



Impact of Climate Change Factors on Weeds and Herbicide Efficacy

Aruna Varanasi, P.V. Vara Prasad, Mithila Jugulam¹

Department of Agronomy, Throckmorton Plant Science Center, Kansas State University, Manhattan, KS, USA

¹ Corresponding author: mithila@ksu.edu

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Abstract

Rising carbon dioxide (CO₂) concentrations and associated changes in global temperature and precipitation are major concerns for future weed management and crop

production. This review focuses on the impacts of climate change factors on the growth of weeds and the potential variations in the efficacy of herbicides under changing climate conditions. Weeds are likely to show greater resilience and better adaptation to changes in CO₂ concentrations and rising temperature in competition with crops due to their diverse gene pool and greater physiological plasticity. Weeds with C₃ and C₄ photosynthetic pathways may exhibit differential responses to higher CO₂ levels and temperatures, which can affect the dynamics of crop–weed competition. In addition to its positive impact on weed growth, climate change factors could influence the efficacy of many herbicides, making weed management a major challenge for sustainable crop production. To enhance our understanding of the impact of climate change factors on herbicide efficacy, it is important to evaluate the effects of environmental conditions on various herbicide modes of action. Environmental factors such as CO₂, light, temperature, relative humidity, and soil moisture differentially affect the uptake, translocation, and activity of different herbicide chemistries. Furthermore, interactions among these environmental factors may have unpredictable effects on herbicide activity. Existing literature suggests that climate change factors impacts vary not only within herbicide modes of action but also among herbicides belonging to same mode of action, so making generalized assumptions for each mode of action is difficult. Extensive research on the impact of climate change factors and their interactions on all commonly used herbicides is necessary to understand the implications for weed management in future climate scenarios.



1. INTRODUCTION

Climate is a major force in Earth's environmental system, and even minor changes in climate can have complex and serious effects on the environment and nature. Climate changes in the past have occurred over hundreds or even thousands of years, but recent changes have received wider attention because of radical shifts occurring in just a few decades. These regional and global climate shifts have started affecting life on our planet in numerous ways, but effects on agriculture and food supply may be one of the greatest threats to sustaining life. Although our understanding of how climate change affects agriculture is still developing, evidence from short-term experiments suggests that it may be affected in several ways. Crop productivity in terms of both quality and quantity, and agronomic practices such as irrigation, fertilization, weed management, and pest control could be affected significantly due to climate change. Furthermore, impacts on soil fertility due to changes in soil organic matter, drainage, and erosion could affect crop production indirectly. Assessment of the effects of global climate change factors [particularly of elevated carbon dioxide (CO₂) concentrations

and rising temperature] on agriculture and farming practices is important to anticipate and adapt practices that maximize agricultural production in future climate scenarios. Achieving sustainable crop production in unpredictable environments necessitates a holistic approach that focuses on not only increasing crop productivity but also effective management of agricultural pests such as weeds.

Weeds, recognized by humans as undesirable plants interfering with agriculture and natural resources, are the oldest and most common problem in profitable crop production. Weeds are complex in nature and have significant negative effects on agriculture, forestry, rangelands, public health, and many human activities. Unlike outbreaks of pests and diseases, which may be random and irregular, weeds are relatively constant and pose severe problems in crop production (Kostov and Pacanoski, 2007). If left uncontrolled, weeds can cause severe crop losses. Yield losses due to weeds vary according to crops, weed species, and farming practices. Crop losses resulting from weed competition will be highest when weeds emerge in high densities with or prior to crop emergence. Some of the most troublesome weeds and typical yield losses incurred due to weed competition in major US field crops are listed in Table 1. Weeds directly reduce crop yields by competing for essential resources such as light, water, nutrients, and space; furthermore, weeds compromise the quality of yields by contaminating the seed and lowering the value of harvested crops. Weeds also interfere with harvest operations, produce harmful chemicals (allelopathy), and serve as hosts for insect pests and diseases (Boydston et al., 2008; Swinton et al., 1994); hence, weed control is a major component of successful crop production.

Weed control can be achieved through cultural, mechanical, biological, and chemical methods. However, labor is expensive in developed countries such as the United States, therefore, crop production relies heavily on chemical weed control methods. Herbicide use on agricultural crops in the United States increased dramatically in the late 1940s and has continued to dominate the US market since that time (Timmons, 2005). Herbicides account for nearly 47% and 25% of the total pesticide use in the United States and worldwide, respectively (Grube et al., 2011). Herbicides have become the major tools for weed management because of their simplicity in use, greater efficacy, and more importantly, due to the reduction in control costs by saving labor and time (McErlich and Boydston, 2013). The advent of herbicides for selective control of weeds has boosted crop production and producers' ability to provide high-quality produce. Herbicides are routinely applied to kill weeds in more than 90% of US crop acreage (Gianessi and

Table 1 Yield loss estimates and major weeds of different US field crops.

| Crop | Troublesome weeds | Yield loss (%) |
|-----------|--|----------------|
| Wheat | <i>Lolium multiflorum</i> , <i>Convolvulus arvensis</i> , <i>Cirsium arvense</i> , <i>Bromus secalinus</i> , <i>Allium vineale</i> | 25 |
| Corn | <i>Sorghum halepense</i> , <i>Chenopodium album</i> , <i>C. arvense</i> , <i>Sorghum bicolor</i> , <i>Abutilon theophrasti</i> | 20 |
| Sorghum | <i>S. halepense</i> , <i>S. bicolor</i> , <i>Xanthium strumarium</i> , <i>Panicum</i> <i>dichotomiflorum</i> , <i>Brachiaria platyphylla</i> | 26 |
| Rice | <i>Echinochloa crus-galli</i> , <i>B. platyphylla</i> , <i>Cyperus esculentus</i> , <i>Heteranthera limosa</i> , <i>Leptochloa fascicularis</i> | 53 |
| Soybean | <i>X. strumarium</i> , <i>S. halepense</i> , <i>C. album</i> , <i>A. theophrasti</i> , <i>Cassia</i> <i>obtusifolia</i> | 26 |
| Cotton | <i>X. strumarium</i> , <i>C. esculentus</i> , <i>Cyperus rotundus</i> , <i>Cynodon</i> <i>dactylon</i> , <i>E. indica</i> | 27 |
| Sugarbeet | <i>A. theophrasti</i> , <i>X. strumarium</i> , <i>Rumex crispus</i> , <i>Polygonum</i> <i>arenastrum</i> , <i>Polygonum lapathifolium</i> | 29 |
| Canola | <i>Sinapis arvensis</i> , <i>Artemisia tilesii</i> , <i>Capsella bursa-pastoris</i> , <i>Rapistrum rugosum</i> , <i>Sisymbrium sophia</i> | 45 |
| Sunflower | <i>Artemisia biennis</i> , <i>C. arvense</i> , <i>Kochia scoparia</i> , <i>Amaranthus</i> <i>palmeri</i> , <i>Amaranthus retroflexus</i> | 16 |
| Drybean | <i>E. crus-galli</i> , <i>C. dactylon</i> , <i>C. arvensis</i> , <i>X. strumarium</i> , <i>C. album</i> | 25 |

Data adapted from Bunce and Ziska (2000) and Gianessi and Sankula (2003).

Reigner, 2007). Among major US crops, weed competition severely affects corn and soybean yields; these crops account for the majority of herbicide use (Vecchia et al., 2009). Despite widespread herbicide use, crop production losses from weeds exceed \$8 billion annually in the United States alone (Loux et al., 2014). Gianessi and Sankula (2003) documented the role of herbicide use in US crop production and estimated costs incurred as a result of herbicide nonuse. Substitution of herbicides with alternate weed control measures such as cultivation and hand-weeding incurred losses of \$13.3 billion in food and fiber production along with an additional \$7.7 billion in increased costs for weed control. The study further emphasizes the importance of herbicide usage for weed management to increase yields and savings for growers, and to reduce soil erosion.

Given the importance of herbicide use for effective weed control, it is essential to understand the factors that govern herbicide performance. Successful weed management relies not only on the chemical properties of a herbicide but also on its interaction with the plant and the environment. Besides plant morphologic and anatomic characteristics, environmental

conditions play a pivotal role in determining the efficacy of herbicides at the time of application. Herbicide absorption into the target plant largely depends on its interaction with atmosphere, soil, or the soil–atmosphere interface. Several environmental factors such as temperature, moisture, relative humidity, and solar radiation influence a plant’s physiologic status and its susceptibility to herbicides. The interactions among these factors further complicate the precise determination of their effects on herbicide performance. In addition, changes in the global climate due to a rise in CO₂ concentration and its associated effects on global temperature and precipitation can have significant impacts on plant growth and herbicide performance.

Understanding the effects of climate change on weed growth and herbicide activity is important to optimize herbicide applications for effective weed control in future. The aim of this review is to provide an overview of the potential impacts of global climate change on weed growth and herbicide efficacy. The effect of climate factors, particularly rising CO₂, increase in surface air temperatures, and changes in precipitation events, on the efficacy of major herbicides with different modes of action will be discussed. Information is also presented on the critical gaps in the current knowledge of environmental influence on the modes of action of different herbicides and possible improvements in herbicide performance in a changing climate to sustain the quantity and quality of crop production.



