

Crops and weeds running to stand still in the red queen's climate change race

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Abstract: The Red Queen Hypothesis formulated by evolutionary biologist Leigh Van Valen describes how coevolving species are engaged in a continuous arms race. The hypothesis was inspired by Lewis Carroll's novel "Through the Looking Glass" where the Red Queen says to Alice "Now, here, you see, it takes all the running you can do, to keep in the same place." In this review we examine how climate change has heightened the arms race between crops and weeds and reflect on how these closely related entities are engaged in a race to adapt to climate change, which represents a serious threat to agricultural productivity. Weeds are adapting to climate change relatively rapidly, whereas crop evolution is restricted by traditional breeding programs to emphasize crop yields and genetic

uniformity. Crops and weeds share much evolutionary history, with crops having been created by domestication of plant species which are often now classified as weeds. For example, in the case of rice, domestication resulted in a lack of infructescence shattering and seed dormancy. However, weedy rice which possesses both ancestral traits is now a serious pest of domestic rice, and continues to evolve, including developing traits for climate change resilience. We highlight the need to utilize knowledge of weed evolution and genomics in crop breeding, even to the point of incorporating genes from weeds as a possibility. Modern gene editing techniques must be utilized extensively to speed up crop improvement and help crops keep up to weeds in the Red Queen's climate change race.

Keywords: Weed Evolution; Crop Breeding; CRISPR; Weed Genomics; Hybridization; Coevolution; GMOs; Crop Wild Relatives

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1. Introduction

In Lewis Carroll's fairytale "Through the Looking Glass," Alice complains to the Red Queen that she is tired from running but is still at the tree where she and the Queen started. The Red Queen retorts: "Now, here, you see, it takes all the running you can do to keep in the same place. If you want to get somewhere else, you must run at least twice as fast as that." This is the basis for Leigh Van Valen's Red Queen Hypothesis that co-evolving species must keep evolving to keep up with each other (Van Valen, 1973). Ever since the agricultural revolution, crops and weeds have been running an evolutionary race, and now both are also running against the winds of climate change (Neve et al., 2009). Climate change acts as a selection pressure on weeds to alter life history characteristics or physiological traits (e.g., stress tolerance, metabolism, or herbicide resistance), sometimes quite rapidly (Clements, Jones, 2021).

Meanwhile, crop breeders must also work quickly to maintain high yielding crops despite climate change (Raza et al., 2019). Although crop breeders wield increasingly sophisticated tools (Marsh et al., 2021), weeds are more responsive to environmental change due to their phenotypic and genotypic plasticity, making it difficult to produce successfully competitive crops in the midst of climate change. Weeds inherently "run faster." Clearly crop improvement faces the urgent need for rapid transformation amidst a rapidly changing climate. Meanwhile one of the strongest evolutionary mechanisms that weeds possess is the ability to "steal genes" from closely related crops (Snow et al., 2001; Huang et al., 2017; Paterson et al., 2020). Many crops have feral counterparts including crops in the following genera: *Avena*, *Beta*, *Capsicum*, *Chenopodium*, *Daucus*, *Helianthus*, *Hordeum*, *Lactuca*, *Medicago*, *Oryza*, *Phaseolus*, *Raphanus*, *Saccharum*, *Sorghum*, and *Zea* (Van Raamsdonk et al., 1996; Huang et al., 2017). These wild relatives stand to benefit from crop improvements through gene flow, further complicating the ongoing arms race between crops and weeds.

In this review we compare the processes by which both crops and weeds are adapting to climate change, with crops adapting primarily via artificial selection and weeds adapting via natural selection. It is interesting to note that human weed control measures could also be seen to apply selection pressure in an unnatural way but this is an inadvertent type of artificial selection. Just as in Lewis Carroll's tale, global agriculture is caught up in a game of chess involving numerous characters (chess pieces)

and challenges, requiring cleverness and creative strategy to advance (Figure 1). Along these lines, we ask whether humanity can somehow harness rapid weed evolution to harvest genetic material for crop improvement. The Red Queen Hypothesis has stimulated many advancements in the study of evolution (Solé, 2022), and in this review we contend that the Red Queen Hypothesis is a useful concept for examining the interplay between crop and weed evolution in the face of climate change.

2. The Red Queen Hypothesis

Although Van Valen's Red Queen Hypothesis (Van Valen, 1973) inspired a considerable body of work in the decade or so that followed and has had a tremendous influence on evolutionary biology over the last 50 years (Solé, 2022), an updated version has emerged more recently (Strotz et al., 2018) which is more appropriate for the comparison between crop and weed evolution under climate change that we are making in this review.

