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Glyphosate Susceptibility in Common Lambsquarters (*Chenopodium album*) is Influenced by Parental Exposure

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Field studies were carried out at two sites in 2005 using common lambsquarters seed collected from long-term research plots near Scottsbluff, NE; Fort Collins, CO; and Torrington, WY, to determine the effect of herbicide selection pressure on glyphosate susceptibility. Parental herbicide exposure influenced the level of glyphosate susceptibility exhibited by a subsequent generation. Common lambsquarters selected from historical plots receiving continuous and exclusive use of glyphosate exhibited lower mortality in response to 420 g ae ha^{-1} glyphosate compared with selections from nonglyphosate treatment histories. Selections from rotating glyphosate treatment histories demonstrated an intermediate tolerance response. Differences in response were also influenced by environmental conditions.

Nomenclature: Glyphosate; common lambsquarters, *Chenopodium album* L. CHEAL.

Key words: Herbicide tolerance, creeping resistance.

Agricultural management practices, such as tillage, crop rotation, and herbicides, tend to favor one or more weed species over others within the weed community (Ball and Miller 1990; Blackshaw et al. 1994; Buhler et al. 1996; Clements et al. 1996; Derksen et al. 1993; Glenn et al. 1997; Manley et al. 2001; Swanton et al. 1993). Over time, continuous application of these management practices will alter the weed community, with species adapted to the selection pressure increasing in relative abundance. Changes in the relative abundance of weed species are often referred to as a ''weed shift.'' If the weed community can be managed with available control tactics, a shift in the weed species composition is generally of little consequence. However, adaptations, such as herbicide resistance or a shift in the weed spectrum toward more difficult-to-control species, can create management problems.

The development of glyphosate-resistant crops allows for a potential three to four crop rotation where glyphosate could be used as the sole herbicide for chemical weed control (Culpepper 2006). Increased selection pressure from continuous glyphosate use in glyphosate-resistant crops will likely cause a shift toward weeds that are more naturally tolerant to glyphosate (Shaner 2000). Common lambsquarters has been noted recently as having the ability to survive and produce seed in glyphosate-resistant crops treated with glyphosate. The escape mechanisms have been suggested to be either avoidance mechanisms or a natural low-level tolerance to the herbicide (Owen and Zelaya 2005; Wilson 2002), but the survival mechanism has not yet been identified.

Several cases of differential susceptibility to glyphosate within a plant species have been reported. Boerboom et al. (1990) reported a threefold difference in glyphosate susceptibility between nine birdsfoot trefoil selections. Field bindweed (*Convolvulus arvensis* L.) is a weed species known to exhibit reduced susceptibility to glyphosate (Sandberg et al. 1980). A single field bindweed population in Indiana contained five biotypes with differing levels of susceptibility to glyphosate (DeGennaro and Weller 1984). The least- and most-susceptible biotypes differed in visual injury by > 70%.

It has been theorized for some time that application of suboptimal herbicide rates over time may select for quantitative resistance mechanisms (Gressel 1995). Recent research has demonstrated that weed populations that exhibit variation in susceptibility to a herbicide may evolve resistance in a relatively short time if suboptimal herbicide rates are applied continuously (Neve and Powles 2005). The theoretical genetic and evolutionary processes involved with this type of selection have been aptly reviewed by Neve and Powles (2005). Common lambsquarters shows high polymorphism at the biotype level and very wide phenotypic plasticity (Cole 1961). Much of this polymorphism can be explained by the simultaneous presence of two ploidy levels in most populations (Al Mouemar and Gasquez 1983; Darmency and Gasquez 1990). Given the high level of polymorphism, it is possible that a given common lambsquarters population will contain various biotypes that exhibit different levels of glyphosate susceptibility. Indeed, differential susceptibility of common lambsquarters biotypes to glyphosate has been reported, although the mechanism has not yet been characterized (King et al. 2004). The objective of this research was to examine common lambsquarters susceptibility to glyphosate in response to field herbicide use history. Details on how common lambsquarters responds to glyphosate selection pressure will be valuable in designing herbicide resistance management strategies.

