**The role of climate change and increasing atmospheric carbon dioxide on weed management:
herbicide efficacy.**

Lewis H. Ziska, PhD, USDA-ARS, Crop Systems and Global Change, 10300 Baltimore Avenue,
Beltsville, MD 20705.
Phone: 301-504-6639, email: l.ziska@ars.usda.gov

Abstract. Rising concentrations of carbon dioxide [CO₂] and a changing climate will almost certainly affect weed biology and demographics with consequences for crop productivity. The extent of such consequences could be minimal if weed management, particularly the widespread and effective use of herbicides, minimizes any future risk; but, such an outcome assumes that [CO₂] or climate change will not affect herbicide efficacy per se. Is this a fair assumption? While additional data are greatly desired, there is sufficient information currently available to begin an initial assessment of both the physical and biological constraints likely to occur before, during and following herbicide application. The assessment provided here, while preliminary, reviews a number of physical and biological interactions that are likely, overall, to significantly reduce herbicide efficacy. These interactions can range from climatic extremes that influence spray coverage and field access to direct effects of [CO₂] or temperature on plant biochemistry and morphology. Identification of these mechanisms will be essential to both understand and strengthen weed management strategies associated with rising levels of [CO₂] in the context of an uncertain and rapidly changing climate.

1. Introduction.

The vulnerability of agricultural productivity to sudden shifts in global climate associated with human emissions of greenhouse gases poses a clear threat to the global food supply. As such, the physical, or abiotic, implications for food security as a consequence of warmer temperatures, rising carbon dioxide concentration [CO₂], erratic precipitation, extreme weather events, have been the subject of much research (Rosenzweig and Parry, 1994; Lobell et al., 2008; Wheeler and von Braun 2013; *inter alia*). Such research efforts are of obvious necessity to quantify the vulnerability of the food supply in the context of climate uncertainty; however, such efforts do not always consider the role of rising [CO₂] or climatic change with respect to pest biology and the consequences for agricultural productivity.

Among biological constraints in agriculture, weeds are, and have been, recognized as representing a significant limitation to achieving potential yields (Oerke, 2006). They can compete directly with crops for physical resources such as light, but also compromise crop quality through contamination and act as a biological reservoir for insect pests and disease (Boydston et al., 2008, Swinton et al., 1994).

Because weed management is necessary to maximize global crop production, the adoption and implementation of a number of control strategies, including mechanical, biological and chemical, are used to maintain weed populations at economically acceptable levels. Such strategies vary greatly depending on culture, natural resources, environment, cropping system, etc. For developed countries such as the United States, Canada, Europe, Australia and Japan, chemical weed control via herbicide application is favored because of uniform application, high efficacy and cost reductions associated with mechanization and time (Gianessi and Sankula, 2003; McErlich and Boydston, 2013). In the U.S. for example, herbicides are routinely used to eliminate weeds in more than 90% of crop acreage (Gianessi and Reigner, 2007). In recent years, the use of herbicides for weed control has increased in developing regions where food security is paramount including China, India and Sub-Saharan Africa; in part, because of the potential for herbicides to improve both crop yields and save labor and energy (Gianessi, 2013).

At present, there are a number of reports indicating that rising [CO₂] and projected changes in climate could favor the growth and development of weeds over crops, with negative consequences for agricultural productivity (Reviewed by Peters et al., 2014; Ziska and McConnell, 2015; Varanasi et al., 2015; Korres et al., 2016). However, if the efficacy of current chemical management efforts can be maintained in such a scenario, then any additional weed pressures related to climate change and [CO₂] would be minimal.

Such an assumption, however, belies an increasing number of studies indicating that climatic change or rising CO₂ concentrations are likely to alter or negatively influence herbicide performance per se (e.g. Ziska et al. 1999; Ziska, 2010; Archambault 2007; Manea et al., 2011). As such, the objective of the current assessment is to derive, from the published literature, a novel synthesis of potential abiotic and biotic mechanisms that characterize how [CO₂] or climatic change impact herbicide efficacy. Such an initial assessment represents an essential step in describing likely impacts and improving herbicide performance with projected changes in [CO₂] or changes in the physical environment.