When Van Valen (1973) proposed the Red Queen Hypothesis, his objective was to try to explain a pattern seen in the fossil record, specifically that survivorship curves of taxa within major taxonomic groups declined in linear fashion when plotted against geological time (Strotz et al., 2018). Van Valen's explanation for the linear pattern was that organisms that share an "adaptive zone" must continually improve their ability to compete with other organisms. Otherwise, the extreme evolutionary pressures of such interactions, taxa inevitably succumb to extinction at the constant rates observed in the fossil record. Such inevitable extinction of competing species is a result of resource limitation and an inability to dominate the other – a "zero sum" game. The Red Queen Hypothesis posits that in a constantly changing environment, organisms must continually evolve new adaptations to survive against ever-evolving adversaries. The Hypothesis explains that species or populations must continually develop new adaptations to avoid extinction (Van Valen, 1973; Dawkins, Krebs, 1979). This theory is often seen in interspecific interactions such as predator and prey evolution such as how a fox lineage may evolve to better catch rabbits but in turn the rabbits will evolve to better outrun the foxes.

There were many critiques of the original version proposed by Van Valen, mostly associated with the purported link between extinction probability rates and species age according to the fossil record (McCune et al., 1982; Vrba, 1993; Vermeij, 1994; Finnegan et al., 2008). However, others have enthusiastically advanced the use of the Red Queen Hypothesis to help explain evolutionary relationships and their outcomes among interacting species, particularly at the population level (Strotz et al., 2018). It is important to understand that different outcomes are possible, and there is not always a winner. Brockhurst et al. (2014) proposed three possible scenarios: "Escalatory, Fluctuating, and Chase." The Escalatory scenario envisions a situation in which the genetic



Figure 1 - In Lewis Carroll's "Through the Looking Glass" the protagonist, Alice, enters a world through a looking glass, and meets up with the Red Queen, and subsequently many other chess piece characters. The Red Queen tells Alice that she too can successfully become a queen if Alice makes the right moves, and as it turns out, overcome many challenges. In many ways, the Red Queen parallels weeds which are adept at rapidly adapting to climate change, whereas Alice as a pawn parallels crops, restricted as they are by conventional breeding programs. As Alice did in the story, global agriculture must overcome many challenges presented by climate change in order to be sustained in these challenging and often unpredictable times

makeup of each interacting species continually improves to exceed whatever the opposing species are dishing out against them. While the Escalatory scenario results in modified traits over time, the Fluctuating scenario pictures a back-and-forth sequence with one species outpacing another for a period of time, followed by reverse fortunes, so in the long-term there is no net evolutionary change in traits. Finally, the Chase scenario sees the possibility that the two interacting entities may evolve differently due to biotic changes across the evolutionary landscape beyond just interactions between the two species under consideration. A given member of the pair of co-evolving species may seldom catch up to the other because the game is always changing. The Chase scenario allows for many other species to potentially be involved in the interaction between the two focal species, which makes sense in a world where multispecies interactions are commonplace. Both the Fluctuating and Chase scenarios represent new wrinkles in Van Valen's original Red Queen Hypothesis which simply describes an escalating arms race (Strotz et al., 2018). The updated version of the Red Queen Hypothesis as described by Strotz et al. (2018) is very much akin to the Chase scenario of Brockhurst et al. (2014), focusing on population interactions, not species extinction dynamics at geological timescales and accounting for the fact species interactions take place within the context of the broader biotic community.

Although Van Valen's version of the Red Queen Hypothesis was centered around biotic interactions, and much of the Red Queen Hypothesis has followed suit, clearly abiotic interactions have an important role to play. Similarly to the Chase scenario pictured by Brockhurst et al. (2014), if the environment around a pair of interacting species is changing, the nature of the interaction is also likely to change. To accommodate this, Barnosky (2001) introduced the "Court Jester hypothesis" to examine how changes in the environment might precipitate changes in species traits. Although such pressures may be less predictable, they may have a great influence on evolution. The Court Jester hypothesis is a highly relevant today as climate change can radically modify species interactions (Schleuning et al., 2020; Antão et al., 2022; Terry et al., 2022). It is argued that the Red Queen Hypothesis best describes interspecific species interaction over a relatively short-time period, rendering abiotic factors less influential in driving evolution at such scales (Strotz et al., 2018; Solé, 2022). However, the ways in which climate change can spur evolutionary change over relatively short durations and at local spatial scales, as seen with many invasive plant species (Clements, Jones, 2021), compels us to consider the Court Jester hypothesis as part of the story.

The updated version of the Red Queen Hypothesis as described by Strotz et al. (2018) and others provides a foundation for understanding the relationship between crops and their wild relatives. This hypothesis becomes a reality in crop fields, where crops and weeds are locked in an evolutionary arms race. For example, rice and its weedy rice relative are said to co-evolve, pitting increasing weediness of the weedy rice against improvements in rice management and varieties (Zhu et al., 2018; Fukagawa, Ziska, 2019).

3. Crop Evolution versus Weed Evolution

Crops and their associated weeds have been undergoing co-evolution since the beginning of the agricultural revolution, however with the addition of climate change they both run to match this new selective force. Climate change adds a new dimension to this race. Crops are becoming more vulnerable to drought, heat stress, and pests, while weeds are evolving to keep pace with the changing climate. Because these weedy crops often have short generation times with strong dispersal abilities, as the environment changes weeds have a higher chance of positively adapting to the changing environments than other plants (Bradley et al., 2010; Clements, DiTommaso, 2011; Anwar et al., 2021). The question then becomes: How can crops keep pace in this accelerated race?

