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Mathematical Modeling of Allelopathy. III. A Model for Curve-Fitting Allelochemical Dose Responses

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ABSTRACT

Bioassay techniques are often used to study the effects of allelochemicals on plant processes, and it is generally observed that the processes are stimulated at low allelochemical concentrations and inhibited as the concentrations increase. A simple empirical model is presented to analyze this type of response. The stimulation-inhibition properties of allelochemical-dose responses can be described by the parameters in the model. The indices, *p%* reductions, are calculated to assess the allelochemical effects. The model is compared with experimental data for the response of lettuce seedling growth to Centaurepensin, the olfactory response of weevil larvae to α-terpineol, and the responses of annual ryegrass *(Lolium multiflorum* Lam.), creeping red fescue *(Festuca rubra* L., cv. Ensylva), Kentucky bluegrass *(Poa pratensis* L., cv. Kenblue), perennial ryegrass *(L. perenne* L., cv. Manhattan), and Rebel tall fescue *(F. arundinacea* Schreb) seedling growth to leachates of Rebel and Kentucky 31 tall fescue. The results show that the model gives a good description to observations and can be used to fit a wide range of dose responses. Assessments of the effects of leachates of Rebel and Kentucky 31 tall fescue clearly differentiate the properties of the allelopathic sources and the relative sensitivities of indicators such as the length of root and leaf.

Key Words: allelopathy, allelochemicals, mathematical modelling, stimulation, dose-response relationship, inverted U-shape response

INTRODUCTION

Molisch (1937) defined allelopathy as any biochemical interaction, whether positive or negative, among plants of all levels of complexity, including microorgan-

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isms. Two important connotations implied in this definition are that allelopathy is a chemical process, which may be harmful or stimulative, and that allelopathy depends on the release of chemical(s) to the environment. Chemicals with allelopathic potential can be in all plant tissues, including leaves, stems, roots, rhizomes, fruits, flowers and pollen, but the most important sources of allelochernicals are leaves and roots (Rice 1984). Allelochemicals may be released from plants into the environment in a number of ways, including root exudates, volatilization, and decomposition of plant residues (Tukey 1969, 1970; Rice 1974; Putnam 1985). Recently, mathematical modeling has been applied to theoretically describe the responses of plants to allellochemicals (An et al. 1993, 1996; Zhen and Ma 2002).

In investigations of allelopathy, bioassay techniques are widely used for the quantitative determination of responses to allelochernicals over a range of doses. Leather and Einhellig (1986, 1988) have extensively reviewed the nature and types of bioassay used. Generally, it is found that stimulation occurs at low concentrations and inhibition appears at high concentrations (Lovett 1979, 1990; Liu and Lovett 1990). The dose-response relationship has, usually, an inverted U-shape in the science of allelopathy, but other kinds of responses are also found, such as an absence of stimulation.

Many allelochemical dose responses are analyzed by ranges of statistical comparison such as Duncan's Multiple Range Test (e.g., Leather and Einhellig 1985; Stevens and Molyneux 1988), Student's t test and the Least Significant Difference (e.g., Paszkowki and Kremer 1988; Toro et al. 1988; Buta and Spaulding 1989). The use of such methods to analyze the data involving a series of dose rates may be, however, statistically inefficient (Dawkins 1983). Linear regression of the dose curves has also been used (Mason-Sedun and Jessop 1988), although the relationship between the doses of allelochernicals and responses of a bioassay organism is not always linear. Like many biological processes, the responses of plant growth and development to allelochernicals are mostly nonlinear.

