Review

Evolved glyphosate-resistant weeds around the world: lessons to be learnt

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Abstract: Glyphosate is the world's most important herbicide, with many uses that deliver effective and sustained control of a wide spectrum of unwanted (weedy) plant species. Until recently there were relatively few reports of weedy plant species evolving resistance to glyphosate. Since 1996, the advent and subsequent high adoption of transgenic glyphosate-resistant crops in the Americas has meant unprecedented and often exclusive use of glyphosate for weed control over very large areas. Consequently, in regions of the USA where transgenic glyphosate-resistant crops dominate, there are now evolved glyphosate-resistant populations of the economically damaging weed species *Ambrosia artemissifolia* L., *Ambrosia trifida* L., *Amaranthus palmeri* S Watson, *Amaranthus rudis* JD Sauer, *Amaranthus tuberculatus* (Moq) JD Sauer and various *Conyza* and *Lolium* spp. Likewise, in areas of transgenic glyphosate-resistant crops in Argentina and Brazil, there are now evolved glyphosate-resistant populations of *Sorghum halepense* (L.) Pers and *Euphorbia heterophylla* L. respectively. As transgenic glyphosate-resistant crops will remain very popular with producers, it is anticipated that glyphosate-resistant biotypes of other prominent weed species will evolve over the next few years. Therefore, evolved glyphosate-resistant weeds are a major risk for the continued success of glyphosate and transgenic glyphosate-resistant crops. However, glyphosate-resistant weeds are not yet a problem in many parts of the world, and lessons can be learnt and actions taken to achieve glyphosate sustainability. A major lesson is that maintenance of diversity in weed management systems is crucial for glyphosate to be sustainable. Glyphosate is essential for present and future world food production, and action to secure its sustainability for future generations is a global imperative.

Keywords: glyphosate; resistance; herbicide; selection; sustainability; evolution

1 INTRODUCTION

Glyphosate has become the world's most widely used herbicide because it is efficacious, economical and environmentally benign.[1,2] Since its 1974 introduction, glyphosate has found a range of uses in agricultural, urban and natural ecosystems. As glyphosate is a non-selective herbicide that controls a very wide range of plant species, it is used in many countries for broad-spectrum weed control just before crop seeding (termed 'burndown'). Glyphosate is also globally used for broad-spectrum weed control between rows of established perennial crops, especially commercial tree, nut and vine crops. Glyphosate is also the global herbicide of choice for weed control in a wide variety of environmental uses in urban and industrial areas, national parks and other amenity areas. In all of these different uses, glyphosate achieves broad-spectrum control of unwanted plants. However, the non-selective effect of glyphosate meant that, until the recent advent of transgenic crops, glyphosate could not be used within crops for selective control of weeds.

A revolutionary new glyphosate use pattern commenced in 1996 with the introduction of transgenic crops (principally soybean, maize, cotton and canola) containing a bacterial gene endowing crop resistance to glyphosate.[2] In transgenic glyphosate-resistant crops (GRCs), glyphosate can be applied to the crop (post-emergence) to remove emerged weeds without crop damage. GRCs enable glyphosate to be used as an in-crop selective herbicide, providing easy, economical, efficient weed control along with other agronomic advantages such as earlier seeding and no-tillage. GRCs are an outstanding commercial success in those countries in which GM crops are grown, with 95% of the more than 100 million hectares of currently grown transgenic crops being GRCs.[3]

This review focuses on the evolution of populations of weed species resistant to glyphosate. When reviewed in 1994 (after 20 years of glyphosate use but before GRCs), there were no known cases of evolved glyphosate-resistant weeds.[4] Clearly, glyphosate resistance in weed species does not evolve rapidly, and, perhaps understandably, this led to speculation that evolution of glyphosate-resistant weeds was unlikely.[5] However, since first reported,[6,7] there are increasing instances of evolved glyphosate resistance in weed species, especially following the advent of GRCs (see below and earlier reviews,[8–10]

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together with the register of herbicide resistant weeds: www.weedscience.com[11]).

