce, 1993.

There have been no studies of competition between C_4 weed and C_4 crop species as a function of carbon dioxide concentration. However, it has been noted that C_4 weed species, as a group, have a larger stimulation of growth at elevated carbon dioxide than C_4 crop species (Ziska & Bunce, 1997), which would presumably favor weeds in competition. The stimulation of growth by elevated carbon dioxide in C_4 weed species results at least partly from a lack of saturation of photosynthesis for carbon dioxide at the current atmospheric concentration (Ziska & Bunce, 1997), which currently remains unexplained (Laisk & Edwards, 1998).

Among plants with C_3 metabolism, elevated concentrations of carbon dioxide usually produce morphological changes which nearly counter balance the stimulation in photosynthesis. In terms of classical growth analysis, elevated carbon dioxide tends to decrease Leaf Area Ratio (by decreasing Specific Leaf Area) almost as much as it increases Net Assimilation Rate (by increasing photosynthesis), such that Relative Growth Rate (RGR) is often increased only about 10% (cf. Poorter, 1993). However, a uniform 10% increase in RGR produces a relative increase in biomass which increases strongly with the absolute value of RGR (Bunce, 1997). It is probably primarily for this reason that the relative increase in biomass at elevated carbon dioxide is larger for fast-growing than for slow-growing species (Bunce, 1997). Weeds of agronomic importance, like crops, tend to have large RGRs, and thus a large relative increase in biomass in response to elevated carbon dioxide (Hunt *et al.*, 1991). While, for plants grown in isolation, there is no evidence that crops and weeds differ substantially in the magnitude of their growth response to elevated carbon dioxide (Bunce, 1997), in the few studies where C_3 weeds and C_3 crops have been grown in competition at different carbon dioxide levels, elevated carbon dioxide has most often favored the weed species (Table 2).

Table 2. Studies in which competition between C_3 weed and C_3 crop species has been examined at elevated carbon dioxide.

Weed	Crop	Environment	Elevated CO_2 favors	Reference
Chenopodium album	soybean	field	weed	1
Chenopodium album	sugar beet	chamber	crop	2
Taraxacum officinale	alfalfa	field	weed	3
Plantogo lanceolata	various grasses	chamber	weed	4
Taraxacum and *Plantago*	various grasses	field	weed	5

References: Ziska, 2001; Houghton and Thomas, 1996; Bunce, 1995; Newton *et al.,* 1996; Potvin & Vasseur, 1997.

Reasons why weeds are often favoured by elevated carbon dioxide in these studies of C_3 species are speculative. It could be that breeding for yield at high stand density has reduced the elongation response to competition in crops species, providing an advantage for weeds. Alternatively, elevated carbon dioxide has been found to speed seed germination in some species with small seeds (Ziska & Bunce, 1993), and weeds typically have smaller seeds than annual crop species. It is certainly to be expected that there will be cases where C_3 crops are more stimulated by elevated carbon dioxide than C_3 weeds. An example of this illustrated in Table 3, where we found that weeds in strawberry plots were less stimulated by elevated carbon dioxide than were the strawberry plants, and that the proportion of weed biomass which was from C_4 species also decreased with increasing carbon dioxide.

Table 3. Weed and strawberry above ground biomass (g m^{-2}) in field plots established in April 1998, in Beltsville, Maryland, and exposed continuously to the current ambient concentration of carbon dioxide, or 300 or 600 μmol/mol^{-1} above the current concentration. Experimental details are available in Bunce (2001).

	CO_2 treatment:		
	Ambient	+ 300	+ 600
Weed above ground biomass in the September 1999	49a	42a	44a
Proportion of weed biomass which was C_4 (%)	20a	8b	4b
Total above ground biomass in June 2000	257c	311b	383a
Proportion of weed biomass (%)	38a	23b	16b

Within rows, numbers followed by different letters were significantly different at P = 0.05.

Another aspect of the biology of weeds which pre adapts them to benefit from global changes in carbon dioxide and temperature is their ability to disperse and extend their range as environmental changes allow. Range extension by weeds is to be expected as atmospheric carbon dioxide rises, whether or not global warming occurs. This is because elevated carbon dioxide concentrations increase the ability of plants to tolerate both high and low temperatures. For warm temperatures, it is thought that two factors are involved. One is that the optimum temperature for photosynthesis of C_3 species increases with carbon dioxide concentration (e.g. Long, 1991), and another is that lower stomatal conductance at elevated carbon dioxide mitigates the dehydrating effects of high temperature stress. At present, increased tolerance of high temperatures at elevated carbon dioxide is primarily theoretical, because there has been very little experimental work on the topic (Taub *et al.*, 2000). Increased tolerance of low temperatures, however, has been repeatedly demonstrated for chilling sensitive plants of tropical or subtropical origin (Sionit *et al.*, 1981; Potvin & Strain, 1985; Boese *et al.*, 1997), as well as other plants (Bunce, 1993). Lower stomatal conductance and mitigation of chilling-induced water stress at elevated carbon dioxide has been demonstrated in some of these cases (Boese *et al.*, 1997).

