



Testing a Convective-dispersive Model of Two-dimensional Root Growth and Proliferation in a Greenhouse Experiment with Maize Plants

V. R. REDDY† and Ya. A. PACHEPSKY*‡

†USDA-ARS, Alternate Crops and Systems Laboratory, Rm. 116, Bldg. 007, Beltsville, MD 20705, USA and

‡USDA-ARS, Hydrology and Remote Sensing Laboratory, Rm. 104, Bldg. 007, BARC-WEST, Beltsville, MD 20705, USA

Received: 30 October 2000 Returned for revision: 5 January 2001 Accepted: 12 February 2001 Published electronically: 5 April 2001

Soil water, solute, heat and gas transport processes are often simulated using convective-dispersive or diffusion-type equations. These models have to be coupled with a root activity model to simulate plant development. To make such coupling easier, a generic convective-dispersive model of root growth and proliferation is proposed. The submodels of root growth rate and root convective and dispersive propagation rates are built so that statistical hypothesis testing can be used to reject an hypothesis on dependence of the rates on root and soil variables. The objective of this work is to test this model using maize plants grown in pots whose walls and bottom mechanically restrict root growth. Treatments included supplying the normal and double the normal amount of fertilizer and water. Plant development was monitored by weekly destructive harvests until 45 d after emergence. Root concentrations were determined in 24 sections of the pots along with shoot parameters. The modular soil and root process simulator 2DSOIL was used to simulate root development. The model explained 73–77 % of variation in the value of the logarithm of the root concentration measured in the experiments. Statistical hypothesis testing led to rejection of the hypothesis that root diffusivity did not depend on root concentration. The hypotheses that there is no geotropic root development and that root growth rate decreases with the growth of root concentration could not be rejected.

Key words: Rootgrowth, modelling, finite element method, maize, greenhouse, convective-dispersive equation.

INTRODUCTION

Simulation of root growth and proliferation is an important part of plant and crop modelling. Strong dependence of simulated crop productivity and environmental quality parameters on the root activity model is widely recognized (Hanks, 1974; Klepper and Rickman, 1990).

Two main directions are developing in modelling root system growth and activity. One explicitly simulates proliferation and spatial distribution of root segments belonging to different root classes. Coordinates and size of each root form the set of root state variables. These models are referred to as 'developmental' (Rose, 1983) or 'architectural' (Pages *et al.*, 1989). Early efforts of a one-dimensional description of the root system architecture (Narda and Curry, 1981; Rose, 1983; Porter *et al.*, 1986; Grant, 1993) were followed by the development of two-dimensional (Shibusawa, 1992) and three-dimensional (Diggle, 1988; Pages *et al.*, 1989) models giving realistic images of root systems and providing tools to test hypotheses related to root development (Bengough *et al.*, 1992; Clausnitzer and Hopmans, 1994).

Another direction in root system simulations uses the continuum model of the root system assuming that (a) root mass or root length per unit of soil volume is a root state variable, and (b) that root state variables can be defined at

any point or for any volume within a soil, without considering the architecture of the root system. Continuum models of root systems include a formulation of a root proliferation submodel either in the form of differential equations of the diffusion-like propagation process (Page and Gerwitz, 1974; Hayhoe, 1981; Brugge and Thornley, 1985) or using root concentrations in soil cells of finite size (Chopart and Vauclin, 1990; Jones *et al.*, 1990; Marani *et al.*, 1992) or in the form of a given function of depth and time (Subbaiah and Rao, 1993).

Authors of continuum models have mainly used a one-dimensional representation of root systems with root concentrations or root segment distribution dependent on a single spatial variable representing depth. However, it was recognized that row crop simulators should include two-dimensional root models (Klepper and Rickman, 1990). The first two-dimensional simulator RHIZOS was for cotton (Bar-Yosef *et al.*, 1982) and was modified for use with soybean crops (Acock *et al.*, 1983).

Since root growth and activity are strongly affected by soil state variables, root activity simulations require a root activity model coupled with soil water, solute, heat and gas transport and soil impedance models (Whisler *et al.*, 1986; Clausnitzer and Hopmans, 1994). The recent process-based soil models are formulated as differential equations expressing conservation laws (Timlin *et al.*, 1996). The equations are solved using an arbitrary subdivision of a soil profile into cells. For compatibility purposes, it seemed to be useful to have a generic root growth and activity model formulated

* For correspondence. Fax 301-504-8931, e-mail ypachepsky@hydrolab.arsusda.gov

using differential equations. A generic convective-dispersive model of root growth and proliferation was proposed by Acock and Pachepsky (1996). Root proliferation was viewed as the result of a diffusion-like, gradient-driven propagation in all directions and convection-like downward propagation caused by geotropism. The finite element method was used to solve the boundary problem for the convective-diffusive equation. The model explained 92 % of the variation in the experimental data of Chen and Lieth (1993) on root growth of potted chrysanthemum cuttings when the following hypotheses were accepted: (1) root diffusivity (colonization of new soil) did not depend on root concentration; (2) there was no geotropic trend in root development; (3) potential root growth increased linearly with root concentration; (4) there were (at least) two classes of roots with different rates of growth and proliferation; and (5) potential root growth rate decreased with distance from the plant stem base. In the experiments used in this work, the root system of the chrysanthemum cuttings consisted of adventitious roots that did not reach the walls of the pots.

