PERSPECTIVE

How may Climate Change affect the activity of Glyphosate on Weeds? Some reflections

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Abstract

The evidence of changes in the global climate being felt by all of the bio-physical environments on the Earth is undisputed. Well-established literature, some of which is summarized herein, shows that the climate change effects will modify agro-ecosystems, including the multiple interactions between crops and weeds. From the perspective of weed management, there is compelling evidence that climate change effects will alter the growth of both C3 and C4 weeds and C3 and C4 crops in their interactions in cropping environments. Such responses will not just modify the outcomes of weed-crop competition, but also affect the efficacy of weed management methods, including the performance of herbicides.

Glyphosate [N-(phospho-methyl) glycine] is unquestionably the world's most used and successful herbicide. Published research, over at least three recent decades, indicates that glyphosate's efficacy and activity on specific weeds may increase or decrease in the wake of elevated atmospheric carbon dioxide (eCO_2) concentrations, global warming and associated climate change effects (such as increased or decreased rainfall and droughts). Changed glyphosate activity under climate change has been attributed to several factors. These include modified plant morphology and physiology (e.g., lower number of stomata, increased leaf thickness and modified cuticle permeability, etc.), which affects plant uptake and also changes in translocation of the herbicide to metabolically-active target sites.

However, there is also evidence that, under some conditions, glyphosate activity on specific weedy taxa or groups of weeds may not be adversely affected by the dominant climate-modifying factors. In this article, we appraise some of the published evidence on glyphosate and reflect upon those factors and how the growth and vigour of weedy taxa might affect the efficacy of glyphosate, under eCO_2 and a warmer global climate. In our view, aside from the broad generalizations, the effects of eCO_2 and warming on glyphosate efficacy on major weeds cannot yet be discerned without more directed research.

Keywords: Climate change, eCO_2, global warming, weeds, crops, glyphosate, herbicidal activity

Introduction

Global climate change is now undisputed and has already caused shifts in temperature, rainfall and other weather patterns across the globe, putting animals, plants and human societies at risk (Stern, 2006; Blasing, 2016). The reasons for climate change are human activities, including the relentless burning of fossil fuels, deforestation, and the rising concentration of greenhouse gases (GHGs), i.e., methane (CH_4), carbon dioxide (CO_2), nitrous oxide (N_2O), and chlorofluorocarbons (CFCs) in the atmosphere.

These three gases are the primary cause of the greenhouse effect, while synthetic CFCs are responsible for the depletion of the ozone (O_3) layer. While enormous quantities of CO_2 are released mainly from the burning of fossil fuels, the other GHGs – methane and nitrogen oxides - are largely released by agriculture and industry. (IPCC, 2001; 2022).

Recent increases in GHGs (Table 1) show that over the past 200 years, human activities have introduced a huge concentration of GHGs into the atmosphere. Because GHGs absorb the infrared radiation (IR) discharged from Earth's surface, they are now contributing to the warming of the Earth's atmosphere much more than they did previously. However, climate projections suggest significantly increased warming by 2100, especially over land. There will also be changes in global precipitation patterns (IPCC, 2001; 2022).

Concentrations of GHGs will also keep on increasing in the 21st Century, due to the activities of a constantly growing human population. The consumption of non-renewable energy resources will also continue for several years. Even if the GHG emissions were decreased immediately, their amount would hike for some time because of the long-term persistence of these gases in the atmosphere and passive uptakes by impact-reducing agents, like the vast oceans and the great vegetation communities (biomes) of the world, which include the forests and grasslands (IPCC, 2021; 2022).

Carbon dioxide emissions are directly attributed to human activities, playing the most significant role in climate change. Atmospheric CO_2 concentration has now risen to above 415 ppm; it was about 300 ppm in the early ages of the industrial era (IPCC, 2022). The *Intergovernmental Panel on Climate Change* (IPCC) predicts that CO_2 concentration will rise to 700 ppm at the end of the 21st Century. Soaring concentrations of CO_2 [eCO_2], as a GHG, will have a profound, direct impact on the global temperature, although a part of warming is also contributed to by CH_4 and other GHGs.

Every 1000 Gt (Giga Tons) of cumulative CO_2 discharges is evaluated to probably cause an increase of 0.27°C-0.63°C in global surface temperature with the best estimate of 0.45°C (IPCC, 2022). It is expected that CH_4 is contributing almost 18% to the total global warming and this is still continually increasing.

If the increasing GHG emission trends are not arrested, the mean temperature of the globe is predicted to rise 1.4-5.8°C by the end of this century, which is an alarming figure that puts many thousands of plant and animal species, as well as humanity, in peril (IPCC, 2021; 2022).

Table 1 A summary of Greenhouse gas concentrations and rates of change*

	CO_2	CH_4	N_2O	# CFC
* Pre-industrial (1750-1800)	280 ppmv	700 ppbv	275 ppbv	0
* Concentration in 1994	358 ppmv	1714 ppbv	311 ppbv	503 pptv
* Rate of change in concentration (up to 1994)	1.5 ppmv/yr	13 ppbv/yr	0.75 ppmv/yr	18-20 ppmv/yr
** Concentration in 2022	413 ppmv	1909 ppbv	335 ppbv	511 pptv
** Rate of change (most recent 12 years)	2.4 ppmv/yr (0.6% per year since 2010	8.8 ppbv/yr (0.5% per year since 2010	0.99 ppbv/yr	Not available
* Atmospheric life (yrs)	50-200	12-17	120	102

* Source: IPCC, 2001; 2022; ppm – parts per million; ppb- parts per billion; ppmv or ppbv– by volume; # Chloro-fluoro-carbons, CFCs, are synthetic gases, discovered in the 1920s and used as refrigerants, propellant sprays, and foaming agents substitute. They are the primary cause of ozone layer depletion.

** Sources: (1) Our World in Data (**https://ourworldindata.org/greenhouse-gas-emissions**); T.J.Blasing (2016). *Carbon Dioxide Information Analysis Centre* (CDIAC). The Most Recent Greenhouse Gas Concentrations (**https://cdiac.ess-dive.lbl.gov/pns/current_ghg.html**); IPCC (2022); (2) The Global Carbon Project (GCP) [1] (**https://www.globalcarbonproject.org/carbonbudget/22/highlights.htm**).

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[1] **The Global Carbon Project** is a Research Project of ***Future Earth*** and a research partner of the ***World Climate Research Programme***. It was formed by the international science community to establish a mutually agreed knowledge-base to support the policy debate and action to slow down and ultimately stop the increase of GHGs in the atmosphere.

Plant growth and metabolic processes, especially photosynthesis, will respond directly to eCO_2, as well as to a warmer climate and other associated changes in climate, such as droughts, extreme hot periods or cold spells, or intermittent, heavy, wet-weather events. Influential reports (Parry, 1990; 1998; Rosenzweig and Hillel, 1998; Luo and Mooney, 1999) and research articles (Ainsworth and Rogers, 2007; Hatfield and Prueger, 2015) have explained in detail how such global climatic changes could modify plant growth rates, developmental processes (phenology), and several physiological processes, such as stomatal conductance, water use efficiency, and CO_2 fixation.

Variations in agricultural production will arise due to direct impacts of eCO_2, higher temperatures, soil moisture deficits and higher exposure of plants to O_3, and combinations of these factors. These factors would have direct effects at the whole plant level, or indirect effects, at the system level, for instance, by modifying crop weed interactions, changing nutrient cycling processes, as well as the incidence of insect pest damages and plant diseases (Fuhrer, 2003).

