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Glyphosate Degradation in Glyphosate-Resistant and -Susceptible Crops and Weeds

Stephen O. Duke

NPURU, ARS, U.S. Department of Agriculture, P.O. Box 8048, University, Mississippi 38677, United States

ABSTRACT: High levels of aminomethylphosphonic acid (AMPA), the main glyphosate metabolite, have been found in glyphosate-treated, glyphosate-resistant (GR) soybean, apparently due to plant glyphosate oxidoreductase (GOX)-like activity. AMPA is mildly phytotoxic, and under some conditions the AMPA accumulating in GR soybean correlates with glyphosate-caused phytotoxicity. A bacterial GOX is used in GR canola, and an altered bacterial glyphosate *N*-acetyltransferase is planned for a new generation of GR crops. In some weed species, glyphosate degradation could contribute to natural resistance. Neither an isolated plant GOX enzyme nor a gene for it has yet been reported in plants. Gene mutation or amplification of plant genes for GOX-like enzyme activity or horizontal transfer of microbial genes from glyphosate-degrading enzymes could produce GR weeds. Yet, there is no evidence that metabolic degradation plays a significant role in evolved resistance to glyphosate. This is unexpected, considering the extreme selection pressure for evolution of glyphosate resistance in weeds and the difficulty in plants of evolving glyphosate resistance via other mechanisms.

KEYWORDS: AMPA, glyphosate, herbicide resistance, GMO, soybean, canola

INTRODUCTION

Glyphosate is the most important herbicide since 2,4-D, and its importance has been amplified by the introduction of transgenic, glyphosate-resistant (GR) crops in 1996.[1,2] More than 80% of the transgenic crops on the vast and ever-increasing farming area planted with these crops are glyphosate resistant. GR crops include soybean, maize, cotton, canola, and sugar beet. The use of glyphosate with GR crops is the most important weed management technology in agronomic crops in the western hemisphere. How metabolic degradation of glyphosate is and is not involved in this technology is an intriguing topic for which there is relatively little peer-reviewed research. Nevertheless, it is surprising that this fascinating area has never been the subject of a review.

The metabolic degradation of glyphosate in soil will be discussed first, because for quite some time glyphosate was thought by many to be degraded only by soil microbes. Genes for the microbial degradation enzymes were sought for the production of GR crops.[3] Then, metabolism in crops, both transgenic and nontransgenic, will be discussed. Although metabolism of glyphosate had been transgenically imparted on one crop (canola),[4] it was later found that soybeans metabolize glyphosate naturally.[5] This topic will be followed by sections on glyphosate metabolism in both susceptible weeds and those that have evolved resistance to glyphosate. The implications of these findings with regard to horizontal gene flow or genes from microbes to plants will be covered. Finally, I will discuss research needs in this understudied aspect of this most important herbicide.

GLYPHOSATE METABOLISM BY SOIL MICROBES

Although the intent of this review is to contrast metabolic degradation of glyphosate in conventional farming systems versus GR cropping systems, a discussion of the metabolism of glyphosate by soil microbes is in order because, for most of the product life of glyphosate, many scientists considered soil microbes to be the only organisms that significantly degrade glyphosate.

Not long after its introduction in 1974, as reviewed by Duke,[6] glyphosate was shown to have a relatively short half-life in soil due to microbial degradation, ranging from a few days to months. As pointed out by Borggaard and Gimsing,[7] a wide variety of soil microbes, including bacteria, actinomycetes, fungi, and unidentified microbes, degrade glyphosate. Two major pathways of degradation have been found in soil. One results in the formation of sarcosine and inorganic phosphate via a C−P lyase. The C−P bond of glyphosate can also be broken nonenzymatically in the presence of manganese oxide,[8] although this type of degradation does not apparently represent a large share of the degradation in soil. Ligninolytic enzymes of soil microflora can also break the C−P bond of glyphosate.[9] The other type of degradation occurs by a glyphosate oxidoreductase (GOX), splitting the glyphosate C−N bond to produce aminomethylphosphonic acid (AMPA) and glyoxylate.

