

## Review

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# Understanding the nexus of rising CO<sub>2</sub>, climate change, and evolution in weed biology

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## Abstract

Rapid increases in herbicide resistance have highlighted the ability of weeds to undergo genetic change within a short period of time. That change, in turn, has resulted in an increasing emphasis in weed science on the evolutionary ecology and potential adaptation of weeds to herbicide selection. Here we argue that a similar emphasis would also be invaluable for understanding another challenge that will profoundly alter weed biology: the rapid rise in atmospheric carbon dioxide (CO<sub>2</sub>) and the associated changes in climate. Our review of the literature suggests that elevated CO<sub>2</sub> and climate change will impose strong selection pressures on weeds and that weeds will often have the capacity to respond with rapid adaptive evolution. Based on current data, climate change and rising CO<sub>2</sub> levels are likely to alter the evolution of agronomic and invasive weeds, with consequences for distribution, community composition, and herbicide efficacy. In addition, we identify four key areas that represent clear knowledge gaps in weed evolution: (1) differential herbicide resistance in response to a rapidly changing CO<sub>2</sub>/climate confluence; (2) shifts in the efficacy of biological constraints (e.g., pathogens) and resultant selection shifts in affected weed species; (3) climate-induced phenological shifts in weed distribution, demography, and fitness relative to crop systems; and (4) understanding and characterization of epigenetics and the differential expression of phenotypic plasticity versus evolutionary adaptation. These consequences, in turn, should be of fundamental interest to the weed science community.

## Introduction

Among pests, weeds are acknowledged as the primary contributor to economic loss in crop production (Pimentel et al. 2000) and other managed systems, including rangelands (Smith et al. 1987) and forests (Webster et al. 2006). Weeds are also known to have a wide variety of other effects on ecosystem dynamics (Mooney and Hobbs 2000), including negative impacts on species diversity and ecosystem services (Forseth and Innis 2004; Pejchar and Mooney 2009).

However, the definition of “weed” is always in the context of the plant system being impacted. As such, it is a human designation, not a biological one. For example, invasive weeds may be defined as plant species outside their native geographic ranges whose presence results in substantial economic (e.g., crop loss) or ecological (e.g., species diversity) consequences (Richardson et al. 2000). But a strict definition of “invasive” can be elusive. For example, if we were to focus on North America, we would find that common lambsquarters (*Chenopodium album* L.) is from Eurasia, but is considered a native weed; kudzu [*Pueraria montana* (Lour.) Merr. var. *lobata* (Willd.) Maesen & S.M. Almeida ex Sanjappa & Predeep] is from East Asia and is generally deemed invasive; whereas native weeds such as ragweeds (*Ambrosia* spp.) are common, but if found beyond their geographic ranges, could be considered invasive.

Given the tremendous variety of agronomic and invasive weeds, as well as the differences among invaded ecosystems, generalizations regarding how weeds will evolve are unlikely. Yet there are some common themes in weed biology that are relevant to evolutionary responses. In this review, we want to explore those responses with the goal of identifying specific evolutionary consequences associated with a rapidly changing climate. We expect that such consequences will be of importance in defining and directing research for *all* weed biology, independent of context, for this century.

What aspects of a rapidly changing climate should concern weed scientists? Atmospheric CO<sub>2</sub> concentrations have risen by ~30% since 1957 and, at current levels of fossil fuel use and deforestation, may exceed 800 ppm by the end of the current century (Field et al. 2014). Concomitant increases in average temperature between 0.15 and 0.3C per decade, with greater temperature extremes, are also expected by 2100. Predictions for altered precipitation are less certain, but include greater likelihood of drought at lower latitudes, increased precipitation at higher latitudes, and an increase in the frequency and intensity of extreme precipitation events (Dore 2005; Qian et al. 2011; Rosenzweig et al. 2001; Swain and Hayhoe 2015).

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There are, in turn, two basic means whereby these global changes will impact weed biology. The first is related to physical changes in the environment. Both weeds and weed management are sensitive to climate, and changes in temperature and precipitation are likely to alter the range, composition, and competitiveness of any weed species (Bradley et al. 2010; Ziska and Dukes 2011). A second impact is the “fertilization” effect of rising CO<sub>2</sub> on plant photosynthesis. Because photosynthesis involves the conversion of CO<sub>2</sub> to sugars and is limited by the current concentration of CO<sub>2</sub>, ongoing increases will stimulate photosynthesis and plant growth. Cool-season species that use C<sub>3</sub> photosynthesis (~85% of plant species, including many weeds) are particularly responsive to increases in CO<sub>2</sub> (Ogren and Chollet 1982; Ziska 2003). In addition to its direct fertilization effect, CO<sub>2</sub> can also increase plant water-use efficiency, with potentially strong effects on invasive plant species establishment (Belote et al. 2003; Blumenthal et al. 2013; Smith et al. 2000).

