

GLYPHOSATE-RESISTANT WEEDS: CURRENT STATUS AND FUTURE OUTLOOK

Vijay K. Nandula,¹ Krishna N. Reddy*,² Stephen O. Duke,³ and Daniel H. Poston¹ review the current situation regarding the development of glyphosate resistant weeds following the increased cultivation of glyphosate-resistant crops and warn of a real loss in glyphosate efficacy if its uncontrolled use continues

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Introduction

Glyphosate [*N*-(phosphonomethyl)glycine] is a non-selective, broad spectrum, systemic, post-emergence herbicide that has been used extensively throughout the world over the past three decades. It inhibits the biosynthesis of aromatic amino acids (phenylalanine, tryptophan, and tyrosine), which leads to several metabolic disturbances, including the inhibition of protein and secondary product biosynthesis (Franz *et al.*, 1997) and the deregulation of the shikimate pathway, leading to general metabolic disruption (Duke *et al.*, 2003).

Since the discovery of its herbicidal properties in 1971 and commercialization in 1974, glyphosate has been used extensively in both crop and non-crop lands. Because of its lack of selectivity, glyphosate use was initially limited to preplant, post-directed, and post-harvest applications for weed control. With the introduction of glyphosate-resistant (GR) crops in the mid 1990s, glyphosate is now widely used for weed control in GR crops without concern for crop injury. GR crops were created by stable integration of a transgene from *Agrobacterium* sp. that encodes for glyphosate-insensitive 5-enolpyruvylshikimate-3-phosphate synthase (EPSPS), the target enzyme of glyphosate in the shikimate pathway (Padgett *et al.*, 1996). Expression of GR EPSPS enzyme helps to maintain normal aromatic amino acid levels in GR crops treated with glyphosate. GR canola, maize, cotton, and soybean have been commercialized in North America since 1996. GR crops are now grown in several countries, with particularly strong adoption in North America, Argentina, Brazil, and China. History, development, and adoption of herbicide-resistant crops in general and GR crops in particular and their impact on weed management are the topics of recent reviews (Dill, 2005; Duke, 2005; Reddy and Koger, 2005).

No evolved resistance to glyphosate was documented until GR rigid ryegrass (*Lolium rigidum*) was found in 1996

(Powles *et al.*, 1998), about 20 years after the introduction of glyphosate. In recent years, the intense use of glyphosate in GR crops has increased selection pressure to evolve natural resistance to glyphosate in several weed populations. This article briefly summarizes the current status and potential future of glyphosate resistant weeds, as well as strategies to prevent future evolution of glyphosate resistant weeds.

Naturally-resistant weed species

Several weed species are inherently more resistant to glyphosate than most other weeds (Table 1). A naturally-occurring, GR biotype of field bindweed (*Convolvulus arvensis*) has been reported with no history of glyphosate use (DeGennaro & Weller 1984). A biotype of birdsfoot trefoil (*Lotus corniculatus*) resistant to labeled glyphosate use rates was identified by Boerboom *et al.* (1990). Recent reports suggest that tropical spiderwort (*Commelina benghalensis*) (Culpepper *et al.* 2004), Asiatic dayflower (*Commelina communis*), Chinese foldwing (*Dicliptera chinensis*), common lambsquarters (*Chenopodium album*), and velvetleaf (*Abutilon theophrasti*) (Owen & Zelaya, 2005) are difficult to control with glyphosate. Natural resistance of these species to glyphosate was not an issue until widespread adoption of GR crops, when many of these species became more problematic as they occupied ecological niches vacated by other weed species in fields of GR crops. This process has been termed "weed shifts."