AMPA is usually reported as the main metabolic product of glyphosate found in soil; however, sarcosine has not been looked for in many of these studies. Examples of soil microbes identified to have the C−P lyase are *Pseudomonas* sp.,[10] *Rhizobium* spp.,[11] and *Streptomcyces* sp.,[12] and examples of those with GOX are *Arthrobacter atrocyaneus* [13] and *Pseudomonas* sp.[14] Via C−P lyase, some microbes can utilize glyphosate as a sole source of phosphorus. If metabolized to AMPA by GOX, to be further

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metabolized, the C−P bond of AMPA must be broken by a C−P lyase. In soils, this step is generally slower than the formation of AMPA.[7] For microbes to use glyphosate or AMPA as a phosphorus source, they must have a C−P lyase. The genes for degradation of phosphonates such as glyphosate and AMPA are regulated by exogenous phosphorus, but the C−P bond of these compounds can be broken in the presence of exogenous phosphate.

One strategy in the early stages of attempts to produce GR crops was to use transgenes from microbes that encode a glyphosate-degrading enzyme. Isolating the gene(s) for the C−P lyase complex proved to be too difficult for this purpose. But, the GOX gene (*goxv247*) from the soil microbe *Ochrobactrum anthropi* was isolated and used as a transgene in GR canola, along with a the gene (*cp4*) that encodes a GR form of 5-enolpyruvylshikimate-3-phosphate synthase (EPSPS), the enzyme target of glyphosate.[15] The gene for glycine oxidase from *Bacillus subtilis* has been mutated to increase its ability to act like a glyphosate oxidoreductase that could be used to generate GR crops, although there is very little sequence similarity (18%) between the GOX gene and that of this glycine oxidase.[16] Whether glycine oxidases or D-amino acid oxidases with GOX-like activity exist in plant species that accumulate AMPA when treated with glyphosate has not been studied.

Other glyphosate-altering enzymes from soil microbes have been found more recently. A glyphosate decarboxylase from a soil fungus has been patented.[17] Three genes from soil *Bacillus licheniformis* (Weigman) encode very weak glyphosate acyl transferases (GAT).[18] The enzymatic product, *N*-acetylglyphosate, is not herbicidal.[19] Eleven iterations of gene shuffling and selection for GAT activity enhanced the activity of this enzyme almost 10000-fold.[18] Siehl et al. [20] provided a detailed biochemical explanation of the remarkable increase in activity. The *gat* transgene confers a high level of resistance to crops and may be utilized in a second wave of GR crops.[19]

Repeated use of a herbicide has been shown to cause what is called accelerated degradation of that herbicide, due to changes in the soil microflora. This can occur through increases in populations of microbial taxa that degrade the herbicide or selection for microbes within a taxa that are more efficient at degrading the herbicide. For example, *s*-triazine herbicides are commonly degraded more rapidly in soils with a history of the use of these herbicides.[21] Whether accelerated degradation of glyphosate occurs is unknown, although the few studies that are germane to this question have not found it. For example, Gimsing et al. [22] determined glyphosate mineralization at three locations in soils that had received glyphosate previously and in soils that were organically managed and therefore had not received glyphosate for at least 15 years. Mineralization was highest in the organically managed soils, indicating that there is no adaptation to glyphosate degradation and that mineralization is controlled by other factors. In Brazilian soil, application of glyphosate every 2 weeks over a period of 2 months did not lead to more rapid degradation over time,[23] but the appearance of accelerated degradation of a herbicide does not normally manifest itself over such a short time span. Similarly, Lancaster et al. [24] found that glyphosate degradation slowed slightly from each previous glyphosate application during a regimen of five applications spaced 2 weeks apart. In two different Brazilian soils, there was either no difference or even slower degradation of glyphosate in soils that had had 6 or 11 years of glyphosate application compared to the same soils that had no history of glyphosate use.[25] If accelerated degradation of glyphosate occurs, it would seem more likely to be more prevalent and robust in GR crops. I am not aware of such a study being conducted.

METABOLISM IN NONTRANSGENIC AND TRANSGENIC CROPS

Most of the early work on the metabolism of glyphosate in crops indicated that glyphosate is metabolized very slowly, if at all.[6,26] This general finding fit the fact that glyphosate is a slow-acting, nonselective herbicide. If a plant metabolized the herbicide rapidly, it should have a degree of natural resistance, just as many crops are resistant to the selective herbicides that are used with them by virtue of rapid metabolism. There was speculation that reports of plant-mediated degradation were due to microbial contamination. It should be pointed out that many of the studies on the metabolism of glyphosate by plants did not account for all of the applied material, and only certain types of metabolism could be determined, depending on the position(s) of the radiolabeled carbon. Such studies with plants are further complicated by the fact that plants lose some foliarly applied glyphosate through root exudation.[27,28]

