

Modelling herbicide dose and weed density effects on crop:weed competition

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Summary

The effects of a range of herbicide doses on crop:weed competition were investigated by measuring crop yield and weed seed production. Weed competitiveness of wheat was greater in cv. Spark than in cv. Avalon, and decreased with increasing herbicide dose, being well described by the standard dose-response curve. A combined model was then developed by incorporating the standard dose-response curve into the rectangular hyperbola competition model to describe the effects of plant density of a model weed, *Brassica napus* L., and a

herbicide, metsulfuron-methyl, on crop yield and weed seed production. The model developed in this study was used to describe crop yield and weed seed production, and to estimate the herbicide dose required to restrict crop yield loss caused by weeds and weed seed production to an acceptable level. At the acceptable yield loss of 5% and the weed density of 200 *B. napus* plants m⁻², the model recommends 0.9 g a.i. metsulfuron-methyl ha⁻¹ in Avalon and 2.0 g a.i. in Spark.

Keywords: modelling, herbicide dose, crop:weed competition, metsulfuron-methyl, dose-response.

Introduction

Increasing environmental concerns and economic pressure have led to a reduction in herbicide use in conventional farming. Farmers are being encouraged to use less herbicide and to combine several control methods such as mechanical methods (e.g. Caseley *et al.*, 1993; Mulder & Doll, 1993) and cultural practices (e.g. Barton *et al.*, 1992; Salonen, 1992). The use of a lower than recommended herbicide dose may result in incomplete weed kill, so that there will still be crop:weed competition, which may or may not cause crop yield loss. There is also the problem of adding new weed seeds to the seedbank. Therefore, there is a need to quantify the effects of reduced herbicide application doses on crop:weed competition.

Many efforts have been made to investigate the effects of reduced doses of herbicide on crop:weed competition in cereal crops, such as spring barley (Richards & Davies, 1991; Salonen, 1992; Christensen, 1993), winter wheat (Richards & Davies, 1991; Lemerle *et al.*, 1996a; Brain *et al.*, 1999) and spring wheat (Salonen, 1992). In parallel with the agronomic approach based on crop yield and weed control, an

economic analysis has also been conducted when reduced doses of herbicide were sprayed on barley (Barton *et al.*, 1992). Studies on reduced doses of herbicide have also been conducted in conjunction with various cultural practices, such as seeding rate (Barton *et al.*, 1992; Brain *et al.*, 1999), crop cultivars (Richards & Davies, 1991; Christensen, 1993; Lemerle *et al.*, 1996b) and row spacing (Barton *et al.*, 1992). Although these studies have provided useful and practical information for specific conditions, it is difficult to establish a general framework. Moreover, models for the prediction of crop yield loss due to weeds usually lead to the recommendation to spray, or not to spray, a herbicide. In reality, however, a more flexible model is needed that will recommend the herbicide dose to use. To develop such a model, it is necessary to carry out experiments on, and model the effects of, sublethal doses of herbicide on crop:weed competition.

Recently, Brain *et al.* (1999) developed a model of the interaction between crop:weed competition and herbicide dose. They combined an empirical model of the relationship between crop yield and weed biomass (related to weed density) derived from a rectangular hyperbola (Cousens, 1985) and an empirical model of

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the relationship between weed biomass and herbicide dose, derived from the standard dose–response curve (Streibig, 1980). The incorporation of the standard dose–response model into the rectangular hyperbola was made with the assumptions that weed competitiveness is linearly related to the leaf area of an individual weed (Kropff & Spitters, 1991) and that the relationship between the total leaf area per m² and the weed biomass is allometric (Jolliffe *et al.*, 1988).

Although this model worked well, it requires an assessment of weed biomass, which is an expensive, and less practical, process, especially for large-scale crop production. Weed biomass depends mainly on soil fertility and temperature, so that it varies with environmental conditions. It also changes over the growing season, so the time at which it should be assessed is unclear. In contrast, weed density is relatively constant through the growing season and easy to assess. The assumptions of Brain *et al.* (1999) implicitly indicate that weed competitiveness is related to weed biomass as well as weed leaf area. Moreover, as the relationship between the individual weed biomass and herbicide dose is well described by the standard dose–response curve, it can be assumed that the decrease of weed competitiveness with herbicide dose can also be explained by the standard dose–response curve. Weed density may be a more practical observation than weed biomass for the combined model. Additionally, by observing weed density, the combination of the rectangular hyperbola and the standard dose–response model may also provide an accurate prediction of weed biomass and seed production, as a result of the complex interaction of sublethal doses of herbicide and weed density.

This study was therefore conducted to examine the relationships between weed competitiveness and herbicide dose and between weed biomass and weed density, so that the former may be incorporated into the rectangular hyperbolic model and the latter into the standard dose–response model. These new combined models can be applied to decision-making for weed control.

Materials and methods

Model development

Crop yield

The rectangular hyperbola is commonly used to describe the relationship between crop yield (Y) and initial weed density (x_0) (Cousens, 1985; Wilson & Wright, 1990) for crops grown at a single density. The equation for this relationship is

$$Y = Y_0 / (1 + \beta x_0) \quad (1)$$

where Y_0 is the weed-free crop yield and β is the competitiveness of the weed (a weed density of $1/\beta$ will reduce the crop yield by 50%).

When a range of herbicide doses is applied, in general, crop yield increases with increasing herbicide dose because the herbicide causes a decrease in the weed biomass and thus decreases weed competitiveness. *A priori*, the relationship between weed competitiveness (β) and herbicide dose is not known, so needs to be parameterized separately at each herbicide dose. There is also a possibility that the herbicide will affect the crop, so that the weed-free crop yield, Y_{0i} , also needs to be parameterized separately for each dose. The general response curve for the i^{th} herbicide dose is then

$$Y = Y_{0i} / (1 + \beta_i x_0) \quad (2)$$

Using eqn 2, a large number of parameters (two at each herbicide dose) are needed to predict crop yield. However, as crop growth is unlikely to be affected by herbicide treatments at less than the recommended dose, it is likely that weed-free crop yield is not affected by herbicide dose, so that eqn 2 can be simplified to eqn 3

$$Y = Y_0 / (1 + \beta_i x_0) \quad (3)$$

where only the weed competitiveness, β_i , changes with dose.