The predictions are that climate change may cause a decrease in agricultural yields of some of the world's major crops, such as wheat (*Triticum aestivum* L.), rice (*Oryza sativa* L.) and maize (*Zea mays* L.) and these effects would be significantly felt in regions and countries that are also most vulnerable. As a consequence of changes in agro-ecosystems, there is a high likelihood of increasing food insecurity across many regions of the world as climate change occurs (Wang et al., 2018; Neupane et al., 2022).

There is also considerable evidence that climate change will have a direct influence on both the abundance and persistence of colonizing taxa (weedy species) in human-modified environments. The spread and geographical distribution of many globally-important weeds are also likely to increase as their ranges expand. Such effects are likely to have major flow-on effects on how weeds will compete with crops in a warmer and CO_2-enriched environment and on weed management in both agricultural and non-agricultural settings (Carter and Peterson, 1983; Patterson, 1985; 1995a, b; Alberto et al., 1996; Patterson et al., 1999; Bunce, 2000; 2001; Ziska, 2000; 2003a, b; Ziska and Dukes, 2011; Chandrasena, 2009; Varanasi et al., 2016; Ramesh et al, 2017).

Ziska and other researchers in the USA first demonstrated that changes in climatic conditions may decrease the efficiency of certain herbicides (Ziska and Bunce, 1997; Ziska et al., 1999; Ziska and Teasdale, 2000; Ziska and Dukes, 2011). They attributed the changes, variability and unpredictable effects on variations in the uptake, translocation, metabolic detoxification, vacuolar sequestration, and other mechanisms by which plants metabolize herbicides (Ziska and Dukes, 2011; Shaner et al., 2012; Varansi et al., 2016). Since the studies intensified in the 1990s, a wealth of evidence has emerged, demonstrating the likely general (adverse) effects of climate change on crop yields (Wilcox and Makowski, 2014; Wang et al., 2018; Raza et al., 2019) and the possible stimulation of growth of many weed species (Ziska, 2003; Ziska et al., 2004; Ziska and Dukes, 2011; Clements et al, 2014; Jabran and Dogan, 2020; Siddiqui et al., 2022).

However, data and information available on climate change effects on the field performance and activities of specific herbicides are somewhat limited, especially on the most widely used global herbicides, which include glyphosate [N-(phosphonomethyl) glycine]. Weed scientists agree that glyphosate is perhaps a '*once-in-a-century*' herbicide, based on its efficacies on a broad spectrum of weed species, commercial success in many countries, and popularity among farmers and weed control practitioners in diverse applications (Duke and Powles, 2008).

The objective of this review is to re-appraise the major findings of the published literature and reflect upon our own research on potential climate change effects on managing weeds with glyphosate. Glyphosate is likely to continue as the world's most used herbicide (Benbrook, 2016; Van Bruggen, et al., 2018; Green, 2018) in the current decade and beyond.

Duke (2018) explained that "*much has happened since the last such review ten years ago [Duke and Powles, 2008], but nothing has happened to detract from the "once-in-a-century herbicide" descriptor that we gave it then*". Glyphosate, however, is under intense scrutiny for its environmental and health effects (Duke, 2018; Kanissery et al., 2019).

Projections are that in the current decade glyphosate usage will still grow at about 5% per annum[2]. As reviewed herein, studies on the interactions between eCO_2, warming and other factors affecting glyphosate efficacy have also continued with high intensity in the last decade with some studies focusing heavily on the likely mechanisms of glyphosate tolerance by treated plants.

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[2] The glyphosate market was valued at US$9.016 billion in 2020. It is expected to grow at a CAGR of 5.1% per year to reach US$12.771 billion by 2027 (**https://www.researchandmarkets.com/reports/5576420/)**.

Major effects of Climate Change

The vast global climate change knowledge repository shows that the changes in the global climate will have flow-on impacts on people's livelihoods, agriculture, and natural ecosystems (Parry, 1990; 1998; Drake and Gonzàlez-Meler, 1997; Rosenzweig and Hillel, 1998; Dukes and Mooney, 1999; Luo and Mooney, 1999; Stern, 2006; Ziska, 2008; Hatfield and Prueger, 2015; Tollefson, 2021).

Table 2 provides a summary of likely effects, of which the first two are relevant to predicting how weeds may respond to climate change and the implications for weed management in both cropped and non-cropped areas. Due to climate change, if the natural habitats of native plant species and vegetation communities undergo significant changes, some weedy species will prosper in those conditions because they have the genetic makeup and inherent adaptations to survive in diverse and stressful conditions (Chandrasena, 2009; Ziska and Dukes, 2011).

Changes that are already on the planet, such as extended periods of elevated temperatures and droughts, increased rainfall and extreme weather events such as floods, cyclones and tornados), are all habitat disturbances. Inevitably, such disturbances will favour the growth of fast-growing, opportunistic, colonizing taxa, which are likely to move into and dominate those habitats (Dukes and Mooney, 1999; Ziska and Dukes, 2011; Hatfield and Prueger, 2015).

In reviewing climate change effects on US Agriculture, Hatfield et al. (2014) summarized the following as the most likely future effects:

- In the last 40 years, there has been an increase in interruptions in agricultural productivity and it is expected to continue throughout the next 25 years. The majority of crops and livestock will face growing negative impacts by mid-century or beyond.
- Several agricultural areas will suffer greater declines in crop and livestock production from stresses, due to the disruptions caused by plant and animal diseases, weeds, insect pests, and other stresses induced by climate change.
- Recent losses of agricultural land and water resources due to extreme weather conditions especially increasing rainfall will continue to pose problems for irrigated and rainfed agriculture unless they are mitigated by the adoption of new resource conservation methods.
- Agriculture and associated socioeconomic systems have already begun to adapt to the current climate change scenarios; however, more modernization and investments will be required to keep the pace of this adoption process as climate change unfolds over the next 25 years.
- The impact of climate change on agriculture will lead to serious concerns about food security, both in the U.S.A. and worldwide, by variations (decreases) in final crop yields and (increases) in commodity prices and also significantly affect food storage, processing, transportation and selling.
- Implementing adaptation initiatives to climate change can help in delaying and decreasing some of the well-established negative impacts.

Effects of eCO_2 on plant growth

Plants will feel the effects of eCO_2 directly through their physiological processes. Elevated CO_2 will affect how they 'fix' CO_2 in photosynthesis and how their stomatal pores respond by opening more or closing. Higher rates of photosynthesis and more efficient gaseous exchange (through stomata) will increase plant growth rates (Carter and Peterson, 1983; Ziska and Bunce, 1997; Dukes and Mooney, 1999; Luo and Mooney, 1999; Ziska and Dukes, 2011; Lee, 2011).

Reviews by Griffiths et al. (2013), Lundgren et al. (2014) and Christin and Osborne (2014) have discussed C_4 photosynthesis, comparing the efficiencies of C_4 plants with C_3 plants and other mechanisms of CO_2 fixation. The most common CO_2-fixation mechanism in plants is C_3 photosynthesis, present in 95% of all species. It involves CO_2 capture and conversion into a 3-carbon sugar (glyceraldehyde-3-phosphate) by the enzyme RuBisCo (Ribulose-1,5-bisphosphate carboxylase-oxygenase). The second-most important mechanism - the C_4 pathway - firstly 'fixes' CO_2 into 4-carbon sugars (oxaloacetic acid and malic acid) and involves a different enzyme (phospho-enol-pyruvate carboxylase, PEP-carboxylase). A third pathway, common in succulents, is *Crassulacean Acid Metabolism* (CAM photosynthesis).