Further testing of the convective-dispersive model of root growth and proliferation, although in a controlled environment, had to include more features that could be encountered in field crops. We focused on two aspects of root growth that are present in crops and could be emulated in a controlled environment. First, the development of the primary (seed, seminal) roots precedes the development of adventitious roots in crops. Second, roots encounter dense and/or dry layers that prevent growth. Our objective was to test the model for the conditions in which the primary root would be allowed to grow and the roots would be restricted in their growth at some stage of plant development. Such conditions were expected to develop in experiments with potted maize plants as conducted in this work.

MATERIALS AND METHODS

Pots 24 cm high with an internal diameter of 12 cm were filled with a 'Jiffy mix' 1 : 1 mixture of Canadian Sphagnum peat moss and vermiculite, and amended with 1.7 g dolomite per litre of mixture. Two doses of 'Osmocote' 14-14-14 fertilizer were used to provide the standard (160 kg per 25 000 plants ha⁻¹) and double the standard amount of fertilizer used when growing maize in Maryland, USA. Drip irrigation was set to provide irrigation treatments equal to one- or two-times the rate of potential daily transpiration. The 'Early Sunglow' maize cultivar was used in the experiment. Two seeds were sown per pot on 1 Jul. 1996. Plants emerged on 5 July and were thinned to one plant per pot on 8 July. Weekly destructive sampling of plants began in the first week and ended in the seventh week after emergence. Three plants were sampled for each sampling time and each level of fertilization. The total number of plants grown was 42 (=two fertilizer applications × seven sampling times × three replications).

Shoot parts were separated from the root in each sampled plant. The above-ground part of the crown roots was included in the shoot. Plant height, leaf area, leaf weight and stem weight were recorded. Root concentrations were determined in 24 sections of each container. The sections

were formed by cutting the soil into six equal vertical layers and by cutting each layer into annuli using circular cuts of 30, 60, and 90 mm from the axis of symmetry. The gravimetric soil water content was measured along with the root mass.

The convective-diffusive model of root growth and proliferation

The root growth model (Acock and Pachepsky, 1996) assumes that a maximum of two classes of roots are present: young roots and mature roots. Root state variables are root mass concentration of young roots, Y , and root mass concentration of mature roots, M , both in kg dry matter m⁻³ of soil. Young roots can grow, proliferate, transform into mature roots and decay. Mature roots can decay.

A general equation for root proliferation flux is chosen in the form:

$$\vec{q} = -\nabla(DY) + \vec{g}Y \quad (1)$$

where \vec{q} is the vector flux of the young root material growing through a unit cross-section of soil (kg m⁻² d⁻¹), D is the root diffusivity coefficient (m² d⁻¹) and \vec{g} is the vector of convective root material transport related to geotropism. Diffusion is assumed to be isotropic and the vector g is directed downwards.

In axisymmetrical cases, eqn (1) can be rewritten as

$$q_x = -xD \frac{\partial Y}{\partial x}; \quad q_z = -D \frac{\partial Y}{\partial z} + gY \quad (2)$$

where x and z are the radial and the vertical coordinates, respectively. In the case of root growth in the vertical plane cross-section, eqn (1) becomes:

$$q_x = -D \frac{\partial Y}{\partial x}; \quad q_z = -D \frac{\partial Y}{\partial z} + gY \quad (3)$$

where x and z are horizontal and vertical coordinates, respectively.

The root mass conservation equation is:

$$\begin{aligned} \frac{\partial Y}{\partial t} &= \frac{1}{x} \frac{\partial}{\partial x} \left[xD \frac{\partial Y}{\partial x} \right] + \frac{\partial}{\partial z} \left[D \frac{\partial Y}{\partial z} - gY \right] + R - d_Y - T_{Y \rightarrow M} \\ \frac{\partial M}{\partial t} &= T_{Y \rightarrow M} - d_M \end{aligned} \quad (4)$$

for the axisymmetrical growth and

$$\begin{aligned} \frac{\partial Y}{\partial t} &= \frac{\partial}{\partial x} \left[D \frac{\partial Y}{\partial x} \right] + \frac{\partial}{\partial z} \left[D \frac{\partial Y}{\partial z} - gY \right] + R - d_Y - T_{Y \rightarrow M} \\ \frac{\partial M}{\partial t} &= T_{Y \rightarrow M} - d_M \end{aligned} \quad (5)$$

for growth in the vertical cross-section. Here R is the growth rate of young roots (kg m⁻³ soil d⁻¹), d_Y is the decay rate of young roots (kg m⁻³ soil d⁻¹), $T_{Y \rightarrow M}$ is the rate of transformation of young roots to mature roots (kg m⁻³ d⁻¹) and d_M is the decay rate of mature roots (kg dry matter m⁻³ soil d⁻¹). Values of R , d_Y , $T_{Y \rightarrow M}$, d_M , D and g are supposed to

reflect soil variables affecting root growth and can depend on root concentration. They are defined in separate submodels as discussed in the next section.

Boundary conditions for eqn (4) or eqn (5) are: zero flux of root material through the soil surface $z = 0$, an axis of symmetry, no horizontal flux of material at $x = 0$, and no material flux through boundaries $x = L_x$ and $z = -L_z$.

The modular soil and root process simulator 2DSOIL (Timlin *et al.*, 1996) was used to simulate root development with a root module developed from eqns (4) and (5). Numerical solution of eqns (4) and (5) has been done using the finite element method (available from the corresponding author). The simulated root growth rate was adjusted at each time step to make the simulated total root mass equal to the measured one. In particular, the growth rate R in eqn [5] had to obey the equation

$$\int_0^L \int_{-L_z}^0 R x dx dz = \frac{dW}{dt} \quad (6)$$

where $W(t)$ is observed dependence of total root mass on time and the integral on the left-hand side is equal to the simulated rate of the total root mass increase. For this purpose, we introduced a matching factor F equal to

$$F = \frac{\frac{dW}{dt}}{\int_0^{L_x} \int_{-L_z}^0 R_{\text{pot}} x dx dz} \quad (7)$$

and calculated actual growth rate (R) in each computational element as

$$R = FR_{\text{pot}} = R_{\text{pot}} \frac{\frac{dW}{dt}}{\int_0^{L_x} \int_{-L_z}^0 R_{\text{pot}} x dx dz} \quad (8)$$

Here R_{pot} is the potential rate of the local root growth defined in the root growth submodel as discussed below.