Although many studies have been conducted to investigate the effect of herbicide dose on crop yield, the recent work by Brain *et al.* (1999) appears to be the first approach to rationalize the relationship between crop yield and herbicide dose. They modelled the relationship by assuming that weed competitiveness (parameter β) is linearly dependent on individual plant leaf area (Kropff & Spitters, 1991), and the relationship between the total leaf area m⁻² and the weed biomass m⁻² at the chosen assessment date is allometric (Jolliffe *et al.*, 1988). Therefore, as the weed leaf area depends on the weed biomass, and weed competitiveness depends on weed leaf area, weed competitiveness will depend on weed biomass. Moreover, it is further assumed that as the relationship between weed biomass and herbicide dose is well described by the standard dose–response curve, then the change of parameter β with herbicide dose can also be modelled using the standard dose–response curve, i.e.

$$\beta_i = \beta_0 / \left(1 + \left(\frac{Dose_i}{e^{LD_{50}}} \right)^B \right) \quad (4)$$

where β_0 is weed competitiveness at no herbicide treatment, LD_{50} is the log of the dose required to reduce weed competitiveness by 50%, and B is the response rate or steepness of the curve. Therefore, if the relationship between parameter β and herbicide dose is described by the standard dose–response curve,

eqn 3 can be reduced to eqn 5 by replacing β_i with eqn 4:

$$Y = Y_0 / \left(1 + \beta_0 x_0 \left(1 + \left(\frac{\text{Dose}}{e^{LD_{50}}} \right)^B \right)^{-1} \right) \quad (5)$$

Thus, any one of eqns 2, 3 or 5 may be required to describe the crop yield for a given experiment, with each equation in the sequence making a stronger assumption than the one before.

Weed biomass and seed production

In order to explain the relationship between weed biomass at a chosen assessment date in a single-species stand and herbicide dose, the standard dose–response curve (eqn 6) has been most widely used (Streibig, 1980):

$$W = W_0 / \left(1 + \left(\frac{\text{Dose}}{e^{LD_{50}}} \right)^B \right) \quad (6)$$

where W_0 represents the weed biomass at no-herbicide treatment at a chosen assessment date, LD_{50} is the log of the dose required to reduce weed biomass by 50%, and B is the response rate or steepness of the curve. In eqn 6, the parameters, particularly W_0 , will change with assessment date, environmental growth conditions and weed density. However in the same environmental conditions, W_0 will be influenced mainly by initial weed density (x_0) at the assessment date. Therefore, if weed density (j) is different, the most general model (Full model) is

$$W = W_{0j} / \left(1 + \left(\frac{\text{Dose}}{e^{LD_{50j}}} \right)^{B_j} \right) \quad (7)$$

where W_{0j} , B_j and LD_{50j} are the parameters for the j^{th} weed density.

As the herbicide dose–response of weeds is physiological, it is assumed that changing weed density will only affect W_0 , but not the parameter LD_{50} and B . Therefore eqn 7 was reduced to eqn 8 with a common LD_{50} and B , so that

$$W = W_{0j} / \left(1 + \left(\frac{\text{Dose}}{e^{LD_{50}}} \right)^B \right) \quad (8)$$

Wilson *et al.* (1995) reported that weed biomass increased hyperbolically with weed density at a fixed crop density. It is thus assumed that weed biomass at no-herbicide treatment has a hyperbolic relationship with initial weed density as follows

$$W_0 = Cx_0 / (1 + Ax_0) \quad (9)$$

where parameter C is the biomass of an individual weed plant without interspecific competition and A is a

measure of intraspecific competition of the weed. Consequently, eqn (8) can be combined with eqn (9) to obtain a model which explains the relationship between weed biomass and herbicide dose at different weed densities simultaneously, i.e.

$$W = Cx_0 / \left(\left(1 + \left(\frac{\text{Dose}}{e^{LD_{50}}} \right)^B \right) (1 + Ax_0) \right) \quad (10)$$

Equation 10 can be also used to estimate weed seed production if it is assumed that seed production is linearly (Wright, 1993) or allometrically (Wilson *et al.*, 1995) related to weed biomass. Thus, any of the eqns 7, 8 or 10 may be required for a given experiment, with each equation in the sequence making a stronger assumption than the one before.

Model development using field data

Field experiment

A field experiment was carried out at Long Ashton Research Station in 1996–97. The experiment consisted of four replicates of a split-split plot design, with six doses of herbicide (metsulfuron-methyl) (including no-herbicide treatment) as the main plot treatments. The main plots were split with two winter wheat cultivars as subplots. Each subplot was further split with four model weed (*Brassica napus* L.) densities (including weed-free). The split-split plot size was 3 m × 3 m.

The two winter wheat (*Triticum aestivum* L.) cultivars, Avalon and Spark, were chosen to have contrasting competitive abilities (Seavers & Wright, 1997), and were drilled at a density of approximately 300 plants m⁻² on 10 October 1996, immediately after four different densities of *B. napus* (oilseed rape, cv. Apex) as a model weed were sown by hand. The target densities of *B. napus* were 0, 25, 50 and 100 plants m⁻².

Metsulfuron-methyl formulated as Ally® (200 g a.i. kg⁻¹, DuPont (UK)), which has a recommended dose of 6.0 g a.i. ha⁻¹, was applied at 0.375, 0.75, 1.5, 3.0 and 6.0 g a.i. ha⁻¹ on 15 April 1997, when the wheat was at growth stage 32 and *B. napus* at 23–24 (Zadoks *et al.*, 1974). The herbicide was applied using a CO₂-pressurized sprayer, Oxford Precision Sprayer (EDM. Engineering, UK), with a 4-m boom carried by two operators. The sprayer was fitted with a LP015F110 fan-tip flat-spray nozzle (Spraying System, USA) and operated at a pressure of 210 kPa and a volume rate of 250 L ha⁻¹.

Assessments were conducted at three times after herbicide application (on 2 May, 25 May and 28 July 1997). Winter wheat was sampled from areas of 0.25 m² for the assessments before harvest, and winter wheat and *B. napus* were sampled from an area of 1.0 m² for the final assessment at maturity. Winter wheat and *B. napus*,

biomass (dried at 90 °C for 24 h) was recorded. Finally, winter wheat grain yield and *B. napus* seed production were measured on 28 July 1997.

Statistical analysis

All measurements were initially subjected to analysis of variance (ANOVA). A variance-stabilizing natural log transformation was used for weed biomass and seed production; no transformation was required for crop yield. Non-linear regression was used to fit the various models, using the transform-both-sides (TBS) technique (Rudemo *et al.*, 1989) when required. Genstat (Genstat Committee, 1993) was used for all statistical analyses. Lack-of-fit of the most complex model (eqn 2 for crop yield; eqn 7 for weed biomass and seed) was also tested to check that the basic models used were appropriate.