2. FACTORS INFLUENCING CLIMATE CHANGE

Climate change refers to a change in the climate variables that persists for extended periods, typically decades or longer. Global climate changes can result from natural forces such as solar activity and volcanic eruptions or human activities such as burning of fossil fuels and deforestation. Since the beginning of the industrial era (1750), human activities have largely contributed to global warming by altering the amounts of greenhouse gases and aerosols (small particles). These emissions accumulate in Earth’s atmosphere and increase in concentration over time, creating the so-called greenhouse effect, which can alter the planet’s energy balance by transmitting incoming solar radiation but absorbing outgoing thermal radiation from the surface (Schneider, 1992). Consequently, continued global warming will be accompanied by an increase in Earth’s mean temperature, changes in the frequency and distribution of precipitation, wind patterns, evapotranspiration, and weather extremities such as droughts, floods, severe storms, and hurricanes (Roeckner, 1992).

Greenhouse gases emitted from natural or anthropogenic sources are the main drivers of climate change and variability. The concentration of greenhouse gases influences the level of absorption and emission of radiation within the atmosphere and at the Earth's surface (Forster et al., 2007). Water vapor is the most abundant and primary greenhouse gas in the atmosphere, but the amount of atmospheric water vapor is largely influenced by natural processes. The direct impact of human activities on the concentration of atmospheric water vapor is minimal and therefore not subject to management and control (Rowntree, 1990). Other trace gases that contribute to the greenhouse effect include CO₂, methane, nitrous oxide, and halocarbons. Although the atmospheric concentrations of these gases are in trace amounts compared with water vapor, their concentrations are largely influenced by human activities and are more responsive to management for limiting global warming effect (MacCracken et al., 1990). The characteristics of CO₂ and other greenhouse gases and their global warming potential relative to CO₂ are shown in Table 2. Among the trace gases, CO₂ contributes most significantly to the global climate change because of its heat-absorbing properties and longer atmospheric lifetime (Andreae and Merlet, 2001; Lacis et al., 2010). At current emission rates, the concentration of CO₂ is predicted to reach ~1000 ppm by the end of the twenty-first century, resulting in an increase of 2–4°C in the Earth's annual surface temperature (IPCC, 2007). Since the Industrial Revolution, human activities have contributed to >40% increase in the atmospheric concentration of CO₂ (Blasing, 2014).

In the last 250 years, burning of fossil fuels, land use, and agriculture are the major anthropogenic sources that have contributed to greenhouse gas emissions. Modern agriculture is one of the main driving forces, contributing about 30% of greenhouse gas emissions (Nitze et al., 2008). CO₂, methane, and nitrous oxide are the three primary greenhouse gases produced from agricultural sources. Agriculture and farming practices such as production and operation of farm machinery and on-farm energy use directly account for 14% of total greenhouse gas emissions. Deforestation for land-clearing purposes affects carbon reuptake and causes an additional 18% of emissions in the form of CO₂. Other agricultural processes such as wetland rice cultivation and enteric fermentation in domestic ruminants contribute to about 54% of methane emissions, whereas about 70% of nitrous oxide emissions are linked to conventional tillage and fertilizer applications (Burney et al., 2010; Nitze et al., 2008). While agriculture could become a significant cause of climate change, it also offers the opportunity to counteract these effects through

Table 2 Characteristics of major greenhouse gases contributed by human activities.

| | Carbon dioxide | Methane | Nitrous oxide | Ozone | CFC-11 | CFC-12 |
|--|---|--|--|---|--|--------|
| Current concentration (ppm) | 395 | 1.7–1.8 | 0.3 | 0.3 | 0.0002 | 0.0005 |
| Percentage increase since 1750 (preindustrial era) | 41 | 144–162 | 20 | 42 | ?* | ? * |
| Atmospheric lifetime (years) | 100–300 | 12 | 121 | Hours-days | 45 | 100 |
| Global warming potential (100-year time horizon) | 1 | 28 | 265 | n.a** | 4,660 | 10,200 |
| Anthropogenic sources | Burning of fossil fuels, deforestation, cement production | Natural gas production, rice paddies, domesticated ruminants, biomass and refuse burning | Commercial fertilizers, nylon production, nitric acid production, automobile exhaust emissions | Fuel combustion, organic compound evaporation | Industries, plastic foams in refrigerants, propellants in aerosol cans | |

*CFC-11 and CFC-12 are industrially manufactured compounds and have no natural sources; hence, their preindustrial concentrations are zero.

**Due to the short lifetime of ozone, global warming potential for a 100-year time zone could not be calculated.

Data from [Blasing \(2014\)](#) and [Patterson \(1995\)](#).

appropriate and timely measures. The negative environmental impacts of agriculture can be mitigated to a large extent through technological advancements such as precision agriculture, which reduces extensive use of fertilizers and pesticides; agricultural intensification on existing land to avoid large-scale deforestation; and greenhouse gas sequestration by capturing these emissions in trees, soils, and plants (Tilman et al., 2011; Mueller et al., 2012; Johnson et al., 2014). Although agriculture has major influence on climate change, the effects of global climate changes on agriculture itself cannot be overlooked.



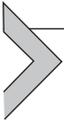
3. IMPACT OF CLIMATE CHANGE FACTORS ON CROP PRODUCTION

Agriculture is an important sector of the US economy. Agricultural trade generates output, income, and employment in both farm and nonfarm sectors and contributes at least \$200 billion to the economy each year (Karl et al., 2009); for example, US agricultural exports totaled \$320.8 billion in 2012 (USDA ERS). Agriculture is highly dependent on specific climate conditions, so its continued success will be affected by climate change factors and variability in weather patterns. Climate change will have multifaceted effects on agriculture by influencing crop growth; soil fertility; weed, insect, and disease infestations; and livestock farming. Climate change can affect agriculture through increased CO₂ concentrations, increased temperatures, variations in precipitation and solar radiation, and weather extremes such as droughts and floods. Global climate change is a major concern for agriculture because of possible negative impacts on the productivity of agroecosystems and crop–weed–pest interactions owing to unfavorable weather. Increases in CO₂ concentration and temperature can cause significant changes in plant growth and development and may have long-term impacts on agriculture (Goudriaan and Unsworth, 1990).

Climate change effects on crop production vary with the nature of climate variability factors. For instance, changes in CO₂ concentrations can be beneficial for some crops (C₃ crops such as wheat, *Triticum aestivum* L.; rice, *Oryza sativa* L.; barley, *Hordeum vulgare* L.; soybean, *Glycine max* L. Merr.; cotton, *Gossypium hirsutum* L., etc.), but the benefits from a single climate change factor can be realized only when other crop growth conditions are at optimum levels. Doubling of CO₂ levels can increase yields for some crops, such as wheat and soybean, by 30%, whereas other crops, such as maize (*Zea mays* L.), might exhibit a much lower response (<10%).

However, if the increase in CO₂ is accompanied by an increase in the temperature above the crop's optimum level or if there is a deficit in the availability of water and nutrients, yield increases may be reduced or reversed (CCSP, 2008). The beneficial effects of elevated CO₂ on most crops is negated by elevated temperature and there are no beneficial effects of elevated CO₂ on C₃ (bean, *Phaseolus vulgaris* L.; Prasad et al., 2002; peanut, *Arachis hypogaea* L.; Prasad et al., 2003) and C₄ crops (grain sorghum, *S. bicolor* L. Moench; Prasad et al., 2006). Changes in temperature will have a considerable impact on plant growth rate and phenologic development in some crops (Porter and Gwaith, 1999; Xiao et al., 2008; Prasad et al., 2008a,b). Increase in CO₂ and warmer temperatures may induce faster growth in determinate crops such as cereals by stimulating photosynthesis and vegetative growth (Kadam et al., 2014). However, grain yield in cereals depends on the length of active photosynthesis (vegetative growth) phase and grain-filling stages. Higher temperatures may negate the positive effects of CO₂ increase on leaf photosynthesis by shortening the growth phases and grain-filling duration through increased pollen sterility, lower grain weight, and poor anther dehiscence (Prasad et al., 2002, 2003, 2006; Barnabás et al., 2008; Powell et al., 2012; Singh et al., 2013; Kadam et al., 2014). The predicted increase in the variability of precipitation patterns may also become a greater concern for crop productivity. Increased frequency of high-precipitation events could influence soil infiltration rates and water availability due to flash floods and increased surface runoff (Hayhoe et al., 2007). Availability of consistent moisture supply throughout the growing season is critical to complete the crop life cycle. Drought stress negatively impacts various physiological, growth, and yield components of grain crops (Prasad et al., 2008b). Drought or water scarcity will become a major limiting factor for plant growth and productivity, especially in regions where summer temperatures are projected to increase and rainfall is projected to decrease (Mishra and Singh, 2010).

