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Multi-dimensional sensitivity analysis and ecological implications of a nutrient uptake model

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Abstract

Mechanistic models of nutrient uptake are essential to the study of plant-soil interactions. In these models, uptake rates depend on the supply of the nutrient through the soil and the uptake capacity of the roots. The behaviour of the models is complex, although only six to ten parameters are used. Our goal was to demonstrate a comprehensive and efficient method of exploring a steady-state uptake model with variation in parameters across a range of values described in the literature. We employed two analytical techniques: the first a statistical analysis of variance, and the second a graphical representation of the simulated response surface. The quantitative statistical technique allows objective comparison of parameter and interaction sensitivity. The graphical technique uses a judicious arrangement of figures to present the shape of the response surface in five dimensions. We found that the most important parameters controlling uptake per unit length of root are the average dissolved nutrient concentration and the maximal rate of nutrient uptake. Root radius is influential if rates are expressed per unit root length; on a surface area basis, this parameter is less important. The next most important parameter is the effective diffusion coefficient, especially in the uptake of phosphorus. The interactions of parameters were extremely important and included three and four dimensional effects. For example, limitation by maximal nutrient influx rate is approached more rapidly with increasing nutrient solution concentration when the effective diffusion coefficient is high. We also note the ecological implications of the response surface. For example, in nutrient-limited conditions, the rate of uptake is best augmented by extending root length; when nutrients are plentiful increasing uptake kinetics will have greater effect.

Introduction

The responses of biological systems to environmental factors such as nutrient addition, climate, pollutants, and atmospheric chemistry concern agronomists and natural scientists alike. Plant responses depend strongly on interactions with below-ground processes; nutrient uptake is one of the most important of these linkages between plant and soil. Mechanistic models of nutrient uptake have been developed over the last three decades. Nye and Spiers (1964) constructed the first steady-state model of mass flow and diffusion of nutrients to a root surface. Further developments included Michaelis-Menten uptake kinetics and a non-steady-state condition (Barber and Cushman, 1981; Claassen and Barber, 1976; Cushman, 1979; Nye and Marriott, 1969; Yanai, 1994). Smethurst and Comerford (1993) modified the steady-state model to allow development of the depletion zone over time and included the effects of new root growth. These models are being applied in increasingly complex and comprehensive ecosystem simulators (Van Heerden and Yanai, 1995).

The predictions of these models are generally in good agreement with measured nutrient uptake (Rengel, 1993). Most of the model testing has been for P and K, nutrients that are supplied mainly by diffusion. Their uptake is relatively rapid compared with their rate of supply from soil; Dunham and Nye (1974) have shown experimentally and theoretically how a

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depletion zone develops in such a case around the root. Uptake models successfully capture these dynamics, showing that if uptake occurs rapidly enough to reduce the nutrient concentration at the root surface, then uptake rates will depend on the rate of supply of nutrient to the surface rather than on maximal plant uptake rates.

Although the models have few equations, the relationships among the parameters are not intuitively obvious. The complexity of the equations means that in many cases model response to parameter alteration can be predicted only by resorting to the full calculation. If nutrient uptake is to be incorporated into linked plant and soil models, then model sensitivity across the full range of all parameter values must be understood, and the most important interactions among the parameters must be identified (Gardner et al., 1981).

The main goal of this study is to find a way to efficiently and comprehensively examine a model of this type. An ordinary sensitivity analysis in one dimension reveals which variables matter the most at a single point in parameter space. For example, Kelly et al. (1992) examined the sensitivity of modelled P uptake in loblolly pine seedlings at a set of baseline parameter values, and showed that root length and average solution nutrient concentration were the most influential. However, it is important to understand model behaviour across a broad range of possible parameter values. The relative importance of parameters defined in a one-dimensional analysis can depend strongly on the values of the other parameters, even in a simple uptake model (Yanai, 1994).

We calculate nutrient uptake using a steady-state model (Nye and Tinker, 1977; Yanai, 1994), which assumes that solute diffusion and solute flow balance uptake. Such models are best suited for insertion into dynamic simulators because the mathematical solution is independent of previous conditions, allowing feedback between plant growth and soil conditions to be simulated. Our goal is to improve our understanding of the model by identifying parameter interactions through a detailed sensitivity analysis. Our analysis is relevant to all the nutrient uptake models described above, which have similar variables and basic equations.

Our first task is to describe the model we use and define the important parameters. We then determine the range of values reported in the literature for each of the parameters required in the model. This allows us to define the limits of our parameter space – in this case a 7-dimensional hypervolume. Initial sensitivity tests within this hypervolume are carried out to determine which are the controlling parameters that require investigation in terms of identifying interactions.

We follow two approaches to analyse interactions of the most important parameters of the model within the specified parameter space. Both rely on analysing model output for many combinations of the parameter values. We selected these combinations so that model behaviour in every part of the hypervolume was examined, though resolution was constrained to allow tractable analysis of the results. The first approach was a statistical analysis of variance (ANOVA), using modelled uptake as the dependent variable to allow systematic identification of interactions. This approach allows us to identify the important sources of model responses and the interactions between parameters.

The second approach is a graphical representation of the response surface, which plots the calculated uptake rate for each parameter combination in such a manner that modelled response to a variation in any parameter can easily be deduced by reference to an associated graphic. Interactions are revealed by inspection of the graphs; the direction and form of the interactions are more obvious than in the ANOVA.

The importance and interactions of the various factors controlling nutrient uptake have implications for the adaptations of plants to different environmental conditions, as have been reviewed by Chapin (1980). Our approach allows a more complete exploration of the parameter space than has hitherto been undertaken. It also allows interactions of more than two parameters to be identified and interpreted.

Model description

Nutrient uptake is calculated using a steady-state model of solute uptake that includes active uptake at the root surface and transport through soil by diffusion and solution flow (Nye and Tinker, 1977; Yanai, 1994). The parameters required by the calculation are listed in Table 1.