Submodels for the growth and proliferation rate parameters

The submodels for growth and proliferation rates express hypotheses about the dependencies of these rates on soil and plant state variables. Several pairs of contrasting hypotheses can be found in existing root growth and proliferation models that are based on the continuum representation (Acock and Pachepsky, 1996).

(a) Some authors believe that there exists a maximum root concentration, and growth ceases when root concentration approaches this maximum (Brugge, 1985; Chen and Lieth, 1993). Other authors assume that root concentration does not limit root growth (Hansen, 1975; Hillel and Talpaz, 1976; Hoogenboom and Huck, 1986).

(b) Whereas the local growth rate is a function of soil state variables in the majority of models, some models treat proliferation rate as a function of the same soil state variables (Bar-Yosef *et al.*, 1982; Hoogenboom *et al.*, 1988; Robertson *et al.*, 1993; Chen and Lieth, 1993) and others

regard this rate as a constant (Page and Gerwitz, 1974; Hansen, 1975; Brugge and Thornley, 1985).

(c) Local root growth rate is usually a function of existing root concentration; some authors base it on mature root concentration (Brugge and Thornley, 1985) others on young root concentration (Huck and Hillel, 1983) or on total root concentration (Acock *et al.*, 1983).

(d) The number of root categories with distinctly different parameters of growth and proliferation can be one (Huck and Hillel, 1983; Chopart and Vaclin, 1990), two (Bar-Yosef *et al.*, 1982; Brugge and Thornley, 1985), three (Ares and Singh, 1974; Marani *et al.*, 1992) or four (Johnson and Thornley, 1985).

(e) Some models include geotropism explicitly as a difference between vertical and horizontal proliferation rates (Hansen, 1975; Acock *et al.*, 1983). Other models are based on the assumption that the propagation of roots downward does not have a deterministic vertical component and may or may not occur depending on the state of soil in the upper part of the profile (Page and Gerwitz, 1974; Huck and Hillel, 1983; Chopart and Vaclin, 1990).

(f) Root proliferation is viewed either as a convective process driven by the local root concentration (Hillel and Talpaz, 1976; Marani *et al.*, 1992; Chen and Lieth, 1993) or as a diffusive process driven by the gradient of root concentration (Page and Gerwitz, 1974; Brugge and Thornley, 1985).

To choose between hypotheses in some of these pairs, we applied a method previously used by Shein and Pachepsky (1995) and Acock and Pachepsky (1996). Namely, we formulated a submodel expressing one of the hypotheses in each pair so that there was a single parameter that should equal zero if the hypothesis under test was correct. Therefore, if the estimated value of the parameter differs significantly from zero, the hypothesis should be rejected.

Since the soil state variables were expected to have values close to optimal, the dependencies of optimal growth and proliferation on root concentration could be studied. We tested the following hypotheses: (1) root diffusivity does not depend on root concentration; (2) there is no geotropic trend in root development; and (3) potential root growth increases linearly with root concentration.

Specifically, to test the hypothesis that root diffusivity does not depend on root concentration, we included in the model a dependence of diffusivity D on root concentration Y in the form:

$$D = D_0 \left[0.01 + \frac{0.99}{1 + \left(\frac{b_1}{Y}\right)^{b_2}} \right] \quad (9)$$

where D_0 is the potential diffusivity attainable at the maximum root concentration. Values of b_1 close to zero mean that there is no dependence of D on Y . Parameter b_2 regulates the shape of the dependence. It can be assumed that there is no dependence of diffusivity D on root concentration Y if the estimated value of the parameter b_2 is close to zero, and $D = 0.5D_0$ at any value of Y .

To test the hypothesis that there is no geotropic trend in root development, we assessed the significance of the difference between the estimated value of g in eqns (1)–(5) and zero. We limited this study with the assumption that there is only one class of roots.

To test the hypothesis that potential root growth R_{pot} does not decrease as root concentration increases, we used the equation:

$$R_{\text{pot}} = b_3 Y(1 - b_4 Y) \quad (10)$$

The relationship can be assumed to be linear if the value of b_4 does not differ significantly from zero. A value of the b_4 other than zero will cause R_{pot} to increase, plateau, then decrease as root concentration increases. Inspection of eqn (8) shows that the parameter b_3 is a multiplier both in the numerator and in the denominator. Therefore, the assumed value of b_3 does not influence the results of the simulations. In this work, the value of b_3 was arbitrarily set equal to 1 d^{-1} .

To estimate the average values and standard errors of the parameters, we used the Marquardt–Levenberg algorithm of non-linear optimization to find a minimum root mean square error (RMSE) of logarithms of the root concentration:

$$\text{RMSE} = \sqrt{\frac{\sum_{i=1}^K (\log n_i^c - \log \bar{n}_i^m)^2}{K}} \quad (11)$$

where n_i^c and \bar{n}_i^m are computed and average measured values of total root concentration $n = Y + M$, respectively and K is the total number of replicated root concentration observations. Using logarithms provided the minimization of relative rather than absolute errors of the model (Clapp and Hornbereger, 1978). This was important in working with root concentration data that varied within four orders of magnitude across a root system for a single plant.