3.1 Crop Breeding Strategies for Climate Change

The threat of climate change and its potential devastating effects on biodiversity and food production, especially given our increasing global population, highlight the crucial need

to protect food security (Vincent et al., 2013). Chen et al. (2018) looked at the productivity of wheat, rice, and maize in 1.5 C and 2.0 C warming scenarios. They found that the increase in temperature would have negative impacts across all three major crops due to decreased growing period and increased frequency of extreme events (Chen et al., 2018). The increase in greenhouse gases resulting in elevated global temperatures and associated extreme weather fluctuations including heat waves, forest fires, typhoons, flooding, and rising sea levels all pose severe threats to agriculture (Yu, Li, 2021; Farooq et al., 2023).

Approximately 12,000 years ago, domestication of major crops began, resulting in three quintessential crops providing 60% of the calories to the human diet: rice, wheat, and maize (Tian et al., 2021). Crop domestication is the anthropogenic process of selecting plant traits for human needs (Tian et al., 2021). When these wild species are domesticated, microevolutionary forces such as genetic drift and gene flow result in the genetic bottlenecks and artificially selected diversity that plant cultivars select (Vigueira et al., 2013). Unfortunately, although this has resulted in the success of food production to date and the fixation of extremely desirable alleles, it has also resulted in severe genetic homogeneity within crop species which increases disease incidence and restricts plasticity to cope with adverse environmental alterations (Tian et al., 2021). While much is known about breeding crops for improved yield, relatively little is understood about the evolution of these plants when climate change or naturogenic causes are leading (Vigueira et al., 2013).

Traditionally, plant breeding is used for crop domestication to reshuffle favorable alleles with the repeated selection of top performing lines resulting from inter-crossing parents (Lyzenga et al., 2021). Although plant breeding has significantly enhanced food production, it has been built on a foundation of homogeneity, making farm crops genetically susceptible to abiotic and biotic factors (Fu, 2015). The potential risk of such homogeneity can be seen through previous epidemics: such as the Irish potato blight in the 1840s and the American corn blight in the 1970s (Fu, 2015). According to commentators like Fu (2015), Lehnert et al. (2022) and others, our understanding of crop genetic diversity in the context of modern plant breeding is severely deficient. Hufford et al. (2019) refer to crop biodiversity as an "unfinished Magnum Opus of nature," celebrating the ingenuity of humans in developing domesticated crops over time to be more and more ideal for human production and consumption. It is unfinished because of some of the crop breeding issues highlighted in our review.

Hufford et al. (2019) point out that crop biodiversity results from three main influences: the nature of the plant itself, the environment, and the actions of humans. Humans tend to narrow the genetic variation of crop plants overall through the domestication process, creating homogeneity that may be vulnerable if the environment under which domestication occurred changes. He and

Li (2023) warn that with the environment changing rapidly due to climate change “the narrow genetic base of elite crop cultivars” makes it very difficult to be innovative through conventional breeding processes. Still Hufford et al. (2019) argue that farmers and others involved in producing and designing crops are very much involved in the continual evolutionary development of crops through various practices designed to attempt to keep crops diverse enough to cope with environmental stresses.

The human population is contingent on the establishment of adequate food production and accelerates with its advancement (Tian et al., 2021). The recent exponential increase in human population can be traced from the Industrial Revolution origins in Great Britain in 1760 and subsequently spreading around the globe, giving birth to a variety of agriculture technologies, including extensive irrigation systems, fertilizers, and pesticides, as accelerated during the green revolution beginning in the late 1960s as worldwide crop production increased three-fold with an increase in cultivated land of only 30% (Khush, 2001; Tian et al., 2021; Shrestha, Horowitz, 2024). By 2050, it is estimated that the world population will reach more than 9 billion, and that food consumption will increase by at least 60% (Tian et al., 2021). Therefore, there is significant pressure to increase food production; however, this must be done so in a sustainable manner. Agriculture expansion and intensification through the reliance on excessive fertilizer, pesticides, and fresh water has contributed to climate change and also the eutrophication and destruction of ecosystems (Tian et al., 2021; Shrestha, Horowitz, 2024).