Solute uptake at the root surface depends on the concentration of solute at the root surface. This concentration will differ from the average concentration in solution, because of gradients created by solute uptake by the root and movement of solute by diffusion and solution flow. The concentration profile around the root can be described by assuming steady state flow. The concentration at the root surface (C_o; mmol m^{-3}) can

Table 1. Symbols and definitions used in the model

α	Root absorbing power (m s^{-1})
b	Soil buffer power (dimensionless): b=θ+ ρK_d, where θ= volumetric soil water content. ρ = soil bulk density (g m^{-3}),and K_d is the slope of the adsorption isotherm (m^3 g^{-1})
C_{av}	Average concentration of substance in the soil solution (mmol m^{-3})
C_o	Concentration of substance at the root surface (mmol m^{-3})
D	Effective diffusion coefficient of the solute through the soil (m^2 s^{-1}): $D = D_l \theta f/b$, where D_l = diffusion coefficient in water (m^2 s^{-1}), θ = volumetric soil water content, and f = impedance factor (dimensionless)
γ	r_o/Db (dimensionless)
$I_{\max}$	Maximal nutrient influx rate (mmol m^{-2} s^{-1})
K_m	Half saturation constant for uptake (mmol m^{-3})
L	Root length (m)
r_o	Root radius (m)
r_x	The mean half distance between root axes (m): $r_x = (V_s/\pi L)^{1/2}$, where V_s = soil volume (m^3)
U	Rate of uptake of solutes by roots in steady state depletion zones (mmol s^{-1})
U_L	Rate of uptake of solutes by roots per unit root length (mmol m^{-1} s^{-1})
v_o	Inward radial velocity of water at the root's surface (m s^{-1})

then be determined as a function of the average concentration in solution (C_{av}, mmol m^{-3}):

$$C_o = C_{av} v_o \left[\alpha + (v_o - \alpha)\left(\frac{2}{2-\gamma}\right)\frac{(r_x/r_o)^{2-\gamma} - 1}{(r_x/r_o)^2 - 1} \right]^{-1} \quad (1)$$

where α = root absorbing power (m s^{-1}), v_o = inward radial velocity of water at the root surface (m s^{-1}), r_x = average radial distance between roots (m), r_o = radius of the root (m), and $\gamma = r_o\, v_o/(Db)$ (dimensionless), where D = effective diffusion coefficient (m^2 s^{-1}) and b = buffer capacity of the soil, or the ratio of exchangeable to dissolved nutrient (dimensionless).

This expression for C_o uses a linear representation of nutrient uptake kinetics, which is appropriate only at low concentrations. To modify the model to allow saturation of ion transporters at high concentrations, we substitute Michaelis-Menten kinetics:

$$\alpha = I_{\max}/(K_m + C_o) \quad (2)$$

where $I_{\max}$ = maximum rate of uptake (mmol m^{-2} s^{-1}), and K_m = concentration at the root surface at half of $I_{\max}$ (mmol m^{-3}). Substitution of this expression for α in Equation 1 allows a quadratic solution to C_o.

When solute concentration at the root surface is obtained, the rate of solute uptake (U; mmol s^{-1}) can be calculated from the root surface area, $2\pi r_o L$, and the uptake kinetics.

$$U = 2\pi r_o L \alpha C_o \quad (3)$$

where L is root length (m). Equations 1 and 3 are presented by Baldwin et al. (1973) and Nye and Tinker (1977). Yanai (1994) gives a derivation of all the equations.

Because uptake is always directly proportional to root length, L (Eq. 3), and L appears nowhere else in the model equations, we know that there are no interactions of L with other parameters. Therefore, in this paper, we chose to consider uptake rate per unit of root length (U_L, mmol m^{-1} s^{-1}), eliminating L from the list of model parameters.

$$U_L = 2\pi r_o \alpha C_o \quad (4)$$

The effect of increasing root length on inter-root competition is included in the model by r_x, the inter-root distance. Although differences in L over time or between systems could be associated with differences in root density, the effect of r_x can be analysed independently of L in a sensitivity analysis of U_L.

We used a steady-state model because time invariant responses are easier to analyse than time series, and independence of initial conditions is guaranteed. One disadvantage of this choice is that we do not consider the effects of soil depletion over time. For example, increasing root length should give diminishing returns if uptake is already close to the rate of supply from soil (Rastetter and Shaver, 1992). Other limitations of the model are due to the simplicity of the single-root approach: the effects of spatial patterns in root and soil properties are not represented.

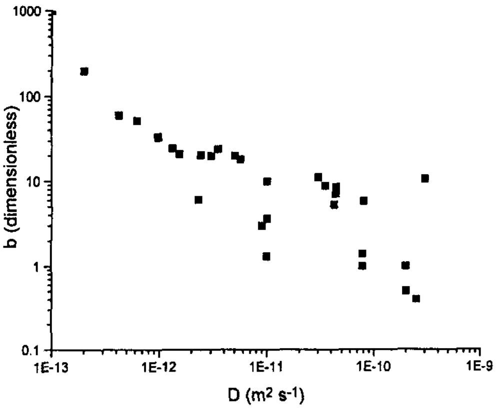

Figure 1. Reported values of the effective diffusion coefficient (*D*) are plotted against corresponding values of soil buffer power (*b*).

Sensitivity analysis

Parameter ranges

We defined parameter ranges within which to examine model behaviour based on a search of the literature. We examined whether *D* and *b*, the soil supply variables, were covariant (they were), and also the uptake kinetic parameters, $I_{\max}$ and K_m (they were not).

The summary of data is shown in Table 2. Measurements of root radii varied between 0.1 and 0.5 mm. We selected 0.4 mm as a representative maximum radius and 0.03 mm as a minimum, corresponding to a hyphal radius (Yanai et al., 1995). Average radial distance between roots (r_x) varied by an order of magnitude, between 2 mm and 30 mm. Initial tests showed little sensitivity of the steady-state model to this parameter, so it was held constant at 10 mm during the graphical analysis. The inward radial velocity of water at the root surface varied by several orders of magnitude in the studies surveyed. In our analyses v_o was varied between 1×10^{-11} and 1×10^{-7} m s^{-1}. The reported average solution nutrient concentration of various ions (C_{av}) also showed considerable variation. The selected range was between 1 and 1000 mmol m^{-3}. The values of the effective diffusion coefficient (*D*) and the soil buffer power (*b*) are linearly related when plotted on a log-log scale ($\log(b) = -6.4 - 0.6 \times \log(D)$; $r^2 = 0.73$, $p=1.5 \times 10^{-9}$; see Fig. 1). This relationship arises because *D* is usually calculated as $D_l \theta f / b$, where D_l= diffusion coefficient in water, θ = volumetric soil water content and f = impedance factor. The relationship of *D* and *b* means that the range of their product is smaller than the individual ranges of the two parameters. Thus, in further analysis, we can safely employ the product *Db* within the range 1×10^{-11} and 3×10^{-9} m^{-2} s^{-1}. The maximal nutrient influx rate varied widely in experimental studies. We selected a range of values between 1×10^{-6} and 1×10^{-4} mmol m^{-2} s^{-1}. The half-saturation of the Michaelis-Menten uptake equation has been found to vary over two orders of magnitude for different species and nutrients. We used a range of 1 to 100 mmol m^{-3} for K_m. However, initial tests showed that within the bounds set by the other parameter ranges, uptake was not very sensitive to variation in K_m. To simplify our analysis, we held this parameter constant at 20 mmol m^{-3} for the graphical analysis.

Statistical analysis

Of the original nine parameters, L was dropped, and *D* and *b* were merged. For the statistical analysis, the remaining seven variables were varied linearly at four levels across their range, giving 16,384 'observations' in the data set.