Optimization was done with the version of the Marquardt–Levenberg algorithm published by Van Genuchten (1981). This version provided both estimates of the average parameter values and estimates of standard errors. To test the significance of the difference between the parameter value and zero we calculated t -statistics as a ratio of the estimated average to the estimated standard error. This ratio was compared with tabulated values of Student's distribution function $t_{N-P, 1-\alpha/2}$ at the significance level $\alpha = 0.05$ with the total number of observations, $N = 144$ (24 sections \times six sampling times).

If any of the parameters used for testing the hypotheses are not close to zero, there is still a chance that we will accept a wrong hypothesis. This may happen because we have fitted a poor model to the data and the deficiency of the model has distorted the result. To minimize this possibility, we fitted our model to the experimental data using all possible combinations of acceptance and rejection of the hypotheses discussed above. The total number of combinations was eight (2^3).

The goodness-of-fit criterion was used to test the hypothesis that the model error is significantly larger than the intrinsic variation in the data (Whitmore, 1991). The mean square lack-of-fit and the mean square pure error statistics have to be computed. The mean square pure error s_e^2 is known to be an unbiased estimator of the model's error (Pollard, 1977):

$$s_e^2 = \frac{\sum_{i=1}^K (n_i^c - \bar{n}_i^m)^2}{K-P} \quad (12)$$

Here P is the number of parameters. The mean square pure error s_e^2 characterizes the intrinsic variation in data:

$$s_e^2 = \frac{\sum_{i=1}^N \sum_j^{m_i} (n_{ij}^m - \bar{n}_i^m)^2}{N-K} \quad (13)$$

where N is the total number of all replications,

$$N = \sum_{i=1}^k m_i, m_i$$

is the number of replications in the i th observation, n_{ij}^m is the j th replication of the i th observation and, \bar{n}_i^m is the average i th observation. The ratio of the lack-of-fit mean square and the square of the mean square pure error, s_e^2 is the statistic for the error comparison. The model errors are significantly larger than intrinsic errors of measurements, if

$$\frac{s_r^2}{s_e^2} > F_{K-P, N-K} \quad (14)$$

where $F_{K-P, N-K}$ is Fisher's ratio. These values together with the significance level 0.05 were used below. Values of $K - P$ varied between 24 and 21 depending on which hypotheses were accepted in the simulations, and $N - K$ was equal to 72 (96-24). We calculated values of F with these degrees of freedom as described by Press *et al.* (1992, p. 222) using their subroutine *betai*. Critical values of $F_{24,72}$ at the 0.05 and 0.01 levels of significance were 1.84 and 2.22, respectively; changing the first degree of freedom to 21 led to values of $F_{21,72}$ equal to 1.88 and 2.29, respectively.

RESULTS

Data for shoot measurements and total root biomass dynamics are shown in Fig. 1. There were almost no differences in plant growth caused by differences in irrigation and fertilizer applications. Only the leaf area measurement showed lower values for the standard irrigation schedule compared with double the level of irrigation. Figure 1 also shows that the variation in whole-plant parameters was relatively low in replications. The maximum variation coefficients were 9, 12, 20, 28, 21 and 28 % in plant height, total number of leaves, leaf area, stem dry weight, leaf dry weight and root dry weight. Typical variation coefficients were about three-times less than the maximum values. The