In a survey of the existing literature, Duke[6] found no metabolism of glyphosate reported in 11 studies of 11 different species during periods of ≤20 days. Studies with *Agropyron repens* found no glyphosate degradation products after 5 months,[29] although only 20% of the applied material was recovered. In apple and pear, 2−8% of glyphosate was found as AMPA after 94 and 80 days, respectively.[30] There were studies in the early days of this research that found significant degradation of glyphosate, but for various reasons, many researchers were suspicious that the metabolic degradation was due to microbial contamination. For example, Rueppel et al.[31] reported slow degradation of glyphosate in maize, cotton, and soybean when it was fed to the plant in a hydroponic solution. Hydroponic solutions are notorious for harboring microbes. In fact, the glyphosate in the hydroponic solution slowly degraded to AMPA according to Franz et al.[26]

Determination of the metabolism of a herbicide in glyphosate-susceptible plants is problematic, in that when glyphosate is applied at herbicidal rates, metabolic processes including metabolic degradation may be impaired. The alternative is to use subtoxic applications, but the smaller amounts of herbicide used make detection and quantification more difficult. Furthermore, subtoxic levels of glyphosate stimulate growth,[32] which may influence degradation. GR crops are ideal for studying degradation, in that there is no toxicity to interfere with the metabolic process.

By the time GR crops became available, interest in studying glyphosate metabolism in crops had largely passed, in part because funding for such research in the public sector had almost completely disappeared. Hence, there is surprisingly little published on this topic, despite the great importance of these crops. We stumbled onto this topic in trying to understand another question regarding GR soybeans.

Soybeans contain estrogenic isoflavones (e.g., genistin) that are reported to provide health benefits to some people. These nutraceuticals are products of the shikimate pathway, the target pathway of glyphosate. We were aware that glyphosate resistance was not complete in reproductive tissues in a least some GR crops (see, e.g., ref 33). Thus, we hypothesized that the highest

Table 1. Effects of Three Different Glyphosate Treatments at Two Different Locations on Shikimate, Glyphosate, and AMPA Composition of Harvested Soybean Seed from Field Plots[a] (Adapted from Reference 5)

	μg/g in herbicide treatment[b]			
seed constituent	none	1	2	3
	Stoneville, MS			
shikimate	26	52	45	55
glyphosate	0.103 a	0.181 b	0.480 b	2.18 c
AMPA	0.263 a	0.602 a	0.729 b	7.27 c
	Columbia, MO			
shikimate	57	29	24	60
glyphosate	0.126 a	0.234 b	0.552 b	3.08 c
AMPA	0.126 a	0.862 b	0.492 b	25.0 c

[a] Means within the same row with different letters are significantly different ($P = 0.05$). There are no differences between means in rows without letters. [b] Herbicide treatment 1 contained 1.26 kg/ha glyphosate 3 weeks after planting, followed by 0.84 kg/ha glyphosate 6 weeks after planting. Herbicide treatment 2 contained 1.26 kg/h glyphosate 6 weeks after planting. Herbicide treatment 3 was 1.26 kg/ha glyphosate applied at full bloom (8 weeks after planting).

legal doses of glyphosate applied at the latest legal time of application to soybeans might reduce the concentration of these compounds in harvested soybeans. We conducted field studies in Mississippi and Missouri in which such applications were made.[5] No effects were seen on isoflavone levels in these seeds. However, we reasoned that to have an effect on these compounds in the seed, we would expect that there would have to be glyphosate in the seed. Therefore, we examined the same seed samples for glyphosate and were surprised to find both glyphosate and AMPA in them (Table 1). The levels were sufficiently high to make microbial degradation unlikely. Plants that were sprayed at full bloom had much higher glyphosate and AMPA levels in the seed than those sprayed 2 weeks earlier (Table 1). Very small amounts of glyphosate and AMPA were found in seeds of unsprayed plants due to drift from sprayed plots. Elevated shikimate levels, an indicator of glyphosate inhibition of EPSPS in plant tissues,[34,35] were not seen in the seed. This was to be expected because GR plants should not accumulate shikimate. Also, although poorly studied, longer term studies have indicated that elevated shikimate levels caused by glyphosate action are transitory (see, e.g., ref 36). The year after our study, a study in Argentina with field-grown GR soybeans was published, which reported similar concentrations of glyphosate in seed as well as in leaves and stems.[37] They found AMPA, but at lower levels than the concentrations than we found, except that in one experiment AMPA levels were higher than glyphosate levels in leaves and stems, with a concentration of about 5 μg/g. We later found no differences between GR soybean varieties in their conversion of glyphosate to AMPA, even though there were differences in the efficacy of glyphosate in causing mild phytotoxicity to the different varieties.[38]