An et al. (1993) described the stimulation-inhibition phenomenon in allelopathy mathematically and defined this type of response as a biological property of allelochernicals. Theoretical models are developed for modeling phytotoxicity released from residues during decomposition (An et al. 1996) and modeling dynamics of allelochernicals from living plants in the environment (An et al. 2002). Wu et al. (2000) used a log-logistic equation (Finney 1979; Streibig 1986) in studying the allelopathic potential of wheat (Triticum aestivum L.) and curve-fitted the root length of annual ryegrass (Lolium rigidum) to wheat sowing density. The log-logistic equation is widely applied in herbicide dose response, but it does not feature stimulation at low doses. Brain and Cousens (1989) modified the log-logistic equation and presented a model that can account for stimulative responses. Schabenberger et al. (1999) developed the statistical test for the modified log-logistic model (Brain and Cousens 1989) in herbicide dose responses. In mathematical modeling of allelopathy, An *et al.* (1993) presented a model based on enzyme kinetics. Sinkkonen (2001) incorporated the enzyme kinetic model to describe the density-dependent chemical

interaction (Weidenhamer et al., 1989). while Dias (2001) used a Weibull function to fit allelochemical effects on the germination process. Some of these models (for example, Dias 2001) often do not possess the nature of stimulation in the equations, while others with the property of stimulation have limited flexibility in curve-fitting to a range of simulation-inhibition curve types (Lovett 1990; Liu and Lovett 1990). The aims of this paper were to develop a highly flexible but simple equation for describing the general pattern of inverted U-shaped dose-response relationships and to use the model to analyze some experimental data of allelochemical effects.

MATERIALS AND METHODS

The Model

Let R be the response of a testing organism, D a dose of an allelochemical, and R_c the response of untreated control in the bioassay. We may write

$$R = R_c + E(D) \tag{1}$$

where $E(D)$ is the effect of the allelochemical. Stimulation corresponds to $E(D) > 0$, and inhibition occurs when $E(D) < 0$. First, consider the case where $E(D)$ is a simple quadratic equation, so that

$$E(D) = \alpha D - \beta D^2 \tag{2}$$

where α, β (> 0) are constants. Stimulation corresponds to $D < \alpha/\beta$, and inhibition to $D > \alpha/\beta$. Equation 1 therefore becomes

$$R = R_c + \alpha D - \beta D^2. \tag{3}$$

Note that when D is large, R will be negative, which is physiologically unacceptable. Consequently, the model will only apply over the range where $R > 0$.

As $\alpha > 0$ and $\beta > 0$, the response curve has a stimulation at low doses, otherwise there is no stimulation.

Equation 3 is basically a quadratic function. The choice of the quadratic equation roots from the consideration of inverted U-shaped biological responses with the mathematical curve shape. In practice, however, a quadratic equation does not usually possess a feature of flexibility in describing biological responses. In order to overcome this, the D term in Equation 3 is replaced by a function of the dose, $g(D)$, so that

$$R = R_c + \alpha g(D) - \beta [g(D)]^2. \tag{4}$$

To analyze the similarities in plant and animal responses to allelochemical stress, Lovett et *al.* (1989) used $g(D) = ln(D+1)$, which gave a good fit to several sets of data. In the present model, this approach is generalized as

$$g(D) = \overbrace{\ln(\ln(...\ln}^{k}(D+\overbrace{1)...+1}^{k})+1) \qquad (5)$$

where k is the number of $ln(D+1)$ transformations. Equation 4 now becomes

$$R = R_c + \alpha \ln(\ln(...\ln(D+1)...+1)+1) - \beta[\ln(\ln(...\ln(D+1)...+1)+1)]^2. \qquad (6)$$

The case of $k = 0$ is denoted as no transformation. Thus, when $k = 0$, Equation 3 is referred. The features of Equation 6 are that the value of the untreated control remains at zero [*i.e.*, $\ln(\ln(...\ln(0+1)...+1)+1)=0$], and the stimulation peak changes from a standard quadratic curve (when $k = 0$). Thus, Equation 6 can account for a wide range of stimulation-inhibition responses. The k may be biologically a sensitive indicator of stimulation. The equation is symmetrical quadratic when the R is plotted against $g(D)$.