The efficiencies of the different photosynthetic pathways are governed by RuBisCo and PEP-carboxylase enzymes, which have different affinities to CO_2. How cells are arranged inside leaves affects the efficiency of CO_2 assimilation by chloroplasts in leaves. C_4 plants have a special type of leaf anatomy, called *Krantz* anatomy in which chloroplast-bearing bundle-sheath cells surround the veins, which supply food and water to leaves. This cell arrangement (an internal 'CO_2 pump') allows CO_2 to be fixed by those special cells and efficiently transfer photosynthetic products from their chloroplasts to the adjacent transport system (phloem) (Griffiths et al., 2013; Lundgren et al. (2014).

As a consequence of the more efficient CO_2 fixation pathway in C_4 species, increasing the external CO_2 concentration above the ambient levels could be expected to have small or negligible effects on the net photosynthesis in C_4 plants. Nevertheless, higher photosynthetic rates, growth stimulation and enhanced biomass production for C_4 plants have been recorded with eCO_2 levels. Such responses are generally due to changes in resource partitioning, accelerated phenology (i.e. floral development, prolonged leaf senescence and enhanced water potentials resulting from stomatal closure at eCO_2 (Carter and Peterson, 1983; Patterson, 1995a; b; Ziska and Bunce, 1997).

While not all plants may respond equally, the combined effects of eCO_2 and higher temperatures will alter a plant's ability to compete with another species, in any given environment (Ziska and Bunce, 1997; Drake and Gonzàlez-Meler, 1997; Ziska and Dukes, 2011). The evidence is that eCO_2 could make some species stronger, enabling them to use both water and nutrients more efficiently and better tolerate stresses, such as drought and fluctuating temperature (Carter and Peterson, 1983; Ziska and Bunce, 1997; Luo and Mooney, 1999; Bunce, 2001; Ziska and Dukes, 2011).

There is a sizable number of previous articles that have attempted to determine the effects of eCO_2 on several C_3/C_4 crop/weed combinations (Patterson et al., 1984; Ziska and Bunce, 1997; Ziska, 2000, 2001, 2003). Unsurprisingly, results reveal that C_4 plants show less response to eCO_2, whether they are a weed or crop than C_3 plants. Further, most research appears to indicate that C_3 weeds are likely to have greater negative impacts on the growth rate and biomass of both C_3 and C_4 plants under eCO_2 than do C_4 weeds.

However, while most studies suggest a larger relative response of C_3 to C_4 plants under eCO_2, it should not be assumed that C_4 plants are incapable of responding to higher CO_2 levels. Species-specific responses to eCO_2 and warmer conditions in C_4 plants are strongly indicated by research. The positive responses of C_4 plants also appear to be independent of any improvement in water relations even in the absence of drought (Ziska and Dukes, 2011).

Colonizing taxa, whether C_3 or C_4, already express innate abilities to withstand environmental stresses. This means that they will most likely benefit more from higher temperatures and eCO_2 than their non-weedy relatives and other slow-growing plants (Luo and Mooney, 1999). Such changes will assist the spread and distribution of many species across the globe, in terms of both altitude and latitude, and their persistence and competitiveness in different habitats (Ziska and Bunce, 1997; Ziska, 2000; 2003; Ziska and Teasdale, 2000; Ziska and Dukes, 2011; Lee, 2011).

Effects of elevated temperature on plant growth

Temperature regulates plants' physiological processes, acting as a determining factor for seed germination, and phenological processes, such as flowering, fruiting and seed formation, all of which are likely to be affected by climate change. Changes in temperature, particularly the frequency and duration of periods of elevated temperatures and eCO_2 may combine to produce important modifications to seasonal rainfall patterns, droughts, local weather, and regional climates, and periods of moisture stress across large landscapes (Parry, 1990; 1998; Rosenzweig and Hillel, 1998; Bunce, 2001).

With global warming, plants, in many parts of the world, will experience not just stress due to higher temperatures but also moisture deficits. However, the way plants feel these effects are unlikely to be uniform in various regions. In the tropics, warming, even by a few degrees, will increase evapo-transpiration from plants to a specific point where the growth rate of some species would suffer due to lower moisture content. However, shifts in rainfall patterns (intermittent and heavy rainfall events and flooding) could balance such responses, under a changing climate scenario.

Temperature is the prominent factor that affects plant growth at high (above 50 ^{0}N) and mid-latitudes (above 45 ^{0}N). In such cold regions, warming would extend the growing season of plants, although the effects on any plant species will be influenced by other factors, such as rainfall. The responses will vary from region to region, and from species to species (Luo and Mooney, 1999; Bunce, 2000; 2001).

Climate change research also shows that the beneficial effects of eCO_2 on most crops might be negated by warming and associated changes, such as extended periods of droughts or intermittent, heavy rainfall events. Persistently higher temperatures will have a considerable impact on the growth rates and phenology of plants (Lee, 2011), such as the flowering time and duration in mass-flowering crop species, as well as the success of pollination, via insects. Similar effects would be felt by weedy taxa, but they would be better adapted to respond to such changes.

In a well-studied example from Australia, Scott et al. (2014) reported that buffel grass (*Cenchrus ciliaris* L.), a C_4 grass, was able to acclimate and grow at warmer temperatures (growth at 35°C versus 25°C) in Australia. The climate suitability modelling prediction is that the spread of buffel grass southwards on the Australian continent is inevitable, as the species shows the capacity to rapidly acclimate and persist under warmer conditions. Although buffel grass is a desirable pasture grass, this range shifting is likely to lead to greatly increased future management costs as it begins to occupy conservation areas and other habitats away from pastures (Scott et al., 2014; Webber et al., 2014).

Combined effects of eCO_2 and warming on plant growth

Over the past two decades, attempts have been made to better clarify crop losses due to weeds that may occur under climate change as plant growth is strongly affected by both CO_2 concentrations and temperature. Research indicates that crop yield losses are likely to be quite significant, due to greater abundance, growth vigour and persistence of weedy taxa in most agro-ecosystems, under future climate change (Ziska, 2000; 2003; Milberg and Hallgren, 2004; Oerke and Dehne, 2004; Oerke, 2006; Ziska and Dukes, 2011; Hatfield et al., 2011; 2014; Liu et al., 2017; Gharde et al., 2018; Neupane et al., 2022).

Evaluating the impacts of elevated temperature and CO_2 on two annual C_3 and C_4 weeds – common lambsquarters (*Chenopodium album* L.) (C_3), and foxtail grass [*Setaria viridis* (L.) P. Beauv] (C_4) in climate chambers, Lee (2011) found that both factors affected the germination, phenology and growth stages of the species. Germination and flowering time were more affected by a 4°C increase in temperature than eCO_2 (1.8 times above ambient CO_2). Higher temperatures delayed seedling emergence by 26 and 35 days, respectively, for lambsquarters and foxtail grass. The flowering times were also delayed by 50 and 31.5 days, respectively for the two species.

The higher temperature alone greatly reduced the biomass and seed production of both species with the effects being more dramatic for the C_4 species. However, eCO_2 compensated for the disadvantage caused by warmer conditions, resulting in increased biomass and seed production of both species. Again, the stimulation of growth by the combined warmer and eCO_2 conditions was more dramatic for the C_4 weed than for the C_3 grass. (Lee, 2011).