2. Chemical Application.

One of the fundamental aspects of herbicide efficacy is related to variation in the physical environment encountered during application. There are a number of climatic changes that are likely, in turn, to affect this aspect of herbicide performance (**FIGURE 1**).

Warmer temperatures or an increase in weather extremes (e.g. precipitation) could reduce field access necessary for herbicide application. Climate change induced inconsistencies in rainfall, wind, relative humidity or soil or air temperature could reduce spray coverage or retention times of active ingredients following application, depending in part, on spray and herbicide placement innovations (Muzik, 1976; Olson et al., 2000). Increases in precipitation (as single extreme events or higher averages) could dilute the herbicide following application as well as exacerbate leaching and potential ground-water contamination (e.g. Froud-Williams, 1996, Carere et al., 2011); windier conditions could increase the risk of drift. Higher temperatures could increase both absorption and translocation of foliar applied herbicides adding to efficacy, but also increase volatility and microbial breakdown (Atienza et al.,

2001). High humidity can reduce droplet drying after application and increase absorption of the herbicide (Anderson et al. 1993). Overall, increased environmental variation, exacerbated by climate change could influence delivery times, spray coverage, volatilization, movement and accidental injury associated with herbicide application (**FIGURE 1**).

3. Plant Based Changes.

Although physical changes in the environment can affect the timing and efficacy of chemical applications, there are a number of biological functions that are also influenced by climate change and increasing levels of atmospheric CO₂. These functions, which run the gamut from short-term biochemical changes to long-term changes in gene flow, hybridization and natural selection, are also likely to affect the efficacy of chemical weed management (**FIGURE 1**).

Biochemistry. Rising [CO₂] or temperature can increase photosynthesis, alter enzymatic activity and affect pigment production (Barnaby and Ziska, 2012). A number of herbicide sites of action are, in turn, specifically designed to disrupt these biochemical processes. Such herbicides include atrazine (Photosystem II inhibitor), amitrole (pigment inhibitor) and glufosinate (inhibitor of the enzyme acetolactate synthase, ALS). As such, [CO₂] or temperature induced increases in growth could, potentially, increase the efficacy of these herbicides. In contrast, there is strong evidence that rising [CO₂] can significantly reduce protein levels in a wide range of plant tissues, including leaves, stems, roots, tubers, seeds and grains (Cotrufo et al., 1998; Taub et al., 2008; Loladze 2014). Less protein would result in less demand for aromatic and branch chain amino acids, with a potential decline in the efficacy of herbicides that act as enzyme inhibitors (e.g. glufosinate, glyphosate) (Varanasi et al. 2015).

Leaves. Leaf orientation and surface area represents the primary target for absorption and translocation following herbicide application. If [CO₂] or temperature stimulates leaf number or area, then such a change would increase herbicide interception and absorption during spraying. In addition, increasing air temperature can affect cuticle and plasma membrane fluidity, improving herbicide uptake and translocation (Johnson and Young, 2002). In contrast, increases in the occurrence of severe stress (drought or flooding) would negatively impact herbicide applications by reducing leaf area or altering leaf

orientation (Zhou et al. 2007). In addition, increasing $[\text{CO}_2]$ or temperature could alter leaf surface characteristics through reduced stomata, increased leaf thickness or changes in cuticular wax viscosity or changes in pubescence so as to reduce chemical absorption (Ziska and Bunce, 2006). Finally, while rising temperature can increase absorption and translocation of most foliar-applied herbicides, sufficiently high temperatures can induce rapid metabolism which can reduce herbicide activity (Kells et al., 1984, Johnson and Young, 2002).

