

Review

Impact of Climate Change on Population Dynamics and Herbicide Resistance in Kochia (*Bassia scoparia* (L.) A. J. Scott)

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Abstract: Climate change has greatly impacted agronomy. Climate forecasts for the coming years predict increases in global temperature, carbon dioxide concentration, and extreme weather events. These changes will continue to influence agricultural production by altering abiotic stress on plants, including crops and weeds. Kochia, one of the most common weeds in North America, is a C4 plant exceptional for its drought tolerance. Kochia has also demonstrated rapid adaption and evolution to the abiotic stress of herbicide application, particularly glyphosate. Abiotic stresses from both climate change and herbicides impact the distribution and expansion of kochia. Being aware of the features and properties of kochia, especially those resulting from herbicide resistance, will help anticipate how kochia responds or migrates under future climate change, and help create proper strategies for kochia weed management.

Keywords: kochia; climate change; weeds; herbicide resistance

1. Introduction

Global climate change predictions forecast changes in climate conditions that are quintessential for successful crop production and weed management. Climate change predictions include elevated temperature, increase in carbon dioxide (CO₂) concentration, and more frequent erratic precipitation events [1]. Climate change is disastrous for threatened species living in a narrow niche [2–4]. However, disruptions due to climate change can be exploited by pests, potentially expanding their range and ecological niche. This will especially be the case if crop cultivars optimized to the prior climate regime are maladapted to their new growing environment and are left less competitive [5–7].

Weeds are noxious pests that are highly competitive, adaptive, and able to withstand multiple stressors, including drought, waterlogging, elevated temperature, and increased CO₂ [6,8,9]. Kochia (*Bassia scoparia* (L.) A. J. Scott) is a diploid ($2n = 18$) weed species and belongs to the *Chenopodiaceae* family. Kochia is native to Eastern Europe and Asia, and is now one of the most common weed species in North American Great Plains [10]. Kochia competes with multiple crops (sugar beet, corn, etc.), causing significant crop yield reduction [11–15]. It is especially well suited to arid and semi-arid climates, and invades a myriad of environments including cropland, rangeland, gardens, roadsides, and almost any disturbed ground. Infestations range in latitude from Mexico to Canada and currently exist in forty-three of the contiguous United States (United States Department of Agriculture *Bassia scoparia* factsheet). Kochia possesses physiological traits that may help it thrive during climate change. In particular, kochia's natural abiotic stress tolerance is deeply associated with a strong artificial abiotic stress tolerance, namely, herbicide resistance.

In this review, we will discuss how kochia, especially herbicide-resistant kochia populations, may respond to a changing climate. Factors considered here include changes in abiotic factors such as temperature, CO₂ concentration, and precipitation, as well as kochia-specific traits such as photosynthetic efficiency, herbicide resistance and fitness penalties, genomics and genetic diversity, and previous work looking at population expansion.

2. Abiotic Stress in Kochia

2.1. Temperature

It is predicted that the mean global temperature will continue to increase over the 21st century with a corresponding increase in the frequency, duration, and magnitude of hot extremes [16]. Increasing temperature can greatly impact plant growth and phenology [17]. Many plant species can tolerate higher temperatures during vegetative growth stages, but not during reproductive growth stages [17].

Crop–weed communities shift under different temperatures, due to factors in the agroecosystem and weed physiological traits. As temperature increases, crop planting dates are likely to shift toward early spring, depending on spring precipitation [18]. Weed communities are also predicted to alter as planting dates become earlier. Additionally, as seed germination timing is influenced by temperature, elevated temperatures in early spring may lead to shifts in weed emergence and overall phenology such as plant height, branching, leaf emergence, etc. [19].

For kochia, a variety of population-specific germination patterns (i.e., emergence rate and timing) have been identified [20]. The range expansion of kochia has already been documented in many regions of North America. Studies in Canada noted that over the past 40 years the frost-free growing season has increased by four days. What appears to be a relatively small increase in the growing season coincided with first reports of kochia invading the more northern regions of Canada (Manitoba, Saskatchewan, and Alberta) [21]. More specifically, climate models project that kochia's range in the United States will expand eastward into the Midwest and Atlantic regions with temperature increases of 1–3 °C [21].

Although mean global temperatures are predicted to increase, there may also be an increase in sudden freezing events in certain areas [22]. Despite being a C₄ plant, kochia is extremely cold-tolerant and it handles the sudden freezes in early spring of the high-plains with ease. Kochia is among the first weeds to germinate, often germinating under snow. Its cold tolerance may be due, in part, to its “kochioid” Kranz anatomy, which is shared with several other halophytes in the *Camphorosmeae* [23]. Cold-tolerant kochia is also expected to migrate and expand its range northward, because increasing global temperature will shrink the size of the cold region toward polar areas.