In the context of this review of evolved glyphosate resistance in weed species, it is instructive to compare the traditional non-selective glyphosate use patterns versus recent selective (in-crop) use in GRCs. For example, glyphosate in burndown usage has been effective for more than three decades, with few occurrences of evolved glyphosate-resistant weed populations. In contrast, glyphosate as a selective in-crop herbicide in GRCs has been used for a maximum of one decade, and glyphosate-resistant weed populations are emerging as a significant problem. Here, the focus is on the combination of factors that result in strong selection intensity for the evolution of glyphosate-resistant weeds, especially in GRCs. Weed spectrum shifts accompanying glyphosate usage[12] will not be considered. Equally, the underlying biochemical or molecular genetic basis of evolved glyphosate resistance has recently been reviewed,[13] and will not be considered here.

2 GLYPHOSATE-RESISTANT WEEDS IN NON-SELECTIVE GLYPHOSATE USAGE

Since its 1974 commercialisation, glyphosate has been used in many parts of the world for non-selective burndown weed control prior to crop seeding. In spite of persistent use on the same crop fields, there are only a few reports of evolved glyphosate-resistant weed populations evident in these situations. There are at least two major reasons why this is so. Firstly, glyphosate is neither active nor residual in the soil, and therefore glyphosate treatment is a short, intense selection event acting only on emerged plants. As weeds often emerge throughout a growing season, this imposes less overall selection pressure than long-term, soil-residual herbicides, which can exert selection over several months of the growing season. Thus, the major glyphosate use pattern of burndown before crop seeding imposes selection only on that cohort of weeds that have emerged early in the growing season. A considerable proportion of the total population (i.e. the later-emerging cohorts) remains unselected, and thus there is reduced selection pressure for resistance in the overall population.[14,15] Additionally, there is often sufficient weed control diversity to minimise the potential for glyphosate-resistant weeds to emerge as a problem. Diversity can be provided by many different factors, some of which may not be readily apparent. Some examples are the use of other herbicides and mechanical (tillage, mowing, hand-weeding, etc.) and/or biological (grazing animals, crop competition) techniques following glyphosate burndown treatment. If there is a sufficiently diverse system, herbicide resistance may evolve only very slowly or not at all. For example, simulation modelling showed that, for burndown glyphosate use before crop seeding, physical tillage in the subsequent crop seeding operation provided diversity that minimised resistance evolution because glyphosate-resistant survivors were killed by tillage at seeding.[14,15] Removal of the tillage by adoption of a no-till seeding system removed this diversity and allowed resistance to emerge. It will be a recurring theme throughout this review that glyphosate-resistant weeds can evolve where there is insufficient diversity in weed management systems. Conversely, maintenance of diversity can lead to glyphosate sustainability.

Glyphosate is widely used in perennial tree, nut and vine crops for weed control between the crop rows, and is often the herbicide of choice for roadside weed control. In such use patterns, glyphosate can be used persistently for many years and there can be several treatments within the growing season. However, glyphosate resistance has evolved in populations of several weedy plant species in situations with such persistent, intense glyphosate selection. This has occurred in weeds of annual crops, perennial tree, nut and vine crops, in weeds infesting roadsides, etc. (Table 1). Notably, but unsurprisingly, glyphosate resistance has evolved most often in the genetically diverse, resistance-prone genera *Conyza* and *Lolium* (both have several species, considerable hybridisation and a resultingly complex taxonomy).[16] In one Australian cropping region, repeated and exclusive glyphosate treatments for fallow weed control and burndown before no-till crop seeding resulted in the evolution of glyphosate-resistant *Lolium* over a considerable area.[17,18] However, where burndown glyphosate usage has been less persistent or intensive, glyphosate retains efficacy on the great majority of Australian *Lolium* populations in fields devoted to cropping.[19,20]

