Modelling interactions between herbicide and nitrogen fertiliser in terms of weed response

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Summary

The effects of nitrogen fertiliser on herbicide dose–response of weeds were investigated by measuring weed biomass after growth at a range of nitrogen levels and treatment with a range of herbicide doses. Increasing weed biomass at no-herbicide treatment (W_0) and the response rate of the dose–response curve (B), with increasing nitrogen were successfully described by the linear model and the exponential model respectively. Conversely, decreasing ED_{50} value with increasing nitrogen was well described by the logistic model. A combined model was then developed by incorporating these models into the standard dose–response model to describe the interactive effects of herbicide dose and nitrogen levels on biomass of *Brassica napus*, *Matricaria perforata*, *Papaver rhoeas* and *Galium aparine*. The model developed allowed the systematic description of increased herbicide performance with increasing nitrogen. The model was also used to predict weed biomass as affected by both herbicide doses and nitrogen levels. The mathematical relationships between herbicide dose–response and nitrogen levels may also be applied to the crop–weed competition model and then to decision making for optimum uses of nitrogen fertiliser and herbicide.

Keywords: modelling, herbicide dose, nitrogen fertiliser, dose–response, combined model.

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Introduction

Weed competitivity is a key component in describing crop–weed interactions and for predicting crop yield loss. Its size is determined by the inherent resource capture efficiencies and the relative responses of crop and weed to environmental factors, such as climatic and soil conditions. Studying the effects of climatic conditions on crop–weed competition is not straight forward, so most studies have concentrated on the effects of soil conditions, such as soil moisture (Wright *et al*., 1999), nitrogen (Farahbakhsh & Murphy, 1988; Rooney *et al*., 1990; Jornsgard *et al*., 1996) and phosphorous (Santos *et al*., 1998).

Nitrogen fertiliser is one of the major inputs in agriculture and recently has been blamed for water pollution, so farmers are now being encouraged to reduce nitrogen fertiliser input. There is also strong pressure on farmers to reduce herbicide use, for both economic and environmental reasons. To give some idea of the effect of reduced herbicide dose on crop production, Salonen (1992) and Christensen (1993) investigated the effects of reduced herbicide rates on crop–weed competition. Several studies have also been carried out on the effects of reduced rates of nitrogen on crop–weed competition (e.g. Wright & Wilson, 1992). Richards (1993) studied the effect of both herbicide and nitrogen on crop production and noted that the combination of reduced rates of herbicide and nitrogen fertiliser may lead to failure in weed control. However, little information is available to support decision making for both herbicide dose and nitrogen rate avoiding weed control failure.

The effect of increased nitrogen often increases weed susceptibility and thus herbicide performance. Previous

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studies (e.g. Lutman, 1971) focused on the physiological and biochemical understanding of nitrogen effects on herbicide performance in relation to herbicide uptake and translocation. No systematic approach has been made to describe a quantitative relationship between herbicide dose–response and nitrogen application. Furthermore, there is a lack of information on the effects of nitrogen on the performance of more recently developed herbicides, such as sulfonylurea herbicides. It has been reported that increased nitrogen fertiliser influenced crop–weed competition by altering each species' individual growth responses to nitrogen (Rooney *et al*., 1990; Iqbal & Wright, 1997). Most studies on the effects of nitrogen on crop–weed competition have been conducted in the field, so that the nitrogen response of weeds may be confounded with the effect of crop competition. Therefore, there is a need to investigate the interaction between herbicide and nitrogen, and their effects on weed growth in monoculture, which can provide basic information to help describe the relationship between herbicide dose–response and nitrogen.

This study was conducted to compare several mathematical models to describe the relationship between herbicide dose–response and nitrogen levels in terms of weed response. If the changes in parameters of the herbicide dose–response model with nitrogen levels can be simply described by empirical models, these models may be incorporated into the herbicide dose–response model to give a combined model. The combined model may be used to predict weed control by a herbicide as affected by both the herbicide dose and nitrogen level.

Materials and methods

Pot experiment

A pot experiment was carried out at Long Ashton Research Station in 1998/1999. The experiment consisted of three replicates for *Matricaria perforata* Merat (mayweed), *Brassica napus* L. (oilseed rape cv. Apex) and *Galium aparine* L. (cleavers), and four replicates for *Papaver rhoeas* L. (common poppy), laid out in a split plot design with six nitrogen levels as main plot treatments and six herbicide doses as sub-plot treatments. The four weed species were sown in a plunge bed on 26 October 1998. They were transplanted into pots (15 cm diameter, 20 cm high and containing silty clay soil) at either four plants per pot for *B. napus* or five plants per pot for the other species on 15 February 1999. The pots were then placed on the plunge bed and regularly watered by a sprinkler system.

The six levels of nitrogen, 0, 22.5, 45, 90, 180 and 360 kg ha^{-1} (based on the area of the pot, 0.018 m^2) were applied as ammonium nitrate (NH_4NO_3); 50% was applied on 17 March 1999 and 50% on 10 May 1999. The soil used in this study contained approximately 75 kg N ha^{-1} (1 ppm of NH_3 and 19.8 ppm of NO_3 measured on 20 October 1998), and approximately 3 ppm of NO_3 (measured on 11 March 1999). The nitrogen content was analysed as described by Keeney and Nelson (1982).

Metsulphuron-methyl at 0, 0.375, 0.75, 1.5, 3.0 and 6.0 g a.i. ha^{-1}, for the control of *P. rhoeas*, *M. perforata* and *B. napus*, and fluroxypyr at 0, 12.5, 25, 50, 100 and 200 g a.i. ha^{-1} for the control of *G. aparine*, were sprayed using a gear and tooth-driven laboratory track sprayer on 7 April 1999. The sprayer was fitted with a 01F80 even spray nozzle (Spraying Systems, Wheaton, IL, USA), set up 45 cm above the target plants and calibrated to achieve application rates in the range of 190–200 L ha^{-1} with a compressed air pressure of *c*. 200 kPa. At the time of herbicide application, plant heights of the test plants were from 5.7, 5.3, 3.6, and 6.1 cm at 0 kg N ha^{-1} to 10.5, 8.6, 8.4 and 8.9 cm at 360 kg N ha^{-1} for *B. napus*, *M. perforata*, *P. rhoeas*, and *G. aparine* respectively. Assessments were made at 63 days after herbicide treatment (9 June 1999). Three plants of *B. napus* and four plants of the other species per pot were sampled and dried at 90°C for 24 h for biomass determination.

