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Inheritance of evolved glyphosate resistance in *Lolium rigidum* (Gaud.)

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Abstract Resistance to the non-selective herbicide, glyphosate, has evolved recently in several populations of *Lolium rigidum* (Gaud.). Based upon the observed pattern of inheritance, glyphosate resistant and susceptible populations are most probably homozygous for glyphosate resistance and susceptibility, respectively. When these populations were crossed and the F_1 progeny treated with glyphosate, the dose response behavior was intermediate to that of the parental populations. This observation, coupled with an absence of a difference between reciprocal F_1 populations, suggests that glyphosate resistance is inherited as an incompletely dominant nuclear-encoded trait. The segregation of resistance in F_1×S backcrosses suggests that the major part of the observed resistance is conferred by a single gene, although at low glyphosate treatments other genes may also contribute to plant survival. It appears from this study that a single nuclear gene confers resistance to glyphosate in one population of *L. rigidum*.

Keywords Glyphosate · Herbicide resistance · Genetics · *Lolium rigidum*

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Introduction

Herbicide resistance has evolved in many different weed species, with an average of nine new cases of herbicide-resistant weed species confirmed each year, worldwide (Heap 2000). Although the appearance of herbicide-resistant weed biotypes has been well documented, less information on the inheritance of resistance is available. To-date, herbicide resistance has appeared in 216 weed biotypes in 45 countries (Heap 2000). Of these, approximately 25 cases have been thoroughly investigated and the mode of inheritance of resistance determined (reviewed by Darmency 1994; Gasquez 1997).

In an overwhelming number of cases studied, a single gene confers herbicide resistance (Darmency 1994; Gasquez 1997). There has been only one example where multiple genes have encoded an evolved herbicide resistance and that is resistance to chlorotoluron in *Alopecurus myosuroides* (Chauvel and Gasquez 1994). Herbicide resistance traits are almost always encoded by the nuclear genome, with the only known example of maternal inheritance being target-site triazine resistance (Darmency 1994) (this is perhaps not surprising given that most herbicides target gene products encoded by nuclear rather than organellar DNA). Similarly, herbicide resistance is most frequently observed as a dominant or partially dominant characteristic, although recessive gene inheritance of trifluralin resistance has been reported (Jasieniuk et al. 1994; Zeng and Baird 1997).

Recently, glyphosate resistance has evolved independently in several *Lolium rigidum* populations (Powles et al. 1998; Pratley et al. 1999). *Lolium* species are major weeds of agricultural and horticultural regions in many countries, and *L. rigidum* is the most economically damaging weed of Australian agriculture. In Australia this species has a long history of herbicide resistance to numerous chemical classes (reviewed by Preston et al. 1996; Preston and Powles 2000), and the development of glyphosate resistance further complicates control strategies for this weed. The objective of this study was to determine the inheritance of glyphosate resistance in a population of *L. rigidum*.

Materials and methods

Seed germination and plant growth

Seeds were germinated on 0.6% (w/v) agar under controlled environment conditions (12 h, 20°C, 30 µE m^{-2} s^{-1} light period; 12 h, 16°C dark period). After 6 days, seedlings were transplanted into standard potting mix (17 cm diameter pots) and thereafter maintained outside during the normal growing season for this species.

Selection of the glyphosate-resistant population (NLR70)

Thirty six two- to three-leaf glyphosate-resistant *L. rigidum* plants (Powles et al. 1998) were treated with glyphosate isopropylamine (900 g a.e.[1] ha^{-1}; with 0.2% by volume non-ionic surfactant), a dose which always kills all susceptible plants. After a 2-week growth period, to ensure all individuals survived the glyphosate application, the seedlings were transplanted into fresh potting mix (25 cm diameter pots; three individuals per pot). These plants were maintained outdoors during the normal growing season for this species (winter-spring). Prior to flowering, entry of foreign pollen was prevented using a transparent plastic sleeve (1200×250 mm) thus leaving the resistant plants to cross-pollinate amongst themselves. Seeds were harvested from the plants and bulked, constituting the NLR70 selected population. This selection process was repeated with 120 seedlings from the NLR70 selected population in the following year, to produce the NLR70 twice-selected population.

Attempt to select glyphosate-resistant plants from a susceptible population (VLR1)

A similar process was performed for a known glyphosate-susceptible *L. rigidum* population (VLR1). Approximately 40,000 VLR1 seedlings were treated with 450 g a.e. ha^{-1} of glyphosate isopropylamine on two occasions, 3 weeks apart. Only 29 plants survived this treatment. These survivors were grown to maturity and were allowed to cross amongst themselves. The progeny (VLR1 selected population) were treated at the two- to three-leaf stage with a single application of 450 g a.e. ha^{-1} of glyphosate isopropylamine. The seven survivors of 408 plants were kept and allowed to cross among themselves to produce the twice-selected VLR1 population.