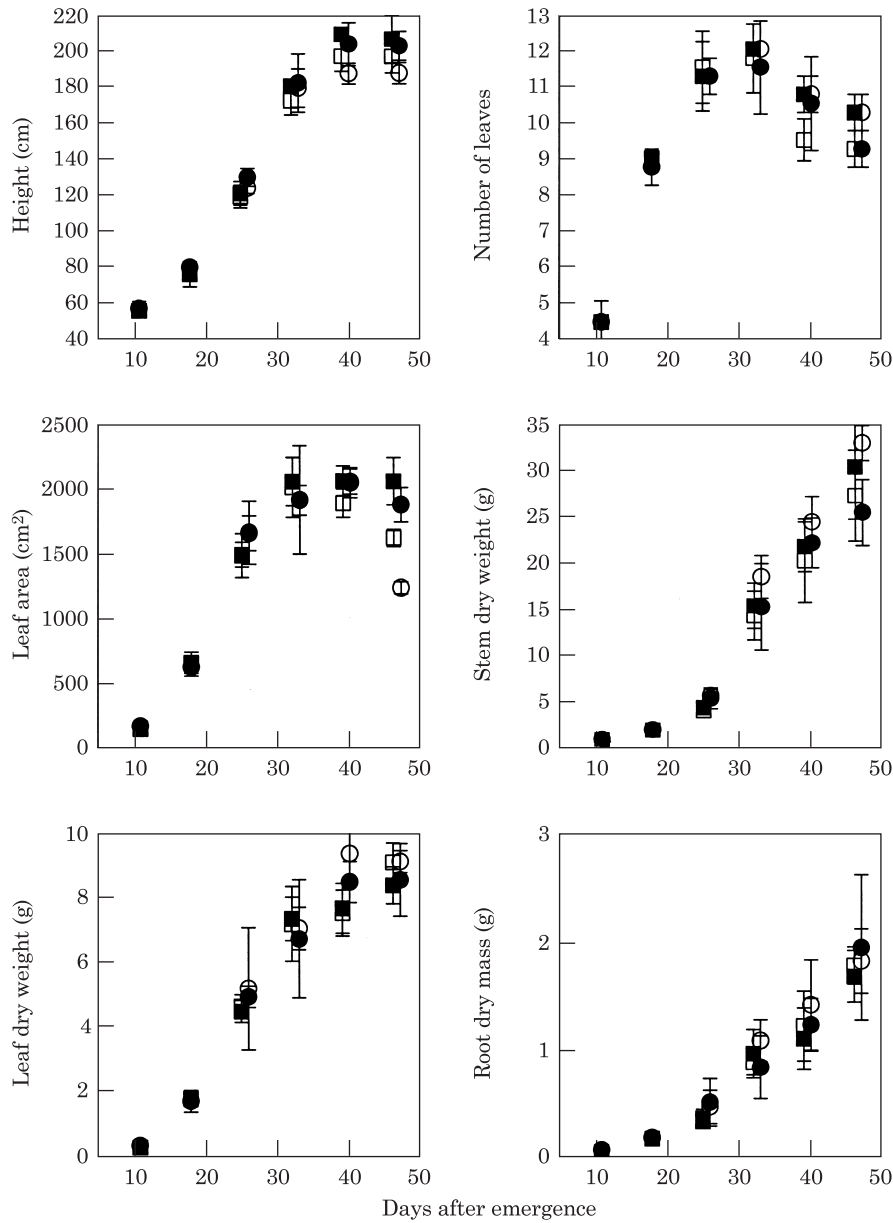


FIG. 1. Plant development in the experiment. ○, ● Standard fertilizer application; ■ □, doubled fertilizer application; ○, □ ordinary irrigation; ●, ■, doubled irrigation.

variability tended to decrease as plants developed. To use the dependence of the total root dry mass W on time in eqns (6)–(8), we fitted a parabola to the data. The resulting equation was $W = 0.0568 + 0.0175(t - 11) + 0.00081198(t - 11)^2$ where W is in g and t in days after emergence (DAE), $R^2 = 0.977$ for this equation.

An example of root development is shown in Fig. 2. Plants established strong seminal roots along the axes of symmetry in the pots early in their development. The nodal roots reached the pot boundaries in the top soil layers at the same time. The crown (brace) roots began to develop around 3 weeks after emergence. They accumulated in the soil close to the walls in the top layer. The rest of soil was

filled with roots in a gradual fashion. The pots' walls and bottoms served as impenetrable boundaries, and a substantial accumulation of root biomass was observed near these boundaries. The variability in root concentration per section was much higher than that in above-ground data. The median value of the variation coefficient was 50 %, and 10 % of the sections had variation coefficients of root concentrations greater than 150 %.

The introduction of a dependence of root diffusivity on root concentration [eqn (9)] led to estimated values of parameter b_1 that differed significantly from zero in any of the eight variants of the model accepting or rejecting the other two hypotheses. Figure 3 shows the effect of

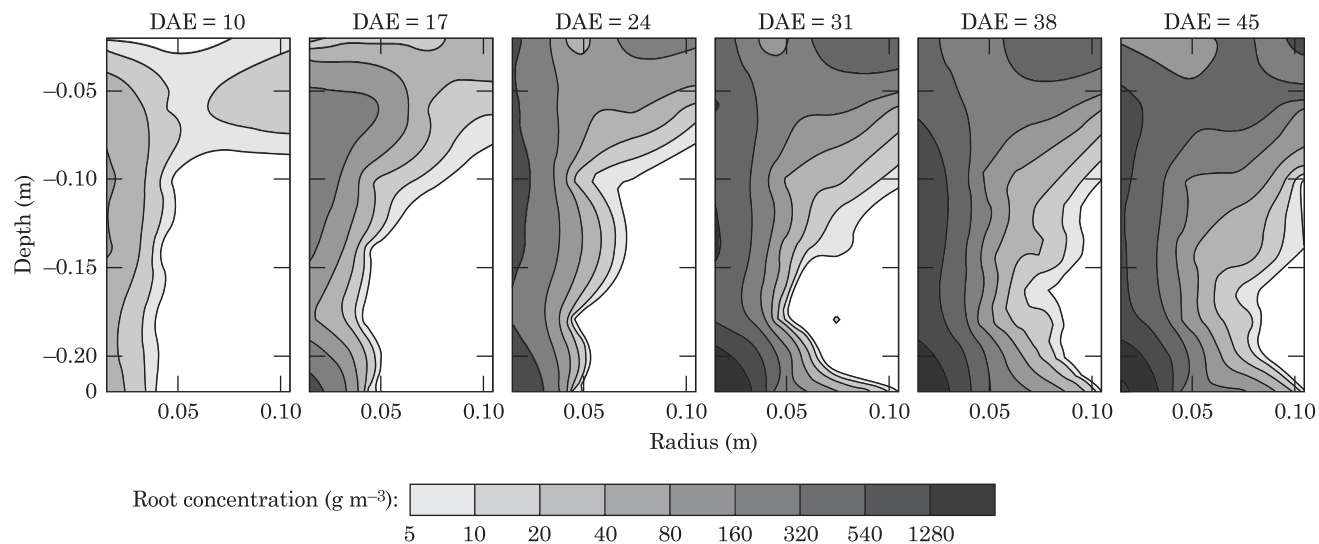


FIG. 2. Root system development in the experiment. Example of the ‘double fertilization-ordinary irrigation’ treatment. Contour plots obtained with the SURFER (Golden Software, Inc.) software version 7.