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

$$F = \left(\frac{RSS_{i+1} - RSS_i}{df_{i+1} - df_i} \right) / \left(\frac{RSS_a}{df_a} \right) \quad (11)$$

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

Results

Modelling crop yield as affected by weed interference and herbicide dose

The weed-free crop yield (*Y*₀) and weed competitiveness (*β*) were estimated at each dose of metsulfuron-methyl by fitting eqn 2 to biomass or grain yield of winter wheat using nonlinear regression. There was no evidence that weed-free crop yield (*Y*₀) was significantly affected by metsulfuron-methyl, but it could be seen clearly that weed competitiveness (*β*) decreased with increasing herbicide dose. To explore this relationship, weed competitiveness were plotted against herbicide dose (Fig. 1), which suggested that the response of weed competitiveness to metsulfuron-methyl could be explained by the standard dose-response curve, regardless of assessment date or crop cultivar. When eqn 3 was fitted, there was no evidence that this fitted less well than eqn 2 as summarized in Table 1, so there was no evidence that *Y*₀ varied with dose. Finally, there was no evidence that eqn 5 fitted less well than eqn 3 (Table 1), so that the final model is a good description of the crop yield. The

parameter estimates of the final model are presented in Table 2, and the predicted competitiveness (*β*) at each dose is presented in Fig. 1, showing that the relationship between weed competitiveness and herbicide could be explained by the standard dose-response curve (eqn 4). This result therefore indicates that the hyperbolic model and the dose response model can be combined to give eqn 5 by modelling the parameter *β* using the standard dose-response curve.

Weed competitiveness without herbicide treatment, *β*₀ (Table 2) was greater in cv. Spark than in cv. Avalon. A component of the weed competitiveness represents crop competitiveness, so that it can be concluded that Avalon was more competitive than Spark in protecting crop yield from weed competition. For grain yield, parameter *β*₀ for Spark (0.0037) was twice as large as that of Avalon. The *LD*₅₀ was greater in Spark than in Avalon. The greater *LD*₅₀ values and parameter *β*₀ for biomass and grain yield of winter wheat (Table 2) suggests that Avalon was more competitive than Spark, so the improved herbicide performance may be related to crop competitiveness.

Modelling weed biomass and seed production as affected by weed density and herbicide dose

Plots of weed biomass and seed production against herbicide dose showed that both weed biomass and seed production decreased with increasing herbicide dose (Fig. 2). To describe the relationship between weed biomass or seed production and sublethal doses of herbicide, eqn 7 was fitted to weed biomass and seed production using the TBS (Rudemo *et al.*, 1989) technique with a log transformation. Neither *LD*₅₀, nor *B*, appeared to be affected by weed density, whereas *W*₀ (weed biomass and seed production at no-herbicide treatment) increased systematically and so eqn 8 was fitted. Finally, as it was expected that the rectangular hyperbolic model would describe the increase in *W*₀ with density as used by Wilson *et al.* (1995), eqn 10 was fitted.

Lack-of-fit tests showed that eqn 7 satisfactorily described weed biomass and seed production in both cvs Avalon and Spark (Table 1). There was no evidence that eqn 8 fitted less well than eqn 7, so that weed density did not affect *LD*₅₀ and *B*, but did affect weed biomass at no-herbicide treatment (*W*₀). Finally, there was no evidence that eqn 10 fitted significantly less well than eqn 8, showing that the relationship between *W*₀ and weed density was well explained by eqn 9. Thus eqn 10 was selected as the model to describe the effect of the complex interaction on weed biomass or seed production. The estimated model parameters are given in Table 3, and the predicted weed biomass at no-herbicide treatment (*W*₀) at each weed density is presented in Fig. 2. This result therefore indicates that the standard

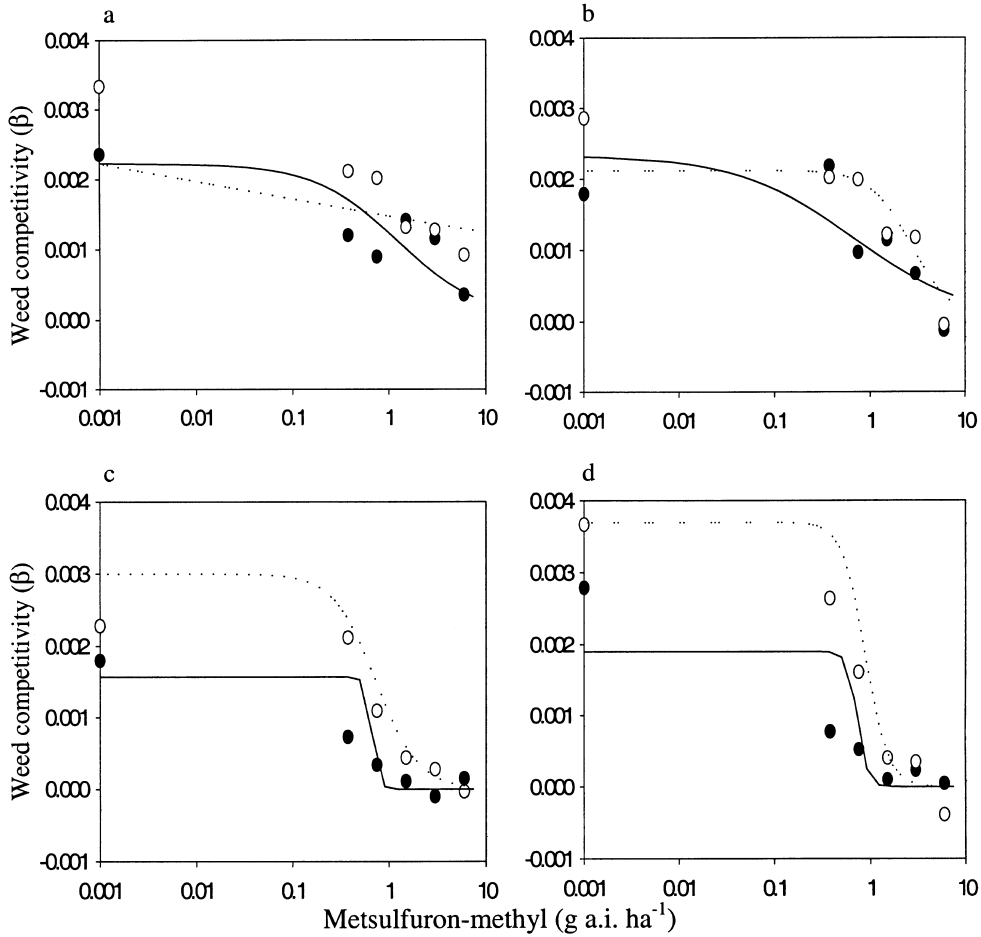


Fig. 1 The relationship between weed competitiveness (β) in Avalon (●), Spark (○) and metsulfuron-methyl. Weed competitiveness were obtained from separate analysis of biomass assessed on 2 May (a), 25 May (b) and 28 July (c) and grain yield (d) by fitting the hyperbolic model (eqn 2) at each dose of metsulfuron-methyl. The continuous lines are fitted lines calculated using eqn 4 and estimated parameters (Table 2).