Whole Plant. Warmer temperatures or additional CO_2 can enhance plant developmental rates following seed emergence (Morison et al., 1999; Poorter and Navas, 2003). For example, Guo and Al Khatib (2003) demonstrated that the growth rates of pernicious weeds, including redroot pigweed, common waterhemp and Palmer amaranth, increased at high temperatures, reducing the amount of time spent at the seedling stage; i.e. the period of greatest herbicide sensitivity. Temperature and $[\text{CO}_2]$ can also affect herbicide efficacy by impacting phenological aspects of whole plant development such as leaf number, anthesis, or rate of senescence (Sicher and Bunce, 1998; Ziska and Bunce, 2006). Increasing $[\text{CO}_2]$ can also influence allometric changes (e.g. differential growth among plant organs) that, in turn, can affect herbicide interactions. For example, Canada thistle grown at ambient and projected CO_2 concentrations, showed a significant increase in root:shoot ratios (Ziska et al., 2004). The increase in root:shoot ratio resulted in a dilution of the active ingredient of the herbicide (glyphosate, sprayed at the manufacturers recommended dose) such that some roots survived. These roots then reproduced new shoots asexually and overall, the herbicide failed to control Canada thistle (Ziska et al. 2004; Ziska 2010). Such $[\text{CO}_2]$ -induced changes in root:shoot allocation may be of particular significance for perennial weeds that are capable of sexual and asexual reproduction since increased temperature or additional $[\text{CO}_2]$ could result in greater rhizome and photosynthate supply to below-ground structures (Rogers et al. 1992).

Plant Community. As temperature, climate and $[\text{CO}_2]$ change, it is likely that weed populations will change in parallel with cropping systems, with consequences for plant community composition and, of course, weed-crop interactions and chemical management (McDonald et al. 2009; Blumenthal et al., 2013; Varanasi et al. 2015). Such changes in weed demographics in conjunction with environmental

gradients are already in evidence. For example, at present, increasing minimum temperatures are associated with a greater increase in perennial relative to annual weeds in cultivated soybean along a North-South latitudinal gradient in the mid-western U.S. with consequences for herbicide application rates (Ziska, 2014). Ziska and Goins (2006) found that long-term (seasonal) exposure to elevated $[\text{CO}_2]$ during the growing season facilitated the number of C_3 weeds relative to C_4 grasses from the weed seed bank with significant changes in weed demographics and populations. The large stimulation in the number and size of C_3 weeds resulted in a significant $[\text{CO}_2]$ by glyphosate interaction with C_3 weed biomass remaining after glyphosate application at recommended doses (Ziska and Goins, 2006).

Evolution and Fitness. Anticipated environmental changes, including $[\text{CO}_2]$, temperature, precipitation, etc. will act to alter evolutionary selection among and within plant communities. At the agronomic level, differential selection between weeds and crops will have obvious consequences for chemical weed management.

Differential selection for weed fitness could, potentially, occur in response to $[\text{CO}_2]$. Carbon dioxide represents the source of carbon for photosynthesis, and is less than optimal in about 94% of all plants species (i.e. those that rely solely on the C_3 photosynthetic pathway). The current concentration of CO_2 already reflects a rapid increase in this resource (i.e., ~25%, from 320 to 400 $\mu\text{mol mol}^{-1}$ since 1965) and could lead to differential selection among crop and weed genotypes with respect to evolutionary fitness. To test for $[\text{CO}_2]$ -induced changes in fitness, two temporally distinct populations of wild oat (*Avena fatua*) were collected in 1966 and again in 2013 from the same location. A comparison of plant relative yield indicated that the more recent wild oat population had adapted to the increase in atmospheric $[\text{CO}_2]$ that had occurred over this period (~320 to 400 $\mu\text{mol mol}^{-1}$) (Ziska, unpublished data). The more recent wild oat population also showed increased competitive ability (greater relative biomass and seed yield) when grown with a cultivated oat line (*A. sativa*, “Clintland 64”) at the current $[\text{CO}_2]$. Obviously, environmentally-induced changes in fitness which favor weeds over crops are likely to heighten the need for chemical weed management, but additional data are needed to confirm these results.