Climate chamber studies by Temme et al. (2015) also showed differential responses of 28 C_3-species, including several weeds (16 forbs, 6 woody, and 6 grasses) to low CO_2 (160 ppm), ambient (450 ppm) and eCO_2 (750 ppm) conditions. The study focused on the leaf growth responses [measured by specific leaf area; leaf area ratio; leaf-mass fraction], relative growth rates and allocation of resources to root systems. Fast-growing species benefitted from eCO_2 by increasing their plant biomass but suffered significantly under low CO_2 (160 ppm). Interestingly, *fast growers grew relatively fast and slow growers grew relatively slowly irrespective of CO_2 levels*. For all species, eCO_2 increased the relative growth rate (RGR) by 8% but low CO_2 had a much more profound effect, decreasing the RGR much more significantly (by 23%).

The differential responses of contrasting plant morphological groups prompted Temme et al. (2015) to state that "*winners will continue to win*" under eCO_2. In their view, flowering plants, which evolved over the past 100-125 or so million years have not had sufficient time in evolutionary terms to adjust their physiology and metabolism (i.e. RuBisCo enzyme-related) to the changing CO_2 levels. In their view, in the future, the dramatic changes in the CO_2 levels will ultimately determine how individual species, their populations and vegetation communities evolve and change [3],

In a recent review, Vila et al. (2021) stated that although the individual effects of climate change and of effects of weeds on crop yields have been evaluated for many global crops, their combined effects have not been well studied. Conducting a meta-analysis by observing 171 cases, which measured the individual responses and integrated effects of weeds and eCO_2, drought or high temperature on 23 crop species, Vila et al. (2021) found the integrated impact of weeds and climate change to be additive and the effects of weeds alone on crop yields can be either similar to the ones that are now (average losses of 28% for a range of global crops and situations) or more detrimental than environmental changes (such as droughts), under climate change. Hence, the management of arable weeds, to reduce their harmful effects on crops, is becoming even more crucial now than ever before, to ensure global food security (Vila et al., 2021).

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[3] Fossil evidence shows that the Angiosperm evolution occurred in the late Cretaceous Period, about 125-100 million years ago.

In addition to increased growth, photosynthetic rates and changes in resource allocation to shoots or underground parts, seed production in many annual weeds could also increase or decrease as the climate warms up and CO_2 levels rise. In one well-studied example, Navie et al. (2005) reported that parthenium (*Parthenium hysterophorus* L.) produced 16,000 seeds per plant under a warm temperate regime (32/24°C) but significantly increased its seed production (19,000 seeds per plant) under a cooler temperate regime (25/16°C). Nguyen et al. (2017), in recent research, confirmed that eCO_2 and warmer conditions, as well as intermittent wetter and drier cycles, under climate change, would greatly enhance the growth and reproductive output of parthenium weed.

Our work, in Turkey (Jabran and Dogan, 2020), with prickly lettuce (*Lactuca serriola* L.), false barley (*Hordeum murinum* L.) and cheatgrass (*Bromus tectorum* L.) showed that warmer conditions (25/15 °C day/night vs. 20/10 °C day/night) and eCO_2 (800-900 ppm) stimulated the growth and biomass production by all three species. The growth stimulation by eCO_2 alone was also more significant than that caused by the higher temperature regime alone.

However, we detected significant interactions of the two climate change factors with nitrogen (N) fertilizer applications [controls with no added N, vs. 60 kg/ha (medium) or 120 kg/ha (high)]. Nitrogen applications stimulated the leaf growth and biomass production of prickly lettuce and cheatgrass more than that of false barley. Based on these results, we identified a clear need to study 'species-specific' interactions of not just the primary climate change factors (CO_2 and temperature) but also with external inputs in agriculture, such as N fertilizers and moisture regimes, under future climate scenarios.

Differential response of Weeds and Crops to elevated CO_2

Over the past three decades, much research has focused on the effects of elevated CO_2 levels on crops and weeds with these different photosynthetic pathways. Of the 15 crops, which supply 90% of the world's calories, 12 are C_3 plants. These include rice, wheat and soybean. The other 10%, including maize, sorghum [*Sorghum bicolor* (L.) Moench], proso millet (*Panicum miliaceum* L.), pearl millet [*Cenchrus americanus* (L.) Morrone] and other millets) and sugar cane (*Saccharum officinarum* L.), are C_4 crops.

The majority of weeds in the world are C_3 plants. Measurements show wide variations in the way weeds respond to higher CO_2, both within populations of the same species and between species. In general, C_3 weeds increase their biomass and leaf area under eCO_2 more than C_4 weeds. Other factors, such as higher temperature, high sunlight, and availability of abundant water and nutrients also affect the weeds' responses (Patterson, 1985; Patterson, 1995a, b).

Elmore and Paul (1983) showed that 14 out of 18 of the *'World's Worst Weeds'* are C_4. Overall, C_4 plants constitute a small portion of the total population of plant species in the world (less than 1000 out of 250 000). The *Weed Science Society of America's Composite List of Weeds* comprises about 2000 species, in 500 genera, and 125 plant families. Of these, at least 146 species, in 53 genera, and 10 families, have the C_4 pathway. In percentage terms, this is 17-fold higher than the C_4 plants among the total world plant population, which indicates the significance of the C_4 pathway for weedy taxa (Elmore and Paul, 1983).

While C_4 plants are photosynthetically more efficient under eCO_2 than C_3, research suggests that eCO_2 levels will stimulate the growth of both C_3 crops and C_3 weeds. A doubling of CO_2 may even cause a 10-50% yield increase in some C_3 crops, which is highly beneficial. Given that C_4 plants are already photosynthetically efficient, eCO_2 levels may not affect them much. Therefore, yield increases in C_4 crops under eCO_2 scenarios are likely to be much lower (only up to about 10%) or none at all (Patterson, 1995a, b; Patterson et al., 1999; Ziska, 2001; 2003a).

Among the 14 most aggressive global weeds are tropical grasses, which are C_4 plants, including barnyard grasses (*Echinochloa* P. Beauv. spp.), paspalum (*Paspalum* L. spp.), large crabgrass [*Digitaria sanguinalis* (L.) Scop.], Bermuda grass [*Cynodon dactylon* (L. Pers.], cogongrass [*Imperata cylindrica* (L.) P. Beauv.], goosegrass [*Eleusine indica* (L.) Gaertn.] and johnson grass [*Sorghum halepense* (L.) Pers.]. While all such species may not show increased growth under higher CO_2, Patterson (1995a, b) and Patterson et al. (1999) suggested that they could become much harder to control because, as C_4 plants, they are well tolerant to heat and moisture stress than C_3 species. Therefore, the simple notion that climate change will only benefit C_3 plants may not be entirely accurate (Patterson, 1995a, b; Patterson et al., 1999).

In some early research, Ziska and Bunce (1997) compared the effect of eCO_2 (720 ppm), on the biomass production of six major C_4 weeds - redroot pigweed (*Amaranthus retroflexus* L.), barnyard grass [*Echinochloa crus-galli* (L.) P. Beauv.], fall panic grass (*Panicum dichotomiflorum* Michx.), foxtail grasses [*Setaria faberi* Herm. and *Setaria viridis* (L.) P. Beauv.], johnsongrass and four C_4 crops – amaranth (*Amaranthus hypochondriacus* L.), sugar cane, sorghum and corn. The photosynthetic rates of eight of the ten species increased by 20% and the increase for C_4 weeds was double that of the C_4 crops, at higher CO_2, which produced significantly higher biomass.