Table 1 Changes in the degrees of freedom and residual sums of squares for the models when fitted to data on winter wheat grain yield and *B. napus* seed production

	Crop grain yield		Weed seed production	
	(Avalon)	(Spark)	(in Avalon)	(in Spark)
Δ d.f.	3	3	1	1
Δ RSS	2.10	2.53	0.02	1.16
F-value	1.709 ^{NS}	2.461 ^{NS}	0.069 ^{NS}	3.889 ^{NS}
		[5]		[10]
		▲		▲
Δ d.f.	5	5	4	4
Δ RSS	3.81	1.26	1.70	2.05
F-value	1.859 ^{NS}	0.734 ^{NS}	1.472 ^{NS}	1.718 ^{NS}
		[3]		[8]
		▲		▲
Δ d.f.	12	12	12	12
Δ RSS	0.41	0.97	3.95	4.75
F-value	0.064 ^{NS}	0.145 ^{NS}	1.141 ^{NS}	1.326 ^{NS}
		[2]		[7]
		▲		▲
		[ANOVA]		[ANOVA]
d.f.	72	72	48	46
RSS	38.54	40.17	13.86	13.72

The numbers in parentheses represent model equations.

Table 2 Parameter estimates for the simulation of biomass and grain yield of winter wheat with different densities of *B. napus* and metsulfuron-methyl at a range of sublethal doses. The numbers in parentheses are standard errors. (d.f. = 92)

Variables	Avalon				Spark			
	Y_0	LD_{50}	B	$\beta_0 \times 10^3$	Y_0	LD_{50}	B	$\beta_0 \times 10^3$
Biomass (t ha ⁻¹)								
2 May	4.16 (0.075)	0.22 (0.943)	0.99 (0.755)	2.23 (0.737)	3.36 (0.059)	-4.50 (13.4)	0.11 (0.294)	3.92 (0.875)
25 May	7.04 (0.613)	-0.40 (1.110)	0.71 (0.531)	2.34 (0.671)	6.68 (0.125)	1.00 (0.545)	2.01 (1.890)	2.12 (0.603)
28 July	14.12 (0.126)	-0.41 (0.119)	12†	1.57 (0.320)	15.15 (0.154)	-0.31 (0.268)	2.01 (0.805)	3.01 (0.498)
Grain yield (t ha ⁻¹)								
28 July	6.63 (0.085)	-0.33 (0.146)	8†	1.90 (0.485)	6.74 (0.097)	-0.13 (0.217)	3.75 (2.23)	3.70 (0.690)

Y_0 , weed-free crop yield of winter wheat (t/ha); B , a response rate of the dose–response curve; β_0 , a measure of weed competitiveness at no-herbicide treatment; LD_{50} , the log of the dose required to reduce weed competitiveness by 50%. †Fixed to facilitate convergence.

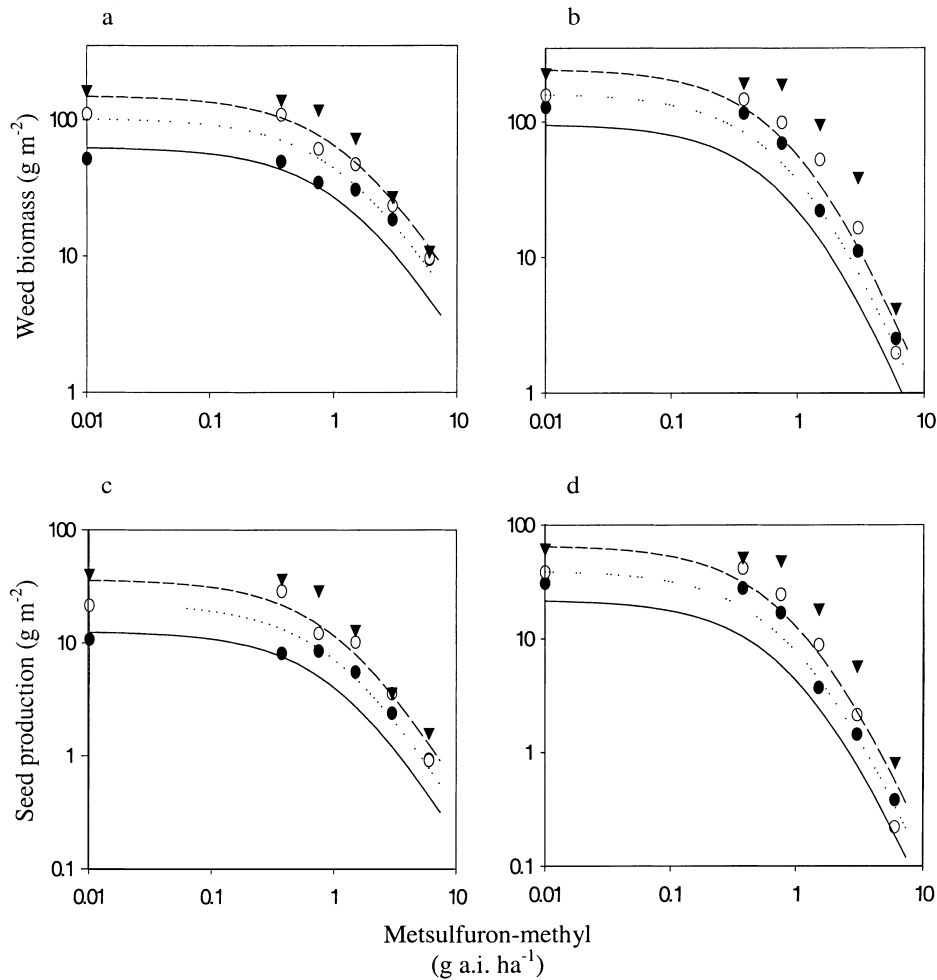


Fig. 2 Dose–response in biomass and seed production of *B. napus* grown in Avalon (a and c) and Spark (b and d) to metsulfuron-methyl at different densities, 25 (●), 50 (○) and 100 (▼) plants m⁻². The continuous lines are the fitted lines from eqn 10.

dose–response model can be modified to a combined model (eqn 10) by replacing parameter W_0 with the rectangular hyperbolic model.

The parameter estimates using the combined model (eqn 10) for the weed biomass, and seed production, data showed that all parameters differ between the two

Table 3 Parameter estimates for biomass and seed production of *B. napus* at harvest on 27 July 1997. The numbers in parentheses are standard errors. (d.f. = 65 and 63 for Avalon and Spark, respectively)

Variables	Avalon				Spark			
	<i>C</i>	<i>LD</i> ₅₀	<i>B</i>	<i>A</i> × 10 ³	<i>C</i>	<i>LD</i> ₅₀	<i>B</i>	<i>A</i> × 10 ³
Biomass	3.22 (0.690)	0.29 (0.225)	1.51 (0.209)	11.39 (5.420)	4.77 (0.969)	0.16 (0.129)	2.40 (0.196)	9.30 (4.834)
Seed production	0.58 (0.120)	0.17 (0.189)	1.87 (0.214)	6.05 (4.010)	1.00 (0.187)	0.12 (0.143)	2.58 (0.119)	5.16 (3.930)

C, individual weed biomass or seed weight at no herbicide treatment (g/plant); *LD*₅₀, the log of the dose (in g a.i. ha⁻¹) required to reduce weed biomass or seed production by 50%; *B*, a rate of response or steepness of the dose–response curve; *A*, a measure of intracompetition effect.

winter wheat cultivars. The individual weed biomass at no herbicide treatment (*C*), was greater in Spark than in Avalon, again suggesting the hypothesis that Avalon is more competitive than Spark. Differences in individual weed plant biomass resulted in different seed productions per weed plant at the no-herbicide treatment. A single *B. napus* plant produced 0.582 g plant⁻¹ of seed when grown with Avalon and 0.998 g plant⁻¹ of seed when grown with Spark. The *LD*₅₀ was slightly, though not significantly, greater in Avalon. It was also noted that the *LD*₅₀ decreased with time (Kim, 1999). This may be due not only to herbicide effects but also to the subsequent increase in weed suppression by winter wheat. Parameter *A*, a measure of intraspecific competition, appears to be similar; for *B. napus* biomass, 0.0114 in Avalon and 0.0093 in Spark, and for seed production, 0.006 and 0.005 in Avalon and Spark, respectively.