To look at the properties of this equation, we write Equation (4) as

$$R = R_c + \frac{\alpha^2}{4\beta} - \beta\left[g(D) - \frac{\alpha}{2\beta}\right]^2. \qquad (7)$$

The maximum value of R, defined as R_m, is

$$R_m = R_c + \frac{\alpha^2}{4\beta}. \qquad (8)$$

Thus, the highest stimulation value (R,,,) is

$$R_h = R_m - R_c = \frac{\alpha^2}{4\beta}. \qquad (9)$$

By defining D_m as the dose that gives the highest stimulation, from Equations 5 and 7. we have

$$D_m = \exp\left(...\left(\exp\left(\exp\left(\frac{\alpha}{2\beta}\right)-1\right)-1\right)...\right)-1. \qquad (10)$$

Define D_p as the dose that results in a $p\%$ reduction in the process, due to the allelochemical. From Equation 4,

$$g(D_p) = \frac{\alpha + \sqrt{\alpha^2 + 0.04 p \beta R_c}}{2\beta} \tag{11}$$

and hence

$$D_p = Exp\left(\ldots \left(Exp\left(Exp\left(\frac{\alpha + \sqrt{\alpha^2 + 0.04 p \beta R_c}}{2\beta} \right) - 1 \right) - 1 \right) \ldots \right) - 1. \tag{12}$$

In particular, the doses corresponding to 0 and 50% reduction, D_0 and D_{50} respectively, are calculated by Equation 12. D_0 is the threshold dose below which stimulations occur, and above which inhibitions appear. D_{50} can be used as a measure of the inhibition potency of an allelochemical or the sensitivity of the testing organism to the allelochemical.

Curve-Fitting Procedure

Equation 6 is illustrated in Figure 1. The approach is to make successive transformations and fit the data to Equation 4 for each transformation. Multilinear regression analysis is used to determine the parameters, $R_{c,i}$, α_i, β_i, where i equals 0, 1, 2, ... for nil, 1, 2, ... logarithmic transformations, respectively. The predicted values, $\tilde{R}_i = R(R_{c,i}, \alpha_i, \beta_i)$, are calculated each transformation. Then, linear regression is used to fit predicted values, $\tilde{R}_i$, to the observed values, R_o:

$$\tilde{R}_i = a + bR_o + \varepsilon. \tag{13}$$

The number of transformations is determined when the k-transformations give the highest coefficient of determination (r^2). The criterion for determination of k is

$$r_{k-1}^2 < r_k^2 > r_{k+1}^2 \text{ or } r_{k+1}^2 - r_k^2 \le 0.01 \tag{14}$$

where the subscription denotes the number of transformations.

RESULTS

Data for the responses of the lettuce root length to the concentration of Centaurepensin (Stevens and Merrill 1985) are used to illustrate the fitting procedure of the model. The number of transformations from k = 0 to 3 is presented in

