



# The Impact of Polyploidization on the Evolution of Weed Species: Historical Understanding and Current Limitations

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Whole genome duplication via polyploidization is a major driver of diversification within angiosperms and it appears to confer the most benefit during times of rapid environmental change. Polyploidization offers expanded access to novel phenotypes that facilitate invasion of new environments and increased resistance to stress. These new phenotypes can arise almost immediately through the novel interactions among or between transcription factors of the duplicated genomes leading to transgressive traits, and general heterosis, or they can occur more slowly through processes like neofunctionalization, and subfunctionalization. These processes are characterized by the changes within homologs of the duplicated genomes, homoeologs. It has been proposed that redundant homoeologs are released from selective constraints and serve as an additional source of adaptive genetic variation, particularly in neo and meso-polyploids. Current practices in weed management create rapid environmental change through the use of chemicals, practices that are meant to cause the extirpation of the designated weed, and represent a strong recurrent selective event—a scenario that should favor polyploidy species. Here we ask the question, “Do polyploids make better weeds?” It is our conclusion that such a question is impossible to answer at this time due to the lack of resources and understanding in weed genomics. The growing contingent of research in weed genomics, however, driven by herbicide resistance evolution is rapidly improving our understanding of weed molecular biology and will aid in improving understanding of the impacts of ploidy levels on weed evolution and adaptation in the future.

**Keywords:** polyploidy, herbicide resistance, evolution, genomics, glyphosate, weeds

## INTRODUCTION

All extant diploid angiosperms have been traced back to polyploid ancestors (Scarpino et al., 2014). Whole genome duplications (WGDs) are major drivers of adaptation and are responsible for the trajectory of flowering plant evolution. Phylogenetic analyses and molecular dating have traced an ancient genome-wide duplication event shared by all extant seed plants (Jiao et al., 2011). Ancient whole genome duplications (WGD), served as a major force in speciation and diversification in highly plastic angiosperm genomes. Compared to gymnosperms, angiosperms are more likely to endure the impact that polyploidy has on a genome, as <5% of gymnosperms are polyploid (Leitch and Leitch, 2008). While polyploidy is gaining traction as a viable and beneficial means

of adaptation, polyploidization has previously been described and is still commonly referred to as an evolutionary “dead end,” as ancient WGD were seen scarce (Arrigo and Barker, 2012; Van De Peer et al., 2017). Polyploidy studies are continuing to rise in prevalence, and more cases of ancient and neopolyploid cases are being discovered and suggests that polyploidization via whole genome duplication is more common than previously thought (Hohmann et al., 2015; Barker et al., 2016; Yang et al., 2018). In rare instances polyploids could have had an evolutionary advantage on their non-polyploid competition, especially in times of stress or environmental upheaval, providing means to survive over their counterparts (Van De Peer et al., 2017). Recent studies provided evidence that there is an increased tolerance to genomic changes in polyploids relative to diploid progenitors, including how polyploid lineages were established and the rates at which this occurs, and the mechanisms they used to spread and maintain themselves (Schoenfelder and Fox, 2015; Shimizu-Inatsugi et al., 2017). Using a literature review and a survey of reported weeds and their ploidy level, we propose to show that polyploids make better weeds. The term weed is a generally vague description designated to virtually any plant deemed undesirable in the context of where it grows. This review focuses on the undesirable plants in an agricultural perspective that have adapted to the human condition (Harlan and de Wet, 1965). Polyploidization is especially important to understand within the study of weed science in the view of climate change and the ever-increasing size of highly managed tracts of land around the world, since both of these selective forces may favor polyploids. Here we ask if polyploidy confers an advantage in the evolution of glyphosate resistance in comparison to their diploid counterparts. Glyphosate resistance is an ideal trait to test since understanding its evolution has both practical and theoretical applications. As a herbicide it was highly effective and the evolution of target site and non-target site required decades (Pratley et al., 1999; Sammons and Gaines, 2014). Understanding if polyploidy confers an advantage in the case of glyphosate will elucidate how resistance to other herbicides will evolve and if special consideration needs to be given to polyploids in application of weed control.

## DEFINITIONS ABOUT POLYPLOIDY

Polyploids are organisms that contain multiple copies of their chromosomes, or simply, a species that has more copies than diploids (Glover et al., 2016). *Polyploidization* itself is defined as whole genome duplication, where it has doubled in the form of either *allopolyploidy* or *autopolyploidy*, or as a combination of both forms (Table 1). *Allopolyploids* are generated through the hybridization of two or more different species each contributing unique subgenomes, while *autopolyploids* arise from the duplication of a single species' genome. On a gene level, the multiple copies of genes or chromosomes in *allopolyploids* are referred to as *homoeologs*. Not to be confused with *homologs*, *homoeologs* are related genes that lie in the different subgenomes of an allopolyploid (Mason and Wendel, 2020). *Homologous genes* share a common ancestor, while *homoeologous genes* have

the same parental origin (Mable, 2003). Within homologous genes, there are *orthologs* and *paralogs*: *orthologs* are genes descended from a common ancestor in different species that share the same function or formed due to a speciation event. *Paralogs* are genes derived from a single gene as the result of a duplication event (Sonnhammer and Koonin, 2002). *Homoeologs* and *orthologs* can be construed as analogous, as *homoeologs* are orthologous genes within a polyploid species that occur on different subgenomes. *Homoeologs* originated through speciation and were recombined in the same genome through *allopolyploidization* (Glover et al., 2016). The correct usage of “homoeolog” has been debated and the sheer amount of different terms can lead to some confusion.