We used ANOVA to determine the sources of variance in the 16,384 calculations made by systematically varying the parameter values. This analysis treats each parameter as a class variable with four levels. In contrast, a regression analysis would make use of the numeric values of the parameters and would test for a specific form of relationship (e.g. linear) between the parameters and uptake rate.

The ANOVA makes no assumptions about the form of the relationship between the parameters and uptake rate. The form of relationship between the parameters, however, must be defined in testing for significant interactions between parameters. The uptake model is multiplicative in form ($U_L = 2\pi R_o \alpha C_o$; Eq. 4). It would not be surprising, therefore, to discover significant departures from additive effects of the various parameters. To test, instead, for departures from multiplicative behaviour, we log-transformed the dependent variable, U_L. (Recall that if $Y = A \times B$, $\log(Y) = \log(A) + \log(B)$; the ANOVA uses the latter structure.) These interactions are the reason for our multidimensional analysis of the uptake model: U_L cannot be predicted by simply multiplying factors associated with each of the input parameters. This fact is revealed by the significance of interaction terms in the ANOVA.

The analysis divides the ANOVA sum of squares between the parameters and their interaction terms. This allows us to rank them according to their influence on calculated uptake. The ANOVA included the seven main effects, 21 two-way interactions, 35 three-

Table 2. Literature values for the uptake model parameters

	Nutrient	Species	Value	Unit	Source
r_o Root radius	N/A	*Glycine max*	0.15	mm	Silberbush and Barber (1983)
		Lolium multiflorum	0.117		Rengel and Robinson (1990)
		Phalaris arundinacea	0.17		Barber and Cushman (1981)
		Pinus elliottii	0.27–0.44		Van Rees and Comerford (1990)
		Pinus taeda	0.35		Kelly et al. (1992)
		Robinia pseudoacacia	0.20		Gillespie and Pope (1990)
		Zea mays	0.50		Olsen et al. (1962)
		Zea mays	0.15		Barber and Ernani (1992)
		Zea mays	0.15		Seeling and Claasen (1990)
		Zea mays	0.19–0.22		Schenk and Barber (1979)
		Zea mays	0.14–0.21		Claassen and Barber (1976)
r_x Average radial distance of root influence		*Glycine max*	0.2	cm	Silberbush and Barber (1983)
		Lolium multiflorum	0.73–3.0		Rnegel and Robinson (1990)
		Pinus elliottii	0.62–2.6		Van Rees and Comerford (1990)
		Pinus taeda	2.0		Kelly et al. (1992)
		Robinia pseudoacacia	0.94		Gillespie and Pope (1990)
		Zea mays	0.14–0.264		Schenk and Barber (1979)
		Zea mays	0.15		Claassen and Barber (1976)
		Zea mays	0.33		Barber and Ernani (1992)
v_o Inward radial velocity of water at root surface			2×10^{-8}	$m\ s^{-1}$	Nye and Marriott (1969)
		Glycine max	5×10^{-9}		Silberbush and Barber (1983)
		Lolium multiflorum	$2.6–13.5 \times 10^{-9}$		Rengel and Robinson (1990)
		Pinus elliotti	$2.2–1.04 \times 10^{-8}$		van Rees and Comerford (1990)
		Pinus taeda	6×10^{-9}		Kelly et al. (1992)
		Robinia pseudoacacia	1×10^{-11}		Gillespie and Pope (1990)
		Zea mays	5×10^{-9}		Barber and Ernani (1992)
		Zea mays	2.2×10^{-8}		Claassen and Barber (1976)
C_{av} Average nutrient solution concentration	K		93–203	$mmol\ m^{-3}$	Van Rees and Comerford (1990)
	K		280		Silverbush and Barber (1983)
	Mg		500–2000		Rengel and Robinson (1990)
	NH_4		200		Barber and Cushman (1981)
	NO_3		2000		Barber and Cushman (1981)
	P		2–60		Gillespie and Pope (1990)
	P		21–126		Schenk and Barber (1979)
	P		15–150		Barber and Ernani (1992)
D Effective diffusion coefficient	K		5×10^{-12}	$m^2\ s^{-1}$	Sanders et al. (1970)
	K	*Glycine max*	3.4×10^{-12}		Silberbush and Barber (1983)
	K	*Pinus elliottii*	$0.2–1.0 \times 10^{-11}$		Van Rees and Comerford (1990)
	K	*Pinus taeda*	3×10^{-10}		Kelly et al. (1992)
	K	*Zea mays*	$0.2–7.8 \times 10^{-11}$		Claassen and Barber (1976)
	Mg	*Loliu multiflorum*	$1.3–2.9 \times 10^{-11}$		Rengel and Robinson (1990)
	Mg	*Pinus taeda*	1×10^{-11}		Kelly et al. (1992)
	N		2.5×10^{-10}		Sanders et al. (1970)
	NH_4	*Phalaris arundinacea*	1×10^{-11}		Barber and Cushman (1981)
	NO_3	*Phalaris arundinacea*	2×10^{-10}		Barber and Cushman (1981)
	P		1×10^{-13}		Sanders et al. (1970)
	P	*Pinus taeda*	8×10^{-11}		Kelly et al. (1992)
	P	*Zea mays*	2×10^{-13}		Barber and Ernani (1992)
	P	*Zea mays*	$0.4–8.9 \times 10^{-12}$		Schenk and Barber (1979)