Materials and Methods

Seed Collection. In 1998, long-term field research plots to investigate weed population dynamics under two crop rotations and four herbicide management regimes were initiated. Studies were established at five university research stations in four states as part of a regional effort to examine weed community shifts resulting from cropping systems using glyphosate-resistant crops (Miller et al. 2003). Experimental sites at Scottsbluff, NE; Torrington, WY; and Fort Collins, CO, were established under irrigated conditions and conservation tillage practices and were used for this research. Experimental sites at Colby, KS and North Platte, NE were established under rain-fed conditions; common lambsquarters was not present at either rain-fed location. Herbicide management treatments included two annual applications of

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Table 1. Herbicide treatment histories for long-term common lambsquarters collection sites.

Treatment	Herbicides and rates[a]		
	Year	Continuous corn	Corn–sugarbeet–spring wheat
High glyphosate (HG)	1998 to 2003	Glyphosate at 840 g ha^{-1} twice	Glyphosate at 840 g ha^{-1} twice
Low glyphosate (LG)	1998 to 2003	Glyphosate at 420 g ha^{-1} twice	Glyphosate at 420 g ha^{-1} twice
Rotating glyphosate (RG)	1998, 2000, 2002	Glyphosate at 840 g ha^{-1} twice	Glyphosate at 840 g ha^{-1} twice
	1999, 2001	Rimsulfuron/thifensulfuron at 18 g ha^{-1} fb dicamba/atrazine at 900 g ha^{-1}	Desmedipham/phenmedipham at 370 g ha^{-1} + triflusulfuron at 18 g ha^{-1} fb desmedipham/phenmedipham at 370 g ha^{-1} + triflusulfuron at 18 g ha^{-1} + clopyralid at 100 g ha^{-1} fb desmedipham/phenmedipham at 370 g ha^{-1} + clethodim at 140 g ha^{-1}
	2003	Acetochlor at 1.69 kg ha^{-1} + isoxaflutole at 66 g ha^{-1} fb nicosulfuron at 35 g ha^{-1} + diflufenzopyr/dicamba at 197 g ha^{-1}	Acetochlor at 1.69 kg ha^{-1} + isoxaflutole at 66 g ha^{-1} fb nicosulfuron at 35 g ha^{-1} + diflufenzopyr/dicamba at 197 g ha^{-1}
No glyphosate (NG)	1998, 2000	Rimsulfuron/thifensulfuron at 18 g ha^{-1} fb dicamba/atrazine at 900 g ha^{-1}	Rimsulfuron/thifensulfuron at 18 g ha^{-1} fb dicamba/atrazine at 900 g ha^{-1}
	1999, 2001	Rimsulfuron/thifensulfuron at 18 g ha^{-1} fb dicamba/atrazine at 900 g ha^{-1}	Desmedipham/phenmedipham at 370 g ha^{-1} + triflusulfuron at 18 g ha^{-1} fb desmedipham/phenmedipham at 370 g ha^{-1} + triflusulfuron at 18 g ha^{-1} + clopyralid at 100 g ha^{-1} fb desmedipham/phenmedipham at 370 g ha^{-1} + clethodim at 140 g ha^{-1}
	2002	Rimsulfuron/thifensulfuron at 18 g ha^{-1} fb dicamba at 280 g ha^{-1}	Bromoxynil/MCPA at 560 g ha^{-1}
	2003	Acetochlor at 1.69 kg ha^{-1} + isoxaflutole at 66 g ha^{-1} fb nicosulfuron at 35 g ha^{-1} + diflufenzopyr/dicamba at 197 g ha^{-1}	Acetochlor at 1.69 kg ha^{-1} + isoxaflutole at 66 g ha^{-1} fb nicosulfuron at 35 g ha^{-1} + diflufenzopyr/dicamba at 197 g ha^{-1}

[a] Abbreviations: fb, followed by; /, package mix; +, tank mix.

glyphosate at 840 g ae ha^{-1} (HG), two annual applications of glyphosate at 420 g ae ha^{-1} (LG), nonglyphosate treatment designed to provide 95% weed control (NG), and a rotating glyphosate treatment (RG). Herbicide treatment histories are provided in Table 1.

