

Review

Weed species shifts in glyphosate-resistant crops

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Abstract: The adoption of glyphosate-based crop production systems has been one of the most important revolutions in the history of agriculture. Changes in weed communities owing to species that do not respond to current glyphosate-based management tactics are rapidly increasing. Clearly, glyphosate-resistant crops (GRCs) do not influence weeds any more than non-transgenic crops. For most crops, the trait itself is essentially benign in the environment. Rather, the weed control tactics imposed by growers create the ecological selection pressure that ultimately changes the weed communities. This is seen in the adoption of conservation tillage and weed management programs that focus on one herbicide mode of action and have hastened several important weed population shifts. Tillage (disturbance) is one of the primary factors that affect changes in weed communities. The intense selection pressure from herbicide use will result in the evolution of herbicide-resistant weed biotypes or shifts in the relative prominence of one weed species in the weed community. Changes in weed communities are inevitable and an intrinsic consequence of growing crops over time. The glyphosate-based weed management tactics used in GRCs impose the selection pressure that supports weed population shifts. Examples of weed population shifts in GRCs include common waterhemp [*Amaranthus tuberculatus* (Moq ex DC) JD Sauer], horseweed (*Conyza canadensis* L), giant ragweed (*Ambrosia trifida* L) and other relatively new weed problems. Growers have handled these weed population shifts with varying success depending on the crop.

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1 INTRODUCTION

The adoption of transgenic herbicide-resistant (HR) crops has increased dramatically worldwide since 1996. Most of the increase in hectares of transgenic crops planted is attributable to glyphosate [*N*-(phosphonomethyl)glycine]-resistant (GR) soybean, maize, canola and cotton. However, the focus of this manuscript will be limited to cotton, maize and soybean grown in the USA and the implications that these GRC-based systems have on weed population shifts.

1.1 Adoption of GRCs

Glyphosate-resistant soybean was introduced in 1996, GR cotton in 1997 and GR maize in 1999. The grower adoption of GR soybean cultivars occurred rapidly and represented an estimated 89% of soybean planted in the USA in 2006.¹ GR cotton cultivar adoption has also increased rapidly since the introduction of the cultivars in 1997.^{2,3} In 2005, 79% of the cotton hectares planted were transgenic HR cultivars, and adoption increased to 83% in 2006. Interestingly, cotton hectares are expected to drop by 20% in 2007, presumably owing to the increased interest in maize grown for ethanol.⁴ GR maize was planted on 36%

of the US hectares in 2006, which represented an 8% increase from 2005. Transgenic HR maize accounted for 21% of the planted area, while transgenic hybrids with insect and herbicide resistance were planted on an estimated 15% of the planted area. The results of this unprecedented change in agriculture have been many, but perhaps most dramatic is the presumed 'simplification' of weed control tactics; growers can now apply a single herbicide (glyphosate) over a wide area without concern for injury to the crop.⁵ While a number of agriculturalists and economists suggest that the adoption of GRCs will reduce herbicide use dramatically, others suggest that herbicide use will actually increase.^{6–8} Regardless, the number of herbicide active ingredients commercially available and applied by growers has declined, thus increasing the ecological implications on the agroecosystem, such as reducing the biodiversity of arable land, facilitating weed population shifts in weed communities and supporting the evolution of GR weed biotypes.^{9–12}

1.2 Changes attributable to GRCs

Historically, a number of changes in agricultural systems have occurred, resulting in significant impacts on weed communities. Conservation tillage practices and

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changes in weed management tactics, specifically herbicides used, have allowed small-seeded annual weeds to become greater economic problems in the recent past.¹³ The widespread use of acetolactate synthase (ALS, EC 2.2.1.6)-inhibiting herbicides facilitated other important changes in weed communities, including the widespread problems with common waterhemp [*Amaranthus tuberculatus* (Moq ex DC) JD Sauer] and, specifically, the selection for ALS-resistant biotypes.¹⁴ More recently, the widespread adoption of GRCs has changed agriculture in many agroecosystems, resulting in considerable changes in weed communities. Examples include, but are not limited to, the escalation of problems from horseweed (*Conyza canadensis* L.) in soybean and cotton systems, Palmer amaranth (*Amaranthus palmeri* S. Wats) in the southeastern US cotton systems and giant ragweed (*Ambrosia trifida* L) in midwest soybean systems.