Climate change may well be the “sword of Damocles” (Figure 2) for agriculture, the critical test of whether humanity can survive the multiple existential threats hanging over us with a changing climate (Yu, Li, 2021). The classical Greek tale of the “sword of Damocles” features Damocles as a courtier to King Dionysis, whose excessive flattery of the king’s prestige and power prompted the king offering to trade places for a time. Dionysis suspended a sword above his throne by a single horse hair to show Damocles how although the king had access to great riches and power, he constantly had to be on the lookout for potential enemies. Damocles learned the lesson immediately and begged the king for permission to abdicate his temporary place on the throne. Like the sword of Damocles, climate change threatens to bring much more severe heat and drought stress in the 21st century if there are not sufficient reductions in greenhouse gas emissions (Ramirez-Villegas et al., 2020). Therefore, a sustainable approach to crop production must not only consider increased productivity, but also abiotic stress resistance in the face of declining environmental quality. Currently, farmers are considering ‘smart crops’, which represent new and improved crops that are resistant to climate change and also excellent in quality and yield (Yu, Li, 2021). To properly construct this new breed of crops we need an advanced understanding of molecular genetics

and plant biotic and abiotic interactions (Yu, Li, 2021). When considering agriculture and its efficiency, two major priorities are crop productivity and weed management with frequent large crop losses due to weed competition and the correspondingly high costs of weed control. Here we explore how crops can be better equipped for climate change and sustainability, especially in light of the success of weeds – their competitors on the global chess board.

Breeding programs must now focus on higher yield, nutrition, and resistance to biotic and abiotic stressors (Lyzenga et al., 2021). Yield and abiotic stress tolerance—which is important for climate change—are particularly complex genetically and are controlled by many small effect loci (Lyzenga et al., 2021). The pressure of climate change and the increase in human population require more intensive techniques than basic plant breeding.

Lyzenga et al. (2021) present a solution through CRISPR/Cas-based gene editing to overcome the time constraints of traditional introgression breeding that can synthesize desirable genetic variants and overcome



Figure 2 - Climate change may be seen as the Sword of Damocles for agriculture, posing an extremely serious threat to its sustainability (Yu, Li, 2021). Painting depicting the Sword of Damocles by Richard Westall – own photograph of painting, Ackland Museum, Chapel Hill, North Carolina, United States of America, Public Domain, <https://commons.wikimedia.org/w/index.php?curid=3437614>

genetic diversity lost through selective breeding. However, Xiong et al. (2022) explain that even with gene editing technologies, plant breeders are still challenged by narrowed genetic bases and uncertain global climates.

Plant breeders do have a variety of techniques available to them for increasing crop genetic diversity and climate resilience (Zenda et al., 2021). One promising avenue for increasing crop genetic diversity is through utilizing the gene pools of crop wild relative species (Vincent et al., 2013). Crop wild relative species are plant species closely related to crops that have not been subjected to the genetic bottlenecks of agriculture cultivation; and therefore, can contain the potential traits that can increase crop yield and production stability (Vincent et al., 2013). Unfortunately, even these wild species are threatened by genetic loss and extinction driven by anthropogenic influences (Vincent et al., 2013).

Cacao (*Theobroma cacao*) cultivation in Columbia and in other growing areas around the world is currently facing challenges due to increased variability in rainfall due to climate change (Lahive et al., 2019). Cacao trees are extremely susceptible to drought and therefore, their success is highly contingent on rainfall availability (González-Orozco et al., 2020). Cacao is also at risk for frosty pod rot disease caused by the fungus *Moniliophthora roreri* which has negatively impacted quality and production even in the most efficient production regions of Latin America. Additionally, increased deforestation from land tenure insecurity, illegal cropping and logging encumbers cacao cultivation. Wild relatives of cacao have increased resistance to excessive humidity and therefore may be less at risk to frosty pod rot disease. However, as is the case for many crop relatives, very little is known about the species richness and endemism of wild relatives of cacao in Colombia. To better equip cacao farmers for increased abiotic stressors such as climate change and disease, more genetic information on wild cacao populations is needed (González-Orozco et al., 2020).

One possible way to improve crops more rapidly than traditional breeding in the face of climate change is through using other techniques to modify their genomes. Genetically modified organisms (GMOs) used in agriculture are relatively controversial. A GMO is defined as genetic material within an organism that has been altered, often due to the addition of foreign genes called transgenes, outside of natural processes via mating and/or natural recombination (Jeschke et al., 2013). One of the most serious issues surrounding GMO crops is that once released, these crops may infiltrate populations of related species via gene transfer. For example, the herbicide resistance transgene from *Brassica napus* was observed to enter the gene pool of a weed-relative *Brassica rapa* in commercial fields (Warwick et al., 2008). The persistence of this gene was documented over a 6-year period without herbicide selection pressure. Although there was indication of increased risk in an agricultural habitat, Warwick et al. (2008) called for more research to understand the

consequences. Such gene transfer obviously runs counter to the purpose of using GMOs to give crops advantages over weeds. In a systematic review, Caradus (2023) listed a number of other documented cases of herbicide resistance transfers from transgenic crops to related weeds, which is especially problematic for outcrossing crops/weeds like *Brassica* spp., where it is virtually impossible to prevent gene flow. Caradus (2023) also lists a number of ways that risks from such transfers can be and are being managed and points out that commercialization of transgenic crops with such risks has been discouraged or pursued with caution.

