

Review

Ten Ways That Weed Evolution Defies Human Management Efforts Amidst a Changing Climate

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Abstract: The ability of weeds to evolve is key to their success, and the relationship between weeds and humans is marked by co-evolution going back to the agricultural revolution, with weeds evolving to counter human management actions. In recent years, climate change has emerged as yet another selection pressure imposed on weeds by humans, and weeds are likewise very capable of adapting to this latest stress of human origin. This review summarizes 10 ways this adaptation occurs: (1) general-purpose genotypes, (2) life history strategies, (3) ability to evolve rapidly, (4) epigenetic capacity, (5) hybridization, (6) herbicide resistance, (7) herbicide tolerance, (8) cropping systems vulnerability, (9) co-evolution of weeds with human management, and (10) the ability of weeds to ride the climate storm humans have generated. As pioneer species ecologically, these 10 ways enable weeds to adapt to the numerous impacts of climate change, including warming temperatures, elevated CO₂, frequent droughts and extreme weather events. We conclude that although these 10 ways present formidable challenges for weed management, the novelty arising from weed evolution could be used creatively to prospect for genetic material to be used in crop improvement, and to develop a more holistic means of managing agroecosystems.



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1. Introduction

Humans and weeds share a long co-evolutionary history. The earliest agrarian weeds emerged as agriculture itself emerged in human history, and many of these species have followed us wherever we have settled and grown crops, with Old World weeds following western colonists to the New World. Now as the major crops have gone global, these same weeds are following grain crops throughout the globe. However, although they may be the same weeds as taxonomically identifiable species (for the most part), weeds are highly variable across their range. Weeds adapt to every situation, and this adaptation throughout the globe is now being spurred on by a global influence generated by humanity—climate change. In the 20th century, weed management made huge advancements, in large part due to the invention of synthetic herbicides. Yet even these powerful tools are being blunted by weed adaptations that are favored by changing climates in many instances. Even aside from climate change, evolution of herbicide resistance has often proved to be the undoing of our weed management systems and their overdependence on chemical control tools.

What is it about weeds that makes them so successful, even in the face of climate change? Charles Darwin provides some powerful clues in the following statement:

We shall best understand the probably course of natural selection by taking the case of a country undergoing some physical change, for instance, of climate. The proportional numbers of its inhabitants would almost immediately undergo a change, and some species might become extinct. We may conclude, from what we have seen of the intimate and complex manner in which the inhabitants of each country are bound together, that any

change in the numerical proportions of some of the inhabitants, independently of the change of climate itself, would most seriously affect many of the others. If the country were open on its borders, new forms would certainly immigrate, and this also would seriously disturb the relations of some of the former inhabitants. [1]

Weeds tend to be pioneer species, dispersing far and wide utilizing a variety of mechanisms. Thus, they are rarely in Darwin's category of becoming extinct, although there are some weed species incapable of adapting to recent agricultural changes, especially in Europe [2,3]. Weeds have a genetic makeup they have inherited from the kinds of natural environments they inhabit (i.e., highly disturbed environments) or from long associations with agroecosystems and other anthropogenically-modified environments. Indeed, as we move further into the Anthropocene, few environments are without extensive anthropogenic influences, and this in itself is pushing us towards a "planet of weeds" [4]. The open borders Darwin speaks of are everywhere, as many weed species enjoy pathways of introduction that allow them to move about much of the globe freely. Certain weed species, such as common ragweed (*Ambrosia artemisiifolia* L.), knotweeds (*Reynoutria* spp.) or *Chenopodium* spp. have such broad climatic niches that they occur through the entire band of temperate zones [5–7]. Similarly, there are tropical weeds such as lantana (*Lantana camara* L.), mile-a-minute (*Mikania micrantha* Kunth) or parthenium weed (*Parthenium hysterophorus* L.) that are gradually encircling the globe in tropical regions [8–10]. This homogenization of the world's weed flora is aided by homogenizing effects of climate change.

Ziska et al. [11] identified some key knowledge gaps critical to understanding the nexus of climate change and weed biology. Namely, how climate change will influence herbicide resistance, weed natural enemies, weed distribution and demography and epigenetics, and other aspects of weed phenotypic plasticity. As weed scientists and ecologists attempt to understand, conduct experiments and model these aspects, it is important to frame the discussion in terms of some key elements that need to be considered as the storm front of climate change approaches.

In this review, we cover ten ways that the constant evolution of weeds makes them a moving target, extremely difficult to control or manage, especially amidst the dynamic of a changing climate. The ten ways we discuss can be broadly divided into two categories: (1) ways that are intrinsic to the nature of weeds and their evolutionary history in broad terms, and (2) ways as a function of their interactions with humans. Under the first category, we discuss general-purpose genotypes, life history strategies, ability to evolve rapidly, epigenetic capacity, and hybridization. Within the second category, we discuss herbicide resistance, herbicide tolerance, cropping systems vulnerability, co-evolution of weeds with human management, and the ability of weeds to ride the climate storm humans have generated.

2. The Ten Ways

2.1. General-Purpose Genotype

Baker [12,13] coined the term general-purpose genotype to describe the extreme phenotypic plasticity exhibited by many weed species. A meta-analysis comparing invasive and non-invasive species across 75 pairs demonstrated overwhelmingly that the invasive species exhibited greater phenotypic plasticity [14]. Although this characteristic of weeds does not hold up for all weed species and should not be taken as a general rule [15], it is clearly a key factor in the success of weeds in defying human management methods, enabling them to flourish in a broad spectrum of environments, often unexpectedly. Darnency [16] emphasizes two main possibilities weeds may respond to selection pressure of recent changes in farming practices: (1) adaptation by general-purpose genotype developed over centuries or (2) ongoing evolutionary adaptations. In either case, weed species have an advantage relative to crop species in terms of response to changing conditions, because of their higher diversity phenotypically and/or genetically.

