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Review

Influence of glyphosate-resistant cropping systems on weed species shifts and glyphosate-resistant weed populations

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ABSTRACT

Glyphosate-resistant (GR) crops have facilitated increases in conservation tillage production practices and simplified weed control in GR corn, soybean, canola and cotton. Increased reliance on glyphosate, many times as the only active ingredient used, has resulted in weed species shifts and the evolution of weed populations resistant to glyphosate. However, weed shifts and the evolution of herbicide resistance are not new in regard to glyphosate use. Similar effects have been documented to many other historically important weed control advancements for agricultural crop production. GR crop technology was developed to utilize glyphosate for postemergence weed control and industry scientists suggested that there was little fear of weed shifts and resistance evolution due to the broad spectrum of weeds controlled by glyphosate. However, over the last decade, the most problematic weeds in agronomic cropping systems have shifted away from perennial grass and perennial broadleaf weeds to primarily annual broadleaf weeds. The evolution of several GR annual broadleaf weeds in GR cropping systems has been documented, and glyphosate resistance mechanisms in weeds are currently poorly understood.

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1. Introduction

Since the introduction of GR crops in 1996, farmers have adopted cropping systems that have resulted in significant changes in crop production and weed management practices (Carpenter and Gianessi, 1999). For instance, GR crops have facilitated an increase

in hectares under conservation and no-till production practices (Young, 2006). Conservation tillage practices are beneficial for reducing soil erosion, improving surface water quality, soil water retention, tillage, and mineral nutrition (Sprague and Triplett, 1986), and reduced herbicide leaching relative to conventional tillage (Fawcett et al., 1994). GR crops also reduced fuel and labor requirements by decreasing the number of hours and energy inputs needed for tillage (Frye, 1984).

Adoption of GR crops greatly increased the use of glyphosate for weed control. Glyphosate use on U.S. corn, cotton, and soybean

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increased eight fold between 1995 and 2005 (USDA-NASS, 2008). Glyphosate has many attractive characteristics including low mammalian toxicity (WSSA, 2007), lower cost than many alternative herbicides (Gianessi et al., 2002), and, when used in GR crops, control of some previously difficult to control weed species due to its broad spectrum effectiveness (Johnson et al., 2000). GR crops have been the most rapidly accepted herbicide-resistant crop technology due to the simplicity and flexibility of broad spectrum weed control (Carpenter and Gianessi, 1999) on larger areas of land with essentially a single herbicide weed control program (Johnson et al., 2000; Martinez-Ghersa et al., 2003; Reddy and Whiting, 2000). Unfortunately, as herbicide costs decreased, seed and technology fees increased, and overall crop production costs have not been reduced (Martinez-Ghersa et al., 2003). Furthermore, the value for chemical companies has transferred from new herbicide development to seed biotechnology development. As a result, chemical companies have de-emphasized their herbicide discovery programs. The overall reduction of herbicide discovery efforts may be detrimental in the long-term since new herbicides are needed to control herbicide-resistant weeds (Rüegg et al., 2007).

GR cropping systems have enhanced the adoption of conservation tillage practices (Young, 2006). In the U.S., the amount of no-till has increased from 6.8 million hectares in 1990 to 25.3 million hectares in 2004 (CTIC, 2004), and this adoption was influenced by GR crops (Young, 2006). Tillage can be an important component in integrated weed management (IWM) practices (Buhler, 1995; Buhler et al., 2001). As tillage has decreased over the last decade, two important things have occurred. The use of multiple herbicides for weed management has decreased and the total amount of glyphosate (kg ae ha^{-1}) applied, the total number of applications, and the kg ae ha^{-1} application $^{-1}$ have increased (USDA-NASS, 2008; Young, 2006). This increase in glyphosate use reflects an increased reliance on glyphosate as a single, repeatedly used weed management tool with less use of other IWM approaches. Unfortunately, the repeated use of glyphosate has had some unintended consequences. First, weed species more difficult to control with glyphosate have become more common and the evolution of GR weeds, now at 9 in the U.S. and 15 species throughout the world (Table 1), is on the rise (Owen and Zelaya, 2005; Powles and Preston, 2006; Heap, 2008).

Weeds have been a persistent problem since the beginning of agriculture. Weed species shifts and evolution of resistance in herbicide based weed control strategies is not a new phenomenon. This review paper will examine how GR cropping systems and the increased reliance on glyphosate as the primary mechanism for weed control has impacted weed species shifts and evolution of GR weeds in U.S. agriculture.

Information presented will compare and contrast the current challenges of weed management in GR crops with other historical advancements in weed control strategies that successfully increased the efficiency of agriculture production. This discussion will provide a historical perspective of weed species shifts and factors involved in evolution of resistance to weed control innovations in crop production, and conclude with implications and insight regarding the necessity to IWM decisions/tools to provide sustainability of herbicide based systems as farmers adopt more herbicide-resistant crop biotechnology.

2. Clarification of the terms: weed species shift, and herbicide resistance

Changes in tillage, crop rotation, herbicide use patterns and other management practices can affect weed species diversity and population demographics. These changes could be from year to year in response to continual disturbance (fluctuational) or a

progression of flora stability over time following a disturbance (successional) (Swanton et al., 1993). Such changes will be referred to in this paper as “weed species shifts” or simply “weed shifts”.

The Weed Science Society of America (WSSA) developed independent definitions for herbicide resistance and herbicide tolerance in an attempt to unify terminology used by weed scientists. WSSA definitions state “herbicide resistance is the inherited ability of a plant to survive and reproduce following exposure to a dose of herbicide normally lethal to the wild type. In a plant, resistance may be naturally occurring or induced by such techniques as genetic engineering or selection of variants produced by tissue culture or mutagenesis.” Herbicide tolerance is defined as “the inherent ability of a species to survive and reproduce after herbicide treatment. This implies that there was no selection or genetic manipulation to make the plant tolerant; it is naturally tolerant” (WSSA, 1998).

Weed scientist should agree, as we will propose in this paper, that herbicide resistance is an evolutionary process despite whether it is monogenic resistance or multigenic “creeping resistance” (Gressel, 2002). The term tolerance should be used to describe weed species populations inherently immune to herbicides. For example, grasses are generally tolerant to the herbicide 2,4-D. For the weed science community to conform to the definitions set forth by the WSSA, the terms “development of tolerance”, “selection of tolerance”, and “evolution of tolerance” are misleading in the context of weed populations. The practicality of the issue from a weed management stand-point is that regardless of the reasons behind the weed response to a herbicide (“tolerant” or “resistant”), the weed is not controlled. Any escape from the control strategies imposed on the weed that allows growth and reproduction necessitates a change in the management of that weed species to prevent a further increase in its population demographics.

3. Weed species shifts and the evolution of resistance to agricultural practices prior to glyphosate-resistant cropping systems

3.1. History of weed control

Weeds have always been a problem in agricultural crop production and changing agricultural practices have and will continue to modify the weed flora (Froud-Williams, 1988). Weed communities have changed over time in response to control practices imposed upon them; whether, those control practices are chosen due to biological and/or social and economical reasons (Ghersa et al., 1994). Reports of weed shifts and resistance evolution since 1996 are predominately concerned with the use of glyphosate. However, the evolution of weeds that avoid weed control tactics is not a new phenomenon. It has been documented in response to several changes that have occurred throughout history. In the early 1900s, agricultural crop production was heavily reliant on manual weed control. In a 1914 “Manual of Weeds”, 17 weed killing methods mentioned; 16 were based on human use of hand tools and one on an animal drawn plow (Georgia, 1914). By the 1940s, tractors replaced a large portion of manual and animal power in agriculture and tillage practices became more advanced. However, the discovery of the weed killing properties of phenoxyacetic herbicides (2,4-D) marked the beginning of the “Chemical Era of Agriculture” (Timmons, 1970). Since that time, many herbicides have been commercialized and they slowly replaced most tillage practices for weed control (Appleby, 2005; Timmons, 1970). Currently, there are 315 herbicide common names approved by the WSSA (WSSA, 2008).

Throughout the modern era of weed control with herbicides, the understanding of weed shifts, herbicide resistance, and the necessity to integrate herbicides and tillage practices became more evident. Extensive and effective weed management practices were

Table 1
 Weed species with biotypes documented by the herbicide resistance action committee (HRAC) as glyphosate-resistant. Data adapted from Heap (2008) located at www.weedscience.org.

Species	Country	Year of first documentation
<i>Amaranthus palmeri</i> , Palmer amaranth	United States of America	2005
<i>Amaranthus rudis</i> , common waterhemp	United States of America	2005
<i>Ambrosia artemisiifolia</i> , common ragweed	United States of America	2004
<i>Ambrosia trifida</i> , giant ragweed	United States of America	2004
<i>Conyza bonariensis</i> , hairy fleabane	South Africa	2003
	Spain	
	Brazil	
	Colombia	
	United States of America	
<i>Conyza canadensis</i> , horseweed	United States of America	2000
	Brazil	
	China	
	Spain	
	Czech Republic	
<i>Digitaria insularis</i> , sourgrass	Paraguay	2006
	Brazil	
<i>Echinochloa colona</i> , junglerice	Australia	2007
<i>Eleusine indica</i> , goosegrass	Malaysia	1997
	Colombia	
<i>Euphorbia heterophylla</i> , wild poinsettia	Brazil	2006
<i>Lolium multiflorum</i> , Italian ryegrass	Chile	2001
	Brazil	
	United States of America	
	Spain	
	Argentina	
<i>Lolium rigidum</i> , rigid ryegrass	Australia	
	United States of America	
	South Africa	
	France	
	Spain	
<i>Plantago lanceolata</i> , buckhorn plantain	South Africa	2003
<i>Sorghum halepense</i> , johnsongrass	Argentina	2005
	United States of America	
<i>Urochloa panicoides</i> , liverseedgrass	Australia	2008

developed using a variety of tools to avoid widespread crop failures due to poor weed control. The commercialization of GR crop technology provided crop producers with a new strategy (post-emergence glyphosate) to control a wide selection of broadleaf and grass weeds with a single active ingredient and was adopted rapidly (Fig. 1) (Carpenter and Gianessi, 1999). It was assumed that this technology would eliminate the worry of shifting weed populations because glyphosate was sold as (and still is believed by many) a non-selective herbicide (WSSA, 2007). Furthermore, some scientists felt it was unlikely that weeds would ever evolve resistance to glyphosate due to its mechanism of action and the difficulty in engineering GR crops (Bradshaw et al., 1997). The authors were partly correct as the evolution of weeds with a mutation at the target site

similar to their engineered mutation has not yet occurred; however, the authors were shortsighted because they did not consider the evolution of other resistance mechanisms.