Table 2. Continued

b Soil buffer power	K		20	(unitless)	Sanders et al. (1970)
	K	*Glycine max*	24.0		Silberbush and Barber (1983)
	K	*Pinus elliottii*	3.6–6.3		Van Rees and Comerford (1990)
	K	*Pinus taeda*	10.6		Kelly et al. (1992)
	K	*Zea mays*	1.4–20.5		Claassen and Barber (1976)
	Mg	*Pinus taeda*	1.3		Kelly et al. (1992)
	N		0.4		Sanders et al. (1970)
	NH_4	*Phalaris arundinacea*	10.0		Barber and Cushman (1981)
	NO_3	*Phalaris arundinacea*	0.5		Barber and Cushman (1981)
	P		1000		Sanders et al. (1970)
	P	*Pinus taeda*	5.8		Kelly et al. (1992)
	P	*Zea mays*	140–178		Olsen et al. (1962)
	P	*Zea mays*	3.0–60.1		Schenk and Barber (1979)
	P	*Zea mays*	200.0		Barber and Ernani (1992)
$I_{\max}$ Maximal nutrient influx rate	K	*Glycine max*	7.05×10^{-7}	$mmol\ m^{-2}\ s^{-1}$	Silberbush and Barber (1983)
	K	*Pinus elliottii*	3.61×10^{-5}		Van Rees and Comerford (1990)
	K	*Pinus taeda*	1×10^{-5}		Kelly et al. (1992)
	K	*Zea mays*	5×10^{-6}		Seeling and Classen (1990)
	K	*Zea mays*	$1.84\text{–}3.77 \times 10^{-4}$		Claassen and Barber (1976)
	Mg	*Lolium multiflorum*	$0.62\text{–}1.2 \times 10^{-6}$		Rengel and Robinson (1990)
	Mg	*Pinus taeda*	$0.19\text{–}1.29 \times 10^{-6}$		Kelly and Barber (1991)
	N	*Phalaris arundinacea*	4×10^{-5}		Barber and Cushman (1981)
	P	*Pinus taeda*	3×10^{-6}		Kelly et al. (1992)
	P	*Robinia pseudoacacia*	1.7×10^{-5}		Gillespie and Pope (1990)
	P	*Zea mays*	3.2×10^{-5}		Schenk and Barber (1979)
	P	*Zea mays*	6×10^{-6}		Barber and Ernani (1992)
K_m Half-saturation	K	*Glycine max*	10.3	$mmol\ m^3$	Silberbush and Barber (1983)
	K	*Pinus elliottii*	29.0		Van Rees and Comerford (1990)
	K	*Pinus taeda*	30.0		Kelly et al. (1992)
	K	*Zea mays*	16.7		Claassen and Barber (1976)
	K	*Zea mays*	70		Seeling and Claassen (1990)
	Mg	*Lolium multiflorum*	53–996		Rengel and Robinson (1990)
	Mg	*Pinus taeda*	8.6		Kelly and Barber (1991)
	N	*Phalaris arundinacea*	15		Barber and Cushman (1981)
	P	*Pinus taeda*	16.0		Kelly et al. (1992)
	P	*Robinia pseudoacacia*	1.8		Gillespie and Pope (1990)
	P	*Zea mays*	5.0		Barber and Ernani (1992)
	P	*Zea mays*	5.8		Sehenk and Barber (1979)

way interactions, and 35 four-way interactions (3990 degrees of freedom). Higher level interactions were not considered.

Graphical analysis

To simplify the graphical analysis, we ignore variation in r_x and K_m, as indicated above. We are left with five parameters of interest: root radius (r_o), inward radial water velocity (v_o), average solution nutrient concentration (C_{av}), the product of the effective diffusion coefficient and the soil buffer power (Db), and the maximal nutrient influx rate ($I_{\max}$).

To examine the interactions of these parameters in some detail, yet to allow clear analysis, we examined each parameter at five levels across its range, logarithmically from the listed low to high value. In the case of r_o, only 3 values were used, representing tree root, crop root and hyphal radii. This approach meant that the uptake model was run 1875 times in total – five

Table 3. Degrees of freedom, analysis of variance, sum of squares, mean squares and F-values from analysis of variance of log-transformed uptake per unit root length per day. Results of all main effect and two factor interactions are shown. Only the most significant 3-factor and 4-factor interactions are listed. In each listed case, $p < 0.0001$

Source	DF	ANOVA SS	Mean square	F-value	Source	DF	ANOVA SS	Mean square	F-value
C_{av}	3	54579.1	18193.0	6672421.5	$r_o \times v_o \times Db$	27	111.4	4.1	1513.1
$I_{\max}$	3	40933.7	13644.6	5004247.5	$v_o \times I_{\max} \times Db$	27	76.3	2.8	1036.2
r_o	3	13449.8	4483.3	1644268.4	$r_o \times C_{av} \times K_m$	27	55.5	2.1	754.0
Db	3	2843.0	947.7	347561.5	$v_o \times C_{av} \times Db$	27	43.0	1.6	584.6
K_m	3	747.6	249.2	91394.9	$r_o \times I_{\max} \times Db$	27	27.9	1.0	378.9
v_o	3	244.8	81.6	29930.8	$r_o \times I_{\max} \times C_{av}$	27	25.9	1.0	352.4
r_x	3	23.8	7.9	2906.9	$r_x \times v_o \times Db$	27	24.1	0.9	327.4
$C_{av} \times Db$	9	1936.1	215.1	78896.5	$v_o \times I_{\max} \times C_{av}$	27	20.3	0.8	275.1
$C_{av} \times K_m$	9	1332.9	148.1	54317.5	$r_o \times C_{av} \times Db$	27	15.4	0.6	209.9
$I_{\max} \times Db$	9	1180.4	131.2	48103.3	$I_{\max} \times K_m \times Db$	27	13.4	0.5	181.8
$I_{\max} \times C_{av}$	9	1069.3	118.8	43575.6	$r_x \times C_{av} \times K_m$	27	10.3	0.4	140.4
$v_o \times Db$	9	692.2	76.9	28209.0	$r_o \times v_o \times I_{\max}$	27	5.9	0.2	80.0
$K_m \times Db$	9	185.5	20.6	7559.7	$r_x \times I_{\max} \times C_{av}$	27	5.6	0.2	75.4
$I_{\max} \times K_m$	9	86.6	9.6	3528.2	$R_x \times C_{av} \times Db$	27	3.8	0.1	51.7
$r_o \times C_{av}$	9	78.9	8.8	3215.0	$r_x \times I_{\max} \times Db$	27	3.7	0.1	50.2
$r_o \times Db$	9	64.1	7.1	2614.0	$r_o \times r_x \times C_{av}$	27	2.5	0.1	33.6
$r_o \times I_{\max}$	9	45.6	5.1	1859.0	$r_o \times I_{\max}\, K_m$	27	2.0	0.1	27.1
$r_o \times v_o$	9	39.9	4.4	1624.0	$r_o \times r_x \times v_o$	27	1.7	0.1	22.7
$v_o \times I_{\max}$	9	25.2	2.8	1027.4	$r_x \times v_o \times I_{\max}$	27	1.3	0.0	17.5
$r_o \times K_m$	9	22.3	2.5	909.4	$r_o \times K_m \times Db$	27	1.1	0.0	14.8
$v_o \times C_{av}$	9	18.5	2.1	753.4	$r_o \times v_o \times C_{av}$	27	0.9	0.0	12.2
$r_x \times C_{av}$	9	17.9	2.0	729.8	$v_o \times I_{\max} \times C_{av} \times Db$	81	59.5	0.7	269.4
$R_x \times Db$	9	9.8	1.1	401.0	$I_{\max} \times C_{av} \times K_m \times Db$	81	45.6	0.6	206.6
$r_x \times v_o$	9	8.7	1.0	355.4	$r_o \times v_o \times I_{\max} \times Db$	81	17.9	0.2	81.0
$R_x \times I_{\max}$	9	8.5	0.9	347.8	$r_o \times I_{\max} \times C_{av} \times Db$	81	9.0	0.1	40.8
$r_x \times K_m$	9	3.9	0.4	160.5	$r_o \times C_{av} \times K_m \times Db$	81	8.7	0.1	39.4
$R_o \times r_x$	9	2.4	0.3	96.0	$r_o \times I_{\max} \times C_{av} \times K_m$	81	5.1	0.1	23.1
$v_o \times K_m$	9	0.4	0.0	14.6	$r_o \times r_x \times v_o \times Db$	81	4.5	0.1	20.4
$I_{\max} \times C_{av} \times Db$	27	587.7	21.8	7983.1	$r_o \times I_{\max} \times K_m \times Db$	81	4.5	0.1	20.3
$C_{av} \times K_m \times Db$	27	398.4	14.8	5412.0	$r_x \times v_o \times I_{\max} \times Db$	81	3.9	0.0	17.7
$I_{\max} \times C_{av} \times K_m$	27	260.8	9.7	3543.1	$r_o \times v_o \times I_{\max} \times C_{av}$	81	2.7	0.0	12.1

values for four parameters and three for root radii. We developed a simple graphical approach to display the results of each of the 1875 modelled uptake rates. This required the preparation of 75 graphs each containing 25 data points.