*Paleopolyploidy* is defined as polyploidy that occurred millions of years ago (Blanc and Wolfe, 2004; Soltis et al., 2009). Genes associated with *paleopolyploidy* can also be referred to as *paleologs*. Determining whether an organism is a *paleopolyploid* or used to be a difficult task because progenitor species could not be identified through cytological tools or DNA markers (Levy and Feldman, 2002). Advances in genomics has eased the process of identification with whole genome assemblies providing the necessary data for synteny plots, gene trees constructed from gene family analyses, and Ks plots from transcriptome assemblies (Husemann and Stoye, 2009; Gao et al., 2018; Leebens-Mack et al., 2019). More recent polyploids have two different categories: *mesopolyploid*, if formed within the last 17 million years, or *neopolyploids* for the species that most recently experienced polyploidization (Ramsey and Schemske, 2002; Cheng et al., 2018). *Neopolyploidy* can also be described as a species that has experienced an artificially induced chromosome duplication (Comai, 2005). *Aneuploidy* is another term associated with polyploidy, as it signifies when there is an abnormal number of chromosomes compared to the wild type, which is commonly found in triploid (and sometimes pentaploid) populations (Müntzing, 1936; Huettel et al., 2008).

## HISTORY OF POLYPLOID EVOLUTION

The earliest concepts of polyploidy came about in the early 1900s. The independent rediscovery of Mendel's work by de Vries, Correns, and Tschermak was the beginning of a golden age of genetics (Corcos and Monaghan, 1990). Geneticists originally associated specific characteristics with morphological characteristics as opposed to genetic characteristics like karyotype (DeVries, 1915; Ramsey and Ramsey, 2014). Using morphological characteristics as a form identification was soon displaced by the acceptance of chromosomes as hereditary units (Roberts, 1929). While certain plants, like maize, had already been determined to be polyploid (Kuwada, 1911), the term polyploidy was coined by Winkler (1917), who created the first artificial polyploid. Winge (1917) had some of the most influential thoughts on the subject, proposing hybridization followed by the doubling of chromosomes (Harlan and De Wet, 1975; Soltis et al., 2014). Stebbins (1950) could be considered one of the most important thinkers on the importance of polyploidy, with fourteen chapters in his book *Variation and Evolution in*

**TABLE 1** | Important terms relating to polyploidy and their definitions.

Term	Definition	References
Polyploidy	Condition where an organism contains more than two sets of homologous chromosomes, or more than a diploid, as a result of whole genome duplications	Glover et al., 2016
Allopolyploidy	Polyploidy generated through hybridization between two distinct species followed by genome doubling	Glover et al., 2016
Autopolyploidy	Polyploidy generated through intraspecific hybridization	Glover et al., 2016
Homolog	A gene in two species that are derived from the same ancestor	Mable, 2003
Ortholog	A homologous gene within two species that share the same function, formed as a result of a speciation event	Sonnhammer and Koonin, 2002
Paralog	A homologous gene within the same species that do not have the same function, formed as a result of a duplication event	Sonnhammer and Koonin, 2002
Homoeolog	Genes that originated due to a speciation event but were recombined due to allopolyploidization	Glover et al., 2016; Mason and Wendel, 2020
Paleopolyploidy	Ancient polyploidy, formed millions of years ago	Blanc and Wolfe, 2004; Soltis et al., 2009
Neopolyploidy	The most recent cases of polyploidy, can be used to describe artificially created polyploids	Ramsey and Schemske, 2002; Comai, 2005
Mesopolyploidy	Bridge between paleo and neopolyploidy, has occurred within the last 17 million years	Cheng et al., 2018
Aneuploidy	Situation where there is an abnormal number of chromosomes in a cell	Müntzing, 1936; Huettel et al., 2008
Subfunctionalization	Process where newly formed genes will retain some subset of the ancestral gene function	Force et al., 1999; Flagel et al., 2008
Neofunctionalization	Process where newly formed genes will obtain some new function	Force et al., 1999
Target site resistance	Herbicide resistance mechanism that is the result of a change to the genetic code	Sammons and Gaines, 2014
Non-target site resistance	Herbicide resistance mechanism that is a result of a change in the metabolism of a plant	Sammons and Gaines, 2014

*Plants* dedicated to the subject. Scientists were tasked with the painstaking endeavor of manually counting chromosomes under a microscope using the squash method, until the genomics era eventually brought about flow cytometry, a more accurate way to measure cellular contents, including DNA and chromosomes (Kron et al., 2007; Windham et al., 2020).

Much of what is understood about the history of polyploidization has come from studying crops (Beasley, 1940; McFadden and Sears, 1946). Thus far, genomic studies on *Triticum* (wheat) and *Gossypium* (cotton) have contributed the most to the current knowledge (Flagel et al., 2008; Moshe Feldman and Levy, 2009). Cultivated wheat is a good example of how studying polyploidization can be useful. Cultivated wheat is classified in three different cytogenic categories: diploid, tetraploid, and hexaploid. While the wild type progenitors for the diploid and tetraploid varieties have been determined, studies have shown that the hexaploidy varieties, like bread wheat (*T. aestivum*) have formed as a byproduct of cultivated tetraploid and wild diploid progenitors as a result of polyploidization (Feldman, 2001; Feldman and Levy, 2005). In allohexaploid bread wheat, there are three identifiable subgenomes, A, B, and D, which is seen as an AABBDD genome. These subgenomes are known to have derived from diploid progenitors *T. uratu* (AA) and *Aegilops tauschii* (DD). The progenitor of the BB subgenome is extinct, but is likely derived from a diploid closely related to *Aegilops speltoides* (Dubcovsky and Dvorak, 2007; Gornicki et al., 2014). The ability to identify these subgenomes provides a

history of polyploidization in wheat, visualizing its progenitors, its center of origin (likely in southwest Asia), and estimating when the polyploidization likely occurred (Vavilov and Love, 1992; Feldman, 2001).