The underlying explanation for this extreme plasticity of many weed species is their nature as pioneer species, adapted to high levels of disturbance by having an array of phenotypes that may be expressed in a given environment. The results of the meta-analysis of 75 species pairs [14] suggests that the fitness advantage gained through plasticity enables invasive species to make better use of resources, as they tended to be able to respond better to increases in resource availability. Specific responses were seen in various plant growth parameters such as shoot or root biomass, photosynthesis or nutrient uptake [14]. Factors related to climate change such as increased temperature, increase atmospheric CO₂, or altered moisture regimes would be expected to prompt similar highly plastic responses in invasive weeds. Non-invasive plants adapted to more stable environmental conditions would by contrast would not be expected to adjust as rapidly to drastic changes in growing conditions.

Alternanthera philoxeroides (Mart.) Griseb. (alligator weed) is capable of growing in both terrestrial and aquatic environments, where it exhibits very different morphology [17]. In testing different populations of *A. philoxeroides* growing in China, Geng et al. [17] found that even the very different morphologies exhibited by terrestrial vs. aquatic forms were due to phenotypic plasticity, not genetic differences. *Lythrum salicaria* L. (purple loosestrife) is another invasive plant that must alter its morphology to adapt to various wetland habitats, and does largely via phenotypic plasticity [18]. When grown in four different soil moisture treatments, 12 genotypes of *L. salicaria* exhibited variation in root and shoot biomass, shoot and inflorescence length, total seed weight, floral mass and morphometric variables, with all of these responses primarily attributable to phenotypic, not genotypic variation [18]. *Ammannia* spp., weeds of rice paddies also exhibit a plastic response in an aquatic environment, with growth traits responding phenotypically to competition with rice [19]. With increased frequency of flooding predicted under climate change [20], plastic responses of invasive plants like *A. philoxeroides*, *L. salicaria* and *Ammannia* spp. could present challenges for management.

Agroecosystems produce ideal environments for weeds with plastic phenotypes to flourish because of the relatively high levels of disturbance created by agronomic practices. Even weed control measures applied in such systems represent disturbances that certain weeds may be able to take advantage of, especially if they are not the specific target. Furthermore, there is the case of herbicide resistance, whereby resistant genotypes can form large patches in fields, thanks in part to the absence of competition from other weed species or genotypes that are susceptible (see further discussion of herbicide resistance in Section 2.6). By contrast to weeds, crop plants are often more hard-wired genetically, with crops generally bred for uniformity to facilitate consistent yields [21,22]. Crop breeders also need to produce crop varieties that are attuned to environmental conditions, but it is fairly inevitable that plastic weeds are better able to adjust to climate extremes. Thus, in years of drought, or other types of extremes such as flooding or storm events, weed problems may become worse, thanks in part to weed phenotypic plasticity.

In Section 2.3, we discuss evolutionary responses, which is a different kind of response to climate change involving selection of genotypes favoring the new climate. However, there is considerable overlap between the two response types. In fact, Franks et al. [23] found that among 38 studies of plant responses to climate change, 26 studies recorded the occurrence of both plastic and evolutionary changes. Thus, the two categories are not mutually exclusive, and indeed plasticity itself can be considered an evolved trait, providing the flexibility that many weeds notoriously exhibit.

2.2. Life History Strategies

Weeds exhibit a broad variety of life history strategies, so as management systems change, weeds that formerly were not a serious issue in a given cropping system may emerge as a new issue. For example, reduced tillage systems promote weeds with different life history strategies than seen under conventional tillage, notably weeds with more perennial life histories, further along in the ecological succession trajectory [24–26].

Similarly, climate change is set to prompt the emergence of new weed issues, through the creation of new niches for weed species or genotypes with life histories better suited for the changing conditions.

A key life history attribute of weeds as pioneer species is dispersal ability, and this dispersal ability may be strongly connected to plant size. Large increases in size can occur due to enhanced atmospheric carbon dioxide, such as the 70% enhanced growth under 719 $\mu\text{mol mol}^{-1}$ CO_2 recorded for *Cirsium arvense* (L.) Scop. (Canada thistle) [27]. The 719 $\mu\text{mol mol}^{-1}$ CO_2 was roughly twice the ambient level at the time in the early 21st century, a level that could well be reached before the end of the century. Ziska et al. [28] suggested that climate change could lead to dramatic increases in dispersal of *C. arvense* and other similar wind-dispersed species with a significant growth response to increases in CO_2 . Both increased height and size could increase dispersal, with larger plants producing more seeds, and seeds dispersing further from taller plants due to aerodynamic factors.

Successful life history strategies for agronomic weeds generally involve synchrony between weed life histories and various aspects of crop life histories and management [29]. For example, successful weed life history strategies may include producing seeds either pre- or post-crop harvest to avoid destruction with harvest, or if weed seed production is synchronized with crop harvest, mimicry of crop seeds may aid in seed dissemination via crop seed contamination. Climate change may disrupt timing patterns for weed and crop phenology, potentially selecting for altered weed life histories, likely comprising polygenic selection [29]. For example, forbs and grasses showed divergent flowering time responses to elevated CO_2 and N addition in a grassland ecosystem [30]. Franks et al. [31] demonstrated that within a few generations, from 1997 to 2004 populations of field mustard, *Brassica napa* L. were able to evolve much earlier flowering times. Flowering time was as much as 8.6 days earlier, in response to a five-year drought from 2000–2004 [31]. Post-drought *B. napa* plants also showed other newly evolved life history characteristics, such as duration of flowering, total number of flowers, number of leaf nodes, and stem diameter, all of which related to the need for accelerated flowering under drought conditions [32].

In addition to dispersal ability and flowering timing, there are many other life history traits that make weeds successful, many of which are discussed in the following section in the context of rapid evolution.