Model development

The standard dose–response curve (Streibig, 1980) was fitted to weed biomass data, transformed if necessary, at each nitrogen level. Possible models for each parameter obtained by visual inspection of the parameter estimates for the dose–response curve at each nitrogen level were tested and then incorporated into the dose–response curve. Finally, the models were simplified by comparing *F*-tests, to obtain a parsimonious, but biologically meaningful final model.

The standard dose–response curve has most commonly been used to explain the relationship between weed biomass and herbicide dose:

$$W = \frac{W_0}{1 + (\mathrm{Dose}/\mathrm{ED}_{50})^B} \qquad (1)$$

where W_0 is weed biomass (g per plant) with no-herbicide treatment, ED_{50} is the effective dose required to reduce weed biomass by 50% (previously described as $e^{LD_{50}}$ by Kim *et al*. (2002) and B is the response rate of the curve or steepness of the curve. In Eqn (1), if different amounts of nitrogen fertiliser are applied, all parameters will change with nitrogen fertiliser (i). Therefore, at different amounts of nitrogen, the most general model (Full model) for weed biomass (W_i) is

Table 1 Summary of model development

Function	Constant	Linear	Exponential	Logistic	Inverse quadratic
$f(i) = W_{0i}$*	–	$W_i = \frac{a+bN}{1+[\text{Dose}/\text{ED}_{50i}]^{B_i}}$	–	–	$W_i = \frac{(a+bN)/(1+cN+dN^2)}{1+[\text{Dose}/\text{ED}_{50i}]^{B_i}}$
↓					
$g(i) = B_i$†	$W_i = \frac{W_{0i}}{1+[\text{Dose}/\text{ED}_{50i}]^{\alpha}}$	$W_i = \frac{W_{0i}}{1+[\text{Dose}/\text{ED}_{50i}]^{\alpha+\beta N}}$	$W_i = \frac{W_{0i}}{1+[\text{Dose}/\text{ED}_{50i}]^{\alpha\beta^N}}$	$W_i = \frac{W_{0i}}{1+[\text{Dose}/\text{ED}_{50i}]^{\alpha/1+\exp(-\gamma(N-\beta))}}$	–
↓					
$h(i) = \text{ED}_{50i}$‡	$W_i = \frac{W_{0i}}{1+[\text{Dose}/\lambda]^{B_i}}$	$W_i = \frac{W_{0i}}{1+[\text{Dose}/\lambda+\omega N]^{B_i}}$	$W_i = \frac{W_{0i}}{1+[\text{Dose}/\lambda\omega^N]^{B_i}}$	$W_i = \frac{W_{0i}}{1+\{\text{Dose}/[\lambda(1+(N\exp(-\omega))^{\theta})^{-1}]\}^{B_i}}$	–

The function $f(i)$ for W_{0i} was incorporated into Eqn (2), followed by the incorporations of $g(i)$ for B_i and then $h(i)$ for ED_{50}.
*W_{0i} in Eqn (2) was replaced by the function $f(i)$, linear and inverse quadratic models.
†After W_{0i} was replaced by the function $f(i)$, B_i was replaced by the function $g(i)$, constant, linear, exponential and logistic models.
‡After W_{0i} and B_i were replaced by their appropriate models, ED_{50i} was replaced by the function $h(i)$, constant, linear, exponential and logistic models.

$$W_i = \frac{W_{0i}}{1 + (\text{Dose}/\text{ED}_{50i})^{B_i}} \tag{2}$$

where W_{0i}, B_i and ED_{50i} are the parameters for the ith amount of nitrogen fertiliser. However, Eqn (2) requires a large number of parameters to predict weed biomass as affected by herbicide and nitrogen, and can predict weed biomass only for a given amount of nitrogen fertiliser. To predict weed biomass as affected by herbicide at a wide range of nitrogen fertiliser doses including the given amount, models to describe the relationships between the parameters and nitrogen should be incorporated into Eqn (2) to give a combined model.

To model the relationship between weed biomass at no-herbicide treatment and nitrogen, linear and inverse polynomial models can be used. In inverse polynomials, the inverse quadratic or linear divided by quadratic polynomial has been widely used for fitting nitrogen fertiliser response data (Nelder, 1966). The inverse quadratic polynomial has provided a good fit to many sets of data describing the relationship between crop yield and the amount of applied nitrogen (George, 1984; Sylvester-Bradley *et al.*, 1987). It is thus a reasonable assumption that the relationship between weed biomass with no-herbicide treatment and the amount of nitrogen (W_{0i}) can be described using the inverse quadratic model given as follows

$$W_{0i} = \frac{a + bN}{1 + cN + dN^2} \tag{3}$$

where a, b, c and d are unknown parameters and N is the amount of applied nitrogen. This gives a model of the form of Eqn (3) by replacing W_{0i} in Eqn (2) as follows

$$W_i = \frac{[(a + bN)/(1 + cN + dN^2)]}{1 + (\text{Dose}/\text{ED}_{50i})^{B_i}} \tag{4}$$