Evolved glyphosate resistance

The widespread adoption of GR crops has not only shifted weed species in these crops towards naturally resistant species, but it also resulted in evolution of GR weed biotypes. To date, a total of eight weed species have evolved resistance to glyphosate (Table 1). They are common ragweed (*Ambrosia artemisiifolia*), 2004, USA; hairy fleabane (*Conyza bonariensis*), 2003, South Africa and 2004, Spain; horseweed (*Conyza canadensis*), 2000–2003, USA (multiple locations); goosegrass (*Eleusine indica*), 1997, Malaysia; Italian ryegrass (*Lolium multiflorum*), 2001–2002, Chile and 2003, Brazil; rigid ryegrass, 1996–2000, Australia (multiple

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GLYPHOSATE-RESISTANT WEEDS

Table 1: Weed species that are resistant to glyphosate*

Weed Species	Year confirmed	Crop situation	Reference
Natural Resistance			
Asiatic dayflower (<i>Commelina communis</i> L.)**	2005	Cotton, peanut, soybean	Owen and Zelaya, 2005
Birdsfoot trefoil (<i>Lotus corniculatus</i> L.)	1990	Regenerated from callus	Boerboom et al., 1990
Chinese foldwing (<i>Dicliptera chinensis</i> (L.) Juss)	2002	Orchard	Yuan et al., 2002
Common lambsquarters (<i>Chenopodium album</i> L.)**	2005	GR Soybean	Owen and Zelaya, 2005
Field bindweed (<i>Convolvulus arvensis</i> L.)	1984	Unknown	DeGennaro and Weller, 1984
Tropical spiderwort (<i>Commelina benghalensis</i> L.)	2004	GR Cotton	Culpepper et al., 2004
Velvet leaf (<i>Abutilon theophrasti</i> (L.) Medic)**	2005	GR Soybean	Owen and Zelaya, 2005
Evolved Resistance			
Buckhorn plantain (<i>Plantago lanceolata</i> L.)***	2003	Orchard & vineyard	Heap, 2005
Common ragweed (<i>Ambrosia artemisiifolia</i> L.)***	2004	GR Soybean	Heap, 2005
Common waterhemp (<i>Amaranthus tuberculatus</i> (Moq.) J.D. Sauer)**	2005	GR Soybean	Owen and Zelaya, 2005
Goosegrass (<i>Eleusine indica</i> (L.) Gaertn.)	1997	Orchard	Lee and Ngim, 2000
Hairy fleabane (<i>Conyza bonariensis</i> L.)***	2003	Orchard & vineyard	Heap, 2005
Horseweed (<i>Conyza canadensis</i> (L.) Cronq.)	2000	GR Soybean	VanGessel, 2001
	2003	Unknown	Mueller et al., 2003
	2003	GR Cotton	Koger et al., 2004
Italian ryegrass (<i>Lolium multiflorum</i> L.)	2001	Orchard	Pérez and Kogan
Rigid ryegrass (<i>Lolium rigidum</i> Gaud.)	1996	Summer & winter crops	Pratley et al., 1999
	1997	Orchard	Powles et al., 1998
	1998	Orchard	Simarmata et al., 2003

* In case of multiple reports of evolved resistance in same weed species, a representative peer-reviewed publication is shown.

** Based on anecdotal evidence. Resistance not confirmed by peer reviewed publications.

*** Reported on website by Heap (2005). Authors are not aware of resistance reported in peer reviewed publications.

locations), 1998, USA, and 2001–2003, South Africa (multiple locations); and buckhorn plantain (*Plantago lanceolata*), 2003, South Africa (Heap, 2005; Koger *et al.*, 2004; Lee & Ngim, 2000; Powles *et al.*, 1998; Pratley *et al.*, 1999; VanGessel, 2001). Glyphosate resistance in common waterhemp (*Amaranthus tuberculatus*) has also been documented (Owen & Zelaya, 2005). Among these eight weed species, common ragweed, common waterhemp, horseweed, and rigid ryegrass are common to cropland, whereas, hairy fleabane, goosegrass, Italian ryegrass, and buckhorn plantain have been selected from orchards and vineyards. The history of herbicide selection pressure and evolution of glyphosate resistance in the above weed species is discussed briefly below.