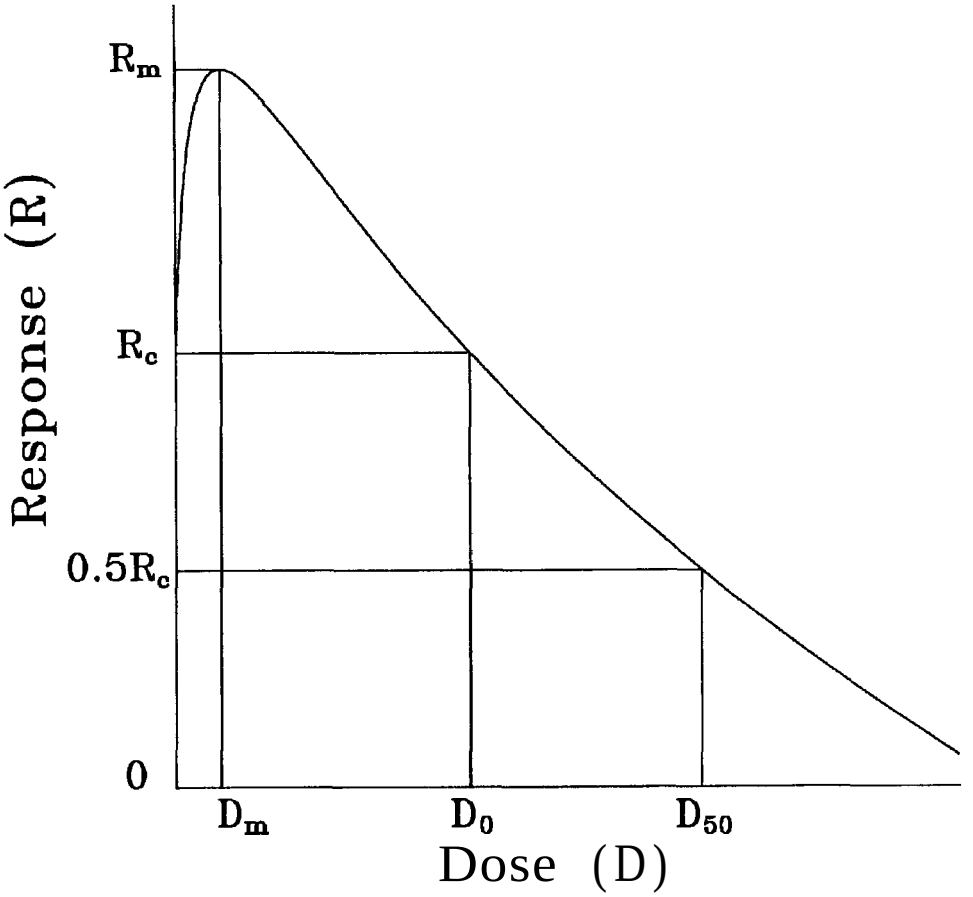

Figure 1. **A hypothetical allelochemical dose-response curve. R_m is the maximum stimulating peak, D_m is the dose that gives the stimulating peak, D_0 is the dose that gives no effect and D_{50} is the dose that gives 50% reduction of untreated control yield.**

Figure 2. The r^2 is increased from 0.74 at nontransformation to 0.96 at one transformation (k = 1). Further increase in number of transformations decreased in r^2 to 0.92 at k = 2 and 0.86 at k = 3. The best fit to the data is obviously one transformation k = 1), which has the highest r^2.

To fit the data of the effect of a-terpineol on the olfactory response of weevil larvae (Selander etal. 1976), the number of transformations giving the highest r^2 was four. Figure 3a compared the fitted values (k = 4) with observed values, while in Figure 3b the transformed data are plotted against the responses.

The estimation of the parameters from the best fit to the data of Stevens and Merrill (1985) and Selander et *al.* (1976) is shown in Table 1. The t-test of an individual parameter shows that the estimation of the parameters is highly significantly different from zero ($p < 0.001$).