In 2003 (the sixth year of the study), six surviving common lambsquarters plants in each plot were identified and marked 10 to 14 d following the final herbicide application. In plots where six surviving plants could not be located, as many plants as were present were marked. In October of 2003, marked plants were clipped at ground level and placed in a large paper bag. Little shattering had occurred before harvest. All plants were placed indoors and allowed to dry at ambient temperature. Once dried, seeds were harvested from each plant using a threshing board and a hand sieve. Seed from each plant was kept separate for the duration of this research. For clarity, all seeds from a maternal plant will be referred to as a selection. After seed collection and cleaning, all selections were stored at 2 C until needed. Germination of freshly harvested seed was poor (< 5%) but increased after being allowed to after-ripen in cold storage for several months.

Field Selection Screen. Field studies were initiated at two research sites in Wyoming in 2005 to screen selections from the 2003 long-term field sites for differential glyphosate susceptibility. Sufficient seed was collected from 168 selections to carry out at least one field study. All 168 selections were planted at the Laramie site, whereas 148 selections were planted at Lingle. Seed was planted on May 10 at Lingle, WY and June 8 at Laramie, WY into 9-m-long rows at a rate of 100 mg of seed per 3 m of row. Both trial sites were overhead irrigated regularly to avoid stress from lack of water. Distance between rows was 15 cm at Lingle and 30 cm at Laramie. Herbicide treatments included 0, 420, or 840 g glyphosate ha^{-1} applied perpendicularly to the rows of common lambsquarters with a CO_2-pressurized knapsack sprayer in 187 L ha^{-1} at 276 kPa. All treatments (including the control) included MON 56151[1] at 0.17% v/v. Herbicide treatments were applied 43 and 44 d after planting at Lingle and Laramie, respectively. At the time of treatment (June 22 at Lingle and July 22 at Laramie), the tallest common lambsquarters plants were 50 and 12 cm in height at Lingle and Laramie, respectively. The difference in size between locations was a response to more optimal growing conditions at Lingle. Environmental conditions for the period 7 d before and 14 d following herbicide applications are provided in Figure 1.

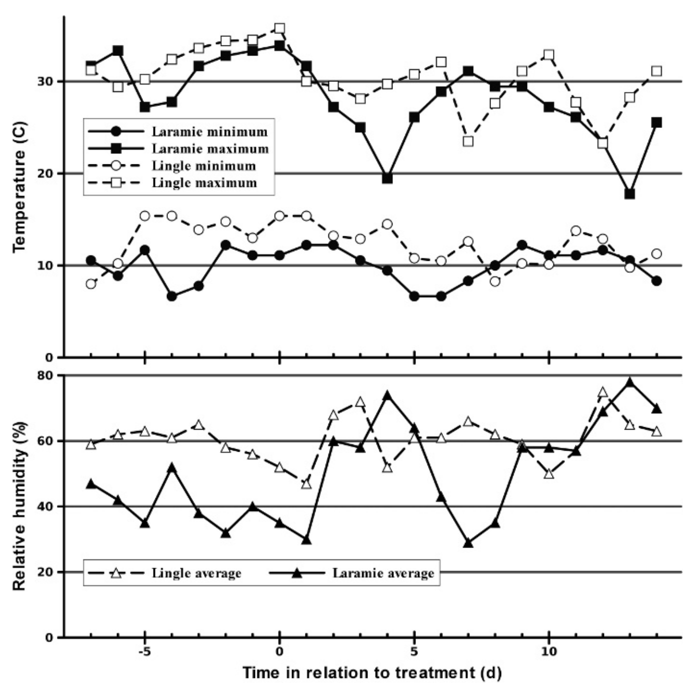

Figure 1. Maximum and minimum temperatures and average relative humidity 7 d before, and 14 d after, herbicide applications at Laramie and Lingle, WY, 2005. Herbicide treatments were applied on July 22 and June 22 at Laramie and Lingle, respectively.

Surviving common lambsquarters plants in 1 m of row for each selection were counted 28 d after treatment, and mortality was calculated by dividing the number of plants in the treated areas by the number of plants in the surfactant control. Pretreatment observations confirmed that selections had similar numbers of plants in each glyphosate rate as the surfactant-treated control (data not shown). Percentage of mortality resulting from either the high-glyphosate rate (840 g glyphosate ha^{-1}) or low-glyphosate rate (420 g glyphosate ha^{-1}) were used as response variables for analysis.