Climatic or [CO₂]-induced changes could also, potentially, affect gene transfer and evolutionary fitness between crops and weeds. This may have particular relevance for herbicide efficacy. As has been evident since the introduction of herbicide tolerant soybean in the mid 1990s, there is an increasing emphasis on GMO-directed herbicide management (e.g., over 90% of the soybean currently grown in the U.S. is Round-up Ready). While this can be a successful means of weed control, long-term effectiveness of this management strategy is dependent on the absence of gene flow between the GMO crop and associated weeds. In soybean, none of the “worst” weeds (e.g. lambsquarters, pigweed) are genetically related to the crop; hence, there is little concern for genetic transference of herbicide resistance to the weed. However, there are a number of crop systems where the worst weeds are wild relatives of the domesticated crop, e.g., sorghum and shattercane, oat and wild oat, cultivated and wild sunflower, potato and nightshade, and limiting gene flow is necessary to achieve continuous chemical control (e.g. Arias and Reiseberg 1994).

One example of how climate or [CO₂] could impact gene flow is associated with weedy rice. Within rice systems, weedy, or red rice (*Oryza sativa*), is increasingly recognized as a major constraint in achieving maximum production (Chauhan, 2013; Zhang et al., 2016). A long-term USDA study indicated that increasing atmospheric [CO₂] from an early 20th century concentration (300 μmol mol⁻¹) to current (400 μmol mol⁻¹) and projected, mid 21st century values (~600 μmol mol⁻¹) resulted in greater synchronicity in flowering times and enhanced outcrossing rates between a cultivated herbicide-resistant line (Clearfield 161) and a weedy red rice accession (StgS) (Ziska et al., 2012). In turn, this resulted in an increase in rice dedomestication and a greater number of weedy, herbicide-resistant hybrid progeny (Ziska et al., 2012). These results, while preliminary, suggest that increasing [CO₂] by altering floral synchrony between related crops and weeds could adversely impact chemical efficacy through hybridization and transfer of herbicide resistance. At present it is unclear, however, if rising temperatures could also elicit similar changes in floral synchrony, gene transfer and herbicide efficacy.

Overall, at the agronomic level, weed-crop associations are likely to respond to differential selection pressures. Crops are cultivated, or selected artificially, for those desirable traits (e.g. disease

resistance) that can be preserved in order to pass on that specific trait through additional selective breeding. In contrast, non-cultivated, wild or weedy plants that compete with the crop are genetically and phenotypically diverse and subject to multiple selection factors. Rapid changes in the environment, emblematic of global climate change, are likely to have differential impacts as a consequence of these different selection pathways. Because crop selection is human-directed for economic traits, it is less subject to environmental perturbations; in contrast, weeds are likely to experience greater selection pressure as a function of environmental uncertainty and climatic change (Nevo, 2001; Hoffman and Hercus, 2000).

To enlarge upon this point, a number of studies have already indicated that for some agronomic pests, evolutionary adaptation can occur in response to global climate change. For example, researchers have documented adaptation to climate change in *Drosophila subobscura* (Rodriguez-Trelles and Rodriguez, 1998). Chakraborty and colleagues have suggested similar changes for plant pathogens (Chakraborty et al., 2000; Chakraborty and Data, 2002). For weeds, rapid genetic changes have also been shown for field mustard (*Brassica nigra*) in response to drought (Franks and Weiss, 2008); for endemic weed species in the mid-western Corn Belt with warming temperatures (McDonald et al., 2009); and, projected increases in the evolution of invasive weeds with climate change (Clements and Ditommaso, 2011). If, as seems likely, human and natural selection for fitness traits between weeds and crops proceed at different time scales, this has obvious consequences for rates of resistance and chemical management; not only for weeds, but other agricultural pests, in a rapidly changing climate.

