Review

Glyphosate-resistant weeds of South American cropping systems: an overview

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Abstract: Herbicide resistance is an evolutionary event resulting from intense herbicide selection over genetically diverse weed populations. In South America, orchard, cereal and legume cropping systems show a strong dependence on glyphosate to control weeds. The goal of this report is to review the current knowledge on cases of evolved glyphosate-resistant weeds in South American agriculture. The first reports of glyphosate resistance include populations of highly diverse taxa (*Lolium multiflorum* Lam., *Conyza bonariensis* L., *C. canadensis* L.). In all instances, resistance evolution followed intense glyphosate use in fruit fields of Chile and Brazil. In fruit orchards from Colombia, *Parthenium hysterophorus* L. has shown the ability to withstand high glyphosate rates. The recent appearance of glyphosate-resistant *Sorghum halepense* L. and *Euphorbia heterophylla* L. in glyphosate-resistant soybean fields of Argentina and Brazil, respectively, is of major concern. The evolution of glyphosate resistance has clearly taken place in those agroecosystems where glyphosate exerts a strong and continuous selection pressure on weeds. The massive adoption of no-till practices together with the utilization of glyphosate-resistant soybean crops are factors encouraging increase in glyphosate use. This phenomenon has been more evident in Argentina and Brazil. The exclusive reliance on glyphosate as the main tool for weed management results in agroecosystems biologically more prone to glyphosate resistance evolution.

Keywords: glyphosate; resistance; evolution; weeds

1 INTRODUCTION

Since crop–pest interactions reduce net primary production of crops, agroecosystems are constantly subjected to energy flows in the form of subsidies that attempt to minimize those biological interactions. Herbicides are the most employed subsidies in modern agriculture, accounting for the greatest use of pesticides.[1] Benefits of herbicide technology must be found not only in crop yield increments driven by efficient weed control but also in profitability.[2]

In the last two decades accelerated evolutionary changes in weeds of arable land have been derived from intense and repetitive use of herbicides.[3] Herbicide resistance is nowadays a common biological phenomenon in many agricultural cropping systems around the planet.[4] Herbicide resistance is a plant trait present at very low frequencies in herbicide-unselected weed populations.[5] The laws that regulate resistance evolution are those involved in any adaptive evolutionary process driven by natural selection.[6] A strong selection pressure (herbicides) over genetically variable organisms (weeds) is necessary for the evolution of herbicide resistance. Herbicide resistance genes endow such a fantastic survival and reproduction advantage that only a few generations under continuous herbicide selection are necessary to enrich a weed population with high levels of herbicide resistance.[5]

Glyphosate [*N*-(phosphonomethyl)glycine] is the most widely used herbicide in the world. The leadership of this herbicide is attributable to its low cost, effectiveness, reduced environmental impact and its excellent crop safety when using glyphosate-resistant crops.[7] In the cropping systems of South America, glyphosate is an essential tool in all weed management programs, especially since the adoption of no-till and glyphosate-resistant crops. The authors review the documented cases of glyphosate resistance evolution in weed species affecting South American cropping systems and evaluate the progress made in this key research area up to the present.

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2 GLYPHOSATE RESISTANCE IN ORCHARD AND WINTER CEREAL FIELDS

Fruit production (apple, grape, lemon, orange) in Argentina, Brazil and Chile represents a major agricultural activity that makes the mentioned countries important suppliers of high-quality fresh fruit to the world market.[8] Weed control in these orchard systems is achieved largely by several applications of glyphosate a year. It is not surprising that the first cases of glyphosate resistance in South America evolved in an obligate outcrossing and genetically diverse grass, *Lolium multiflorum* (Lam.). A history of 10 years of intense glyphosate use (an average of 3.7 kg ae ha^{-1} $year^{-1}$) in fruit orchards from central Chile led to selection of glyphosate-resistant *L. multiflorum* populations (Fig. 1).[9] Assays evaluating aerial vegetative biomass and seed germination after glyphosate exposure revealed a 2–5-fold resistance ratio between resistant populations and a glyphosate-susceptible *L. multiflorum* reference population (Table 1).[9,10] Subsequent studies assessing the physiological and molecular bases endowing glyphosate resistance found no differences in glyphosate leaf absorption and translocation between resistant and susceptible biotypes.[11] A recent report evaluating a single *L. multiflorum* population documents a target-site mutation in the 5-enolpyruvylshikimate-3-phosphate (EPSPS) gene, causing a proline-to-serine amino acid substitution at residue 106 of the EPSPS protein as the mechanism endowing glyphosate resistance.[10]