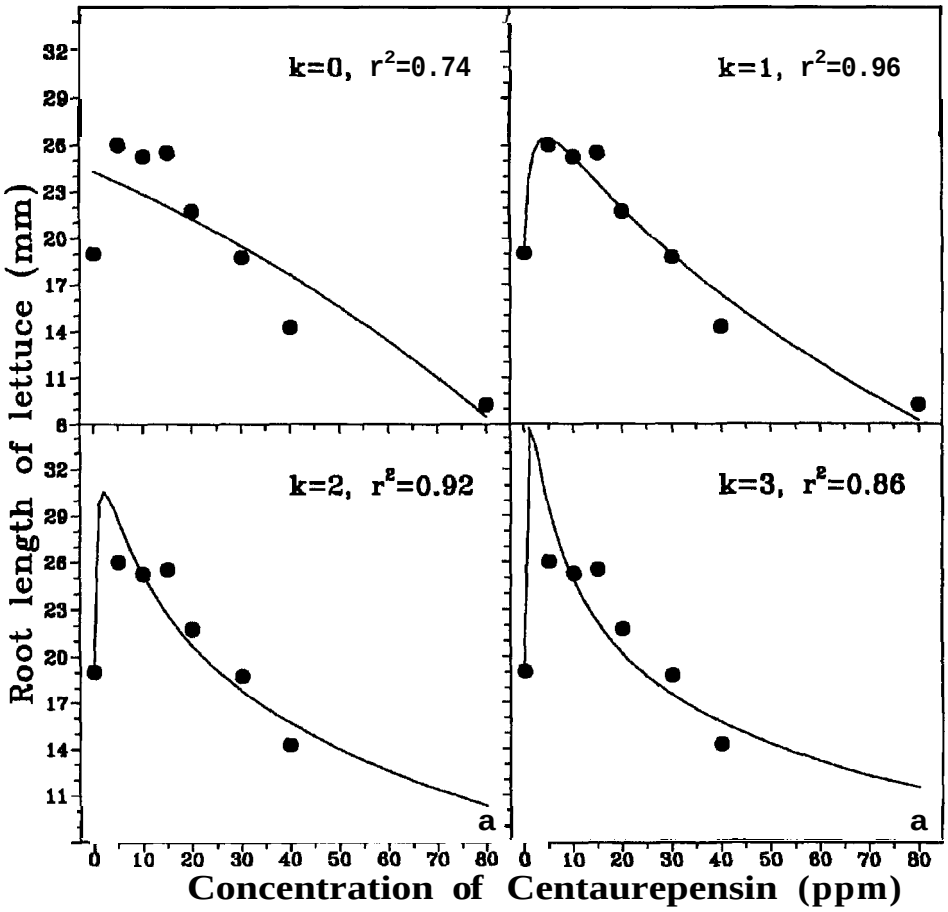

Figure 2. **Details of k = 0, 1, 2, and 3 in the procedures of curve-fittings (the solid lines) of Equation (6) to observations (solid dots) in the responses of the lettuce root length to Centaurepensin (Stevens and Merrill 1985).**

Table 2 shows the estimation of parameters of Equation 6 to fit the data of Buta and Spaulding (1989) with the effect of tall fescue leachates on grass seedling growth. The values of r^2 and standard errors indicate that the regressions and estimations of parameters were reasonably precise. For example, the estimations of all untreated controls, R_c are not significantly different from 100 ($P > 0.05$). Figure 4 showed that the responses of grass leaf length had fewer k-transformations than that of grass root length. This indicated lower sensitivity in grass leaf growth than in grass root growth because the number of $ln(D+1)$-transformation indicates the sensitivities of the test species. The analysis of the means of D_0 and D_{50} supports the finding that grass root growth showed higher sensitivity to both tall fescue leachates than did grass leaf growth (Table 3).

