GLYPHOSATE – HOW IT BECAME A ONCE IN A HUNDRED YEAR HERBICIDE AND ITS FUTURE

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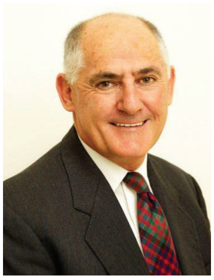

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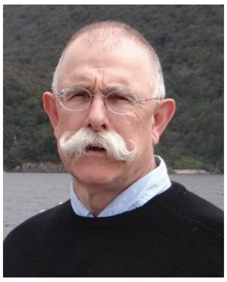

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More than a decade ago we termed glyphosate a "once in a century herbicide" (Duke & Powles, 2008). We designated glyphosate with this distinction in 2008 even though we were only 60 years into the age of synthetic herbicides. As synthetic herbicide use began about 1945, we are fast approaching the 75th year of the herbicide era. Also, it is nearly 50 years since first use of glyphosate. Glyphosate has been by far the world's most used herbicide for about two decades, and it currently makes substantial contributions to world food production. The history of how this molecule attained such importance and our views on the growing biological challenges (herbicide resistance evolution) to its future use in feeding a growing world population are discussed.

Glyphosate discovery and its unparalleled success

The glyphosate molecule was first synthesized by the Swiss company Cilag in 1950, but this company apparently did not test it as a herbicide (Franz *et al.*, 1997). Glyphosate was found to be herbicidal by Monsanto Co. during the early 1970s, a time when this company was heavily involved in herbicide discovery. We note that the glyphosate molecule has few of the physicochemical properties commonly thought to be requisites of good herbicides (Dayan, 2018; Tice, 2001; Zhang *et al.*, 2018).

Thus, such a compound might not be considered for evaluation as a herbicide today. In the early 1970s, companies screened all new compounds, whether they fit a discovery concept or not. Of great importance is glyphosate's strict specificity for its target, 5-enolpyruvylshikimate-3-phosphate synthase (EPSPS). EPSPS, an enzyme of the shikimic acid pathway, is required for synthesis of aromatic amino acids (phenylalanine, tyrosine, and tryptophan), as well as plant defense compounds, hormones, enzyme cofactors and other metabolites needed by plants. Serendipitously, the number of target site EPSPS molecules in plants is low enough that most weeds are killed by around 1 kg/ha glyphosate. Recent evolution of some glyphosate-resistant (GR) weeds has been by EPSPS gene amplification producing higher levels of EPSPS molecules (first reported by Gaines *et al.*, 2010). Thus, higher glyphosate application rates are required to block the shikimic acid pathway. Conversely, lowering levels of EPSPS in weeds with elevated EPSPS levels via RNAi technology makes them susceptible to field rates of glyphosate (Sammons, 2015). Thus, the number of target site molecules in a plant can be critical to whether a herbicide for that target is viable. Although the discoverers of glyphosate knew nothing about this, they were lucky that the target site is amenable to economical levels of this remarkable herbicide. The relatively high initial cost of glyphosate for end-users in the 1970s too often resulted in low use rates. Thus, EPSPS levels were sufficiently low for use of economical doses of the herbicide.

Another asset of glyphosate is that it is an uncompetitive inhibitor of its target, EPSPS. No other herbicide is an uncompetitive inhibitor. Uncompetitive inhibitors of enzymes of biosynthetic pathways are predicted to have much greater effects on overall metabolism, due to their predicted substantial effects on accumulation of metabolic intermediates (Cornish-Brown, 1986). One of the clues that led to discovery of EPSPS as the target site of glyphosate is the accumulation of large amounts of shikimic acid in glyphosate-treated plants.