Increasing CO<sub>2</sub> and altered temperature and precipitation are therefore likely to affect all aspects of weed biology (Peters et al. 2014; Ziska and Dukes 2011), including establishment (Clements et al. 2004), competition (Valerio et al. 2011), distribution (Bradley et al. 2010; Thuiller et al. 2008), and management (Waryszak et al. 2018). Overall, our ability to characterize evolutionary adaptation of weeds to climate and CO<sub>2</sub> has not been given adequate consideration (Moran and Alexander 2014). Yet such consideration may be particularly relevant, given that weeds are, in general, capable of rapid genetic change (Neve et al. 2009). The focus of the current review is to examine interactions between these impacts and adaptive evolution.

In examining how climate change can alter evolutionary aspects of weed biology, we acknowledge, given the eclectic nature of what constitutes a “weed,” the difficulty in developing conclusive evolutionary insights. However, we hope that a review of existing data can provide general trends related to evolutionary adaptation for three interrelated aspects of weed science: demographics, competition, and management. By examining these biological interactions, we also hope to gain insight into future research priorities that will help elucidate how elevated CO<sub>2</sub> and/or climate change will alter selective pressures, fitness, and observed evolutionary responses that will be of fundamental importance in weed biology and weed science.

## Weeds and Evolution

In examining evolution, it is important to distinguish between acclimation and adaptation, particularly for weeds. It is commonly accepted that weeds often have “general-purpose genotypes” (Baker 1974) and could, potentially, respond to rapid environmental change primarily through plasticity or acclimation of traits such as phenological or morphological characteristics (Davidson et al. 2011) with potential diminishment of the correlation between environmental and phenotypic variation. Conversely, weeds also have characteristics that may favor rapid adaptive evolution with climate shifts: large populations, short life cycles, strong dispersal abilities, and in the case of introduced or invasive weeds, novel selection pressures (Clements et al. 2004; Neve et al. 2009; Prentis et al. 2008).

Any time that environmental conditions change, there is potential for concomitant shifts in natural selection and for adaptive evolution to occur. For weeds, this can take place when introduced to new locations with novel conditions or when existing environmental conditions (e.g., herbivores, competitors) change (Clements and

DiTommaso 2011; Mooney and Cleland 2001; Sakai et al. 2001). For example, herbicide use can lead to selection for, and the evolution of, herbicide resistance (Heap 2014; Powles and Yu 2010). However, adaptive evolution will not always occur, as there are acknowledged limitations and constraints (Hoffmann et al. 2014). For example, many weedy species have failed to adapt to serpentine soils despite living in proximity to them, possibly due to lack of genetic variation for tolerance to serpentine soils (Brady et al. 2005).

A change in climate could also result in ecological sorting rather than adaptive evolution within populations. For example, earlier onset of spring due to global warming could select for earlier emergence within populations, or could favor species that already emerge earlier, or both (Willis et al. 2010). Consequently, how and to what extent weeds will evolve in response to climatic and other environmental changes, the types of changes most likely to lead to evolution, and which species are most likely to adapt to climatic changes are empirical questions important to weed science.

A key prerequisite for adaptive evolution is genetic variation, because the rate of evolutionary response to selection is directly proportional to the amount of genetic variation in a population (Fisher 1958). Evidence is mixed regarding the level of genetic variation within weed populations. Founder effects, consistent selection pressures, and selfing may all reduce variation, while the presence of large seedbanks that maintain viability of previous biotypes and repeated introductions may enhance or restructure genetic variation over time (Clements et al. 2004; Dlugosch and Parker 2008). Measurements of genetic variation in weed populations include examples of weed species with ample variation and others in which variation is quite limited (Neve et al. 2009).

Despite potential limitations, there is increasing empirical evidence for rapid microevolutionary change within agronomic and invasive weed species (Maron et al. 2004; Neve et al. 2009). In agronomic systems, herbicides represent extraordinarily strong selective pressures, and the evolutionary potential of weeds is perhaps best illustrated by the rapid and widespread documentation of herbicide resistance (Heap 2014). In the study of invasive weeds, considerable effort has been devoted to understanding how species have evolved following their introduction to new ranges. Release from specialist herbivores in the introduced range has been hypothesized to allow evolution of reduced defense and increased growth or competitive ability (Blossey and Notzold 1995). Common garden studies partially support this idea, suggesting that rapid evolution in both growth and defense is relatively common in species in introduced ranges. (Blossey and Notzold 1995; Felker-Quinn et al. 2013; Zhang et al. 2018). These examples suggest that the traditional paradigm of weed evolution as a very slow process is incomplete and that rapid evolutionary change (years or decades) can be pervasive within weed biology and could include evolution in response to climate (Clements et al. 2004; Ravet et al. 2018).