4. Uncertainties and Critical Needs.

Chemical weed management is determined, in large part, by quantifiable damage that is associated with the presence of a given weed, and where and when those weeds grow. It is becoming increasingly clear that climate change and rising [CO₂] are likely to exacerbate weed populations, alter weed-crop demographics and influence overall weed damage (e.g., Varanasi et al., 2015). Furthermore, these same associated changes may also be simultaneously affecting the overall efficacy of herbicidal control, either through reducing optimal application times and circumstances; or alternatively, through weed biology and

differential crop-weed evolution. It is therefore urgent to understand the basis for any climatic or CO₂ shifts in herbicidal action; such an imperative is further emphasized as over-reliance on herbicides has resulted in unprecedented levels of single and multiple resistance within weed populations (Heap, 2014).

While the review presented here provides an initial synthesis regarding the probable interactions between herbicide efficacy and climate or [CO₂], there remain a number of critical needs regarding temporal and spatial impacts before, during and following herbicide application (**FIGURE 1**). Critical information includes, but is not limited to: (a) Quantification of mutation rates associated with climatic extremes that could alter herbicidal mode of action at the biochemical level; (b) An assessment of climate or [CO₂] induced changes in morphology (e.g. leaf thickness, number) and phenology (e.g. time spent in the seeding stage) that influence uptake and translocation of herbicide; (c) For weeds that have developed herbicide resistance, documentation of [CO₂] or climate induced changes in fecundity between resistant and sensitive populations to determine future selection; (d) Derivation of herbicide use rates resulting from reductions in efficacy associated with climate or [CO₂] and potential increases in weed resistance specific for a cropping system; and, (e) Identification or synthesis of non-chemical weed management strategies that could strengthen weed management with projected changes in climate and [CO₂].

5. Conclusions.

The potential effects of climate change on crop production and the consequences for food security are self-evident. However, pest management is an integral part of agricultural production as well, and as such, the impacts of climate change or [CO₂] on management, should also be considered. Globally, weeds represent the greatest potential limitation to crop production (e.g., Oerke, 2006). As weeds are primarily controlled in the U.S. by chemical means, any interaction between climate and [CO₂] on herbicide efficacy, particularly given the already rapid rise in herbicide resistance, should be of immediate concern. In that regard it is hoped that the initial assessment provided here will serve as a starting point for additional inquiry.

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Climate and increasing CO₂ can effect weed distribution, weed demographics and favor weed over crop growth at the time of herbicide application^{1,2,3}

Before

During herbicide application projected changes in climate, including extremes in wind, rain; as well as warmer and more variable temperatures can influence spray patterns and retention times^{4,5,6}

During

Following herbicide application, CO₂-induced changes in leaf morphology, or variation in root:shoot ratio can dilute herbicide uptake and distribution⁷. In addition, climate and/or CO₂ can reduce leaf protein levels (i.e. site of herbicide action)⁸ and herbicide persistence⁹.

After

Figure 1. Overview of potential climate, [CO₂] and their interactions on herbicidal control of agricultural weeds before, during and after herbicide application. Before: climate- or [CO₂] - induced changes in weed species populations, and [CO₂]-induced selection of weeds over crops will influence timing and herbicide selection; During: Variation and long-term trends in wind, temperature and precipitation can influence efficacy of spray patterns and herbicide retention times following spraying; After: Climate or

460 [CO₂] can have long-term physiological effects, such as reducing protein levels, that could potentially
461 reduce herbicidal mode of action.

462 ¹ Patterson 1995

463 ² Ziska and Goins, 2006

464 ³ McDonald et al. 2009

465 ⁴ Spillman JJ 1984

466 ⁵ Trenberth 1998

467 ⁶ Nguyen et al., 2015

468 ⁷ Ziska et al. 2004

469 ⁸ Taub et al.2008

470 ⁹ Bailey SW 2003