The general view (Ziska and Dukes, 2011) is that weed-crop competition, irrespective of whether they are C_3 or C_4 species, could become more intense under future climate change, particularly under rising concentrations of CO_2. Ziska (2003b) had earlier reported that in a 'weed-free' environment, eCO_2 (250 ppm above ambient) caused a remarkable rise in leaf size and weight of sorghum (a C_4 crop) but had no remarkable impact on the seed yield or above-ground biomass comparative to ambient CO_2 levels.

At ambient CO_2 levels, the presence of velvetleaf (*Abutilon theophrasti* Medik.), a C_3 weed, had no effect on either the sorghum grain yield or total dry matter production. However, at eCO_2, a 3-fold increase in velvetleaf growth and biomass caused significant yield and biomass losses in sorghum. In comparison, redroot pigweed (C_4), growing at ambient CO_2, caused a remarkable reduction in the aboveground dry matter production of sorghum but not grain yield. Although, at eCO_2, the C_4 weed became much more aggressive and caused significant losses in both sorghum grain yield and dry matter, indicating potentially higher yield loss in a commonly grown C_4 crop from weedy competition in a future climate with eCO_2 (Ziska, 2003b).

Such research has clearly established that under eCO_2 and warmer conditions, growth rates and dry matter accumulation of both C_3 and C_4 weeds could increase, particularly if other favourable conditions prevail (i.e. moisture). In one study from Southeastern USA, Runion et al. (2008) reported significantly increased growth of sicklepod (*Cassia obtusifolia* L.; C_3 legume) and Johnsongrass [*Sorghum halepense* (L.) Pers.; a C_4 grass] under eCO_2 (575 ppm) when compared with ambient CO_2 (375 ppm). Under eCO_2, both plants allocated more resources to leaf and shoot growth than to reproductive structures and became more competitive (Runion et al., 2008).

Climate Change effects on Glyphosate – an Appraisal

The overwhelming evidence from research indicates that climate change will most likely have a significant effect on the biology and ecology of weedy species, as well as their abundance and persistence. Climate change will also most likely directly affect herbicide applications and herbicide effectiveness in field situations. Effects will most likely occur through altered plant (leaf or stem) uptake, translocation (via phloem or xylem) and metabolism of herbicides at the cellular level, including detoxification or sequestration (Chandrasena, 2009; Ziska and Dukes, 2011; Clements et al., 2014; Ziska, 2016; 2020; Fernando et al., 2016; Ramesh et al., 2017; Siddiqui et al., 2022).

The early studies (Bunce, 2000) had already shown that rising CO_2 concentration could cause many changes in plant leaves, including a reduction of stomatal numbers and stomatal conductance by up to 50% in some plants. With eCO_2, cuticles on plant leaves may also become waxier and thicker and less permeable even to surfactant-assisted, formulated herbicides. Such changes in leaf morphologies, along with changes in cuticular wax chemistries may reduce the uptake of foliar-applied herbicides with concomitant decreases in the efficacy of foliar-applied herbicides, most of which are phloem-mobile and translocate following a typical ''source-to-sink" pattern (Ziska et al., 2000; Ziska, 2003; 2008; 2016; 2020).

Glyphosate is undoubtedly the world's most-used and best-known herbicide (Dukes and Powles, 2008; Sammons and Gaines, 2014; Van Bruggen, et al., 2018; Green, 2018).). As a non-selective, foliar-applied, systemic chemical, glyphosate controls a wide range of weeds in both agricultural and non-agricultural settings. Glyphosate's history proves that it has been a remarkably successful weed control tool that has performed well under diverse conditions all over the world (Duke and Powles, 2008; Benbrook, 2016; Heap and Duke, 2017; Duke, 2018).

Once absorbed through leaves and stems, glyphosate is highly mobile inside the plant body, being translocated to meristematic tissues, such as developing leaves, shoots, and roots. Glyphosate affects plants by suppressing chloroplast enzymatic activity inside the shikimate pathway, resulting in the build-up of shikimate (shikimic acid). The specific enzyme inhibited by glyphosate is EPSPS (5-enolypyruvylshikimate-3-phosphate synthase). It is also known that under optimum growth conditions, nearly 20% of total photosynthetically-fixed carbon is predicted to move through the shikimate pathway.

The inhibition of the enzyme and the pathway then causes a reduction in the biosynthesis of aromatic amino acids, many aromatic secondary metabolites, plant proteins and hormones essential for growth (Shaner et al., 2012). The phytotoxic effects that result from the above effects of glyphosate include wilting of leaves, chlorosis, necrosis, and plant death, which generally occur within one to three weeks after glyphosate applications (Shaner et al., 2012; Sammons and Gaines, 2014; Heap and Duke, 2017).

However, published research indicates that under future climate change scenarios, the efficacy of glyphosate may increase, decrease or remain constant, depending upon the types of weeds treated, rates and timings of applications and other local, influential factors that affect the growth of the targeted species. Some of the most significant findings are summarized in **Table 3** and discussed briefly below.

In some of the earliest studies, Lewis Ziska and co-workers (Ziska et al., 1999) demonstrated that under eCO_2, a C_3 weed – lambsquarters was considerably tolerant of glyphosate at the recommended control rate. In contrast, redroot pigweed, a C_4 species, was well controlled by the recommended rate of glyphosate, or one-tenth of it. The main reasons for the differential response of the C_3 and C_4 species to glyphosate might be the effects on plant morphology and physiology, brought about by eCO_2. Plant size alone could not explain the tolerance between the two levels of CO_2 in the C_3 weed's recalcitrance, indicating that under eCO_2, physiological changes may have occurred. Based on the results, Ziska et al. (1999) predicted that the control of some C_3 weeds with glyphosate could become more difficult under future climate change.

Pline et al. (1999) also showed that foliar uptake of ^{14}C-glyphosate by 'Roundup-ready' (RR) soybean (*Glycine max* L.) grown at 15 or 35°C was similar up to 7 days after treatment (DAT). However, translocation was significantly higher at 35°C than at 15°C, indicating the potential for glyphosate injury to the genetically-modified crop, supposed to be glyphosate-resistant.

Long-term exposure of couchgrass [*Elymus repens* (L.) Desv. ex Nevski.] to eCO_2 (720 ppm) significantly increased its resistance to glyphosate, which became difficult to control (Ziska and Teasdale, 2000). Ziska (2001) showed early evidence that eCO_2 increased leaf area sizes and biomass of C_3 weeds and predicted that such a change would assist C_3 weeds, such as common cocklebur (*Xanthium strumarium* L.) to evolve glyphosate resistance.

Sharma and Singh (2001), working with Florida beggarweed [*Desmodium tortuosum* (Sw.) DC.]. showed that the uptake and translocation of ^{14}C-glyphosate were significantly higher at 22°C or 95% relative humidity (RH) than at 16°C and 35°C, or 45% and 70% RH. Such findings indicate that with global warming, changes in humidity could lower the overall efficacy of some herbicides.

In another example, Zhou et al. (2007) found that glyphosate efficacy was considerably reduced when applied on drought-stressed velvetleaf. Adding to this research, Mithila et al. (2008) showed that the lowered efficacy of glyphosate on velvetleaf and lambsquarters under low N was primarily due to reduced herbicide acclimatization to meristems. The authors argued that low N may reduce the net acclimatization of carbon in plants, which results in a reduction in the net transport of sugar molecules, and also glyphosate, taken up by the treated weeds. In their view, decreased glyphosate efficacy under low soil N in some weed species would explain why some weeds survived glyphosate treatments in field situations (Mithila et al., 2008).