Although GR soybeans had been grown for several years at the time of our study, no one had reported glyphosate and AMPA in the plants. A much earlier study had found soybean cell cultures to metabolize glyphosate to AMPA.[39] In a study with nonglyphosate-resistant pea (*Pisum sativum* L.), much higher levels of glyphosate and lower levels of AMPA were found at the early maturation stage of seed development[40] than we found in mature seeds of soybean.

AMPA had been reported to be phytotoxic to soybean by Hoagland.[41] It was significantly less phytotoxic than glyphosate. Nandula et al. [38] found the efficacy of AMPA as a phytotoxin on glyphosate-susceptible canola to be >30-fold less than that of glyphosate. The mode of action of AMPA is unknown, but it apparently has a mode of action different from that of glyphosate, as AMPA increases anthocyanin accumulation in plants, whereas glyphosate reduces it.[41] The accumulation of AMPA leads us to speculate that the occasional reports of mild injury to GR soybeans by glyphosate (see, e.g., refs 42,43) might be due to accumulation of phytotoxic levels of AMPA.[44]

Under greenhouse conditions, we did dose−response studies with technical grade AMPA and glyphosate on GR soybeans.[44] Applications of glyphosate or AMPA that caused similar amounts of AMPA to accumulate in green tissues caused similar reductions in chlorophyll content, supporting the hypothesis that AMPA accumulation is responsible for the occasional reports of mild glyphosate damage to GR crops. Shikimate levels were unaffected by even the highest levels of glyphosate and AMPA used. In this study, glyphosate and AMPA levels in treated leaves were highest one day after treatment, both decreasing over a period of 22 days. Glyphosate levels did not decrease as rapidly as those of AMPA, indicating that AMPA may degrade and/or translocate more rapidly than glyphosate in green treated leaves. The finding that glyphosate levels were higher than AMPA levels and stable in untreated, developing leaves, whereas AMPA levels decreased between 7 and 22 days after spraying in these tissues, suggests that AMPA degradation may account for most of its loss over time.

Conversion of glyphosate to AMPA by soybean indicates that this species possesses a GOX-like enzyme. GR canola contains two transgenes for resistance, the *cp4* and *goxv257* genes. Nontransgenic canola apparently has no GOX enzyme, because metabolism studies had shown no AMPA to accumulate in glyphosate-treated plants.[45] The question arose as to whether AMPA accumulates to higher levels in GR canola than in soybean, and, if so, if it causes injury.[38] If the answer to both questions was yes, one would expect the glyphosate resistance factors for GR soybean and canola to be different. This is not the case, as we found the resistance factor (GR_{50} of the resistant/GR_{50} of the susceptible) to be about 50 for both GR soybean and canola.[38] We were surprised to find that resistance factors for these crops had not been published before. Even though we found AMPA applied like a herbicide to canola to be as phytotoxic to canola[38] as we had earlier found it to be to soybean,[44] accumulating to similar levels in the plant tissues, no phytotoxicity of glyphosate has been reported in GR canola in the field.

Lower glyphosate accumulation levels in GR canola than in soybean suggested that it is more rapidly broken down in canola.[38] The finding that AMPA levels do not accumulate to higher levels in GR canola than in soybean suggests that AMPA is metabolized more rapidly to a nonphytotoxic compound in canola than in soybean.