Generation of F_1 and backcross populations

Individuals of the resistant *L. rigidum* population (R=NLR70), preselected with glyphosate (900 g a.e. ha^{-1}), and the known susceptible population (S=VLR1) were crossed to produce the F_1 generation. One plant each of the known R and S populations was re-potted into a single pot (25 cm diameter). Prior to flowering, the pots were encased within a transparent plastic sleeve (1200×250 mm) to ensure cross-pollination and to restrict entry of foreign pollen. Seeds were harvested from both R and S parents and kept separately to constitute individual F_1 families.

The F_1 backcross populations were obtained by crossing one plant each of the F_1 hybrids (maternal R) back to the S parental plants. Thirteen individual F_1 plants, each from different families, were used, yielding 13 backcross families.

Herbicide treatments

Herbicide was applied with a laboratory moving-boom sprayer, equipped with T-jet fan nozzles, travelling at a speed of 1 m s^{-1}. The output volume from the sprayer was 128 l ha^{-1} at a pressure of 250 kPa. Plants were returned outdoors after treatment and the response to herbicide application recorded after 21 days.

Glyphosate-selected resistant and susceptible populations

The glyphosate-resistant NLR70, NLR70 selected and NLR70 twice-selected populations were subjected to glyphosate dose-response experiments. Germinated seedlings were transplanted to 17 cm-diameter pots containing potting soil, with 12 seedlings per pot, and grown outdoors. Glyphosate isopropylamine (with 0.2% by volume surfactant) was applied at a range of rates from 0 to 3,600 g a.e. ha^{-1} to plants at the two- to three-leaf stage of development. For each herbicide rate, four replicate pots per population were used. The susceptible VLR1, selected VLR1 and twice-selected VLR1 populations were treated similarly, except that the rates of glyphosate isopropylamine ranged from 0 to 900 g a.e. ha^{-1}.

Plants were recorded as alive if they demonstrated active growth following application of the herbicide. Mortality data were subject to probit analysis using the computer program POLOPC (1987) to determine LD_{50}s. Probit analysis gives equations of the form:

$$Y=5+(a+b\log z) \quad (1)$$

where Y is the expected probit, *a* is the intercept and *b* is the slope of the probit line, and $\log_z$ is the log of the dose rate (Finney 1971). The LD_{50} can be calculated from this equation by solving for a probit of 5.

F_1 dose-response experiments

Glyphosate dose-response experiments were conducted on the S, R and F_1 plants maintained outdoors during autumn and winter (normal growing season). Germinated seedlings were transplanted to 17 cm-diameter pots containing potting soil with 12 seedlings per pot. Glyphosate isopropylamine (with 0.2% by volume surfactant) was applied at a range of rates from 0 to 3,600 g a.e. ha^{-1} (four different rates per population) to plants at the two- to three-leaf stage of development. For each herbicide rate, four replicate pots of the S and R populations, and one pot for each of four F_1 families (maternal S and R origins) were used. Results from each group of maternal F_1 families (either S or R) were combined.

Glyphosate-treatment of F_1 backcrosses

The F_1×S backcross population, with S, R and F_1 controls, was assessed for glyphosate resistance. Germinated seeds were transplanted to rectangular trays (285×310 mm) containing potting soil, 63 seedlings per tray, and grown outdoors. Preliminary experiments (data not shown) were conducted, to determine the most suitable glyphosate concentrations for plant control. Thus, glyphosate isopropylamine (with 0.2% by volume surfactant) was applied at rates of 225 and 338 g a.e. ha^{-1} to plants at the two- to three-leaf stage of development. For each herbicide rate, 48 individuals of the S and R populations, 96 individuals from four F_1 families (maternal S and R origins), and 585 individuals from 13 F_1×S families were used. The results from each group of F_1 and F_1×S families were combined.