Rigid and Italian ryegrass

The ability of rigid ryegrass to accumulate resistance mechanisms and acquire cross-resistance is attributed to its widespread distribution within cropping regions, prolific seed set, cross-fertilization, as well as significant genetic variability and phenotypic plasticity. The first evidence of evolved resistance to glyphosate in a weed species was reported by Powles *et al.* (1998). A rigid ryegrass population from an orchard in Australia (Orange, New South Wales), exposed to 2 to 3 glyphosate applications per year for 15 years, exhibited a 7- to 11-fold resistance compared to a susceptible population (Figure 1). In a second report on glyphosate resistant rigid ryegrass from Australia, a ryegrass

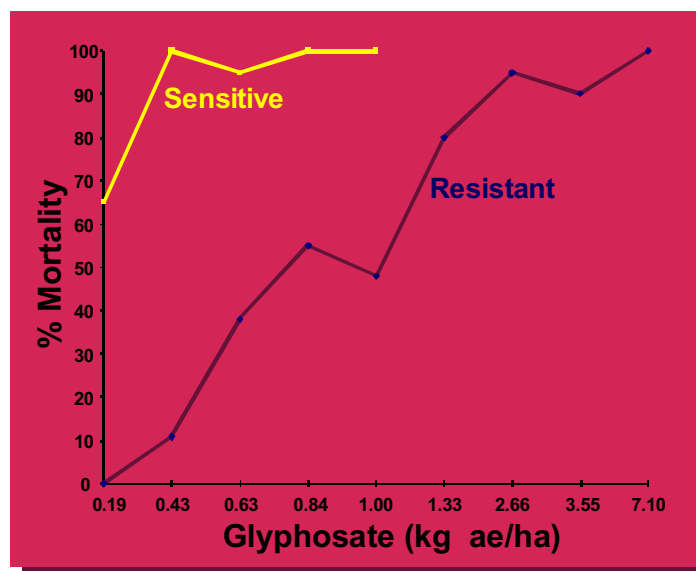


Figure 1. Dose-response relationships for glyphosate on resistant and susceptible biotypes of rigid ryegrass from Australia. Courtesy of Scott R. Baerson.

biotype selected from a population (Echuca, Northern Victoria) exposed to glyphosate applications for 15 years was nearly 10-fold more resistant compared to a susceptible biotype (Pratley *et al.*, 1999). ¹⁴C-glyphosate uptake, translocation, and metabolism comparisons between the resistant and susceptible rigid ryegrass biotypes revealed no

differences (Feng *et al.*, 1999). The transcription of genes for sensitive EPSPS went up 3-fold in the most resistant biotype, but the investigators did not attribute all of the resistance to this difference between GR and susceptible biotypes (Baerson *et al.*, 2002a). Lorraine-Colwill *et al.* (2003) showed that glyphosate accumulates preferentially in the roots of susceptible plants, whereas more of it accumulates in the leaf tips of resistant plants. They concluded that an alteration to the cellular transport of glyphosate confers resistance.

Italian ryegrass populations from a fruit orchard in Chile exposed to three glyphosate applications annually for 8 to 10 years, evolved 2- to 4-fold resistance compared to susceptible population (Pérez & Kogan, 2003). This is the first case of glyphosate resistance reported from South America. In Italian ryegrass, Pérez *et al.* (2004) reported no differences in uptake and translocation of glyphosate between GR and susceptible populations.

Horseweed

Horseweed is a summer/winter annual broadleaf weed species that is native to northern North America (Koger *et al.*, 2004). Widespread evolution of glyphosate resistance in horseweed populations could be attributed to its ability to germinate and establish in undisturbed soils, to colonize no-till fields, to adapt to varying habitats (crop and noncrop lands), together with the popularity of reduced or no-till tillage practices, its vast seed production potential and wind dispersal of seed (Koger *et al.*, 2004; VanGessel, 2001).