While increased tolerance of temperature extremes with rising carbon dioxide applies equally to weeds and crops, as does global warming, the primary concern for weed control is the potential poleward range extension of some particularly aggressive weeds whose agronomic impact is currently limited by low temperatures. For example, Bunce & Ziska (2000) compiled data indicating that weeds have a larger impact on maize and soybean crops in the southern than in the northern United States, because of the different weed species involved. Accurate predictions of effects of environmental changes on weed distributions will require thorough analysis of which aspects of plant biology (e.g. seed germination, growth, reproduction, over-wintering) are limited by which aspects of the environmental temperature (e.g. length of growing season, mean growing season temperature, extremes of temperature). I doubt that we have this information in hand for many weed species. Of course there can be biological controls of weed distribution and abundance, for example by diseases and insects. Because the organisms involved probably have individualistic responses to environmental factors like temperature, biological control systems could have complex responses to environmental changes (Gutierrez, 2000), and studies are lacking.

Reduced stomatal conductance with increasing carbon dioxide is often cited as a response pre adapting plants to have increased tolerance of drought as atmospheric carbon dioxide concentration rises (cf. Drake *et al.*, 1997). Herbaceous species certainly have a larger absolute decrease in conductance than do trees, for example, but seem also to have a larger relative decrease in conductance (Bunce, 1992; Norby *et al.*, 1999). In extensive herbaceous vegetation, however, only minor (e.g. 5%) reductions in evapotranspiration are predicted to result from much larger (e.g. 50%) reductions in stomatal conductance at the leaf scale (Wilson *et al.*, 1999). This is because stomatal control of transpiration decreases with increasing spatial scale (McNaughton & Jarvis, 1991). While the impact of decreased stomatal conductance at elevated carbon dioxide on crop water loss may not be very important, reduced stomatal conductance would more directly translate into reduced exposure to atmospheric pollutants, such as ozone and oxides of nitrogen or sulfur (Polle & Pell, 1999). While the growth of many crop and forest species is sensitive to air pollutants (Polle & Pell, 1999), I am not aware of studies indicating the extent to which weed growth is inhibited by air pollution.

Even if weed species distributions did not change, nor did their tolerance of stresses, control of weeds would likely become more difficult as the concentration of carbon dioxide in the atmosphere rises and temperatures increase. There are several reasons for this expectation, most related to the more rapid growth rate at elevated carbon dioxide and warmer temperature. More rapid growth means that weeds will pass through the stage when they can be effectively controlled by post-emergent chemicals more quickly, narrowing the window of opportunity for control and increasing the probability of ineffective control of weeds. Similarly, for weed control by tillage, weeds which reproduce vegetatively, by rhizomes, for example, are likely to do so earlier in the season at elevated carbon dioxide and with warmer temperatures. Elevated carbon dioxide also often disproportionally increases plant mass below ground (Rogers *et al.*, 1994), making mechanical control less effective for weed species which spread by below-ground organs, even if tilled at the same above ground biomass. Experiments in glasshouses have indicated that glyphosate is less effective in killing or suppressing the growth of *Chenopodium album* and *Elytrigia repens* plants when plants have been grown at elevated carbon dioxide than when grown at the current ambient concentration of carbon dioxide (Ziska *et al.*, 1999, Ziska & Teasdale, 2000). For *Chenopodium album,* the results from the glasshouse experiments have been confirmed in field experiments (Ziska, personal communication). In field experiments, we also found that glyphosate was less effective in controlling *Cirsium arvense* (Canada thistle) grown at elevated carbon dioxide (Ziska and Bunce, unpublished data). Reasons for the lower effectiveness of glyphosate at elevated carbon dioxide have not been established. However, since in these experiments, pesticide applications were standardized in terms of active ingredient per unit of ground area, the amount of active ingredient per unit of plant material was less at elevated carbon dioxide. Differences in herbicide uptake due effects of growth at elevated carbon dioxide on leaf surfaces can not be ruled out. It seems probable that in many situations weed control may become less effective or more expensive as the climate changes.