The study was analyzed as a randomized complete-block design with three replications at two experimental sites. The trial location (either Lingle or Laramie), collection site (either Scottsbluff or Torrington), and historical herbicide treatment (either HG, LG, RG, or NG) from which each selection was collected were used as factors in the analysis. Data were pooled across the original blocking criteria from each collection site because it was the response of the entire population from the historical herbicide treatments that was of interest. An unequal number of plants were collected from the various historical herbicide treatments, resulting in an unequal sample size for that factor. At the Laramie site, 41, 63, 22, and 27 selections were planted and analyzed from the HG, LG, RG, and NG historical herbicide treatments, respectively. At the Lingle site, 36, 55, 22, and 24 selections were planted and analyzed from the HG, LG, RG, and NG historical herbicide treatments, respectively. A mixed-effects, unbalanced ANOVA was used to determine the effect of historical herbicide treatments from the Scottsbluff and Torrington sites on the response of the selections to glyphosate. Selections from the Fort Collins site were used in construction of the histograms but were excluded from ANOVA (15 selections at Laramie, 11 selections at Lingle) because only plants from the low-glyphosate treatment were collected. Trial site, collection location, historical herbicide treatment, and all interactions between these three factors were considered fixed effects in the model. Each selection was considered a replicate of the collection location and historical herbicide treatment from which it was collected. Each selection appeared three times at each trial site and thus was considered a repeated measure in space. Heterogeneity of variance was identified between levels of the historical herbicide treatment factor with respect to the low-glyphosate rate mortality response variable but not the high-glyphosate rate mortality response. A between-subject heterogeneous variance model was chosen for analysis of the low-glyphosate rate mortality response to account for this heterogeneity using the MIXED procedure in SAS[2] (Littell et al. 1996). No such modification was required for the high-glyphosate rate mortality response.

Results and Discussion

Histograms representing the mortality response from the 420 g glyphosate ha^{-1} at the Laramie experimental site were positively skewed for all historical herbicide treatments, and no differences between histograms were apparent (data not shown). Because this rate resulted in very low mortality at this experimental site, it is not surprising that differences between historical herbicide treatments were not evident. In contrast, differences between historical herbicide treatments are unmistakable in response to the 840 g ha^{-1} rate of glyphosate (Figure 2). The distribution in mortality response for plants from the HG treatment at Laramie experimental site appeared very balanced with mortality ranging from 0 to 100% with a peak near 50%. Skewness (a measure of lack of symmetry) for this group is near 0. In contrast, the RG and NG treatments, and to a lesser extent the LG treatment, resulted in distributions that were heavily skewed to the left with the only noticeable peak near 100%. When interpreting these histograms, it is important to remember that seed was collected only from common lambsquarters plants that survived herbicide applications in 2003. Little inference can be made about the population as a whole in each plot history; inference should be limited to the portion of the seed bank resulting from plants that survived herbicide treatment. Seed produced by plants emerging after herbicide treatments or possessing other avoidance mechanisms were excluded from this sample and may enrich the level of susceptibility in the total seed bank.

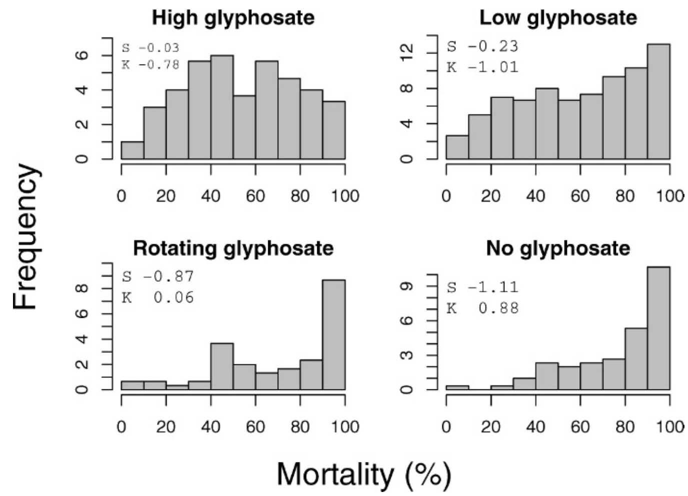

Figure 2. Mortality of common lambsquarters in response to 840 g glyphosate ha^{-1} as influenced by four herbicide treatment histories, Laramie, WY. Abbreviations: S, skewness; K, kurtosis.