Eqn (3) appears to be most biologically appropriate when the amount of applied nitrogen includes the amount that causes plant growth inhibition. However, when the amount of nitrogen is not high enough, other models, particularly a linear model, may be more appropriate to describe the relationship between weed biomass and nitrogen. As Eqn (3) can be easily simplified to the linear model $W_{0i} = a + bN$, Eqn (4) can be further reduced to Eqn (5) as follows,

$$W_i = \frac{a + bN}{1 + (\text{Dose}/\text{ED}_{50i})^{B_i}} \tag{5}$$

Once an appropriate model for W_{0i} is incorporated into Eqn (2), for example to give Eqn (5), the parameter B can be re-estimated by fitting Eqn (5) to biomass data. To describe the relationship between the re-estimated parameter B and nitrogen, constant, linear, exponential and logistic models can be used. If the exponential model is selected to be the most appropriate one among them, the selected model is then incorporated into Eqn (5) to give Eqn (6) as follows,

$$W_i = \frac{a + bN}{1 + (\text{Dose}/\text{ED}_{50i})^{\alpha\beta^N}} \tag{6}$$

where α and β are unknown parameters. If the parameter B is constant regardless of nitrogen levels, the exponential model for the parameter B in Eqn (6) can be easily simplified to a constant model to give Eqn (7) as follows:

$$W_i = \frac{a + bN}{1 + (\text{Dose}/\text{ED}_{50i})^{\alpha}} \tag{7}$$

Finally, after setting two models for W_{0i} and the parameter B incorporated into Eqn (2), e.g. to give Eqn (6) or (7), the most appropriate model to describe the relationship between the parameter ED_{50} estimated by fitting Eqn (6) or (7) to biomass data and nitrogen can be selected by comparing candidate models such as constant, linear, exponential and logistic models. The selected model can then be incorporated into Eqn (6) or (7) by replacing ED_{50i} to give a final model. The final model can be used to estimate weed response to herbicide at a range of nitrogen levels. The overall process of model development is summarised in Table 1.

Statistical analysis

All weed biomass data were initially subjected to an analysis of variance (ANOVA). A variance-stabilizing transformation with the natural $\log_e$ or square root was used for weed biomass. Nonlinear regression was used to fit various components of the models, in some cases, using the transform-both-sides (TBS) techniques (Rudemo *et al.*, 1989). Genstat (Genstat Committee, 1993) was used for all statistical analyses. Lack-of-fit of the most complex model (Eqn 2, Full model) was tested to check that the basic model used was appropriate.

There was no evidence of lack-of-fit of the most complex model, so each model was compared with its predecessor by calculating the *F*-value as follows

$$F = \frac{[(\mathrm{RSS}_{j+1} - \mathrm{RSS}_j)/(\mathrm{df}_{j+1} - \mathrm{df}_j)]}{(\mathrm{RSS_a}/\mathrm{df_a})} \qquad (8)$$

where RSS and df represent the residual sum of square and the degree of freedom, respectively, j+1 represents the reduced model from its predecessor (j) and a represents ANOVA. If the *F*-value was lower than the tabulated *F*-value (5% level) with (df_{j+1}–df_j, $\mathrm{df_a}$) degrees of freedom, the reduced model could be accepted.

Results

Initial analysis of weed biomass data

For the initial data analysis (ANOVA), weed biomass data were square root transformed for *B. napus*, *M. perforata* and *P. rhoeas*, and natural log transformed for *G. aparine*, to stabilize the variance. There were significant effects of each treatment on weed biomass (Table 2) and there was a significant interaction between herbicide and nitrogen for all four weed species, indicating that the herbicide dose–responses of each weed species were influenced by nitrogen treatment. Considering the size of *F*-values, the interaction of herbicide and nitrogen appeared to be more significant for the biomass of *M. perforata*, *P. rhoeas* and *G. aparine* than for *B. napus*.

To investigate the relationship between weed biomass and herbicide dose, the standard dose–response curve was fitted to the weed biomass data at each nitrogen level independently using the TBS technique (Rudemo *et al.*, 1989). The completely separate standard dose–response curves (Eqn 2) well described weed biomass at each nitrogen level (Fig. 1).

The parameter estimates for Eqn (2) (Table 3) showed the changes of each parameter with increasing nitrogen levels. Regardless of weed species, weed biomass (W_0) at no-herbicide treatment increased significantly with increasing nitrogen. Parameter *B*-values for *B. napus*, *G. aparine* and *M. perforata* appeared not to significantly change with increasing nitrogen. However, the value for *P. rhoeas* obviously increased with nitrogen, from 1.5 at 0 kg N ha^{-1} to 4.62 at 360 kg N ha^{-1}. The ED_{50} values for *B. napus* was about 1.732 g a.i. ha^{-1} of metsulphuron-methyl on average and also appeared to be fairly constant regardless of nitrogen levels. However, the values for the other weeds decreased continuously with increasing nitrogen levels; from 1.567 g and 4.468 g a.i. ha^{-1} of metsulphuron-methyl at 0 kg N ha^{-1} to 0.525 g and 0.87 g a.i. ha^{-1} at 360 kg N ha^{-1} for *M. perforata* and *P. rhoeas*, respectively, and for *G. aparine*, from 225.7 g a.i. ha^{-1} of fluroxypyr at 0 kg N ha^{-1} to 130.8 g a.i. ha^{-1} at 360 kg N ha^{-1}.

Modelling weed biomass (W_0) at no-herbicide treatment with increasing nitrogen

As shown in Fig. 1 and Table 3, it was clear that at no-herbicide treatment, weed biomass (W_0) increased with increasing nitrogen. The weed biomass (W_0) at no-herbicide treatment (Table 3), estimated by using Eqn (2) at each nitrogen level, was thus plotted against nitrogen and the linear and inverse quadratic models were fitted using nonlinear regression; the parameter estimates are presented in Table 4. Table 4 showed that weed biomass at no-herbicide treatment increased with increasing nitrogen and the increase was well described by the linear and inverse quadratic models. Overall, *B. napus* showed the most rapid response to nitrogen considering its response rate, 0.01589 g of plant biomass per kg N ha^{-1}, followed by *G. aparine*, *P. rhoeas* and *M. perforata*. *Matricaria perforata*, *P. rhoeas* and *G. aparine* appeared to have similar nitrogen responses, with biomass increasing steadily up to 360 kg N ha^{-1}. In comparison, the response rate of *B. napus* appeared to decrease before 360 kg N ha^{-1}. Nonetheless, it was

Table 2 Summary of *F*-values from the analysis of variance of transformed weed biomass with square root for *Brassica napus*, *Matricaria perforata* and *Papaver rhoeas*, and natural log for *Galium aparine*

	Source of variation		
Weed species	Nitrogen	Herbicide	Nitrogen × herbicide
B. napus	4.5**	107.2**	2.0*
M. perforata	4.6**	154.4**	4.2**
P. rhoeas	5.6**	35.0**	5.1**
G. aparine	230.0**	50.6**	4.9**

Significance at *$P = 0.05$ and **$P = 0.001$.