Phenotyping of backcross individuals

Tillering plants were divided into segments of two to three tillers, yielding nine segments (or clones) from each individual plant. The clones were trimmed to approximately 1 cm of root and 2 cm of shoot material and planted into 5 cm-diameter pots containing potting soil (one clone per pot) and grown outdoors. When the clones had grown 2 to 3 cm of fresh leaf material they were treated

[1] a.e.=acid equivalent, the theoretical yield of parent acid, glyphosate, from the formulated salt

Table 1 Glyphosate dose required for 50% mortality of the resistant and susceptible glyphosate-selected *L. rigidum* populations. Values are LD_{50}s calculated by probit analysis of the full dose response, from two separate experiments. Values in parenthesis represent the 95% confidence intervals

Susceptible populations	LD_{50} (g a.e. ha^{-1})	Resistant populations	LD_{50} (g a.e. ha^{-1})
VLR1	136 (83, 181)	NLR70	514 (395, 614)
VLR1 selected	138 (110, 163)	NLR70 selected	465 (370, 538)
VLR1 twice-selected	168 (141, 195)	NLR70 twice-selected	476 (377, 555)

with glyphosate isopropylamine (with 0.2% by volume surfactant) at rates of 338, 450, and 563 g a.e. ha^{-1}. Preliminary experiments established that higher concentrations of glyphosate were needed to control clones compared to *L. rigidum* seedlings. Thus, each original plant was treated at each of the herbicide rates in triplicate (3 rates×3 clones); 24 plants each of S, R and F_1 (S and R maternal origin) populations and 114 F_1×S individuals were used. Individual plants were phenotyped according to the combined response of all nine clones to the herbicide, 28 days after application (as compared to the behavior of control populations).

Results and discussion

Homozygosity of the glyphosate-R population/ background resistance in the S population

The three glyphosate-resistant NLR70 populations (original NLR70, selected and twice-selected NLR70) demonstrated similar responses to glyphosate treatment. Plants from all three populations showed zero mortality after application of glyphosate isopropylamine at rates that killed susceptible plants. The concentration of herbicide required to kill 50 % (LD_{50}) of the resistant population NLR70 was 514 g a.e. ha^{-1}, whilst the LD_{50}s for the selected populations were 465 and 476 g a.e. ha^{-1} (Table 1) for NLR70 selected and twice-selected, respectively. These values show that repeated selection of the NLR70 population with glyphosate did not alter the dose response. Therefore, it is highly likely that the original NLR70 population was homozygous for the glyphosate resistance trait.

When the glyphosate-susceptible population was repeatedly selected with glyphosate, very few individuals survived the recommended field rate (450 g a.e. ha^{-1}). The LD_{50} for the original susceptible population (VLR1) was, in this instance, 136 g a.e. ha^{-1} (Table 1). A single generation of selection did not significantly alter this, giving a population with an LD_{50} of 138 g a.e. ha^{-1}. The twice-selected susceptible population had a slightly higher LD_{50} (168 g a.e. ha^{-1}). Treatment with 900 g a.e. ha^{-1} killed all individuals of all VLR1 populations. These experiments over three generations demonstrate that recurrent selection for glyphosate-resistant individuals within a glyphosate-susceptible population is no simple task. These experiments further suggest that there is some variation for glyphosate tolerance present in VLR1. This is to be expected in the highly genetically variable and cross-pollinated *L. rigidum*.

These experiments have demonstrated that the parental glyphosate resistant and susceptible plants used in this study were very likely to be homozygous for glyphosate resistance and susceptibility, respectively (Table 1).

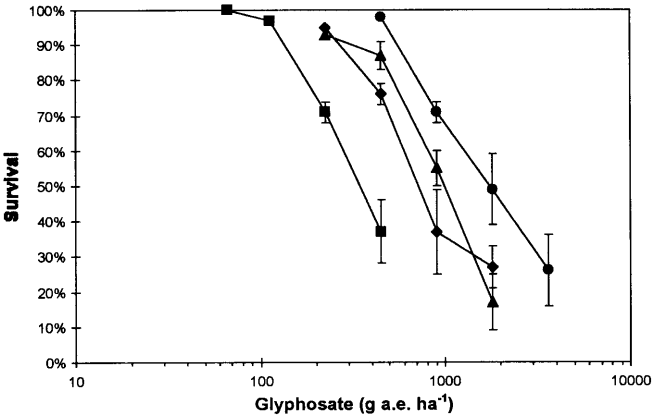

Fig. 1 Dose response of the susceptible (■), F_1 maternal S (◆), F_1 maternal R (▲), and resistant (●) populations of *L. rigidum* to glyphosate isopropylamine (log scale). Data is from a single dose response experiment with four replicates conducted on seedlings growing in pots. Points are mean survival±SE

F_1 dose-response curves

The resistant *L.rigidum* population was much less affected by glyphosate than the susceptible population, requiring 10-fold higher rates for substantial mortality (Fig. 1). The F_1 population demonstrated an intermediate response to glyphosate. A very similar level of glyphosate resistance was observed for F_1 seed obtained from both maternal S and R parents (Fig. 1). As the reciprocal F_1 plants had similar responses to glyphosate, the genetic control of the glyphosate resistance mechanism resides in the nuclear genome and is not localised to the maternal cytoplasm.