Although common lambsquarters plants were much larger at Lingle compared with Laramie, environmental factors strongly favored glyphosate efficacy at the Lingle site. Environmental conditions at Laramie were, on average, drier and cooler than at Lingle (Figure 1). Differences in relative humidity and minimum temperatures were especially evident in the 7 d before, and 1 d following, herbicide application. Research under controlled environments has repeatedly demonstrated that cool, dry conditions result in reduced absorption, translocation, and overall efficacy of glyphosate (Dall'Armellina and Zimdahl 1989; Jordan 1977; Klevorn and Wyse 1984; Masiunas and Weller 1988; Reddy 2000). Although the environmental differences between the Lingle and Laramie sites were not as great as those in many controlled studies, it is likely that the differences in temperature and relative humidity between the sites contributed to the large differences in mortality. Mortality from the 840 g ha^{-1} rate at Lingle was high regardless of treatment history. However, the HG treatment distribution was less skewed compared with the other three treatment histories (Figure 3). These data demonstrate the strong influence of environment on glyphosate efficacy. It is likely that many differences in glyphosate susceptibility within a species may not be noticeable under environmental conditions that favor glyphosate efficacy (such as warm, humid environments).

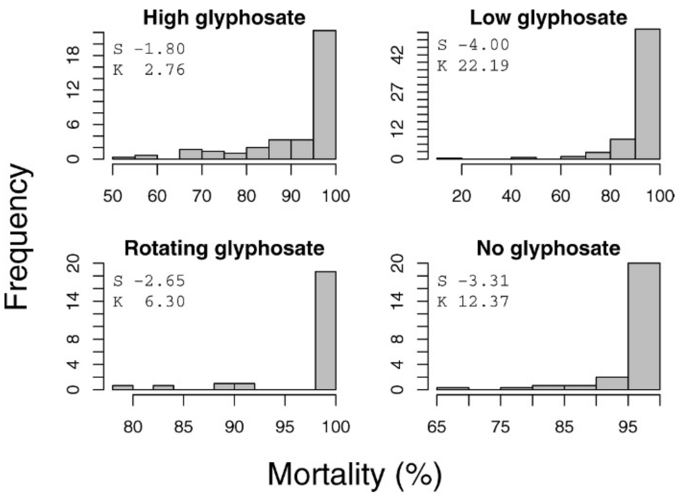

Figure 3. Mortality of common lambsquarters in response to 840 g glyphosate ha^{-1} as influenced by four herbicide treatment histories, Lingle, WY. Abbreviations: S, skewness; K, kurtosis.

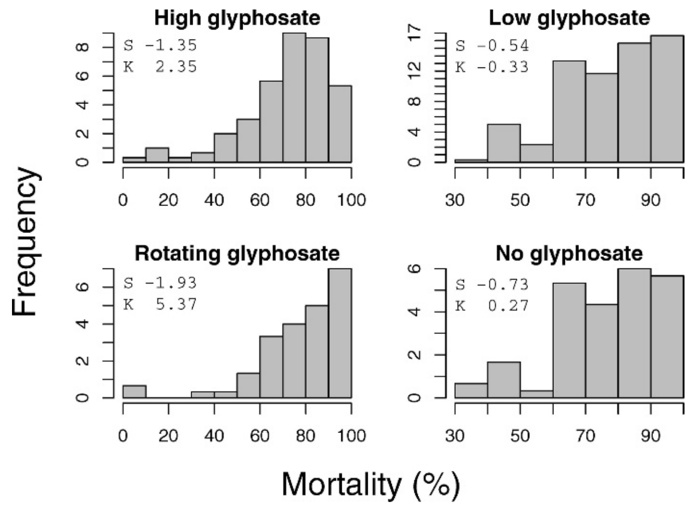

Figure 4. Mortality of common lambsquarters in response to 420 g glyphosate ha^{-1} as influenced by four herbicide treatment histories, Lingle, WY. Abbreviations: S, skewness; K, kurtosis.