The recent emergence of CRISPR/Cas-based gene editing has created a new option for producing GMO crops that may be more palatable than traditional GMO techniques that involve incorporating genetic material from other organisms. Gene editing causes a mutation within the plants own genome, without the insertion of foreign DNA (Garland, 2021). Despite this difference, the European Union has still placed restrictions on gene editing (Garland, 2021). Gene editing has been proven to be more successful and less error prone in comparison to other ways of altering the plant genome (Garland, 2021). Plant gene editing research is making progress in crop adaptation to climate change by providing crops with the necessary traits to withstand adverse climate scenarios (Garland, 2021). Not surprisingly this new technology has caused debate in terms of what is considered GMO or non-GMO (Salt, 2023). To date, most countries accept that genome-editing without the addition of foreign material is equivalent to conventional breeding methods and therefore, non-GMO. This classification comes with less restrictions on use and increased responsibility to ensure these transgenic plants do not result in their unintended release into the natural environment (Salt, 2023).

A major question being considered by crop breeders is whether genes from more successful wild species can be extracted and edited into crop genomes to reinvigorate domestic species in various ways (Mohd Hanafiah et al., 2020; Bhupenchandra et al., 2024). It somehow makes sense that weeds, which are extremely resilient to abiotic stressors, should be considered as a source of genetic material to bolster domestic crops.

3.2 Rapid Weed Evolution Under Climate Change

The story of the origin and evolution of plants known as weeds is interlinked with the development of crops, and the story continues to play out on a fairly rapid scale under climate change (Clements, Jones, 2021). Humans have attempted to reserve areas of land strictly for agricultural use to grow crops but because non-crop plants need very similar resources of light, minerals and water humans are always battling weeds adapted to persist in these systems (Bunce, Ziska, 2000; Ellstrand et al., 2010; Upadhyaya et al., 2022). The word “weed” is often used to label any plant pest that interferes with agricultural practices (Bunce, Ziska, 2000; Ellstrand et al., 2010). There

are thousands of weed species, and around 250 of these are considered agriculturally problematic. These agricultural weeds are one of the leading causes of decreased crop yields with an estimated 10% worldwide reduction in crop productivity (Vigueira et al., 2013). Weeds have evolved to inhabit agricultural ecosystems but lack intentional artificial selection pressures from humans (Neve et al., 2009; Vigueira et al., 2013). Human agricultural practices do act as selection pressures on weeds, but because these pressures are unintentional, weed evolution in agricultural fields occurs due to natural selection. Essentially, these agricultural weeds are neither wild nor domesticated having evolved alongside crop domestication; they may bear both the traits that were selectively favored in crops such as herbicide resistance and the wild traits such as seed dispersal (Vigueira et al., 2013; Matzrafi et al., 2021). Through comparing recent lineages with ancestral populations, population genetic structure patterns can be analyzed to trace the evolution of weediness.

Weedy crops represent a special case of weed evolution that is particularly relevant to the climate change race between weeds and crops. There are three major processes by which weedy crops may evolve: directly descending from the crop, hybridization between crops and wild types, and from de-domestication of crops (Ellstrand et al., 2010; Wedger, Olsen, 2018). As weeds are typically phylogenetically diverse, it is likely that in many cases weed genomes stem from multiple pathways (Vigueira et al., 2013). For example, several *Lolium* grass species that are prominent both as crops and weeds, are obligate outcrosses that are very capable of hybridization, which promotes geographic expansion in the weedy varieties (Matzrafi et al., 2021). Weedy rice is often found to have originated from a de-domestication event but is also seen hybridizing with the cultivated rice crop in certain regions (Roma-Burgos et al., 2021). The rapid evolution of weedy crops alongside cultivated crops calls for more in-depth investigation of these processes to improve crop/weed management (Arnaud et al., 2010). Successful crop and weed hybridization within cultivation fields leads to high levels of genetic diversity and increases the adaptability of populations. These weedy crops are often said to have descended from crop-wild hybrids in an adaptive evolution sense due to the selective pressures associated with crop cultivation (Arnaud et al., 2010).

In many cases, weedy crops are likely better at adapting to the stresses of climate change; through genetic modification than the crops themselves (Mohd Hanafiah et al., 2020; Bhupenchandra et al., 2024). If this is the case, we could utilize their genomic advantages for crop improvement, helping crops keep up with the weedy crops in the Red Queen climate race. As we discussed previously, technology such as CRISPR/Cas9 is a precise tool for editing crop genomes to include traits for enhanced climate adaptability (Lyzenga et al., 2021). Improvement traits are often obtained from germplasm collections however wild relatives hold a much wider range or trait variations that can be

utilized (Lyzenga et al., 2021). Genes of these wild relatives are generally ideal for CRISPR/Cas gene editing due to their simple genetic architecture (Lyzenga et al., 2021).

Another avenue of research has explored the use of CRISPR/Cas-based gene editing to accelerate domestication and value of wild relatives of cultivated crops (Lyzenga et al., 2021). The *de novo* domestication harnesses the beneficial genetic variations found among the wild relatives while using genetic modification to accelerate the domestication to have equal or better yields than the original domesticated crop (Lyzenga et al., 2021). Therefore, utilizing the weedy relatives by domesticating them instead of breeding them with our previously domesticated plants may have genuine potential.