There is increasing concern of weed shifts and resistance evolution in GR crops; therefore, it is important to review documentations of how previous weed control and cropping system strategies have always impacted weeds and their composition of weed populations. This following section will review how various mechanical tools such as tillage, the cropping system, and the herbicides 2,4-D, atrazine, and several acetolactate-synthesis (ALS) inhibitors have impacted weed populations.

3.2. Tillage and cropping system effects on weed populations

Tillage is widely used for seedbed preparation and in-season weed control in many agronomic cropping systems. Tillage can affect weed emergence, weed management, weed seed production, and distribution of weed seeds in the soil (Buhler, 1995). Tillage practices including the type of tillage implements used contribute to weed shifts by differential movement of seeds to soil burial depths more or less suited for specific germination and emergence requirements (Grundy et al., 2003). Swanton et al. (2006) compared the effects of tillage (moldboard plow, chisel plow, and no-till) and crop rotations (continuous corn, corn-soybean, corn-soybean-winter wheat) on emerged and seedbank weed species diversity and density. They found tillage had a larger affect on weed diversity and density than crop rotation. As tillage intensity declined, (moldboard > chisel > no-till) total weed density declined while weed species diversity increased, and no crop yield differences between tillage systems were reported. Mulugueta et al. (2001) also found similar results when comparing the same three tillage systems in corn and soybean production. Swanton et al. (2006)

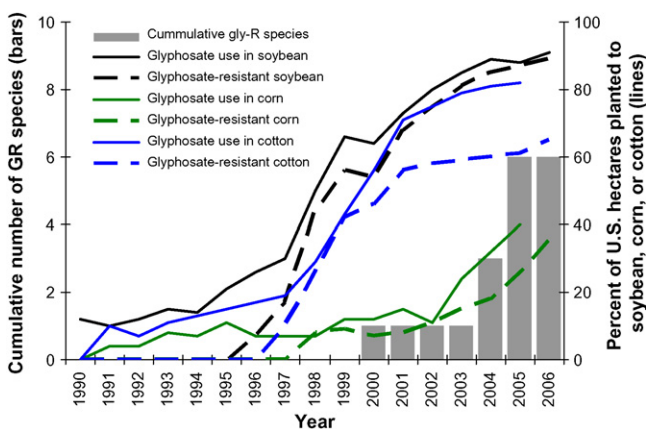


Fig. 1. Rate of GR crop adoption and glyphosate use in the U.S. compared to the number of 2 weeds that have evolved resistance in GR cropping systems in the U.S.

suggested the increased diversity associated with no-till systems was not detrimental to crop yields because many of the additional species found in the no-till system were not summer annual species and therefore less competitive with the crop during the growing season. While this may be accurate, their conclusion fails to consider that increased species diversity associated with the no-till system increases the possibility of enhancing the populations of weed species that have greater tolerance to the herbicides used in that system.

In addition to tillage practices, cropping systems also play a role in determining weed population composition. Crop rotations alleviate selection pressure by diversifying the patterns of disturbance, shading, and preventing the proliferation of weed species well suited to practices associated with a single crop (Buhler et al., 1997). Cardina et al. (2002) found that in a no-till system, a corn–corn–corn rotation had a 45% higher density of yellow wood-sorrel (*Oxalis stricta* L.) and common chickweed (*Stellaria media* L. Vill.) seed in the seedbank than a corn–oats (*Avena sativa* L.)–alfalfa (*Medicago sativa* L.) rotation. The authors concluded these weeds increased because they were the least affected weeds in the community by the microenvironment competition with corn. In another study, Buhler et al. (2001) found the density of all weed species fluctuated substantially from 2810 to 70,780 weed seeds m⁻² in the upper 20 cm of soil in 3 years of a corn–soybean–corn rotation following oat–hay (alfalfa grass mixture) production. Buhler et al. (2001) concluded that using tillage plus a corn–soybean rotation significantly reduced weed seeds near the soil surface. Other studies conducted have also shown in general, the more diverse the cropping rotation, the more diverse the weed species will be in the community (Anderson and Beck, 2007; Anderson et al., 2007; Cardina et al., 2002; Heggenstaller and Liebman, 2005; Murphy et al., 2006; Swanton et al., 2006; Westerman et al., 2005) thus increasing the opportunity for weed species shifts. Increased weed diversity is also observed when cover crops are used in an integrated weed management approach although emergence and growth of some species can be suppressed (Chikoye et al., 2005; Ngouajio and Mennan, 2005; Samarajeewa et al., 2005; Teasdale et al., 2005).

While not all of the increases in species diversity and density caused by changes in tillage and cropping systems may be detrimental to crop yields, increased diversity and density also increases the chance of selection for weeds that are tolerant, resistant, or can avoid glyphosate. An example of this was the evolution of GR horseweed (*Conyza canadensis* L. Cronq.). Horseweed has long been known to be associated with no-till systems (Kapusta, 1979; Triplett and Lytle, 1972) and especially no-till soybean (Barnes et al., 2004), and GR populations were first documented in no-till GR soybean (VanGessel, 2001) and subsequently in extensive field surveys conducted by Davis et al. (2008).

3.3. Herbicide effects on weed populations

In addition to tillage and crop rotation, herbicides play a key role in weed shifts and the speed at which weed shifts occur. In a 6-year study, Menalled et al. (2001) found that species density and diversity were lowest in a high herbicide input system coupled with conventional tillage, intermediate in a no-till system with high herbicide inputs, and highest in conventional tillage systems with low herbicide inputs or organic cropping systems with no chemical inputs. They also found that the organic system and low herbicide input system were dominated by red clover, quackgrass, and common lambsquarters, the no-till system with high herbicide inputs contained primarily large crabgrass and fall panicum. A multivariate ordination analysis suggested herbicides are likely the most important component of management for reducing weeds in integrated systems (Menalled et al., 2001).

Heavy reliance on a single herbicide has resulted in weed shifts since their introduction in the 1940s. Harper (1956) was the first person to seriously consider population changes imposed by herbicides. 2,4-D was very effective in control of broadleaf weeds, especially in monocot crops, but because of this specificity, the use of 2,4-D alone was not sufficient for protecting yields in crops that were infested with both grass and broadleaf weeds. In 1948, just 1 year after commercialization of 2,4-D, Lee (1948) stated, "It is apparent that the use of 2,4-D alone is not the answer to weed control in corn fields. Cultivation is necessary to destroy grassy weeds". This may have been one of the earliest documentations describing a weed shift due to herbicide use, and the importance of herbicide and tillage integration. In production fields where 2,4-D was used annually, weed communities by the 1950s were dominated by grasses. Weed research in the corn belt of the U.S. reflected these weed shifts with much research in the 1950s and 1960s focusing on johnsongrass (*Sorghum halepense* L. Pers.) and wild oats (*Avena fatua* L.) control (Table 2).

Resistance evolution in weeds to 2,4-D has been remarkably low despite its many years of use (Gustafson, in press). Repeated use of 2,4-D in Hawaiian sugarcane production raised questions about the evolution of herbicide resistance in weeds in the late 1950s. Hanson (1962) reported intraspecific biotype differences in 2,4-D susceptibility in spreading dayflower (*Commelina diffusa* Burm. f.) following 2,4-D use in Hawaii sugarcane production. Ultimately, that population was not considered "2,4-D-resistant", but herbicide selectivity for shifting weed populations to resistant individuals was clearly demonstrated.

The introduction of the triazine herbicides in the mid-1950s, particularly atrazine, an inhibitor of photosystem II (WSSA, 2007), not only were a substantial advance in herbicide options for corn and sorghum (*Sorghum bicolor* (L.) Moench ssp. bicolor) producers, but led to the first documentation of herbicide resistance. The first weed biotype historically considered "resistant" was a biotype of common groundsel (*Senecio vulgaris* L.) documented in 1970 to have evolved triazine resistance in a Washington nursery (Ryan, 1970). Atrazine use also led to the first weed with resistance to a widely used herbicide in U.S. agronomic crop production. In 1972, smooth pigweed (*Amaranthus hybridus* L.) was documented to be resistant to atrazine in Maryland corn production (Heap, 2008). Rapid evolution of atrazine resistant weed biotypes occurred in many localized production systems.

Atrazine is and was widely used because it has both foliar and residual activity in the soil on many grass and broadleaf weeds common to corn producing areas. However, it also resulted in selection pressure for weed species which could germinate later. The residual properties of atrazine provided persistent screening for resistant biotypes by providing an extended period of selection pressure, a process described by Sammons et al. (2007). By the 1970s, weed shifts were demonstrated in corn production where weeds such as fall panicum (*Panicum dichotomiflorum* Michx.) and redroot pigweed (*Amaranthus retroflexus* L.) had become dominant (Triplett and Lytle, 1972). Redroot pigweed populations increased by emerging later in the season and subsequently avoiding the herbicide application. However, unlike the wide germination timing of redroot pigweed, fall panicum could metabolize atrazine (Thompson et al., 1971). While it cannot metabolize atrazine at the same rate as corn, its ability to metabolize the herbicide was adequate to create a weed shift toward predominantly fall panicum in addition to redroot pigweed. The use of both 2,4-D and atrazine clearly demonstrated the ability of herbicide use to cause weed shifts, and both are still commonly used for weed control in crop production (USDA-NASS, 2008), thus they have not been rendered obsolete despite the evolution of resistant biotypes.