In addition to altering the length of the crop growing season and other crop characteristics, rapidly changing climate can create difficulties in the management of agricultural pests and weeds. Global warming will result in warmer nights and winters and extreme temperature events that are more likely to affect perennial weeds and may potentially expand the habitable range of some insects and disease pests (Hatfield et al., 2011). Climate change may differentially affect crops and weeds, and any adaptation in crop management practices is likely to affect weed growth and distribution.



4. EFFECTS OF CLIMATE CHANGE FACTORS ON WEED PHYSIOLOGY AND GROWTH

Atmospheric CO₂, temperature, and water or nutrient availability are important abiotic variables that directly affect weed physiology and growth. Weeds respond quickly to resource changes and have a greater likelihood to adapt and flourish in various types of habitats due to their greater genetic diversity and physiological plasticity compared with crops. As with crops, weeds with C₃ or C₄ photosynthetic pathways exhibit differences in their response to changing climate. The effects of elevated CO₂ and temperature on some of the major C₃ and C₄ weeds are summarized in [Table 3](#).

Weeds with C₃ and C₄ photosynthetic pathway vary in their responses to elevated CO₂ concentrations due to physiological differences in photosynthetic biochemistry. CO₂ is the sole source of carbon for plants, and increased CO₂ concentrations directly affect physiological processes such as photosynthesis and stomatal conductance ([Drake et al., 1997](#)). In plants with C₃ photosynthetic pathway, CO₂ is first accepted by a sugar, ribulose biphosphate (RuBP), and the reaction is catalyzed by the ribulose biphosphate carboxylase-oxygenase (Rubisco) enzyme. Because of the dual activity of Rubisco (carboxylation and oxygenation), both CO₂ and O₂ compete for the same site on Rubisco, resulting in a 20–60% loss of substrate (carbon) through photorespiration (oxygenation) ([Bowes, 1996](#)). Increased CO₂ concentrations will stimulate carboxylation, thereby reducing the loss of CO₂ through photorespiration; thus, C₃ plants typically exhibit an increase in net photosynthetic rates with increased CO₂ levels. On the other hand, plants with C₄ photosynthetic pathway have alternate CO₂ fixation mechanisms. CO₂ is initially fixed in the mesophyll cells by phosphoenolpyruvate carboxylase (PEPcase), which has a higher affinity for CO₂ than Rubisco. The resultant 4-carbon organic acid formed in this reaction regenerates CO₂ in the bundle sheath cells for fixation by Rubisco. Because of this internal mechanism that concentrates CO₂ for Rubisco, carboxylation is promoted over oxygenation and photorespiration is inhibited. Therefore, unlike in C₃ plants, increased CO₂ concentrations will have less of an effect on the net photosynthetic rates of C₄ plants. Many C₃ weeds have shown significant increases in growth, with substantial decreases in the yields of competing crops, as a result of increased CO₂. [Ziska \(2000\)](#) reported a 65% increase in the biomass of a C₃ weed, common lambsquarters (*C. album* L.), with an analogous reduction in seed yield of soybean by 39% at elevated CO₂ concentrations. On the contrary,

Table 3 Effects of elevated CO₂ and temperature on major C₃ and C₄ weeds.

| Photosynthetic pathway | Physiological differences | Major weeds | | Climate change parameter | | References |
|---|---|---------------------|---------------|--|--|--|
| | | Species | Common name | Elevated CO ₂ | Rise in temperature | |
| C ₃ type | Chloroplasts present only in mesophyll cells | <i>Avena fatua</i> | Wild oat | High stimulation of photosynthesis and growth | Increase in photorespiration and decrease in net photosynthesis | O'Donnell and Adkins (2001) Miri et al. (2012) Davis and Ainsworth (2012) Ziska et al. (2004) Valerio et al. (2013) Ziska (2013) Jia et al. (2011) Zelikova et al. (2013) |
| | | <i>C. album</i> | Lambsquarters | | | |
| | <i>C. arvense</i> | Canada thistle | | | | |
| | <i>A. theophrasti</i> | Velvetleaf | | | | |
| CO ₂ fixed by RUBP carboxylase | <i>L. multiflorum</i> | Italian ryegrass | | | | |
| | <i>Polygonum convolvulus</i> | Wild buckwheat | | | | |
| High photorespiration | <i>C. arvensis</i> | Field bindweed | | | | |
| Optimum temperature 15–25°C | <i>X. strumarium</i> | Cocklebur | | | | |
| | <i>Erepens</i> | Quackgrass | | | | |
| | <i>Bromus tectorum</i> | Cheatgrass | | | | |
| C ₄ type | Chloroplasts present in mesophyll and bundle sheath cells | <i>K. scoparia</i> | Kochia | Lower stimulation of photosynthesis and growth | Stimulation of photosynthesis and growth at high CO ₂ | McDonald et al. (2009) Mahajan et al. (2012) Valerio et al. (2011) Satrapová et al. (2013) Zheng et al. (2011) Rodenburg et al. (2011) |
| | | <i>S. halepense</i> | Johnsongrass | | | |
| | <i>S. bicolor</i> | Shattercane | | | | |
| | <i>E. indica</i> | Goosegrass | | | | |
| CO ₂ fixed by PEP carboxylase | <i>E. crus-galli</i> | Barnyardgrass | | | | |
| Low photorespiration | <i>Digitaria sanguinalis</i> | Large crabgrass | | | | |
| | <i>A. retroflexus</i> | Redroot pigweed | | | | |
| Optimum temperature 30–40°C | <i>C. dactylon</i> | Bermudagrass | | | | |
| | <i>C. rotundus</i> | Purple nutsedge | | | | |
| | <i>A. palmeri</i> | Palmer amaranth | | | | |

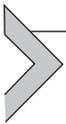
redroot pigweed (*A. retroflexus* L.), a C₄ weed, showed no change in biomass at elevated CO₂, and yield loss in soybean decreased from 45% to 30% in competition with this weed. Similarly, elevated CO₂ was found to increase the seed yield and biomass of weedy or wild rice compared with cultivated rice as the competitive density increased, indicating greater reduction in the yields of cultivated rice in the presence of C₃ weeds in future CO₂ concentrations (Ziska et al., 2010). In another study, Ziska (2001) reported the effects of elevated CO₂ on the growth of grain sorghum (C₄) with and without common cocklebur (*X. strumarium* L.) (C₃) competition. At elevated CO₂, biomass and leaf area were higher for common cocklebur and significantly lower for sorghum in competitive mixtures, indicating that growth of C₄ crops could be reduced in the presence of C₃ weeds as future CO₂ levels increase. Elevated CO₂ is also speculated to be the major cause of a substantial increase in the growth and distribution of invasive and noxious species. In a study conducted on the effects of doubled CO₂ on the growth of invasive plants in New Zealand, Sheppard and Stanley (2014) reported an increase in the total biomass and leaf area of queensland umbrella tree (*Schefflera actinophylla*) by 45% and 35%, respectively. Cheatgrass (*B. tectorum*), which was accidentally introduced to North America from Central Asia, quickly invaded western US rangelands and displaced the native species in these areas because of its ability to flourish in dry habitats. Furthermore, cheatgrass has changed the fire regimes in these regions due to its high combustibility. At higher levels of CO₂, cheatgrass can produce greater biomass adding more fuel for wildfires (Poorter, 1993).

Enhanced greenhouse effects because of higher CO₂ concentrations are predicted to increase global surface temperatures and the frequency of extreme temperature events (IPCC, 2007, 2014). Plants are likely to experience high-temperature stress, which can affect growth rates because of changes in temperature thresholds during specific developmental phases. The degree of photosynthetic stimulation and growth response varies between C₃ and C₄ plants as the temperature increases. In C₃ plants, temperatures above 25°C increase photorespiration and inhibit CO₂ assimilation (Jordan and Ogren, 1984). Conversely, temperature increase has little effect on CO₂ assimilation in C₄ plants because CO₂ pumps in mesophyll cells maintain low photorespiration rates at all temperatures (Hatch, 1987); consequently, C₄ species are better adapted to heat stress and may show stimulation of meristematic regions, rapid canopy growth, and root proliferation at high temperatures that often inhibit growth in C₃ species (Morgan et al., 2001). Weeds may show a greater range of responses to increasing temperatures because of their wider gene pool

compared with crops, which enables them to adapt to diverse environment conditions (Treharne, 1989). Weeds with rapid dispersal and establishment will be able to spread into new territories and may alter the composition and integrity of ecosystems. As warmer winters make higher latitudes more conducive to plant growth and higher temperatures make lower latitudes less habitable, many weeds are expected to expand their geographical range and cause greater losses to crop, rangeland, and forest productivity (Patterson, 1995; Parmesan and Yohe, 2003). Effects of elevated CO₂ and temperatures on potential weed migrations have been documented in multiple cases. For example, kudzu (*Pueraria lobata*) is an invasive C₃ weed that can cause crop and forest losses of some \$500 million per year, including control costs and property damage (Blaustein, 2001). Its habitat range is typically restricted to the southeastern United States because of the low winter temperatures in the north. However, increase in winter temperatures has expanded this species' range of invasion to the Midwest and northern states, potentially incurring higher losses to US economy (Ziska and George, 2004). Similarly, the growth rate of fitchgrass (*Rottboellia cochinchinensis*), a highly competitive C₄ weed in many cropping systems, including sugarcane, corn, cotton, soybean, grain sorghum, and rice systems, is projected to increase and cause the weed to invade the central Midwest and California with only a 3°C increase in temperature (Patterson et al., 1999).