Perhaps the most important impact on agroecosystems was the recognition by growers that the GRCs and glyphosate provided an effective and consistent 'system' for weed control with less tillage.⁵ Thus, crop production in no-tillage and other conservation tillage systems increased dramatically, largely owing to GRCs.^{2,15} The GRC-based 'conservation' tillage systems represent significant economic savings for growers, including the more important feature of environmental savings from reduced soil erosion.^{16,17}

1.3 Impacts of GRCs on the weed community and general biological diversity

While there have been reports of a marked decline in the abundance of plant and animal species attributable to agriculture, there is no conclusive evidence that GRCs have a direct effect on biological diversity or species abundance within the planted fields.^{2,18–20}

The effects of GRCs on the ecosystem have not been great.²¹ However, the indirect impact of GRCs on the agroecosystem, particularly as a result of changes in tillage and weed management tactics, is important and has major implications on organism populations.²² Of the two factors, tillage and weed management tactics, the former is likely more important with regard to the impact on the biodiversity of plants, vertebrates and invertebrates.² Interestingly, reports support both an increase and a reduction of biological diversity when GRCs are imposed on the agroecosystem; however, most assessments do not address the long-term implications.^{2,23–26} Furthermore, the impact on weed community and biological diversity depends on the specific crop and the relative effectiveness of the conventional weed management tactics compared with the effectiveness of the tactics in the GRCs.^{27,28} For example, in sugar beet and spring oilseed rape the weed abundance was considerably reduced in the GRCs compared with the conventional crop, while in maize the weed population density was lower in the conventional system, reflecting the relative effectiveness of the weed management tactics.²⁸

Effects on the weed community diversity also reflect the relative intensity of weed management tactics. For example, when single glyphosate applications were made, weed community diversity was greater compared with high-intensity use of glyphosate, suggesting that some limited use of glyphosate would not have a significant effect on weed community diversity.²⁹ Thus, there appears to be both favorable and unfavorable data describing the effects of GRCs on biological diversity.³⁰ The critical consideration is that these effects of the GRCs on the weed communities and biological diversity are highly dependent on specific crop and management tactics. Any unfavorable effects on weed communities and general biological diversity could be ameliorated by subtle manipulation of the GRC-based systems.

2 WEED POPULATION SHIFTS

Agriculture practices impart selection pressure on weed communities that inevitably result in weed population shifts.³¹ The most influential selective forces that act on a weed community are tillage (disturbance) and herbicide regimes. The adoption of GRCs does not directly impart selection pressure on the weed community. However, the production systems used in GRCs increase selection pressure on the weed community owing to the predominance of conservation tillage and the limited number of herbicides (glyphosate) used to control weeds. Increased selection pressure increases weed population shifts.^{27,28} The selection pressure imparted by glyphosate will cause weed shifts attributable to the natural tolerance of a particular species to glyphosate or the evolution of glyphosate resistance within the weed population. Mechanisms by which weeds are naturally tolerant to glyphosate are not well defined, and research investigating these mechanisms is limited. However, there is considerable effort in describing the mechanism(s) of evolved resistance to glyphosate. While authors have distinguished between evolved herbicide resistance and increasing populations of naturally tolerant weeds, an ecological change in the agrosystem had to occur for the shift in the weed community to become a factor.^{32,33} Thus, a definition describing weed population shifts should include both evolved herbicide-resistant weed populations and naturally tolerant weed populations which developed as a result of the selection pressure(s) imposed by the crop production system. Specifically for GRCs, both 'types' of weed population shift have occurred in response to grower adoption of GRC-based systems and the resultant application of glyphosate. However, it must be considered that the initial factor was the ability of the weed community to adjust/adapt to the tillage system which has a greater overall impact on the agroecosystem.³⁴

2.1 Ecological adaptation of weed populations

Weed population shifts can be attributable to the 'ecological adaptation' of weed populations to changes

in tactics used in crop production. For example, in a long-term study investigating the effect that different tillage systems can have on weed population shifts, it was found that no-tillage had the greatest impact on the weed community compared with conventional tillage.³⁵ Woolly cupgrass [*Eriochloa villosa* (Thunb) Kunth] is an excellent example of a weed population shift in conservation tillage systems that is attributable primarily to ecological adaptation due to a number of biological characteristics such as seed fecundity, germination over a wide range of conditions and depths within the soil and a high level of competitiveness.³¹ There are no reports of evolved herbicide-resistant woolly cupgrass populations. However, woolly cupgrass is sensitive to glyphosate, and thus, while current control in GRCs with glyphosate is excellent, the potential for evolved glyphosate resistance likely exists within woolly cupgrass populations.