Polyploidization is a seemingly irreversible process, but all polyploid plants eventually undergo the process of diploidization. The process of a polyploid becoming a diploid again is a result of *genomic downsizing*, where genomes have been significantly reduced as a result of loss of DNA fragments, segmental DNA loss, and gene silencing, mainly to stabilize the genome (Wendel and Adams, 2005; Bird et al., 2019). Genomic downsizing most likely occurs immediately following a chromosomal duplication event. Drastic alterations to the genome are referred to as *genome shock*; a plant might not be prepared for such intense changes to its genome and these stabilization events could possibly occur to counteract the shock (McClintock, 1983). There is a case to be made that there are no true extant diploids, and should be considered to be paleopolyploids (Levy and Feldman, 2002). Combined with the fact that all diploid angiosperms are descended from polyploid ancestors, genomic downsizing over the course of millions of years could contribute to this claim (Force et al., 1999; Feldman and Levy, 2005). An example of this is present in corn (*Zea mays*); it has paleopolyploid characteristics and has origins as a segmental allopolyploid, but its genome was so drastically altered and silenced that it is a cytogenic diploid (Gaut and Doebley, 1997; Soltis and Soltis, 1999).

Duplicate genes in polyploids have many different pathways they can take: they can develop a new function (*neofunctionalization*), retain the ancestral function (*subfunctionalization*), or accumulate deleterious mutations and decay (Force et al., 1999). In the process of trying to maintain its status as a diploid, some plants will undergo the process of *instantaneous subfunctionalization*, which occurs immediately following genomic merger in order to retain all duplicate genes (Flagel et al., 2008). Different loss-of-function mutations can develop in both copies, but both copies must be retained in order to keep its ancestral function (Cheng et al., 2018). Upland cotton (*Gossypium hirsutum*) demonstrates subfunctionalization in the reciprocal silencing of its *adhA* homoeolog; the homoeolog is silenced rather than deleted, retaining all copies present (Adams et al., 2003). Larger populations are more likely to experience neofunctionalization rather than subfunctionalization because the genetic drift in large populations is going to be so slow that parental alleles are likely going to be silenced by deleterious mutations before fixation can occur (Soltis et al., 2010).

## ADVANTAGES OF POLYPLOIDY IN EVOLUTION

Polyploidization allows organisms to react and survive; by their very nature, polyploids have a much higher range of genetic diversity than diploids, which certain environmental factors, such as habitat disturbance, nutritional stress, physical stress, and climate changes, can trigger new phenotypes, like increased allelopathic effect (Hegarty and Hiscock, 2007; Ramsey, 2011; Te Beest et al., 2012; Omezzine et al., 2017). New phenotypes may arise through heterosis, gene redundancy, or the formation of transgressive traits (Comai, 2005; McCarthy et al., 2016; Wei et al., 2019). The effects of heterosis was first identified by Darwin, whose experimental crosses resulted in more vigorous hybrids, i.e., heterosis (Darwin, 1876). There are two main models involved in heterosis: the dominance model and overdominance model. The dominance model hypothesizes that the slightly deleterious recessive alleles are complemented by superior dominant ones in hybrids (Hochholdinger and Baldauf, 2018). The overdominance model is used to describe polyploidization, as the progressive heterosis associated with polyploids is more complex due to the increasing vigor with increasing number of genomes (Birchler et al., 2010). While heterosis generally results in polyploids with better phenotypic performance than its parent species, plants with transgressive traits display extreme phenotypes outside of the range of its progenitors (McCarthy et al., 2016). Heterosis and transgressive traits have been shown to be potential improvements for epigenetic mechanisms in allopolyploids, like histone modification or cytosine methylation (Renny-Byfield and Wendel, 2014). Gene redundancy acts as a protective feature, shielding polyploids from the effects of deleterious mutations with the numerous copies present (Wendel, 2000). Even allelopathy (the ability to suppress growth in another plant), which is present in both diploids and polyploids, has been shown to increase in polyploids compared to diploids (Colquhoun, 2006; Omezzine

et al., 2017). Hexaploid barnyardgrass (*Echinochloa crus-galli*) shows considerable allelopathic tendencies and Omezzine et al. (2017) was able to show that allelopathy increased as ploidy increased in fenugreek (*Trigonella foenum-graecum*) (Omezzine et al., 2017).

Allopolyploids provide some evidence of increased fitness over their progenitors. When diploid parents are crossed, typically their offspring have an increase in performance; polyploids produced more viable seed in extreme heat and drought conditions and differences in stomatal pore sizes that improved drought survival over their diploids counterparts (Madlung, 2013; Godfree et al., 2017). For example, cultivated wheat (*T. aestivum*) is an allohexaploid that has managed to survive over its B genome donor (Feldman and Levy, 2009). Allopolyploids also have more potential for ecological adaptation over their diploid counterparts, as shown through diploid and allopolyploid species of *Cardamine*; while different diploid species had a tendency to prefer only one environment, the allopolyploid species was able to grow and survive in all the environments tested (Shimizu-Inatsugi et al., 2017). The ability to alter phenotypes, as in functional trait divergence or generalized trait plasticity is one of the leading hypotheses regarding overall increased fitness in polyploid species (Van De Peer et al., 2017; Wei et al., 2019). Polyploid crops have huge adaptation potential and further studies are necessary to show the role of genetic variation resulting from polyploidy in this potential (Ramsey and Ramsey, 2014; Schiessl et al., 2017).