Precipitation is another important climate variable that influences the growth and distribution of vegetation. Although CO₂ concentrations and temperature rise in future are predictable, distribution and variation in the intensity of precipitation patterns remains much more uncertain. Moisture is a key factor required for weed seed germination and establishment. Climate change can affect the frequency and intensity of rainfall and result in occurrences of extreme events such as floods and droughts; consequently, weeds adapted to these conditions will have a higher competitive advantage. Changes in precipitation patterns and water availability will not only alter plant size but also affect seed production and dispersal (Rodenburg et al., 2010, 2011). Under prolonged drought conditions, composition of weed species will change, leading to a shift in the vegetation. For example, cheatgrass and yellow star thistle (*Centaurea solstitialis*) are annual weeds known to survive and outgrow other species under drought conditions (Gerlach et al., 1998; Vollmer and Vollmer, 2006). While cheatgrass completes its life cycle on available moisture, yellow star thistle competes with native plants by developing deeper root system (Hatfield et al., 2011). C₃ and C₄ weeds also vary in their response to water stress conditions. Stomatal conductance

decreases with increased CO₂ concentrations because of partial closure of stomata, which lowers the transpiration rate and improves water use efficiency by 70–100% in both C₃ and C₄ plants (Kimball and Idso, 1983). Under hot and arid conditions, however, the higher water use efficiency of C₄ plants may lead to a greater competitive advantage over C₃ plants (Osmond et al., 1982). Under limited soil water conditions, C₄ plants are able to produce more biomass, root growth, and seeds than C₃ plants (Long, 1999).



5. EFFECTS OF CLIMATE CHANGE FACTORS ON CROP–WEED COMPETITION

Since climate change imposes new limitations on resources essential to plant growth, crop–weed interactions and crop losses from weeds are likely to be affected. Therefore, a broader understanding of the potential interactions between crops and weeds in the context of climate change, particularly CO₂, high temperature, and drought, is essential to evaluate the vulnerability of crop production at various regions of the world (Valerio et al., 2013).

Elevated CO₂ levels could affect the growth rates of crops and weeds by altering worldwide temperature, precipitation, and radiation patterns. Increased CO₂ levels will directly affect photosynthetic activity and crops' ability to compete with surrounding weed species, which could modify weed distribution patterns (Chandrasena, 2009). Higher CO₂ levels also could result in an increase in temperatures, leading to altered plant growth and crop yields. Higher photosynthetic rates at elevated CO₂ in C₃ crops (rice, wheat, soybean, etc.) mean they will respond more favorably to higher CO₂ levels than the C₄ weeds (palmer amaranth (*A. palmeri*), waterhemp (*Amaranthus rudis*), kochia (*K. scoparia*), etc.) (Elmore and Paul, 1983). In contrast, C₃ weeds (lambsquarters, velvetleaf (*A. theophrasti*), common ragweed (*Ambrosia artemisiifolia*), and giant ragweed (*Ambrosia trifida*)) will respond more favorably to increased CO₂ levels and offer stiffer competition to C₄ crops (maize, sorghum, sugarcane, etc.). At elevated CO₂ concentrations, relative yield and competitive ability of C₃ plants, soybean and lambsquarters were significantly higher than that of C₄ plants, millet and pigweed (Miri et al., 2012). The same study reported higher competitive ability of pigweed and lambsquarters compared with millet and soybean crops, respectively.

Increasing CO₂ levels can favor either the crop or the weed in the same field. In a grass weed–crop (Lucerne, *Medicago sativa* L.) setting, it was found

that growth of the lucerne crop was favored by increasing CO₂ levels (Bunce, 1993). Growth of redroot pigweed in a sorghum field was favored by increasing atmospheric CO₂ levels (Ziska, 2003). Evidence suggests that broadleaf C₃ weeds are preferentially selected at elevated CO₂ levels (Ziska and Goins, 2006). The effects of elevated CO₂ on crop–weed competition are also influenced by temperature. Patterson et al. (1988) observed rapid growth of cotton at elevated CO₂ levels relative to velvetleaf and spurred anoda (*Anoda cristata*), and increasing temperatures had a synergistic effect on cotton growth. Alberto et al. (1996) studied the interaction between temperature and CO₂ on rice–barnyardgrass (*E. cruss-galli*) competition and reported that elevated CO₂ favored the crop at day/night temperatures of 27/21°C but favored the growth of barnyardgrass at 37/29°C. Valerio et al. (2013) reported the interactive effects of CO₂ levels (400 and 800 μmol mol⁻¹) and temperatures (21/12°C and 26/18°C day/night) on tomato plants grown in competition with and without two common weeds, lambsquarters (C₃) and redroot pigweed (C₄). Elevated CO₂ intensified weed competition from both weed species, but crop losses were higher at 26/18°C than at 21/12°C.

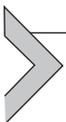
Not many studies have been performed to evaluate the interactive effects of drought and increased CO₂ levels on crop–weed competition. In high CO₂/drought conditions, C₄ weeds could outcompete C₃ crops (Knapp et al., 1993). Elevated CO₂ may have varying implications on nutrient dynamics between crops and weeds. Rising atmospheric CO₂ concentration altered the competition between rice and barnyardgrass in favor of rice (Zeng et al., 2011). Absolute uptake and tissue concentrations of C, N, P, K nutrients were greater in rice than in barnyardgrass at elevated CO₂, which enhanced the tillering, leaf area index, net assimilation rate, and biomass of rice. In another study, N was found to be the limiting factor for biomass increase in rice at elevated CO₂ levels compared with barnyardgrass (Zhu et al., 2008). Thus, climate change could influence the outcomes of crop–weed competition in different ways, which further necessitates specific weed management strategies that are more flexible and adaptable to future climate scenarios.



6. IMPACT OF CLIMATE CHANGE FACTORS ON WEED MANAGEMENT AND HERBICIDE EFFICACY

Weeds cause extensive damage to cropland and noncropland areas and to public health. Weed management becomes the primary focus for farmers and weed scientists around the world. Several options exist for weed control,

including cultural, mechanical, chemical, and biological methods; however, chemical weed management through the use of herbicides is the most economical and widely used alternative for most developed countries, including the United States. In recent years, herbicide use has increased in other parts of the world, including China, India, and Sub-Saharan Africa because of their potential to improve crop yields and save labor and energy, thereby reducing the cost of farming (Gianessi, 2013). Although the focus of weed management is shifting toward integrated strategies to reduce the impact of herbicide use on the environment and the development of herbicide-resistant weeds, herbicides remain the mainstay of weed control due to their ease of application and cost-effectiveness. Given the importance of herbicide use in sustainable crop production, it is essential to understand if climate change influences the efficacy of herbicides to control weeds in future. Several studies have focused on the impact of climate change on crop productivity, but less attention has been given to the impact on weed management, particularly herbicide efficacy and its subsequent effects on the development of herbicide-resistant weeds. Changes in herbicide susceptibility due to environmental stress could have serious consequences for crop-weed competition and may contribute to higher production losses in future.



7. ENVIRONMENTAL FACTORS THAT AFFECT HERBICIDE ACTIVITY

To realize the impact of climate change on herbicide efficacy, it is important to understand how environmental conditions affect herbicide performance. Successful use of herbicides depends on environmental conditions prior to, during, and after herbicide application. The environment influences not only growth and physiology of the plants but also the herbicide and the interaction between the plant and herbicide. In the previous sections, we reviewed how climate change influences weed physiology and growth. Here, we discuss the effects of environmental factors such as light, CO₂, temperature, soil moisture, relative humidity, rainfall, and wind on herbicide action in plants. These factors can affect herbicide efficacy directly by altering the penetration and translocation of herbicides within the plant or indirectly by changing the growth and physiological characteristics of the plants. While foliar-applied herbicides are influenced by many environmental factors, soil-applied herbicides are influenced mainly by soil moisture and temperature.