All documented reports of GR horseweed have come from the USA. Monoculture of GR soybean has resulted in less than acceptable control of horseweed populations within 3 years of using only glyphosate for weed control in Delaware (VanGessel, 2001). Greenhouse screenings of one such population from Delaware revealed 8- to 13-fold glyphosate resistance compared to a susceptible population, representing the first documented evidence of evolved glyphosate resistance in a GR crop, as well as the first broadleaf weed to evolve glyphosate resistance. Koger *et al.* (2004) documented horseweed biotypes from a field planted to GR cotton for three consecutive years (2000–2002) and a field planted to GR soybean (2000) followed by GR cotton (2001 and 2002). These biotypes exhibited an 8- to 12-fold level of resistance to glyphosate compared to a susceptible biotype in Mississippi (Figure 2). Obviously, rotation of GR crops (cotton and soybean) is not a prudent option to prevent evolution resistance in horseweed.

Feng *et al.* (2004) found reduced movement of ^{14}C -glyphosate out of a treated single leaf and reduced translocation to other leaves, roots, and crown in the Delaware resistant biotype compared to corresponding plant parts of a susceptible biotype. Similarly, the level of ^{14}C -glyphosate that translocated out of the treated leaf was lower in the resistant biotypes compared with susceptible biotypes. The difference ranged from 28 to 48% between respective resistant and susceptible biotypes from different states in a study comparing absorption and translocation pattern of ^{14}C -glyphosate in resistant and susceptible horseweed biotypes from Mississippi, Arkansas, Delaware, and



Figure 2. Glyphosate-resistant (left column) and susceptible (right column) horseweed biotypes from Mississippi. Two fully expanded leaves of plants in bottom row were treated with glyphosate, and plants in the upper row were not treated. Ten microliter of glyphosate (0.84 kg ae/ha in 190 L of water; 1X field rate) solution was placed on each leaf as 20 droplets. Three weeks after treatment, the susceptible plant was killed, and the resistant plant survived, suggesting reduced translocation of glyphosate (Koger and Reddy, 2005).

Tennessee (Koger & Reddy, 2005). All resistant horseweed biotypes were 8- to 12-fold more resistant to glyphosate than a susceptible biotype (Koger *et al.*, 2004). The above results strongly suggest that resistance in horseweed biotypes is due to reduced translocation of glyphosate to growing parts of the plant.

Goosegrass

Goosegrass, an annual grass, thrives in a wide range of environment that includes south Asia, eastern and southern Africa, and North America. It is considered one of the ten “most important herbicide-resistant species” and its populations have evolved resistance to many herbicides, including acetolactate synthase inhibitors, acetyl-CoA carboxylase inhibitors, bipyridiliums, dinitroanilines, and glyphosate (Heap, 2005). A goosegrass biotype originating from a fruit orchard in Malaysia is 8- to 10-fold resistant to glyphosate (Lee & Ngim, 2000). The mechanism of glyphosate resistance in other GR goosegrass biotypes from Malaysia was apparently partly due to an EPSPS target site mutation of proline to serine at position 106 (Baerson *et al.*, 2002b), representing the first report for a glyphosate resistance mechanism involving an altered EPSPS enzyme in any plant species. The GR form of EPSPS from goosegrass has been patented for potential use in creating GR crops.

Common waterhemp, common ragweed, hairy fleabane, and buckhorn plantain

Not much is known about these weeds regarding the nature of selection pressure, resistance mechanism or genetics. These weeds are reported on a website by Heap (2005) and a review by Owen and Zelaya (2005); however peer-reviewed

publications are not available. Biotypes of common waterhemp (*Amaranthus tuberculatus*) were reported in 1998 in GR soybean to be more resistant than other biotypes (Owen & Zelaya, 2005). However, variation among natural biotypes (Patzoldt *et al.*, 2002) suggests that selection has been for existing biotypes, rather than evolved resistance.