Glyphosate is a slow-acting, non-selective herbicide, often requiring several days for phytotoxicity symptoms to occur and a week or more for complete plant death. In the mid-1970s, Monsanto scientists told one of us (Duke) that there was concern before the product was commercialized that its slow action might limit sales. Farmers like to see weeds wither and die quickly. However, the extended time that it takes glyphosate to kill a plant gave it an advantage over paraquat, the leading non-selective herbicide at that time. In contrast to glyphosate, paraquat is a very fast acting herbicide. If applied when sunlight is strong, paraquat kills green tissue so rapidly that it is not sufficiently translocated throughout the plant. In this circumstance, paraquat-treated weeds can suffer damage but regrow from meristems in parts of the plant that are not directly contacted by the herbicide (e.g., rhizomes). Conversely, glyphosate is very phloem mobile, and its slow action allows it to move to all meristems, killing all parts of the plant. These features make it more effective than other herbicides on perennial weeds. Furthermore, during the time that glyphosate is translocating, there is little or even no metabolic degradation of glyphosate in most plant species (Duke, 2011), allowing herbicidal glyphosate doses to accumulate in meristematic tissues far from the site of application.

A few years after glyphosate was first marketed, Steinrücken and Amrhein (1980) discovered its molecular target, EPSPS. Loss of these amino acids impairs protein synthesis and production of aromatic amino-derived enzyme co-factors and plant pathogen defenses. Glyphosate efficacy is much better in the presence of plant pathogens (reviewed by Hammerschmidt, 2018). Discovery of the glyphosate target site stimulated much research seeking herbicides that would target EPSPS or other enzymes of the shikimate pathway, but no other herbicides that target EPSPS or any other shikimate pathway enzymes have been commercialized. Thus, unlike most other herbicide modes of action, no other products with similar activity have been available, leaving this market to glyphosate alone. Initially, the major limitation of glyphosate was its non-selectivity, meaning that for its first 20 years glyphosate sales were globally modest. For example, by the mid-1990s, the annual glyphosate use in the US was about 13 million kg year, an amount similar to that of trifluralin (Fig. 1) and much less than that of metribuzin (https://water.usgs.gov/nawqa/pnsp/usage/maps/compound_listing.php), both moderately important herbicides at the time. At this time, paraquat use was only about 2 million kg per year in the US, and the use rates and crop use patterns show that the market niches of these two non-selective herbicides were different (Figs. 1 and 2). We rely on US data because the types and quality of data for pesticide use in the USA over the long time period of Figs. 1 and 2 are not available for many other countries.

Glyphosate was a successful herbicide, but its utility was limited because it could not be used in crops. Glyphosate was (and still is) used before and after the crop season (burndown), and for vegetation management in non-crop situations. Largely, the only use with crops was as a harvest aid in mature grain crops to hasten crop desiccation for improved mechanized harvesting (Griffin *et al.*, 2010). The uses of glyphosate and its market share were similar in the rest of world to that in the USA before 1996. Before 1996, considerable effort was made to use glyphosate during crop production by specialized application technology such as rope wick and carpet applicators to wipe glyphosate on weeds that were taller than the crop and shielded sprayers to spray weeds between crop rows (Derting, 1987). But, these approaches to use glyphosate as a selective herbicide were not very efficient, required specialized application equipment, and often resulted in unacceptable crop damage and therefore had very limited adoption. Many recognized that if glyphosate could be used in growing crops it would be an ideal broad-spectrum herbicide, superior to all selective herbicides being used to control crop-infesting weeds.

Ground breaking biotechnology research utilizing the then nascent transgene technology led to Monsanto Company's introduction of glyphosate-resistant (GR) soybean, cotton, maize, canola, alfalfa, and sugar beet, beginning with GR soybeans in 1996 (Duke, 2014). These crops were made resistant to glyphosate with a bacterium-derived transgene coding for a GR form of EPSPS. This biotechnological breakthrough to endow crops with resistance to glyphosate revolutionized glyphosate use and made it the most used herbicide worldwide, even though GR crops do not include two major crops (rice and wheat), and GR crops are not grown in many countries. With the introduction of GR crops in the USA in 1996, glyphosate use increased more than tenfold (Fig. 1), while the use of most other herbicides used in soybean, maize and cotton decreased considerably (for example, see trifluralin, imazethapyr, and acifluorfen in Figs. 1 & 2). GR crops revolutionized weed control, making it much simpler, less expensive, and more effective. Glyphosate/GR crop technology was economically very attractive to farmers (Brookes & Barfoot, 2017). As a result, adoption of GR crops was very rapid, reaching close to 95% adoption for maize, cotton and soybeans in the US, with similar adoption rates in the countries of South America where these crops are grown, particularly Brazil and Argentina (Duke, 2018). Adoption of GR sugar beet in the US went from zero to essentially 100% within two years of introduction (Morishita, 2018). GR