7.1 Light

Light is one of the most important environmental factors that influences plant growth and development. Variation in light intensities changes the anatomy, morphology, and growth of plants, which further affects herbicide performance. Light is the source of energy for photosynthesis, and the rate of photosynthesis determines the rate of phloem translocation of assimilates (Devine, 1989). Net photosynthetic rate typically increases with light intensity, and higher photosynthesis and subsequent phloem translocation will increase the movement of foliar-applied systemic herbicides; for example, the efficacy of clethodim and tralkoxydim was reduced in ultraviolet light, which indicates that spraying these grass herbicides later in the day when light intensity is higher may improve their efficacy (McMullan, 1996). Light is also essential for seed and leaf development (Ohadi et al., 2010). Stomatal conductance and leaf cuticle development are positively correlated with light intensity (Hull et al., 1975; Raschke et al., 1978). At high light intensity, stomata remain open, thus improving tissue penetration for foliar-applied herbicides. Furthermore, plant branching and leaf thickness increase to reduce the damage caused by excessive light energy and to ensure the proceeding of photosynthesis (Matos et al., 2009; Wentworth et al., 2006). Conversely, at low light intensity, plants tend to produce thinner leaves with greater specific leaf area and plant height to capture available light and meet the demand for photosynthesis (Steinger et al., 2003). These adaptations in plant growth and leaf anatomy influence the amount of herbicide that is absorbed and retained by the plant; for example, higher plant branching increases surface coverage and absorption of postemergent (POST) herbicides, whereas thicker leaves slow the diffusion of herbicides resulting in reduced herbicide activity (Riederer and Schonherr, 1985).

7.2 Carbon Dioxide

The importance of CO₂ influence on herbicide efficacy has come to our attention in recent years as a result of the steady rise in atmospheric CO₂ since the industrial revolution. High CO₂ concentrations in the atmosphere are likely to have pronounced effects on weed biology, consequently altering herbicide performance on weeds. One of the most prominent effects of elevated CO₂ levels is the reduction in stomatal conductance, which could increase up to 50% in some plants (Bunce, 1993). Reduced stomatal conductance can alter the efficacy of both foliar- and soil-applied herbicides. Furthermore, at elevated CO₂ levels, leaf thickness increases and the number of open stomata decrease; thus, reducing the amount of foliar-applied

herbicide that is directly absorbed into the plants, thereby protecting the weeds from damage by POST herbicides. Decreased stomatal conductance also results in reduced transpirational flow, which further reduces the uptake of soil-applied herbicides (Bunce and Ziska, 2000; Ziska, 2008). In addition, an increase in the net photosynthetic rates at high CO₂ levels, particularly in C₃ weeds, could result in rapid seedling growth. Because the seedling stage is the most sensitive stage for effective weed control, the timing of POST herbicide application could be altered. Common lambsquarters is a C₃ weed that has shown higher tolerance to glyphosate as a result of increased growth and biomass at elevated CO₂ (Ziska et al., 1999). Glyphosate efficacy at elevated CO₂ concentrations was also reported to decrease in C₄ invasive weeds such as Rhodes grass (*Chloris gayana*), weeping lovegrass (*Eragrostis curvula*), and dallisgrass (*Paspalum dilatatum*) owing to increased biomass and leaf area (Manea et al., 2011). Greater CO₂ concentrations may stimulate rhizome or tuber (below-ground) growth relative to aboveground growth in most perennial weeds, which may render herbicide control of such weeds more difficult (Patterson et al., 1999). Ziska et al. (2004) reported increased growth and root:shoot ratio of field-grown Canada thistle (*C. arvensis*) under elevated CO₂ levels, which resulted in the reduced efficacy of glyphosate because of the dilution effect caused by large stimulation of below-ground growth.

7.3 Temperature

Temperature has both direct and indirect effects on herbicide efficacy. Temperature has complex effects on plant growth and development. Photosynthesis, phloem translocation, respiration, and protoplasmic streaming are some temperature-dependent physiological processes. Changes in the rate of these processes will indirectly affect herbicide penetration and translocation. Germination, seedling growth rate, and leaf anatomy (leaf area, leaf shape, and cuticle development) can be influenced by air and soil temperature, which, in turn, determine the time when plants are most susceptible to herbicides (Hull et al., 1975). Guo and Al-Khatib (2003) showed that seedling growth rates of redroot pigweed, common waterhemp, and palmer amaranth increased at high temperatures and suggested that the amount of time for POST herbicide applications to be most effective (when the seedling are younger) decreases at high temperatures.

Temperature can directly affect herbicide performance through its effects on the rate of herbicide diffusion, viscosity of cuticle waxes, and physicochemical properties of spray solutions (Price, 1983). Higher temperatures may lower the viscosity of cuticular lipids, thereby increasing the permeability and

diffusion of herbicides through the cuticle; for example, uptake and translocation of ^{14}C -glyphosate was found to be higher at 22°C than at 16°C in *Desmodium tortuosum* (Sharma and Singh, 2001). Similarly, Roundup Ready Soybean translocated more ^{14}C -glyphosate to meristematic tissues at 35°C than at 15°C , indicating potentially increased glyphosate injury at higher temperatures (Pline et al., 1999). Flumiclorac also showed higher activity on common lambsquarters (sevenfold) and redroot pigweed (threefold) as temperatures increased from 10°C to 40°C (Fausey and Renner, 2001). Although high air temperatures tend to speed both absorption and translocation of most foliar-applied herbicides, in some cases high temperatures also may induce rapid metabolism, which subsequently reduces herbicide activity on target plants (Kells et al., 1984; Johnson and Young, 2002). A threefold increase in the absorption and translocation of mesotrione in velvetleaf and common cocklebur was observed at 32°C . In contrast, mesotrione efficacy on common waterhemp and large crabgrass (*D. sanguinalis*) decreased by six- and sevenfold at the same temperature (Johnson and Young, 2002). Similarly, mesotrione efficacy on palmer amaranth decreased significantly with an increase in temperature from 25°C to 40°C , indicating a possible increase in metabolism of mesotrione at higher temperatures (Godar et al., 2015). Warmer temperatures also may result in reduced herbicide uptake due to rapid drying of spray droplets to solid deposits (Devine et al., 1993). Temperature also affects the volatility of some herbicides, such as synthetic auxins resulting in vapor drift and possible injury on nontarget broadleaf plants (van Rensburg and Breeze, 1990; Strachan et al., 2010). Visual symptoms of injury due to dicamba drift on soybean increased from 0% to 40% as temperature increased from 15°C to 30°C (Behrens and Lueschen, 1979). Although these effects are observed mainly with foliar-applied herbicides, soil temperature affects the movement and permeability of soil-applied herbicides within the plant. High soil temperatures may lower the efficacy of soil-applied herbicides by increasing volatility and microbial breakdown. High temperature had a profound effect on the volatilization of the triallate herbicide from soils. Triallate losses increased from 14% to 60% in sandy soil and 7% to 41% in loamy soil when temperatures increased from 5°C to 25°C (Atienza et al., 2001).

7.4 Relative Humidity

Relative humidity primarily influences the activity of foliar-applied herbicides through its effects on herbicide uptake. Relative humidity could influence the efficacy of foliar-applied herbicides through interactions between the herbicide droplet, leaf cuticle, and availability of water in or around droplets

(Devine et al., 1993). Both air temperature and relative humidity influence transpirational flow; thus, affecting chemical absorption and movement. High temperature and low humidity increase evaporation, which, in turn, reduces droplet size and increases herbicide drift. At high humidity, however, the effects of high temperature on droplet drying is reduced due to increased leaf retention time, hence increased herbicide absorption. Plants grown at high humidity usually develop softer cuticles than plants grown at low humidity, which tend to have thicker cuticles and thus less herbicide penetration. In general, humidity has a greater effect on herbicide uptake than temperature. The efficacy of glufosinate ammonium on green foxtail (*Setaria faberi*) and barley was greater at high humidity than at high temperature (Anderson et al., 1993). Humidity typically affects herbicide uptake through its impact on cuticle hydration and the rate of droplet drying after herbicide application (Muzik, 1976; Price, 1983). Therefore, humidity is considered more important at the time of spraying than during the postspraying period. Increased herbicide uptake at high relative humidity may lead to greater translocation of herbicides. The effects of humidity are much higher on water-soluble herbicides than on lipophilic herbicides. At high humidity, cuticle hydration and stomatal opening increases, which further increases the permeability of water-soluble herbicides into the leaf surface (Kudsk et al., 1990). The susceptibility of common waterhemp and large crabgrass to mesotrione was four- and two-fold higher at 85% relative humidity compared with 30%, respectively (Johnson and Young, 2002). Wild oat plants grown at high (>95%) relative humidity demonstrated significantly increased glufosinate ammonium efficacy compared with those grown at low (40%) relative humidity; furthermore, uptake of ^{14}C -glufosinate ammonium was higher when wild oat plants were exposed to high relative humidity for 30 min before and after treatment compared with those left at continuously low relative humidity (Ramsey et al., 2002). Uptake and efficacy of most herbicides was generally found to be higher when plants were exposed to high humidity after spraying than before, suggesting that delayed droplet drying could be the mechanism for higher efficacy at high humidity levels rather than cuticle hydration (Ramsey et al., 2005).