Wheat (currently 400 000 ha planted area) and other winter cereals (barley and oat) are important and traditional crops grown in southern Chile that are usually infested with high densities of *L. multiflorum*. Recent reports also indicate evolution of glyphosate resistance in these *L. multiflorum* populations. An evaluation of a single population collected from these glyphosate-treated fallow fields revealed a fivefold resistance to glyphosate in relation to a glyphosate-susceptible population (Espinoza N, personal communication, 2007). Interestingly, this glyphosate-resistant *L. multiflorum* exhibits low levels of resistance to the wheat-selective acetolactate synthase (ALS) inhibitors iodosulfuron

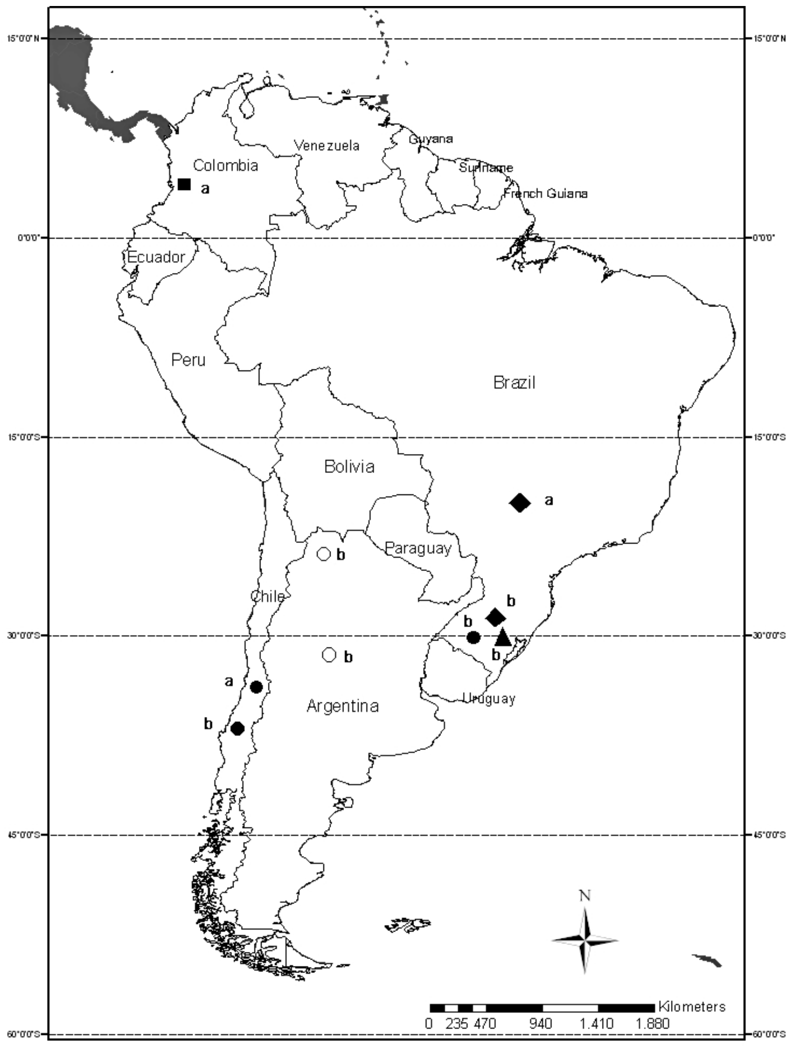

Figure 1. Geographical locations of confirmed cases of evolved glyphosate resistance in weed species of South American agriculture. *Lolium multiflorum* (●), *Conyza bonariensis* and *C. canadensis* (♦), *Euphorbia heterophylla* (▲), *Parthenium hysterophorus* (■) and *Sorghum halepense* (○). Letters (a, b) denote cropping systems of selected glyphosate-resistant weeds: a, fruit orchards; b, fallow and/or glyphosate-resistant soybean fields.