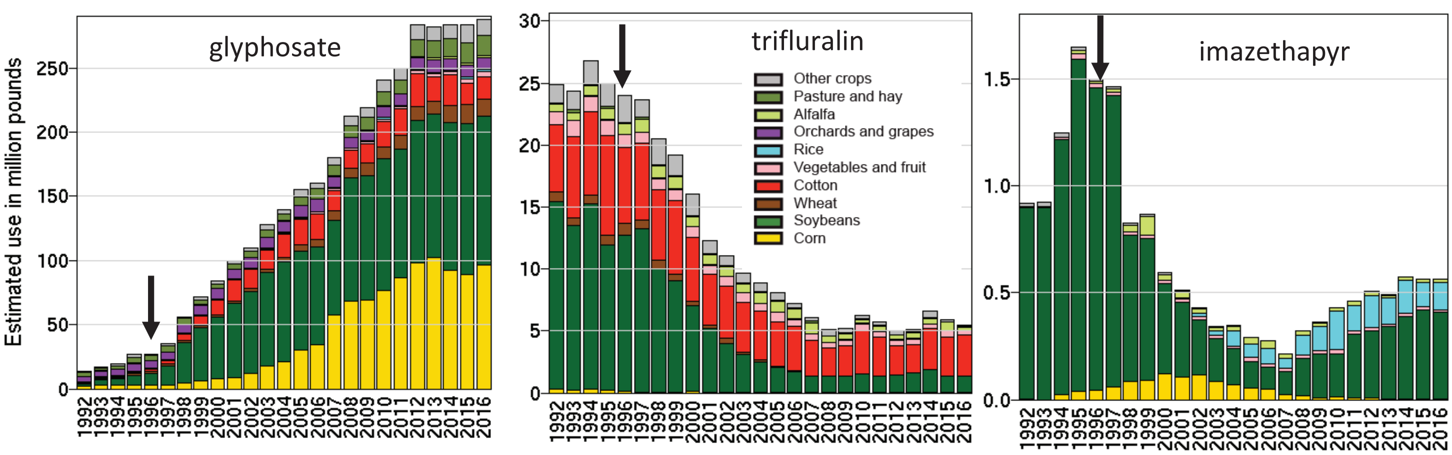

Figure 1. Glyphosate, trifluralin, and imazethapyr use in the USA over the past 25 years. The arrows represent the introduction of the first glyphosate-resistant crop in 1996. Constructed from figures of the United States Geological Survey Pesticide National Synthesis Project (https://water.usgs.gov/nawqa/pnsp/usage/maps/compound_listing.php).