7.5 Precipitation and Soil Moisture

Precipitation can directly influence herbicide uptake by washing the spray droplets off leaf surfaces or by diluting the herbicide to a less-effective form. This effect is more pronounced if precipitation occurs shortly after herbicide application. Herbicide applications are generally not recommended immediately

after rainfall because wet leaf surfaces have a higher tendency to bounce off the spray droplets (Spillman, 1984). The intensity and duration of precipitation determine the rainfastness of the herbicide. Rainfastness is the ability of an herbicide to quickly dry and penetrate into the leaf tissues so it remains effective after rainfall. Herbicides with lipophilic properties usually have better rainfast properties than water-soluble herbicides (Kudsk and Kristensen, 1992). Ester formulations of auxinic herbicides are absorbed more quickly than amine and salt formulations, which are more susceptible to wash-off. Low levels of precipitation or dew may improve leaf retention and herbicide efficacy by rewetting spray droplets on the surface (Olesen and Kudsk, 1987). On the other hand, lower precipitation amounts throughout the season may result in water stress conditions that affect both plant growth and herbicide efficacy (Zanatta et al., 2008).

Soil temperature and moisture directly influence soil-applied herbicides by affecting herbicide concentration, solubility, and movement in the soil and through the plant via transpiration (Moyer, 1987). Low soil moisture content may result in increased adsorption of herbicides to the soil particles, thus reducing their availability for uptake by plant roots (Dao and Lavy, 1978). Adequate soil moisture is particularly necessary for pre-emergent herbicides for movement into the zone of weed seed germination and effective weed control. Soil moisture effects on foliar-applied herbicides are related to herbicide absorption, translocation, and metabolism (Hinz and Owen, 1994; Peregoy et al., 1990). Cheatgrass and spring wheat were injured more from sulfonylurea herbicides applied when soil moisture was at saturation compared with one-third moisture content (Olson et al., 2000). Efficacy of imazamethabenz on blackgrass (*Alopecurus myosuroides*) increased with increasing soil moisture (Malefy and Quakenbush, 1991). Corn injury by EPTC and butylate was higher at 33% than at 15% soil moisture (Burt and Akinsoratan, 1976). Plants grown under moisture stress develop leaves with an upright orientation to minimize leaf surface area that intercepts light and temperature. This orientation has negative consequences for foliar absorption because upright leaves cannot retain spray droplets for a long time (Levene and Owen, 1995). Prolonged periods of moisture stress reduce photosynthesis due to stomatal closure and causes leaf thickening, tissue dehydration, and greater leaf senescence which, in turn, reduces herbicide diffusion and subsequently lowers herbicide absorption and translocation (Kogan and Bayer, 1996). Pereira et al. (2011) found that the efficacy of sethoxydim was lower in goosegrass (*E. indica*) plants grown under water-deficit conditions. Similarly, plantain signalgrass (*Urochloa plantaginea*) plants grown under water stress were not effectively controlled by ACCase-inhibiting herbicides when applied during the later growth stages (Pereira, 2010).

7.6 Wind

Wind may have a less pronounced influence on herbicide performance. Nonetheless, windy conditions can interfere with surface application and cause spray drift, thereby reducing spray application efficiency (Combella, 1982). Wind reduces herbicide retention by moving spray off and away from plants and particularly affects deposition of smaller droplets on the leaf surface (Nordbo and Taylor, 1991). Furthermore, spray deposits tend to dry rapidly under windy conditions, with a subsequent reduction in herbicide uptake. Wind can also cause cuticle damage through leaf collisions and abrasions from soil particles (Thomson, 1974). Wind also affects evapotranspiration from the leaf surface; thus, altering herbicide absorption from soil. However, in the case of contact herbicides, wind may increase herbicide action, especially at high temperatures and low humidity (Muzik, 1976).



8. IMPACT OF CLIMATE CHANGE FACTORS ON THE EFFICACY OF HERBICIDES WITH DIFFERENT CHEMISTRIES

Herbicides act on various sites in plants. Based on their specific site of action and symptoms of injury, herbicides are grouped into different modes of action. Table 4 outlines a brief overview of herbicide classifications based on the primary mechanism of action, including the chemical families, active ingredients, and major injury symptoms of commonly used herbicides in each group. Herbicide action generally depends on a metabolic function in the plant that is essential for normal plant growth and development. Consequently, any change in the climatic conditions that affects the metabolic pathways in the plants adversely affects herbicide performance. In addition, climate change can affect herbicide properties and alter the physicochemical processes through which the herbicide is absorbed and translocated in the plant. Herbicides belonging to different modes of action have different physicochemical properties, which further implies that climate change effects can vary among the different herbicide chemistries. Therefore, it is important to understand the impact of climate change on the underlying physiological and biochemical mechanisms that determine herbicide efficacy of each mode of action. Here, we review existing studies of how climate change has influenced some of the herbicides in each mode of action. This information will be helpful not only in identifying potential modes of action that are least affected by climate change but also in assessing

Table 4 Herbicide chemistries and symptomatology.

| Herbicide classification | Site of action | Chemical family | Active ingredients | Activity | Major injury symptoms |
|---------------------------------|--|--|--|---|--|
| Growth regulators | Auxin receptors | Benzoic acid Carboxylic acid | Dicamba Clopyralid, fluroxypyr, picloram | Effective on perennial and annual broadleaf weeds | Twisting, drooping, and curling in stems, cupping and crinkling in leaves |
| Amino acid synthesis inhibitors | Auxin transport inhibitors Acetolactate synthase (ALS) inhibitors | Phenoxy acetic acids | 2,4-D, MCPA | Effective on both grasses and broadleaf weeds | In grasses, stunting, purple coloration, and “bottle brush” appearance on roots; in broadleaf plants, red or purple leaf veins and yellowing of new leaves |
| | | Semicarbazone Imidazolinones | Diflufenzopyr Imazamox, imazapic, imazamethabenz | | |
| | Sulfonylureas | Nicosulfuron, thifensulfuron, tribenuron, chlorsulfuron, metsulfuron | | | |
| | Triazopyrimidines None accepted | Flumetsulam, cloransulam Glyphosate | Nonselective herbicide with broad-spectrum weed control | | |
| | 5-Enolpyruvylshikimate-3-phosphate (EPSPS) synthase inhibitors | Phosphoric acid | Glufosinate | Nonselective herbicide with broad-spectrum weed control | Yellowing, browning, and death of affected plants Chlorosis, wilting, necrosis followed by death of affected plants |
| Photosynthetic inhibitors | Photosystem II inhibitors | Triazines Triazinones Benzothiadiazoles Nitriles Ureas Phenylcarbamates | Atrazine, simazine Metribuzin Bentazon Bromoxynil Linuron, diuron Desmedipham | Broadleaf herbicides with some activity on annual grasses | Yellowing in the veins and leaf margins, speckling, spotting, or bronzing, and death of the affected part |
| Lipid synthesis inhibitors | Acetyl-CoA carboxylase (ACCCase) inhibitors | Aryloxyphenoxypropionates (APPs) | Fenoxaprop, fluazifop, quizalofop, diclofop, clodinafop | Effective only on annual and perennial grasses | New leaves turn yellow and die. Stem sheath and leaf margins may become reddish blue |
| | | Cyclohexanediones (CHDs) Phenylpyrazolins | Clethodim, sethoxydim Pinoxaden | | |

(Continued)

Table 4 Herbicide chemistries and symptomatology.—cont'd.

| Herbicide classification | Site of action | Chemical family | Active ingredients | Activity | Major injury symptoms |
|----------------------------------|---|----------------------|---|---|---|
| Seedling root growth inhibitors | Microtubule inhibitors | Dinitroanilines | Pendimethalin, trifluralin, ethalfluralin | Effective on small-seeded broadleaf and grass weeds | In grasses, stunting and purple discoloration with stubby and thick roots; in broadleaf plants, swollen and cracked hypocotyls |
| Seedling shoot growth inhibitors | Lipid synthesis inhibitors (not ACCase) | Thiocarbamates | Triallate, EPTC, butylate | Effective on small-seeded broadleaf and grass weeds | In grasses, improper leaf unfolding, buggy whipping, and leaf crinkling; in broadleaf plants, stunting, leaf puckering, and drawstring appearance |
| | Long-chain fatty acid inhibitors | Chloroacetamides | Alachlor, acetochlor, metolachlor, dimethenamid | | |
| Cell membrane disrupters | Protoporphyrinogen oxidase (PPO) inhibitors | Oxyacetamides | Flufenacet | Effective on both grasses and broadleaf weeds | Contact herbicides that cause rapid yellowing and drying up of the affected plant part |
| | | Pyrazoles | Pyroxasulfone | | |
| | | Diphenyl ethers | Acifluorfen, fomesafen, lactofen | | |
| Pigment inhibitors | Photosystem I electron diverters Diterpene synthesis inhibitors 4-Hydroxyphenylpyruvate dioxygenase (HPPD) inhibitors | Aryl triazinones | Sulfentrazone, carfentrazone, fluthiacet | Effective on annual grass and broadleaf weeds | Injured leaves appear yellow or white and eventually become translucent |
| | | N-phenylphthalimides | Flumiclorac, flumioxazin | | |
| | | Pyrimidinediones | Saflufenacil | | |
| | | Bipyridiliums | Paraquat, diquat | | |
| | | Isoxazolidinones | Clomazone | | |
| | | Isoxazoles | Isoxaflutole | | |
| | | Pyrazoles | Pyrasulfotole | | |
| Pyrazolones | Topramezone | | | | |
| Triketones | Mesotrione, tembotrione | | | | |

research gaps in the current knowledge and suggesting potential areas that need to be focused in the future to sustain current weed control strategies in the face of global climate change.