2.3. Rapid Evolution

The general-purpose genotype providing weeds flexibility under changing climate conditions and shifts to prominence of particular life histories both involve pre-adaptation. As discussed previously, such phenotypic variability is intrinsic to weed species evolved in highly disturbed environments for millennia. However, neither of these attributes—plasticity or life history variation—require evolutionary adaptability. Weeds which are capable of evolving in relatively short timeframes [15,33–35], provide another means of making weed management a challenge under climate change [11,34,36]. Furthermore, because it is clear from abundant evidence that weeds are capable of evolving herbicide resistance rapidly, there is no reason to assume this capability to evolve rapidly does not also apply to weedy traits [37].

As invasive plants invade new habitats with different climatic and other abiotic conditions, primarily due to human agency, it is interesting to observe how well they adapt to local conditions. A meta-analysis of 134 plant species in 54 plant families comparing native to invasive species found that the invasive plants were just as capable of adapting to local conditions as their native relatives [38]. This adaptive capability was seen as a strong indication of the ability of the invasive plants to evolve rapidly to novel conditions [38].

Climate change results in changing environmental conditions, thus creating selection pressure on all species, including weeds, which may result in evolutionary change. Because weeds are pioneer species, they have many life history traits that can be selected for under climate change [36], including the traits that Baker [13] determined as constituting the ideal weed characteristics. Baker's [13] 10 ideal weed characteristics can be summarized under

6 categories (Table 1): (1) germination, (2) growth, (3), competitive ability, (4) breeding system, (5) seed production, and (6) dispersal traits. Below we discuss each of the rapid evolution possible under climate change for these 6 categories of traits.

Table 1. Categories of traits within Baker’s ideal weed characteristics [13] arranged by stages in the weed life cycle.

Trait Category	Ideal Weed Characteristic (Number from Baker [13])
Germination	Germination requirements fulfilled in many environments (1)
	Discontinuous germination and great longevity of seed (2)
Growth	Rapid growth through vegetative phase to flowering (3)
Competitive	The ability to compete interspecifically by special means, ability, e.g., rosette, choking growth, allelochemicals (10)
Breeding system	Self-compatible but not completely autogamous or apomictic (5)
	If cross-pollinated, unspecialized visitors or wind-utilized (6)
Seed production	Continuous seed production for as long as growing conditions permit (4)
	Very high seed output in favourable environmental circumstances (7)
Dispersal	Produces some seed under a wide range of environmental conditions, is tolerant and plastic (8)
	Adaptations for short- and long-distance dispersal (9)

2.3.1. Germination

Germination characteristics are likely to be under relatively high selection pressure, as the relative success or failure of weeds to recruit from seed and passage through the critical seedling stage comprise a crucial gateway to evolutionary fitness [39,40]. This gateway partly interacts between environmental factors and seed dormancy mechanisms. Gu et al. [41] showed that a simple multigenic system for dormancy genes in weedy rice (*Oryza sativa* L.) was responsible for the dormancy levels exhibited by the weed, varying with ripening under different seasons or temperatures. Weedy rice likely originated from domestic rice in a variety of different ways, such as adaptation of wild *O. sativa* to agricultural habitats or de-domestication of cultivated rice [42]. The fact that weedy rice may exhibit dormancy ranging to several years in length when domestic rice varieties exhibit little or no dormancy shows how readily novel seed germination characteristics can arise. There are also several other seed germination traits that distinguish weedy rice from cultivated rice including seed shattering and greater cold tolerance allowing weedy rice to produce seeds under colder temperatures and emerge from greater burial depths than cultivated rice [42–44].

2.3.2. Growth

Baker’s (1974) third ideal characteristic of rapid growth in the vegetative phase is a trait that has evolved to an extreme extent in certain weeds. For example, *Mikania micrantha* Kunth, appropriately named mile-a-minute, is a scrambling vine native to Central and South America that has invaded large areas of Asia and the Pacific Islands, in large part due to its rapid growth rate [9]. *M. micrantha* vines are capable of growing as fast as 20 cm per day [45]. An analysis of the *M. micrantha* genome revealed that the rapid growth was partly due to the capability of *M. micrantha*, as a C₃ plant, to absorb CO₂ at night using a mechanism similar to plants with CAM, in combination with augmented stem photosynthesis efficiency and nitrogen absorption [46].

In their assessment of the *M. micrantha* genome, Liu et al. [46] examined its genetic history compared to other Asteraceae. In addition to bearing the marks of numerous gene duplication events in common with its relatives, there were many recent segmental duplication events evident in the *M. micrantha* genome. The way Liu et al. [46] phrased it, “the *M. micrantha* genome experienced a recent explosion of lineage-specific segmental duplications.” Photosynthesis was clearly a key evolutionary driver of these events,

with *M. micrantha* featuring more genes related to photosynthesis than any other aster species [46]. “Recent” was defined as within the last million years, but still the mechanism of duplication events is clearly a significant one in this species and other weeds capable of rapid growth rates. Because such increased growth rates may be connected to changes in photosynthetic genes, changes in CO₂ concentrations and climatic conditions could stimulate evolutionary change in weed photosynthetic efficiency. Plants already possessing highly efficient photosynthesis like *M. micrantha* could take advantage of such conditions to expand their ranges and biotypes adapted to particular areas could emerge. An example of this kind of change is *Bromus madritensis* L. (foxtail brome), which evolved a change in stomatal conductance in just 7 years, allowing this invasive grass to take advantage of enriched levels of CO₂ [47].

2.3.3. Competitive Ability

One advantage of high growth rate is accompanying competitive ability, but there are many other competitive mechanisms that could also undergo rapid evolution in weeds [32]. One valuable approach to studying changes in competitive ability is the “resurrection approach,” whereby weed seeds from an earlier period are planted alongside modern seeds. Franks et al. [48] showed that 2014 accessions of *Avena fatua* L. (wild oat) were more competitive than accessions derived from the 1960s, in response to a 25% increase in CO₂. Ziska [49] compared competitive parameters such as leaf area and above-ground biomass between the *A. fatua* populations and cultivated oats (*A. sativa* L.). Over the same timespan (mid-20th century to 2014), *A. fatua* had been selected for higher competitive parameters with the enhanced CO₂ levels, whereas *A. sativa* domestic lines showed a more muted response [49]. This disparity makes sense because crops are not generally bred for competitive ability as yield is the primary priority, especially if weed-free growing conditions are assumed by plant breeders.