Another major advancement in herbicide discovery was the development of, and introduction into the weed control market,

Table 2
The 5 most commonly cited weeds in the North Central Weeds Science Society titles between 1948 and 2007.

Rank	1948	1955	1967	1972	1977	1982	1987	1992	1997	2002	2007
1	Canada thistle (<i>Cirsium arvense</i>)	Canada thistle (<i>Cirsium arvense</i>)	Field bindweed (<i>Convolvulus arvensis</i>)	Canada thistle (<i>Cirsium arvense</i>)	Common milkweed (<i>Asclepias syriaca</i>)	Eastern black nightshade (<i>Solanum ptychanthum</i>)	Canada thistle (<i>Cirsium arvense</i>)	Canada thistle (<i>Cirsium arvense</i>)	Common sunflower (<i>Helianthus annuus</i>)	Common sunflower (<i>Helianthus annuus</i>)	Common lambsquarters (<i>Chenopodium album</i>)
2	Field bindweed (<i>Convolvulus arvensis</i>)	Field bindweed (<i>Convolvulus arvensis</i>)	Western ironweed (<i>Vernonia baldwinii</i>)	Field bindweed (<i>Convolvulus arvensis</i>)	Field bindweed (<i>Convolvulus arvensis</i>)	Giant foxtail (<i>Setaria faberi</i>)	Downy brome (<i>Bromus tectorum</i>)	Common ragweed (<i>Ambrosia artemisiifolia</i>)	Common waterhemp (<i>Amaranthus rudis</i>)	Common waterhemp (<i>Amaranthus rudis</i>)	Common waterhemp (<i>Amaranthus rudis</i>)
3	Leafy spurge (<i>Euphorbia esula</i>)	Large crabgrass (<i>Digitaria sanguinalis</i>)	Wild buckwheat (<i>Polygonum convolvulus</i>)	Johnsongrass (<i>Sorghum halepense</i>)	Johnsongrass (<i>Sorghum halepense</i>)	Johnsongrass (<i>Sorghum halepense</i>)	Musk thistle (<i>Carduus nutans</i>)	Giant foxtail (<i>Setaria faberi</i>)	Giant foxtail (<i>Setaria faberi</i>)	Giant foxtail (<i>Setaria faberi</i>)	Giant ragweed (<i>Ambrosia trifida</i>)
4	Perennial sow thistle (<i>Sonchus arvensis</i>)	Leafy spurge (<i>Euphorbia esula</i>)	Wild oat (<i>Avena fatua</i>)	Wild oat (<i>Avena fatua</i>)	Wild buckwheat (<i>Polygonum convolvulus</i>)	Quackgrass (<i>Elytrigia repens</i>)	Velvetleaf (<i>Abutilon theophrasti</i>)	Johnsongrass (<i>Sorghum halepense</i>)	Palmer amaranth (<i>Amaranthus palmeri</i>)	Horseweed (<i>Coryza canadensis</i>)	Horseweed (<i>Coryza canadensis</i>)
5	Russian knapweed (<i>Acroptilon repens</i>)	Quackgrass (<i>Elytrigia repens</i>)	Yellow nutsedge (<i>Cyperus esculentus</i>)	Yellow nutsedge (<i>Cyperus esculentus</i>)	Yellow nutsedge (<i>Cyperus esculentus</i>)	Wild proso millet (<i>Panicum miliaceum</i>)	Woolly cupgrass (<i>Eriochloa villosa</i>)	Velvetleaf (<i>Abutilon theophrasti</i>)	Velvetleaf (<i>Abutilon theophrasti</i>)	Velvetleaf (<i>Abutilon theophrasti</i>)	Volunteer corn (<i>Zea mays</i>)

herbicides that inhibit acetolactate synthase (ALS) in the branch chain amino acid biosynthesis pathway (EC 4.1.3.18) (Singh and Shaner, 1995). ALS inhibitors were first commercialized in 1982 and many additional members of this group were introduced throughout the 1980s and 1990s. The many different ALS-inhibiting herbicides have unique ranges of weed and crop selectivity from five chemical classes (imidazolinones, pyrimidinylthiobenzoates, sulfonlamino-carbonyl-triazolinones, sulfonlureas, and triazolopyrimidines) (WSSA, 2007). Like glyphosate in GR cropping systems, ALS inhibitors were widely and rapidly adopted in many cropping systems because of their benefits including low application rates, broad spectrum weed control, wide application windows, elevated crop safety, and low mammalian toxicities.

Unfortunately, many weed populations quickly evolved ALS-resistance. Tranel and Wright (2002) concluded this was due to repeated applications and high selection pressure applied for mutant ALS R alleles. The first ALS-inhibitor resistant weed identified was prickly lettuce (*Lactuca serriola* L.) which evolved after just 5 years of repeated chlorsulfuron use in wheat (Mallory-Smith et al., 1990). Currently, there are 95 ALS-inhibitor resistant species worldwide (Heap, 2008). Tranel and Wright (2002) reviewed literature and concluded there were five highly conserved amino acids on the ALS enzyme which were responsible for all of the known target site ALS resistances and mutations that confer ALS resistance and can vary between and within weed species. However, despite a high relative rate of resistance evolution documented by Gustafson (in press), like atrazine, the ALS-inhibiting herbicides are still widely used in many current cropping systems (USDA-NASS, 2008).

In conclusion, previous herbicide advancement, 2,4-D, atrazine, and ALS inhibitors, and their use caused weed shifts and selection of herbicide-resistant populations. In spite of this, 2,4-D was still used on 21% to 33% of U.S. wheat, corn, cotton, and soybean hectares in 2004 (USDA-NASS, 2008). Atrazine was still used on 64% of U.S. corn hectares in 2005 and ALS inhibitors were used on 35% of soybean hectares in 2006 (USDA-NASS, 2008).

4. Glyphosate-resistant cropping systems

4.1. Development of GR technologies

Glyphosate is marketed as a non-selective postemergence herbicide for control of annual and perennial weed species (WSSA, 2007). Glyphosate was classified as a herbicide after it was discovered by J. E. Franz in 1971 at Monsanto (Monsanto Agricultural Products Co., St Louis, MO, USA), and was commercialized under the trade name Roundup® (Franz, 1985). Today, glyphosate is sold as an isopropylamine salt, trimethylsulfonium (trimesium) salt, sesquisodium salt, potassium salt, and ammonium salt (WSSA, 2007) under several hundred trade names by Monsanto and other chemical companies.

The mode of action for glyphosate is inhibition of aromatic amino acid biosynthesis specifically inhibition of 3-phospho-5-enolpyruvylshikimate synthase (EPSP synthase, EC 2.5.1.19) which reduces the plant's ability to form aromatic amino acids tryptophan, tyrosine, and phenylalanine and other important secondary compounds (Steinrücken and Amrhein, 1980; Bradshaw et al., 1997). Glyphosate is a foliar applied herbicide which once absorbed is readily translocated in the xylem and phloem throughout the plants with primary sinks being actively growing vegetative tissue and reproductive tissue, however, it has no soil residual activity (WSSA, 2007).

Due to the broad spectrum activity of glyphosate on plant species and its favorable environmental and animal toxicology aspects, there was interest in whether resistance to glyphosate was possible and if so, whether this could be used to develop herbicide-resistant crop plants. Selection experiments using a microbe (a CP4

strain of *Agrobacterium tumefaciens*) resulted in isolation of mutants that demonstrated high levels of glyphosate tolerance due to an alteration in the target EPSPS that prevented glyphosate inhibition of enzyme activity (Bradshaw et al., 1997; Delannay et al., 1995; Padgett et al., 1995). The CP4 EPSPS gene was isolated, cloned, and inserted with an appropriate promoter in the germplasm of soybean line 40-3-2 using particle acceleration (Padgett et al., 1996). This gene transformation resulted in soybean plants resistant to high levels of glyphosate (Bradshaw et al., 1997; Delannay et al., 1995; Padgett et al., 1995). This event was patented as the Roundup Ready® gene technology, expressed in soybeans and released into the commercial marketplace in 1996 by the Monsanto Company (Delannay et al., 1995).

4.2. Use of glyphosate-resistant crop technology

Glyphosate-resistant crops, first released in 1996, have been the most rapidly adopted agriculture technology by the farming community in the U.S. By 2006, greater than 90% of the soybean hectares, 60% of the cotton hectares, and approximately 40% of the corn hectares were GR in the U.S. (Sankula, 2006). When GR crops were introduced, some scientists believed it was highly unlikely that resistance due to an altered and insensitive EPSPS would occur because of the extremely complex molecular manipulations that were required to develop GR crops (Bradshaw et al., 1997). Other scientists suggested that use of glyphosate would inevitably cause shifts in weed species under continual selection pressure from the herbicide (Duke, 1996; Shaner, 2000). Prior to GR crop introduction there were no reports of weeds resistant to glyphosate, however, since their introduction in 1996, glyphosate resistance has been documented in 15 weed species throughout the world (9 in the U.S.) (Heap, 2008) (Table 2). The evolution of GR weeds has been closely associated with the frequency of glyphosate use (Fig. 1).