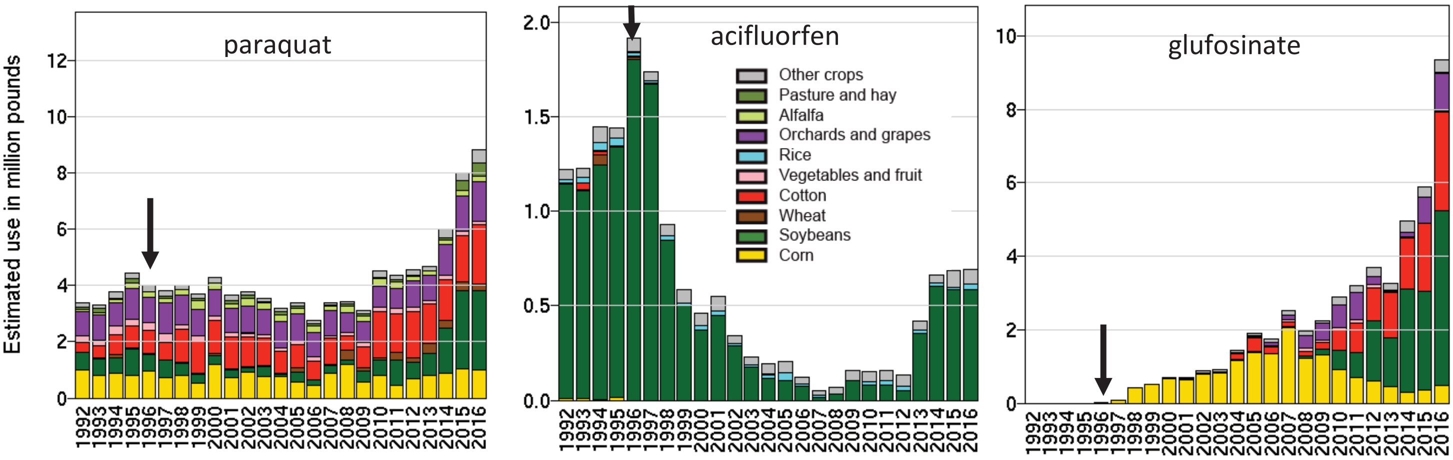

Figure 2. Paraquat, acifluorfen, and glufosinate use in the USA over the past 25 years. The arrows represent the introduction of the first glyphosate-resistant crop. Constructed from figures of the United States Geological Survey Pesticide National Synthesis Project (https://water.usgs.gov/nawqa/pnsp/usage/maps/compound_listing.php).

crops enabled reduced- and no-tillage agriculture, and had several other environmental advantages (Cerdeira & Duke, 2006). For farmers growing GR crops, there was a golden age weed management , with easy, inexpensive, and reliable weed control for at least a decade from 1996 onwards. GR crops (with and without Bt) became the most planted transgenic crops worldwide.

This golden age of glyphosate for weed control was difficult for corporations involved in herbicide discovery. The dominance of glyphosate and GR crops substantially reduced the value of the market for other herbicides (Figure 3), almost certainly contributing to the current paucity of new herbicide products/new modes of action that would have been valuable in herbicide resistance management (Duke, 2012). Some companies discontinued herbicide discovery research, and others reduced their efforts significantly. During this time, the consolidation of companies involved in pesticide discovery (Copping, 2018) accounted for even further reductions in herbicide discovery research. The number of patents for new herbicides plummeted compared to those for fungicides and insecticides.

Glyphosate-resistant weeds are eroding the value of glyphosate

Life depends on the powerful force of evolution that ensures species persistence in the presence of lethal selection pressures. For weedy plants, herbicides are a frequent catastrophic challenge causing high weed mortality. Yet, herbicides have not driven weed species to extinction; rather, genetic variability in large weedy plant populations ensures some survivors. Under persistent herbicide selection these initially rare resistant survivors reproduce and are enriched over generations until herbicide failure is evident. There are many examples of herbicide-resistant weed evolution from the past half-century of global herbicide use (reviewed by Powles & Yu, 2010, see Heap website 2018). For some herbicides, there is rapid resistance evolution, whereas for others resistance evolution is slow.

Some considered that if weeds evolved resistance to glyphosate it would be low and slow (Bradshaw *et al.*, 1997).

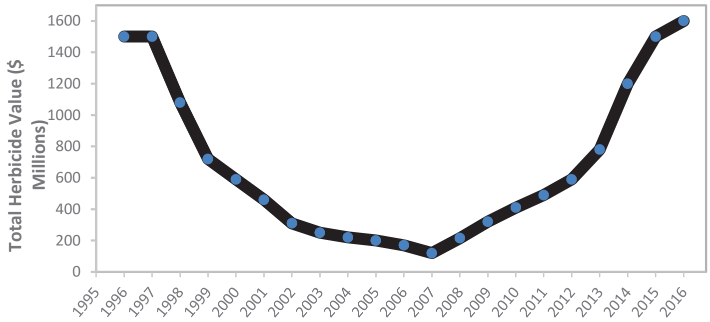

Figure 3. Value of all herbicides other than glyphosate used in soybeans in the US.