Although it was theorized that reduction in allocation to plant defense in invaded ranges has facilitated enhanced competitive ability [50], a meta-analysis demonstrated that this was not always the case [51]. However, the meta-analysis did show rapid evolution of invasive plants occurred following their introductions, with some invasive plants showing higher competitive ability assessed via vegetative growth and reproductive effort. Some invasive plants maintained high levels of defense against herbivores in the introduced range [51]. Another more recent meta-analysis supported a Shifting-Defense hypothesis, whereby the most common scenario was alien invasive plants being released from specialist herbivores but still having to deal with generalist herbivores in their newly invaded ranges [52].

2.3.4. Breeding System

A large proportion of weeds are autogamous or primarily selfing, but occasional outcrossing still allows for evolutionary adaptation [15,53]. Uniparental reproduction allows pioneer species to colonize and multiply in new areas with relatively few conspecific individuals present [53]. Breeding systems predicted to have higher colonization ability include hermaphrodites with male and female organs on the same flower and monoecious plants with organs on separate flowers on the same plant [53]. Although breeding system does exhibit some taxonomic bias, breeding systems themselves are subject to evolution and many closely related plant taxa exhibit a variety of breeding systems [53,54]. Thus, environmental changes may provide selection pressures potentially leading to altered breeding types. Plants that exhibit clonal growth in particular may be prone to form asexual populations in invaded regions, such as the widespread introduction of male-sterile *Reynoutria japonica* Sieb. & Zucc. (Japanese knotweed) in Europe and North America [55].

A good example of a recent breeding system alteration spurred by invasion is the case of *Eichhornia paniculata* (Spreng.) Solms (Brazilian water hyacinth), which has invaded various parts of Central America and the Caribbean from its native Brazil [54]. Because its Brazilian pollinators are absent in the invaded regions, sexually reproducing tristylous

flowering morphs that promote outcrossing in the native environment are absent in favor of selfing forms [56]. Barrett et al. [54] envisage that the prediction of increased flooding and storm events under climate change provide conditions favoring breeding system changes in other aquatic or semi-aquatic plants, and clearly other invasive plants with multiple breeding system modes, particularly those involving clonality such as perennial grasses might exhibit similar evolutionary tendencies. These evolutionary dynamics are difficult to predict because the relative emphasis on reproduction and dispersal changes over different phases of invasion [57].

2.3.5. Seed Production

Several ideal characteristics listed by Baker [13] involve seed production, and as a fundamental aspect of fitness, fecundity is strongly correlated to evolution of many of the other traits already discussed here, i.e., larger or more competitive plants tend to produce more seeds. Many of the world's worst weeds are characterized by high levels of seed production, so if changing climates select for even higher seed production, these species will become even more prolific and difficult to control. One such weed is *Parthenium hysterophorus* L. (parthenium weed) which is of widespread concern throughout Asia and Oceania, and shown to produce more seeds under changing climate conditions in Australia featuring increased atmospheric CO₂, and with increased temperatures to a point [58]. Furthermore, droughts also caused increased allocation to reproduction, but less seed filling and longevity. These details indicate some of the selection pressures that might cause genetic changes over times; the two biotypes in this study did show differences in seed production characteristics [58].

There are also numerous studies indicating how seed production is influenced by environmental conditions, and how different species are impacted differently by climate stresses. The weed *Amaranthus palmeri* S. Watson (Palmer amaranth) is known for high levels of seed production, but this was reduced by 55% when moisture levels were at 75% of field capacity [59]; by contrast, *Echinochloa colona* (L.) Link (jungle rice) seed production maintained the same level at 50% of field capacity [60]. Thus, plants like *E. colona* are well-suited to proliferate and continue evolving drought tolerance as drought frequency increases as predicted under climate change. For example, the rangeland weed, *Centaurea solstitialis* L. (yellow starthistle) is predicted to expand its range in the western U.S. because of increasing drought frequency [61–63]. Like most other plants, seed production is related to plant size, and research has shown that *C. solstitialis* is capable of evolving greater size in invaded habitats [64].

2.3.6. Dispersal

High levels of fitness are associated with production of large numbers of seeds, but particularly important for the fitness of an invasive species, is the ability to disperse effectively. In fact, studies have shown increased dispersal ability has evolved in populations of some invasive plant species at the edges of their ranges [65,66]. A coastal invasive species in eastern Australia dispersed by winged seeds, *Gladiolus guenzii* Kunze exhibited greater dispersal ability along the edges of its range, as measured by wind loading ratio: seed mass/wing area [66]. Interestingly, *G. guenzii* also exhibited increasing capacity for selfing along the invasion edges in Australia [67]—the adaptive tendency we discussed in Section 2.3.4. Three traits associated with increased seed dispersal for *M. micrantha*, plume loading, seed mass and pappus radius were found to be selected for in populations undergoing range expansion [65].

Because climate change will often have the strongest impact at the edge of species ranges, it is predicted that along the edge of ranges is precisely where selection pressures due to climate change will be greatest, including selection favoring dispersal ability, but much more empirical research on this prediction is needed [68]. Increased dispersal ability and accompanying dispersal under climate change threatens to be one of the most dire consequences of the anticipated changes due to large-scale alterations in cli-

mate. For example, a study of the predicted increase in *Ambrosia artemisiifolia* L. (common ragweed) in Europe, estimated by 2050 ragweed pollen levels would be 4 times higher than levels in 2015, in addition to the agronomic damage caused by the greatly expanded distribution of *A. artemisiifolia* [69]. Factors contributing to this predicted spread include increased seed distribution due to climate change, land-use changes, and evolution of seed dispersal ability.