Overall, it is evident that weed populations can evolve quickly in response to intense selection pressures associated with novel environmental conditions arising from both introduction and management, in accord with the wider recognition that evolution can occur on ecological timescales (Neve et al. 2009; Thompson 1998). Consequently, weeds may often have the capacity to rapidly evolve in response to climatic changes. Further investigations into these evolutionary responses is likely to be a fruitful area of inquiry. Particularly useful may be studies using the resurrection approach (Franks et al. 2018) to study weed evolution, such as work done by Kuester et al. (2016), who found evolutionary responses and

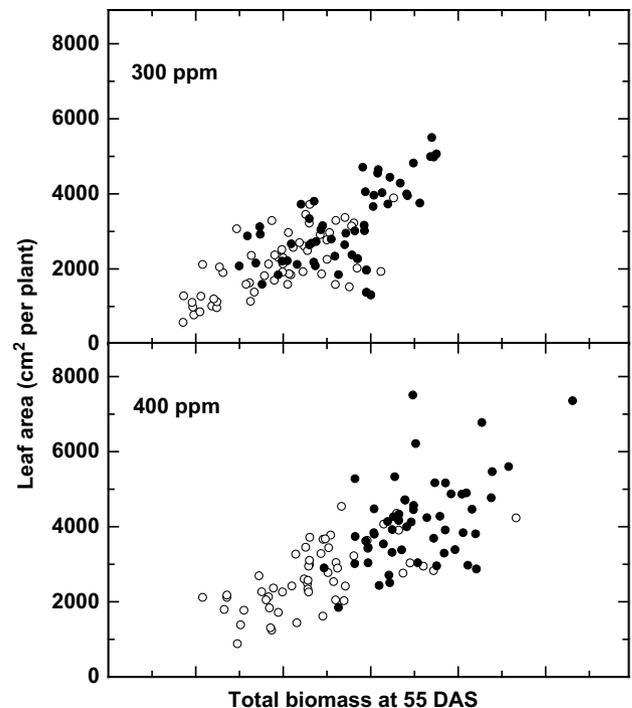
genetic changes in an agronomic weed following the use of herbicides.

### Observed Evolutionary Responses of Weeds to Climate and Climate Change

Much of what we know about how weeds evolve in response to climate comes from range expansions, where it is the weed that moves in relation to the climate, rather than the climate shifting around the weed. Clements et al. (2004, 2008) have summarized specific shifts in agronomic and invasive weed species and the adaptive traits associated with this type of northward expansion. For example, populations of the invasive forb common St. Johnswort (*Hypericum perforatum* L.) display clonal variation in its nonnative range that appears to have evolved since introduction (Maron et al. 2004). Plants from more northern latitudes were found to have higher growth and seed production in four different common gardens. Latitudinal clines in phenology have been identified for an array of species, including tall goldenrod (*Solidago altissima* L.) and giant goldenrod (*Solidago gigantea* Alton) introduced to Europe and Japanese stiltgrass [*Microstegium vimineum* (Trin.) A. Camus] introduced into the eastern United States, saltcedar (*Tamarix ramosissima* Ledeb.) and Chinese tamarisk (*Tamarix chinensis* Lour.) introduced into the western United States, and jimsonseed (*Datura stramonium* L.) introduced into Canada (Friedman et al. 2011; Novy et al. 2013; Weaver et al. 1985; Weber and Schmid 1998). In all cases, plants from northern populations grew, flowered, or set buds earlier in the season. Other traits displaying clonal variation included cold tolerance and plant and seed size.

Additional evidence suggests that adaptation to recent changes, particularly the rapid increase in CO<sub>2</sub> (+20% since 1980), may have already altered the relative fitness of crops and weeds. Bunce (2001) studied the growth response of four annual weeds over a narrow CO<sub>2</sub> range, from 90 ppm CO<sub>2</sub> below to 90 ppm CO<sub>2</sub> above ambient levels and demonstrated that the efficiency at which plants use CO<sub>2</sub> declined significantly at CO<sub>2</sub> concentrations above ambient, suggesting that weeds have been adapting to recent CO<sub>2</sub> increases. Comparisons of six cultivated and six wild or weedy biotypes of rice (*Oryza sativa* L.) indicated a greater overall growth response among wild relative to cultivated rice (*Oryza sativa* L.) to recent (300 to 400 ppm) increases in CO<sub>2</sub> (Ziska and McClung 2008) (Figure 1), suggesting that rapid evolution of weedy biotypes may have increased their fitness relative to the crop. Greater seed yields were also recorded for Stuttgart, a weedy biotype, relative to Clearfield™, a cultivated rice line for the same CO<sub>2</sub> range (Ziska et al. 2010). Similarly, using a resurrection approach (Franks et al. 2018), seed of two temporally distinct populations of wild oat (*Avena fatua* L.) from the same location, one from the 1960s and one from 2014 (a relative CO<sub>2</sub> increase of 80 ppm, or 25% from 1960), demonstrated different competitive abilities against a cultivated oat (*Avena sativa* L.) line, with the more recent (2014) *A. fatua* population having greater growth and competitive ability at current CO<sub>2</sub> levels (Ziska 2017).