Indeed, weeds do not easily evolve resistance to glyphosate, with the first global case not reported until 1998 (Powles *et al* 1998, Pratley *et al* 1999), more than 20 years after the introduction of glyphosate. However, the 1996 introduction and subsequent massive adoption of GR soybean, maize and cotton in the Americas greatly increased glyphosate use. What followed was a decade of outstanding weed control with glyphosate. We term the decade 1996–2006 as the golden decade of glyphosate in which glyphosate easily and efficiently removed a wide range of weed species present in GR crop fields. However, almost universal adoption of GR crops meant glyphosate was persistently applied without weed management diversity on huge weed populations across vast areas. This was a potent evolutionary scenario for GR weeds to evolve and represents one of the world's clearest examples of human-induced, large-scale selection for rapid evolution. It was an evolutionary inevitability that GR weeds would result, with a first appearance of GR *Conyza* in GR soybean (Van Gessel, 2001). GR weeds then steadily increased across GR crop areas of the US mid-west/south (Heap, 2018) and, to a lesser extent, in Argentina and Brazil. GR weed species are now present in at least half of the 150 million hectares of GR soybean, maize and cotton fields in these countries. The GR *Amaranthus* weed problem is particularly dramatic. First reported in Georgia (Culpepper *et al.*, 2006), GR populations of pernicious *A. palmeri* (Palmer pigweed) now infest much US crop land, including northern US states and Argentina and Brazil which had never known this weed. In northern US states devoted to GR soybean and maize, GR *A. tuberculatus* (water hemp) now widely infests crop fields. In Argentina, GR *Sorghum halepense* (johnsongrass) is becoming widespread.

Amaranthus spp., *Sorghum halepense, Echinochloa* spp., *Lolium* spp. and several other major weed species with glyphosate resistance, are known as "driver weeds" because their adverse impacts on crop yield drives grower decision making and expenditure. Unfortunately, driver weed species are often the most resistance-prone. Driver weeds often have high genetic variability and fecundity on which evolution acts to enrich resistant biotypes. Driver weeds are evolving glyphosate resistance in GR crop areas of the Americas and around the world. It is noteworthy that GR weeds are not a major issue in Canada, despite significant areas of GR crops. Undoubtedly, this is because there has been much greater diversity in crops and weed control herbicides in Canada that has acted to minimize the selection intensity, meaning GR weed evolution has been minimal relative to south of the Canadian border. This Canadian example of crop and herbicide diversity should be heeded throughout the world. Similarly, few weeds have evolved resistance in continuous GR maize in the US, where several other herbicides have been routinely used with glyphosate.

While outside the scope of this article, there is a great deal of research on the biochemical and molecular basis of evolved glyphosate resistance in weeds. The first GR weeds showed only modest levels of glyphosate resistance, endowed by either a reduced translocation/vacuolar sequestration resistance mechanism (Lorraine-Colwill *et al.*, 2002; Ge *et al.*, 2010) or a Pro-106 Ser mutation in the EPSPS gene (Baerson *et al.*, 2002). However, since then, a surprising diversity of glyphosate resistance mechanisms has become evident. Particularly interesting are high levels of glyphosate resistance due to gene amplification of the EPSPS gene (first reported by Gaines *et al.*, 2010) or two codon changes in EPSPS (Yu *et al.*, 2015) and stacking of resistance gene traits within individual plants to give highly resistant GR weeds (glyphosate resistance mechanisms recently reviewed by Sammons & Gaines., 2014).