In the central valley intensive agricultural region of the state of California, glyphosate-resistant *Conyza* and *Lolium* are now a significant problem along

Table 1. Global reports of evolved glyphosate-resistant weeds (not in transgenic GRCs)

Species	Region	Country
Conyza spp.	N America	USA
	S America	Brazil
	Europe	Spain
	Middle East	Israel
	Africa	South Africa
	Asia	China
Lolium spp.	N America	USA
	S America	Chile
		Brazil
	Europe	France
		Spain
	Africa	South Africa
	Asia	Australia
Echinochloa colona	Asia	Australia
Eleusine indica	Asia	Malaysia
		Taiwan
Parthenium hysterophorus	S America	Colombia
Plantago lanceolata	Africa	South Africa

roadsides, irrigation channel banks and tree, nut and vine crops. In this area, glyphosate has been persistently used for interrow weed control, and a random survey revealed 55 of 60 *Lolium* populations (92%) to be glyphosate resistant.[21] In the same region, glyphosate-resistant *Conyza* infests hundreds of kilometres of glyphosate-treated irrigation channel banks (K Humbree, private communication, 2007). *Conyza* and/or *Lolium* populations have evolved glyphosate resistance in orchard, tree, nut and vine crop situations around the world. This has occurred where glyphosate has been used persistently in Europe (France, Spain), the Middle East (Israel), South Africa, South America (Chile, Colombia, Brazil) and Asia (Australia, China).[21–31] In Israel, a random survey of roadside *Conyza* populations found 50% of the 60 collected samples to be glyphosate resistant (B Rubin, private communication, 2007). In Malaysian oil-palm plantations with persistent glyphosate use there are now widespread populations of *Eleusine indica* L. resistant to glyphosate.[32,33] Similarly, glyphosate-resistant *E. indica* is evident in orchards in Taiwan.[34] Glyphosate-resistant populations of *Parthenium hysterophorus* L. are present in Colombia.[35]

The common factor in all of these examples where glyphosate-resistant weeds have evolved is that there had been persistent glyphosate usage with little or no diversity in weed control practices. However, it is important to recognise that glyphosate continues to be effective where there is sufficient diversity in weed control practices and not an overreliance on glyphosate alone.

3 GLYPHOSATE-RESISTANT WEEDS IN TRANSGENIC GLYPHOSATE-RESISTANT CROPS (GRC)

3.1 USA

The adoption of GR soybean, cotton, maize and canola has been dramatic in the USA. In 2007, GR soybean comprised 90%, cotton 91% and maize 60% of the entire USA plantings of these crops.[2,3] In southern cropping regions, GR soybean, cotton and maize dominate in rotation on the same fields. In central and northern cropping regions, GR soybeans are almost universal and often in rotation with GR maize. Clearly, glyphosate selection pressure on weeds is intense in US soybean, maize and cotton agroecosystems, especially as the advent of GRCs has resulted in glyphosate largely replacing selective herbicides. This widespread adoption of GRCs and heavy glyphosate reliance are understandable from a producer viewpoint: glyphosate provides excellent weed control, generally not requiring the additional adjuvants or complicated herbicide tank mixtures or sequences that are often needed with other crop and weed management systems.[36–40] GRCs tolerate glyphosate well, and glyphosate can be effective against large weeds, ensuring that there is flexibility in the timing of glyphosate treatment(s). The simplicity, consistency and flexibility of glyphosate weed control in GRCs have all contributed to widespread adoption. This is evident in several recent surveys of US producers that reveal a very high level of grower adoption and satisfaction with GRCs.[41–49] When producers adopt GR crops, they often cease using other herbicides, reduce tillage and rely almost exclusively on glyphosate for in-crop weed control, thereby greatly reducing diversity. Given the high level of satisfaction with GRCs and the wide range of weed species controlled by glyphosate, it is unlikely that producers will reduce their heavy reliance on glyphosate unless forced to by recalcitrant weed populations (i.e. weed species shift and/or resistance evolution).