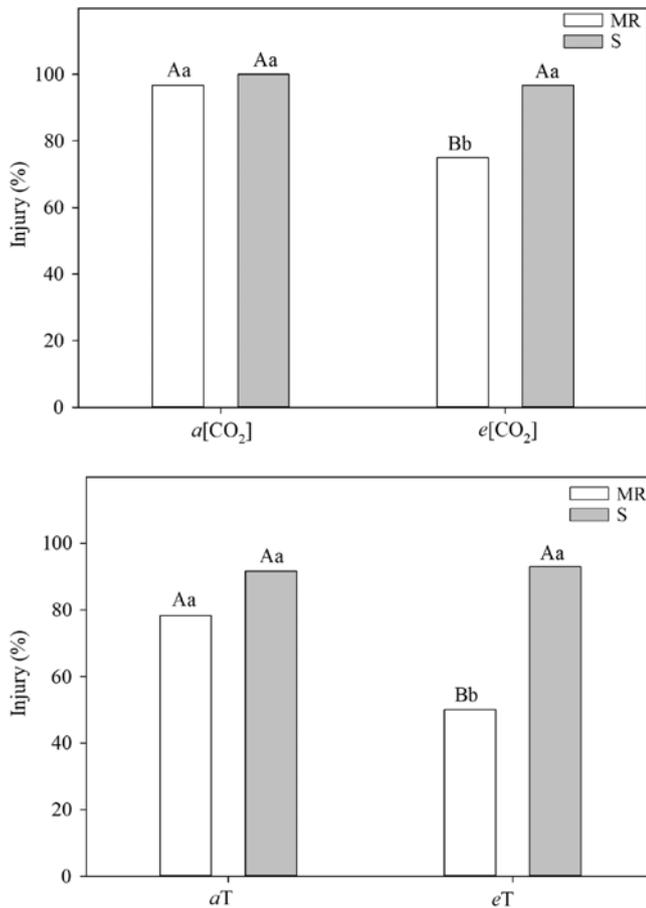
Direct experimental evidence for weed evolution in response to climate change is rare, but there are a few examples. Experiments using seed of the annual weed birdsrape mustard (*Brassica rapa* L.) collected before and after a severe drought demonstrated that drought exerts strong selection pressure, that flowering time is heritable, and that *B. rapa* responded to selection by evolving earlier flowering and lower water-use efficiency (a drought escape strategy) within just a few generations (Franks 2011; Franks et al.



**Figure 1.** Change in leaf area in response to biomass at 55 d after sowing (DAS) for six wild and six cultivated rice biotypes (closed and open circles, respectively). Differential changes to CO<sub>2</sub> between weedy and cultivated rice may influence evolutionary selection and fitness. Adapted from Ziska and McClung (2008).

2007). Similarly, in a much wetter environment, the limestone grassland of Britain, 13 yr of experimental drought appear to have led to evolution of drought escape in the common weed buckhorn plantain (*Plantago lanceolata* L.) (Ravenscroft et al. 2014). When grown in a common garden, populations collected from plots subjected to drought displayed greater reproductive allocation. Further work demonstrated differences in genetic variation consistent with these phenotypic differences (Ravenscroft et al. 2015). Finally, the annual invasive grass foxtail brome (*Bromus madritensis* L.), was examined as part of the Mojave Desert CO<sub>2</sub> enrichment experiment. The study found that within 7 yr, the grass populations subjected to increased CO<sub>2</sub> had evolved reduced stomatal conductance, allowing them to lose less water but still obtain enough CO<sub>2</sub> in the enriched environment, demonstrating rapid adaptive evolution to increased CO<sub>2</sub> in this weed species (Grossman and Rice 2014).

There is also experimental evidence that climate change may be increasing gene flow between herbicide-resistant crops and weedy relatives. For many global rice systems, weedy or red rice is recognized as a major production constraint (Chauhan 2013; Ziska et al. 2015). A long-term USDA study comparing outcrossing rates between cultivated and weedy rice at three different CO<sub>2</sub> concentrations (300, 400, and 600 ppm; or mid-20th-century, current, and mid-21st-century values, respectively) noted greater synchronicity in flowering times and enhanced outcrossing rates between a cultivated rice mutant that is resistant to a class of herbicides (imidazolinone, Clearfield™ 161) and a weedy red rice accession (StgS) (Ziska et al. 2012). Consequently, as CO<sub>2</sub> increased, the number of weedy herbicide-resistant hybrid progeny also increased (Ziska et al. 2012). While additional information on other environmental parameters (e.g., temperature) is needed, CO<sub>2</sub> per se could alter



**Figure 2.** Differential effects and standard error of herbicide application on multiple-resistant (MR) and susceptible (S) biotypes of junglerice [*Echinochloa colona* (L.) Link]. Different letters above columns indicate a significant difference at the  $P < 0.05$  level; capital letters refer to treatment (CO<sub>2</sub> and temperature) differences, and lowercase letters refer to MR and S biotypes. *a* and *e* refer to ambient and elevated treatment conditions for CO<sub>2</sub> concentration [CO<sub>2</sub>] and temperature (T). Note the reduction in efficacy at warmer temperatures and higher CO<sub>2</sub> levels for the MR biotype. Adapted from Refatti et al. (2019).

floral synchrony and gene flow between crops and weeds, with subsequent consequences for hybridization, herbicide resistance, and evolution.