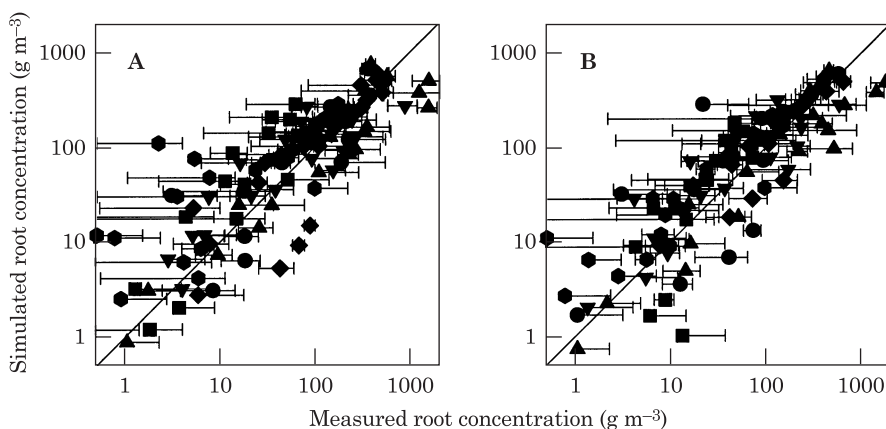


FIG. 3. Simulations of the root growth and proliferation as affected by the dependence of the root diffusivity coefficient on the root concentration simulation of root growth and proliferation; A, constant diffusivity; B, diffusivity grows linearly with root concentration.

introducing a linear increase in diffusivity with the increase in root concentration. The determination coefficient R^2 increased from 0.703 to 0.748, the root mean square error [eqn (11)] decreased from 0.456 to 0.391, and the mean relative error halved in the ‘double fertilizer, ordinary irrigation’ treatment depicted in Fig. 3. Other treatments showed similar improvements in fits (Table 1). Further inspection of these data showed that better results might be obtained if the rate of diffusivity increase per unit of root concentration was lower at low root densities and increased as the root concentration increased. The equation

$$D = D_0[n - 3.5(1 - \exp(-n/3.6))] \quad (15)$$

where n is the root concentration in g m^{-3} and $D_0 = 2.9 \times 10^{-8} \text{ m}^5 \text{ d}^{-1} \text{ g}^{-1}$ provided the best overall correspondence between measured and simulated root concentration distributions in terms of mean square relative error.

Estimates of the geotropic trend parameter g were close to zero and not significantly different from zero in any of

the eight variants of the model, accepting or rejecting the other two hypotheses. We could not find any decrease in potential growth rate related to increase in root concentration as projected by eqn (10). None of the estimated values of parameter b_4 differed significantly from zero in the eight variants of the model accepting or rejecting the other four hypotheses.

Figure 4 depicts the results of calculations made with root diffusivity dependence on root concentration according to eqn (15), with no geotropic trend parameter, and with no decrease in potential root growth related to the increase in root concentration. Each cell in this figure represents the physical sections of the containers that were formed by cutting the soil into equal vertical layers and by cutting each layer into annuli. The graphs within the cells show calculated and measured dependencies of root concentration (vertical axis) on time after planting (horizontal axis). The model correctly simulates trends in root development in most sections. The largest errors occur in the section on the

TABLE 1. Statistics of the performance of the model

Dependence of root diffusivity on root concentration	Statistics	Treatments			
		1F1W	1F2W	2F1W	2F2W
No dependence	R^2	0.687	0.711	0.703	0.691
	RMSE	0.482	0.440	0.456	0.460
Linear dependence	R^2	0.727	0.751	0.748	0.717
	RMSE	0.420	0.429	0.391	0.427
Non-linear dependence [eqn (15)]	R^2	0.775	0.763	0.762	0.781
	RMSE	0.401	0.370	0.385	0.405
	F -ratio, DAE = 17	0.280	0.330	0.175	0.219
	F -ratio, DAE = 24	0.541	0.291	0.146	0.664
	F -ratio, DAE = 31	0.760	1.003	0.941	0.880
	F -ratio, DAE = 38	0.429	0.398	0.200	0.250
	F -ratio, DAE = 45	0.883	0.337	0.253	0.411

Treatments involved use of normal (1F) and double the normal (2F) amounts of fertilizer and levels of irrigation equal to one-(1W) or two-(2W) times the rate of potential daily transpiration. DAE, Days after emergence.

bottom directly under the plant and in the section that is 8 cm deep and 3 cm from the axis (Fig. 4).

The above results were obtained using a cell size of 1 cm in the numerical solution of eqn (5). Two simulations were repeated with a cell size of 0.1 cm. Results did not differ substantially (data not shown).

Although errors were significant in some sections, the overall goodness-of-fit was satisfactory for the model, and the hypothesis that the error of the model is significantly larger than the intrinsic variation in data was rejected for all four experiments. The F -ratios computed with eqn (14) were all less than the critical values (Table 1). No dependence of F -ratios on time was observed, although the model appeared to perform better at the beginning and end of the simulated period (Table 1).

DISCUSSION

The convective-diffusive model of root growth and proliferation described reasonably well the experimental data on root growth of potted maize plants. The best R^2 value was 0.78 (Table 1)—smaller than the value of 0.92 that we obtained using experimental data on potted chrysanthemum plants. The root mean square error was about 0.4, which means that a 2.5-times error is typical. However, Fig. 3 shows that large relative errors are mainly associated with the low root concentration values. Points showing large root concentration values are generally located near the one-to-one line. One reason for this may be that large relative error is unavoidable when root concentrations are low because of the difficulties in extracting small roots. A high variability in root concentration data was observed in all treatments. This variability was the reason that the goodness-of-fit statistical criterion indicated that the model errors did not differ significantly from variability in the data, or that, in other words, the model was not less accurate than the data it was tested with.