8.1 Amino Acid Inhibitors

This group of herbicides inhibits amino acid synthesis in susceptible plants. Based on the type of amino acids that are inhibited, they can be classified as (1) ALS inhibitors, which inhibit the production of branched-chain amino acids (leucine, isoleucine, and valine) by blocking acetolactate synthase enzyme; (2) EPSPS inhibitors, which block the EPSPS enzyme in the shikimic acid pathway and inhibit the production of aromatic amino acids (tryptophan, phenylalanine, and tyrosine); and (3) glutamine synthetase inhibitors, which inhibit the glutamine synthetase enzyme, which is essential for assimilation of ammonia into organic nitrogen, resulting in phytotoxic accumulation of ammonia and reduced production of glutamine and other amino acids.

Amino acids are essential building blocks for protein synthesis. Proteins are required for the production of new cells and for the functioning of many plant processes. Plants synthesize amino acids from carbohydrates (produced by means of photosynthesis) and nitrogen (obtained from the soil) through collateral metabolic pathways. Any change in the environmental conditions that affect carbohydrate production through photosynthesis or nitrogen absorption from the soil can alter amino acid production in plants, subsequently affecting the efficacy of herbicides that inhibit amino acid synthesis. For example, elevated CO₂ may increase the starch content with a subsequent reduction in protein content per gram of tissue (Bowes, 1996). Less protein may lead to less demand for amino acid synthesis, which in turn may alter the efficacy of amino acid inhibitors. Long-term exposure (231 days) to elevated CO₂ concentration of 720 μmol mol⁻¹ increased glyphosate tolerance in quackgrass (*E. repens*) compared with ambient CO₂ concentration of 380 μmol mol⁻¹. It was speculated that this could have been owing to either a reduction in stomatal conductance that may have decreased glyphosate absorption or high leaf starch concentrations, which is common in C₃ plants exposed to CO₂ enrichment (Ziska and Teasdale, 2000). Research from previous studies indicates that the environmental impact on the efficacy of amino acid inhibitors is species-specific. Although the efficacy of imazamethabenz on wild oat (*A. fatua*) control increased by 15.7% at double-ambient CO₂ levels, efficacy of metsulfuron on redroot pigweed decreased by 4.6%, and no change in the efficacy of imazethapyr was observed on chickweed (*Stellaria media*) (Archambault et al., 2001). Efficacy of some

amino acid inhibitors also can vary with the ability of plants to metabolize under changing environmental conditions; for example, at 46 g ha^{-1} , percent injury from a sulfonylurea herbicide increased with an increase in the day/night temperature regimes from $5/3^\circ\text{C}$ to $25/23^\circ\text{C}$ and was highest for cheatgrass (33–95%), followed by wild oat (28–53%), jointed goatgrass (*Aegilops cylindrica*) (10–32%), and spring wheat (1–8%), suggesting that slower plant growth at the $5/3^\circ\text{C}$ temperature may have inhibited herbicide effectiveness in all species (Olson et al., 2000). Variation in the plant response suggests that spring wheat plants were able to metabolize the herbicide rapidly at all temperatures compared with the other three grass weeds. Similarly, control was higher for the weedy species at full soil moisture capacity compared with one-third moisture content. Lower herbicide efficacy at one-third soil moisture may be due to physiologically inactive plants or less herbicide dissolution in the soil solution, which may decrease its uptake by plant roots (Wu et al., 1974; Olson et al., 2000). Zhou et al. (2007) reported that drought and flooding resulted in lower glyphosate efficacy in velvetleaf plants due to alterations in leaf orientation (leaves tilted downward). This result indicates that changes in future precipitation patterns due to global warming that lead to more frequent droughts and floods may also decrease the effectiveness of herbicides. In contrast, increased ambient air temperature and high relative humidity were found to improve the efficacy of some amino acid inhibitors; for example, the efficacy of glyphosate and imazethapyr were significantly higher when common ragweed was treated between noon and 18:00 h (Stoppes et al., 2013). As air temperature increases, cuticle and plasma membrane fluidity increases in the leaves, resulting in improved herbicide uptake and translocation (Johnson and Young, 2002). Relative humidity was found to have a more pronounced effect on the phytotoxic action of glufosinate ammonium than temperature. Under controlled conditions, glufosinate efficacy on green foxtail was significantly higher at 95% relative humidity than at 40% (Anderson et al., 1993). Glufosinate translocation was higher in palmer amaranth, redroot pigweed, and common waterhemp grown at 90% relative humidity compared with 35%, indicating greater control at high humidity levels (Coetzer et al., 2001).

8.2 Photosynthetic Inhibitors

These herbicides inhibit photosynthesis in susceptible plants by impeding the electron transport system in light reactions. Photosynthetic inhibitors include herbicides that bind to the D-1 quinone protein of photosystem II and inhibit plastoquinone binding; thus, interrupting the process of photosynthetic

electron transfer. This process compromises the synthesis of ATP and NADPH in the chloroplast, resulting in the inability to fix CO₂. Electrons also are diverted from the electron transport chain, which causes oxidative stress due to the generation of free radicals that cause rapid cellular damage.

Elevated CO₂ concentrations and temperature alter the photosynthetic activity in plants and may subsequently affect the action of herbicides that interfere with photosynthesis. Effects of elevated CO₂ levels on photosynthetic inhibitors varied with species; for example, the efficacy of linuron on wild buckwheat (*P. convolvulus*) was reduced by 15% at double-ambient CO₂ levels, whereas no change was observed for bromoxynil on kochia (*K. scoparia*) or metribuzin on common lambsquarters (Archambault et al., 2001). In contrast, efficacy of most photosynthetic inhibitors showed a consistent increase with increased temperature, light intensity, or soil moisture. Control of velvetleaf and common ragweed was maximized when atrazine was applied at 15:00 h, when the air temperature was highest. The efficacy of bromoxynil on velvetleaf was reduced by up to 45% when applied at 24:00 h, when the air temperature was lowest (Stewart et al., 2009). Mulder and Nalewaja (1978) reported a 26% increase in atrazine toxicity on barley shoots as temperature increased from 10°C to 17°C at all the rates used in the study (0.5, 0.75, and 1 kg ha⁻¹). Uptake of bentazon was greatest for velvetleaf plants grown under high temperature and high moisture content compared with plants grown under high temperature and drought stress conditions. It was suggested that plant epicuticular wax increased under drought stress conditions, which could have affected the absorption of bentazon. Bentazon absorption also increased with increasing light intensity, suggesting that absorption may depend on the supply of ATP available in plants (Hatterman-Valenti et al., 2011).

8.3 Lipid Synthesis Inhibitors

These chemicals block the activity of the enzyme ACCase that catalyzes the conversion of acetyl-CoA to malonyl-CoA. Malonyl-CoA is required for fatty acid synthesis. Inhibition of fatty acid synthesis through ACCase blocks formation of lipids that are essential components of cell membranes. As a result, many plant processes, such as thylakoid membrane formation, chloroplast formation and multiplication, and cell division, are disrupted; thus, ceasing growth in susceptible plants. Lipid synthesis inhibitors include two herbicide families, aryloxyphenoxypropionates (APPs) and cyclohexanediones (CHDs). APPs are applied and absorbed as inactive ester formulations, which are later converted into the active acid form in the sensitive species.

Climate factors influence the efficacy of lipid synthesis inhibitors through their impacts on the physicochemical processes that affect herbicide absorption, translocation, and metabolism. For example, at low rates, diclofop toxicity to wild oat was higher at a lower temperature (10°C) than at a higher temperature (24°C) (Mulder and Nalewaja, 1978). Diclofop was reported to metabolize rapidly in wheat and wild oat plants to water-soluble conjugates (Shimabukuro et al., 1977); however, the rate of metabolism would probably decrease at lower temperatures, thereby increasing phytotoxicity. Although low soil moisture reduced the efficacy of fluzifop (Dickson et al., 1990), low temperatures and soil moisture deficit prior to application influenced the efficacy of clodinafop on *Avena* spp. (Medd et al., 2001). Research has also shown that efficacy of CHD herbicides decreased in ultraviolet light due to photodegradation (McMullan, 1996). The effects of rising CO₂ on lipid synthesis inhibitors is species-specific. At double-ambient CO₂ levels, clodinafop efficacy increased by 8.6% on wild oat, whereas sethoxydim efficacy was not affected. Efficacy of fluzifop was not affected by elevated CO₂ levels in both wild oat and green foxtail (Archambault et al., 2001).