Prediction

A main aim of the modelling approach to crop:weed competition is to predict crop yield and weed seed production. Incorporating other factors, i.e. herbicide dose, considerably complicates the prediction process. However, the model presented here provides a valuable tool for predicting the effect of these factors.

Crop yield

Using the final model (eqn 5) and estimated parameters (Table 2), crop biomass and grain yields were predicted in Figs 3 and 4 respectively. The decrease in winter wheat biomass with increasing weed density at no-herbicide treatment increased with time, regardless of winter wheat cultivar (Fig. 3). The extent of decrease in biomass of cv. Spark (Fig. 3b, d and f) was markedly greater than with cv. Avalon (Fig. 3a, c and e). The effect of herbicide treatment also became more obvious with time. There was no significant difference in weed-free crop yield of the two cultivars, 6.6 and 6.7 t ha⁻¹ for Avalon and Spark respectively (Fig. 4). At the no-herbicide treatment, the predicted grain yield of Avalon decreased to 5.6 t ha⁻¹ with 100

B. napus plants m⁻² (Fig. 4a), whereas that of Spark decreased to 4.9 t ha⁻¹ (Fig. 4b). Metsulfuron-methyl below 0.3 g a.i. ha⁻¹ did not change the pattern of this decrease. Above 0.3 g a.i. ha⁻¹, the pattern of decrease changed rapidly until 1.65 g a.i. ha⁻¹ for Avalon and 3.0 g a.i. ha⁻¹ for Spark. At higher doses, the effect of weed competition was totally eradicated. In terms of herbicide performance therefore Avalon had a greater advantage than Spark.

Weed biomass and seed production

Using the estimated parameters (Table 3) and the combined model (eqn 10), weed biomass was predicted separately in cvs Avalon and Spark (Fig. 5). The prediction showed that *B. napus* grows better in Spark than in Avalon. For instance, the model predicted that *B. napus* biomass at 100 *B. napus* plants m⁻² with no-herbicide treatment will be 150 g m⁻² in Avalon and 250 g m⁻² in Spark at harvest (Fig. 5a and b), whereas at the same weed density but with 1.0 g a.i. ha⁻¹ of metsulfuron-methyl, weed biomass will be about 70 g m⁻² in both Avalon and Spark. Figure 5 also shows the predicted *B. napus* seed production as affected by weed density and herbicide dose. It was predicted that with no-herbicide treatment, *B. napus* produces more seeds in Spark than in Avalon. For example, at 100 *B. napus* plants m⁻², without herbicide treatment the model predicted 35 and 72 g m⁻² of *B. napus* seed in Avalon and Spark plots respectively. However, the herbicide dose–response of *B. napus* was more obvious in Spark than in Avalon, so that with doses of metsulfuron-methyl greater than 1.5 g a.i. ha⁻¹, the model predicts that more seeds will be produced in Avalon than Spark.

Discussion

Although much effort has been made to optimize herbicide use and maintain profits, the results (Defelice *et al.*, 1989; Barton *et al.*, 1992; Spandl *et al.*, 1997) have only provided individual solutions for certain conditions. For the study of crop:weed competition in field conditions, additive experiments (Harper, 1977)