The dependence of root diffusivity on root concentration was found necessary to improve performance of the model. The introduction of such a dependence is based on the idea

that fresh roots cannot colonize a new soil cell unless parent roots are present in an adjacent cell (Hillel and Talpaz, 1976; Huck and Hillel, 1983). This is a viable assumption when layers of finite thickness are considered, but if the layers become small enough, parent root formation and proliferation can be thought of as occurring simultaneously. We did not find such a dependence to be present when the experimental data for chrysanthemum cuttings were examined. Our conjecture was that the difference was related to the biomass distribution in the root systems of the two plants. Root systems of both maize and chrysanthemum are defined as fibrous. However, there is a greater difference in mass of roots of sequential orders in maize than in chrysanthemum. In maize, roots of the first order are much more massive than roots of following orders. We hypothesized that the larger the local root concentration, the more lower-order roots are present, and more root proliferation may be expected. Admittedly, the apparent smaller increase in values of D with root concentration at low densities may be related to the inability to find and collect very fine roots.

A geotropism factor was not needed to explain the experimental data. While many root activity models include geotropism, several successful models do not (Page and Gerwitz, 1974; Huck and Hillel, 1983; Chopart and Vauclin, 1990). It may be that, what appears to be geotropism in observations of root behaviour is actually hydrotropism, which is a dominant trend (Jaffe *et al.*, 1985). However, the experimental data we used are for maize growing adventitious roots, and results might be different for seedlings or plants with a distinct taproot. The limited size of pots could prevent geotropism being observed in this work. The technique of hypothesis testing proposed in this paper should be used to study this problem with other experimental data.

We used the observed dependence on time for the factor F introduced in eqn (7) to fit calculated total growth rate of the root mass to measured rates. A mechanistic shoot model has to be coupled with the proposed root model to ensure proper allocation of carbon to roots and to generate the correct pattern of dependence of W on t . Carbon allocation

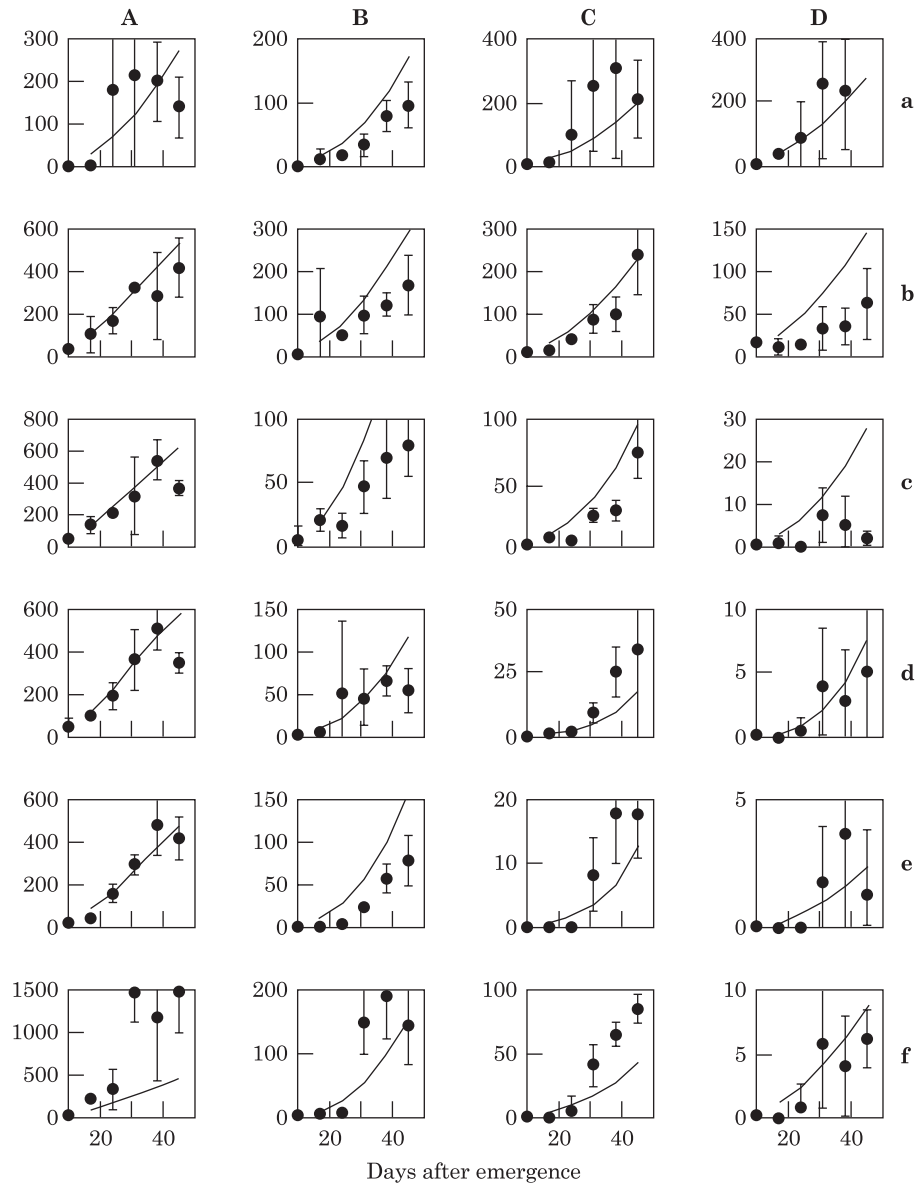


FIG. 4. Observed (symbols) and calculated (lines) dependencies of root concentrations (vertical axis) on time (horizontal axis) and on spatial coordinates. A–D, Soil in the 0–3, 3–6, 6–9 and 9–12 cm annuli, respectively, a–f, soil at depths 0–4, 4–8, 8–12, 12–16, 16–20 and 20–24 cm, respectively.

to roots was distributed between all computational cells in proportion to the root concentration present in each cell. Generally, this assumption worked well, although the root concentration near the lower impermeable border was underestimated. It is possible that the plant allocates additional resources to the parts of the root system that are able to support a tall and heavy plant. Plants grew more than 2 m tall in the experiment whereas the root system was confined to a 24 cm soil layer.