Manea et al. (2011) also reported that glyphosate efficacy in controlling three out of four C_4 grass weeds - Rhodes grass (*Chloris gayana* Murb.), African love grass (*Eragrostis curvula* Schard.) and dallis grass (*Paspalum dilatatum* Poir) was significantly reduced under eCO_2. In contrast, smutgrass (*Sporobolus indicus* R. Br.) was well controlled by glyphosate under both ambient CO_2 and eCO_2. The authors suggested that glyphosate efficacy was equivalent to the number of plant tissue in which it has to act; i.e. a significant amount of biomass would dilute glyphosate within the plant, making it less effective. As a result, if the growth of some C_4 grasses is stimulated by eCO_2, they would resist glyphosate and increased glyphosate rates would be required for their control (Manea et al. (2011).

While some studies report that eCO_2 and elevated temperatures affect the growth of weeds, and reduce glyphosate efficacy, not all studies agree with such a finding. In one study, Marble et al. (2015) recorded that the growth of hard-to-control, globally important, C_4 sedges - purple nutsedge (*Cyperus rotundus* L.) and yellow nutsedge (*Cyperus esculentus* L.) increased under eCO_2 (608 ppm) compared with ambient CO_2 (405 ppm). However, at three weeks, a single application of glyphosate or halosulfuron, either alone or in mixtures, at recommended rates, controlled both sedges adequately, regardless of CO_2 concentration.

In our view, the results of the study (Marble et al., 2015) were influenced by the age of the treated plants, which were only four weeks old at the time of treatment. We concur with the authors that more mature plants or hardier nutsedge populations (possibly with greater numbers of underground tubers) may require more than one herbicide application, but these may not necessarily be higher glyphosate rates. Whether or not eCO_2 affected the translocation of glyphosate or halosulfuron to the tubers or roots of the sedges was not determined in the study, which was a limitation.

Table 3 A Summary of findings in climate change-related studies on the effects of eCO_2, temperature and other factors affecting glyphosate activity

Study	Significant findings of modified (reduced) activity	Probable reasons
Pline et al. (1999)	• Uptake and translocation of glyphosate to meristems was significantly higher at 35°C (HT) than at the lower 15°C temperatures (LT), indicating increased glyphosate injury to Roundup-Ready (RR) soybean at higher temperatures.	• Increased translocation out of leaves at HT.
Sharma and Singh (2001)	• Temperature and relative humidity (RH) both influenced glyphosate uptake and translocation by Florida beggarweed (*Desmodium tortuosum*), which was optimally controlled at 22°C and 95% RH.	• Increased uptake and translocation at higher temperatures and RH.
Ziska, Teasdale and Bunce (1999)	• Irrespective of CO_2 (ambient 360 ppm vs. elevated 720 ppm), the growth of redroot pigweed (*Amaranthus retroflexus*), a C_4 species, was significantly reduced by a lower glyphosate rate (0.112 kg ai ha^{-1}) and was fully killed by a higher rate (1.12 kg ai ha^{-1}). At eCO_2, the lower glyphosate rate had no effect on the growth of a C_3 species - lambsquarters (*Chenopodium album*), while the higher rate reduced its growth, but did not eliminate the weed.	• Increased biomass production and vigour resulting in possible dilution of the herbicide in tissues.
Ziska and Teasdale (2000).	• Sustained growth, photosynthesis and increased tolerance to glyphosate observed in a C_3 perennial weed, quackgrass (*Elytrigia repens*), grown at elevated carbon dioxide.	• Dilution of the herbicide in the large biomass and tissues.
Reddy (2000)	• Glyphosate control of the woody redvine (*Brunnichia ovata*), was greatly affected by post-treatment temperature. Uptake and translocation were highest in plants maintained at 35/30 ^{0}C (14/10 h, day/night) and were lowest in plants maintained at 25/20 ^{0}C. Translocation of glyphosate out of leaves continued up to 8 DAT.	• Increased translocation out of leaves at a higher temperature
Ziska, Faulkner and Lydon (2004)	• In Canada thistle, under eCO_2 (ambient + 350 ppm CO_2) both root and shoot biomass increased. Root growth was stimulated more strongly by eCO_2 than shoot growth. Reduced glyphosate efficacy at eCO_2 treatments was not due to differential herbicide uptake. Instead, tolerance was more a dilution effect, related to the large stimulation of roots, relative to shoot biomass, at eCO_2.	• Increased biomass production, resulting in dilution of the herbicide in tissues.
Zhou et al. (2007)	• Drought and flooding conditions lowered the efficacy of glyphosate on button weed due to the weed suffering from stressful conditions.	• Reduced uptake and translocation
Mithila et al. (2008)	• Reduced glyphosate efficacy on velvetleaf and lambsquarters, grown under low N, was a result of decreased herbicide translocation to meristems under N stress.	• Decreased translocation.
Manea et al. (2011)	• eCO_2 stimulated the biomass production of all four C_4 grasses tested. Under eCO_2, glyphosate control of smut grass (*Sporobolus indicus*) was unaffected. • But, the control of Rhodes grass (*Chloris gayana*), African love grass (*Eragrostis curvula*) and dallis grass (*Paspalum dilatum*) were significantly reduced.	• Dilution of g*lyphosate* in the larger biomasses of the grasses under eCO_2.
Marble et al. (2015)	• eCO_2 increased the growth and vigour of purple and yellow nutsedge shoot and underground growth. Glyphosate efficacy was, however, not affected.	• Increased uptake and translocation.
Zhang et al. (2015)	• Glyphosate-susceptible (GS) and glyphosate-resistant (GR) goosegrass (*Eleusine indica*) biotypes showed a differential response to eCO_2 (800 ppm) when compared with ambient CO_2 levels (400 ppm). • eCO_2 increased the glyphosate tolerance in the S biotype, but reduced the resistant level in the R biotype, due to reduced photosynthesis, and decreased carboxylation efficiency at eCO_2 levels compared with atmospheric CO_2 levels.	• Modified uptake and translocation.
Ganie et al. (2017)	• Glyphosate-resistant and glyphosate-susceptible common ragweed (*Ambrosia artemisifolia*) and giant ragweed (*Ambrosia trifida*) biotypes were both more effectively controlled by glyphosate at higher temperatures (HT, 29/17 ^{0}C d/n) compared with lower temperature (LT, 20/11 ^{0}C d/n). Glyphosate translocation was much higher at HT for common ragweed, while in giant ragweed, both uptake and translocation were significantly higher at HT compared with LT.	• Increased uptake and translocation.