The study of neopolyploids furnishes strong insights in the evolution of polyploid species. *Spartina anglica* (common cordgrass), is an invasive neoallopolyploid weed species that arose in the last 200 years (Baumel et al., 2002). The neododecaploid weed arose at the end of the nineteenth century as a result of a genome duplication between the already hybrid species *Spartina X townsendii*, which is a cross between hexaploids *Spartina alterniflora* and *Spartina maritima* (Ainouche et al., 2004). The duplication of the two unique subgenomes in *Spartina X townsendii* cements *S. anglica* as an allopolyploid as opposed to an autopolyploid. Compared to its progenitors, *S. anglica* has been shown to have increased fitness with its prolific seed production, fertility, and extensive lateral clonal growth, which was not seen in its sterile progenitor *Spartina X townsendii*. Baumel et al. (2002) was able to demonstrate that rapid, non-Mendelian changes involving preferential sequence elimination or modification of methylation patterns may occur in the earliest stages of polyploid stabilization. Other neopolyploids, like *Senecio* and *Tragopogon* have also been established within the last 200 years (Abbott and Lowe, 2004; Soltis et al., 2004). The development new polyploids aids in understanding gene silencing, cytosine methylation, and parental “non-additivity” play an active role in polyploidization and improving overall understanding of the process (Adams and Wendel, 2005).

## WEEDS AND UNCONSCIOUS SELECTION

Aside from polyploidy, one way weeds have been able to thrive in a world that strives to exterminate them is through unconscious

selection, or actively breeding plants in an environment different from their wild habitat, usually human-made (Zohary, 2004). Crops once considered weeds have been domesticated through *unconscious selection*, as they could not be differentiated from the crop they were growing alongside. The phenomenon of weeds imitating desired crops was noticed and thoroughly discussed by Nikolai Vavilov, who covered the process in “Origin and Geography of Cultivated Plants” (Vavilov, 1922). Vavilov looked into the centers of origins of crops, determining that there is more diversity in a species in an area where a species originated (McElroy, 2014). The process of an undesirable species evolving to mimic desirable ones as a means of survival has become known as *Vavilovian mimicry* (Pasteur, 1982). This phenomenon was first noticed, and well-established, between rye (*Secale cereale*) and wheat (*Triticum*) (Vavilov, 1922).

Before the time of chemical management, the only way to eliminate weeds when harvesting was by hand or hand-held implements. Since rye is remarkably visually similar to wheat, farmers often could not differentiate the two. When harvesting, rye would be selected for alongside the wheat, and when the harvested seed was replanted, unwanted rye would grow as well. Eventually, rye evolving alongside a desirable crop made it desirable as well. Rye could also perform better in colder climates than weaker wheat species did, but its increased fitness could possibly be contributed to crossing between the weed species and the crop it grew alongside (Harlan, 1965). This same principle of mimicry can be applied to modern day crop and companion weeds with cultivated rice (*Oryza*) and barnyardgrass (*Echinochloa crus-galli*, specifically ssp. *oryzicola*). In the seedling stage, barnyardgrass growing in paddy fields are virtually indistinguishable from rice, which makes manual weeding extremely difficult (Barrett, 1983). Barnyardgrass has also demonstrated allelopathetic tendencies in rice paddies, which provides even more difficulty in its management (Khanh et al., 2007; Guo et al., 2017)?

Another subset of Vavilovian mimicry is *seed mimicry*, where weeds may or may not look morphologically similar to the crop they contaminate, but the seeds produced by both crop and weed are identical in size and shape. While this might not be a problem when weeding by hand, but once mechanical winnowing came into play, the weed seeds only need to trick the machine (Harlan, 1982). An example of this is evident between balloonvine (*Cardiospermum halicacabum*) and soybean (*Glycine max*), which are morphologically dissimilar, however their seeds are indistinguishable in size and shape by a machine, which aids in the weed survival (Johnston et al., 1979). One final way weeds are unconsciously selected is through genetic mimicry. As weeds continue to grow, it is likely that they will develop herbicide resistance as an adaptation to human management practices.

As chemical herbicides became the primary weed management practice, herbicide resistance developed as the weed's survival mechanism. The more herbicides are continuously sprayed on crops, the more likely resistance to such herbicides will result in those weeds (Powles and Yu, 2010). Gene flow works in both ways; crops and weeds don't grow independently, genetic material can be shared between them, which is what leads to hybridization between the two (Harlan

and De Wet, 1975; Gould, 1991). While unconscious selection plays a major role in basically how all weeds are bred, the real question is are polyploids the better weed? Do more polyploids exhibit characteristics of Vavilovian mimicry within the genetic subset? Before we answer these questions, it is important to look further into modern day weed management practices, specifically regarding herbicide and the effect it has on crops and weeds in general.

## HERBICIDE RESISTANCE

In this modern era, herbicide resistance is the biggest problem currently faced with weeds. The two types of herbicide resistance typically dealt with are target site resistance (TSR) and non-target site resistance (NTSR). TSR develops directly against a mode of action, specifically as a mutation to the genetic code, as a single nucleotide polymorphism (SNP). NTSR relates to metabolism, as there are no direct changes to the genetic code (Sammons and Gaines, 2014). This can be seen as reduced absorption, translocation, or sequestration of the herbicide in the vacuole (Powles and Yu, 2010). To simplify our analysis of the effect of polyploidization on the formation of herbicide resistance traits, we have chosen to focus on well-described TSR mechanisms, specifically the glyphosate mechanism. Target site resistance provides a stronger case for increased weed survivability in polyploids, as multiple chromosome copies alone provide an environment for mutations to occur in at least one copy, and if that copy is expressed resistance should occur (Otto, 2007).