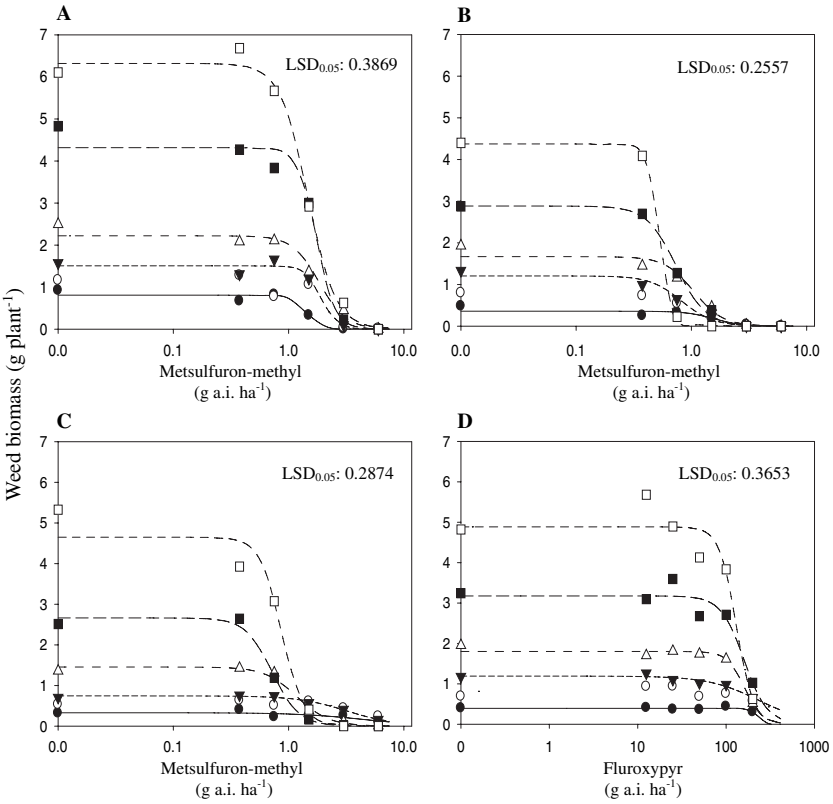

Fig. 1 Herbicide dose–responses in biomasses of *Brassica napus* (A), *Matricaria perforata* (B), *Papaver rhoeas* (C) and *Galium aparine* (D) at different levels of nitrogen, 0 (●), 22.5 (○), 45 (▼), 90 (▽), 180 (■) and 360 (□) kg N ha^{-1}. LSD values are least significant differences of mean values of square root-transformed biomass for *B. napus*, *M. perforata* and *P. rhoeas*, and natural log-transformed biomass for *G. aparine*. The continuous lines are fitted lines from Eqn (2) and parameter estimates in Table 3.

Table 3 Parameter estimates for the standard dose–response curves of four weed species to metsulphuron-methyl (*Brassica napus*, *Matricaria perforata* and *Papaver rhoeas*) and to fluroxypyr (*Galium aparine*) at different levels of nitrogen

Weed species	Parameter estimates	Nitrogen (kg ha^{-1})					
		0	22.5	45	90	180	360
B. napus	W_0	0.808 (0.140)	1.077 (0.158)	1.508 (0.189)	2.220 (0.243)	4.317 (0.324)	6.320 (0.433)
	B	6.52 (4.90)	8.49 (7.73)	6.08 (2.33)	3.73 (1.06)	5.48 (1.11)	3.61 (0.61)
	ED_{50}	1.419 (0.207)	2.100 (0.706)	1.914 (0.323)	1.846 (0.292)	1.744 (0.150)	1.468 (0.135)
M. perforata	W_0	0.359 (0.069)	0.715 (0.092)	1.205 (0.162)	1.669 (0.174)	2.883 (0.255)	4.373 (0.368)
	B	3.65 (1.73)	4.68 (1.45)	3.176 (0.785)	3.476 (0.791)	3.412 (0.562)	8.21 (2.79)
	ED_{50}	1.567 (0.406)	1.328 (0.161)	0.822 (0.141)	1.047 (0.147)	0.739 (0.077)	0.525 (0.068)
P. rhoeas	W_0	0.330 (0.087)	0.574 (0.087)	0.744 (0.116	1.455 (0.177)	2.663 (0.268)	4.650 (0.320)
	B	1.50 (1.75)	2.50 (2.47)	2.01 (1.07)	3.111 (0.820)	3.741 (0.743)	4.619 (0.677)
	ED_{50}	4.468 (2.775)	5.270 (1.555)	3.212 (1.050)	1.176 (0.206)	0.721 (0.080)	0.870 (0.064)
G. aparine	W_0	0.393 (0.022)	0.815 (0.064)	1.192 (0.104)	1.801 (0.115)	3.176 (0.211)	4.885 (0.313)
	B	10.07 (4.94)	1.86 (1.93)	1.525 (0.880)	4.38 (1.88)	3.31 (1.17)	4.521 (0.876)
	ED_{50}	225.7 (13.3)	319.6 (170.3)	232.1 (52.0)	162.4 (16.7)	160.3 (16.2)	130.8 (11.5)

Parameter estimates in Eqn (2) were estimated using the transform-both-sides technique and the numbers in parenthesis are standard errors. W_0, weed biomass (g plant^{-1}) at no-herbicide treatment; ED_{50}, the effective dose required to reduce weed biomass by 50%; B, a response rate of the dose–response curve.

concluded that the change of weed biomass at no-herbicide treatment with nitrogen was well described by the linear and inverse quadratic models, indicating that the parameter W_{0i} in Eqn (2) could be replaced by the linear model or the inverse quadratic. However, the linear model appears to be more advantageous than the inverse quadratic model in this situation, as no significant decrease of biomass was observed even at 360 kg N ha^{-1} and fewer parameters are required for the linear model.