While weed shifts caused by glyphosate use and the evolution of GR biotypes were both expected, there were many diversified approaches to manage weeds that could have been used to slow the evolution of GR weed biotypes (Boerboom, 1999; Buhler, 2002; Knezevic and Cassman, 2003; Neve, 2007). Three herbicide use patterns that were largely abandoned during the rapid adoption of GR cropping systems included: (1) the use of tank mixtures with other herbicides, (2) the use of alternative herbicides in rotation with glyphosate, and (3) the use of residual herbicides before or at planting. However, because GR crops are so commonly grown in US agriculture, the temptation to rely solely on glyphosate for weed control is real and must be addressed proactively to avoid reducing the value of this technology to U.S. crop producers. Main obstacles to a diversified approach was the ease of using a single herbicide, glyphosate, as a complete weed control herbicide program in GR crops and widespread opinion that weed resistance to glyphosate is rare (Johnson et al., 2008).

Table 3
Glyphosate rate need to control weeds of various sizes according to a glyphosate label.

Weed	Min. rate (ml)	Max. size at min. rate (cm)	Max. rate (ml)	Max. size at max. rate (cm)	Index ^a
Hophornbeam copperleaf	473	2.5	1420	15	284
Sida spp.	473	2.5	1420	15	284
Eclipta	473	10	946	30	79
Texas panicum	473	15	1420	60	55
Crabgrass	473	30	710	45	32
Common cocklebur	473	30	946	60	32
Pigweeds	473	30	946	60	32
Hemp sesbania	710	5.0	1420	20	213
Morningglories	710	5.0	1420	15	237
Sicklepod	710	5.0	1420	20	213
Carolina geranium	946	10	1420	23	156
Florida pusley	946	30	946	30	63

^a Index = (min. rate/max. size at min. rate) + (max. rate/max. size at max. rate).

Diversified approaches are more complex and additional herbicides equate to additional costs. Also, adoption of diversified practices may be low because producers do not feel evolution of GR weeds is a major concern, and/or they do not understand the role repeated glyphosate use has in GR weed evolution (Johnson and Gibson, 2006).

4.3. Glyphosate-induced weed species shifts

From 1996 to 2007 a primary component contributing to weed species shifts has been the widespread use of glyphosate, the resultant heavy selection pressure linked to the adoption of GR crops, and the concomitant reduction in the amount of tillage used in agronomic crops. Firbank et al. (2006) documented that fields of GR corn had higher weed seedbank densities in the first 2 years of GR use compared to a conventional herbicide system. Jeschke and Stoltenberg (2006) found that 8 years of continuous glyphosate used alone in a corn–soybean rotation resulted in greater weed species richness compared to more diverse management systems which included tillage and/or non-glyphosate herbicides. In their study weed species composition over the 8 years included common lambsquarters, pigweed (*Amaranthus*) species, and giant foxtail (*Setaria faberi* Herrm.) as the weeds which were predominate across most treatments. However, treatments consisting of only one postemergence application of glyphosate were dominated by giant ragweed (*Ambrosia trifida* L.), shattercane, and large crabgrass (*Digitaria sanguinalis* L. Scop.). Field survey research in Indiana has shown that GR horseweed, giant ragweed, and tolerant common lambsquarters populations were among the most prevalent among late-season weed escapes in Indiana soybean fields in 2003, 2004, and 2005 (Davis et al., 2008).

Hilgenfeld et al. (2004) conducted a 2-year, multi-site study on weed species shifts in GR soybean systems. This particular study found that continuous use of glyphosate for weed management could alter the presence of weed species found within a given field. This was due to the inconsistent control of all the species and allowing some species such as ivyleaf morningglory (*Ipomoea hederacea* (L.) Jacq.) and shattercane (*Sorghum bicolor* (L.) Moench) disproportionately replenish the seedbank. Wilson et al. (2007) found that over a 5-year period in glyphosate-based cropping systems in the western U.S. corn belt, weed populations shifted from a kochia (*Kochia scoparia* L. Schrad.) and wild-proso millet (*Panicum miliaceum* L.) dominated population to a predominately narrowleaf lambsquarters (*Chenopodium desiccatum* A. Nels.) population. Several weed scientists agree that weed species shifts are of great concern because the species that are becoming more abundant are species that are either resistant or more difficult to control with glyphosate, and the utility of GR cropping systems will continue to deteriorate (Culpepper, 2006). Thus to conclude this section, it is imperative to reiterate that several studies have shown that

glyphosate use has shifted populations to competitive and difficult to control weeds such as giant ragweed, horseweed, common and narrowleaf lambsquarters, morningglory, and shattercane (Davis et al., 2008; Hilgenfeld et al., 2004; Jeschke and Stoltenberg, 2006; Wilson et al., 2007).

It has also been interesting to track the weeds that weed scientists were conducting research on over the course of time in the Midwest. From 1948 until the early 1980s, perennial weeds were the predominant weed species under investigation in the corn belt (Table 3). By 1997, no perennial weeds were among the top 5 most commonly cited weeds in NCWSS annual meeting proceedings. By 2007, the top 5 most commonly cited weeds in the proceedings had either evolved resistance to glyphosate, or contained an R gene (volunteer corn), or were always somewhat tolerant to glyphosate (Tables 3 and 4).

4.4. Crop producer perspective on weed shifts caused by glyphosate

Written crop producer surveys were conducted to assess farmer perceptions of problematic weeds in Midwest fields in Ohio in 1990 (Loux and Berry, 1991) and Indiana in 1996 (Childs et al., 1997), 2000, 2003 (Nice and Johnson, 2005), and 2005 (Kruger et al., submitted for publication). Results from these surveys showed giant ragweed and common lambsquarters were among the ten most problematic weeds in both states for all surveys (Table 4). Canada thistle (*Cirsium arvense* (L.) Scop.), common cocklebur (*Xanthium strumarium* L.), velvetleaf (*Abutilon theophrasti* Medik.), and burcucumber (*Sicyos angulatus* L.) were among the ten most problematic weeds in four of the five surveys. Of the top ten weeds reported in Indiana in 1996, the year GR soybeans were first commercially grown, four of the ten weeds were monocot species (Table 4). By 2005, only two of the top ten weeds were monocots. Weeds, such as common waterhemp and dandelion appeared on surveys from 2003 to 2005, but not on surveys prior to 2003 which might be a reflection of reduced tillage and/or glyphosate use patterns (Young, 2006). Both species adapt well to no-till systems as common waterhemp is an annual with very small seeds and dandelion is a perennial with expansive tap roots. Dandelion is also a difficult weed to control using only glyphosate in no-till systems (Dewell et al., 2004). Increased prevalence of common waterhemp is concerning because selected biotypes have shown inherent variability in response to glyphosate (Smith and Hallett, 2006), and it has evolved resistance to glyphosate in several states (Heap, 2008). Horseweed was also perceived as problematic in 2003 and 2005 which supported the results of field surveys conducted by Davis et al. (2008). Overall, surveys in Indiana suggest broadleaf weeds that are either resistant or difficult to control with glyphosate have become more problematic than monocot species.

Crop producer surveys have been also been conducted by telephone communication to a much larger geographical area to gain their perspectives on weed management problems in GR cropping systems and whether shifts and/or herbicide-resistant weed species are evolving (Kruger et al., submitted for publication). The survey was conducted from farmers using GR corn, soybean, and cotton cropping systems both in continuous GR crop rotations and GR crops rotated with non-GR crops in Illinois, Indiana, Iowa, Mississippi, Nebraska, and North Carolina. Producers across all cropping systems indicated they felt their most problematic weeds were reduced after the introduction of GR crop technology. However, the most commonly mentioned problematic weeds still occurring across all cropping systems and all states were giant and common ragweed, johnsongrass, velvetleaf, morningglory species, sicklepod, and Amaranthus species (Kruger et al., submitted for publication). Their survey documented broadleaf species may be of most concern to producers. It should also be noted that giant

Table 4
 The ten most problematic weeds in the Eastern corn belt, U.S. from 1990 to 2005.

Rank	1990	1996	2000	2003	2005
1	Canada thistle (<i>Cirsium arvense</i>)	Giant ragweed (<i>Ambrosia trifida</i>)	Giant ragweed (<i>Ambrosia trifida</i>)	Giant ragweed (<i>Ambrosia trifida</i>)	Giant ragweed (<i>Ambrosia trifida</i>)
2	Foxtail species (<i>Setaria</i> spp.)	Canada thistle (<i>Cirsium arvense</i>)	Canada thistle (<i>Cirsium arvense</i>)	Common lambsquarters (<i>Chenopodium album</i>)	Johnsongrass (<i>Sorghum halepense</i>)
3	Velvetleaf (<i>Abutilon theophrasti</i>)	Hemp dogbane (<i>Apocynum cannabinum</i>)	Johnsongrass (<i>Sorghum halepense</i>)	Canada thistle (<i>Cirsium arvense</i>)	Foxtail species (<i>Setaria</i> spp.)
4	Common ragweed (<i>Ambrosia artemisiifolia</i>)	Common lambsquarters (<i>Chenopodium album</i>)	Common lambsquarters (<i>Chenopodium album</i>)	Common cocklebur (<i>Xanthium strumarium</i>)	Burcucumber (<i>Sicyos angulatus</i>)
5	Common cocklebur (<i>Xanthium strumarium</i>)	Horseweed (<i>Conyza canadensis</i>)	Shattercane (<i>Sorghum bicolor</i>)	Velvetleaf (<i>Abutilon theophrasti</i>)	Dandelion (<i>Taraxacum officinale</i>)
6	Giant ragweed (<i>Ambrosia trifida</i>)	Johnsongrass (<i>Sorghum halepense</i>)	Hemp dogbane (<i>Apocynum cannabinum</i>)	Horseweed (<i>Conyza canadensis</i>)	Waterhemp species (<i>Amaranthus</i> spp.)
7	Morningglory species (<i>Ipomoea</i> species)	Burcucumber (<i>Sicyos angulatus</i>)	Burcucumber (<i>Sicyos angulatus</i>)	Waterhemp species (<i>Amaranthus</i> spp.)	Horseweed (<i>Conyza canadensis</i>)
8	Quackgrass (<i>Elytrigia repens</i>)	Shattercane (<i>Sorghum bicolor</i>)	Velvetleaf (<i>Abutilon theophrasti</i>)	Burcucumber (<i>Sicyos angulatus</i>)	Velvetleaf (<i>Abutilon theophrasti</i>)
9	Common lambsquarters (<i>Chenopodium album</i>)	Giant foxtail (<i>Setaria faberi</i>)	Common ragweed (<i>Ambrosia artemisiifolia</i>)	Chickweed (<i>Caryophyllaceae</i> spp.)	Common lambsquarters (<i>Chenopodium album</i>)
10	Pennsylvania smartweed (<i>Polygonum pennsylvanicum</i>)	Fall panicum (<i>Panicum dichotomiflorum</i>)	Common cocklebur (<i>Xanthium strumarium</i>)	Dandelion (<i>Taraxacum officinale</i>)	Common cocklebur (<i>Xanthium strumarium</i>)
Source	Loux and Berry (1991)	Childs et al. (1997)	Nice and Johnson (2005)	Nice and Johnson (2005)	Kruger et al. (submitted for publication)

and common ragweed and multiple *Amaranthus* species have been documented with GR populations, and the evolution of those GR populations were in GR crop systems (Heap, 2008).