Each individual graph shows the results at a fixed r_o, Db and v_o. The y-axis shows the nutrient uptake rate in mmol m^{-1} root per day. The x-axis covers the range of C_{av} on a logarithmic scale, and on each graph there are five different lines, one for each level of $I_{\max}$. Thus each line shows the increase in uptake at a given $I_{\max}$, Db, v_o and r_o, with increasing solution nutrient concentration (C_{av}). Each group of 25 graphs shows the results for a fixed root radius; the graphs are so arranged that v_o increases from the top row to the bottom, and Db increases from the left-hand column to the right-hand, as indicated in the margins. The three sets of graphs should be compared to determine the difference in uptake sensitivity with differing root radii. The y-axis on the graphs have been scaled so that the ratio of the y-axis maximum to root surface area is constant. This means that the graphs can be directly compared, ignoring the y-axis scaling, to see how uptake by a similar surface area of roots of different radii varies.

Results

Part 1: Analysis of variance

The results of the analysis of variance for the 16,384 modelled uptake rates are summarised in Table 3. The table shows how much of the variation in modelled uptake rates can be explained by the main effects and two-, three- and four-way interactions of the parameters. It shows all seven parameters are highly significant individually; of the seven parameters the most important are average solution nutrient concentration (C_{av}) and maximal nutrient influx rate ($I_{\max}$). The remaining parameters are ranked in importance r_o, Db, K_m, v_o and r_x.

The most important two-factor interactions involve C_{av}, Db, K_m and $I_{\max}$. Another noteworthy two-factor interaction is that between v_o and Db. Only the most significant three- and four- factor interactions are shown in Table 3 (F-value > 10.0). The most significant three factor interaction is between $I_{\max}$, C_{av} and Db. The most significant four factor interaction is between v_o, $I_{\max}$, C_{av} and Db.

We recalculated the ANOVA with uptake rate expressed per unit root surface area, rather than per unit root length. The only change in the results was an alteration in the main effect of r_o; its mean square value fell to 39.4, and its F value to 14,441. So, although still highly significant, the relative importance of this main effect is much reduced. The results of the analysis of the interactions with r_o were not altered.

Part 2: Graphical trends

The three sets of graphs (Fig. 2) show the strong relationship of uptake rate to C_{av}, which increases along the x-axis of each graph. In general, uptake increases with C_{av}; this is a first-order or main effect that would be detected in an ordinary one-dimensional sensitivity analysis. However, the rate of increase in uptake with increasing C_{av} declines at high C_{av}, in accordance with the Michaelis-Menten saturation contained in the model. The reduction in the slope of uptake with C_{av} would be even more striking if the graphs were not log-scaled. This dependence of dU/dC_{av} on the value of C_{av} is one of the reasons to examine the overall shape of the response surface rather than relying on a sensitivity analysis at one point in parameter space.

Comparison of the five lines on each graph reveals that those with higher maximal nutrient influx rates ($I_{\max}$) show the strongest response to rising C_{av}. When $I_{\max}$ is low, uptake is near saturation, and increases in C_{av} have little impact on uptake. This effect of C_{av} on uptake is dependent on the value of $I_{\max}$; this is a two-parameter interaction.

Comparison of graphs in the same row shows the effect of changing Db (the product of the effective diffusion coefficient and the buffer power). At low Db, uptake is strongly reduced: uptake is limited by the rate of movement of nutrient to the root surface, rather than by the uptake of nutrient by the plant itself. The uptake system is far from saturation, and the characteristic Michaelis-Menten curves are not expressed. Parameter interactions can be identified; with decreasing Db, a higher C_{av} is required to saturate the uptake system. Full Michaelis-Menten dynamics are no longer evident. Another two-parameter interaction is that of $I_{\max}$ and Db; when supply limitations are minimised (high Db) then uptake is more responsive to increases in maximal uptake rate. $I_{\max}$, C_{av} and Db also interact strongly together: the $I_{\max}$ limitation to uptake is approached more rapidly with increasing C_{av} if the value of Db is high. This is the most significant three-parameter interaction as indicated by the ANOVA.

The effect of radial water velocity (v_o) is indicated by comparison of graphs in the same column. Although the effect of v_o over the range of values used in uptake models does not produce as much variation as the other parameters displayed in these graphs, it is clear that low v_o (the upper rows) can reduce uptake rates. Perhaps more importantly, the effect of v_o on uptake is strongest when Db is low – another two-parameter interaction. At low Db, the rate of delivery of solute to the root surface is more limiting than the plant uptake capacity; water movement contributes to this rate of delivery. The three-parameter interaction of $I_{\max}$, C_{av} and Db varies across the range of v_o; the interaction of v_o with these three parameters is the strongest four-parameter interaction identified by the ANOVA.

Comparing the three sets of graphs at different root radii (r_o), reveals that this interaction of low v_o and Db is most pronounced at high r_o (0.4 mm). This interaction of r_o, v_o and Db was among the strongest of the three-parameter interactions (ANOVA, Table 3).