Ecological adaptation of weeds is, in part, a function of the weed population diversity within the weed community and reflects specific weed population density. When weed population density and diversity are low, the impact of a single weed control tactic on those species will be greater. Weed diversity in GR soybean was a factor of the number of glyphosate applications per season and geographic location.²⁹ Single glyphosate applications had higher weed species diversity than any management tactic, including the untreated control. Single glyphosate applications controlled the dominant species, thus providing an ecological opportunity for other species to increase in importance in the agroecosystem. If two glyphosate applications were used, weed population diversity was lower.

Weed population density and diversity declined for multiple glyphosate applications and supplemental interrow cultivation, compared with soil-applied residual herbicides.³⁶ However, risks for weed population shifts for GRCs were assessed to be no greater than those associated with other herbicides and conventional crops. Others suggested that GRCs and recurrent glyphosate applications would augment specific adapted weeds and result in significant shifts in weed populations.³⁷

2.2 Ecological factors influencing weed population shifts

Weeds are highly effective at adapting to changes in agroecosystems, and understanding the processes that allow weeds to succeed has considerable implications for management.³⁸ Plant ecology describes species divergence and evolution in response to various ecological selection pressures, while weed scientists have historically focused narrowly on the impact of specific weed management tactics and other production practices as the primary factors affecting weed population shifts.³⁹ By investigating the ecology of weeds and not just their responses to management practices, a greater insight into understanding the

impact of GRC systems on weed communities will be gained and more effective management tactics can be developed.

2.2.1 Influence of selection pressure on weed population shifts

For weed population shifts to occur, genetic variability must be present within the weed population, and recombination of the genetic characteristics occurs in response to the selection imposed by the agroecosystem.⁴⁰ In natural systems, neither the presence of the genetic traits nor the selective forces are the dominant factor resulting in the ecological adaptation of plant populations, but rather they must operate in concert. To affect a shift in weed populations in agroecosystems, the need for strong selection pressure in order to cause a weed population shift is greater when there is lower genetic variability. For example, it is possible to contrast the selection pressures required to affect a shift in weed populations that are resistant to ALS-inhibiting herbicides (relatively high frequency of the resistance trait) versus a shift attributable to glyphosate (relatively low frequency of the resistance trait) and see the interaction of the genetics and selection pressure. The key consideration for ecological adaptation of weed populations and resultant shifts in agroecosystems is the significant selection pressure that is imposed both by tillage and herbicide use.

Grower perspectives and attitudes enter into the ecological equation and are seemingly contrary to a logical understanding of the problem.⁴¹ While growers recognize the likelihood of weed population shifts, they do not accept/understand the effect of the selection pressures that the crop production system imposes upon the weed community, as evidenced by the widespread occurrence of ALS-inhibitor herbicide resistance in multiple weed species. Interestingly, scientists also apparently fail to understand the implications of selection pressure on the ecological adaptation of weed populations.⁹ For example, Watkinson *et al.*⁹ predicted that GRC-based systems would either eradicate weed populations or reduce them to low levels. This pronouncement intuitively infers that extremely high selection pressure is being imposed on the weed communities. High selection pressure typically results in specific weed populations within weed communities with adaptive traits that overcome the management tactic and subsequently increase in population density.⁴² Importantly, for polygenic traits that code for characteristics supporting the ecological adaptation of a species, relatively low levels of selection pressure (i.e. low rates of a herbicide) will facilitate a weed population shift.⁴³ While there is good evidence that short-term selection pressure can affect weed population shifts, in more complex crop production systems a longer time period should be considered in order fully to assess the potential for weed population shifts.⁴⁴ Regardless of the specific form or time, sufficient selection pressure is imposed by crop production systems, particularly

in GRC-based systems, to result inevitably in the ecological adaptation of 'new' weed populations in the agroecosystem. The pervasive question is whether or not these changes represent significant risks to agriculture.