Common ragweed was reported to have evolved resistance to glyphosate in GR soybean in Missouri in 2004. A hairy fleabane population in South Africa derived from an orchard/vineyard was controlled only 17% with a glyphosate rate that was twice the normal use rate (1.08 kg ae/ha). A resistant population of hairy fleabane in Spain was 10-fold more resistant than a susceptible population. In 2003, a resistant buckhorn plantain population from an orchard in South Africa was controlled only 18% with a 2.88 kg/ha glyphosate rate, which was twice the recommended rate for control of this weed.

The mechanisms of herbicide resistance in weeds are reduced herbicide absorption, reduced translocation of herbicide from the site of absorption to the target site, rapid metabolic detoxification of herbicide, and altered herbicide target site. Thus far, only two of these mechanisms, reduced translocation of glyphosate in the resistant rigid ryegrass and horseweed biotypes and an altered target site in goosegrass, appear to play a major role in glyphosate resistance.

Future outlook

Farmers in the USA have rapidly adopted GR crops, planting about 85% of soybean, 60% of cotton, and 18% of maize hectares to GR varieties in 2004 (Duke, 2005). Consequently, use of glyphosate has increased dramatically with concomitant decreases in the use of other (non-glyphosate) herbicides. For example, the total active ingredient of glyphosate application increased from 107,000 kg/year in 1995 to 1,500,000 kg/year in 2002 in maize, from 320,000 kg/year in 1995 to 3,863,000 kg/year in 2001 in cotton, and from 2,867,000 kg/year in 1995 to 27,206,000 kg/year in 2002 in soybean (<http://www.usda.gov/nass/pubs/histdata.htm>). Furthermore, with the expiration of the glyphosate patent in 2000, several generic formulations of glyphosate are now commercially available at discounted prices. This translates to lower cost of weed control and improved profits for farmers with most GR crops. The problem of weed species evolving resistance is expected to increase with intense use of glyphosate and continued adoption of GR crops without rotation with non-GR crops. Already, the appearance of evolved resistant biotypes to glyphosate heralds this problem on a global scale.

Glyphosate-resistant weed management strategies

The increasing adoption of GR crops has exerted tremendous herbicide selection pressure on weed populations over the past decade. Farmers should not rely completely on GR crops to manage weeds to the exclusion of other weed management options. Alternating herbicides with different modes of

action or tank mixing herbicides with different modes of action are common recommendations in resistance management programs; however, these practices are often ignored by farmers for economic reasons as the cost of weed control is cheaper with GR crops using glyphosate alone. Increased awareness of weed resistance by farmers, field scouting for early detection, monitoring of farms for weed species and population shifts, and record keeping are critical to delay or prevent resistance from occurring. Cultural (crop rotation, winter crops in rotation, cover crops), mechanical (tillage before planting, cultivation), and chemical (herbicide rates, tank mixtures, sequences, application timing, herbicide rotation with different modes of action) weed control practices must be used as dictated by grower needs to control resistant weeds. Rotation between GR cultivar and non-GR cultivar of the same crop could aid in delaying the evolution of glyphosate-resistance in weeds. Thus, prudent use of glyphosate with other chemistries based on weeds, farm size, and economics by growers is critical in managing GR weeds.

Conclusions

Introduction of GR transgenic crops has revolutionized weed management. GR crops as weed management tools have allowed farmers to manage weeds more effectively and economically. High levels of adoption of GR crops by U.S. farmers have dramatically increased the use of glyphosate, with a concomitant decrease in use of other herbicides. This has impacted weed communities. Evolution of weeds resistant to glyphosate and weed species shifts towards naturally resistant species in GR crops require alternative strategies to manage weeds. GR crops should not be relied upon solely with the use of their respective herbicides to the exclusion of other weed control methods, but should be used within integrated management systems. The problem of GR weeds is real, and farmers have to understand that continuous use of glyphosate without alternative strategies will likely result in the evolution of more GR weeds. Even in the short term, no one can predict the future loss of glyphosate efficacy due to weed species shifts and evolution of glyphosate resistance. This will depend on whether mitigation strategies are adopted by farmers and the inherent predisposition of many different weed species to evolve resistance or to move into agricultural ecosystems.

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