Polyploids develop glyphosate resistance at a faster rate than their diploid relatives. Glyphosate was first introduced by Monsanto in 1974 with the trade name “Roundup” and in the last decade has become the most used herbicide worldwide. It is a non-selective herbicide that targets the shikimic acid pathway and its ability produce folates and aromatic amino acids (Malik et al., 1989; Valavanidis, 2018). Target site resistance in glyphosate resistant plants results in mutations at the Pro106 location to either Thr, Leu, Ser, Ala, or a double substitution of Thr102 to Ile + Pro106 to Ser (TIPS) (Yu et al., 2015). With the introduction of Roundup Ready® (RR) crops as a staple in crop production, gene flow from RR crops has the potential to result in glyphosate resistant weeds, which presents a major problem for weed management (Mallory-Smith and Zapiola, 2008). Based on data from weedscience.org, weedy polyploid species like annual bluegrass (*Poa annua*), oat (*Avena*), junglerice (*Echinochloa colona*), and barnyardgrass (*Echinochloa crus-galli*) are just a few of the species reported resistant to glyphosate (Heap, 2019).

## SHOULD POLYPLOID SPECIES SHOULD MAKE BETTER WEEDS AND BE MORE COMMON WITH HERBICIDE RESISTANCE?

Theoretically, target site resistance should be more common in polyploid weeds, since theoretically polyploids have a more flexible expression profile that allows them to silence adaptive

**TABLE 2 |** Weed species currently (9 June 2020) reported as resistant to glyphosate according to The International Survey of Herbicide Resistant Weeds and corresponding reported genomic data.

Family	Common name	Species	Chromosome number (2n)	Ploidy	1C (Mbp)	Glyphosate Resistant	TSR	NTSR	Genome	References
Amaranthaceae	Palmer amaranth	<i>Amaranthus palmeri</i> <sup>1</sup>	32	?	465	Yes	?	Yes	No	Gaines et al., 2011
Amaranthaceae	Spiny amaranth	<i>Amaranthus spinosus</i> <sup>1</sup>	34	2X	929	Yes	Yes	Maybe	No	Nandula et al., 2014
Amaranthaceae	Tall waterhemp	<i>Amaranthus tuberculatus</i> (syn. <i>rudis</i> ) <sup>1</sup>	32	?	701	Yes	Yes	Yes	Yes	Nandula et al., 2013
Amaranthaceae	Smooth pigweed	<i>Amaranthus hybridus</i> (syn: <i>quitensis</i> )	?	?	686	Yes	Yes	Yes	No	Perotti et al., 2019
Amaranthaceae	Kochia	<i>Kochia scoparia</i>	18	2X	1095	Yes	Yes	Maybe	No	Wiersma et al., 2015
Asteraceae	Common ragweed	<i>Ambrosia artemisiifolia</i> <sup>1</sup>	36	4X	1134	Yes	?	?	No	Ganie and Jhala, 2017
Asteraceae	Giant ragweed	<i>Ambrosia trifida</i> <sup>1</sup>	24	2X	1868	Yes	?	?	No	Norsworthy et al., 2010
Asteraceae	Hairy fleabane	<i>Conyza bonariensis</i>	18	?	2043	Yes	?	Yes	No	Kleinman and Rubin, 2017
Asteraceae	Horseweed	<i>Conyza canadensis</i>	18	2X	440	Yes	Yes	?	Yes	Beres et al., 2020
Asteraceae	Sumatran fleabane	<i>Conyza sumatrensis</i>	54	?	?	Yes	?	?	No	Santos et al., 2014
Asteraceae	Hairy beggarticks	<i>Bidens pilosa</i>	72	?	1666	Yes	Yes	Yes	No	Alcántara-de la Cruz et al., 2016
Asteraceae	Greater beggarticks	<i>Bidens subalternans</i>	48	?	2915	Yes	Yes	?	No	Takano et al., 2020
Asteraceae	Plumeless thistle	<i>Carduus acanthoides</i>	22	?	?	Yes*	?	?	No	Heap, 2019
Asteraceae	Ragweed parthenium	<i>Parthenium hysterophorus</i>	34	?	?	Yes	Yes	Yes	No	Bracamonte et al., 2016
Asteraceae	Common sunflower	<i>Helianthus annuus</i>	34	2X	3596	Yes	No	Yes	Yes	Singh et al., 2020
Asteraceae	Willow-leaved lettuce	<i>Lactuca saligna</i>	18	2X	2332	Yes	?	?	Yes	Amjad et al., 2018
Asteraceae	Prickly lettuce	<i>Lactuca serriola</i>	18	?	(likely 2) 2606	Yes*	?	?	No	Heap, 2019
Asteraceae	Annual sowthistle	<i>Sonchus oleraceus</i>	32	4X	1568	Yes	?	?	No	Cook et al., 2014
Asteraceae	Russian thistle	<i>Salsola tragus</i>	36	?	?	Yes	?	?	Yes**	Kumar et al., 2017
Asteraceae	Coat buttons	<i>Tridax procumbens</i>	36	?	?	Yes	Yes	No	No	Li et al., 2018
Poaceae	Wild oat	<i>Avena fatua</i>	42	6X	12,646	Yes*	?	?	No	Heap, 2019
Poaceae	Sterile oat	<i>Avena sterilis</i> ssp. <i>ludoviciana</i>	42	6X	12,617	Yes	?	Yes	No	Fernández-Moreno et al., 2016
Poaceae	Australian fingergrass	<i>Chloris truncate</i>	40	?	?	Yes	No	Yes	No	Ngo et al., 2018b
Poaceae	Tall windmill grass	<i>Chloris elata</i>	?	?	?	Yes	No	Yes	No	Brunharo et al., 2016
Poaceae	Radiate fingergrass	<i>Chloris radiata</i>	40	?	?	Yes*	?	?	No	Heap, 2019
Poaceae	Feather fingergrass	<i>Chloris virgate</i>	20	?	?	Yes	Yes	No	Yes**	Ngo et al., 2018a
Poaceae	Sweet summer grass	<i>Brachiaria eruciformis</i>	18	?	?	Yes*	?	?	No	Heap, 2019
Poaceae	Ripgut brome	<i>Bromus diandrus</i>	56	8X	11687	Yes	No	Yes	No	Malone et al., 2016
Poaceae	Rescuegrass	<i>Bromus catharticus</i>	42	?	?	Yes*	?	?	No	Heap, 2019
Poaceae	Red brome	<i>Bromus rubens</i>	28	4X	4802	Yes?	?	?	No	Heap, 2019
Poaceae	Gramilla mansa	<i>Cynodon hirsutus</i>	?	?	?	Yes?	?	?	No	Heap, 2019
Poaceae	Sourgrass	<i>Digitaria insularis</i>	36	?	?	Yes*	?	Yes	No	Lopez Ovejero et al., 2017
Poaceae	Junglerice	<i>Echinochloa colona</i>	54	?	1320	Yes	Yes	Yes	No	Alarcón-Reverte et al., 2015
Poaceae	Barnyardgrass	<i>Echinochloa crus-galli</i>	54	?	1372	Yes*	?	?	Yes	Heap, 2019
Poaceae	Goosegrass	<i>Eleusine indica</i>	20	2X	709	Yes	Yes	No	Yes	Yu et al., 2015
Poaceae	Tropical sprangletop	<i>Leptochloa virgata</i>	40	?	?	Yes	Yes	Yes	Yes	Alcántara-de la Cruz et al., 2016