2.2.2 *Issues of relative scale on weed population shifts*

Observations from studies investigating ecological adaptation of weed populations and weed shifts must take into account the relative scale used in the study. For example, a study with relatively small plots might miss a weed population shift when a similar study with larger plot size would provide better information. In many instances, researchers must adopt methods based more on convenience and logistics rather than the potential for elucidating far-reaching results.⁴⁵ There are inconsistencies in the results of several long-term studies that investigated the impact of GRC-based weed management systems on weed population dynamics, particularly when anecdotal observations from commercial agriculture are considered.^{36,42,46} The scale of the experiment could be responsible for the inconsistent data; traditional small-plot techniques are not suited to capturing the variable effects of production systems, tillage and weed management tactics on weed communities. Consider that more than 41 million hectares of GM HR crops are planted.³³ Thus, to evaluate the impact of GRCs on weed communities effectively, the scale of experimentation should be increased dramatically. The widespread adoption of GRCs further reinforces the impact that production agriculture has on the agroecosystem and, given the scale of GRC use, ensures that the rare mutation(s) that allows the weed to adapt to the production practices will be selected and thus become a major component of the agrosystem.⁴⁷ Large-scale experiments such as the farm-scale evaluations (FSEs) have been designed to address the issues associated with identifying weed shifts within the weed communities that are difficult to quantify, and to bridge the differences between 'traditional' smaller-scale research and the anecdotal observations from commercial fields.⁴⁸ However, even the FSEs are hampered to some degree by the use of an experimental scale that may not capture the impact of the crop production system on the landscape. Perhaps the inclusion of model simulations will provide a longer-term perspective.⁴⁴ However, a better strategy would be to increase the size of the experimental units (commercial fields), the number of fields in the study and the cropping systems included, as is projected for the multistate project currently under way in the US midwest, southeast and Mississippi River delta.⁴⁹

2.2.3 *Site properties*

Weed species diversity and abundance can vary considerably across a field, and specific site properties are likely factors that influence the ecological success of the weed communities.⁵⁰ These site properties may be topographical or soil characteristics and can be

associated with agronomic and weed management practices as well as the year-to-year variation in fields that are attributable to seasonal environmental conditions. Specific crops and production systems also affect weeds within fields, and, while the impact of GRCs on site properties may not be different from the impact of non-GR crops, the weed management used in the production of the GRCs is different and can affect site properties.^{24,27,28} However, when the effects of management systems with GRCs and non-GR crops were compared, the effects on weed diversity were suggested to be transient over time.²⁸

It is important to recognize that conservation tillage, which is a major component of the GRC-based systems, plays a major role in affecting the localized site properties. Tillage impacts on the weed seedbank by affecting species composition, spatial distribution and population density.³⁴ Reports on the relative impact of tillage on weed communities differ. For example, weed diversity is reported to respond positively to reduced tillage by some researchers, while others report no effect.^{34,51} These different reports are likely confounded by the crop and production system. The effect of tillage interacts with other management factors such as crop rotation and weed management tactics.⁵² No-tillage systems, which have become a significant component of GRC-based systems, favor species that are able to germinate at or near the soil surface. Examples of weed population shifts attributable to no-tillage production systems include shallow-germinating summer annuals such as common lambsquarters and common waterhemp. Wind-dispersed species are also favored in conservation tillage systems.⁵³ Thus, the lack of tillage changes the site properties to allow specific adapted species to predominate, which reflects to some degree the weed shifts observed in GRCs. Importantly, the change in site properties can result in relatively rapid changes in the weed community.³⁵

2.2.4 *Effect of crop rotation on weed population shifts*

Crop rotation is suggested to be an effective means of managing a number of different pest complexes.^{34,54} Crop rotation allows alternative weed management tactics to be used and thus may reduce weed population densities and maintain weed species diversity and ultimately have a negative effect on weed population shifts.⁵⁵ However, the effectiveness of crop rotation in impacting on weed population density is dependent on the characteristics of the crop and the success of the weed management tactics. The increased diversification found in complex crop rotations dilutes the selection pressure that favors specific weed populations and subsequently reduces the potential for weed population shifts.⁵⁶ However, the effects of crop rotation on weed communities are difficult to isolate from the management tactics that are used for the production of the crops.³⁴ In some studies, cropping sequence is reported to be the dominant factor in affecting the weed seedbank, while, in other research, crop rotation did not impact

on weed numbers.^{52,57} Factors such as herbicide use and tillage system are important components of a crop production system and thus have significant impacts on the weed population dynamics that cannot be separated from the specific effect of the crop rotation on the weed community.⁵⁵ Regardless, crop rotations that create differences in soil disturbance and resource competition, which result in an inhospitable and unstable agroecosystem, will have a significant impact on reducing the likelihood of weed population shifts.⁵⁶ These characteristics do not describe GRC-based production systems, and thus there is probably little positive impact of crop rotation on reducing the potential for weed population shifts in GRCs.