These differences may become more pronounced when less-favorable conditions for glyphosate efficacy are present, such as those observed at the Laramie site.

When the rate was reduced to 420 g glyphosate ha^{-1} at Lingle, the distributions shifted to the left of the mortality spectrum (Figure 4). In the HG treatment, there is a peak at 80% mortality; no other historical treatment has a peak at < 90% mortality. Although the differences are more subtle at Lingle, these results support the findings from the less-favorable environment at Laramie that the selection pressure resulting from the high glyphosate historical treatment results in more-tolerant progeny from surviving plants. Common lambsquarters plants that survived glyphosate applications in the long-term research plots indeed produced progeny with reduced glyphosate susceptibility compared with plants that were not exposed to the herbicide.

Data from the two field trials were subjected to ANOVA using historical treatment and collection location (Scottsbluff or Torrington) as factors. The trial site by historical treatment interaction was significant with respect to mortality from 840 g glyphosate ha^{-1}, so data were analyzed separately by trial site for this response variable. Collection location was not significant for either response variable ($P > 0.7$) nor were any interactions with collection location ($P > 0.2$) at either trial site. This indicates that selections from the Torrington and Scottsbluff long-term research plots responded similarly when collected from the same historical herbicide treatments.

Glyphosate applied at 420 g ha^{-1} resulted in less common lambsquarters mortality under the environmental conditions experienced at the Laramie location (Table 2). Differences between historical herbicide treatments were observed, with plants collected from the HG historical treatment exhibiting less mortality than any other historical treatment. The LG treatment had lower mortality compared with the NG treatment after application of 420 g ha^{-1} glyphosate when pooled over trial locations and collection sites. Mortality followed a logical pattern, with the mortality ranging from the lowest value (42%), where historical selection pressure was heaviest (HG), up to the highest value (54%), where no glyphosate selection pressure had been applied over the previous 6 yr (NG). Although the RG treatment was not statistically different from the LG or NG treatments, its intermediary position implies that some degree of reduced susceptibility found in this population may indeed have arisen from generations before those collected for this study.

Analysis of mortality resulting from the 840 g ha^{-1} rate of glyphosate revealed significant interactions between trial site and historical treatment. Differences between historical treatments similar to those described above were observed at the Laramie trial site, where HG and LG treatments showed reduced mortality after application of the high glyphosate rate compared with RG and NG treatments (Table 3). Although the overall ANOVA was marginally significant ($F_{df=3,129} = 2.20$, $P = 0.091$), differences between historical treatments were not observed at the Lingle site in response to 840 g glyphosate ha^{-1}, where mortality ranged from 93 to 99%. Common lambsquarters in the Laramie trial showed differences in mortality relating to treatments applied the year of collection; HG and LG received glyphosate applications in the year of collection, whereas the RG and NG treatments received nonglyphosate herbicide treatments the same year. It is unclear from the data how much influence the

Table 2. Common lambsquarters mortality after application of 420 g glyphosate ha^{-1} at two trial locations in 2005 as influenced by four herbicide treatment histories.

Trial location	Historical herbicide treatment	Mortality[a]
		%
Laramie	Pooled	19 a
Lingle	Pooled	77 b
Pooled	High glyphosate[b]	42 A
Pooled	Low glyphosate	47 B
Pooled	Rotating glyphosate	50 BC
Pooled	No glyphosate	54 C

[a] Least-square means for trial location or historical treatments followed by the same letter are not significantly different (0.05). Lowercase and uppercase letters are for comparison of trial locations and historical herbicide treatments, respectively.

[b] Historical herbicide treatment descriptions: high glyphosate, exclusive use of glyphosate applied twice per year at 840 g ha^{-1}; low glyphosate, exclusive use of glyphosate applied twice at 420 g ha^{-1}; rotating glyphosate, received high glyphosate treatment in even numbered years and no glyphosate treatment in odd numbered years; no glyphosate, received nonglyphosate treatment each year. Detailed treatments are provided in Table 1.