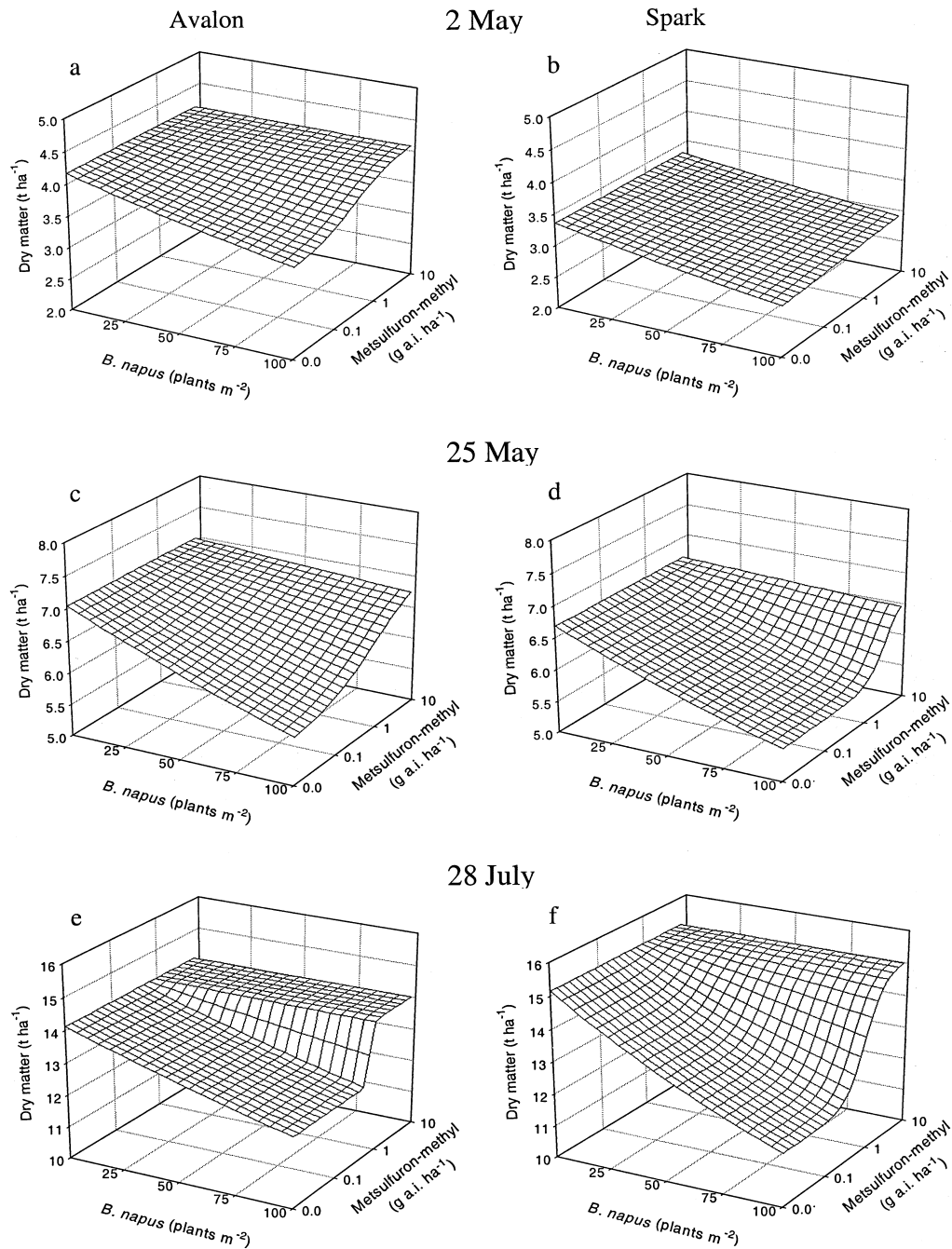


Fig. 3 Predicted biomass of winter wheat as affected by crop:weed competition and sublethal doses of metsulfuron-methyl, using eqn 5 and the parameter estimates given in Table 2.

have been used widely, most often with several weed densities (including weed-free) and a constant crop density. For the study of herbicide dose–response of weeds, several herbicide doses (including no-herbicide) are tested. The combination of these two types of study, as presented here, provides a better approach for optimizing herbicide use. In this respect, the studies of Christensen (1993) and Brain *et al.* (1999) would be very close to this approach. However, Christensen's

(1994) model for the relationship between crop:weed competition and herbicide performance, used a single weed density and measured only weed biomass to compare competitiveness of cereal crop species and cultivars. Brain *et al.* (1999) modelled the complex interaction between herbicide doses and crop:weed competition, but their model requires weed biomass data instead of weed density. In practice, the biomass assessment is expensive and not practical for farmers to

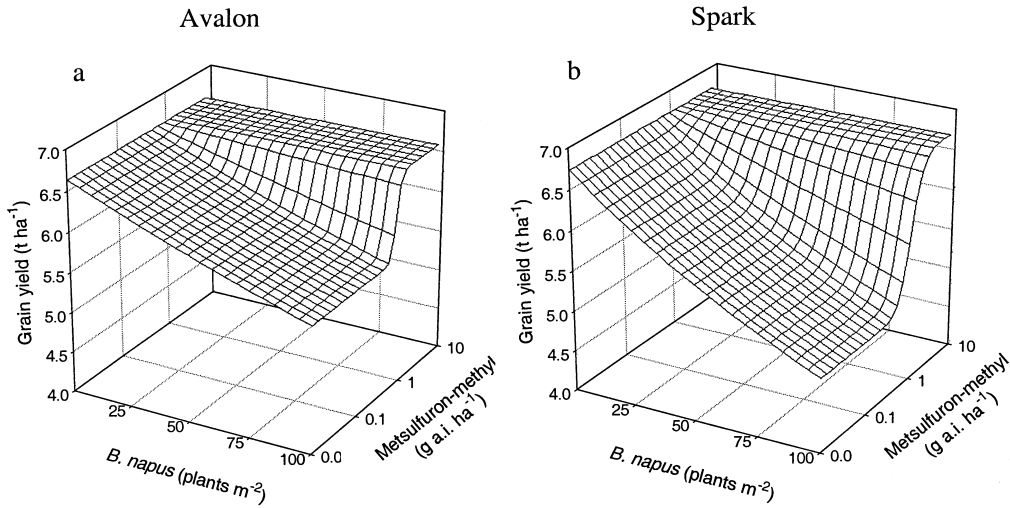


Fig. 4 Predicted grain yield of Avalon (a) and Spark (b) as affected by crop:weed competition and sublethal doses of metsulfuron-methyl, using eqn 5 and the parameter estimates given in Table 2.

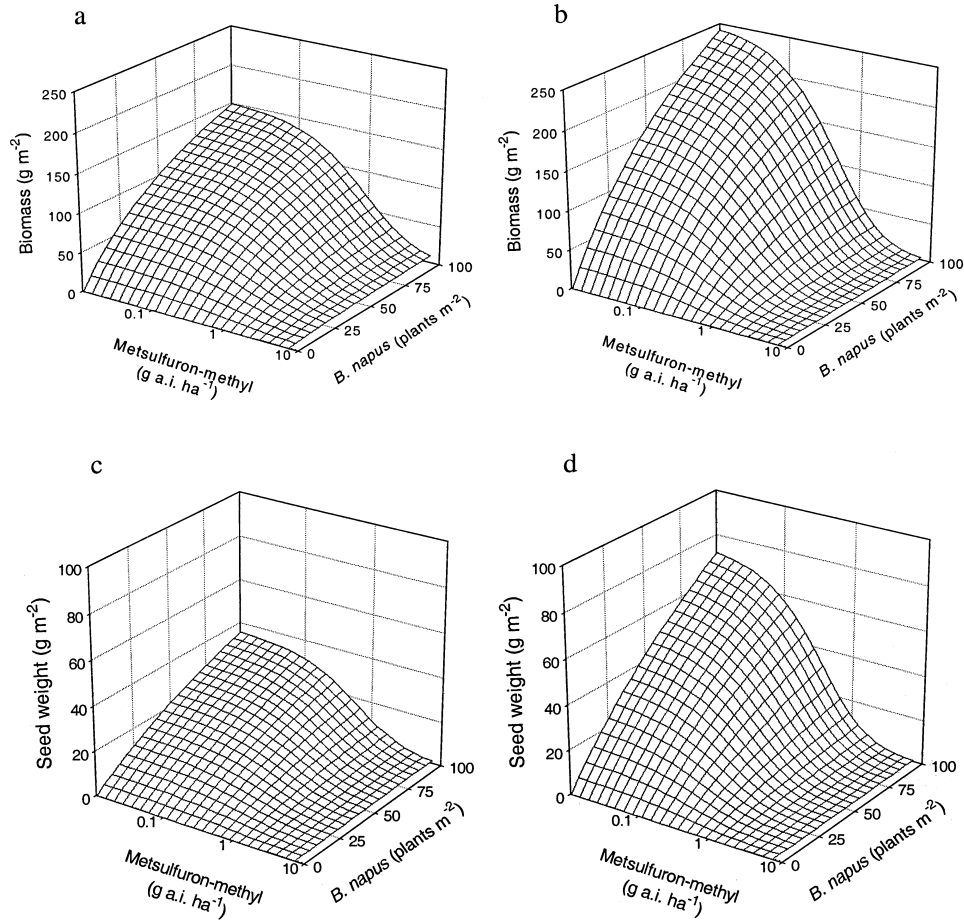


Fig. 5 Predicted biomass (a and b) and seed production (c and d) of *B. napus* as affected by *B. napus* density and metsulfuron-methyl in Avalon (a and c) and Spark (b and d) using eqn 10 and parameter estimates given in Table 3.

adopt. In comparison, the two models (eqns 5 and 10) presented here are able to predict crop yield and weed seed production respectively. These models are based

on weed density observed early in the spring, which remained relatively constant until the final assessment (data not included). In winter crops, weed density in

the spring would vary less over the growing season compared with weed biomass (Brain *et al.*, 1999). The rearrangement of these final models may also provide an answer to how much herbicide is required (see Figs 6 and 7).