2.2. Carbon Dioxide (CO₂)

Atmospheric CO₂ concentration is predicted to increase under climate change scenarios. According to www.climate.gov, since 1972, atmospheric CO₂ concentrations have increased from 324 ppm to 414 ppm, with an average increase of 2.3 ppm per year [24]. Increasing CO₂ will directly impact photosynthesis, transpiration, and respiration, but the direction of the response is dependent on the types of photosynthesis. For C₄ plants, increasing CO₂ will not affect the photosynthetic rate, due to their physiology that concentrates CO₂ levels around Rubisco [25]. For C₃ plants, current levels of atmospheric CO₂ do not saturate the Rubisco enzyme. Therefore, elevated CO₂ will stimulate C₃ photosynthesis by reducing the loss of CO₂ through photorespiration and increasing the concentration gradient of CO₂ from air to leaf [25–27]. For crassulacean acid metabolism (CAM) plants, the scenario is similar to C₄ plants, although CAM stomates work differently by staying closed during the day and open at night [28].

Most weed species studied so far are genetically and phenotypically diverse compared to the crops they invade. It has been repeatedly demonstrated that high genetic diversity is critical in ensuring plant survival in rapidly changing environments [3,9]. In particular, weeds' genetic diversity may produce a diversity of growth and reproductive responses to elevated CO₂. Kochia is a C₄ plant that

often infests C3 crops (e.g., rice, oats, wheat). Although C3 crops may respond more positively to elevated CO₂ when compared to kochia, the final outcome will depend on other climate factors such as precipitation [29].

A further consequence of increased CO₂ is the potential for increasing glyphosate tolerance in some weed species. This shift in glyphosate tolerance due to increased CO₂ has been shown to be especially profound in C3 weed species, but has also been demonstrated to a lesser extent in C4 plants such as kochia [30–33]. The physiological reasons for this shift in glyphosate tolerance seem to be multifaceted and are due to biochemical, physiological, and morphological properties [33].

2.3. Precipitation and Photosynthetic Efficiency

While variations in temperature and CO₂ concentration are relatively easy to forecast, changes in precipitation patterns, intensities, and distributions are more uncertain [34]. Precipitation in the US is predicted to become more erratic, with the majority of the total rainfall occurring in May and June, and less during the growing season when it is most critical [35]. The link between water use efficiency and CO₂ fixation means that drought conditions during the growing season can have a profound effect on primary productivity [36,37].

Similar to many of its relatives in the Chenopodiaceae, kochia is quite drought tolerant—requiring only 15 cm of annual rainfall—and can grow in highly alkaline soils [10]. Furthermore, as a C4 plant, kochia is predicted to have an advantage over C3 weeds or crops under drought conditions. C4 plants separate the light-capturing and carbon-capturing reactions in time and space, allowing light harvesting during the day and gas exchange at night [38]. However, C3 plants perform both the light-capturing and carbon-capturing reactions simultaneously, which necessitates gas exchange via stomata opening during the hottest time of the day, and limits their growth when under drought stress. Drought conditions resulting from climate change should therefore affect kochia less profoundly than its crop competitors. However, the combination of elevated CO₂ concentrations and reduced precipitation may reduce the overall effect, as plant response to drought is intrinsically coupled with CO₂ concentration [39].

Kochia range expansion may be dramatically affected by precipitation. For example, a 20% increase in precipitation is projected to limit the eastward expansion of kochia from the Western United States, even with a temperature rise of 1–3 °C [21]. In contrast, a 20% decrease in precipitation is projected to amplify with the effect that rising temperature will have on kochia's range by making the climate of the western part of the midwest similar to the high-plains of Colorado and Wyoming.

3. Herbicide Resistance in Kochia

Herbicide control of kochia has used only a few modes of action, and therefore the selection pressure for resistance to these compounds has been high. Kochia populations with resistance to photosystem II (PSII) inhibitors, acetolactate synthase (ALS) inhibitors, synthetic auxins, and glyphosate have been identified. The first case of kochia resistance to a herbicide was to atrazine (a PSII inhibitor) in 1976 [40]. Since then, intensive herbicide application to control kochia has led to increasing numbers of herbicide-resistant kochia populations reported across much of North America [41]. Even worse, a kochia population has been found with multiple resistance to all four herbicide modes of action listed above [42].

In kochia, herbicide resistance mechanisms to PSII inhibitors, ALS inhibitors, and glyphosate have been shown to be target-site-based, either from mutation (single nucleotide polymorphisms or insertion/deletions) or duplication of target-site genes [42–47]. Resistance to glyphosate arises from tandem duplication of the target-site gene [43]. For resistance to PSII inhibitors, the mutations Gly-264-Ser [42,48,49] and Val-219-Ile [49] have been found in the *psbA* gene. For resistance to ALS inhibitors, mutations at site Pro-197 [42,50,51], Asp-376 [51], Trp-574-Leu [42,48,51], and combinations (Pro-197 + Asp-376, or Pro-197 + Trp-574) have been reported in the *ALS* gene [51,52].