As mentioned previously, there are at least 15 genera of crops with wild weedy relatives (Van Raamsdonk et al., 1996; Huang et al., 2017). The best studied crop weed relative, and also one of the world's most economically damaging weeds is weedy rice (Ellstrand, 2019; Mohd Hanafiah et al., 2020; Gu, 2022). Thus, research on weedy rice offers key insights into how weed evolution may possibly be utilized to develop better crops.

3.2.1 The case of weedy rice evolution

Rice is a staple that comprises 20% of human calorie intake and has been shaped by the relentless forces of evolution and human creativity (Fukagawa, Ziska, 2019). Early farmers began domesticating what was once weedy grass into what would become a key food source for the world. They domesticated the crop by gathering and eating seeds from weedy grass, promoting the planting of selected seeds, and creating the variety of rice we access today (Lyzenga et al., 2021). Traditionally rice is cultivated in paddy fields, flat land with 10 cm of water submerging the crops, proving useful in combating weeds (Fukagawa, Ziska, 2019). Through this domestication of wild rice emerged a domestication bottleneck as the persistent selection of crops with similar genes severely reduced the genetic diversity of the crop species compared to its wild relatives (Dempewolf et al., 2017).

Weedy rice, one of the world's worst weeds, is a crop mimic of cultivated rice but undergoes infructescence shattering (fruiting head) and exhibits greater dormancy compared to cultivated rice (Bunce, Ziska, 2000; Ellstrand et al., 2010; Ellstrand, 2019). Recent evidence from whole-genome resequencing supports origins from cultivated rice ancestors. These agricultural weeds have acquired traits which allow them to thrive in the changing agricultural environment; as Vigueira et al. (2013) comment, these traits can be grouped as an "agricultural weed syndrome" which favor agricultural settings in being able to compete and persist. The syndrome includes rapid growth, high nutrient use efficiency, crop mimicry, herbicide resistance and seed dormancy. These genetic traits are often evolved from the crop itself from standing variation and re-evolution through genetic mutations of alleles. In the case of the

infructescence shattering trait characteristic of weedy rice the *sh4* gene was a gene lost through domestication and it is apparent that weedy rice re-evolved a functional *sh4* gene through mutational suppression (Vigueira et al., 2013).

When this weedy rice co-occurs with rice, crop yields are reduced and due to the almost identical physiology and morphology of weedy rice, it is nearly impossible to control through chemical or physical means (Ellstrand et al., 2010). In addition to the economic costs of the weeds in these systems, as the weeds co-inhabit the crop fields their evolutionary dynamics affect the crops. Controlling weedy rice requires herbicides or further crop breeding which the surrounding weeds in turn may adapt to, in accordance with the Red Queen hypothesis, creating a cycle of crop modification and weed adaptation (Vigueira et al., 2013). Genomic studies to better understand the weedy rice genome, give clues to the driving forces of crop-weed interactions (Vigueira et al., 2013; Guo et al., 2018). This includes how the wild (weedy) rice may provide insights on how to improve crop breeding in the face of climate change (Mohd Hanafiah et al., 2020). For example, it has been shown that weedy rice may be better adapted to elevated temperatures and CO₂ levels (Ziska et al., 2012). In their review, Mahd Hanafiah et al. (2020) listed 9 different genes and/or gene families in weedy rice associated with resilience to biotic or abiotic stressors, that could be utilized in producing more climate resilient rice varieties.

3.3 Herbicide use and weed-crop evolution under climate change

Although the focus of this paper is the influence of climate change on weed-crop competition, it is important to emphasize that the evolution of weeds in agronomic situations has been strongly driven by another abiotic influence: herbicides. Herbicides represent another “Court Jester” (Barnosky, 2001) alongside climate change, and ever since World War II, the Court Jester called “Herbicides” has been doing a lot of jesting in agronomic fields throughout the world. Herbicide-resistant crops have also been produced to participate in this arms race which also represents a prominent genetic modification on the crop side. Most research on weed evolution has been focused on evolution of weeds to herbicides and the need to prevent widescale evolution of herbicide resistance (Gressel, 2009; Neve et al., 2009; Baucom, 2019; Matzrafi et al., 2021). There is no doubt we can learn much about crop-weed evolution through the lens of adaptation to herbicides. However, our focus in this paper is on climate change, so here we will confine the discussion to how climate change influences the long-running herbicide use arms race.