The LD_{50} of the susceptible population, in this instance, was 354 g a.e. ha^{-1}, whilst the LD_{50} for the resistant population was 1833 g a.e. ha^{-1}. These values are considerably higher than those reported for other experiments (e.g. Table 1). Some variation in LD_{50} values between experiments conducted at different times of the year is to be expected as seasonal conditions affect the level of control observed after glyphosate application. The absolute values for each population fluctuate between experiments; however, the ratio of LD_{50}s for the glyphosate susceptible and resistant populations remains similar (Powles et al. 1998).

Table 2 Number of F_1×S individuals surviving glyphosate treatment (338 g a.e. ha^{-1}) and chi-square analysis for goodness of fit of the observed segregation ratios to the 1:1 ratio predicted by the single gene hypothesis

F_1×S family	Observed plant numbers		Expected plant numbers		Total individuals	χ^2 Prob.
	Alive	Dead	Alive	Dead		
1	7	38	15	30	45	<0.05
2	15	29	15	29	44	0.934
3	17	28	15	30	45	0.544
4	14	31	15	30	45	0.734
5	13	27	13	27	40	0.893
6	14	29	14	29	43	0.895
7	13	31	15	29	44	0.578
8	14	29	14	29	43	0.895
9	20	24	15	29	44	0.093
10	23	20	14	29	43	<0.05
11	19	24	14	29	43	0.138
12	3	40	14	29	43	<0.05
13	19	24	14	29	43	0.138
Total	191	374	189	376	565	0.880
Behavior of parental controls:						
S	0	41			41	
F_1(S)	29	19			48	
F_1(R)	40	14			54	
R	41	7			48	

The LD_{50} values for the combined F_1 (S) or F_1 (R) families were 857 and 937 g a.e. ha^{-1} respectively. The lower resistance of the F_1 families when compared with the glyphosate-resistant population indicates that resistance is not fully dominant over susceptibility. Incomplete dominance of herbicide resistance is common, but the degree of dominance demonstrated by the resistance allele varies considerably (Mallory-Smith et al. 1990; Betts et al. 1992; Purba et al. 1993; Boutsalis and Powles 1995; Murray et al. 1995; Tardif et al. 1996). A study of bipyridyl herbicide resistance in *Arctotheca calendua* (Purba et al. 1993) determined the LD_{50} of reciprocal F_1 progenies at 80 g a.i. ha^{-1}, compared to 30 g a.i. ha^{-1} for the susceptible population and 200 g a.i. ha^{-1} for the resistant population. Conversely, the LD_{50} for chlorsulfuron-resistant *Sonchus oleraceus* and heterozygous F_1 populations was >45 g a.i. ha^{-1}, whilst the LD_{50} of the susceptible population was <4 g a.i. ha^{-1} (Boutsalis and Powles 1995). Similar results were obtained for a *L. rigidum* biotype resistant to haloxyfop-ethoxyethyl (Tardif et al. 1996). The LD_{50}s for susceptible and resistant *Lolium* populations were 12 and >3,500 g a.i. ha^{-1}, respectively, whilst the LD_{50} of the F_1 populations was 1,300 and 2,600 g a.i. ha^{-1} (maternal S or R parent, respectively). In each of these examples the genetic inheritance of herbicide resistance is described as incompletely dominant; however, a greater degree of dominance is exhibited by the resistance allele in the chlorsulfuron and haloxyfop-ethoxyethyl cases (semi-dominant), as opposed to the paraquat resistance gene. The glyphosate resistance mechanism in *L. rigidum* is inherited in a semi-dominant manner, similar to that of chlorsulfuron resistance (Boutsalis and Powles 1995) and haloxyfop-ethoxyethyl resistance (Tardif et al. 1996).

Segregation of resistance trait in F_1xS backcross population

To ascertain whether the genetic control of glyphosate resistance resides on a single allele or involves multiple genes, the F_1 population was backcrossed to the susceptible parent, yielding the F_1×S populations. These plants were treated with two different rates of glyphosate (225 and 338 g a.e. ha^{-1}). The number of survivors of the treated S, R, and F_1 plants (determined 3 weeks after glyphosate treatment) was used to calculate the expected mortality from glyphosate application at each rate, assuming a single gene with partial dominance. The number of surviving F_1×S backcross individuals was compared with the predicted values (assuming 1:1 segregation of F_1 to susceptible phenotypes in the backcross generation). The calculated chi-square probability value for the combined F_1×S backcross population (13 families) was consistent with the partially dominant single-gene hypothesis at the 338 g a.e. ha^{-1} treatment (Table 2).