Kruger et al. (submitted for publication) also noted that 6–11% of respondents did not know what their most problematic weeds were after implementing a GR cropping system. The authors suggested this may be a reflection of their confidence in the effectiveness of glyphosate for controlling weeds in GR crops. This may be an alarming observation that suggests an increasing number of producers are not scouting their fields, which is an important component of IWM. Other alarming results concerning producer attitudes about resistance were also documented by Johnson and Gibson (2006) who found nearly two-thirds of surveyed growers did not express a high level of concern for GR weeds despite frequent occurrence of GR horseweed in the surveyed area, and just over one-third did not contribute resistance evolution to repeated herbicide use. The education of crop producers about the necessity of IWM systems, the causes of resistance evolution, and the documentation of GR weed populations will be increasingly important for the viability of GR cropping systems to slow the increasing evolutionary rate of GR weeds.

4.5. Evolution of glyphosate resistance in weeds

Due to the difficulty in engineering site of action resistance to glyphosate into crops, it was speculated that resistance in weed species would not occur because a point mutation at the EPSPS enzyme as the basis of resistance was highly unlikely (Bradshaw et al., 1997). A major concern with this conclusion was that other mechanisms of resistance were largely discounted as possible (metabolism, sequestration, translocation). However, there have been many reports since glyphosate was first introduced in the 1970s of weeds that vary in their susceptibility to glyphosate. DeGennaro and Weller (1984) identified field bindweed (*Convolvulus arvensis* L.) biotypes which varied up to 70% in visual injury, root and shoot dry weight, and shoot re-growth when exposed to a 2.24 kg/ha application of glyphosate. Furthermore, as much as a 40% increase in tolerance to glyphosate was observed as the plants aged.

Observed variation of response to glyphosate should not be totally surprising. The glyphosate label has a wide range of listed rates for control of different species and size of plants (Table 3). These rates fluctuate in regard to both size and development as indicated by the nearly nine fold difference in an index calculated by the equation [(minimum rate/maximum size at minimum rate) + (maximum rate/maximum size at maximum rate)]. The first GR weed identified was rigid ryegrass (*Lolium rigidum* Gaudin) in 1996 in Victoria, Australia and later other biotypes were identified in the U.S. (1998), South Africa (2001), and France (2005) (Heap, 2008). These events occurred independently as the cropping situations and glyphosate use patterns varied among the sites (Lyon et al., 2002). The original GR rigid ryegrass biotype evolved after 15 years of annual glyphosate use prior to continuous summer and winter annual crop production (Pratley et al., 1999). Since this first report, there have been over 40 confirmed cases of GR rigid ryegrass in Australia. A year later, goosegrass (*Eleusine indica* (L.) Gaertn.) was documented in a Malaysian orchard after seven applications of glyphosate were made during a 3-year period (Lee and Ngim, 2000). Horseweed was the third GR weed worldwide, but was the first GR weed documented to have evolved in a GR cropping system in Delaware, U.S. (VanGessel, 2001). Horseweed was also the first annual GR broadleaf weed. GR biotypes evolved after only 3 years of continuous GR soybean production where glyphosate was used exclusively for both preplant and in-crop weed control. Since this initial report, GR horseweed has been reported in 15 other states from Delaware to California and from Michigan to Mississippi

(Heap, 2008). GR horseweed has been reported in other countries including Brazil, China, Spain, and the Czech Republic (Heap, 2008). An Indiana survey conducted from 2003 to 2005 by Davis et al. (2008) showed the frequency of GR horseweed was as high as 38% in all Indiana soybean fields in the SE region of the state and infested over 100,000 ha surveyed statewide. As evidenced by this high frequency in some geographies, GR horseweed may be a compounding problem for large geographies because in-field and seedbank demographics were shown to increase in systems that rely on glyphosate (Davis et al., 2007) and seeds are easily transported long distances by wind (Dauer et al., 2006).

Other weeds that have since been reported to be GR that evolved in U.S. GR cropping systems include common ragweed (*Ambrosia artemisiifolia* L.), giant ragweed (*A. trifida* L.), common waterhemp, and Palmer amaranth (*Amaranthus palmeri* S. Wats.) (Heap, 2008). Populations of GR giant ragweed have been documented in Ohio, Indiana, Kansas, Minnesota, and Tennessee. Populations of GR common ragweed have been documented in Arkansas, Missouri, and Kansas (Heap, 2008). These GR *Ambrosia* species are a serious concern for farmers because they create greater weed control challenges and they are very competitive species with crops causing large yield losses. Johnson et al. (2007) observed up to 19% corn yield loss at giant ragweed densities of 0.5 plants m⁻² under season-long interference. Furthermore, Harrison et al. (2001) observed corn yield loss could be predicted up to 90% for densities of 1.4 plants m⁻², and Baysinger and Sims (1991) observed nearly complete soybean yield loss from season-long competition of 22 and 36 giant ragweed plants m⁻².

Common waterhemp also evolved GR biotypes in GR soybean fields in Missouri, Illinois, Kansas, and Minnesota (Heap, 2008). It is also competitive with crops, is a prolific seed producer, and there are biotypes resistant to several other herbicide mode of actions (Heap, 2008) making it a GR weed of great concern to crop producers. The evolution of GR common waterhemp populations was predicted by Smith and Hallett (2006) due to inherent variability of response to glyphosate. Smith and Hallett (2006) showed common waterhemp populations collected from Illinois and Indiana to have 10% plant survival to 0.63 kg ae ha⁻¹ in populations suspected to be resistant. The 10% survival rate was too low to consider these populations, as a whole, to be GR; however, surviving plants were cloned and found to be GR up to nine times the putative susceptible clones and GR₉₀ values were estimated to be 13–16 kg ae ha⁻¹ (Smith and Hallett, 2006). The first field population of common waterhemp documented GR was in a Missouri field that had been planted with GR soybeans and treated with glyphosate continuously for 8–9 years (University of Missouri, 2005). In succeeding field experiments with this GR population, greater than 50% of plants 15 cm tall survived when treated with 6.9 kg ae ha⁻¹ glyphosate (Legleiter et al., 2006). Furthermore, this GR population was also resistant to ALS and protox-inhibiting herbicides, and the Illinois population of GR common waterhemp was also multiple-resistant with ALS-inhibiting herbicides (Heap, 2008).

The four GR weeds previously mentioned will have a significant impact on corn and soybean production in the U.S. corn belt. In the southern and southeast U.S., GR Palmer amaranth is a highly competitive weed in GR cotton (Culpepper and York, 2008). GR populations were first observed in Georgia cotton fields after 4 years of continuous GR cotton where the producer was also using pendimethalin and paraquat for weed control (Culpepper et al., 2006). Since then, GR Palmer amaranth has also been documented in cotton and soybean fields in Arkansas and Tennessee. Much like GR giant ragweed in the Midwest corn and soybean production, GR Palmer amaranth is a very competitive weed and yield losses up to 100% are possible (Culpepper et al., 2006).

GR Palmer amaranth and common waterhemp are additionally problematic, especially in geographies these species share, because

they have a high potential for introgression of resistance traits due to dioecious reproduction (Trucco et al., 2007; Wetzel et al., 1999). Among the *Amaranthus* species, there are many different herbicide-resistant biotypes documented by Heap (2008). Due to the multiple herbicide resistances found in *Amaranthus* populations, the dioecious reproductive habits and potential for high frequencies of gene transfer, and the widespread distribution of waterhemp in much of the Midwest and Palmer amaranth in the Southern U.S., glyphosate resistance in *Amaranthus* species will be very detrimental to crop yields and profitability if alternative approaches are not adopted by producers to slow the evolutionary rate of GR weed populations.

4.6. Resistance mechanisms

Evolution of glyphosate resistance in weeds stems from inherent variability in populations in response to the herbicide. Inherent variability was demonstrated by Smith and Hallett (2006) in common waterhemp collections prior to the documentation of GR common waterhemp field populations. One of the primary concerns with the evolution of GR weed populations is the lack of understanding of the mechanisms of resistance and genetics of the resistant traits. Information describing the genetic heritability of existing GR weeds will provide powerful knowledge about the potential for the evolution and spread of GR in other weeds. For example, the fact that GR is a single incompletely dominant locus on a nuclear gene in horseweed provides valuable insight into why the spread of GR biotypes was so pervasive and rapid, and why there were multiple founding events for this trait (Zelaya et al., 2004). However, GR waterhemp evolved much slower. Early evidence suggested that the limited segregation for the GR trait was because resistance was governed by a polygenic event (Zelaya and Owen, 2002). Furthermore, GR resistance can be a potentially important consideration when weeds hybridize (Zelaya et al., 2007).