2.4. Epigenetics

In addition to rapid evolution, many invasive plants have the ability to respond quickly to abiotic environmental factors by altering their gene expression. In a constantly changing environment, plants need to be flexible in order to survive stresses such as fluctuating light, temperature, water, and salt levels. In order to be flexible, plants can undergo epigenetic modification, which is the alteration of chromatin without modifying the DNA sequence [70]. Chromatin refers to the DNA sequence along with histone proteins, which allow the DNA to be folded into a more compact, higher order structure. This structure can be influenced by stimuli like abiotic environmental factors, leading to changes in gene expression, mainly transcription [71].

There are three major types of epigenetic modifications to plants: histone variants, histone modifications, and DNA methylation. As mentioned, the DNA is compacted and wrapped around the histone proteins; this structure determines the accessibility of the DNA to transcription factors and thus can impact gene expression. One of the ways the chromatin structure can change is by exchanging a histone for a histone variant, a similar protein with differences in the amino acid sequence. The variants have different affinities for DNA and binding proteins, leading to changes in the chromatin compaction. For example, the linker (H1) histone variant H1.3 in *Arabidopsis* allows the plant to respond better to combined light and water stress. A study by Rutowicz et al. [72] found that plants with the H1.3 variant have higher alteration of gene expression, increased growth rate, increased photosynthetic ability, and increased stomatal density compared to wild type plants.

Similarly, histones can also be altered after translation, through chemical modifications to amino acid residues such as methylation, acetylation, and phosphorylation. Acetylation of histones reduces the charge between the histone and DNA, subsequently facilitating the start of transcription; deacetylation has the opposite effect. In a study of *Arabidopsis*, it was found that histone acetylation levels were increased within 2–5 h after exposure to drought stress, leading to a corresponding increase in transcription of several drought-responsive genes [73]. Amidst a changing climate, the ability to rapidly respond to environmental stresses such as drought are essential for invasive plants to maintain a competitive edge over native species.

DNA methylation is the most common type of epigenetic modification, occurring when the cytosine position 5 is converted to 5-methylcytosine; this adaptation is related to coping with severe environmental stresses by affecting gene expression. DNA methylation has been associated with a number of different environmental stresses, including high temperatures [74], cold temperatures [75], salinity [76], drought [77], and heavy metals [78]. The ability to adapt in this manner to environmental stresses is especially important for clonal invaders. Like DNA mutations, epigenetic mutations can increase the range of variation for natural selection to act on, thereby increasing adaptation of individuals. For clonal species that do not reproduce sexually, epigenetic mutations are a way for phenotypic variation to arise. This is imperative for invading new, heterogeneous ecosystems. For instance, a study of the clonal invader *Alternanthera philoxeroides* (alligator weed) found that under salinity stress, epigenetic diversity within a population was significantly increased [79]. Similar results were found when studying *Reynoutria japonica* (Japanese knotweed) another clonal invader [80]. Another study of alligator weed found that when comparing populations in different environments, the epigenetic modifications were significantly different, despite sharing a nearly identical DNA sequence [81]. In clonal populations, where genetic

diversity is low, this mechanism can rapidly increase adaptive potential to novel environments without waiting generations for natural selection to act, increasing invasive success. However, it is important to note that most stress-related epigenetic modifications to chromatin only last until the stress exposure ends, although emerging evidence suggests that some modifications can be passed down to progeny through a “memory” of the stressed state [82]. Epigenetic modification is an effective, though intermediate, method of rapid evolution for invasive species, especially in novel environments. With the implications brought by climate change, adaptations to changing environmental conditions will be even more important for invasive species to thrive. Populations will likely experience novel climates without expanding their geographic range, including hotter, drier summers and warmer, wetter winters, as well as more frequent and severe storms.

2.5. Hybridization

Genetic diversity of a weed species can also be increased through hybridization with another species, resulting in new genetic combinations and allowing for more rapid adaptive evolution. Hybridization can be a way for genetically impoverished species, such as those impacted by founder effects or bottlenecks, to gain genetic diversity that can then be acted upon by natural selection. This greatly increases the chances of success when invading new areas. Clonal species are also at risk for genetic loads, and hybridization is one way to overcome this issue.

Hybrid weed species often exhibit hybrid vigor, also known as heterosis, where the progeny exhibits improved biological function when compared to both parent species. Generally, the hybrid will exhibit more aggressive growth, with an improved ability to spread to new areas and compete within invaded areas, and may also have greater biomass and higher fertility [83]. An excellent example of heterosis can be found in the hybrid *Reynoutria* × *bohemica* Chrtek & Chrtková (Bohemian knotweed), a cross between *Reynoutria japonica* Japanese knotweed, a clonal species, and *Reynoutria sachalinensis* (Friedr. Schmidt Petrop.) Nakai (giant knotweed). Despite primarily reproducing vegetatively and existing in its invasive range as a sterile clone, *R. japonica* is one of the most aggressive invaders in the northern hemisphere [83]. *R. sachalinensis*, which has had multiple introductions to North America and Europe, has high genetic diversity and can reproduce both vegetatively and by seed [84]. An interspecific hybrid between *R. japonica* and *R. sachalinensis* was first reported in Europe in the late 19th century. However, it seems that the importance of the hybrid in the spread of the taxon has risen in more recent years, and is now considered to be the most common of the three knotweed taxa across North America [84] and much of Europe [83]. Introgression between *R. japonica* × *bohemica* hybrids and the *R. japonica* parent is also well documented in North America and Europe; interestingly, these *R. japonica* × *bohemica* most closely related to *japonica* hybrids have demonstrated the most aggressive growth, as well as higher numbers of flowers and seeds, when compared to *R. japonica*, *R. sachalinensis*, and a true intermediate *R. japonica* × *bohemica* hybrid [83]. Parepa et al. [85] also reported that the hybrid species outcompetes native vegetation better than either parent species, decreasing native plant biomass by over 20%, and at the end of the experiment reached a biomass 3 times greater than either parent species.