### Climate Change, Selection, and Demography

Understanding factors influencing weed demography (population growth and spread) is of critical importance to weed biology. A changing climate may alter demography directly through differential selective pressures on weed species and indirectly through changes in the abiotic and biotic aspects of the ecosystems or through mediated changes in human management. Direct selection pressures are evident in how elevated CO<sub>2</sub> and higher temperatures differentially alter weed growth, leaf production, plant height, and seed production (Liu et al. 2017; Patterson 1995; Walck et al. 2011; Ziska 2011). For example, under elevated CO<sub>2</sub> (500 to 800 ppm), flowers, fruits, seed production, and seed mass were all increased, but at different degrees, for a range of agronomic and invasive species (Jablonski et al. 2002). Variable stimulation of growth and seed production has also been noted for both recent and projected CO<sub>2</sub> increases for agronomic and invasive weeds (Blumenthal et al. 2013; Dukes 2002; Dukes et al. 2011; Smith et al. 2000; Ziska 2003). CO<sub>2</sub>-induced stimulation of plant height (height is associated with greater seed dispersal;

Thomson et al. 2011) has also been observed for red (weedy) rice (Gealy et al. 2003). Temperature can also influence the extent and timing of plant growth, as well as seed germination and emergence (Benech-Arnold et al. 2000). In warmer regions, increases in temperature are also likely to select for tolerance or avoidance of drought and heat (Franks et al. 2007). Whether these initial responses are indirect (plastic) or direct (genetic), if CO<sub>2</sub> and temperature elicit inter- or intraspecific responses that result in greater exploitation of additional carbon and/or longer growing seasons to increase seed production (Grossman and Rice 2014; Hovenden et al. 2006), evolutionary selection will occur.

As weed managers adapt to a changing climate, changes in management may also alter selection pressures and weed demography. In cropping systems, producers are likely to shift to new crops better suited to new climates (Olesen et al. 2011). In rangelands and forests, plant community changes may be driven by differential movement and local extinction of native species, as well as by changes in disturbance regimes (Thomas et al. 2004; Thuiller et al. 2005). For example, changes in fire regimes due to the introduction and spread of flammable weeds such as downy brome (*Bromus tectorum* L.) are expected to be widespread, leading to dramatic shifts in plant communities (Early et al. 2016) and, presumably, strong selection pressures on extant species.

One of the most interesting forecasts regarding climate and weed demography was made almost 30 yr ago for *P. montana*, a well-established weed of the southeastern United States. Specifically, Tom Sasek and Boyd Strain at Duke University observed that the latitudinal distribution in 1990 was limited to regions in the southern United States where minimal winter temperatures were not below  $-15^{\circ}\text{C}$  (Sasek and Strain 1990: Figure 7), and they suggested that warming winter temperatures could result in the northward migration of this species. How much of this latitudinal migration is solely attributable to increasing minimum winter temperatures is unclear (see Coiner et al. 2018), but the northward spread of *P. montana* is consistent with the Sasek and Strain hypothesis. Various models have since been developed for predicting invasive species movement with climate change (e.g., Bradley 2010; Bradley et al. 2010).

Rapid range shifts can lead to a variety of evolutionary responses. In addition to contributing to novel selection pressures, range shifts may also increase genetic variation, as previously separate populations interbreed, potentially increasing responses to selection and facilitating adaptation (Bell and Gonzalez 2011; Hufbauer et al. 2015). However, dispersal could also negatively affect adaptation in weeds if populations are locally adapted and dispersal introduces maladaptive alleles (Bourne et al. 2014; Lenormand 2002). Local adaptation was thought to be less common in introduced weeds than in other species; however, a recent review found that invasive plants were just as locally adapted as native species (Oduor et al. 2016).

While dispersal can influence rapid evolution positively, the reverse can also occur, with rapid evolution facilitating range expansion (Szűcs et al. 2017). For example, in a common garden study of the invasive perennial weed *Senecio inaequidens* DC, populations collected farther from the initial site of invasion were found to have larger dispersal structures and therefore greater dispersal potential, suggesting that novel environments can select for greater dispersal ability (Mahy and Mahy 2010). Interestingly, projected warming may be exceeding maximum rates of plant migration that were observed in postglacial time periods (Malcolm et al. 2002), resulting in preferential evolutionary selection for the most mobile plants (Boeye et al. 2013). Characteristics associated with

long-distance dispersal are commonly found among invasive plants (Rejmanek 1996), suggesting that, potentially, they may be among the fastest to migrate with warming temperatures (Dukes and Mooney 2000). The ecological processes of dispersal and migration could be augmented by evolution if there is selection for increased dispersal or adaptation to novel conditions in the migrating invasive weed, meaning that current projections of future distributions of invasive weeds that do not take evolution into account may be overly conservative (Clements and DiTommaso 2011).

### Competition and Fitness

Competition is a central aspect of weed biology, because it is through interspecific competition, or the reduction in fitness of two species over shared resources, that weeds reduce production in natural and managed systems. Yet competitive ability is not fixed, it reflects the environmental conditions under which competition occurs and can evolve as plant density or other factors influencing competitive advantage shift (Grace 1990). Consequently, differential selection to climate and/or CO<sub>2</sub> between weeds and the natural or managed plant community (e.g., forest plantations, rangelands, crops) may have significant economic and environmental repercussions.