Table 1. Documented cases of glyphosate-resistant weeds in cropping systems of South America. Summary of the involved agroecosystem, weed species, resistance factor and mechanism endowing glyphosate resistance

Weed species	Location	Cropping system	Resistance estimated parameter (g ae ha^{-1})	R/S[c]	Mechanism of resistance	References
Lolium multiflorum	Central Chile	Fruit orchard	GR_{50}: 290 (S)[a]		No differential absorption and translocation	9,11
			630 (R)[b]	2.2		
			1180 (R)	4.0		
			LD_{50}: 32 (S)	5.0	Target-site EPSPS gene mutation	10
			160 (R)			
	Southern Chile	Fallow	GR_{50}: 149 (S)	4.6		Espinoza N (personal communication)
			683 (R)			
L. multiflorum	Southern Brazil	Apple orchard	GR_{50}: 288 (S)	16.7	Reduced translocation	13, 14, 15, 19
			4833 (R)			
		Fallow				
Conyza bonariensis	Central Brazil	Citrus orchards	LD_{50}: 135 (S)	10.4–14.7	Unknown	22
			1404–1992 (R)[d]			
			GR_{50}: 149 (S)			
			226–746 (R)[e]	1.5–5.0		
C. canadensis	Central Brazil	Citrus orchards	LD_{50}: 145 (S)	7.1–10.8	Unknown	22
			1032–1570 (R)[d]			
			GR_{50}: 70 (S)	6.1–6.6		
			435–471 (R)[e]			
Parthenium hysterophorus	West Colombia	Fruit orchards		2.5–3.5	Unknown	23
C. bonariensis	Southern Brazil	Transgenic soybean	LD_{50}: 289 (S)	2.4	Unknown	25
			705 (R)			
C. canadensis	Southern Brazil	Transgenic soybean	LD_{50}: 284 (S)	2.4	Unknown	25
			677 (R)			
Euphorbia heterophylla	Southern Brazil	Transgenic soybean	LD_{50}: 131 (S)	3.3	Unknown	27
			433 (R)			
Sorghum halepense	Northern Argentina	Transgenic soybean	LD_{50}: 213 (S)	4.5	Unknown	28
			966 (R)			
			[f]GR_{50}: 77 (S)	8.0		
			617 (R)			
			[g]GR_{50}: 620 (S)	4.3		
			2641 (R)	4.3		
	Central Argentina	Corn, transgenic soybean	[f]GR_{50}: 178 (S)	≥5.25	Unknown	Trucco F and Tranel PJ (unpublished)
			935 (R)			

[a] (S) denotes glyphosate-susceptible population, (R) denotes glyphosate-resistant population.
[b] (R) Indicates the lowest glyphosate concentration used in the assay that totally controlled the glyphosate-susceptible population.
[c] Calculated as GR_{50}(R)/GR_{50}(S) or LD_{50}(R)/LD_{50}(S).
[d] LD_{50} values obtained from two assessed populations.
[e] GR_{50} values obtained from two assessed populations.
[f] Estimated parameter after evaluation of plants at young stage.
[g] Estimated parameter after evaluation of plants at adult stage.

and flucarbazone-sodium, suggesting the existence of at least two mechanisms endowing resistance (i.e. multiple resistance).[12]