R. japonica × *bohemica* has been found to have incredibly high genetic and phenotypic diversity, with multiple genotypes existing within patches, confirming that the hybrid can reproduce vegetatively or by seed [84]. Despite reproducing clonally, *R. japonica* does exhibit heritable variation between populations, likely from epigenetic variation, which plays a role in its invasive success [80]. Some evidence indicates that epigenetic variation can play a key role during hybridization events, helping to stabilize new genotypes, and could be a factor in the rapid adaptation of hybrid species to novel environments and new climatic zones, though further research is needed to confirm this [86]. The hybrid between these two invasive knotweed taxa has created an even more invasive species, highlighting the importance of hybridization as a means of further invasion.

Heterosis is also observed in the hybrid between two invasive toadflax species, *Linaria vulgaris* Mill. (yellow toadflax) and *Linaria dalmatica* (L.) Mill. (Dalmatian toadflax) [87]. Not only is the hybrid fertile, but it has also been found to be more resistant to human management efforts. Environmental suitability modelling for the *Linaria* hybrid revealed a large potential invasive range, including areas where neither parent species is found, highlighting the hybrid's phenotypic plasticity [87]. Common garden experiments across the parent species range showed the hybrid to have significantly higher biomass and fertility compared to the parents [88]. In water-limited environments, such as those where *L. dalmatica* typically thrives, the hybrid species has been found to break dormancy earlier than the parent species, allowing it to use available water without heavy competition from other species. This strategy will likely provide a continued advantage amidst a changing climate, given that future models have projected a decrease in spring and summer precipitation, more frequent drought, as well as higher temperatures.

Hybridization also poses a risk to agricultural settings, as hybridization can occur between crops and weeds. Allele flow between transgenic herbicide resistant crops and closely related non-resistant, herbicide sensitive weeds has been recently documented. In *Conyza*, for instance, hybridization of a transgenic glyphosate resistant (GR) crop and glyphosate sensitive (GS) species resulted in a resistant hybrid [89]. Not only was this hybrid resistant, but it displayed a significantly higher level of resistance than its GR parent, despite employing the same mechanism of resistance [89]. Introgression between the hybrid and either the weed or crop parent also results in a resistant hybrid. These hybrid GR weeds prove to be more difficult for landowners and farmers to control than a typical GR weed, requiring integrated management practices [89]. The transfer of herbicide resistance through hybridization has been documented in several cases, including between *Brassica* crops (canola) and their weedy relatives [90], between crop and wild rice (*Oryza* spp.) [91], and between crop and wild wheat (*Aegilops* spp.) [92].

Beyond the transfer of resistance to weeds, hybridization between crops and weeds can pose other threats, such as decreasing crop yield. For example, sugar beet crops have a well-documented history of hybridization with wild beets, and the hybrid produces seeds that are indistinguishable from the cultivated, certified seeds [93]. These seeds are often inadvertently spread alongside sugar beet seeds, and the difference can only be seen during bolting and flowering. The hybrid will flower during its first year, contrary to the crops which are biannual and are harvested for their roots before flowering, decreasing overall sugar beet yield. These hybrids also have the potential to produce many seeds, which would exacerbate the problem the following year. Because the weeds and crop beets are closely related, they cannot be treated with herbicides and require integrated management techniques, which generally involve higher costs and time for land managers.

Hybridization often results in progeny with improved fitness, and these heterotic hybrids may be more likely to adapt to climate change. Traits like aggressive growth, high fertility, and increased biomass will likely be useful in overcoming environmental stresses such as high temperatures and drought. Additionally, hybridization may also be driven by climate change due to altered timing of flowering and pollen release caused by seasonal temperature changes. Recent studies have indicated that some weeds, such as *Ambrosia* spp. (ragweeds), will increase pollen production in Europe by as much as four times by 2050, based on climate modelling [69]. In addition, warmer spring temperatures have begun to influence timing of flowering, with the timing shifting earlier in several observed species, including both weeds and crops [88,94,95]. In the U.S., early flowering has been reported in several species of *Brassica*, driven by strong directional selection due to increasing spring temperatures [95]. Ultimately, increases in pollen as well as shifts in timing of flowering and pollination of both weedy species and agricultural crops may result in the production of new hybrids that were previously not reproducing at overlapping times. As temperature and precipitation continues to shift due to anthropogenic climate change, we may observe an increase the number of weedy hybrids.

2.6. Herbicide Resistance

Herbicide resistance represents a crucial way for weeds to defy human management efforts, since the broad scale application of herbicides in the 1950s, where for most cropping systems around the world herbicides became *the* critical tool for controlling weeds. Yet this tool has been jeopardized by the dramatic rise in herbicide resistance cases in the last several decades, with resistance seen for 23 of 26 of the herbicide modes of action, observed in a broad spectrum of weeds in 71 different countries [96]. Much has been written elsewhere about the serious problems herbicide resistance presents for weed management, but here we will focus on how these serious problems are exacerbated by climate change. A key driver of herbicide resistance evolution is the frequency of herbicide application and exposure [97] and such exposure may or may not increase under climate change. Changes in herbicide exposure in relation to climate change are predicted to depend on management factors, such as the potential for additional applications due to enhanced weed growth or herbicide tolerance (see Section 2.7), or environmental factors either affecting herbicide exposure directly (e.g., rainfall pattern changes) or indirectly (e.g., changes in weed growth or reproduction, phenology or other physiological aspects).

However, what may be of greater concern regarding herbicide resistance specific to climate change is the increased dissemination of herbicide resistance biotypes due to climates that favor greater weed spread, at local and regional levels. Two chief means of spread of herbicide resistant agricultural weeds are (1) spatial dissemination via wind dispersal, farm machinery or other means, and (2) temporal dissemination via persistent seed banks or bud banks in the case of perennial weeds [98]. Herbicide resistant weeds are spreading throughout the globe, to an alarming extent in every region [99]. Warming temperatures, changing moisture and storm regimes that facilitate further range expansion of weeds also facilitate expanding distribution of herbicide resistant weeds [100].