Many weeds have the C<sub>4</sub> pathway, which shows a minimal response to CO<sub>2</sub>, whereas crops often have the C<sub>3</sub> pathway, which shows a stronger response. As such, it has been hypothesized that crops would outcompete weeds as CO<sub>2</sub> rose (Ziska and Dukes 2011). However, early studies did not capture the complexity of agroecosystems where, on average, each crop competes with 8 to 10 weed species (Bridges 1992). Moreover, a competitive advantage for C<sub>3</sub> crops over C<sub>4</sub> weeds is likely to occur only under rising CO<sub>2</sub> without concomitant changes in climate. For example, at higher temperatures and increased drought, C<sub>4</sub> weeds can still benefit (Alberto et al. 1996; Valerio et al. 2011) relative to C<sub>3</sub> crops.

For invasive weeds, data regarding the response of an individual invasive to rising CO<sub>2</sub> can provide a sense of the growth or reproductive potential of that species relative to the community at large (Ziska 2003). In that regard, projected CO<sub>2</sub> concentration value levels have been shown to preferentially select (within native plant communities) for weed species such as Japanese honeysuckle (*Lonicera japonica* Thunb.) (Belote et al. 2003), cherry laurel (*Prunus laurocerasus* L.) (Hattenschwiler and Korner 2003), red brome (*Bromus rubens* L.) (Smith et al. 2000), mile-a-minute (*Mikania micrantha* Kunth.), Chinese wedelia (*Wedelia chinensis* L. Pruski.), beach morningglory [*Ipomoea pes-caprae* (L.) R. Br.] (Song et al. 2009), and Dalmatian toadflax [*Linaria dalmatica* (L.) Mill.] (Blumenthal et al. 2013). Similarly, warming can favor invasive species relative to natives through the process of species sorting, but this effect appears to be inconsistent, perhaps because warming can increase water stress (Blumenthal et al. 2013; Compagnoni and Adler 2014; Sandel and Dangremond 2012; Walther et al. 2009; Williams et al. 2007).

Because of methodological difficulties, experimental manipulation of both CO<sub>2</sub> and temperature for plant communities in situ are rare. The combination of these changes had no net effect on common catsear (*Hypochaeris radicata* L.) or lesser hawkbit (*Leontodon saxatilis* Lam.) in a Tasmanian grassland, but increased invasion of yellow starthistle (*Centaurea solstitialis* L.) in a California grassland (Dukes et al. 2011), and of *L. dalmatica*, *B. tectorum*, and diffuse knapweed (*Centaurea diffusa* Lam.) in a Wyoming mixed-grass prairie (Blumenthal et al. 2013, 2016;

Reeves et al. 2015). These data, while limited, suggest that ongoing increases in atmospheric CO<sub>2</sub> and temperature could, potentially, lead to altered competition and relative increases in the abundance of invasive weeds relative to native plants within communities.

Given that both weeds and the desired or natural plant species will face novel selective pressures, another relevant question regarding competition is determining the differential growth and fecundity of weeds relative to the managed plant species within a given system. For managed plant communities, including pastures, forest plantations, and crops, genetic uniformity is utilized as a means of increasing productivity. Indeed, a great deal of effort by breeders is designed to identify and maintain desirable economic traits for a narrow selection of available germplasm. While selection to CO<sub>2</sub> and/or climate could, in the short term, reduce genetic diversity among weedy species, it seems likely that the difference in relative response between weeds and desired plant species (representing a narrow subset of genetic variation) will be enhanced, with greater negative impacts on the potential productivity of managed plant systems.

### Weed Management and Herbicide Resistance

The ability to detect and respond to weed threats is of obvious importance, and there are several management strategies that are used globally to keep weed populations at acceptable levels (i.e., below an economic threshold). Such practices vary, but usually include cultural, mechanical, chemical, and biological options. For developed countries, chemical application of herbicides remains the most widely used means to control weed populations; indeed, herbicides are the most widely applied class of pesticides (Colborn and Short 1999; Ziska and McConnell 2015).

The evolutionary potential of weeds is perhaps best illustrated by the rapid and widespread documentation of herbicide resistance (Heap 2014). The occurrence of resistance can vary and is a function of species, herbicide mode of action, and usage of the herbicide. Currently, the issue of herbicide resistance is recognized as a major issue in weed management and is the subject of ongoing research. Yet this research does not, in general, consider climate change and CO<sub>2</sub> and how these factors could also affect the selection and evolution of herbicide resistance (Nguyen et al. 2015; Ziska 2016).

Changes in climatic conditions such as wind speed, humidity, and soil/air temperature will influence herbicide coverage, persistence, and efficacy, thus altering patterns of selection on herbicide responses (Bailey 2003). Carbon dioxide or temperature changes could influence growth phenology, with less time spent in the seedling stage, which is the period of greatest herbicide sensitivity. Carbon dioxide-induced changes in leaf morphology or variation in root:shoot ratio can affect herbicide uptake and distribution. In Canada thistle [*Cirsium arvense* (L.) Scop.], for example, additional CO<sub>2</sub> can stimulate root over shoot growth, diluting shoot-applied herbicide; failure to kill roots, in turn, results in regeneration of the whole plant (Ziska et al. 2004). Interestingly, similar increases in root:shoot ratio have been observed for other invasive weeds in response to recent CO<sub>2</sub> increases, although whether this allocation shift contributes to decreased herbicide efficacy has not been tested (Ziska et al. 2011; Figure 5).