Other four-parameter interactions can be discerned by inspection of the graphs. On the log-scale, Michaelis-Menten dynamics are represented by a sigmoid curve of uptake with C_{av} most obvious at high $I_{\max}$ and high Db. This is a three-parameter interaction, already discussed above. The additional effect of variation in root radius (r_o) is evidenced by comparison of the three pages of graphs. The sigmoid curve

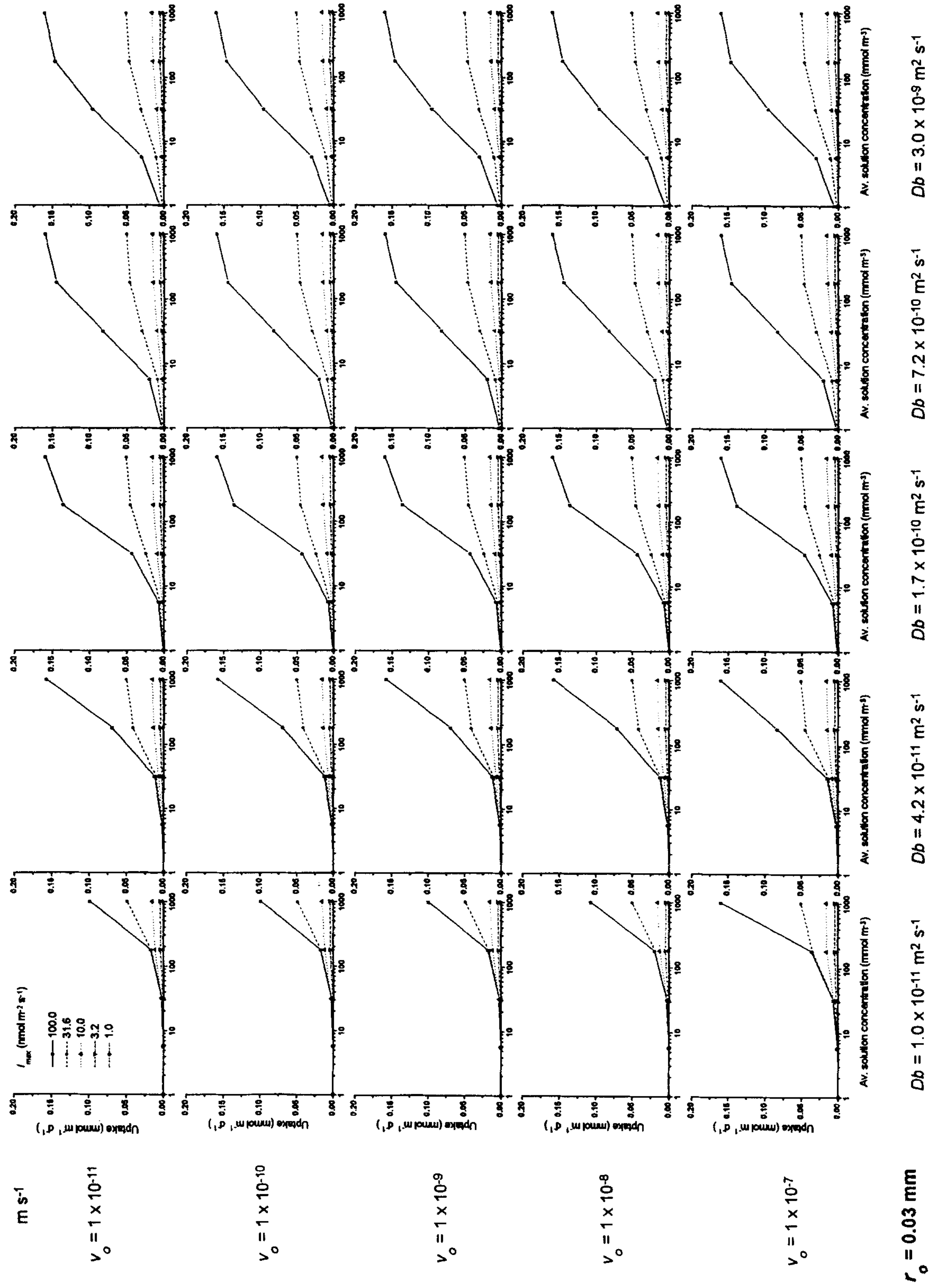

Figure 2. Response surfaces of the nutrient uptake model: root radius (r_o) = 0.03 mm (**a**), 0.15 mm (**b**) and 0.40 mm (**c**).