Modelling parameter B as affected by nitrogen

After the linear model for W_{0i} was incorporated into Eqn (2) to give Eqn (5), the modified model was again

Table 4 Parameter estimates for the models tested to describe the relationship between weed biomass at no-herbicide treatment (W_0) and nitrogen

Weed species	Model tested	Parameter estimates				r^2
		a	*b*	*c*	*d*	
B. napus	Linear	0.861 (0.189)	0.01589 (0.00111)	–	–	0.981
	Inverse quadratic	0.817 (0.045)	0.00877 (0.00152)	−0.003906 (0.000423)	7.99×10^{-6} (0.59×10^{-6})	0.999
M. perforata	Linear	0.583 (0.131)	0.01105 (0.0078)	–	–	0.981
	Inverse quadratic	0.373 (0.090)	0.01735 (0.00463)	0.00106 (0.00220)	1.02×10^{-6} (3.47×10^{-6})	0.998
P. rhoeas	Linear	0.314 (0.058)	0.01223 (0.00034)	–	–	0.997
	Inverse quadratic	0.311 (0.059)	0.00996 (0.00223)	−0.00192 (0.00113)	4.08×10^{-6} (1.93×10^{-6})	0.999
G. aparine	Linear	0.597 (0.127)	0.01244 (0.00075)	–	–	0.986
	Inverse quadratic	0.427 (0.054)	0.01576 (0.00246)	−0.00033 (0.00104)	2.82×10^{-6} (1.64×10^{-6})	0.999

The data of weed biomass used to fit the models were the parameter estimates (W_0) in Table 3. The numbers in parenthesis are standard errors. Linear model: $a+bN$; inverse quadratic model: $(a + bN)/(1 + cN + dN^2)$.

Table 5 Parameter estimates for the functions tested to describe the relationship between parameter *B* and nitrogen (N)

Weed species	Model tested	Parameter estimates			r^2
		α	β	γ	
Brassica napus	Linear	6.583 (0.772)	−0.0088 (0.0046)	–	0.48
	Constant	5.566 (2.918)	–	–	–
Matricaria perforata	Exponential	3.365 (0.585)	1.0018 (0.00075)	–	0.547
	Linear	3.334 (0.675)	0.0081 (0.00398)	–	0.509
	Constant	4.277 (2.366)	–	–	–
Papaver rhoeas	Logistic	5.020 (1.600)	46.1 (91.9)	0.0077 (0.0069)	0.793
	Exponential	2.326 (0.306)	1.002 (0.0006)	–	0.743
	Linear	2.204 (0.323)	0.007 (0.0019)	–	0.770
	Constant	3.016 (1.158)	–	–	–
Galium aparine	Linear	6.880 (1.490)	−0.0117 (0.0088)	–	0.309
	Constant	5.514 (8.171)	–	–	–

The data of parameter *B* used to fit the models were estimated by fitting the original raw data set to Eqn (5). The values in parenthesis are standard errors. Constant model: α; linear model: $\alpha+\beta N$; exponential model: $\alpha\beta^N$; logistic model: $\alpha/[1+exp(-\gamma(N-\beta))]$.

fitted to the weed biomass data and a new set of parameter estimates was calculated (data not shown). The parameter *B*-values estimated for each weed species were then plotted against nitrogen to identify the relationship with nitrogen. Several possible models were compared to describe the behaviours of parameter *B* with nitrogen and the results are summarized in Table 5.

Parameter *B* for *B. napus* appeared not to show a clear trend of change with increasing nitrogen. If parameter *B* is constant, it would be estimated to be approximately 5.566; otherwise its change may be described by a linear model with the intercept and slope 6.58 and −0.0088 respectively (Table 5). For *M. perforata*, parameter *B* appeared to be increasing with nitrogen levels, because of the high value at 360 kg N ha^{-1} (Table 3). Three possible models describing the relationship between parameter *B* and nitrogen were compared, exponential, linear and constant models. The exponential model gave a better fit than the others (Table 5). For *P. rhoeas*, parameter *B* increased with increasing nitrogen (Table 3), so logistic, exponential and linear models were used in comparison with the constant model. The relationship between parameter *B* and nitrogen was well explained by these models (Table 5). For *G. aparine*, in a similar way to *B. napus*, parameter *B* appeared to be constant. The linear model described the relationship between parameter *B* and nitrogen very poorly; its slope −0.0028 with a rather large standard error, indicating that the slope may not be significantly different from zero and thus parameter *B* constant (Table 5).

Modelling ED_{50} value as affected by nitrogen

The new estimates of the ED_{50} values (data not shown) calculated by fitting Eqn (5) to the weed biomass were plotted against nitrogen levels. The ED_{50} values generally decreased with increasing nitrogen, with the exception of *B. napus*. Possible models, such as logistic, exponential, linear and constant models, were proposed to model the change in the ED_{50} with increasing nitrogen levels.

The ED_{50} values for *B. napus* appeared to be unaffected by nitrogen, indicating that nitrogen did not affect the dose–response of *B. napus* to metsulphuron-methyl. In contrast, the ED_{50} values for the other weed species clearly declined with increasing nitrogen (Table 3). For *M. perforata*, *P. rhoeas* and *G. aparine*, the logistic curve was generally better to explain the decrease of the ED_{50} values with increasing nitrogen than the other models (Table 6).

Comparison of models

Investigations of each parameter revealed that weed biomass (W_0) at no-herbicide treatment and the parameters B and ED_{50} changed with increasing nitrogen. Lack-of-fit tests showed that Eqn (2) satisfactorily described weed biomass as affected by herbicide at a range of nitrogen levels irrespective of weed species (Fig. 2). There was no evidence that Eqn (2) fitted less well than Eqn (5) for all tested weeds, indicating that the relationship between W_0 and nitrogen was well explained by the linear model. When Eqn (7) was fitted for *B. napus* and *G. aparine*, there was no evidence that Eqn (7) fitted less well than Eqn (5), so the changes in parameter B for both weed species were not large enough to significantly affect the fit of the model. However, when eqns 6 and 7 were fitted for *M. perforata* and *P. rhoeas*, there was no evidence that Eqn (6) fitted less well than Eqn (5), but evidence that Eqn (7) fitted less well than Eqn (5), indicating that the relationship between parameter B and nitrogen was well explained by the exponential model for these two weeds. Finally, when Eqn (11) was fitted for *B. napus*, there was no evidence that Eqn (11) fitted less well than Eqn (7), so there was no evidence that the ED_{50} varied with nitrogen (Fig. 2). When Eqn (9) was fitted for *M. perforata* and *P. rhoeas*, F-value revealed that there was no evidence for *M. perforata* that Eqn (9) fitted less well than Eqn (6) but evidence for *P. rhoeas* that Eqn (9) fitted less well than Eqn (6). Direct comparison of Eqn (9) with the Full model (Eqn 2) for *P. rhoeas* showed no evidence that Eqn (9) fitted less well than the Full model. When Eqn (10) was fitted for *G. aparine*, there was evidence that Eqn (10) fitted less well than Eqn (7). However, direct comparison of Eqn (10) with the Full model (Eqn 2) showed no evidence that Eqn (10) fitted less well than the Full model. These findings thus indicated that the relationship between ED_{50} value and nitrogen was well described by the logistic model for *M. perforata*, *P. rhoeas* and *G. aparine*.