2.2.5 Relative speed of weed population shifts

Predictions of how quickly weed shifts (accounting for both evolved resistance and natural tolerance) would develop have varied. Early predictions suggested that shifts in weed populations, glyphosate resistance specifically, would be unlikely to evolve.⁵⁸ This prediction was reinforced recently with a suggestion that, owing to a number of characteristics unique to glyphosate, resistance would evolve slowly and at a relatively low level in weed populations.⁵⁹ Other predictions suggested that weed population shifts, both evolved resistance and natural tolerance to glyphosate, were inevitable and would occur sooner rather than later.^{13,60} Shifts to tolerant weed species were predicted to occur between 5 and 8 years after the adoption of GRCs, and species with resistance to glyphosate would evolve more slowly, but other authors reported that the speed at which weed shifts were expected to occur was uncertain.^{30,61}

Models predicted that herbicide resistance associated with a single dominant gene would evolve within 4–8 years with consistent selection.⁶² However, the prevailing thought was that weed population shifts in GRCs with the concomitant use of glyphosate would lag considerably behind weed population shifts attributable to other herbicides. However, resistance to glyphosate in isolated common waterhemp plants was observed 2 years after the commercialization of GR soybean, and, in horseweed, glyphosate resistance was widely distributed 3 years after grower adoption of GR soybean.^{63–65} Interestingly, numerous characteristics of horseweed, such as high levels of seed production, facilitated seed dispersal and adaptation to conservation tillage, did not fully explain the occurrence of glyphosate-resistant populations that evolved quickly across the eastern and midwestern USA. The report that glyphosate resistance in horseweed was attributable to a single semi-dominant gene, in spite of the estimated low frequency of occurrence within weed populations, provided the final piece of the puzzle that accounted for the speed of the widespread evolution of glyphosate resistance in horseweed.^{66,67} In the case of common waterhemp, the progression from an occasional glyphosate-resistant individual within a common waterhemp population to a homogenous

glyphosate-resistant population has taken longer than observed for horseweed. The longer time required for the shift in common waterhemp is attributable, in part, to the dioecious reproductive habit demonstrated by common waterhemp and supported by cursory evidence that the genetic basis for glyphosate resistance is polygenic.⁶⁵

Other significant biological factors impact on the speed at which weed population shifts occur. Notably, general ecological fitness, as illustrated by growth and seed production characteristics of weeds, greatly influence the speed of weed population shifts.⁶⁸ While a weed species might be adapted to a particular agroecosystem, if it is not as ecologically fit as other weeds within the community, it is unlikely that the species will become a dominant member of the weed community unless recurrent selection pressure is invoked (i.e. glyphosate). Also of considerable importance are seedbank characteristics. These include seed population density and seed longevity. Seed dormancy obviously has a significant role in the variability in weed seedbanks.⁶⁹ The more stable (long lived) the weed seedbank, the slower the shift in the weed community because the gene pool is diluted. However, if a species is extremely well-adapted owing to other characteristics, such as high levels of seed production and inherent competitive ability (e.g. woolly cupgrass), it may become dominant even though the seedbank decline can be rapid.⁷⁰ Finally, seed dispersal is a critical component of weed community shifts. Generally, the greater the number of dispersal vectors that a species utilizes, the more successful the species will be in an ecosystem.⁷¹ However, environmental conditions such as prevailing winds or rainfall impart an effect on weed seed dispersal. Furthermore, given that long-distance dispersal is important for the survival of species that exist within fragmented ecosystems (i.e. agroecosystems), species that have specialized dispersal mechanisms (i.e. pappus) can be successful in spite of the lack of multiple dispersal vectors. Horseweed is an excellent example of a weed species with a specialized dispersal mechanism that has facilitated widespread, economically important weed population shifts in a relatively short period of time.

2.3 Evolved glyphosate resistance in GRCs

Weed populations shifts have occurred in response to the adoption of GRCs.⁶¹ The evolution of resistance to glyphosate is now an accepted fate of recurrent use of glyphosate in GRCs. It is now apparent that there were fewer constraints on the evolution of glyphosate resistance than originally proposed, and resistance to glyphosate has evolved in many species and is widely distributed.^{33,72} A detailed account of GR weeds is given in other papers within this publication and is not within the scope of this manuscript. However, as GR weeds also represent *de facto* shifts in weed populations, a brief overview is provided here.