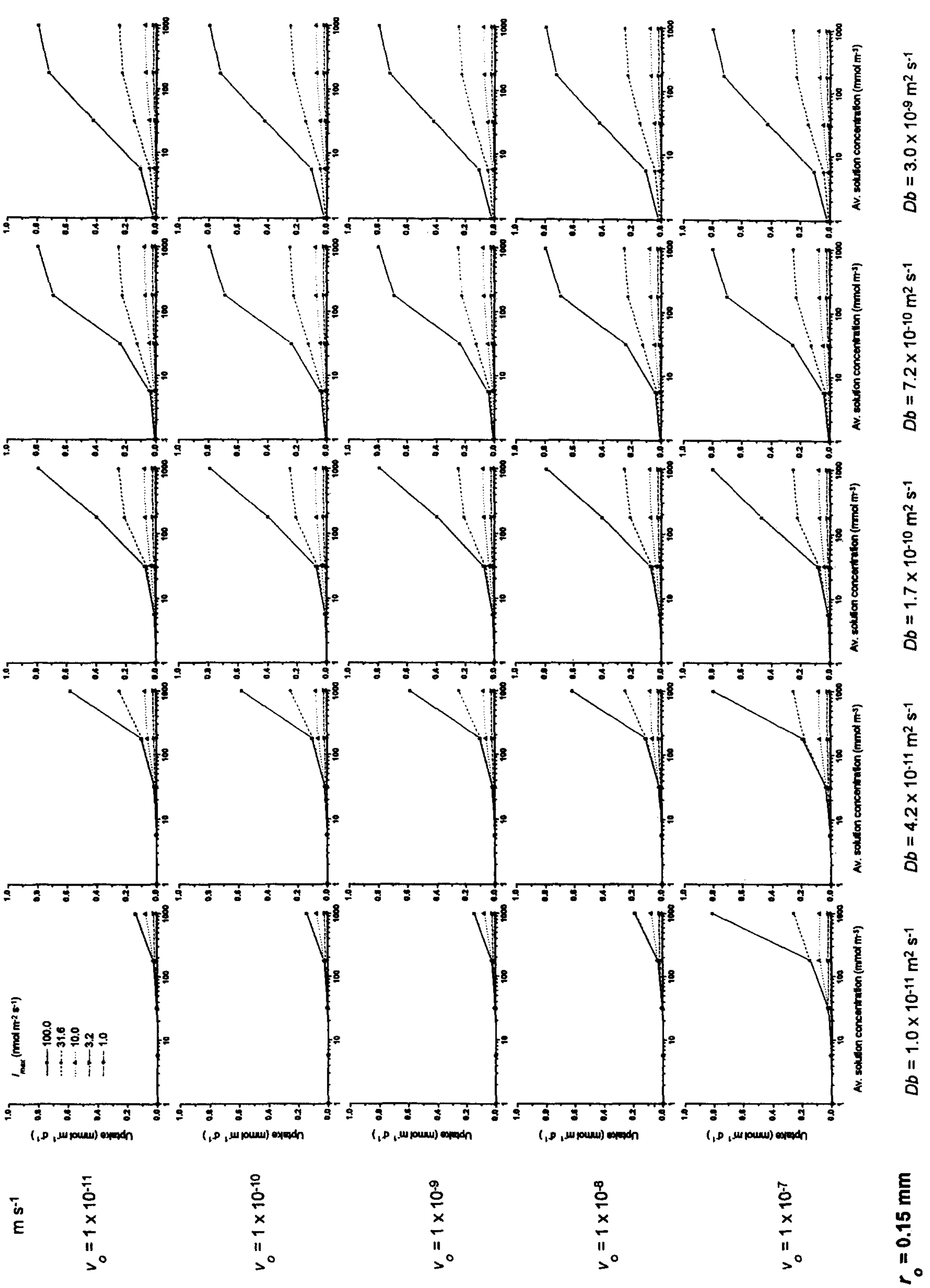

Figure 2b. Legend see page 319

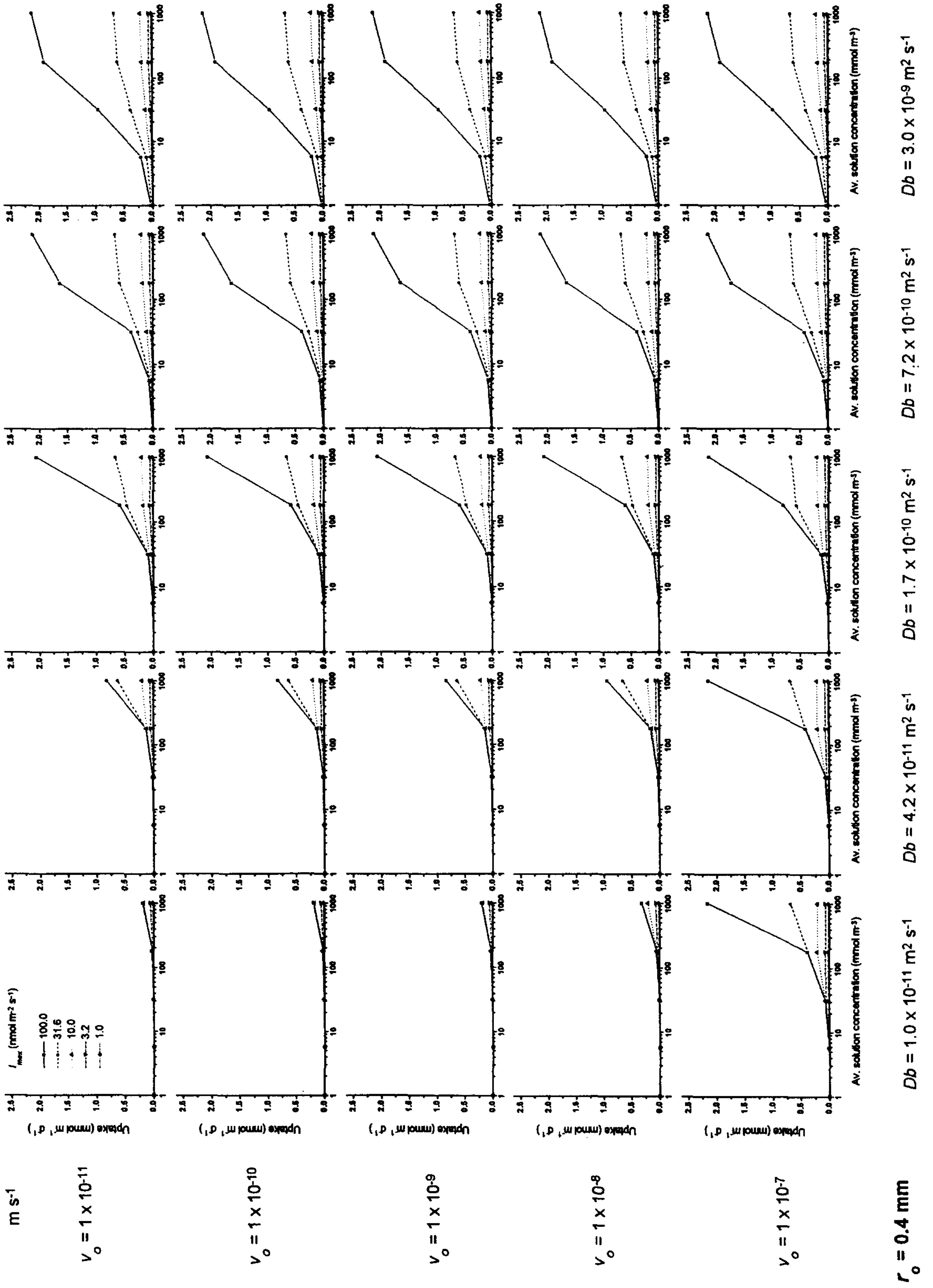

Figure 2c. Legend see page 319

representing Michaelis-Menten dynamics is still clearly visible at median Db when r_o is 0.03 mm, but not when radii are increased to 0.4 mm. The shape of each $I_{\max}$ curve indicates whether uptake kinetics or rate of soil supply is the limiting factor to nutrient uptake. The graphs indicate that the response of uptake to $I_{\max}$ and C_{av} varies with Db, across columns, and with r_o, between pages. This is a four-factor interaction, which is also identified by the ANOVA.

In comparing the three sets of graphs at different root radii, note that the scaling of the y-axis alters in proportion to root radius. Uptake rates increase significantly with increased r_o, but on a surface area basis (by which the y-axis scales are comparable) there is markedly less alteration. However, at slower Db and C_{av}, finer root systems do show a higher uptake on a per surface area basis. In other words, when $I_{\max}$ is not limiting, increasing r_o has a negative effect on uptake calculated on a surface area basis; uptake does increase with r_o, but not as much as surface area.

Discussion

Approaches to sensitivity analysis

We chose to explore model behaviour in multiple dimensions using two complementary approaches, the statistical and the visual. Statistical analysis of the variance in model output provided an objective measure of the importance of model parameters across the range of values selected, and the interactions of parameters with one another. It would have been difficult from visual inspection alone to determine which interactions were strongest. On the other hand, although the statistical analysis reveals the strength of the interactions, it is of little help in revealing the nature of the interactions. We did not use linear regression or any other quantitative model in testing sources of variation because we did not want to make any assumptions about the form of the main effects or the interactions, many of which we knew to be non-linear. The explanatory variables in the ANOVA, the parameters input to the model, were therefore treated as class variables (each had four levels), without reference to their values. As a result, the statistical analysis does not identify whether parameters contributed positively or negatively to variation in output, as would be the case in a linear regression. Instead, the nature of the effects is defined by the mean value of the output for each combination of parameter values. For our system, in the case of threeway interactions, with four levels of each parameter, there are 64 combinations, and therefore 64 means to be inspected. A graphical approach would be called for even if we wanted only to visualise the results of the ANOVA.