Final model and its application

As a result of the model comparisons, the final models were selected for each weed species. Eqn (9) is therefore generalised common model for weed species tested in this study.

$$W = \frac{a + bN}{1 + \{\text{Dose}/[\lambda(1 + (N\exp(-\omega))^{\theta})^{-1}]\}^{\alpha\beta^N}} \qquad (9)$$

By fitting Eqn (9) to the transformed weed biomass, parameter estimates were calculated (Table 7). The simulation of weed biomass using Eqn (9) and the parameter estimates given in Table 7 is shown in Fig. 3.

The standard dose–response curve with constant parameters B and ED_{50} (Eqn 11) is likely to be the

Table 6 Parameter estimates for the functions tested to describe the relationship between ED_{50} and nitrogen (N)

Weed species	Model tested	Parameter estimates			r^2
		λ	ω	θ	
B. napus	Linear	0.53 (0.088)	−0.00012 (0.00052)	–	0.014
	Constant	1.688 (0.226)	–	–	–
M. perforata	Logistic	1.174 (0.098)	5.683 (0.250)	1.55 (0.746)	0.877
	Exponential	1.220 (0.068)	0.9976 (0.0005)	–	0.888
	Linear	1.191 (0.058)	−0.002 (0.0003)	–	0.896
	Constant	0.957 (0.287)	–	–	–
P. rhoeas	Logistic	5.590 (0.579)	3.988 (0.197)	2.241 (0.774)	0.952
	Exponential	5.805 (0.674)	0.9874 (0.0035)	–	0.900
	Linear	4.186 (0.886)	−0.0122 (0.0052)	–	0.577
	Constant	2.768 (2.173)	–	–	–
G. aparine	Logistic	269.4 (26.2)	5.536 (0.368)	0.916 (0.373)	0.879
	Exponential	256.2 (17.4)	0.998 (0.0007)	–	0.838
	Linear	246.1 (17.8)	−0.396 (0.105)	–	0.782
	Constant	200.0 (60.7)	–	–	–

The data of parameter ED_{50} used to fit the models were estimated by fitting the original raw data set to Eqn (6) for *Matricaria perforata* and *Papaver rhoeas* and Eqn (7) for *Brassica napus* and *Galium aparine*. The numbers in parenthesis are standard errors. Constant model: λ; linear model: $\lambda + \omega N$; exponential model: $\lambda\omega^N$; logistic model: $\lambda/[1 + (N \exp(-\omega))^{\theta}]^{-1}$.

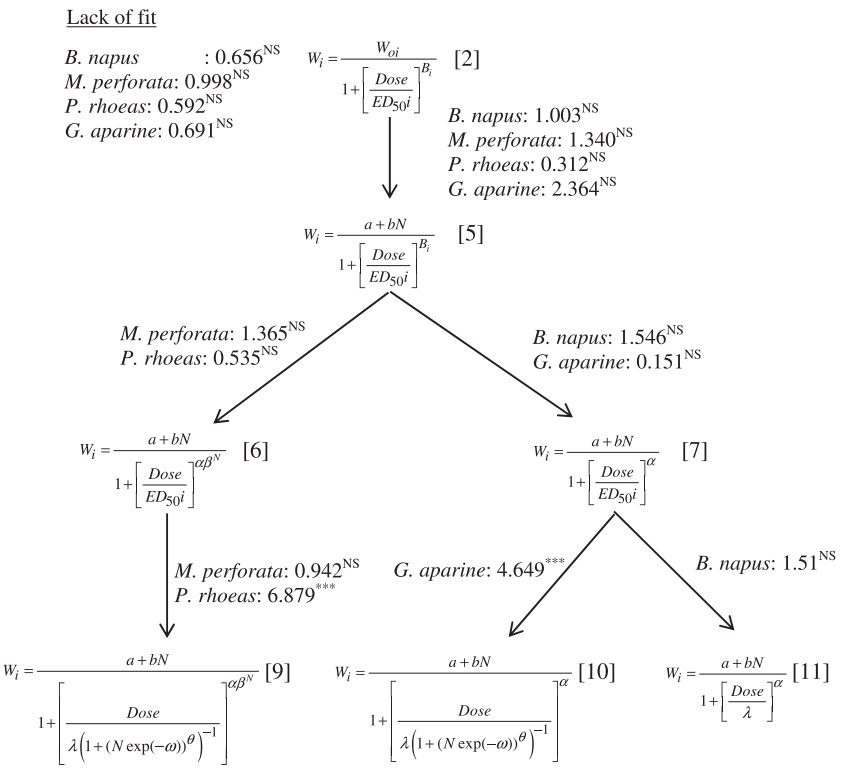

Fig. 2 Model tree and *F*-values from sequential comparison of models by *F*-test for the biomass of tested plants as affected by herbicide and nitrogen.