To date all of the weeds that have evolved resistance to glyphosate demonstrate low levels of resistance and show moderate to substantial levels of injury when treated with higher rates of glyphosate. However, only 3 of 15 GR weed species have been investigated to determine the mechanism of resistance. Resistance at the site of action, similar to that expressed by weeds resistant to ALS inhibitors, is total and would be a major concern since the herbicide regardless of dose is ineffective. Scientific evidence suggests that modification of the EPSPS (5-Enol-pyruvylshikimate-3-phosphate synthase), the target site for glyphosate, would not result in total resistance, and in fact, is highly unlikely as any enzyme alteration would lead to unfit biotypes (Bradshaw et al., 1997; Sammons et al., 2007). A low-level resistance as determined in the few GR weeds characterized is due to other mechanisms including herbicide sequestration, limited herbicide translocation or slow metabolism (Feng et al., 2004; Lorraine-Colwill et al., 2003; Sammons et al., 2007). The one exception reported to this pattern is goosegrass (Ng et al., 2003) where resistance is partially due to a change at the EPSPS binding site of glyphosate.

Sammons et al. (2007) suggest that since all GR weeds demonstrate a low level of resistance, it does not represent a serious problem from a management perspective since target site resistance is the most difficult type of resistance to manage. Low-level resistance, it is argued, can be overcome by adjusting the rate of glyphosate applied. The approach would be for farmers to adjust the rate of glyphosate they use in order to target the most difficult to control weeds in their field. Sammons et al. (2007) argue that this management tactic would delay or totally prevent GR evolution in weeds. Furthermore, arguments were made that tank-mixing glyphosate with a different mode of action would be an effective management tactic. However, care would need to be used in selecting the specific tank-mix partner herbicides in order to avoid evolution of resistance to other herbicides and antagonistic

interactions between herbicides that would result in reduced weed control. They further suggest that even though a rate adjustment approach is easiest and would work, farmers should not disregard other proven resistance management tactics such as applying tank mixtures of herbicides with different mechanisms of action, tillage, crop rotation, and other diversified weed management approaches. The challenge with this strategy is that glyphosate prices doubled between 2007 and 2008 and crop producers will be tempted to reduce rates to reduce costs.

Other approaches to address weed resistance and allow herbicides to remain effective for management of the most problematic agronomic weeds involve engineering genes for other types of herbicide resistance into crop plants. There is a great deal of interest in this approach and there are many reports describing discoveries of genes responsible for conferring resistance to an array of herbicides (Behrens et al., 2007; Castle et al., 2004; Service, 2007). Crop plants resistant to dicamba (Behrens et al., 2007), glyphosate (Castle et al., 2004), glufosinate (Pline et al., 1999), all via metabolism genes, 2,4-D (mechanism unknown) (Wright et al., 2005), PROTOX (Xianggan and Nicholl, 2005), and ACCase inhibitors, ALS inhibitors, triazines are either on the market or under development (Service, 2007). The concept is that resistance of crop plants to other herbicides would provide additional herbicidal methods to control weeds and delay, prevent or manage weed resistance to a wide variety of herbicides. Regardless of whether or not multiple herbicide-resistance traits in a single crop plant will overcome this problem, we know that many weeds have evolved resistance to a number of herbicides that are widely used in the U.S. (Heap, 2008).

4.7. Future implications

Weed control practices in large-scale crop production have managed weeds to reduce the impact to yields and/or economic gain. They have not focused on seemingly impractical weed eradication. Therefore, despite the different types of advancements in crop and weed management systems to achieve these goals, weeds have continued to be (and always will be) a pest control requirement for agricultural production due to their remarkable ability to adapt to all varieties of weed management approaches. Weeds evolve resistance to herbicides, and all forms of management practices lead to shifts in the dominant and problematic weed populations to species or biotypes that avoid the strategies designed to control them. This is evidenced by the numerous weed shifts influenced by tillage, cropping, and herbicide systems, the numerous populations that have evolved resistance to herbicides (Heap, 2008), and the previously discussed changes in problematic weeds over time as demonstrated by farmer surveys. Currently, annual broadleaf weed species such as *Ambrosia* species, *Amaranthus* species, *Chenopodium* species, *Ipomoea* species, and horseweed appear to have increased in difficulty for many crop producers to control. Annual grass species such as johnsongrass and GR volunteer corn appear to have also increased in difficulty to control for many producers.

The advantage weeds have to adapt to management practices is based on the tremendous amount of genetic variability within species. Crops have been improved by ideotype breeding and harvest index breeding (i.e. reduction in genetic variability), while weeds have adapted and survived agriculture because of their tremendous genetic variability and man imposed selection pressure. Until weed managers realize that the best management practices rely on a variety of tools and not the simplistic approach of one tool, such as glyphosate, being the 'perfect storm', we will continue to evolve herbicide-resistant weed populations and reduce the value of broad spectrum herbicides like glyphosate.

The evolution of herbicide resistance, particularly glyphosate resistance, could deplete the control options for most problematic

weeds. GR has become the most widely used trait in corn, soybean, and cotton production and is used in canola, and sugarbeets. The GR trait has been the most rapidly adopted new crop technology ever. This technology is a valuable weed management tool and, therefore, it is important to understand farmer attitudes and perceptions about GR and the potential for evolution of GR weeds in order to design the most effective and proactive weed management practices for GR cropping systems. Scientists (and chemical company decision makers) must couple this technology and farmer practices with our science-based knowledge of resistance evolution to help guide farmer educational programming aimed at increasing awareness and knowledge of this subject and modifying farmer behavior towards weed and resistance management.