We tried various methods of graphing model output (uptake rate per unit root length), most of which are not presented here. We graphed the mean uptake produced by values of one parameter or a few parameters, averaging across all values of the other parameters, as suggested by the results of the ANOVA. These averages proved very difficult to interpret, in part because of non-linearity in the model: for example, the mean value of C_o, concentration at the root surface (an important intermediate calculation in the model), would not agree with the mean value of uptake rate. In general, in a non-linear model, the means of inputs do not produce the mean output, and therefore means do not illustrate model behaviour very well. A second problem was that graphing means did not allow us to chart the boundary of model behaviours such as the accumulation or depletion of solute at the root surface, which depend on the values of many parameters. Finally, graphs of means do not allow observation of interactions with the parameters not pictured.

The graphical method that we found most useful was not to average at all, but to view every point individually (Fig. 2). In this way, each value of model output can be associated with values of all the parameters that produced it. We tried methods of graphing surfaces, but ultimately found two-dimensional graphs to be the least confusing to read.

By including multiple lines on an x-y graph, we represent two dimensions in a graph: by arranging a series of such graphs in rows and columns, we represent two additional dimensions; the use of multiple pages gives a fifth dimension. This very detailed view of the response surface made it possible to identify high-level interactions that would have been difficult to discover or interpret in any other way. Although the five dimensions are conceptually equivalent and orthogonal, they are not equally easy to visualise using this method, and a variety of choices should be examined. It is easiest to detect interactions pictured within an x-y graph, and more difficult to observe interactions across lines, columns, or pages (pages should be printed on acetate and overlain).

Ecological implications

We can explain the interactions of soil and plant factors in controlling nutrient uptake by distinguishing whether the rate of nutrient uptake is more limited by the potential rate of delivery to the root, which depends on soil properties, or by the potential rate of uptake into the root, which depends on root physiology. When the rate of delivery of nutrient is less than the potential rate of uptake, a nutrient depletion zone develops around the root. In this case, the concentration of the nutrient at the root surface (C_o) is less than the average nutrient solution concentration (C_{av}). In contrast, when the potential rate of delivery by soil exceeds the ability of the root to take it up, nutrients accumulate at the root surface, and C_o is greater than C_{av}. In this case, the rate of uptake by the root (defined by $I_{\max}$ and K_m) is limiting the rate of uptake.

The interactions involving $I_{\max}$ and C_{av} describe the difference between supply limitation and uptake limitation. When $I_{\max}$ is low relative to C_{av}, uptake will be determined by $I_{\max}$, and will not be sensitive to the factors that influence the supply of nutrients by soil. On the other hand, when $I_{\max}$ is relatively high, uptake depends on the rate of supply by soil. Nutrient is delivered to the root through the soil by a combination of diffusion and mass flow. Diffusive transport depends on the effective diffusion coefficient (D) and buffer power (b). Mass flow depends on the radial velocity of water (v_o). Both diffusion and mass flow also depend on the average nutrient concentration in solution (C_{av}). These variables interact: if diffusion rates are high, the contribution of mass flow is less important to nutrient uptake than if diffusion is very slow.

We can use the graphical output to investigate specific ecological questions in terms of controls on nutrient uptake, using the information provided in Table 2. The literature values show that phosphorus tends to have low Db values, nitrate and ammonium generally occupy the middle of the range, while Db for potassium is highly variable. We can conclude that P uptake will most often be limited by the rate of diffusion. Uptake of P will be facilitated by rapid plant water uptake (high v_o). On a surface area basis, P uptake is most efficient at low r_o (i.e. hyphal radii), especially if v_o is low. For NO_3 and NH_4, there is less impact of v_o on uptake, because Db values are generally higher. Root radius (r_o) will still be influential, especially in the middle range of solution nutrient concentrations if $I_{\max}$ is high; smaller radii have a higher uptake per unit surface area in this part of parameter space.

The $I_{\max}$ values for P tend to be low, between 3.0 and 32.6 nmol m^{-2} s^{-1}. The average solution nutrient concentrations in the literature search for P are between 2 and 150 mmol m^{-3} (Table 2); solution concentrations in unmanaged systems can be even lower – between 0.1 and 2.0 mmol m^{-3} for forests (Kimmins et al., 1985; Yanai, 1991). Given that Db values for P are also generally low, we can see that in the region of parameter space occupied by P, uptake is relatively insensitive to $I_{\max}$. Thus investment in high P uptake capacity will generally give poor returns. In the case of NO_3 and NH_4, nutrient concentrations and soil characteristics (Db) are such that uptake is more sensitive to $I_{\max}$, and measured values of this parameter tend to be higher than those for P.

For plants evolving in low-nutrient environments, natural selection should tend to result in adaptations that optimize nutrient uptake under limiting environmental conditions (Chapin, 1980). The model parameters that describe plant properties ($I_{\max}$, r_o, v_o, L) have different importance to nutrient uptake rates under different soil conditions; plants benefit from augmentation of a particular parameter only under conditions in which uptake is sensitive to that parameter. For example, the analyses shows that maximal nutrient influx rate ($I_{\max}$) is a very important parameter, but also that $I_{\max}$ interacts strongly with C_{av}, such that increasing $I_{\max}$ at low C_{av} gives poor returns, as discussed above. Plants also affect the rate of mass flow of the soil solution (v_o), through transpiration. Nutrient uptake is sensitive to v_o only when diffusion rates are low. We could hypothesise that in such a situation, species with high transpiration rates should experience a nutritional advantage over their competitors, though this might not outweigh the cost of drought stress.

Root length and morphology (L and r_o) are directly under plant control: their effect on uptake should indicate whether it is more advantageous to the plant to invest in thickening roots or in lengthening them. Nutrient uptake is positively related to root surface area, so increasing root radius (r_o) increases nutrient uptake rates per unit length of root. This benefit is less when the rate of delivery of nutrient to the root zone is limiting, and more when the rate of transport into the root is limiting. However, even in the extreme case of root limitation, when uptake equals $I_{\max}$, the effect on uptake will only be proportional to the increase in surface area. The surface area gained for an increase in volume becomes smaller as the root grows thicker. In contrast, an investment in root length will always show a proportional increase in uptake (ignoring effects of root density, represented by r_x). This means that plants get a higher return in nutrient uptake per unit biomass by investing in long, fine root systems and mycorrhizae (Yanai et al., 1995).

An investment in longer root systems, rather than in higher maximal uptake rates, will tend to be more efficient, although the relative costing of such investments is unclear. An increment in root length requires an investment in carbon (i.e. root structure) and in machinery for nutrient uptake (i.e. a nitrogen requirement). An increase in $I_{\max}$ would not require such an investment in carbon. We could hypothesise that in conditions of abundant nutrients (e.g. fertilised plots), an investment of N to increase $I_{\max}$ should give strong returns in nutrient uptake, allowing carbon to be deployed towards aboveground productivity rather than root biomass. With a low C_{av}, any investment in improving $I_{\max}$ will give poor returns; nutrient uptake is best enhanced by increasing L, an investment requiring both carbon and nutrients.

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