Table 7 Parameter estimates for the final model (Eqn 9) for each weed species

Parameter estimates		Weed species			
		Brassica napus	*Matricaria perforata*	*Papaver rhoeas*	*Galium aparine*
W_0	a	0.829 (0.0927)	0.471 (0.065)	0.315 (0.053)	0.4177 (0.0224)
	b	0.01607 (0.00099)	0.01228 (0.00084)	0.01191 (0.00082)	0.01465 (0.00065)
B	α	4.333 (0.463)	2.941 (0.467)	2.145 (0.241)	3.813 (0.532)
	β	1	1.002131 (0.000654)	1.00288 (0.00047)	1
ED_{50}	λ	1.655 (0.0846)	1.080 (0.124)	7.52 (4.10)	274.4 (40.6)
	ω	∞	5.762 (0.135)	1.55 (1.26)	5.501 (0.483)
	θ	0	2.098 (0.604)	0.495 (0.0119)	0.748 (0.185)
r^2	0.91	0.937	0.844	0.932	
Model in Fig. 2	Eqn (11)	Eqn (9)	Eqn (9)	Eqn (10)	

The parameters were estimated by fitting the transformed biomass data to the final model (Eqn 9). The numbers in the parentheses are standard errors. a and b are the unknown parameters for the linear model; α and β, parameters of the constant model for *B. napus* and *G. aparine* and of the exponential curve for *M. perforata* and *P. rhoeas*; λ, ω and θ are the parameters of the constant for *B. napus* and of the logistic curve for *M. perforata*, *P. rhoeas* and *G. aparine*.

best for describing the biomass of *B. napus* as affected by metsulphuron-methyl and nitrogen. Increasing nitrogen did not change the form of the dose–response of *B. napus* to metsulphuron-methyl (Fig. 3A). For *M. perforata* and *P. rhoeas*, the standard dose–response curve was modified by replacing the parameter B and ED_{50} with the exponential curve and the logistic curve respectively (Eqn 9). Nitrogen treatment affected the dose–response curve to metsulphuron-methyl, resulting in poor control of *M. perforata* and *P. rhoeas* at lower nitrogen levels (Fig. 3B and C respectively). For *G. aparine*, the standard dose–response curve was modified by replacing the parameter B and ED_{50} with the constant value and the logistic curve (Eqn 10), indicating that nitrogen influenced the performance of fluroxypyr in controlling *G. aparine* (Fig. 3D).

Discussion

Considerable benefits may accrue from the optimum application of fertilisers to crops and, as a result, there has been much interest in the timing and amount of nitrogen applied in relation to crop yield (e.g. Ball *et al.*, 1996). However, as weeds in the crop field also benefit

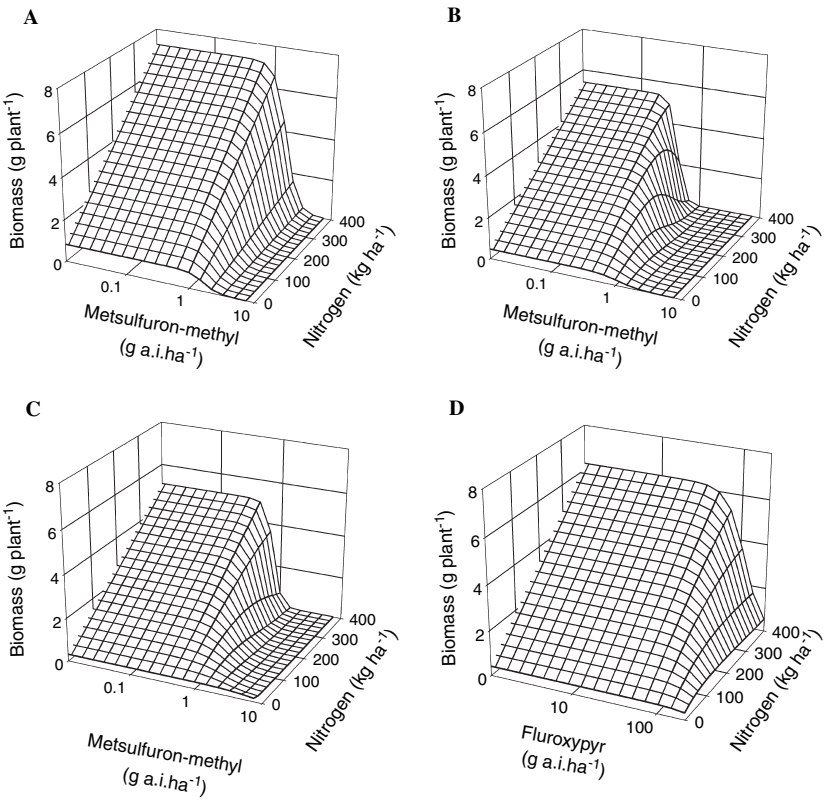

Fig. 3 Predicted biomass of *Brassica napus* (A), *Matricaria perforata* (B), *Papaver rhoeas* (C) and *Galium aparine* (D) using the final models, Eqn (11), Eqn (9), Eqn (9) and Eqn (10), respectively, and parameter estimates given in Table 7.

from the application of nitrogen, the optimum nitrogen application should consider the nitrogen response of weeds and its effect on crop–weed competition. An increased supply of nitrogen generally increases weed growth, so that both crop yield loss and weed seed production consequently increase, although the absolute crop yield may also increase. Decisions regarding herbicide application should also consider the nitrogen response of weeds, not only in terms of weed biomass but also morphological and physiological characteristics. There is some evidence that nitrogen levels influence herbicide performance, generally increasing with increasing nitrogen levels.

The results presented here agree with Lutman *et al.* (1974) and provide a closer insight into the relationship between nitrogen response and herbicide dose–response of weeds. The model approach also suggests that the relationship might be predictable, although this has yet to be validated with further data sets.

Nitrogen response of weed species

Many studies have investigated the effects of nitrogen on weed growth, mainly in relation to crop–weed competition (e.g. Wright & Wilson, 1992). Although these studies provide a practical understanding of the nitrogen response of weeds in field conditions, often the effect of nitrogen on weed growth has been confounded with the effect of crop–weed competition on weed growth. Therefore, to quantify the genuine nitrogen response of weeds, experiments with weeds grown in monoculture were required under a wide range of nitrogen levels. In this sense, our results clearly showed that weed biomass increased significantly with increasing nitrogen levels and was well described by the linear model. Each weed species responded to nitrogen differently. In general, *G. aparine* has been considered a nitrophilous species, significantly increasing biomass at higher nitrogen levels (e.g. Grime *et al.*, 1988; Rooney *et al.*, 1990; Wright & Wilson, 1992), but few studies have been done on *M. perforata* and *P. rhoeas*. Our results suggest that *B. napus*, *M. perforata* and *P. rhoeas* may also be nitrophilous, as they show significant increase of biomass with increasing nitrogen and a similar response rate to *G. aparine*. Nitrogen supply can affect plant growth and productivity by altering both leaf area and photosynthetic capacity (Sinclair, 1990; Frederick & Camberato, 1995). Increasing nitrogen supply results in increased leaf nitrogen content (Frederick & Amberato, 1995), which is positively correlated with the light-saturated rate of net photosynthesis (Hunt & Van Der Poorten, 1985).