(Continued)

**TABLE 2 |** Continued

Family	Common name	Species	Chromosome number (2n)	Ploidy	1C (Mbp)	Glyphosate Resistant	TSR	NTSR	Genome	References
Poaceae	Annual ryegrass	<i>Lolium multiflorum</i>	14	2X	2661	Yes	Yes	No	No	Jasieniuk et al., 2008
Poaceae	Perennial ryegrass	<i>Lolium perenne</i>	14	2X	2695	Yes	Yes	Yes	Yes	Yang et al., 2018
Poaceae	Rigid ryegrass	<i>Lolium rigidum</i>	14	2X	2687	Yes	Yes	Yes	No	Pratley et al., 1999
Poaceae	Smooth barley	<i>Hordeum murinum</i> ssp. Glaucum	14	2X	5390	Yes*	?	?	No	Heap, 2019
Poaceae	Annual bluegrass	<i>Poa annua</i>	28	4X	2812	Yes	Yes	No	No	Cross et al., 2015
Poaceae	Johnsongrass	<i>Sorghum halapense</i>	40	?(sus. 4)	1614	Yes	No	Yes	No	Vila-Aiub et al., 2012
Poaceae	Liverseedgrass	<i>Urochloa panicoides</i>	44	?	?	Yes*	?	?	No	Heap, 2019
Poaceae	Arrochillo	<i>Paspalum paniculatum</i>	20	?	?	Yes*	?	?	Yes**	Heap, 2019
Plantaginaceae	Buckhorn plantain	<i>Plantago lanceolata</i>	12	2X	1174	Yes*	?	?	No	Heap, 2019
Brassicaceae	Birdsrape mustard	<i>Brassica rapa</i> syn campestris	20	2X	784	Yes*	?	?	Yes	Heap, 2019
Brassicaceae	Wild radish	<i>Raphanus raphanistrum</i>	18	?	?	Yes	?	?	Yes	Ashworth et al., 2014
Rubiaceae	Woody borreria	<i>Hedyotis verticillata</i>	?	?	?	Yes	?	?	No	Chuah et al., 2005

\*Indicates that there was no paper associated with the article, just reported on weedscience.org (Heap, 2019).

? indicates that there was no data available for that column.

\*\*Indicates that there is only a partial genome present.

**TABLE 3 |** Ploidy and glyphosate resistance status of the world's worst weeds as described by Holm and Herberger (1969), Holm et al. (1977).

Common name	Scientific name	Ploidy	Glyphosate resistant?
<b>1969</b>			
Purple nutsedge	<i>Cyperus rotundus</i>	?	No
Bermudagrass	<i>Cynodon dactylon</i>	6X	No
Barnyardgrass	<i>Echinochloa crus-galli</i>	6X?	Yes
Junglerice	<i>Echinochloa colona</i>	?	Yes
Goosegrass	<i>Eleusine indica</i>	2X	Yes
johnsongrass	<i>Sorghum halapense</i>	4X?	Yes
Cogongrass	<i>Imperata cylindrical</i>	2X?	No
Water hyacinth	<i>Eichhornia crassipes</i>	4X	No
Purslane	<i>Portulaca oleracea</i>	?(mixed)	No
Common lambsquarter	<i>Chenopodium album</i>	2X	No
<b>1977</b>			
Purple nutsedge	<i>Cyperus rotundus</i>	?	No
Bermudagrass	<i>Cynodon dactylon</i>	6X	No
Barnyardgrass	<i>Echinochloa crus-galli</i>	6X?	Yes
Junglerice	<i>Echinochloa colona</i>	?	Yes
Goosegrass	<i>Eleusine indica</i>	2X	Yes
Johnsongrass	<i>Sorghum halapense</i>	4X?	Yes
Cogongrass	<i>Imperata cylindrical</i>	2X?	No
Spiny amaranth	<i>Amaranthus spinosus</i>	2X	Yes
Sour paspalum	<i>Paspalum conjugatum</i>	2X?	No
Tropic ageratum	<i>Ageratum conyzoides</i>	?(mixed)	No