Considerable research has demonstrated that herbicide efficacy is affected by climate change, and in the majority of cases climate change is seen to reduce herbicide efficacy (Ziska et al., 2004; Matzrafi et al., 2016; Varanasi et al., 2016; Ziska, 2016; Matzrafi, 2019). Indeed, Waryszak et al. (2018) suggested a re-evaluation of herbicide use under elevated

CO₂ levels is warranted. Alteration of weed ecophysiology under climate change may be strongly tied to alteration of enzyme systems targeted by herbicides (Matzrafi, 2019). Higher CO₂ levels under climate change may reduce herbicide efficacy by increasing weed growth rates or belowground allocation (Patterson et al., 1999; Ziska et al., 2004). With increasing temperatures under climate change, herbicide efficacy may increase or decrease depending on particular conditions involved (Varanasi et al., 2016). On one hand, herbicides may be more rapidly absorbed or translocated at higher temperatures, but on the other hand increased evaporation of herbicides from the soil may mitigate more rapid uptake of herbicides (Kells et al., 1984; Atienza et al., 2001; Johnson, Young, 2002). Drier soil conditions can reduce absorption of herbicides by plant roots and lead to the development of thicker cuticles in weed leaves. Because drought conditions may increase cuticle thickness in weed leaves, drought conditions fostered by climate change could reduce herbicide efficacy (Olson et al., 2000; Skelton et al., 2016; Kumar, Kumar, 2017).

Because these various ways herbicide efficacy could be modified by climate change are fairly species specific, it is likely that certain weeds will come out as the winners in this climate change race between weeds and herbicide use. In fact, it has been argued that weeds that are most likely to evolve non-target site herbicide resistance are the very same weeds that are most likely to be more difficult to control when subject to changing climate (Kleinman et al., 2016; Matzrafi et al., 2016; Matzrafi, 2019). Ziska (2020) points out that although the evolution of herbicide resistance is widely recognized as an important strategic concern among weed scientists and agronomists more broadly, it is also imperative to incorporate into the equation the gathering evidence of the impacts of factors like rising CO₂, temperatures, and drought frequency on weed evolution. Although for a time glyphosate use in concert with transgenic crops resistant to glyphosate was a promising paradigm to reduce herbicide resistance and create a relatively stable weed management system, it was short-lived as glyphosate resistant weeds emerged under the tremendous selection pressure due to reliance on a single mechanism on a continental scale (Ziska, 2020). Still, it is clear that glyphosate will continue to be used extensively for some time to come despite changes in both herbicide resistance dynamics and climate, and that thorough research on various weed species and cropping systems is needed to map out the best path forward (Jabran et al., 2022).

Herbicide resistance is often facilitated by generations of weeds that can survive via soil seed banks, and another hopeful paradigm for management of herbicide resistance is harvest weed seed control. Even this paradigm is not foolproof, however. Through natural selection wild radishes (*Raphanus raphanistrum*) may alter their flowering time to evade harvest weed seed control (Sun et al., 2021). Altered flowering timing is a major adaptation to climate change as well.

Although herbicide resistance is an important and complex topic, we have just addressed it in a limited way to provide some clarity on the context of the agronomic system where climate influences act. We now turn to the potential value of learning from weed evolution to climate change, and potentially borrowing genes directly from “the enemy.”

3.4 Learning from the Red Queen: Forging New Alliances

In “Through the Looking Glass” the Red Queen is justifiably seen as an antagonistic figure but she is not all bad. In fact, she is the one who told Alice that she too could become a queen if she advanced to the end of the chessboard. As a chess queen, the Red Queen is capable of moving quickly and in all directions, unlike the lowly pawn that Alice was. This comparison in many ways parallels the comparison between weeds (Red Queen) vs. crops (Alice) in the evolutionary landscape. If crops are to be improved to be better adapted to the multifaceted threat of climate change, it then makes sense to try to learn as much as possible from the weeds. We have learned much from studying how weeds traverse the ecological filters which are comparable to the many perplexing obstacles Alice faced in her quest to advance to the final square in Lewis Carroll’s story (Figure 3). Although Alice and the Red Queen at times seem like opposites, they are both clearly human and speak the same language. Similarly, crops and weeds share the language of DNA, and in fact as we have reviewed here, many weed species share many of the same genes, with some being feral crops (e.g., weedy rice) and others receiving genes transferred from crops, such as transgenes for herbicide resistance in some cases (Warwick et al., 2008; Sohn et al., 2022). The ability of weeds to adapt quickly and even to take advantage of stolen

genes from crops represents a challenge for agriculture, but yet also an opportunity, if we can learn from weed adaptation and even use innovations found in weed genomes.

At this point in time, often referred to as the Anthropocene because of how much humanity has modified the environment and the climate (Lewis, Maslin, 2015), the weed (Red Queen) seems better equipped to deal with this brave new world than the crop (Alice). Yet crop varieties, as the contributors to the “unfinished Magnum Opus of nature” are well designed to feed us, refined a long history of careful breeding and well refined agronomic techniques (Hufford et al., 2019). Perhaps after years of crops and weeds running in parallel and in competition, it is a good time to form new alliances between the two sides, as weeds and crops both face highly restrictive ecological filters due to climate change (Figure 3). Is it too far-fetched to imagine incorporating weed genes in crops?