Paradoxically, the introduction of GRCs in the USA could have enabled increased diversity of herbicides, as the glyphosate mode of action is unique. This added diversity could have benefited efforts in weed/herbicide resistance management, as glyphosate can be combined with other herbicides in a tank mixture, or as part of a sequential herbicide programme. However, the reality is that most GRC producers currently rely on glyphosate alone, with markedly reduced diversity in weed management tools employed. For example, GRCs have enabled producers to reduce tillage,[49] with concomitant environmental benefits, but this results in reduced diversity in the weed management techniques practised.

The massive adoption of GRCs in soybean-, maize- and cotton-growing regions of the USA has resulted in strong selection intensity favouring any weeds possessing gene traits enabling glyphosate survival (Table 2). The first evolved glyphosate-resistant weed reported in a GRC (2001) was *Conyza canadensis* L.[50] In the few years since this first report, glyphosate-resistant *Conyza* now infests at least 2 million hectares of GRCs in the USA.[51] Glyphosate-resistant *Lolium* has also been reported.[52] More worrisome are glyphosate-resistant populations of far more economically damaging weed species (Table 2). In central states there are now several known glyphosate-resistant populations of the very vigorous, highly competitive and economically damaging weeds *Ambrosia artemissifolia* L. and

Table 2. Global reports of evolved glyphosate-resistant weeds in glyphosate-resistant crops (GRCs)

Species	Region	Country
Conyza spp.	N America	USA
	S America	Brazil
Lolium spp.	N America	USA
Ambrosia artemissifolia	N America	USA
Ambrosia trifida	N America	USA
Amaranthus palmeri	N America	USA
Amaranthus tuberculatus	N America	USA
Amaranthus rudis	N America	USA
Sorghum halepense	S America	Argentina
Euphorbia heterophylla	S America	Brazil

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Ambrosia trifida L.[11] In the southern cotton-growing states there are many reports of glyphosate-resistant populations of *Amaranthus palmeri* S Watson, the most damaging weed of US cotton crops.[11,53,54] In northern states, there are glyphosate-resistant populations of the widespread and very competitive *Amaranthus tuberculatus* L.[55] and *Amaranthus rudis* L.[11,56–58] This evolution of glyphosate-resistant *Ambrosia* and *Amaranthus* populations is obviously a serious issue.

3.2 Argentina and Brazil

In parallel with the USA, GR soybean has been massively adopted in Argentina. Virtually the entire (99%) 16 million hectare Argentine soybean crop is GR, and nearly all of this is in no-till production systems with little diversity in weed control, and almost exclusive reliance on glyphosate. Additionally, in Argentina (as in the USA), GR maize is being adopted at a rapid rate. Therefore, the selection pressure is intense for evolution of glyphosate-resistant weeds. So far, the very damaging weed *Sorghum halepense* (L.) Pers. has evolved glyphosate resistance across a significant area of the GR soybean crop in the Salta province.[59] The evolution of glyphosate-resistant weeds in South America has been reviewed.[60]

Brazil did not allow GRCs until well after Argentina, the USA or Canada, and therefore GRC adoption has only occurred over the past few years. However, rapid adoption of GR soybean, maize and cotton is now under way. Thus far, glyphosate-resistant populations of *Conyza*[61] and *Euphorbia heterophylla* L.[62] have evolved in Brazilian GR soybean areas (Table 2). Paraguay and Uruguay are also adopting GRCs, although there are currently no reports of glyphosate-resistant weeds in these countries.