The effects of climate change on herbicide efficacy may also depend on herbicide mode of action. Climate and/or CO<sub>2</sub> could alter pigment production, photosynthesis, and overall metabolic activity. Herbicide modes of action are designed to disrupt these

processes (e.g., atrazine is a photosystem II inhibitor; amitrole is a pigment inhibitor); consequently, where CO<sub>2</sub> and/or climate change stimulate growth, these herbicides may become more effective. Conversely, there is general recognition that rising CO<sub>2</sub> and/or rising temperatures could reduce protein levels in a wide range of plant tissues (e.g., Loladze 2014; Taub et al. 2008). Less protein would result in less demand for aromatic and branched-chain amino acids, with potential declines in the efficacy of herbicides that act as enzyme inhibitors (e.g., glufosinate, glyphosate) (Varanasi et al. 2015).

At present, there is an emphasis on GMO-directed herbicide management. But long-term effectiveness of such a strategy is dependent on the absence of gene flow and transference of resistance between the GMO and associated weeds. Yet, depending on the degree of genetic similarity, climate and CO<sub>2</sub> may alter gene flow, with consequences for herbicide efficacy.

As illustrated previously, for many global rice systems, weedy or red rice is recognized as a major production constraint (Chauhan 2013; Ziska et al. 2015). A long-term USDA study comparing outcrossing rates between cultivated and weedy rice at three different CO<sub>2</sub> concentrations (300, 400, and 600 ppm; or mid-20th-century, current, and mid-21st-century values, respectively) noted greater synchronicity in flowering times and enhanced outcrossing rates between a cultivated rice mutant that is resistant to a class of herbicides (imidazolinone, Clearfield™ 161) and a weedy red rice ascension accession (StgS) (Ziska et al. 2012). Consequently, as CO<sub>2</sub> increased, the number of weedy herbicide-resistant hybrid progeny also increased (Ziska et al. 2012). While additional information on other environmental parameters (e.g., temperature) is needed, CO<sub>2</sub> per se could alter floral synchrony and gene flow between crops and weeds, with subsequent consequences for hybridization, herbicide resistance, and evolution.

### Evolutionary and Revolutionary Knowledge Gaps and Critical Needs

Overall, a review of current studies indicates that managing plant systems within the context of climate change will depend, in part, on related shifts in weed limitations to productivity, increased understanding and assessment of climate-induced evolutionary change, and related changes in management efficacy. Climate and CO<sub>2</sub> will act directly (e.g., CO<sub>2</sub> fertilization effects; Ziska 2001) and indirectly (e.g., biogeographical location; Bradley et al. 2010; McDonald et al. 2009) on selection, and weeds appear to have the requisite genetic variation to respond (Clements et al. 2004; Franks et al. 2007; Ravenscroft et al. 2015).

In this context, we would highlight several research gaps that, if addressed, would improve our ability to understand and predict evolutionary responses of weeds to elevated CO<sub>2</sub> and climate change. Evolutionary issues related to demographics, competition, and management, while presented independently here, should be considered in an integrative context specific to addressing and prioritizing research needs.

### Differential Herbicide Resistance

One of the most practical research needs is an integrated assessment of how climate change and rising CO<sub>2</sub> will affect the development and spread of herbicide resistance (Fernando et al. 2016; Waryszak et al. 2018). As emphasized by Franks (2016), herbicide resistance remains a prosaic example of how rapid contemporary evolution functions in response to strong selection pressures.

Indeed, recent data suggest that rising CO<sub>2</sub> and/or temperature per se could select for resistant biotypes (Figure 2).

Yet a host of issues specific to climate and CO<sub>2</sub> require further elucidation in that regard: (1) potential changes in mutation rates that could alter herbicide mode of action; (2) morphological (leaf thickness, stomatal number) and phenological (root:shoot ratio) shifts with consequences for uptake and translocation of herbicides; (3) documentation of whether selection shifts for resistant and susceptible biotypes occurs (e.g., do resistant weedy biotypes show a stronger growth and yield response to rising CO<sub>2</sub>? (see Refatti et al. 2019); and (4) observed increases in herbicide application rates associated with reduced efficacy and consequences for increased occurrence of resistance due to greater herbicide selection pressures.

### Biological Constraints

In addition to chemical control, there is evidence that climate can influence other aspects of weed management; with subsequent consequences for selection and evolution. In perennial managed systems, including rangelands and forests, biological control can be the most efficient and effective method for controlling weeds (Clewey et al. 2012). However, climate change may alter the efficacy of weed biological control through changes in plant nutrient content, which often declines with elevated CO<sub>2</sub>; increases in insect activity with temperature; and shifts in phenology of both agents and host weeds (Reeves 2017; Reeves et al. 2015). Adaptive responses to such changes are difficult to predict, given that both biological control agents and host weeds will have the potential to adapt to new selective pressures (Holt and Hochberg 1997). However, the specificity of agent–host interactions suggests that differential adaptation and selection could also have important consequences for weed fitness and future management.