Potential application of the models to decision-making for weed control

Although many models have been developed and tested to aid decision-making for weed control, they have only provided simple answers, such as estimated crop yields, economic threshold weed density and whether or not to spray herbicide. In model-based approaches, such as those of Christensen (1993), and Brain *et al.* (1999), their models were further modified to calculate the dose of herbicide required to limit crop yield loss to less than a given level. Likewise, in our study, if a threshold of acceptable percentage yield loss is denoted by $p\%$, eqn 5 can be rearranged to give the dose, D_p , required to reduce the yield loss to less than $p\%$

$$D_p = \exp(LD_{50}) \left(\frac{(100-p)\beta_0 x_0}{p} - 1 \right)^{\frac{1}{b}} \quad (12)$$

This herbicide dose (D_p) could then be estimated for this experiment, using the parameter estimates given in Table 2 and eqn 12. The results are presented in Fig. 6. For example if an acceptable yield loss is 5%, and the weed density was 200 plants m^{-2} , a metsulfuron-methyl dose of 0.9 g a.i. ha^{-1} would still provide effective control in Avalon (Fig. 6a), whereas more than 2.0 g a.i. ha^{-1} of metsulfuron-methyl would be required in Spark (Fig. 6b). Similarly, if $p = 2\%$ and the weed density is

200 plants m^{-2} , Avalon would require 1.0 g a.i. ha^{-1} of herbicide, whereas Spark would require 2.5 g a.i. ha^{-2} . If weed density data are available, and the parameters of eqn 12 are known for a given site/year, eqn 12 will predict the appropriate dose of herbicide. The risk of failure in weed control and crop production can be minimized. Furthermore, this model can be used in economic analysis before herbicide application to optimize economic benefits.

Findings from many studies show clearly that effective long-term weed management requires greatly reduced weed seed production (e.g. Swanton & Weise, 1991; Swanton & Murphy, 1996; Jordan, 1997). Therefore, decision-making for weed control needs to consider the long-term economic threshold based on weed seed production. However, all seeds produced in one season may not be added to the seedbank or establish in the following season. Once new weed seeds are added in the seedbank, they will be dispersed in the soil profile by physical factors such as mechanical cultivation (see, Brain & Marshall, 1999 and Marshall & Brain, 1999). Some of them will germinate and the others will remain in the soil or lose their viability. Only a proportion of seeds produced in one season will be established in the following season. Based on this information, an acceptable level of weed seed production can be estimated. If an acceptable seed production (q) based on total seed production and population dynamics is assumed, eqn 10 can be rearranged to give the minimum dose, D_q , required to restrict the weed seed production to lower than q g m^{-2}

$$D_q = \exp(LD_{50}) \left(\frac{Cx_0}{q(1+Ax_0)} - 1 \right)^{\frac{1}{b}} \quad (13)$$

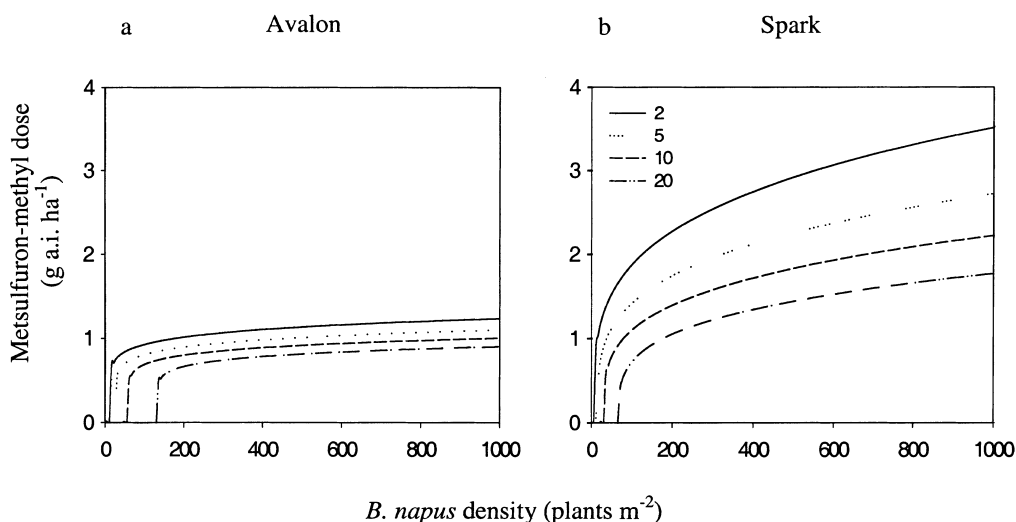


Fig. 6 Estimated doses of metsulfuron-methyl required to restrict grain yield losses of Avalon (a) and Spark (b) to less than $p\%$ for a range of *B. napus* densities. The dose was calculated using eqn 12 and parameter estimates (Table 2).

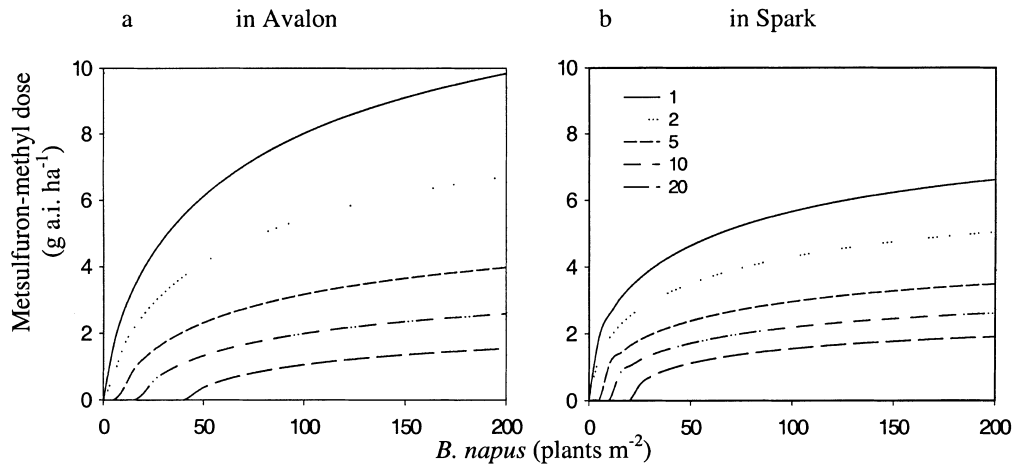


Fig. 7 Estimated metsulfuron-methyl doses (D_q) to restrict seed production of *B. napus* in Avalon (a) and Spark (b) to less than $q \text{ g m}^{-2}$ for a range of q -values (1, 2, 5, 10 and 20 g m^{-2}) vs. *B. napus* density, calculated using eqn 13 and parameter estimates from Table 3.