Given the dominance of GRCs in soybean, cotton and maize agroecosystems in Argentina, Brazil and the USA, more species than currently known (Table 2) will inevitably evolve glyphosate resistance. A number of other important weed genera and species are at risk, including (but not restricted to) grass weeds such as *Digitaria*, *Setaria* and *Sorghum*, or dicotyledonous species such as *Abutilon theophrasti* Medik, *Amaranthus* spp. (*A. hybridus* L., *A. retroflexus* L., *A. powelli* L.), *Chenopodium album* L., *Kochia* species and *Xanthium strumarium* L. These genetically diverse weed species have already demonstrated the ability to evolve resistance to a number of other herbicide modes of action, and they are now under intense glyphosate selection. Therefore, as they evolve glyphosate resistance, they will also retain genes endowing resistance to previously used herbicides. This is already evident in multiple-herbicide-resistant *Lolium* in Australia and South Africa.[31,63]

3.3 Canada

Relative to the massive GRC adoption in the USA and Argentina, it is instructive to contrast the situation in Canada. While GR soybean and maize are grown in the Ontario province, in the western grainbelt provinces (Alberta, Manitoba, Saskatchewan) canola is the only GRC. In this agroecosystem, the non-GR cereal crops wheat and barley dominate, with canola as an important rotational crop. In 2006, of the 6 million hectares of canola in Canada, 70% was GR. Canola engineered for resistance to the herbicide glufosinate competes directly with GR canola, and therefore producers are able to diversify by alternating between GR and glufosinate-resistant canola. It is important to recognise that, on average, canola is grown on a particular cropping field in only one year in four. As the rotational cereal and any other crops are not GR, it is thus likely that a GR crop is grown on a particular field only once in 4 years. Clearly, the glyphosate selection intensity on weed species in this Canadian canola–cereal cropping agroecosystem is much less than in the USA, Argentine or Brazilian GR soybean, maize and cotton agroecosystems. Unsurprisingly, there are currently no known cases of evolved glyphosate-resistant weeds in Canada. This is undoubtedly due to the diversity (as it refers to glyphosate) evident in the non-GRC cereal/GR canola Canadian cropping system, relative to that in the GR soybean–maize–cotton agroecosystems to the south. Thus, GR canola should remain sustainable in Canada if this diversity is maintained. There are important lessons to be learnt for other parts of the world in this sustainable use of a GRC in Canada.

4 CONCLUSIONS AND IMPERATIVES FOR GLYPHOSATE SUSTAINABILITY

A major lesson evident from more than three decades of glyphosate use to control billions of plants worldwide is that, where diversity in weed management systems is maintained, weed control by glyphosate can be sustainable. Indeed, in spite of long-term use, the evolution of glyphosate-resistant weed populations in non-GRC, burndown systems has been very limited. Thus, functionally competent gene traits endowing glyphosate resistance are relatively rare and not easily enriched in plant populations.[13–15] This is why glyphosate is a remarkably robust herbicide from a resistance avoidance viewpoint. However, as reviewed above, it is clear that, where there is very intense glyphosate selection without diversity, glyphosate-resistant weed populations will evolve. In particular, the evolution of glyphosate-resistant weed populations is a looming threat in areas where transgenic glyphosate-resistant crops dominate the landscape and in which glyphosate selection is intense and without diversity. If current practices continue in these areas, then glyphosate-resistant weeds will become a major problem. This being so, the reintroduction and/or maintenance of diversity in these agroecosystems are essential if glyphosate is to be sustainable. What specifically constitutes ‘diversity’ will vary according to region, ecosystem, enterprises, economics and many other factors. However, diversity will involve herbicide rotations, sequences, combinations of robust rates of different modes of action and use of non-herbicide weed control tools.[15] Such diversity must be introduced now in the GRC areas of the USA, Argentina and Brazil if glyphosate is to be sustained. Mixtures of glyphosate with effective doses of different herbicides are already being adopted, and transgenic crops with additional herbicide resistance genes are in development.[64–66] Alternative herbicides and integration with non-herbicidal weed control tools will be required.

For those in regions of the world that have not yet adopted GRCs and/or intensive glyphosate usage, there are lessons to be learnt from the GRC experience in the Americas. Through avoiding intense glyphosate reliance and by maintenance of diversity, the longevity of the precious herbicide resource glyphosate and excellent GRC technologies can be sustained for future harvests and future generations.

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