A good example of a weed that is benefitting from both herbicide selection pressures and climate change is *Bassia scoparia* (L.) A. J. Scott (kochia), which exhibits widespread herbicide resistance, especially to glyphosate [101]. In North America, its range and impact has been extending rapidly in the northern U.S. and Canada, partly through widespread herbicide resistance, and partly through extended growing seasons due to climate warming, changed rainfall patterns, enhanced atmospheric CO₂, all of which favor its physiology [101–103]. Many other factors also promote its spread, including potential for rapid evolutionary change, epigenetic factors, its tumbleweed mode of spread, and seed longevity, which increases the long-term persistence of resistant biotypes [101]. All in all, kochia presents a good cautionary tale, that beyond the widely recognized issue of herbicide resistance, the combination of resistance and climate change threatens to make the problem worse.

2.7. Herbicide Tolerance

Given the high degree of efficacy expected from herbicides, weeds that are not killed by herbicide applications are not given much attention, especially when control is rated at 90% or higher. There is some concern over the potential for tolerance to eventually lead to resistance, but in this section, we will focus on the potential effects of climate change on herbicide tolerance, specifically, on what climatic conditions may tend to favor herbicide tolerance.

Because many environmental factors such as temperature, carbon dioxide and moisture levels affect herbicide efficacy, it is abundantly clear that climate change is currently having, and will have major impacts on herbicide effects, generally reducing their efficacy [104,105]. Increasing temperatures can reduce herbicide efficacy because of more rapid plant metabolism at higher temperatures and/or increased evaporation from the soil, although these effects vary by site and for particular weed species [106–108]. When Benedetti et al. [109] exposed *Echinochloa colona* (L.) Link (junglerice) to repeated low doses of herbicides under two heat stress levels (30 and 45 °C), they found that several genes were upregulated in junglerice that tended to increase herbicide tolerance.

Increased atmospheric CO₂ concentration may have considerable impacts on crop-weed relations, especially considering that concentrations are projected to rise as much as 4× current levels by the end of the 21st century [110]. Increased levels of atmospheric CO₂ will reduce herbicide efficacy due to a variety of factors including increased growth rates and increased allocation to underground storage organs in target weeds [111,112]. Perennial weeds such as *Cirsium arvense* L. (Canada thistle) under a pre-emergence glyphosate regime may exhibit increased biomass due to enhanced CO₂ levels, with concomitant reductions in crop yields [113].

Drier conditions predicted under climate change, including more frequent droughts may decrease herbicide efficacy in at least two distinct ways: by reducing absorption of herbicides in weed roots or by reducing herbicide absorption in weed leaves that develop thicker cuticles to resist drought conditions [114–116]. Taken together, these lines of evidence collectively point to a serious loss in the expected effectiveness of herbicides, given future predicted climate regimes. Indeed, if one goes beyond the study of single weed species, as Waryszak et al. [117] did, examining effects of elevated CO₂ levels on herbicidal control of 14 weed species, including C₃ and C₄ weeds, and weedy shrubs, reduced efficacy may call for a wholesale re-evaluation of herbicide use.

2.8. Cropping Systems Vulnerability

The world is changing in many ways due to climate change, with many of these shifts happening in the way things have been done the same way for a long time, and once the tipping point is reached, there is no going back [118,119]. One of these tipping points is in the nature of cropping systems and the need for rapid adaptation. There are concerns that crop variety development cannot keep up to the rapid changes in climate that are anticipated [120], and part of the issue is the increased unpredictability of pest control in current cropping systems under climate change [121]. More resilient cropping systems, including better use of conservation tillage, cover crops, crop rotations and perennial crops may be imperative to combat the inherent vulnerability of present practices [122]. However, there is often a natural trend towards growing crops better adapted to conditions as temperate regions become warmer, in response to favorable economics.

In view of predicted cropping system changes under climate change, there are two major ways these agroecosystems could become more vulnerable to weeds: (1) use of cropping systems that are inherently more vulnerable, (2) greater ability of the weed flora to adapt to climate change than the crops. Numerous reports have warned of greater vulnerability of cropping systems under climate change, across many parts of the globe [120,123–125]. It has been shown that although soybean yields respond favorably to enhanced CO₂ levels, the presence of weeds compromises this ability [126].

In temperate regions, the poleward expansion of weed distributions is predicted as climates in these regions become warmer with climate change, and this expansion is already occurring, with numerous examples of weeds moving northward in North America [15,127–129] and Europe [130,131] (Kollmann and Bañuelos 2004; Hyvönen et al., 2012), and southward in Australia [33,132]. However, the movements of these weeds are also highly determined by selection of cropping systems, which is a key mechanism by which weeds and their propagules are transported [133]. The choice to begin growing crops in different regions to adapt to climate change, will thus likewise influence shifts in weed distributions. Many C₄ weeds are more competitive than C₃ weeds, which have tended to be in the majority in cooler temperate zones, and an increased mix of C₄ and C₃ weeds in a given region could create more weed competition with crops [134]. Moreover, areas such as Australia and California already facing some extreme high temperature and drought conditions due to climate change have recorded changes in weed-crop competition relationships, usually in favor of the weeds [134,135].

Although we have referred to a variety of studies that have attempted to predict cropping systems vulnerability to increased spread and impact of invasive plants, there is a shortage of empirical studies on such predictions [134,136]. Pyšek et al. [136] call for

additional research to better link changes in distribution of invasive species to shifts in temperature or precipitation under climate change. They highlight the importance of such research to assess interactions among invasive species and with other species, such as the critical interaction with crops touched on here.

2.9. Co-Evolution with Human Management

The world is in the midst of a great experiment, an experiment unwittingly designed to research the effect of our management of weeds on the evolution of said weeds [15]. John Harper, often considered the father of modern weed ecology, said in 1956 that, “arable weeds constitute an ecological group . . . that have been selected by the very practices that were originally designed to suppress them” [137]. It is clear that the artificial selection for crop traits favoring uniformity in general is no match for the potentially rapid evolution of weeds via natural selection [138,139]. We are also experimenting with climate effects, through our actions to cause climate change, thereby turning up the temperature on the great experiment.