2.3.1 *Conyza canadensis*

Horseweed (*Conyza canadensis*) continues to escalate as a significant weed problem in GRCs and represents a weed shift attributable to ecological adaptation to the lack of disturbance in the agroecosystems and evolved resistance to glyphosate. Anecdotal reports suggest that glyphosate-resistant horseweed populations are now frequent in the mid-Atlantic, midsouth, Mississippi River delta and midwest regions of the United States and represent a serious problem in no-tillage cotton production. Herbicide resistance in a weed like horseweed is the worst-case scenario for GRC-based production systems, given the ecological adaptation of the species to agroecosystems with no tillage, the high level of fecundity and the wind-facilitated long-distance transport of seeds.^{71,73} Importantly, the genetic heritability of the glyphosate resistance trait increases the potential for population shifts in GRCs.⁶⁶ Furthermore, the ability of horseweed to hybridize with other *Conyza* spp. and the occurrence of glyphosate-resistant hairy fleabane (*Conyza bonariensis* L.) are indicative of the high level of ecological adaptation by the genus.^{67,74} The difficulty of managing horseweed with alternative herbicides, particularly in cotton, reinforces the fact that horseweed is a significant agronomic problem. Unless tillage is reintroduced into the agroecosystem, cotton growers may have few options to manage horseweed consistently and effectively.⁷⁵ The mechanism of glyphosate resistance in horseweed is thought to be attributable to differential translocation of the herbicide.⁷⁶

2.3.2 *Amaranthus species*

Common waterhemp (*Amaranthus tuberculatus*) is an example of a species well adapted to the prevailing agroecosystems in the midwest that has also evolved resistance to most ALS-inhibitor herbicides and has now evolved resistance to glyphosate.^{64,65,77} The first investigated reports of control problems with glyphosate were in 1998 in fields near Badger and Everly, Iowa.^{64,65} Cursory evidence suggests that the genetically heritable glyphosate response is polygenic.⁶⁵ Recent anecdotal reports from growers indicate that the difficulties of effectively managing common waterhemp with glyphosate are increasing rapidly. While these problems may be a function of poor management tactics or may reflect biological adaptation such as delayed emergence, evidence also supports an escalation of glyphosate resistance in populations.^{78,79} Given the ability of common waterhemp to adapt to ecologically diverse agroecosystems and numerous herbicide mechanisms of action, management options are often few. However, recent reports suggest that the common waterhemp seed-bank is relatively short lived and, with diligence, can be managed effectively within 5 years.^{80,81}

Recently, another dioecious pigweed, Palmer amaranth (*A. palmeri*), was confirmed to have evolved resistance to glyphosate.^{82,83} Palmer amaranth represents a significant problem for GRCs in the southeast

USA and is more competitive than common waterhemp. The specific mechanism of glyphosate resistance is not currently known.

2.3.3 *Other species*

Several other weed species have evolved resistance to glyphosate. These weeds were well adapted to the agroecosystem and had become prevalent members of their respective weed communities. For example, further selection with recurrent applications of glyphosate in GRCs resulted in glyphosate-resistant populations of wild poinsettia (*Euphorbia heterophylla* L.) in Brazil and Johnsongrass (*Sorghum halepense* L.) in Argentina.^{84–86}

2.4 Naturally adapted species

A number of weeds have been described as having inherent tolerance to various herbicides. Adaptation to herbicide management is likely of less importance than ecological adaptation to the agroecosystem, specifically the tillage regime and specific environmental conditions that prevail. Concern for tolerance to glyphosate has been an important consideration for many years, but was brought to prominence with the adoption of GRCs. A number of weeds have previously been reported as adapted to GRC-based systems and naturally tolerant to glyphosate, but in most instances these weeds remained isolated problems. However, several weeds that have historically demonstrated exceptional ecological adaptation to the prevailing agroecosystem increased in prevalence across the midwest with the adoption of GRCs.