Despite auxinic herbicides being some of the first mass-produced herbicidal compounds, resistance to auxinic herbicides has been slower to evolve than for the other modes of action; however, resistance to 2,4-D, dicamba, and fluroxypyr are becoming more common [53,54]. Both target-site and non-target-site (reduced translocation) resistance mechanisms confer auxinic resistance in kochia [55,56]. A glycine to asparagine amino acid change within a highly conserved region of KsIAA16, an AUX/indole-3-acetic acid (IAA) protein, was shown to endow resistance to dicamba, with possible cross-resistance to 2,4-D and fluroxypyr [56]. Additionally, constitutively increased chalcone synthase expression in a resistant population may be related to reduced dicamba translocation, and therefore aid in resistance [55].

As climate change is predicted to favor the expansion of weed species such as kochia, there will be a greater need for methods to control them. However, the abundance of resistance mechanisms currently evolved in kochia populations, as well as a lack of new herbicide chemistries, suggests that herbicides alone will not be a long-term control strategy [57–60]. The combination of climate change and prevalent herbicide resistance alleles may result in very few options for effective control of kochia by the end of the 21st century if new, alternative control technologies are not developed.

Herbicide Resistance, Fitness, and Adaptive Potential

When hypothesizing about the interaction of herbicide resistance and climate change, another key aspect to consider is the impact of pleiotropic phenotypes associated with certain resistance mutations. Usually these phenotypes are detrimental to the plant and result in a fitness penalty compared to susceptible counterparts. In general, anything that changes an organism's ability to successfully reproduce is considered a fitness penalty. In weeds, fitness is often measured in terms of seed characteristics such as seed yield, weight, germination, and dormancy [61]. These traits are all profoundly impacted by environmental conditions [6], and climate change is likely to amplify these impacts.

For example, a kochia population resistant to dicamba/fluroxypyr was found to be less competitive than susceptible kochia, with reduced germination dynamics, vegetative growth and seed production [62]. On the other hand, fitness penalties may also be ambiguous, as in the case of glyphosate-resistant kochia. Glyphosate-resistant kochia populations from Western Kansas, Western Canada and Midwestern US showed reduced seed longevity and slower rate of germination than glyphosate-susceptible populations [63,64]. However, glyphosate-resistant kochia populations collected from Northern Montana showed either delayed and reduced germination or no differences when compared to susceptible populations, even under a broad experimental temperature range [65]. Delayed and reduced germination characteristics of glyphosate-resistant kochia populations may offer options for weed seedbank management by altering pre-emergence herbicide timing, tillage timing, or other cultural control practices. Herbicide resistance has also been associated with increased fitness: seeds of a kochia population resistant to ALS inhibitors germinated faster and at a higher frequency than the susceptible population [66,67], showing possible benefits from resistance.

Effects of herbicide resistance on fitness have been studied under current environmental conditions, but how these pleiotropic phenotypes will manifest under a hotter and dryer regime is still unknown. Increasing competitiveness of kochia due to climate change may mitigate the mild or moderate fitness penalties arising from herbicide resistance pleiotropic phenotypes and allow strongly penalizing mutations (such as the KsIAA16 dicamba resistance mutation [68]) to persist in the population for longer.

4. Genomics and Genetic Diversity of Kochia

Recently, the first draft of the *Kochia scoparia* genome was published, with a second, reference-quality assembly in progress [46]. Similar to the genomes of fellow chenopods quinoa and sugar beet, the kochia genome has large amounts of heterozygosity, repetitive content, and transposable element activity, which has made full assembly of this weedy genome difficult [69,70]. However, studying these genomic features may be the key to understanding kochia's success in terms of abiotic stress tolerance and rapid resistance evolution.

The story of glyphosate resistance evolution in kochia provides key evidence about the role of novel genetic diversity in shaping the evolutionary trajectory of a weed population. Glyphosate resistance in kochia is caused by tandem duplication of the target gene, 5-enolpyruvylshikimate-3-phosphate synthase (EPSPS) [43,45]. The tandem duplication involves the insertion of a series of mobile genetic elements flanking the EPSPS locus [46]. EPSPS is co-duplicated with several other genes whose phenotypic impact remains unknown. The novel EPSPS copy number variant (CNV) and subsequent glyphosate-resistant phenotype has led to extreme selective pressure on resistant individuals and this resistant allele. Due to the heavy selection pressure of glyphosate application, the low fitness penalty EPSPS CNV seems to incur, and the reproductive abilities of kochia, the EPSPS CNV can be quickly spread to fixation within a small kochia population. Furthermore, genes linked with the EPSPS CNV will also increase in frequency and the overall population structure altered significantly [47,71].