Many recent advances in the study of weed genomics in fact promise to identify potential weedy genes to be utilized in crop breeding (Huang et al., 2023; Montgomery et al., 2024). At the same time, the study of weed genomics lags behind that of research on genomics of other organisms, with only 32 weed genomes sequenced, which represents a much smaller effort than that accomplished for crops (Huang et al., 2023; Montgomery et al., 2024). If the value of weed genomics work for both improving weed management and crop breeding could be realized, the critical importance of weed genomics would no doubt be better appreciated.

Beyond the somewhat radical technique of inserting adaptive genes from weeds into crops, there are many other numerous ways humanity can learn from weed evolution in response to climate change. If stronger efforts could be made to better understand the adaptations weed species are

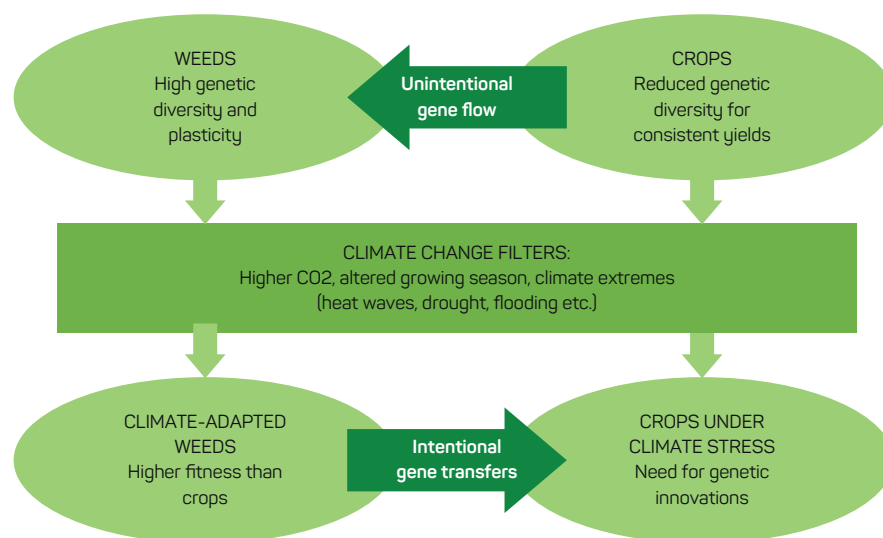


Figure 3 - Diagram illustrating the general advantage weeds have over crops in adapting to climate change and associated ecological filters such as higher carbon dioxide levels, altered growing season, and climate extremes, indicating how that while gene flow from crops to weeds is generally unintended and unwanted, there may be some value in transferring climate-adapted weed traits to crops

making to climate change through studying weed genomics and various other aspects of weed biology, there might be numerous unanticipated benefits of such research. New alliances need to be formed between weed scientists and crop breeders in order to see how agriculture may actually benefit in some ways from the weeds that have long been seen only as blights on the agricultural landscape.

4. Conclusions

With the effects of climate change on agroecosystems ever more apparent, we need to up our agricultural chess game with more evolutionary thinking. There is much at stake here with the effects of climate change continually worsening and thus climate change increasingly threatening to be the sword of Damocles for agriculture (Yu, Li, 2021; Figure 2). The reasons weeds persist are clearly tied to their ability to evolve – in fact, evolution is the driving force behind weed persistence (Neve, Caicedo, 2022).

Weedy relatives of crops, with their superior adaptability to climate change, hold genetic keys to resilience. By understanding and harnessing these traits, we can develop crops that are not just survivors but thrive in changing climates. As the human population grows our need for agricultural production equally increases, raising alarm on global food security. Using the crop wild relatives such as weedy rice may have the potential to contribute some beneficial traits for our cultivated crops. Because these wild crop relatives have not been subject to the genetic bottleneck of agricultural domestication, they contain a wide range of adaptation and habitat genes that would aid in adapting to our changing climate. Numerous wild relatives of crops such as wheat, barley, oat, maize, rice, cotton and soybean represent valuable reservoirs for increasing the genetic pools of our cultivated rice (Mammadov et al., 2018). At this point genetic modification tools are advancing rapidly and we also have gained some understanding of the genomic advantages of weedy crops. By integrating these tools and insights, we can develop crops that are more resilient to

the stresses of climate change, improving food security for future generations.

However, to further understand the co-evolution between weeds and crops, future research directions should focus on thoroughly understanding the genetic basis of weedy crop resilience and field trials to test genetically modified crops in diverse environmental conditions to evaluate performance and adaptability. It is evident that hybridization between crops and their weedy relatives can readily create problematic weeds to further intensify the agricultural arms race. This threat necessitates not just innovation, but foresight in our breeding strategies.

In conclusion, the race dictated by the Red Queen Hypothesis is not one we can opt out of, especially given the effects of the climate change crisis on agriculture at present. Instead, we must use the knowledge and technology at our disposal, from the ancient wisdom of our farming ancestors to the latest in genomic research, to ensure that our crops can keep pace in the ever-evolving challenge of agriculture. The future of our food security depends on our ability to adapt and innovate.

Author's contributions

All authors read and agreed to the published version of the manuscript. DC: conceptualization of the manuscript. DC, JB, and LM: literature review and writing.

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