2.4.1 *Common lambsquarters*

Common lambsquarters is adapted to conservation tillage systems and has been a difficult weed to manage in many crops, irrespective of the tactic used. Anecdotal observations across the midwest have suggested that common lambsquarters populations were not responding to glyphosate in GR soybean. Common lambsquarters was a prevalent species in field experiments where one and two applications of glyphosate to GR soybean were compared.²⁶ However, the escape of common lambsquarters was attributed to biological adaptation (delayed emergence). Other factors such as weed size and light response are also reported to affect the variable response of common lambsquarters populations to glyphosate.^{87–89} However, common lambsquarters populations were confirmed as glyphosate resistant in Ohio, and current assessments in Indiana and Wisconsin also suggest the presence of glyphosate-resistant populations.⁹⁰ Interestingly, common lambsquarters populations in Ontario, Canada, were reported to be relatively sensitive to glyphosate in 2004; whether these populations remain sensitive is suspect.⁹¹

2.4.2 *Giant ragweed*

Giant ragweed has been a significant weed problem in Ohio and Indiana for a number of years and is

described as the major weed problem in those states.⁹² In GRCs, giant ragweed populations increased over time in a long-term study conducted in Wisconsin.³⁶ While there does not appear to be information describing the ecological adaptation of giant ragweed to the crop production systems in these states, anecdotally it is apparent that this species is adapted to no-tillage. Furthermore, selection from ALS-inhibiting herbicides effected a rapid population shift to the resistant biotype.^{92,93} Given the prevalence of GRCs in the midwest and the resultant selection pressure from recurrent applications of glyphosate, it is not surprising that the glyphosate-resistant giant ragweed populations evolved rather quickly and are now widely distributed across Ohio and Indiana.⁹² Anecdotal reports from growers in Iowa and Wisconsin suggest that there is a high probability that glyphosate-resistant giant ragweed populations have or will soon evolve in these states.⁹⁴

2.4.3 Velvetleaf

Velvetleaf (*Abutilon theophrasti* Medik) has historically been described as difficult to control with glyphosate. However, the tolerance of this economically important weed to glyphosate was not an issue until the widespread adoption of GRCs. Recent reports suggested that the survival of velvetleaf after exposure to glyphosate can be high.⁹⁵ The tolerance mechanism in velvetleaf is reportedly associated with the differential disruption of cellular processes in source leaves and sink tissues, in addition to a mitigation of water movement to the shoot.⁹⁶ Glyphosate response by velvetleaf is also affected by environmental stress and application time of day.^{97,98} These responses are likely important factors in the inconsistent control of velvetleaf observed by growers. However, overall velvetleaf populations do not appear to be increasing dramatically as a result of GRCs, and may likely be declining because the species is not well adapted to the prevailing conservation tillage systems that are a significant component of GRCs.²

2.4.4 Asiatic dayflower

Asiatic dayflower (*Commelina communis* L.) has been a serious, albeit scattered weed problem in soybean, peanut and cotton fields in the midwest, midsouth and southeast USA for a number of years. Recent information suggests that Asiatic dayflower is spreading, although not quickly (Boerboom C, private communication, 2007). In GR cotton, for example, Asiatic dayflower is difficult to control with glyphosate.⁹⁹ Apparent natural tolerance to glyphosate and other biological characteristics (i.e. extended germination period) contribute to the inability of growers effectively to manage this weed.¹⁰⁰ The mechanism(s) of tolerance to glyphosate exhibited by Asiatic dayflower has not been reported. Recent research has not demonstrated any consistent herbicide control tactics, and it is anticipated

that Asiatic dayflower populations will continue to increase, given the predominance of GRCs.¹⁰¹

2.4.5 Tropical spiderwort

Tropical spiderwort (*Commelina benghalensis* L.) rapidly increased in prominence to become one of the more problematic weeds in GR cotton production in the southeast USA.^{102,103} Tropical spiderwort is ecologically adapted to the high-input agriculture that is prevalent in the southeast USA. Furthermore, tropical spiderwort is relatively tolerant to most herbicides used in cotton and soybean production systems, including glyphosate.¹⁰³ Field experiments did not elucidate effective and consistent alternative herbicide strategies to provide control of this weed. *Commelina* spp. are also reported to be extremely difficult to manage in plantation crops grown in Central and South America, and are tolerant of glyphosate (Pitty A, private communication, 2007). It is anticipated that populations of tropical spiderwort will continue to spread in the southeast USA.