More broadly, a wide variety of interactions between weeds, pathogens, and pollinators may be influenced by climate change, with consequences for evolution. While not specific to weeds per se, it is of interest to note that in transgenic *Bacillus thuringiensis* (Bt) cotton (*Gossypium hirsutum* L.), elevated CO<sub>2</sub> reduced Bt protein production relative to the ambient CO<sub>2</sub> condition (Coviella et al. 2000). The impact of climate and CO<sub>2</sub> suggests that ecological dynamics are likely to be affected (e.g., temporal shifts in pollen production and pollinators with warming temperature) and that there is a close coupling between ecological and evolutionary dynamics. To date, there has been little research on the role of climate and/or CO<sub>2</sub> on biotic constraints to weed biology and the subsequent consequences for selection pressure. Yet inter-specific checks and balances on populations may be altered by rapid evolutionary change imposed by climate/CO<sub>2</sub>.

### Demography

Climate and CO<sub>2</sub> are also likely to alter the evolutionary basis for ecotype differentiation and the ability of weeds to disperse and colonize quickly. There are several field-based studies indicating that elevated CO<sub>2</sub> could select for more invasive weed species (reviewed in Ziska 2011). However, the basis for their selection is unclear. Specific factors related to demographics, including seed dormancy, germination, emergence, and dispersal, are acknowledged, but a comprehensive understanding of how climate/CO<sub>2</sub> alters these selective factors is lacking. There is an immediate need to understand and document the role of climate/CO<sub>2</sub> in changing demography and evolutionary potential (Ravet et al. 2018). The evolutionary potential specific to demographic change can be

evaluated in terms of genetic variation; associated selection pressures, including hybridization; changes in life histories (e.g., annuals to perennials); acclimation capacity; photoperiodism (Saikkonen et al. 2012); and human activities and agronomic shifts in cultivation (Clements and DiTommaso 2011). Information related to how evolution may influence population growth and spread associated with climate change would be of critical benefit in updated models of projected weed distribution and impact (e.g., Bradley et al. 2010; McDonald et al. 2009).

### Epigenetics and Climate

Given the acknowledged acclimatory responses of weeds (e.g., Baker 1974), differentiating between physiological acclimation and evolutionary adaptation to climate/CO<sub>2</sub> is of obvious importance (Franks et al. 2014). At the crux of such differentiation is the role of epigenetics. However, the role of epigenetics, heritable phenotype changes that do not involve alterations in the DNA sequence, and the influence of climate/CO<sub>2</sub> on their function is almost completely unknown. Yet epigenetic changes that are heritable could influence evolution.

Many of the most troublesome weeds are polyploids (Barrett 1982). For weeds, taxa with high chromosome numbers can potentially produce a variety of recombinant progeny and an enhanced degree of genetic variation. This variation, in turn, may be of benefit in adaptive evolution to a changing environment (Chen 2007); consequently, understanding such an influence is key to determining suitable phenotypes, as well as adaptation and fitness in response to climate change. For example, a study of alligatorweed [*Alternanthera philoxeroides* (Mart.) Griseb.], an invasive weed of both terrestrial and aquatic systems, reported genome-wide epigenetic reprogramming in response to environmental variability (Gao et al. 2010). Given this degree of sensitivity, it seems essential to document and understand climate/CO<sub>2</sub> effects on weed epigenetics and the consequences for evolutionary adaptation.

### Conclusions

As emphasized by Neve et al. (2009), other academic disciplines that study pests, such as entomology and pathology, are primarily concerned with biology, from the biochemical to the ecosystem, and the secondary application of this knowledge to management. Conversely, for weed science, we would argue that the success of chemical management has led to a primary technological and management focus with less emphasis on weed biology per se.

But now weed science faces twin challenges. The first is related to the rapid increase and spread of herbicide resistance; the second to the environmental uncertainty represented by climate change and rising levels of CO<sub>2</sub>. The evolutionary aspects of these two challenges are interrelated. Weed management is still paramount, but it is becoming clear that a more efficacious approach must include a renewed emphasis on fundamental research in weed biology, from the cellular to the ecosystem, for all circumstances in which unwanted plants pose an environmental or economic constraint. And in that context, a greater understanding of weed evolution is essential to maintaining and improving future productivity in managed plant systems (Harker 2013)

The overview presented here emphasizes this point for environmental change, provides a review of weed evolution, and tries to assess the evolutionary consequences specific to three research areas: demographics, competition, and management. Demographic traits, including seed biology, germination, life span, and fecundity will be

influenced by climate/CO<sub>2</sub>, with consequences for selection and adaptation. Similar influences on crop–weed interactions can be expected, with initial evidence suggesting that differences in genetic variation between crops and weeds may already be leading to differential responses to recent CO<sub>2</sub> increases. Management, in turn, is perhaps exemplified by herbicide resistance, the selection role that climate and CO<sub>2</sub> would play in that regard, and the unknown consequences of CO<sub>2</sub>/climate influences on gene flow between crops and weeds. Finally, any effort to review a subject provides a tempting platform for new ideas and future direction, and some suggestions are offered. However, it should be kept in mind that these are by no means exhaustive, and other perspectives from different disciplines are welcome.

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