ADAPABILITY OF WEEDS TO CLIMATE CHANGE FACTORS

The previous section dealt with responses to climate change factors for weed populations as they currently exist, without considering the possibility that weeds may evolve in response to projected changes in the environment.

The relatively small stimulation in relative growth rate, mentioned earlier, which typically occurs when C_3 plants are grown at elevated carbon dioxide concentrations suggests that the plants do not efficiently utilize the extra photosynthate produced. It has been hypothesized that this conservative response of plants may reflect their adaptation to the low carbon dioxide concentration (about 280 μmol/mol^{-1} which occurred for about 10000 years before the current exponential increase began about 200 years ago (Sage & Cowling, 1999). It was suggested that adaptations to the stresses associated with low carbon dioxide prevent plants from taking full advantage of increased carbon dioxide. This idea raises several questions: to what concentration of carbon dioxide are weeds adapted, will they undergo evolution as the atmospheric carbon dioxide concentration rises, how rapidly will this occur, and will it result in more competitive weeds? It has been demonstrated that carbon dioxide concentration can be a selective agent (Ward *et al.*, 2000), and that substantial genetic variation in responsiveness to carbon dioxide occurs in many plant species (reviewed by Ward & Strain, 1997), so that evolution may be expected as the carbon dioxide concentration in the atmosphere changes.

We conducted experiments with four annual weed species common to eastern and central North America, *Abutilon theophrasti*, *Chenopodium album*, *Datura stramonium*, and *Xanthium strumarium*, to determine the carbon dioxide concentration to which the plants are adapted. By analogy with plant adaptation to other growth limiting resources, it was assumed that the efficiency of the use of carbon dioxide would remain high up to the level of the carbon dioxide to which the plants were adapted, and that the efficiency would decrease at higher concentrations. Seeds from local Beltsville, Maryland populations were grown at 280, 370 and 460 μmol/ mol^{-1} carbon dioxide concentration in controlled environment chambers, and several measures of the efficiency of carbon dioxide utilization were made for each growth condition. The results (Bunce, 2002) indicated that for all of the species the efficiency of utilization of carbon dioxide was nearly constant between 280 and 370 μmol/mol^{-1} of carbon dioxide, and significantly lower at 460 μmol/mol^{-1}. For example, down-regulation of photosynthesis and reduction in specific leaf area occurred only at the highest carbon dioxide concentration, and leaf area per plant increased up to, but not above 370 μmol/ mol^{-1}. These results suggest that these annual herbaceous weeds are adapted to approximately the current atmospheric concentration of carbon dioxide, rather than the pre-industrial concentration. This suggests that evolution in these species in response to the changing atmospheric concentration of carbon dioxide has been rapid, and that we can anticipate further evolution in weed populations which will increase their growth rate at elevated carbon dioxide.

Numerous studies have indicated that widespread species such as weeds have populations which vary in their temperature responses, indicating adaptation to local temperatures. Of course, there are limits to adaptation to temperature within a species, or else distributions would not be limited by temperature. The projected increases in global temperatures are probably less than the variation in temperature found within the range of most weed species. Furthermore, elevated carbon dioxide may increase the ability to tolerate high temperatures. Weeds are therefore likely to be able to fully adapt to global warming except at the extremes of their distributions.

Genetic variation in the response of growth to carbon dioxide concentration has also been found within the few crop species which have been examined for such variation (cf. Ziska *et al.*, 2001). However, it is doubtful that crop breeding will rapidly increase the response of crop growth to elevated carbon dioxide. This is because any selection for increased responsiveness to carbon dioxide will be indirect for crops, and because traits resulting in increased crop yield at elevated carbon dioxide have not been identified. Many crop breeders use "modern elite" varieties as the starting point in breeding programmes, and such varieties may not posses the most useful traits for a higher carbon dioxide world. For example, in rice (Alberto *et al.*, 1996) and wheat (Manderschied & Weigel, 1997) greater responses of yield to elevated carbon dioxide occurred in older than newer varieties. In soybeans, the largest yield response occurred in the cultivar Mandarin (Ziska *et al.*, 2001), whose genes are probably not represented in any modern varieties.

Because of their greater genetic variation and the more direct selection for fitness, it seems likely that weeds will evolve more rapidly than crops to more fully exploit the increasing availability of carbon dioxide. Thus experiments with existing weed populations, which often indicate a potentially greater impact of weeds on crops under climate change conditions, probably underestimate the difficulty of controlling weeds in agriculture as the climate changes.

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