2.4.6 Other species

Dicliptera chinensis (Jussieu) was previously reported to be naturally tolerant to glyphosate, but no new reports on this have been published.¹⁰⁴ However, there are a number of interesting anecdotal reports of additional weeds that appear to be increasing in GRCs. Evening primrose (*Oenothera biennis* L.) has been reported to be an isolated but significant problem in specific Iowa fields where GRCs are cultivated. Evening primrose is a biennial, and biennials are not commonly associated with crop production fields. However, with the adoption of GRCs and the concomitant use of no-tillage, it is likely that some biennial plants could adapt to these systems. Reports suggest that evening primrose is not sensitive to glyphosate. Wild parsnip (*Pastinaca sativa* L.) is another biennial plant that has been reported to be invading GRCs (and other non-GR cultivars) in Iowa. Wild parsnip is commonly found in roadsides, ditches and right-of-ways, but until recently was not observed to be a significant problem in row crops. Pokeweed (*Phytolacca americana* L.) is a perennial weed that has increased in fields. It is unlikely that the ecological adaptation is attributable to GRCs other than the fact that GRC-based systems are predominately no-tillage. Furthermore, the use of glyphosate provides effective control of most annual weeds, thus providing an ecological opportunity for pokeweed to increase in the weed community. Finally, field horsetail (*Equisetum arvense* L.) appears to be effectively invading row crop fields from field margins. Field horsetail is extremely tolerant of most herbicides, including glyphosate, but the primary factor is its adaptation to the conservation tillage systems that are prevalent in the midwest USA.

2.5 Impact of weed population shifts on GRCs

The pervasive question that must be answered is, if there is a weed population shift due to ecological

adaptation, natural tolerance to glyphosate or evolved glyphosate resistance, is this economically important? While it is apparent that weed population shifts and the evolution of glyphosate resistance are inevitable consequences of the widespread adoption of GRCs, the relative economic importance has not been determined for all species and is likely a factor of the competitive ability of that weed species.⁴⁵ However, recent activities by national crop associations, agrochemical manufacturers, seed companies and Cooperative Extension Service personnel to bring these issues to the front and the surprising, based on previous responses, consensus that there are significant problems in GRCs, as demonstrated by weed population shifts, are an indication of the importance of the issue. There is a need to establish stewardship to protect GRCs and extend the utility of glyphosate as an effective herbicide. It is important closely to observe weed communities and mark weed population shifts early in their adaptation in order to direct research to develop management tactics for these weeds.

3 CONCLUSIONS

Glyphosate is the leading herbicide worldwide.¹⁰⁵ The adoption of GRCs will continue, and this adoption is strengthened, in part, by the demand for biofuels, which resulted in a 19% increase in maize hectares in the USA in 2007.¹⁰⁶ The widespread adoption of GRCs has dramatically impacted on weed communities by facilitating weed population shifts, whether attributable to ecological adaptation or a further focus of selection pressure resulting in the evolution of glyphosate-resistant biotypes. While the risk of weed resistance to glyphosate was suggested to be low, the speed at which these changes have occurred has caused significant concern in agriculture.¹⁰⁷ However, given the level of selection pressure that these GRC systems impart on the agroecosystem, it is not surprising that the changes in the weed communities have occurred as rapidly as demonstrated.⁴⁷ Weed population shifts are not predicted to slow in the immediate future. It is important for growers to recognize the potential economic implications of weed population shifts and to determine the best strategies to minimize the economic effects of these shifts.⁷⁵ Interestingly, the adoption of alternative strategies for weed management is anticipated to reduce economic risks of yield losses that can commonly occur with the weed management tactics used in GRCs, as well as reducing the selection pressure which results in weed population shifts that no longer respond to glyphosate. In order best to accomplish this, the ecological perspective of weed management must be considered and robust systems that focus on the overall agroecosystem rather than individual species must be developed.¹⁰⁸

An important question is the impact that the adoption of GRCs will have on the agroecosystem

and the biodiversity of farmland.^{109,110} While the projections are that the impacts of GRCs on the agroecosystem are likely to be small, it is critical that research be conducted to alleviate the fears of society.²¹ Furthermore, the research must be conducted on a scale and with a design fully to accommodate the impacts of GRC-based systems on weed communities and agroecosystem biodiversity.¹¹¹ Again, it is important to recognize that, in themselves, GRCs do not have a great impact on the agroecosystem; the trait can be described as benign to the environment. However, the accompanying management tactics have demonstrated important impacts on the agroecosystem, specifically the facilitation of weed population shifts. The ecological basis and mechanisms of these shifts must be identified and supplemental management tactics adopted to provide appropriate stewardship for the GRCs.

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