? Indicates that the data was not available.

alleles or loci with fitness costs when the allele offers no adaptive advantage (Otto and Whitton, 2000; Otto, 2007). TSR fitness costs have been identified, but the level of costs varies among

different plant species (Vila-Aiub et al., 2009) and modes of action. In general, fitness costs have been associated with ALS, ACCase, and photosystem II (PSII) herbicides, which is especially evident in PSII herbicides because of the reduced photosynthetic capacity (Jansen and Pfister, 1990). Fitness costs in ACCase inhibitors should have no association with polyploidy because ACCase inhibitors only affect the plastid isoform (Murphy and Tranel, 2019). Glyphosate's role as the most widely used herbicide provides the lens for the focus of herbicide resistance in polyploids compared to other herbicides due to the possibility of both target and non-target-site resistance. Studies have shown that herbicide resistance alleles do not universally endow some type of fitness cost, but there is more of a cost in diploid species over polyploid (Vila-Aiub et al., 2009; Yanniccari et al., 2016). A reduction in fitness has been identified in glyphosate resistant goosegrass (*Eleusine indica*), rigid ryegrass (*Lolium rigidum*), and perennial ryegrass (*Lolium perenne*) (Preston et al., 2009; Yanniccari et al., 2016; Han et al., 2017). However, fitness costs in glyphosate resistant biotypes seem to be present on a case-by-case basis. The TIPS double mutation in the *E. indica* population came at a very high resistance cost, resistant *L. rigidum* populations may or may not have a fitness penalty, depending on the resistance allele present, and the fitness cost in *L. perenne* is not associated with a target-site mutation, but rather high EPSPS activity. The Pro-106-Ser mutation, the most common target-site in glyphosate resistant biotypes, endows a low-level glyphosate resistance and is seemingly negligible in fitness costs compared to mutations endowing high level resistance, like the TIPS mutation (Vila-Aiub et al., 2019). There has been no investigation comparing the fitness cost of herbicide resistant polyploid species to the cost seen in diploid species, or even delving into the costs of herbicide resistance in any polyploid species. While there have been reviews showing the fitness costs of different herbicides,

all data and conclusions are drawn from diploid species (Vila-Aiub et al., 2009). More studies should be performed in order to ascertain whether polyploidy plays a role in reduced fitness in association with herbicide resistance.

In order to examine how polyploidy affects weed survival, a survey of weeds was done on those reported as glyphosate resistant (Heap, 2019). A list of weeds reported as glyphosate resistant was assembled and the polyploidy, chromosome counts, and C-values were compared in **Table 2**. Out of 48 species selected, 12 are known to be diploid, four tetraploid, two hexaploid, one octoploid, and the remaining 29 species have a ploidy level that has not been confirmed, based on data from the Kew C-value database and the Chromosome Counts Database (Rice et al., 2015; Pellicer and Leitch, 2020). A few assumptions can be drawn about the species with unconfirmed ploidy: they could be diploid, polyploid, or have mixed ploidy, but thus far no studies have been done to confirm their ploidy. Ploidy determination is just one part of a bigger issue; according to the genome database from NCBI, out of the 48 species surveyed, only nine have fully sequenced genomes and two have RefSeq genomes. So along with the fact that there is little to no data to draw conclusions from, the majority of studies reporting glyphosate resistant are lacking in research beyond spray trials. Target site resistance should be considered a major factor for resistance and studies that just ignore the benefits of sequencing data can be detrimental. When sequencing data is in play, one can more accurately confirm TSR or NTSR, rather than just claiming NTSR.

## BUT, DO POLYPLOIDS MAKE BETTER WEEDS?

Two questions need to be asked: “Are polyploids better weeds?” and “Are polyploids more likely to be resistant to herbicides?” The weeds historically referred to as the “world’s worst weeds,” has had relatively no changes, or at least no reported changes, to this list since first reported in 1969, and last updated in 1977 (referenced in **Table 3**) (Holm and Herberger, 1969; Holm et al., 1977). Based on data from the Plant C-Value database and the International Herbicide-Resistant Weed database, little can be determined whether ploidy or glyphosate resistance has any determining factor on what makes a better weed (Heap, 2019; Pellicer and Leitch, 2020). Barnyardgrass (*E. crus-galli*), which is known to be glyphosate resistant, a possibly hexaploid weed, would support the case for polyploidy providing better weeds; barnyardgrass has easily adapted to human activity, along with other polyploids like rye (*S. cereale*) and annual bluegrass (*Poa annua*) (Ye et al., 2014; Cross et al., 2015). A case could also be supported with the glyphosate resistant diploid species goosegrass (*Eleusine indica*), as there is a fitness cost associated with the double EPSPS gene mutation TIPS endowing glyphosate resistance (Han et al., 2017). Polyploids have adapted and survived due to polygenic selection over millennia (Stebbins, 1950). Comparatively herbicide resistance, both TSR and NTSR, is more often than not monogenic: this can be seen as a divergent single nucleotide polymorphism (SNP), a single unregulated

metabolic enzyme, or even as a widely duplicated gene (Délye, 2013; Jugulam and Shyam, 2019).