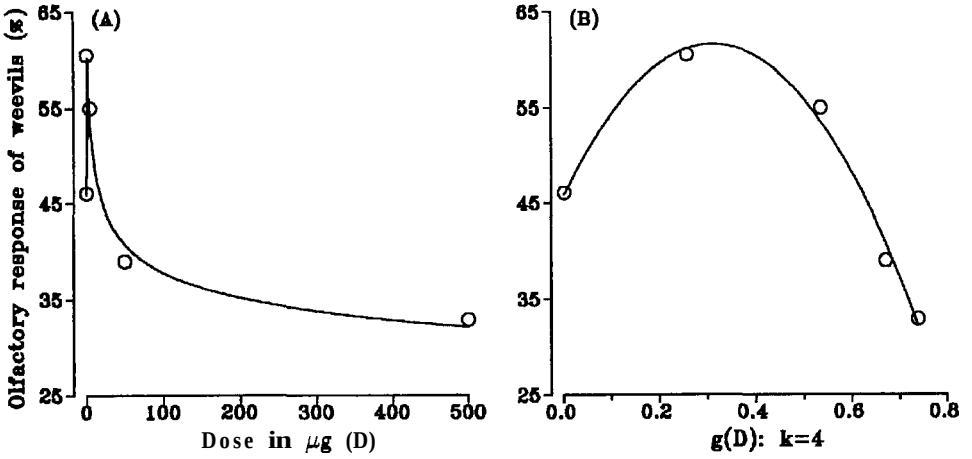

Figure 3. **Equation (6) fitted to the data of Selander *et al.* (1976) with the responses of weevils to α-terpineol; (A): plotting D against *R*, (B): plotting *g(D)* against *R*.**

Table 1. Summary of the curve-fitting results for the responses of the lettuce root length to Centaurepensin (Stevens and Merrill 1985) and the olfactory response of weevil larvae to α-terpineol (Selander *et al.* 1976). Standard error is shown in brackets.

Parameters	Centaurepensin v.s. lettuce	a-terpineol v.s. weevils
K	1	4
R_c	19.36 (1.37)	44.41 (2.27)
α	8.63 (1.21)	119.54 (14.89)
β	2.55 (0.27)	179.27 (18.46)
r^2	0.96	0.99

Table 2. Estimates of parameters of Equation (6) fitted to the data of Buta and Spaulding *(1989)* with the effect of tall fescue (*Festuca arundunacea* Schreb) leachates on grass seedling growth. Standard error is shown in brackets.

Leachate		Annual ryegrass	Ensylva	Kenblue	Manhattan	Rebel
			Grass leaf length			
Kentucky 31	K	1	0	0	2	2
	R_c	100.17 (0.22)	105.98 (3.79)	106.32 (3.93)	99.94 (0.71)	98.53 (4.05)
	a	20.07 (0.26)	0.39 (0.27)	0.089 (0.28)	26.58 (2.11)	69.35 (12.03)
	β	6.99 (0.06)	0.006(0.003)	0.0044 (0.003)	38.71 (1.17)	55.13 (6.66)
	r^2	1.0	0.87	0.93	1.00	0.99
Rebel	K	0	1	2	1	0
	R_c	100.28 (1.43)	101.55 (2.06)	98.47 (4.23)	103.39 (4.35)	93.18 (4.18)
	a	-0.25 (0.10)	23.33 (2.50)	65.23 (12.56)	9.03 (5.28)	-1.51 (0.30)
	β	0.005 (0.001)	6.70 (0.53)	57.85 (6.96)	6.14 (1.12)	0.0078 (0.003)
	r^2	1.00	0.99	0.99	0.99	0.98
			Grass root length			
Kentucky 31	K	0	1	2	3	2
	R_c	108.22 (4.96)	99.81 (1.35)	99.37 (11.86)	100.16 (3.43)	99.84 (3.46)
	α	-2.18 (0.036)	16.18 (1.64)	98.18 (35.22)	92.87 (16.71)	46.48 (10.27)
	β	-0.012 (0.0036)	6.22 (0.35)	83.97 (19.52)	174.21 (15.91)	56.58 (5.69)
	r^2	0.99	1.00	0.96	1.00	1.00
Rebel	K	4	2	3	5	2
	R_c	99.95 (7.96)	98.93 (3.41)	100.20 (4.93)	100.16 (2.27)	99.74 (2.41)
	α	206.38 (55.55)	81.38 (10.12)	108.67 (24.02)	338.69 (21.31)	1.03 (7.16)
	β	463.72 (76.98)	65.69 (5.61)	184.97 (22.88)	948.18 (39.27)	30.55 (3.97)
	r^2	0.98	0.99	0.99	1.00	1.00

DISCUSSION AND CONCLUSION

Behrens (1970) pointed out that the application of appropriate methods to data from biological assays would greatly improve the value of the results obtained. The technique described in this study may be a useful tool in overcoming problems associated with comparing dose-response curves in bioassays and quantifying the toxicity of allelochemicals.