References

- Anderson, R.L., Beck, D.L., 2007. Characterizing weed communities among various rotations in central South Dakota. *Weed Technol.* 21, 76–79.
- Anderson, R.L., Stymiest, C.E., Swan, B.A., Rickertsen, J.R., 2007. Weed community response to crop rotations in western South Dakota. *Weed Technol.* 21, 131–135.
- Appleby, A.P., 2005. A history of weed control in the United States and Canada—a sequel. *Weed Sci.* 53, 762–768.
- Barnes, J., Johnson, B., Gibson, K., Weller, S., 2004. Crop rotation and tillage system influence late-season incidence of giant ragweed and horseweed in Indiana soybean. *Crop Manag.*, doi:10.1094/CM-2004-0923-02-BR (Online).
- Baysinger, J.A., Sims, B.D., 1991. Giant ragweed (*Ambrosia trifida*) interference in soybeans (*Glycine max*). *Weed Sci.* 39, 358–362.
- Behrens, M.R., Mutlu, N., Chakraborty, S., Dumitru, R., Jiang, W.Z., LaVallee, B.J., Herman, P.L., Clemente, T.E., Weeks, D.P., 2007. Dicamba resistance: enlarging and preserving biotechnology-based weed management strategies. *Science* 316, 1185–1188.
- Boerboom, C.M., 1999. Nonchemical options for delaying weed resistance to herbicides in Midwest cropping systems. *Weed Technol.* 13, 636–642.
- Bradshaw, L.D., Padgett, S.R., Kimball, S.L., Wells, B.H., 1997. Perspectives on glyphosate resistance. *Weed Technol.* 11, 189–198.
- Buhler, D.D., 2002. Challenges and opportunities for integrated weed management. *Weed Sci.* 50, 273–280.
- Buhler, D.D., 1995. Influence of tillage systems on weed population dynamics and management in corn and soybean in the Central USA. *Crop Sci.* 35, 1247–1258.
- Buhler, D.D., Hartzler, R.G., Forcella, F., 1997. Implications of weed seedbank dynamics to weed management. *Weed Sci.* 45, 329–336.
- Buhler, D.D., Kohler, K.A., Thompson, R.L., 2001. Weed seed bank dynamics during a five-year crop rotation. *Weed Technol.* 15, 170–176.
- Cardina, J., Herms, C.P., Doohan, D.J., 2002. Crop rotation and tillage system effects on weed seedbanks. *Weed Sci.* 50, 448–460.
- Carpenter, J., Gianessi, L., 1999. Herbicide tolerant soybeans: why growers are adopting Roundup Ready varieties. *Agric. Biol. Forum* 2, 65–72.
- Castle, L.A., Shiehli, D.L., Gorton, R., Patten, P.A., Chen, Y.H., Bertain, S., Cho, H.-J., Duck, N., Wong, J., Liu, D., Lassner, M.W., 2004. Discovery and directed evolution of a glyphosate tolerance gene. *Science* 304, 1151–1154.
- Chikoye, D., Udens, U.E., Ogunyemi, S., 2005. Integrated management of cogongrass (*Imperata cylindrical* L. Ruesch.) in corn using tillage, glyphosate, row spacing, cultivar, and cover cropping. *Agron. J.* 97, 1164–1171.
- Childs, J., Jordan, T.N., Blackwell, R.L., 1997. Survey of Problem Weeds in Indiana: 1996. Purdue University Cooperative Extension Services, WS-10.
- CTIC (Conservation Tillage Information Center), 2004. National Crop Residue Management Survey Conservation Tillage Data. West Lafayette, IN. www.ctic.purdue.edu/CTIC/CRM.html.
- Culpepper, S.A., 2006. Glyphosate-induced weed shifts. *Weed Technol.* 20, 277–281.
- Culpepper, S.A., Grey, T.L., Vencill, W.K., Kichler, J.M., Webster, T.M., Brown, S.M., York, A.C., Davis, J.W., Hanna, W.W., 2006. Glyphosate-resistant Palmer amaranth (*Amaranthus palmeri*) confirmed in Georgia. *Weed Sci.* 54, 620–626.
- Culpepper, S.A., York, A.C., 2008. Glyphosate-resistant Palmer amaranth impacts Southeastern agriculture. In: Proc. IL. Crop Protect. Technol. Conf. 60, Champaign, IL, pp. 61–63.
- Dauer, J.T., Mortensen, D.A., Humston, R., 2006. Controlled experiments to predict horseweed (*Conyza canadensis*) dispersal distances. *Weed Sci.* 54, 484–489.
- Davis, V.M., Gibson, K.D., Johnson, W.G., 2008. A field survey to determine distribution and frequency of glyphosate-resistant horseweed (*Conyza canadensis*) in Indiana. *Weed Technol.* 22, 331–338.
- Davis, V.M., Gibson, K.D., Bauman, T.T., Weller, S.C., Johnson, W.G., 2007. Influence of weed management practices and crop rotation on glyphosate-resistant horseweed population dynamics and crop yield. *Weed Sci.* 55, 508–516.
- DeGennaro, F.P., Weller, S.C., 1984. Differential susceptibility of field bindweed (*Convolvulus arvensis*) biotypes to glyphosate. *Weed Sci.* 32, 472–476.
- Delannay, X., Bauman, T.T., Beighley, D.H., Buettner, M.J., Coble, H.D., DeFelice, M.S., Derting, C.W., Diedrick, T.J., Griffin, J.L., Hagood, E.S., Hancock, F.G., Hart, S.E., LaVallee, B.J., Loux, M.M., Lueschen, W.E., Matson, K.W., Moots, C.K., Murdock, E., Nickell, A.D., Owen, M.D.K., Paschal II, E.H., Prochaska, L.M., Raymond, P.J., Reynolds, D.B., Rhodes, W.K., Roeth, F.W., Sprankle, P.L., Tarochino, L.J., Tinius, C.N., Walker, R.H., Wax, L.M., Weigelt, H.D., Padgett, S.R., 1995. Yield evaluation of a glyphosate-tolerant soybean line after treatment with glyphosate. *Crop Sci.* 35, 1461–1467.
- Dewell, R.A., Johnson, W.G., Creech, J.E., Davis, V.M., 2004. Management options for dandelion control in no-till systems. *Proc. North Cent. Weed Sci. Soc.* 59, 39.
- Duke, S.O., 1996. Herbicide-resistance crops—background and perspectives. In: Duke, S.O. (Ed.), *Herbicide-Resistant Crops*, Agricultural, Environmental, Economic, Regulatory, and Technical Aspects. CRC Press, Inc., pp. 1–9.
- Fawcett, R.S., Christensen, B.R., Tierney, D.P., 1994. The impact of conservation tillage on pesticide runoff into surface water: a review and analysis. *J. Soil Water Conserv.* 49, 126–135.
- Feng, P.C.C., Tran, M., Chiu, T., Sammons, R.D., Heck, G., Cajacob, C.A., 2004. Investigations into glyphosate-resistant horseweed (*Conyza Canadensis*): retention, uptake, translocation, and metabolism. *Weed Sci.* 52, 498–505.
- Firbank, L.G., Rothery, P., May, M.J., Clark, S.J., Scott, R.J., Stuart, R.C., Boffey, C.W.H., Brooks, D.R., Champion, G.T., Haughton, A.J., Hawes, C., Heard, M.S., Dewar, A.M., Perry, J.N., Squire, G.R., 2006. Effects of genetically modified herbicide-tolerant cropping systems on weed seedbanks in two years of following crops. *Biol. Lett.* 2, 140–143.
- Franz, J.E., 1985. Discovery, development and chemistry of glyphosate. In: Grossbard, E., Atkinson, D. (Eds.), *The Herbicide Glyphosate*. Butterworth and Company, pp. 3–7.
- Froud-Williams, R.J., 1988. Changes in weed flora with different tillage and management systems. In: Altieri, M.A., Liebman, M. (Eds.), *Weed Management in Agroecosystems: Ecological Approaches*. CRC Press, Inc., pp. 213–236.
- Frye, W.W., 1984. Energy requirements in no-tillage. In: Phillips, R.E., Phillips, S.H. (Eds.), *No Tillage Agriculture: Principles and Practices*. Van Nostrand Reinhold, pp. 127–151.
- Georgia, A.E., 1914. *A Manual of Weeds*. Norwood Press.
- Ghersa, C.M., Roush, M.L., Radosevich, S.R., Cordray, S.M., 1994. Coevolution of agroecosystems and weed management. *BioScience* 44, 85–94.
- Gianessi, L.P., Silvers, C.S., Sankula, S., Carpenter, J.E., 2002. Case study 26—herbicide tolerant soybean. In: *Plant Biotechnology: Current and Potential Impact for Improving Pest Management in U.S. Agriculture an Analysis of 40 Case Studies—June 2002*. www.ncfap.org/40CaseStudies/CaseStudies/SoybeanHT.pdf.
- Gressel, J., 2002. Evolution of resistance to herbicides. In: *Molecular Biology of Weed Control*. Taylor and Francis, pp. 78–121.
- Grundy, A.C., Mead, A., Burston, S., 2003. Modelling the emergence response of weed seeds to burial depth: interactions with seed density, weight, and shape. *J. Appl. Ecol.* 40, 757–770.
- Gustafson, D.I., in press. Sustainable use of glyphosate in North American cropping systems. *Pest Manag. Sci.* 64. doi:10.1002/ps.1543.
- Hanson, N.S., 1962. Weed control practices and research for sugar cane in Hawaii. *Weeds* 10, 192–200.
- Harper, J.L., 1956. The evolution of weeds in relation to resistance to herbicides. In: *Proc. 3rd Br. Weed Control Conf.*, pp. 179–188.
- Harrison, S.K., Regnier, E.E., Schmoll, J.T., Webb, J.E., 2001. Competition and fecundity of giant ragweed in corn. *Weed Sci.* 49, 224–229.
- Heap, I., 2008. International survey of herbicide resistant weeds. *Weed Science Society of America*. www.weedscience.org.
- Heggenstaller, A.H., Liebman, M., 2005. Demography of *Abutilon theophrasti* and *Setaria faberi* in three crop rotation systems. *Weed Res.* 46, 138–151.
- Hilgenfeld, K.L., Martin, A.R., Mortensen, D.A., Mason, S.C., 2004. Weed management in a glyphosate resistant soybean system: weed species shifts. *Weed Technol.* 18, 284–291.
- Jeschke, M.R., Stoltenberg, D.E., 2006. Weed community composition after eight years of continuous glyphosate use in a corn–soybean annual rotation. *Proc. North Cent. Weed Sci. Soc.* 58, 59.
- Johnson, W.G., Gibson, K.D., 2006. Glyphosate-resistant weeds and resistance management strategies: an Indiana grower perspective. *Weed Technol.* 20, 768–772.
- Johnson, W.G., Bradley, P.R., Hart, S.E., Buesinger, M.L., Massey, R.E., 2000. Efficacy and economics of weed management in glyphosate-resistant corn (*Zea mays*). *Weed Technol.* 14, 57–65.
- Johnson, W.G., Ott, E.J., Gibson, K.D., Nielsen, R.L., Bauman, T.T., 2007. Influence of nitrogen application timing on low density giant ragweed (*Ambrosia trifida*) interference in corn. *Weed Technol.* 21, 763–767.
- Johnson, W.G., Weller, S.C., Owen, M.D.K., Shaw, D.R., Wilcut, J.W., Jordan, D.L., Wilson, R.G., Young, B.G., 2008. U.S. grower perspectives on glyphosate resistance management and alternative weed management practices. *Proc. Weed Sci. Soc. Am.* 48, 302.
- Kapusta, G., 1979. Seedbed tillage and herbicide influence on soybean (*Glycine max*) weed control and yield. *Weed Sci.* 27, 520–526.
- Knezevic, S.Z., Cassman, K.G., 2003. Use of herbicide-tolerant crops as a component of an integrated weed management program. *Crop Manag.*, doi:10.1094/CM-2003-0317-01-MG (Online).
- Kruger, G.R., Johnson, W.G., Weller, S.C., Owen, M.D.K., Shaw, D.R., Wilcut, J.W., Jordan, D.L., Wilson, R.G., Young, B.G., submitted for publication. U.S. grower views on problematic weeds and changes in weed pressure in glyphosate-resistant corn, cotton, and soybean cropping systems. *Weed Technol.*
- Lee, O.C., 1948. The effect of 2,4-D as a selective herbicide in growing corn and sorghums. *Proc. North Cent. Weed Sci. Soc.* 5, 18–21.
- Lee, L.J., Ngim, J., 2000. A first report of glyphosate-resistant goosegrass (*Eleusine indica* (L) Gaertn) in Malaysia. *Pest Manag. Sci.* 56, 336–339.
- Legleiter, T.R., Monnig, N., Bradley, K., 2006. Evaluation of programs for the management of glyphosate-resistant common waterhemp in soybean. *Proc. North Cent. Weed Sci. Soc.* 61, 209.