There is evidence that both glyphosate and AMPA accumulate to lower concentrations in GR crops than in susceptible ones. When the two types of soybeans were sprayed with a dose of glyphosate that causes a 50% reduction in growth rate (GR_{50}) of the susceptible variety (0.25 kg/ha), >5 times more glyphosate and AMPA were found in the susceptible than in the resistant

Table 2. Metabolites of Glyphosate Reported in Weed Species[a]

weed species	AMPA	sarcosine	glycine	ref
Agropyron repens	X			47
Convolulus arvensis	X	X	X	48
Ipomoea purpurea	X	X	X	49
Alternanthera philoxeroides	X			50
Equisetum arvense	X			51
Senna obtusifolia[b]	X			46
Cassia occidentalis[b]	X			46
Desmanthus illinoensis[b]	X			46
Pueraria montana[b]	X			46
Conyza canadensis	X			46

[a] Most of these studies did not look for any metabolite other than AMPA. X = detected. [b] Legumes.

variety when determined 7 days after treatment.[46] There was a 300-fold increase in the shikimate levels in the susceptible variety. In the same type of experiment, a susceptible maize variety had a >2-fold higher glyphosate concentration than a resistant variety at 7 days after treatment with the GR_{50} dose (0.093 kg/ha), but no AMPA was found in either variety. There were no effects on shikimate accumulation at this time point after spraying.

The reasons for higher glyphosate levels in glyphosate-treated susceptible than in resistant tissues in both soybean and maize are probably due to the lack of phytotoxicity in the transgenic varieties. In both transgenic maize and soybean, growth was not inhibited, so the plants that were sprayed at 3 weeks of age grew significantly during the week after spraying. Therefore, the glyphosate was distributed over more plant tissue than in the susceptible plants. There could also have been more loss of glyphosate due to root exudation in the resistant varieties,[27,28] although Laitinen[28] found that AMPA is apparently not exuded by roots. In the healthy tissues of the resistant soybean, there could also have been a greater rate of metabolic degradation, resulting in an even greater differential between susceptible and resistant varieties. This might explain the greater difference in soybean than in maize.

METABOLISM IN GLYPHOSATE-SUSCEPTIBLE AND -RESISTANT WEEDS

Our results with crops suggest that some plants species metabolize glyphosate with a GOX enzyme, whereas others do not. What about weeds, and could metabolism contribute to either natural or evolved resistance to glyphosate? AMPA has been detected after glyphosate treatment of several weed species over the years (Table 2). Many papers that found little or no metabolism of glyphosate in several weeds are excluded from Table 2, but are discussed in earlier reviews.[6,52] Sandberg et al. [49] speculated that the small amount of metabolites they found could be due to contamination of their [^{14}C]glyphosate with small amounts of the metabolites found. However, others found large proportions of radiolabeled material from radiolabeled glyphosate to be AMPA. For example, Marshall et al. [51] reported that although they found almost 4% of the radioactivity in radiolabeled glyphosate to be AMPA, >50% of the radiolabel in treated shoots of *Equisetum arvense* was AMPA. We determined the amount of glyphosate and AMPA in cowpea and eight weeds species 7 days after spraying with the GR_{50} rate of glyphosate for each species.[46] Results of that study are provided in Table 3.

At this point, it appears that some plants possess a GOX enzyme and others do not. Those plants in which AMPA has not been reported could have very low levels of GOX or very high levels of an enzyme that degrades AMPA. Many of the species of both crops and weeds that have been found to metabolize glyphosate to AMPA are legumes. Whether this plays a role in the natural, nonselected resistance of some of these species has not been proven, but it is hard to believe that the high conversion rates of some legumes (Table 3) would not confer at least some level of natural tolerance.

Some morning glory (*Ipomoea*) species are harder to kill at field rates than most weeds.[53,54] This natural resistance (termed tolerance by some) was present before glyphosate was used. There is some evidence that selection with glyphosate has increased the level of natural resistance,[55] although there is no morning glory species on the list of 19 species recognized by the Herbicide Resistance Action Committee to have evolved resistance to glyphosate.[56] Considering that a morning glory [49] and a related species[48] metabolize glyphosate, this purported case of evolved resistance[55] should be examined for changes in the metabolic degradation of glyphosate.

Relatively few of the 19 weed species reported to have evolved resistance to glyphosate have a well-researched mechanism of resistance. The mechanism of resistance of at least one *Conyza* species is sequestration of glyphosate into vacuoles.[57] The mechanism of resistance to *Amaranthus palmeri* is gene amplification of an EPSPS gene.[58] Other cases appear to involve mutation of EPSPS to give a low level of resistance (reviewed by ref 59) and reduced translocation of glyphosate (see, e.g., refs 59,60). No one has found enhanced detoxification of glyphosate to be involved in evolved glyphosate resistance (see, e.g., refs 59−62). This is unexpected, in that the gene for GOX appears to occur in some weed species, suggesting that selection for mutations to confer higher activity with glyphosate as a substrate or gene amplification to enhance activity could occur. One could argue that resistance by metabolic degradation alone might not be sufficient for effective weed resistance, as it has not been chosen for as a sole means for producing GR crops.[4] However, the levels of resistance of almost all weeds that have evolved resistance are much lower than that of GR crops.