Lolium multiflorum populations have also evolved resistance to glyphosate in fruit orchards from southern Brazil (Fig. 1). In the Brazilian state of Rio Grande do Sul, weed control in rows of apple trees has been performed recurrently with glyphosate (an average of 3.15 kg ae ha^{-1} $year^{-1}$) over the past 15 years. A study reveals the existence of a population exhibiting 16-fold resistance when compared with a glyphosate-susceptible control.[13] Evidence shows reduced glyphosate translocation from the treated leaves to other organs of the resistant plants. At 64 h after glyphosate treatment, only 20% (10% in roots and 10% in shoots) glyphosate was recovered from plants of the resistant population, whereas 48% (28% in roots and 20% in shoots) of the absorbed glyphosate was found in plants of the susceptible population.[14] The evaluated resistant population also showed higher above-ground biomass in relation to a susceptible biotype when exposed to acetyl co-enzymeA carboxylase (ACCase) inhibitors.[14,15] However, evidence supporting cross-resistance to graminicides in this glyphosate-resistant population is inconclusive. In the absence of herbicide selection, this glyphosate-resistant *L. multiflorum* population showed a remarkable 40% less vegetative growth and

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44% less reproductive biomass yield in comparison with a control glyphosate-susceptible population.[14] These growth penalties suggest a pleiotropic effect or fitness cost associated with glyphosate resistance. Given the dissimilar genetic backgrounds of the glyphosate-resistant and susceptible populations that were compared, these results should be taken with caution.[16–18]

Lolium multiflorum is usually grown as pasture and cover crop in no-till systems in southern Brazil. During fallow, volunteer *L. multiflorum* plants are controlled with glyphosate. Under these cropping conditions, Roman *et al.*[19] also reported a case of evolved glyphosate resistance in a *L. multiflorum* population that notably survived 5.7 kg ae ha^{-1} of glyphosate.

In central Brazil (Sao Paulo state), glyphosate-resistant *Conyza bonariensis* (L.) and *C. canadensis* (L.) populations have been documented in citrus orchards where glyphosate has been the predominant herbicide used since the early 1990s with field rates ranging from 720 to 1440 g ae ha^{-1} (Fig. 1).[20–22] For these two species, resistant-to-susceptible ratios based on plant survival after glyphosate exposure have been estimated to be as high as 14.7 (*C. bonariensis*) and 10.8 (*C. canadensis*) (Table 1).[22] Alternative herbicides such as metsulfuron (ALS inhibitor), metribuzin (photosystem II inhibitor) and 2,4-D (auxin analog herbicide) have shown high efficacy in controlling these glyphosate-resistant *Conyza* species.[22]

Similarly, *Parthenium hysterophorus* L., a composite annual herbaceous plant native to Central and South America, has evolved resistance after 15 years of continuous glyphosate selection in fruit orchards of Colombia (Department of Valle del Cauca). Greenhouse and field dose–response experiments have shown a 3.5 resistance index in this invasive weed population.[23]

3 GLYPHOSATE RESISTANCE IN TRANSGENIC SOYBEAN

Brazil and Argentina are respectively the second and third largest soybean producers in the world, accounting for nearly 50% of the total soybean production.[24] The massive adoption (99%) of glyphosate-resistant soybean cultivars by Argentinean farmers has resulted in a very heavy reliance on glyphosate to control weeds in fallow and soybean fields over the last decade. Likewise, since the official release in 2003, the same trend has been observed in Brazil, where 40–50% of the current soybean acreage is grown with glyphosate-resistant soybean varieties.

Four weed species have evolved glyphosate resistance in no-till glyphosate-resistant soybean cropping systems (Table 1). Glyphosate-resistant *C. bonariensis* and *C. canadensis* populations have been reported to infest respectively 500 ha and 100 ha in southern Brazil.[25] Vargas *et al.*[26] found a *C. bonariensis* population displaying high levels of glyphosate resistance at 2.8 kg ae ha^{-1} when compared with a susceptible population controlled at 720 g ae ha^{-1}. From this experiment, a resistance ratio greater than 4 was calculated for the glyphosate-resistant *C. bonariensis* population.