Quantifying allelopathic potential in terms of the use of a numerical index derived from a bioassay, rather than from a single index, is favored (Lehle and

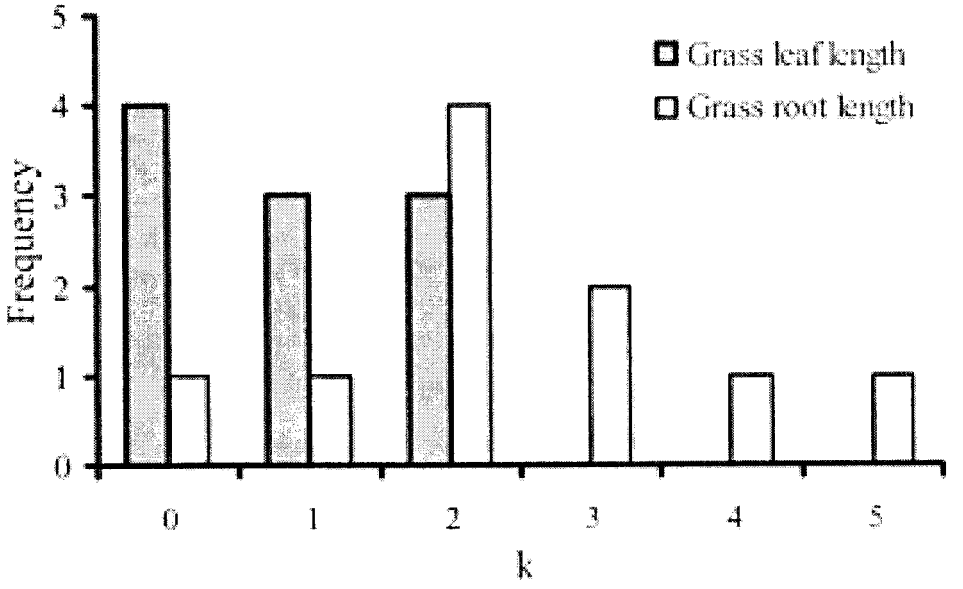

Figure 4. **Statistics in number of $ln(D+1)$ transformations of the data of Buta and Spaulding (1989).**

Table 3. The effect of two tall fescue leachates on mean D_0 and D_{50} of five grasses.

Leachates	Kentucky 31		Rebel	
	D_0	D_{50}	D_0	D_{50}
Grass leaf length	22.94	99.97	8.37	73.34
Grass root length	5.01	38.59	3.38	29.22

Putnam 1982). Our model permits the use of the data from a bioassay to estimate the dose of allelochemical or potentially allelopathic material such as plant extracts and leachates required for 0% (Do) and 50% (D_{50}) reduction to untreated controls. In the example of the effect of tall fescue leachates on grass seedling growth, D_0 and D_{50} of Kentucky 31 leachates on the grass leaf growth are much higher than that of Rebel leachates. This demonstrates that, as Buta and Spaulding (1989) concluded, Rebel leachates were more active in terms of effect on leaf growth. Considerably higher D_0 and D_{50} of Kentucky 31 leachates on root growth were also shown. These results might lead to a conclusion that the toxicity of Rebel leachate was higher than that of Kentucky leachate. In addition, our analysis of the data of Buta and Spaulding (1989) by application of the model indicates that the inhibitory and stimulatory activities of the two fescue leachates on grass root growth were much higher than that on leaf growth. Buta and Spaulding (1989) could not obtain this conclusion due to the use of a conventional method such as the Least Significant Difference.

The term of dose concentration used in the curve-fitting of the presented model is not restricted to a concentration of a single allelochemical. For example, the growth inhibitors leached from excised leaves of tall fescue grass (Butta and Spaulding 1989) were identified as at least three compounds: abscisic acid, caffeic acid, and ρ-coumaric acid. All of these compounds are allelochemicals (Rice 1984). The effect of the tall fescue leachates on the grass seedling growth tested derives from the combinations of these allelochemicals, together with other possible, unidentified, allelochemicals or nutrients. Thus, the dose concentration means the proportion of all substances or compounds involved in the tested solution.