Applying what is known about polyploidization in crops to weeds, one could try to assume an advantage for polyploid weeds. Factors that favor polyploid crop domestication should translate over to polyploid weed species. Heterosis, gene redundancy, and high genetic variability discussed above should act the same in weeds as they do in crops. Even in older, more established polyploid populations, you can see the benefit compared to diploids. Studies have shown that polyploids in general have the capacity to be more invasive over diploid species. Stevens et al. (2020) showed that tetraploid seeds tended to be larger than those of diploids, which contributed to tetraploid seeds being more dormant than the diploid seeds, less likely to germinate in stressful environments and therefore better adapted to said environments. Polyploid species have also been found to be more fecund and competitive than diploids, as seen in studies done with spotted knapweed (*Centaurea stoebe*) (Broz et al., 2009; Rosche et al., 2017). Studies on the three geo-cytotypes of *C. stoebe*, a native Eurasian diploid, a native Eurasian tetraploid, and an introduced North American tetraploid provided evidence that the polycarpic nature of the tetraploid biotypes allowed these biotypes to survive after the initial flowering and flower more than the monocarpic diploid biotype, and the introduced biotype even more than the native (Broz et al., 2009). Pandit et al. (2011) showed in an extensive study on rarity and invasiveness that diploid plants were more likely to be rare, while polyploids were more likely to be invasive. It has also been determined that polyploid species are less likely to experience inbreeding depression, due to the balancing effect of the presence of multiple gene copies (Rosche et al., 2017). The combination of higher seedling growth rates and diminished inbreeding depression creates an argument that polyploids are more invasive and therefore more competitive than diploids. Annual bluegrass (*P. annua*) has established itself on every continent and barnyardgrass continue to invade rice paddies, and when combined with the likelihood for developing herbicide resistance, namely glyphosate resistance, it creates some formidable weed species. And as mentioned before, there is even evidence that target site resistance in diploid plants significantly reduces fitness levels (Preston et al., 2009; Yanniccari et al., 2016; Han et al., 2017).

However, there are currently more reported diploid species resistant to glyphosate than there are polyploid. There are diploid species that are considered to be some of the most widespread and difficult weed species to manage, like smooth pigweed (*Amaranthus hybridus*) and horseweed (*Conyza canadensis*), that have high levels of glyphosate resistance with no fitness cost reported (Beres et al., 2018, 2020; Perotti et al., 2019). Purple nutsedge (*Cyperus rotundus*) and yellow nutsedge (*Cyperus esculentus*), whose ploidy levels (according to the Plant C-Value database) have not been reported, are considered some of the worst weeds on the planet because of control difficulty (Pereira et al., 1987; Arias et al., 2011; Pellicer and Leitch, 2020). And although its ploidy has, surprisingly, not yet been reported, Palmer amaranth (*Amaranthus palmeri*), is increasing one of the most difficult weeds to control (Rayburn et al.,



2005; Gaines et al., 2011). Such fitness costs have not yet been reported in polyploid species and further investigation is required to determine if herbicide resistance has any negative effects in polyploids.

The sheer magnitude and complexity of polyploid genomes makes it difficult to perform large-scale genetics studies (Schuessl et al., 2017). While there have been polyploid genomes fully sequenced, the genomes sequenced have been relatively small, genome size wise, outside of the massive undertaking of sequencing the allohexaploid wheat genome (Zimin et al., 2017). Advances in genomics has made whole genome sequencing easier and cheaper as a whole, but it improving the possibility of sequencing polyploid genomes. Despite this, barnyardgrass remains the only polyploid weed genome sequenced (Kyriakidou et al., 2018). There is an obvious need for a well-established weed genomics database; while there are still challenges to this undertaking, it is a necessary step that needs to be taken in order to advance the understanding of polyploidy in weeds, and weed genomics in general (Patterson et al., 2019).

## CONCLUSIONS

Based on the data that is available to us, *no conclusions can be drawn that polyploids make better weeds than non-polyploids*. At this point in time, there is no truly reliable database for genetic data on weed species, and even the available data on polyploid crops is lackluster. The Plant C-Value database is currently the most reliable, and while it offers data some data

on polyploidy, including ploidy level and chromosome numbers, its purpose is to provide C-value data, not polyploid data. Even the list of the worst weeds in the world has not changed in the past 40 years, which should be highly unlikely, as the science is constantly changing. Research into weed genomics has room for improvement, and the development of weed genomics provides potential for greater understanding in how weed species evolve and the role polyploidy is playing and has played in weed evolution (Ravet et al., 2018; Patterson et al., 2019). The International Weed Genomics Consortium provides an outlet for collaborative research into weed genomics, with a growing genomics repository for weed species. The complexity of polyploids makes genomic work difficult; ploidy needs to be determined, chromosome copy number, and even then, certain genes might have more copies than are actually being tested. Next generation sequencing lends itself to providing more insight into polyploidy and its role in weed genomics. While there are more sources providing insight into weed genomics and a pathway for polyploid weeds, more extensive and in-depth research is required in order to fully comprehend the scale that polyploidy plays in understanding weeds.

## AUTHOR CONTRIBUTIONS

JM and NH conceived the idea, developed the outline for the paper, and edited the paper. CR wrote the paper. JM and CR developed the tables. All authors contributed to the article and approved the submitted version.

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**Conflict of Interest:** The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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