In a southern Brazilian area of 100–200 ha over a plain agricultural landscape (Fig. 1), control failures of the summer annual weed *Euphorbia heterophylla* (L.) after yearly glyphosate applications have been reported as well. In this soybean-cropped area, Brazilian producers have been successfully implementing weed control programs with glyphosate doses (360–540 g ae ha^{-1}) below the recommended field rates (720–1080 g ae ha^{-1}). Investigating these glyphosate escapes, Vidal *et al.*[27] report that *E. heterophylla* populations have evolved resistance to the current glyphosate-selective environment (Table 1). A characteristic phenotypic response of the resistant *E. heterophylla* individuals to the glyphosate selection effect was the emergence of new shoots from lateral buds.[27]

Sorghum halepense (L.), a successful perennial weed of summer crops, has been recognized as one of the most troublesome weeds of agriculture. In Argentinean cropping systems, the use of glyphosate and no-till have been exceptionally effective agronomic practices to keep *S. halepense* populations at low densities in corn and soybean fields. However, in recent years, producers of glyphosate-resistant soybean crops from northern Argentina (provinces of Salta and Tucumán) (Fig. 1) have observed a significant reduction in glyphosate efficacy in the control of this rhizomatous weed. Experimental evaluations using plants derived from rhizomes and seeds have recently demonstrated that reported glyphosate control failures are due to evolved resistance in several *S. halepense* populations from northern[28] and central (province of Córdoba) Argentina (Trucco F and Tranel PJ, unpublished) (Fig. 1 and Table 1). Assessment of shikimate accumulation in glyphosate-treated leaves revealed a different response between glyphosate-resistant and -susceptible *S. halepense* populations. In a glyphosate dose dependent manner, significantly more shikimate accumulated in the susceptible individuals than in the resistant ones.[29] The molecular basis endowing glyphosate resistance in *S. halepense* is currently under investigation.

4 SHORT- AND LONG-TERM ACTION STRATEGIES

Regardless of the geographical location, it is evident that the agroecological environments of South American cropping systems in which weed species have evolved glyphosate resistance are similar: strong glyphosate selection pressure over genetically diverse weed populations infesting large cropped areas with minimal crop rotation. The current favorable international market conditions for commodities, in combination with low glyphosate prices, strongly indicate that planted areas with glyphosate-resistant crops (soybean, corn) will continue to increase not only in Argentina and Brazil but also in other countries such as Paraguay and Uruguay, making those key conditions that favor evolutionary changes (i.e. glyphosate resistance) in weed populations persist and exacerbate the situation.

The adoption of integrated management strategies to prevent or reduce the impact of glyphosate-resistant weeds is critical to maintain sustainable agricultural systems. However, the implementation of these strategies requires a knowledge of the genetics, physiology and ecology of herbicide-resistant weed populations.[30,31] Furthermore, the prediction of the occurrence and evolution of glyphosate resistance also involves an understanding of the biological attributes that play a major role in how they interact with environmental factors to influence the outcome of herbicide resistance in weed populations. For example, the evolution of glyphosate resistance in *S. halepense* is a major threat to glyphosate-resistant soybean productivity in northern fields of Argentina. The current estimated infested area (100 000 ha), the perennial habit and the existence of two growth propagation strategies (seeds and rhizomes) in this 'C 4' weed pose a challenge in terms of management of resistance. Studies including the expression of cross-resistance or multiple resistance, the mechanism/s endowing resistance, heritability and flow of resistance gene/s (dominance, seed dispersal) and expression of fitness costs associated with glyphosate resistance are essential to help optimize those agronomic practices (spray timing, use of herbicides with dissimilar mode of action and herbicide mixtures, prevention of weed seed contamination) to mitigate the impact of glyphosate-resistant *S. halepense*. However, in the long term, an integrated approach that considers systematic crop and herbicide rotations (less reliance on glyphosate as the only burndown herbicide), crop cultivars with higher competitive ability, minimal tillage or cultivation and changes in the crop seeding date and density will likely reduce the rate of glyphosate resistance evolution in weeds (reviewed by Matthews[32] and Diggle and Neve[33]).

The academic sector should lead the process of knowledge acquirement in these key biological aspects of resistance, and proactive efforts to design and implement herbicide resistance preventive and curative actions should be jointly coordinated with the private (agrochemical companies, farmer associations) and public (governments) sectors. This is an important task mainly in those cropping areas where farmers have no background knowledge of herbicide resistance and are dealing with this Darwinian evolutionary event for the first time. Only then can the useful life of glyphosate be maximized.

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