Glyphosate Use in the Futu[illegible]

Currently, across large areas devoted to GR crops, particularly in the USA, Brazil and Argentina, GR weeds have become very problematic, reducing the cost and efficacy advantages of GR crops significantly. In the Americas, GR weeds have forced farmers to much greater expenditures on herbicides for weed control. The rapid US farmer adoption of GR soybean with almost exclusive glyphosate use caused a precipitous decline in use of other herbicides (Figures 1 and 3) from 1996 onwards for a decade. Growers relied exclusively on glyphosate for weed control in GR crops. However, as GR weed challenges emerged in US GR crop fields, growers were forced to add alternative herbicides to control glyphosate resistant weeds. Grower weed control costs tripled, as evidenced by the rapid resurgence of herbicide use in US soybean crops (Figure 3). For example, acifluorfen use rebounded (Figs 1). Paraquat use in soybeans and maize increased (Fig. 2), as did imazethapyr (Fig. 1) and metribuzin use in soybeans. Glufosinate-resistant crops, which had little initial market penetration during the glyphosate golden decade, were turned to because of GR weeds, resulting in record sales of glufosinate in recent years in the US (Fig. 2). Use of other, older herbicides has gone up too. GR weeds are also now being controlled with dicamba in soybeans with transgenes for both dicamba and glyphosate resistance. GR crops with genes for resistance to 2,4-D and for HPPD inhibitor herbicides are becoming available in the US. It must be noted that despite the major problems with GR weeds, farmers still use glyphosate to control weeds that remain susceptible to glyphosate. Thus, although glyphosate use in the US reached a plateau in 2012 (Fig. 1) its use has not declined. The dynamics over which glyphosate use will decline are multi-factored and difficult to predict.

There is considerable pessimism about the role of herbicides in weed management in global agriculture in future decades. Increasing numbers of GR weeds with decreasing herbicide options account for part of this pessimism. Weeds resistant to several herbicides with several modes of action (multiple resistance) are an increasing problem, leaving few herbicide options in some situations. At the rate this problem is increasing, farmers will need new herbicides and/or weed control options other than herbicides. Currently, growers achieve weed control with a diversity of herbicides, including continued reliance on glyphosate for control of many weed species. But, due to multiple herbicide resistance, maintaining this level of weed control usually requires more herbicides and more expertise in weed management. This has high costs for the farmer and more potential environmental impact. So, will the age of herbicides last a century, and how much longer will glyphosate play a major role in weed control?

Conclusions

By removing crop-infesting weeds, it is indisputable that herbicides have made great contributions to world food production. World population growth and increasing meat consumption demands that crop yields must increase dramatically to feed the world. However, major issues including climate change, water restrictions, loss of arable land, limited genetic capacities of crops, and herbicide-resistant weeds are formidable challenges that will make needed increases in crop production ever more difficult. Sustainable, intensive agriculture is the only future alternative to removing more land from its natural state for crops in order to fulfill humanity's food needs (Balmford *et al.*, 2018). We believe that for the major field crops that feed the world, wise use of herbicides will continue to be part of crop production technology for the foreseeable future. Loss of the once in a hundred year herbicide glyphosate as part of this future would be costly. It is possible that robotic weeding and other weed control technologies will add to or even replace herbicides in some high value crops in coming decades (Westwood *et al.*, 2018). However, in the world's great major field crops, wheat, rice, maize, soybean, etc., herbicides will be essential for many years to come. The specter of the loss of herbicide control of weeds, especially the world's greatest herbicide, glyphosate, must encourage greater diversity in weed control, including multi-mode of action formulated herbicide mixtures and sequences to better manage evolving herbicide resistance. Cultural and other non-chemical methods of weed management will help in diversifying herbicide resistance management to help the longevity of good herbicides for future harvests. There are encouraging signs, such as the widespread adoption of non-chemical harvest weed seed control techniques in Australia (Walsh *et al*., 2013), but much remains to be achieved. New herbicide discovery is paramount, including a search for a herbicide potentially able to replace glyphosate. What is abundantly clear is that glyphosate is still a once-in-a-century herbicide and all efforts should be made to sustain its efficacy so that it can continue to contribute to global food production. In the shrort term, sustainably producing food for more than 10 billion people will be significantly more difficult without glyphosate.

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