- Lorraine-Colwill, D.F., Powles, S.B., Hawkes, T.R., Hollinshead, P.H., Warner, S.A.J., Preston, C., 2003. Investigations into the mechanism of glyphosate resistance in *Lolium rigidum*. *Pestic. Biochem. Physiol.* 74, 62–72.
- Loux, M.M., Berry, M.A., 1991. Use of a grower survey for estimating weed problems. *Weed Technol.* 5, 460–466.
- Lyon, D.J., Bussan, A.J., Evans, J.O., Mallory-Smith, C.A., Peeper, T.F., 2002. Pest management implications of glyphosate-resistant wheat (*Triticum aestivum*) in the Western United States. *Weed Technol.* 16, 680–690.
- Mallory-Smith, C.A., Thill, D.C., Dial, M.J., 1990. Identification of sulfonylurea herbicide-resistant prickly lettuce (*Lactuca serriola*). *Weed Technol.* 4, 163–168.
- Martinez-Ghersa, M.A., Worster, C.A., Radosevich, S.R., 2003. Concerns a weed scientist might have about herbicide-tolerant crops: a revolution. *Weed Technol.* 17, 202–210.
- Menalled, F.D., Gross, K.L., Hammond, M., 2001. Weed aboveground and seed-bank community responses to agricultural management systems. *Ecol. Appl.* 11, 1586–1601.
- Mulugeta, D., Stoltenberg, D.E., Boerboom, C.M., 2001. Weed species-area relationships as influenced by tillage. *Weed Sci.* 49, 217–223.
- Murphy, S.D., Clements, D.R., Belaousoff, S., Kevan, P.G., Swanton, C.J., 2006. Promotion of weed species diversity and reduction of weed seedbanks with conservation tillage and crop rotation. *Weed Sci.* 54, 69–77.
- Neve, P., 2007. Challenges for herbicide resistance evolution and management: 50 years after Harper. *Weed Res.* 47, 365–369.
- Nice, G., Johnson, B., 2005. Indiana's top ten most problematic weeds. Purdue University Cooperative Extension Services. www.btny.purdue.edu/WeedScience/2005/topten05.pdf.
- Ngouajio, M., Mennan, H., 2005. Weed populations and pickling cucumber (*Cucumis sativus*) yield under summer and winter cover crop systems. *Crop Protect.* 24, 521–526.
- Ng, C.H., Wickneswari, R., Salmijah, S., Teng, Y.T., Ismail, B.S., 2003. Gene polymorphisms in glyphosate-resistant and susceptible biotypes of *Eleusine indica* from Malaysia. *Weed Res.* 43, 108–115.
- Owen, M.D.K., Zelaya, I.A., 2005. Herbicide-resistant crops and weed resistance to herbicides. *Pest Manag. Sci.* 61, 301–311.
- Padgett, S.R., Kolacz, K.H., Delannay, X., Re, D.B., Lavalley, B.J., Timius, C.N., Rhodes, W.K., Otero, Y.I., Barry, G.F., Eichholtz, D.A., 1995. Development, identification and characterization of a glyphosate tolerant soybean line. *Crop Sci.* 35, 1451–1461.
- Padgett, S.R., Re, D.B., Barry, G.F., Eichholtz, D.E., Delanny, X., Fuchs, R.L., Kishore, G.M., Fraley, R.T., 1996. New weed control opportunities: development of soybeans with a Roundup Ready™ Gene. In: Duke, S.O. (Ed.), *Herbicide Resistant Crops*. CRC Press, Inc., pp. 53–84.
- Pline, W.A., Wu, J., Hatzios, K.K., 1999. Effects of temperature and chemical additives on the response of transgenic herbicide-resistant soybeans to glufosinate and glyphosate applications. *Pestic. Biochem. Physiol.* 65, 131–199.
- Powles, S.B., Preston, C., 2006. Evolved glyphosate resistance in plants: biochemical and genetic basis of resistance. *Weed Technol.* 20, 282–289.
- Pratley, J., Urwin, N., Stanton, R., Baines, P., Broster, J., Cullis, K., Schafer, D., Bohn, J., Krueger, R., 1999. Resistance to glyphosate in *Lolium rigidum*. I. Bioevaluation. *Weed Sci.* 47, 405–411.
- Reddy, K., Whiting, K., 2000. Weed control and economic comparisons of glyphosate-resistant, sulfonylurea-tolerant, and conventional soybean (*Glycine max*) systems. *Weed Technol.* 14, 204–211.
- Rüegg, W.T., Quadranti, M., Zoschke, A., 2007. Herbicide research and development: challenges and opportunities. *Weed Res.* 47, 271–275.
- Ryan, G.F., 1970. Resistance of common groundsel to simazine and atrazine. *Weed Sci.* 18, 614–616.
- Samarajeewa, K.B.D.P., Horiuchi, T., Oba, S., 2005. Effect of Chinese milk vetch (*Astragalus sinicus* L.) as a cover crop on weed control, growth, and yield of wheat under different tillage systems. *Plant Prod. Sci.* 8, 79–85.
- Sammons, R.D., Heering, D.C., Dinicola, N., Glick, H., Elmore, G.A., 2007. Sustainability and stewardship of glyphosate and glyphosate-resistant crops. *Weed Technol.* 21, 347–354.
- Sankula, S., 2006. Quantification of the impacts on U.S. agriculture of biotechnology-derived crops planted in 2005. National Center for Food and Agricultural Policy, Washington, DC. www.ncfap.org/whatwedo/pdf/2005biotecimpacts-finalversion.pdf.
- Service, R.F., 2007. AGBIOTECH: a growing threat down on the farm. *Science* 316, 1114–1117.
- Shaner, D.L., 2000. The impact of glyphosate-tolerant crops on the use of other herbicides and on resistance management. *Pest Manag. Sci.* 56, 320–326.
- Singh, B.K., Shaner, D.L., 1995. Biosynthesis of branched chain amino acids: from test tube to field. *Plant Cell* 7, 935–944.
- Smith, D.A., Hallett, S., 2006. Variable response of common waterhemp (*Amaranthus rudis*) populations and individuals to glyphosate. *Weed Technol.* 20, 466–471.
- Sprague, M.A., Triplett, G.B., 1986. No-tillage and Surface-tillage Agriculture. John Wiley & Sons, Inc.
- Steinrücken, H., Amrhein, N., 1980. The herbicide glyphosate is a potent inhibitor of 5-enolpyruvylshikimic acid-3-phosphate synthase. *Biochem. Biophys. Res. Commun.* 94, 1207–1212.
- Swanton, C.J., Booth, B.D., Chandler, K., Clements, D.R., Shrestha, A., 2006. Management in a modified no-tillage corn-soybean-wheat rotation influences weed population and community dynamics. *Weed Sci.* 54, 47–58.
- Swanton, C.J., Clements, D.R., Derksen, D.A., 1993. Weed succession under conservation tillage: a hierarchical framework for research and management. *Weed Technol.* 7, 286–297.
- Teasdale, J.R., Parthan, P., Collins, R.T., 2005. Synergism between cover crop residue and herbicide activity on emergence and early growth of weeds. *Weed Sci.* 53, 521–527.
- Thompson Jr., L., Houghton, J.M., Slife, F.W., Butler, H.S., 1971. Metabolism of atrazine by fall panicum and large crabgrass. *Weed Sci.* 19, 409–412.
- Timmons, F.L., 1970. A history of weed control in the United States and Canada. *Weed Sci.* 18, 294–306.
- Tranel, P.J., Wright, T.R., 2002. Resistance of weeds to ALS-inhibiting herbicides: what have we learned? *Weed Sci.* 50, 700–712.
- Triplett Jr., G.B., Lytle, G.D., 1972. Control and ecology of weeds in continuous corn grown without tillage. *Weed Sci.* 20, 453–457.
- Trucco, F., Zheng, D., Woodyard, A.J., Walter, J.R., Walter, J.R., Tatum, T.C., Rayburn, A.L., Tranel, P.J., 2007. Nonhybrid progeny from crosses of dioecious amaranths: implications for gene-flow research. *Weed Sci.* 55, 119–122.
- University of Missouri, 2005. Waterhemp 'Potentially Resistant' to Herbicide Found in Northwest Missouri Soybean Fields. www.plantmanagementnetwork.org.
- USDA-NASS, 2008. Agricultural Chemical Use Database. USDA-NASS, Washington, DC. www.pestmanagement.info/nass.
- VanGessel, M.J., 2001. Glyphosate resistant horseweed from Delaware. *Weed Sci.* 49, 703–705.
- Weed Science Society of America (WSSA), 1998. Herbicide resistance" and "herbicide tolerance" defined. *Weed Sci.* 12, 789.
- Weed Science Society of America (WSSA), 2007. *Herbicide Handbook*, ninth ed. pp. 243–246.
- Weed Science Society of America (WSSA), 2008. Common and chemical names of herbicides approved by the WSSA. www.wssa.net/Weeds/Tools/Herbicides/HerbicideNames.htm.
- Westerman, P.R., Liebman, M., Medaled, F.D., Heggenstaller, A.H., Hartzler, R.G., Dixon, P.M., 2005. Are many little hammers effective? Velvetleaf (*Abutilon theophrasti*) population dynamics in two- and four-year crop rotation systems. *Weed Sci.* 53, 382–392.
- Wetzel, D.K., Horak, M.J., Skinner, D.Z., Kulakow, P.A., 1999. Transfer of herbicide resistance traits from *Amaranthus palmeri* to *Amaranthus rudis*. *Weed Sci.* 47, 538–543.
- Wilson, R.G., Miller, S.D., Westra, P., Kniss, A.R., Stahlman, P.W., Wicks, G.W., Kachman, S.D., 2007. Glyphosate-induced weed shifts in glyphosate-resistant corn or a rotation of glyphosate-resistant corn, sugarbeet, and spring wheat. *Weed Technol.* 21, 900–909.
- Wright, T.R., Lira, J.M., Merlo, D.J., Hopkins, N., 2005. Novel herbicide resistance genes. *World Patent Appl. No.* 107437.
- Xianggan, L., Nicholl, D., 2005. Development of PPO inhibitor resistant cultures and crops. *Pest Manag. Sci.* 61, 277–285.
- Young, B.G., 2006. Changes in herbicide use pattern and production practices resulting from glyphosate-resistant crops. *Weed Technol.* 20, 301–307.
- Zelaya, I.A., Owen, M.D.K., VanGessel, M.J., 2004. Inheritance of evolved glyphosate resistance in *Conyza canadensis* (L.) Cronq. *Theor. Appl. Gen.* 110, 58–70.
- Zelaya, I.A., Owen, M.D.K., 2002. *Amaranthus tuberculatus* (Mq/ex DC) J. D. Sauer: potential for selection of glyphosate resistance. In: 13th Australian Weeds Conference 13, pp. 630–633.
- Zelaya, I.A., Owen, M.D.K., VanGessel, M.J., 2007. Transfer of glyphosate resistance: evidence of hybridization in *Conyza* (Asteraceae). *Am. J. Bot.* 94, 660–673.