In effect, we are placing agronomic fields already impacted by weed competition into greenhouses, via the “greenhouse effect.” Greenhouses often provided a rarified atmosphere for insect pests and pathogens to flourish more than in outdoor environments exposed to weather extremes. However, weed pests are not normally as big of a problem as other pests in greenhouses because they do not tend to invade greenhouses *en masse*. With temperate areas of the globe warming, weeds now have access to warmer temperatures facilitating growth and, in many instances, herbicide resistance, along with increased CO₂ levels, another frequent additive in artificial greenhouses. Just as our agronomic methods select for weeds, so does our facilitation of the greenhouse effect. The milder conditions and elevated CO₂ levels in temperate zones tend to help both weeds and crops, except along with climate warming comes climate extremes, which as discussed previously also favor many weeds that may be more drought tolerant than crops or have their dispersal promoted by extreme weather.

2.10. Riding the Climate Change Storm

Climate change literally leads to increased storm frequency and severity [140,141]. Although climate change is metaphorically like a storm moving across the globe and affecting all flora and fauna in its path, organisms like weeds and other invasive species are the most likely organisms to “ride out the storm.” In the wake of Tropical Storm Irene in 2011, *Reynoutria japonica* (Japanese knotweed) increased its distribution in Vermont via fragments spread by the storm’s fury [142]. Likewise, the invasive sedge, *Carex kobomugi* Ohwi proliferated after Hurricane Sandy in 2012, performing much better than the local native coastal grass *Ammophila breviligulata* Fernald (American beachgrass) [143]. A planet heavily scarred by climate change could well become the “planet of weeds” referred to earlier [4].

3. Conclusions

If the 10 ways described here by which weeds defy human management efforts become more serious as the climate changes, business as usual or small modifications in the way weeds are managed will not suffice (Table 2). Each of these 10 challenges to weed management (and others) call for the design and implementation of more resilient cropping systems rather than simply relying on attempts to improve herbicidal control, which itself can be compromised by climate change. Such improvements may include, but are not limited to, better use of conservation tillage, cover crops, crop rotations and perennial crops [122]. In fact, the best approach to managing the multiple ways that weeds can thwart weed control management under climate change is through an integrated approach that incorporates a variety of agronomic tactics including cultural weed control methods, biological control, crop competitiveness, and a proactive overall strategy to ensure the forces that drive selection of weedy traits are kept off balance.

Table 2. Ten ways that that weed evolution defies human management efforts amidst a changing climate.

Weed Evolution Element	Challenges to Human Management Amidst Climate Change
1. General-purpose Genotype	Difficult to account for weed phenotype variation as exacerbated by climate change
2. Life History Strategies	Life history strategies subject to change under climate change so management must adjust
3. Rapid Evolution	Many weed traits capable of evolving rapidly in response to climate change, requiring management to pivot
4. Epigenetics	Difficult to predict weed phenotype variation even intra-generationally
5. Hybridization	Abrupt genotype change on a large scale creating new weeds to manage
6. Herbicide Resistance	Additional spread of herbicide resistant weeds likely under climate change
7. Herbicide Tolerance	More climatic variation leading to more variable effectiveness of herbicide applications
8. Cropping Systems Vulnerability	Weed communities better adapted to respond to climate change than cropping systems
9. Co-evolution with Human Management	Management of weeds tends to select for better adapted weeds more difficult to manage; climate change adds another selection factor
10. Riding the Climate Change Storm	Weeds are well adapted for climate extremes which may help further spread them and increase their overall persistence amidst changing climates

4. Management Implications

Human selection pressures are ubiquitous [144]. We are the ones igniting the wildfires of weed evolution, and so perhaps we need to think more about fighting fire with fire [145]. Ideally, crop cultivars should be designed to counter the effects of both weed competition and climate change [139]. In fact, because weeds “break the rules” constituting the normal constraints of evolution creating novelty in the process, their innovative adaptations may actually be a great benefit to humanity [146].

For example, given the evolutionary potential of weeds as enhanced under climate change, an “evolutionary plant breeding” approach could be developed [147], both to counter evolutionary advances of weeds and incorporate the lessons weeds have taught us. The close evolutionary relationship between crops and weeds should facilitate this approach [37]. This approach to crop breeding could even directly incorporate some of the evolutionary advances weeds have made in response to climate change, such as the idea of incorporating *Sorghum halepense* (L.) Pers. (Johnsongrass) genes into sorghum (*S. bicolor*) breeding programs to develop varieties suited for a broader range of climates [148]. Similarly, it has been suggested that we should prospect for favorable rice traits in weedy rice—in this case, both the weed and crop are classified as *Oryza sativa* but exhibit considerable trait differentiation as discussed in Section 2.3.1 [42].

Similarly, Small and Raizada [149] argue that drought-tolerant, nitrogen fixing “weeds” should be investigated as potential crops in subtropical regions. Given that both crops and weeds are under strong selection pressures, with crops artificially being selected for adaptation to changing conditions, including climate change, and weeds adapting along with them, it is clear that agronomists must be vigilantly aware of the implications of evolutionary theory in these times [150]. The innovative photosynthetic system possessed by the fast-growing invasive mile-a-minute vine (*M. micrantha*) could perhaps be investigated as a potential quantum leap in crop improvement [46].

As Mahaut et al. [146] contend, although the usual response to the various ways that weeds defy human management is frustration, the novel strategies of weeds have much to teach us. We have much to learn from the ten weedy issues described here amidst a changing climate: (1) general-purpose genotypes, (2) life history strategies, (3) ability to evolve rapidly, (4) epigenetic capacity, (5) hybridization, (6) herbicide resistance, (7) herbicide tolerance, (8) cropping systems vulnerability, (9) co-evolution of weeds with human management, and (10) the ability of weeds to ride the climate storm humans have generated.

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