The mortality observed when treatment occurred at the lower glyphosate rate (225 g a.e. ha^{-1}; Table 3) was less than expected (217 plants controlled by glyphosate treatment compared with the 278 expected). These values give a chi-square probability of 2.4×10^{-7}, significantly less than 0.05. The greater number of observed survivors may be due to the effects of one (or more) minor genes that confer glyphosate tolerance at low rates. Certainly, the effects of any minor genes were not apparent at 338 g a.e. ha^{-1} of glyphosate (Table 2).

To clarify this discrepancy, individual plants were phenotyped (glyphosate treatment of clones at different rates) yielding very consistent results. The phenotype of each plant was determined according to the behavior of the S, R, and F_1 control plants at each of the glyphosate rates tested (338, 450, and 563 g a.e. ha^{-1}). All individuals phenotyped as “susceptible” were killed by 450 g a.e.

Table 3 Number of F_1×S individuals surviving glyphosate treatment (225 g a.e. ha^{-1}) and chi-square analysis for goodness of fit of the observed segregation ratios to the 1:1 ratio predicted by the single-gene hypothesis

F_1×S family	Observed plant numbers		Expected plant numbers		Total individuals	χ^2 Prob.
	Alive	Dead	Alive	Dead		
1	19	26	23	22	45	0.281
2	25	17	21	21	42	0.230
3	25	17	21	21	42	0.230
4	31	14	23	22	45	<0.05
5	31	10	21	20	41	<0.05
6	21	20	21	20	41	0.902
7	28	17	23	22	45	0.108
8	30	10	20	20	40	<0.05
9	28	14	21	21	42	<0.05
10	26	18	22	22	44	0.241
11	26	18	22	22	44	0.241
12	19	25	22	22	44	0.348
13	33	11	22	22	44	<0.05
Total	342	217	281	278	559	<0.001
Behavior of parental controls:						
S	10	35			45	
F_1(S)	39	11			50	
F_1(R)	43	9			52	
R	42	2			44	

Table 4 Chi-square analysis of the segregation for glyphosate resistance in F_1×S backcross populations. Plants were assessed 28 days after treatment with glyphosate. Phenotype classes are S (susceptible behavior) and non-S (non-susceptible behavior)

F_1×S family	Phenotype			χ^2 Probability (1:1 ratio)
	S	Non-S	Total	
1	12	12	24	1.00
2	11	13	24	0.68
3	8	11	19	0.49
4	10	14	24	0.41
5	13	10	23	0.53
Observed	54	60	114	0.57
Expected	57	57	114	

ha^{-1} of glyphosate (or less), while those phenotyped as "non-susceptible" plants (including all F_1 and R) had most clones surviving at this rate. For each of the five backcross populations screened (Table 4), the hypothesis of a single-gene trait was confirmed at the 0.05 significance level. The pooled data (114 individuals in total, plants phenotyped in triplicate) also gave phenotypic ratios consistent with this hypothesis, with a chi-square probability value of 0.57. From these results it appears that a single gene encodes glyphosate resistance in this population of *Lolium*.

Conclusion

Glyphosate resistance in *L. rigidum* population NLR70 is clearly a nuclear inherited trait as reciprocal crosses demonstrate that resistance is pollen-transmitted (Fig. 1). Glyphosate resistance is also stably maintained through at least two generations (Table 1). In this *L. rigidum* population, glyphosate resistance is inherited in a semi-dominant manner (Fig. 1, Tables 2–4). Although other genes may play some small role in maintaining survival at low doses of glyphosate, F_1×S backcross populations exhibit phenotypic ratios that are consistent with those expected for a single-gene trait (Tables 2–4). These results with glyphosate-resistant plants are similar to those found with resistance to many other herbicide modes of action, which are predominantly encoded by single nuclear genes with dominant or incompletely dominant expression (reviewed by Darmency 1994; Gasquez 1997). Thus glyphosate resistance appears to be encoded by a single nuclear gene. Although the function of this gene is not yet known, efforts to elucidate the mechanism of resistance actively continue in our laboratory (Lorraine-Colwill et al. 1999).

The glyphosate-resistant population of *L. rigidum* exhibits strong resistance to normal field application rates of glyphosate when the resistance allele is present in either the homozygous or heterozygous condition (Fig. 1). Therefore, under normal field use, resistance in such populations would be expressed largely as a dominant trait, and this would increase the rate of resistance evolution. The level of glyphosate resistance conferred by this allele, coupled with the simple mode of inheritance and self-incompatibility of the species, suggests that the glyphosate resistance gene has the potential to rapidly increase in frequency in *L. rigidum* populations under continued glyphosate selection.

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