Table 3 (continued)

Study	Significant findings of modified (reduced) activity	Probable reasons
Jabran and Doğan (2018)	• Growth, leaf and biomass production of cheatgrass, false barley and prickly lettuce increased under both eCO_2 and higher temperatures. All three species were well controlled by glyphosate at standard and double rates. • More than 80% control of plants grown under eCO_2 and higher temperatures was also achieved by lower glyphosate rates	• Modified uptake and translocation.
Bajwa et al. (2019)	• Growth and reproduction of parthenium increased under eCO_2, but its control by glyphosate was not affected by eCO_2. Herbicide injury developed more slowly at eCO_2 (700 ppm), compared to ambient (400 ppm), which showed that under eCO_2, glyphosate translocation was initially slow. However, the survival rate of treated plants was higher under eCO_2, compared with ambient CO_2 at recommended (0.8 kg a.i. ha^{-1}) and lower rates of glyphosate.	• Modified uptake and translocation.
Matzrafi et al. (2019)	• Glyphosate translocated quickly from leaves of Canadian fleabane and lambsquarters to shoot meristems and roots under eCO_2 [ambient 400 ppm vs. eCO_2 720 ppm], increased temperatures [18/12°C vs. 32/26°C], and the combination of both factors in both species. • The combined effects of both factors led to higher survival rates as compared to each factor alone. Early induction of reproduction and loss of apical dominance occurred in glyphosate-treated plants under high temperatures and eCO_2 levels.	• Modified translocation and tissue-specific sequestration, leading to decreased sensitivity.
Cowie et al. (2020)	• Parthenium growth was stimulated by eCO_2 (Plants grown under 600 and 800 ppm accumulated 23% and 55% more biomass compared to ambient CO_2). • Glyphosate treatments significantly reduced plant biomass (81%, 78% and 76% respectively, in the 400, 600 and 800 ppm treatments).	• Modified photosynthetic responses

The effects of eCO_2 stimulating the growth of shoot systems also lead to more resources being partitioned to underground parts of plants, such as taproots, tubers or rhizomes. Evidence of this effect was described in some early research. For example, in Canada thistle (*Cirsium arvense* L.), the stimulation of underground biomass (taproots) resulted in inadequate control of the weed by standard glyphosate rates (Patterson et al., 1999; Ziska et al., 2004). Ziska's early studies (2003a) showed growth stimulation of several weeds by eCO_2, and greater subterranean biomass production by Canada thistle (+72%) and spotted knapweed (*Centaurea maculosa* Lam.) (+60%). Despite species-specific responses, the consensus of these studies is that CO_2–induced increases in root or rhizome biomasses could make perennial weeds, particularly grasses, much harder to control under eCO_2.

Shaner et al. (2012) explained that glyphosate efficacy would be different in C_3 and C_4 weeds and pointed out that as a result of eCO_2 some C_3 weeds can evolve glyphosate-resistant more easily as compared to the C_4 weeds. Glyphosate-resistant populations of goosegrass (*Eleusine indica*), a C_4 grass, have been increasing in prominence in many tropical Asian countries and in parts of China (Chen et al., 2015). Studying these in China, Zhang and co-workers (2015) recorded a highly significant differential response in glyphosate-resistant (R) and glyphosate-susceptible (S) goosegrass biotypes to eCO_2 (800 ppm vs. ambient 400 ppm). Elevated CO_2 caused an 11% increase in glyphosate tolerance in the S biotypes but reduced the resistant level in the R biotypes by 60%.

Clearly, eCO_2 had a greater impact on the biochemical processes of the goosegrass R biotype, which were adversely affected by eCO_2 (lower photosynthetic performance, stomatal limitations and shoot biomass). Such effects resulted in the decline of their glyphosate tolerance and were largely explained by reduced photosynthesis and decreased carboxylation efficiency at high CO_2 levels compared with ambient CO_2 levels (Zhang et al., 2015).

Zhang et al.'s results, however, sharply contrasted with those of Manea et al. (2011) who had earlier recorded increased resistance to glyphosate in several, growth-stimulated C_4 grasses. Glyphosate resistance is likely to impart a considerable cost for resistant plants through several tolerance mechanisms. Reviewed elsewhere (Shaner, 2009; Roso and Vidal, 2010; Shaner et al., 2012; Salas et al., 2012). Sammons and Gaines, 2014; Fernando et al., 2016), the mechanisms of glyphosate tolerance include the following: (a) biochemical changes, such as increased EPSPS enzyme concentrations in different tissues; (b) unknown transport protein-related factors that may affect the critical phloem-loading step in tolerant plants; (c) reduced movement of the herbicide through the transpiration flow (in the xylem, after entering through the stem); (d) the inability of the herbicide to re-enter the phloem; (e) metabolic detoxification of glyphosate; (f) sequestration of glyphosate within chloroplasts and/or cells associated with phloem; and (g) enhanced production of EPSPS in some tissues and regions.

However, it is also clear that such physiological mechanisms of glyphosate tolerance may be modified by plant growth under eCO_2, warming and other climate change factors (such as moisture stress). The outcomes are largely uncertain, and generalizations are difficult to make with the current status of knowledge, except that some responses appear highly variable and could well be species-specific.

In our research, over two typically cool growing seasons (2013-2015) in Turkey (Jabran and Dogan, 2018), we studied the interactions of higher temperatures, eCO_2 and glyphosate on the growth and control of cheatgrass, false barley and prickly lettuce. Study treatments included: (1) ambient CO_2 (400-450 ppm) and temperature (20/10 ^{0}C day/night); (2) elevated temperature (25/15 ^{0}C day/night) + ambient CO_2; (3) eCO_2 (800-900 ppm) + ambient temperature and (4) eCO_2 + higher temperature. We found that eCO_2 and higher temperatures combined to consistently increase the total biomass and leaf area production of all three species, relative to ambient, control conditions. Growth stimulation by eCO_2 was stronger than any negative effect of higher temperature and also explained the increased growth under the combined conditions (Jabran and Dogan, 2018).

Different glyphosate rates provided somewhat variable control of the three weeds. The standard rate (1.44 kg a.i. ha^{-1}) and its double rate (2.88 kg a.i. ha^{-1}) completely and consistently controlled the weeds under all climatic conditions. The lower rates of 0.72 and 1.08 kg a.i. ha^{-1} also achieved >80% kill of all three weeds under all the climatic conditions, leading to our finding that eCO_2 did not change the efficacy of glyphosate (Jabran and Dogan, 2018)

Elevated CO_2 levels appear to clearly improve the growth and development of plants. The effects are likely to be caused by (a) improved photosynthetic rates, (b) reduced photorespiration, (c) increased water availability, through decreased cuticle thickness and lower stomatal numbers, and (d) improved source-to-sink transport, sink size and biomass production. However, higher temperature day/night regimes may adversely affect the growth rate of plants by having opposite effects, such as increasing evaporation, transpiration and metabolism rates.

Ganie et al. (2017) found that glyphosate resistance was sensitive to temperature in both susceptible and resistant biotypes of common ragweed (*Ambrosia artemisifolia* L.) and giant ragweed (*Ambrosia trifida* L.). All biotypes were well controlled by glyphosate as resistance decreased under higher temperatures (29/17 ^{0}C d/n) compared with lower temperatures (20/11 ^{0}C d/n). This finding led to the recommendation that glyphosate should be applied on warmer days in spring and mid-to-late afternoons in the growing seasons (Ganie et al., 2017).

Elevated temperature and eCO_2 levels both cause low sensitivity of many weeds to glyphosate, possibly due to low absorption and translocation rates (Matzrafi et al., 2019). Recently, Matzrafi et al. (2019) showed that the sensitivity of both Canadian fleabane (*Conyza canadensis* (L.) Cronquist. and common lambsquarters to glyphosate was much less under eCO_2, warmer conditions, and the combination of both factors. The higher temperature had a greater effect on plant survival than eCO_2 on both species. Moreover, the combination of elevated temperature and eCO_2 resulted in the loss of apical dominance and rapid necrosis in treated plants.

The reason for reduced glyphosate activity was the rapid translocation of the herbicide out of treated leaves to shoot meristems and roots in plants subjected to higher temperatures and eCO_2. This caused decreased sensitivity of the plants and reduced glyphosate efficacy, possibly due to altered herbicide translocation and/or tissue-specific sequestration. The authors suggested that over-reliance on glyphosate for weed control under changing climatic conditions may result in more weed control failures (Matzrafi et al., 2019).