8.4 Growth Regulators

Growth regulator herbicides are synthetic auxins that mimic natural growth hormones and alter hormonal regulation in sensitive plants. Auxinic herbicides are more stable in plants than natural auxins and are transported systemically in sensitive plants. They are used selectively against dicot weeds in cereal crops (Grossmann, 2010). These herbicides disrupt numerous biochemical pathways such as those necessary for nucleic acid metabolism, cell elongation, cell division, and protein synthesis. Auxinic herbicide action is mediated by specific receptors that trigger a host of transcriptional and biochemical responses to auxin overdose in the tissue. Further interactions with other hormones in the cell such as ethylene and abscisic acid lead to abnormal growth patterns in affected plants, ultimately leading to senescence and cell and plant death. Auxinic herbicides are categorized as one of the three types: phenoxy acids such as 2,4-D, 2,4-DP, MCPA, or MCPP; benzoic acids such as dicamba; or picolinic acid compounds such as picloram, triclopyr, and clopyralid.

Environmental stress may have variable effects on growth regulator herbicides and is usually species-dependent; for instance, regardless of temperature increase, dicamba/diflufenzopyr provided greater than 95% control of common ragweed, common lambsquarters, and redroot pigweed. In contrast, control of velvetleaf was reduced by 7% to 15% at a low temperature

(Stewart et al., 2009). Likewise, water stress capable of slowing plant growth significantly decreased translocation of picloram and reduced efficacy in Canada thistle and Russian knapweed (*Acroptilon repens*) (Morrison et al., 1995). Efficacy of 2,4-D on wild buckwheat control increased by 26.9% at double-ambient CO₂ levels, but clopyralid efficacy on common groundsel decreased by 8.9% (Archambault et al., 2001).

8.5 Seedling Growth Inhibitors

Seedling growth inhibitors include three groups of herbicides: microtubule assembly inhibitors (dinitroanilines), seedling shoot and root growth inhibitors (acetanilides), and seedling shoot inhibitors (carbamothiates). All these herbicides inhibit seedling germination and emergence and must be preplant-incorporated or pre-emergent-applied to be effective. They interfere with new plant growth by inhibiting cell division or lipid and protein synthesis. Plants take up these herbicides from soil through developing roots and shoots. Because these herbicides are soil-incorporated, their efficacy is significantly affected by soil factors such as moisture, temperature, organic matter, and type of soil (Jursík et al., 2013). Dry soil conditions generally decrease the activity of these pre-emergent herbicides because of herbicide adsorption, but intense precipitation after the application may result in leaching (Soukup et al., 2004). Leaching potential depends on the type of soil. In general, herbicide leaching is high in sandy soils compared with clay soils because of their low sorption capacity; for example, a higher rate of subsurface leaching was recorded for metolachlor in sandy soils than in clay soils (Inoue et al., 2010). Jursík et al. (2013) reported a decrease in the activity of pethoxamid under dry soil moisture conditions. Under controlled experiments, low soil temperatures around 10°C also reduced the activity of alachlor and EPTC (Mulder and Nalewaja, 1978). Similarly, activity of acetochlor also decreased with increasing soil organic matter (Vasilakoglou et al., 2001).

8.6 Cell Membrane Disrupters

Several herbicide families with similar primary mechanisms of action are grouped into this category. The major mode of action in susceptible plants is rapid destruction of cell membranes and leakage of cell contents through the formation of free radicals. These herbicides are diverse compounds with sites of action in photosystem I (bipyridyliums) or the PPO enzyme (PPO inhibitors). Paraquat and diquat are examples of bipyridyliums, which divert electrons from the photosynthetic electron transport chain in photosystem I

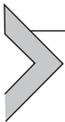
to generate hydroxyl radicals through the formation of superoxide and hydrogen peroxide. These toxic-free radicals can induce lipid peroxidation, leading to chlorophyll breakdown and loss of photosynthetic activity through the disruption of cell membranes (Babbs et al., 1989). PPO inhibitors include diphenyl ethers, triazolinones, phenylphthalimides, and pyrimidinediones, which inhibit the PPO enzyme that is required for chlorophyll and heme biosynthesis.

Cell membrane disrupters are primarily contact herbicides, so thorough spray coverage is essential for effective control. These herbicides are light-activated and generate symptoms rapidly under bright, sunny conditions (Wright et al., 1995). Absorption and efficacy of acifluorfen, a PPO inhibitor, varied with variation in soil moisture and light intensity. Although acifluorfen absorption decreased with increasing light intensity under field capacity moisture content, the opposite was true under drought stress conditions. This is due to the rapid cell membrane disruption under optimum moisture and high light intensity which reduced further penetration as light intensity increased (Hatterman-Valenti et al., 2011). Paraquat efficacy decreased with an increase in the ultraviolet (UV-B) radiation in velvetleaf, large crabgrass, and feather fingergrass (*Chloris virgata*) weeds. Increased UV-B radiation increased the leaf wax content of these species, consequently reducing paraquat absorption and efficacy (Wang et al., 2006). Temperature also influenced the efficacy of some PPO inhibitors; for example, the efficacy of flumiclorac and fluthiacet on common lambsquarters and redroot pigweed was significantly higher at 40°C than at 10°C (Fausey and Renner, 2001). Similarly, acifluorfen absorption was greater at 35/26°C than at 27/18°C, which resulted in better control of pitted morning glory (*Ipomoea lacunosa*) (Oliver and Lee, 1982). Because PPO inhibitors are contact herbicides, high temperatures generally favor the penetration of these herbicides due to reduced viscosity of leaf epicuticular waxes, resulting in increased herbicide diffusion.

8.7 Pigment Inhibitors

Herbicides belonging to this mode of action either interfere with the carotenoid pigment biosynthetic pathway (isoxazolidones) or block the enzyme HPPD (isoxazole, triketones, pyrazoles, and pyrazolones), an important enzyme for quinone synthesis. Carotenoids are essential compounds that prevent plant pigments from photo-oxidative damage. Quinones are required for functioning of electron transport in photosynthesis. Loss of carotenoids and quinones lead to chlorophyll destruction and loss of photosynthetic activity in susceptible plants.

Research on the effects of environmental stress on the activity of pigment inhibitors is limited. [Johnson and Young \(2002\)](#) reported that the effects of temperature and relative humidity on the foliar activity of mesotrione (HPPD-inhibitor) are largely species-specific. Efficacy of mesotrione increased by up to threefold in velvetleaf and common cocklebur at 32°C compared with 18°C because of increased absorption and translocation. In contrast, mesotrione efficacy was higher at 18°C for common waterhemp (sixfold) and large crabgrass (sevenfold). Similarly, mesotrione absorption and translocation was higher by fourfold and twofold at 85% relative humidity compared with 30% in common waterhemp and large crabgrass, respectively. This result may be due to increased hydration of the cuticle, which typically improves the penetration and efficacy of water-soluble herbicides such as mesotrione. Efficacy of mesotrione on palmer amaranth also decreased at high day/night temperatures of 32.5/22.5°C compared with 25/15°C. At high temperatures, decreased translocation and increased metabolism of mesotrione was observed in palmer amaranth, which resulted in the quick recovery of plants. Furthermore, as part of the plant defense mechanism, palmer amaranth increased its expression of HPPD enzyme at high temperatures to tolerate the toxic effects of mesotrione ([Godar et al., 2015](#)).



9. SUMMARY AND IMPLICATIONS FOR FUTURE RESEARCH

Global climate change factors has serious implications for not only crop growth and productivity but also herbicide performance and the effectiveness of chemical weed management. The steady rise in atmospheric CO₂ concentrations and its potential effects on other climate variables such as temperature, precipitation, relative humidity, and radiation may have important consequences for sustainable weed control and crop production. The studies reviewed here suggest that any positive impact of climate change on crop growth may be nullified by higher responses from weeds. Weeds tend to show better survival mechanisms under changing climate because of their greater interspecific genetic variation and physiological plasticity. Furthermore, herbicide properties are significantly influenced by environmental conditions before, during, and after application. Current weed management strategies that rely heavily on herbicide usage may have altered effects on these aggressively growing weeds in future climatic conditions.

This warrants immediate action in terms of extensive research on the potential effects of changing climate variables on different herbicide chemistries. In particular, it is necessary to develop experiments with multiple climate variables to study the interactive effects of climate change on weed control. Much research has been focused on single factor experiments that have little predictive value in reality because plant responses to interacting climate factors differ greatly from single factor responses. Furthermore, information from existing studies pertains more to controlled environment conditions that may not relate to responses under field conditions. Limited research has been carried out to predict the effects of global climate change on weed management under field conditions; therefore, it is essential to design long-term field studies with experimental conditions that simulate the future climate to predict the effects of global climate change more accurately. Information generated through such studies will help identify the potential weed control measures that need to be adopted to cope with challenges emerging from aggressive weed growth and possibly increased herbicide resistance under changing climate.

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