To describe the relationship between weed biomass at no-herbicide and nitrogen, the linear model was employed in this study. However, this model may have problems of extrapolation even just outside the range of

the data, as it cannot allow for the decrease in biomass often seen at the high levels of nitrogen. In this sense, the inverse quadratic model may be more appropriated, as it has provided a good fit to many sets of data including the decrease of biomass at high levels of nitrogen. Therefore, the linear model for W_{0i} in Eqn (9) could be substituted by the inverse quadratic model in future work where the range of nitrogen includes levels that cause growth inhibition.

Effects of nitrogen fertiliser on the herbicide dose–response of weeds

Our results clearly showed that there was often a significant interaction between herbicide and nitrogen, with increased nitrogen levels enhancing herbicide performance by increasing the response rate (parameter B) or by decreasing the ED_{50}. The herbicide dose–response curves were different for each weed species. For *B. napus*, nitrogen treatment only scaled the dose–response curve to metsulphuron-methyl up or down, but did not alter the shape of the curve. However, for *M. perforata* and *P. rhoeas*, the dose–response curve to metsulphuron-methyl changed by increasing B and decreasing ED_{50} with increasing nitrogen levels. For *G. aparine*, nitrogen treatment affected the dose–response curve to fluroxypyr by only decreasing the ED_{50}, but did not alter parameter B. Similar results have been found in previous studies. Wolf *et al.* (1950), Pfeiffer and Holmes (1961) and McWhorter (1971) examined the effects of nitrogen, showing that it can increase the susceptibility of soyabean (*Glycine max* (L.) Merr.), barley (*Hordeum vulgare* L.) and johnsongrass (*Sorghum halepense* (L.) Pers.) to 2,4-D, barban and dalapon respectively. Griffiths (1968) found that higher nitrogen status led to improved control of perennial ryegrass (*Lolium perenne* L.). Lutman *et al.* (1974) also reported that several species in the Gramineae family grown at a high nitrogen level were more susceptible to paraquat than those grown at a low level. The potential mechanisms for such relationships can be explained by herbicide interception and retention, foliar uptake of herbicide and herbicide translocation. Hammerton (1967) showed that high fertility increased spray interception and retention. Nitrogen fertility may change trichome length and quantity of epicuticular wax on leaves, which could affect herbicide uptake indirectly by their effects on leaf wettability (Holloway *et al.*, 1980). Richmond and Martin (1958) showed that apple leaves deficient in nitrogen had less waxy material in their cuticles than leaves from normal plants. As the finding that the xenobiotic penetration into young leaves was greater than older leaves (King & Radosevich, 1979), nitrogen levels may affect the composition of cuticle and herbicide uptake. A few studies have indicated a correlation between herbicide and assimilate translocation (e.g. McAllister & Haderlie, 1985), with an increased nitrogen application increasing the quantity of assimilate and its translocation, thus resulting in an increased herbicide translocation. However, these mechanisms may differ between herbicides and weed species. Further study may be required to investigate mechanisms for this relationship in detail.

The mathematical description with empirical models gave a clearer understanding of the behaviour of the herbicide dose–response curve with increasing nitrogen: linear, exponential and logistic models for the changes of the parameters W_0, B and ED_{50} respectively. The linear model for W_0 can be easily expanded to the inverse quadratic to cover the decrease in biomass at high levels of nitrogen, and the exponential model for B and the logistic model for ED_{50} can be reduced to constant parameters B and ED_{50} by constraining the parameter $\beta = 1$ and $\omega = \infty$ respectively. This complex interaction of herbicide dose and nitrogen on weed biomass was well explained by the final model (Eqn 9) developed in this study. The model allowed the systematic description of increased herbicide performance with increasing nitrogen. Therefore, it may be possible to predict the herbicide dose–response as affected by nitrogen application or soil nitrogen content.

It can be argued that the herbicide efficiency is decreased when a low level of nitrogen is applied, but the weed biomass is also strongly decreased at the same time. It is thus possible to obtain an overall decrease of the weed biomass at a low nitrogen level, suggesting that the change of the herbicide dose required to reduce weed biomass to a selected level with nitrogen may be different from the case of ED_{50}. However, in weed management, the weed biomass resulting from herbicide application is not so important as the survival of weed. After herbicide application, the biomass of remaining weed grown at a high nitrogen level may be high but its survivability may be too low for the weed to recover. Conversely, the biomass of remaining weed grown at the low nitrogen level may be low but its survivability may be high enough for the weed to recover and become competitive when additional fertiliser is applied. Therefore, the decrease in the herbicide efficacy at the low nitrogen level is more important in weed management than the decrease of weed biomass at the low nitrogen level.

Implications of the nitrogen and herbicide dose–response

With increasing environmental concerns, low input systems with less herbicide and nitrogen inputs are being developed for crop production. However, our

results suggest a cautious approach when combining reduced inputs, because weeds grown under lower nitrogen levels may be more herbicide tolerant than those grown under higher nitrogen levels. Richards (1993) had previously highlighted that this combination may lead to failure in weed control. Therefore, when making decisions about herbicide doses and the amount of nitrogen to apply, the interaction between herbicide dose–response and nitrogen needs careful consideration. Further study is needed to obtain more accurate parameters experimentally derived from field studies. Nevertheless, as the interaction between herbicide and nitrogen may affect crop–weed competition, the mathematical relationships between herbicide dose–response and nitrogen levels presented in this study may also be applied to the crop–weed competition model for crop yield prediction and aid decision making for optimum uses of nitrogen fertiliser and herbicide.

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