Table 3. Common lambsquarters mortality after application of 840 g glyphosate ha^{-1} at two trial locations from two collection sites in 2005 as influenced by four herbicide treatment histories.

Trial location	Historical herbicide treatment	Mortality
		%
Laramie	High glyphosate[a]	55 a[b]
	Low glyphosate	58 a
	Rotating glyphosate	80 b
	No glyphosate	77 b
Lingle	High glyphosate	93 A
	Low glyphosate	95 A
	Rotating glyphosate	99 A
	No glyphosate	98 A

[a] Historical herbicide treatment descriptions: high glyphosate, exclusive use of glyphosate applied twice per year at 840 g ha^{-1}; low glyphosate, exclusive use of glyphosate applied twice at 420 g ha^{-1}; rotating glyphosate, received high glyphosate treatment in even numbered years and no glyphosate treatment in odd numbered years; no glyphosate, received nonglyphosate treatment each year. Detailed treatments are provided in Table 1.

[b] Least-square means for historical herbicide treatments within a trial location followed by the same letter are not significantly different (0.05). Lowercase and uppercase letters are for comparison of treatments at the Laramie and Lingle locations, respectively.

previous 5 yr of herbicide selection pressure has had on these populations.

The progeny observed in this research may have arisen from two distinct types of selection. Neve and Powles (2005) have demonstrated that rigid ryegrass (*Lolium rigidum* Gaudin) plants resistant to field use rates of diclofop could be produced after only three generations of selection at reduced herbicide rates. It is not known if 6 yr of low-rate glyphosate use in the LG treatment has resulted in a similar quantitative selection process. Furthermore, it is possible that the higher glyphosate rates applied in the HG treatment will be selecting for fewer genes with greater impact to achieve reduced glyphosate susceptibility compared with plants from the LG treatment. Future research is needed to determine the similarities and differences between the LG and HG treatments.

Rotating glyphosate applied alone with nonglyphosate herbicides on an annual basis resulted in an intermediate response in common lambsquarters susceptibility to glyphosate compared with the continuous, exclusive use of glyphosate or continuous nonglyphosate systems. This trend indicates that some effect of long-term selection pressure was observed and that rotating herbicide modes of action on an annual basis exert less selection pressure than continuous, exclusive glyphosate use. Rotation of herbicides has been suggested as a strategy for delaying or preventing the appearance of herbicide-resistant weeds (Gressel and Segel 1990). However, Neve and Powles (2005) point out that rotation of herbicides may actually exacerbate herbicide resistance if it is a "generalist" form of resistance; that is, a mechanism that could result in cross-resistance to other modes of action. As no mechanism for the differences in glyphosate susceptibility have been isolated for common lambsquarters, it is not known whether reduced susceptibility to other herbicides may be present. In addition, Gressel and Segel (1990) theorize that fitness of resistant plants will determine whether rotation of herbicides is an effective resistance management strategy. It is unknown at the current time whether the common lambsquarters plants that exhibit less susceptibility to glyphosate are less fit than their more susceptible counterparts are.

A second resistance management strategy that has been advocated is mixtures of herbicides applied at the same time (Gressel and Segel 1990). The herbicide treatments from which the common lambsquarters seed was harvested for this research did not include weed management programs that incorporated either a residual herbicide followed by glyphosate or glyphosate tank-mixed with an herbicide with another mode of action; therefore, no comparisons between these management strategies can be made based on this research.

This research indicates that parental exposure to exclusive use of glyphosate influences the following generation of common lambsquarters with respect to glyphosate susceptibility. The differences observed between common lambsquarters selections were influenced by environmental conditions before and following application as well as the glyphosate rate applied. This interaction between environment and biotype may explain the variable response often observed in glyphosate tolerance research on common lambsquarters, and also the variable field response many weed scientists have observed in growers fields from year to year (Culpepper 2006; Owen and Zelaya 2005; Scursoni et al. 2006).

Sources of Materials

[1] Roundup WeatherMAX surfactant system, MON 56151, Monsanto Company, Saint Louis, MO.

[2] SAS version 8.1, SAS Institute Inc., Cary, NC.

Acknowledgments

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