Equation 6 is a simple nonlinear equation. After $g(D)$-transformation the regression can be conducted by the least squares method. A multilinear regression program can be used. This may, computationally, be much easier than any nonlinear regression because initial estimates of parameters in a nonlinear regression program are essential. This can cause a number of regression problems, such as lack of smoothness in the convergence of residual sum of squares (Lehle and Putnam 1982). It should be noted that k in Equation 6 is an integer and cannot be determined by a nonlinear regression technique, but we found it is the best to be determined by assessment of r^2 for individual regression. Figure 2 clearly has demonstrated the regression procedure, in which a program has been written based on the least squares method. In the program the comparisons of r^2 and standard error of each parameter estimated are conducted. It was found that, as k increases the r^2 is increased, reaching a peak at k = i, then decreasing from i+1 transformations, while the standard error decreases until reaching a minimum at i-transformations, then increasing from i+1 transformations. Therefore, it is straightforward to select the best regression for a certain set of experimental data. However, in the case of using an available linear regression program it should start from k = 0,1,2,.., then determining the k by manual comparison of the r^2 and/or standard error. This may be tedious when a large number of data sets are to be fitted. (The procedure of the linear

regression and k-value determination was written in Fortran 77L. The executable version can be obtained by writing to the senior author.)

For an empirical model, the number of parameters is of importance in obtaining a better fitting of the model with observed data (Liu and Scott 2001). Among the previous stimulation-inhibition models, parameters ranged from 5 in the log-logistic herbicide dose-response model (Brain and Cousens 1989) to 8 in the residue phototoxic model (An ***et al.*** 1996). To satisfy the assumptions implicit in the regression analysis, the more parameters the model has, the more observed data are required. In general, the number of observations must be greater than the number of parameters. In addition, a set of initial values of the parameters must be estimated at the start for running a nonlinear regression package (White 1997). These prerequisites heavily limit the application of the models. As a consequence, the direct-search method may be used as an alternative. In this method, parameters are often fitted by calculating many combinations of possible values and, finally, selecting the values for parameters that give a minimum residual sum of squares of the difference between the observations and the corresponding values of the model (An ***et al.*** 1993). Due to the nonflexibility of the models, the great divergence from the model predictions to observations is generally observed (An ***et al.*** 1993, 1996; Schabenberger ***et al.*** 1999; Sinkkonen 2001). The current model (Equation 6) has virtually three parameters, as the k-value is not involved in the linear regression. Because the multiple-linear regression is based on the Equation 4, the regression of the model to the best fit to the actual data is straightforward (Figure 2) and can be always performed as soon as the number of observations is reasonably large (a minimum of three required). However, if nontransformation ($k = 0$) is used, the quadratic equation (Equation 3) is less flexible than other models (An ***et al.*** 1993). Thus, in the case of nontransformation, or lack of significant stimulation, the other models, such as log-logistic function, may be used.

In conclusion, it is evident from the examples of the application that the model description of data from different sources agreed well. The biologically significant indices, such as maximum value for stimulation and specific doses for percentage of reduction are derived. The model was also reasonably appropriate for assessment of the sensitivity of the responses in bioassay. Three criteria, recommended by Lehle and Putnam (1982) for selecting an appropriate biological model, are: the form of the model should fit the raw biological observations closely; the form of the model should be biologically reasonable; and the model should not be restrained by assumptions. In this paper the model presented appears to provide a reasonable description of wide ranges of data. Apart from this, the estimations of the parameters of the model and, thereafter, of the indices, are computationally easy due to the model being based on a quadratic equation. This model is considerably flexible and can be useful in fitting a wide range of stimulation responses at low doses and inhibitions as increasing doses.

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