In more recent studies, similar types of responses have been observed in other C_3 weeds, such as lambsquarters, thornapple (*Datura stramonium* L.), *C. arvense*, and parthenium (Bajwa et al., 2017; 2019). In recent research, Bajwa and co-workers (2019) showed that the growth and reproduction of parthenium increased under eCO_2, but its control by glyphosate after 21 DAT was not affected by the growing conditions under higher CO_2. Herbicide injury developed more slowly at eCO_2 (700 ppm), compared to ambient CO_2 (400 ppm), which showed that under eCO_2, glyphosate translocation was initially slow. The survival rate of treated plants was also higher under eCO_2, compared with ambient CO_2 at recommended (0.8 kg a.i. ha^{-1}) and lower rates of glyphosate.

In other recent studies, Cowie et al. (2020) confirmed that parthenium showed higher growth and reproduction rate under eCO_2. Compared to parthenium, grown under ambient CO_2 (400 ppm), plants at 600 and 800 ppm CO_2 produced 23.4% and 54.5% more biomass, respectively. Glyphosate treatment, however, dramatically declined plant biomass at all three CO_2 treatments 400, 600 and 800 ppm, by 81%, 78% and 76% respectively.

From the physiological point of view, glyphosate-treated plants showed a severe reduction in chlorophyll content (by >90%) and several photosynthetic efficiency parameters (i.e. maximum quantum efficiency; photon absorption and electron transport). However, these effects were slower to develop in plants cultivated under eCO_2. Low efficacy of glyphosate also occurred but only with plants grown under eCO_2 and this effect was mainly due to improved biomass production. The recovered parthenium plants also grew up to reproductive maturity and produced seeds, which leads to the possibility that under eCO_2 conditions, parthenium may become harder to control by glyphosate (Cowie et al., 2020).

Conclusions

Research on how climate change factors may affect glyphosate activity has produced some significantly mixed results. These have been hitherto explained based on differences in (a) plant growth – increased biomass production under eCO_2 and resource partitioning to underground parts, (b) changes in leaf morphologies, plus changes in cuticular and epicuticular waxes, affecting uptake by either leaves or stems; (c) translocation in the phloem and xylem, affected by physiological processes; (d) possible detoxification and/or sequestration of glyphosate in different tissues (largely in glyphosate-tolerant plants).

Photosynthetic responses of plants to eCO_2 and warming, as well as the interactions of plant growth and metabolism in the presence or absence of N fertilizers and or moisture deficits also complicate the results. Overall, we agree that the mechanisms by which glyphosate activity might be adversely affected by the rapidly changing climate factors are still unclear and may be ‘species-specific’, as has been previously suggested by Mithila et al. (2008).

Studies are yet to demonstrate whether higher temperatures would lower the viscosity and increase the permeability of cuticular and epicuticular lipids, thereby enhancing the foliar uptake of glyphosate or other herbicides through the cuticle.

Climate change components, especially eCO_2 levels, generally cause stomata to close and reduce stomatal conductance (a measure of stomatal opening, the rate of CO_2 entering, or water vapour exiting through stomata), while increasing leaf areas. As suggested by Ziska (2016) and Varanasi et al. (2016), a decline in stomatal conductance and a reduction in the demand for aromatic amino acids may also affect glyphosate activity after it has entered a plant. Their view is that declined protein levels produced in plant tissues under eCO_2 could directly reduce the efficiency of enzyme-inhibiting herbicides, including glyphosate.

Under climate change, the combined effects of eCO_2 and higher day/night temperature regimes are likely to increase the growth, biomass and vigour of many weeds in most situations. These effects could also affect herbicide efficiency either through reduced uptake rates of active ingredients or by increased biomass, which enables plants to better withstand the effects of the herbicide. In general, elevated temperatures alone may have either neutral, negative or slightly positive effects on the growth of weed species as they balance their physiological demands of water and nutrients required for growth against the stresses caused by higher temperatures. While individual plant responses will inevitably be constrained by the resources available to them (Mithila et al., 2008; Manea et al., 2011), they will be modified by other climate components.

Because of the predicted changes in plant physiology and morphology, the activity of foliar-applied herbicides, such as glyphosate, is likely to be modified. If the foliar uptake of glyphosate is decreased, under climate change, due to changes in cuticle thickness and permeability in leaves or other structures, it could result in reduced translocation and efficacy of glyphosate on weeds that are usually susceptible to glyphosate.

If climate change effects result in greatly enhanced biomass production and changes in resource allocation to shoots and roots or other subterranean parts in some weeds, such as both C_3 and C_4 grasses, it could lead to differential translocation of the herbicide to active sites. Dilution of the herbicide in larger biomasses could be a strong reason for the differential responses.

It is well-known that the combined effects of factors i.e., CO_2, soil moisture, sunlight, relative humidity and temperature can differentially impact the plant absorbance, translocation, metabolism and action of phloem-mobile herbicides, such as glyphosate. It is also clear that variations in soil N levels can impact plant growth and development, which in turn may have an effect on biochemical and physiological processes, such as the absorbance, translocation, and activity of herbicides. This is why it is essential to well understand the complex influences of eCO_2, global warming, and other influential and changing factors (such as N fertilization and moisture regimes), on the growth and herbicide tolerance of weeds (Chandrasena, 2009; Ziska and Dukes, 2011; Varanasi et al., 2016; Ziska, 2016; Ramesh et al., 2017; Jabran and Dogan, 2018).

In our view, supported by others (Duke and Powles, 2008; Benbrook, 2016; Heap and Duke, 2017), the extensive use of glyphosate is not likely to slow down but continue in the next decade or so in most countries. Given this glyphosate use trend and the current discourses on environmental risks associated with it, research must strive to better understand the factors that significantly influence glyphosate activity. As Kanissery et al. (2019) recently argued, research must focus on increasing understanding among glyphosate users about its careful utilization and this necessitates further studies to avoid, mitigate or eliminate the problems due to its overuse.

Our studies also have shown clearly that when plants can respond to eCO_2 with a higher growth rate and large, leafy biomass production, such effects can improve their tolerance of glyphosate and possibly other herbicides. This suggests that in a world with higher concentrations of CO_2, increased application rates of glyphosate might be required, which could have significant economic and environmental consequences. Nevertheless, our review, and those of others (Ziska and Dukes, 2011; Varanasi et al., 2016; Ziska, 2016; Ramesh et al., 2017), find that interactions among a range of factors operating in the field may have unpredictable effects on herbicide activity.

Available literature also indicates that the effects of climate change components can be highly variable, not only within groups of herbicides with the same mode of action but also varies with different modes of action Making a generalized statement about each mode of action continues to be difficult. More detailed studies on the effects of climate change components and their relations on all frequently used herbicides and their activity on selected, globally-important weedy taxa is essential to understand the consequences for future weed management under climate change scenarios.

Based on this review, more generally, we recommend further research to focus on the interaction of future climate factors on glyphosate activity on climate-hardened weedy plants and not juveniles (such as used by Cowie et al., 2020), and species representing major families and/or groups of weeds.

As Waryszak et al. (2018) recently suggested, the evidence from a spate of research on climate change factors affecting the activity of glyphosate and other herbicides needs that over-reliance on herbicides for controlling weeds needs a “*rethink*” under eCO_2 and associated changes. Although our own research found contrary evidence, the increased resistance of many species to glyphosate warrants further research regarding the effects of climate change variables on the herbicide’s activity on target weeds and other factors that are known to affect its overall effectiveness.

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