Furthermore, we know that many soil microbes have genes for either GOX or a C−P lyase enzyme that will degrade glyphosate. Some of those who warn of the potential harm of transgenic crops discuss horizontal gene transfer from plants to microbes and vice versa as if it were rather common (see, e.g., refs 63−66), although some who work in this area view it as an exceedingly rare phenomenon.[67] With the selection pressure of the most widely used herbicide in the world over many years, one would think that there would be at least one case of horizontal transfer of such a gene from a microbe to a weed. This real world case of incredible selection pressure makes a good case against the probability of horizontal gene transfer from microbes to higher plants.

RESEARCH NEEDS AND PERSPECTIVES

The literature on glyphosate metabolism in plants has been extremely sparse after a flurry of literature within 10 years after the introduction of glyphosate. There are many more papers during the past decade on improved methods for chemical

Table 3. Effects of Glyphosate at the GR_{50} Rate on Glyphosate and AMPA Concentration in Several Plant Species 7 Days after Treatment (Adapted from Reference 46)

plant species	glyphosate treatment (g/ha)	glyphosate (μg/g of tissue)	AMPA (μg/g of tissue)	glyphosate/AMPA ratio
Vigna unguiculata[a]	201	26.8	4.8	6
Senna obtusifolia[a]	252	6.4	1.8	4
Cassia occidentalis[a]	75	5.9	0.3	21
Sesbania exaltata[a]	456	38.7	nd[b]	
Desmanthus illinoensis[a]	272	3.3	1.5	2
Pueraria montana[a]	77	5.6	0.3	19
Abutilon theophrasti	122	0.7	nd	
Conyza canadensis	170	26.3	0.3	84
Lolium perenne	220	7.4	nd	

[a] Legumes. [b] nd, not detected.

analysis of glyphosate and its metabolites than there are papers using the methods to answer substantive questions regarding the fate of glyphosate in crops and other plants, including weeds. This is surprising when one considers the importance of GR crops and evolved resistance of weeds to glyphosate. There are still significant questions that have not been answered.

Is glyphosate metabolized by plant endophytes? We know that many microbes metabolically degrade glyphosate and that many plants harbor microbial endophytes that can have profound effects on the chemical and other properties of plants.

Few studies in peer-reviewed papers have looked for metabolites other than AMPA. A recent paper [68] reported that the major identified metabolite of glyphosate injected into the lead tree (*Leucaena leucoephala*) was sarcosine, concluding that a C−P lyase was responsible. However, most of the metabolism occurred between 45 and 90 days after injection, making microbial involvement a possibility. Nevertheless, whether there is a plant C−P lyase deserves further study.

Simply looking at glyphosate and its metabolites at one point in time after application can be very misleading. The few papers that have found glyphosate metabolism in plants, including ours, do not examine the kinetics and flux of glyphosate conversion to AMPA and loss of AMPA due to further metabolic degradation. Because glyphosate readily translocates and is even exuded from roots, making such a study is complicated. Studies examining the kinetics of the degradation of glyphosate and its metabolites over time after application are much needed.

Neither plant GOX nor the genes encoding it have been isolated or elucidated. This seems to be a highly important project. A plant gene encoding GOX might be useful in genetically engineering crops for resistance. Understanding the actual purpose of this enzyme in the biochemistry and physiology of the plants that possess it could also be important. Furthermore, there must be a plant enzyme that degrades AMPA. What is its true function in the plant? Is the GOX gene induced by exposure of the plant to glyphosate?

What is the mode of action of AMPA? It is much less active than glyphosate and apparently has a different mode of action. Can plants be made resistant to AMPA, or can AMPA degradation be increased to reduce the potential for glyphosate injury to those that contain GOX? Are weeds that are resistant to glyphosate by means of sequestration[57] also resistant to AMPA by the same mechanism?

These are but a few of the questions that remain unanswered about glyphosate degradation in transgenic and conventional crops and in both naturally and evolved resistant weeds.

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