Equation 13 can be used to estimate the herbicide dose required to restrict the seed production of *B. napus* to less than $q \text{ g m}^{-2}$ (Fig. 7). As a result of more *B. napus* seed production in Avalon at doses of metsulfuron-methyl $> 1.5 \text{ g a.i. ha}^{-1}$, a higher dose of metsulfuron-methyl will be required to restrict seed production to 5 g m^{-2} in Avalon than in Spark. In contrast, if the acceptable seed production is more than 10 g m^{-2} , a lower dose of metsulfuron-methyl will be required in Avalon than in Spark. The recommended herbicide dose based on crop yield loss can be adjusted by considering weed seed production and population dynamics. Therefore, the final recommendation of herbicide dose can be made on the basis of both crop yield loss and weed seed production.

Crop cultivar effects on herbicide performance

It is speculated that improved crop competitiveness may help to minimize herbicide use. Many studies have found that improvement in crop competitiveness was achieved by selecting competitive cultivars (e.g. Richards & Whytock, 1993) and increasing crop density (e.g. Lemerle *et al.*, 1996b). There have been several reports showing increased herbicide performance as a result of improved crop competitiveness (Richards & Whytock, 1993; Courtney, 1994). The results showed that weed competitiveness (β_0) at no-herbicide treatment was smaller in cv. Avalon than in cv. Spark, indicating that Avalon was more competitive than Spark. Herbicide performance, as a result of crop competitiveness, was also greater in Avalon with smaller LD_{50} than Spark. Similar results were reported by Lemerle *et al.* (1996a), showing that more competitive cultivars were less dependent on herbicide to achieve grain yield potential than less competitive cultivars. Increased crop competitiveness by increasing

crop density (Wilson *et al.*, 1995) may also achieve better herbicide performance for crop yield. Brain *et al.* (1999) found that the LD_{50} value in their combined model was smaller at the high crop density than at the low crop density. Therefore, improving crop competitiveness by using more competitive cultivars or increasing crop density may help minimize weed competitiveness and increase herbicide performance. Richards & Whytock (1993) also showed a similar result. Also, increasing crop density normally improves herbicide performance (Courtney, 1994; Brain *et al.*, 1999).

The use of strongly competitive cultivars is likely to slow down the rate of build-up of weed seeds in the soil (Salonen, 1992). At the no-herbicide treatment, *B. napus* produced more seeds in Spark than Avalon, indicating that Avalon was more suppressive to *B. napus* than Spark. This difference in crop competitiveness might be related to the growth character and morphological characteristics of the cultivars. Avalon had wider, longer and more recurved leaves than Spark, which had narrow and erect leaves (Seavers & Wright, 1999). As a result of these different characteristics, Avalon intercepted more light than Spark, allowing less light for *B. napus* growth (Kim, 1999). Previous studies have shown that Spark is a poor competitor (Richards & Whytock, 1993; Seavers & Wright, 1997; Champion *et al.*, 1998), whereas Avalon has been found to be more competitive than Spark (Seavers & Wright, 1997). The results from this study confirm the results of these previous studies. The results also showed that the herbicide dose-response of *B. napus* in terms of biomass and seed production was influenced by the crop cultivars, which is different from the findings by Christensen (1993) and Lemerle *et al.* (1996a), who showed that crop cultivar affected the weed biomass at no-herbicide treatment but not the herbicide dose-response. Several studies have suggested

that the herbicide dose requirement for weed control can be reduced in more competitive crop cultivars (e.g. Lemerle *et al.*, 1995). Salonen (1992) reported that the level of weed suppression by reduced herbicide doses was determined by not only environmental conditions and weed spectrum, but also by the crop competitiveness. Therefore, the more competitive cultivar is likely to retard the rate of weed seed build-up in the soil, lead to less dependence on herbicides, and result in reduced costs of weed control (Salonen, 1992). However, there is still controversy regarding weed seed production, particularly at higher herbicide dose treatments. In this study, *B. napus* seed production at above 3.0 g a.i. metsulfuron-methyl ha⁻¹ was greater in Avalon than in Spark. As a consequence, the LD_{50} was slightly greater in Avalon but parameter B was smaller compared with that in Spark. Whiting & Richards (1990) suggested that herbicide efficacy was reduced with cultivars of extensive ground cover, possibly because of interception of the herbicide by the crop foliage. Lemerle *et al.* (1996a) also speculated that at high seed rates herbicide may be intercepted by the crop rather than by the weed, therefore reducing efficacy. However, Christensen (1993) found that relative differences in weed biomass between cultivars were the same irrespective of the herbicide dose. Brain *et al.* (1999) found that the LD_{50} value decreased at the high crop density, indicating increased herbicide efficacy. In this experiment, herbicide deposition was not assessed, so it is difficult to surmise whether differences in the parameters LD_{50} and B were caused by more herbicide interception by Avalon than by Spark. Alternatively, the greater seed production in Avalon at higher doses may be due to its earlier maturity compared with Spark. In general, Avalon is considered an early maturing cultivar compared with Spark (Jarman & Pickett, 1996). This early maturation may allow more light to reach the regrowing *B. napus* below the crop canopy. When all plants were harvested, *B. napus* still had green leaves and the late regrowth was observed, particularly at the herbicide treatments > 3.0 g a.i. ha⁻¹. This late regrowth did not cause crop yield loss, but may have contributed to seed production. Although it appeared that Avalon required more herbicide than Spark as presented in Fig. 7, this may not be true in real situations. As mentioned previously, the two cultivars were harvested at the same time although Avalon matured much earlier than Spark. Avalon left in the field for a long period of time after maturation allowed late regrowth of *B. napus* to produce more seeds than Spark. If Avalon is harvested at the proper time, this would be avoided. Nevertheless, this aspect should also be considered in the long-term weed management strategy.

Validation and future work

Owing to their relative simplicities (four parameters) compared with the model of Brain *et al.* (1999) based on weed biomass (five parameters), these models may be more applicable to complex and varied conditions, such as multiple-weed interference, different fertilizer levels and different application timings of herbicide. This approach provided an initial framework for modelling the complex interaction between herbicide and crop:weed competition. However, as this experiment was conducted with an artificial weed in a single year/site, further experimentation for a range of edaphic and climatic conditions (different years and sites) is required for validation and parameter adjustment.

Our approach can be applied to rectangular hyperbolic models based on leaf area (Kropff & Spitters, 1991; Kropff & Lotz, 1992) and so has a wide applicability. As eqn 10 can predict weed seed production, this equation can be incorporated into existing population dynamics models, so that a new generation model will be able to estimate an acceptable level of weed seed production (q), and an optimum herbicide dose required to limit weed seed production to less than q .

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