Structural rearrangements and changes in epigenetics can provide a huge advantage to species that need to adapt to rapidly changing environments [72,73]. Unlike the single nucleotide polymorphism mutation rate, which is determined primarily by genome size, structural rearrangements such as gene duplication occur at varying rates, where populations undergo periods of activity and dormancy [74,75]. Furthermore, many different abiotic stresses have been found to accelerate both transposable element activity and copy number variation [76–79]. Structural variation does not affect the coding sequence or the regulatory elements of a gene, which may help avoid many of the pleiotropic effects often associated with single nucleotide polymorphisms. Structural variants, such as all mutations, are predicted to usually cause a fitness penalty and therefore should be suppressed. However, kochia is an R-selected species, producing many offspring, and rare beneficial mutations can therefore manifest in the large offspring pool and spread; in turn, these successful mutants may also perpetuate a relaxed suppression of structural variant generation [64,71].

5. Kochia Population Expansion

Kochia is diverse in both genotype and phenotype, even in North America, where it has only had since the late 1800s (a relatively short period of time) to adapt [10]. It has been estimated that plants within populations are as genetically similar as those between populations, indicating that strongly isolated populations probably do not exist and gene flow occurs over a broad geographic range [80]. Several reproductive traits may be influencing kochia's genetic variability. First, kochia's flowers are protogynous: stigmas emerge first, receive pollen, and dehisce before the flower's own pollen production occurs. This largely prevents self-fertilization, which only occurs when no other plants are available for out-crossing [81,82]. Second, kochia is a tumbleweed, which makes its rapid dispersal very likely, especially across its current range, the windy great plains of North America [41,83].

In addition to geographical range shifts via migration, climate change will modify the size of the niche that kochia can inhabit, which will lead to changes in overall weed community composition [7]. Niches will be modified by extreme weather events predicted to become more common under future climate scenarios. Niche gaps will result from these disturbances and are potential hot spots for weedy plant invasion [84]. Once species migrate to a new location, purifying natural selection will occur, leading to local adaptation. It is often the case that species with high amounts of genetic diversity, such as kochia, quickly establish themselves in the new environment after migrations occur [9]. These evolutionary processes are categorized as trait shifts and encompass shifts in weed phenology and physiology [7].

Temperature and precipitation will be the largest abiotic factors that determine how kochia's invaded range changes in the coming decades [85,86]. Under increased temperatures, weed species experience shifts in geographical locations, resulting in the invasion of species into new locations as well as localized extinctions [85]. Furthermore, under predicted climate change scenarios, growing degree days will accumulate faster, resulting in weed species reaching maturity earlier in the growing season [87]. Taking into consideration kochia's ability to survive and thrive in a variety of temperature

regimes and kochia's past history of northward invasion, it stands to reason that it will continue to move northward, invading an even larger proportion of Canadian land.

Increased moisture stress will also greatly impact weed species diversity, competition, and interactions with crops [86]. However, how a particular species distribution responds to drought is a multifactorial problem involving the weed species itself and the agroecosystem [85]. For example, in extended drought conditions, weed communities would shift to favor more deep-rooted species, whereas early emerging species, which are often shallow rooted and depend on resources in the upper soil profile, will be suppressed [88]. Drought conditions can also favor weed seed survival in the soil as dry soil conditions promote seed longevity and reduce predation [5,89]. Kochia thrives in arid and semi-arid climates, and if these climates expand, kochia's distribution will expand as well.

6. Conclusions

Global climate change will challenge all plant species; however, weedy species are especially well suited to meeting the challenge. The plethora of adaptive traits that make weeds competitive with crops (despite our best attempts to control them) overlap with traits that may help them overcome climate change. Weed populations are large and can have incredible genetic diversity on which evolution can act during this period of rapid climate change. Furthermore, as non-weed species are forced to migrate or go extinct due to climate change, ecosystems will be destabilized, and more resources will become available. Weeds can expand to fill open ecological niches and capitalize on these perturbances, similar to how they fill open niches when agricultural fields are disturbed.

Kochia scoparia is no exception to these predictions and may in fact epitomize what is to come. It has a battery of abiotic stress resilience traits, a large population size and geographic distribution, high levels of genetic diversity, and the ability to spread novel alleles over great distances. Researchers have already documented kochia's northward spread deeper into Canada due to the addition of four growing degree days, and this range expansion is unlikely to stop anytime soon, especially as we lose the ability to chemically control kochia with common herbicides due to herbicide resistance evolution. Understanding the traits that allow weeds such as kochia to be successful may be one of our greatest tools for controlling weeds. Predicting how climate change will impact weed population expansion will be essential to prepare for the future.

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