It should be noted that the model simulates the effect of restrictions by restraining root proliferation according to boundary conditions of eqn (5). As roots meet obstacles they begin to accumulate. Their concentration grows locally according to eqn (10) that is used in any location within the

soil. However, the increase in root concentration near an obstacle occurs not only because of local growth but also because new roots arrive from neighbouring cells. Therefore, accelerated root growth near pot walls compared with growth far from walls is expected and can be observed in both experimental data and simulations.

Functions given by eqns (9) and (10) are quite flexible in describing non-linear dependencies of root diffusivity and potential root growth on root concentration. Examples of dependencies described by these functions are given in Fig. 5. However, these functions should not be expected to give the best fit to actual dependencies. The role of these functions is to detect the presence of dependencies of D and R_{pot} on root concentration rather than to give the best fit.

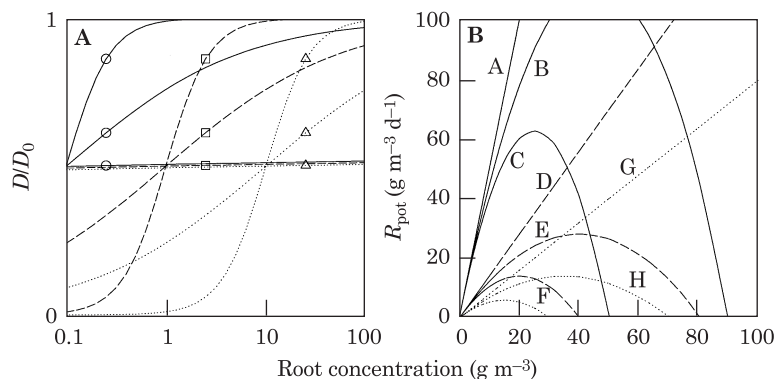


FIG. 5. Examples of dependencies of root diffusivity (A) and potential root growth rate (B) on root concentration as given by eqns (9) and (10) with various values of parameters: A, $b_2 = 0.01$ (—), 0.5 (---) and 2 (⋯); $b_1 = 1$ (○), 10 (□) and 100 (△) g m^{-3} . B, $b_3 = 5 \text{ d}^{-1}$ (A–C), 1.4 d^{-1} (D–F), 0.8 d^{-1} (G–I); $b_4 = 0$ (A), 0.020 (B), 0.011 (C), 0 (D), 0.025 (E), 0.013 (F), 0 (G), 0.033 (H) and 0.14 (I) $\text{m}^3 \text{ g}^{-1}$.

Figure 5A shows that the value of D remains constant when parameter b_2 is close to zero. If fitting the model to data shows that this parameter is not statistically different from zero, then a constant value of D is sufficient. On the other hand, if the fitted value of b_2 is different from zero, then there is a dependence of D on root concentration, and an equation better than eqn (9) is needed. In this work, eqn (15) was selected to describe this dependence. Similarly, Fig. 5B shows that potential root growth depends linearly on root concentration when parameter b_4 is close to zero. If fitting the model to data shows that this parameter is not statistically different from zero, then R_{pot} is proportional to root concentration, and the constant root growth rate per unit root mass R_{pot}/Y is sufficient. On the other hand, if the fitted value of b_4 is different from zero, there is a dependence of R_{pot}/Y on root concentration, and an equation better than eqn (10) should be sought. The value of b_4 was not significantly different from zero in this work, and therefore no modifications to eqn (9) were required.

The model [eqn (5)] permits the use of arbitrarily small computational cells. This seems to contradict the actual finite size and specific shape of plant roots. However, transport of water and solutes in soils also occurs in pores with a finite size and specific shape. Nevertheless, differential equations similar to the system [eqn (5)] are successfully used to simulate water and solute transport. The convective-dispersive equation showed its applicability to simulate root distributions with and without mechanical restrictions to root growth.

The absence of differences between treatments (Fig. 1) indicated that plants grew in optimal conditions at all times. The indices of the model performance were similar among the treatments (Table 1). The uniformly favourable conditions of soil temperature, water and nutrient content in the experiment of Chen and Lieth (1993) and in this work meant the data sets were ideal for testing hypotheses about effects of geotropism and root concentration. Gradients in soil environmental conditions could have swamped these subtle effects; instead, we were able to treat the model parameters as independent of soil state variables. They have to be functions of soil environmental variables to evaluate

the model with data on root response to temperature, water and nutrient distribution in soil.

CONCLUSIONS

The generic convective-dispersive model of root growth and proliferation explained 73–77% of the variation in the value of the logarithm of the root concentration measured in the experiments with maize plants grown in pots whose walls and bases provided mechanical restrictions to root growth. The goodness-of-fit statistical criterion indicated that the model errors did not differ significantly from variability in the data. The submodels of root growth rate and root convective and dispersive propagation rates were built so that statistical hypothesis testing could be used to reject an hypothesis on dependence of the rates on root and soil variables. We tested hypotheses that (a) root diffusivity did not depend on root concentration; (b) there is no geotropic trend in root development; and (c) root growth rate decreases with the growth of root concentration. Hypothesis (a) was rejected, but hypotheses (b) and (c) could not be rejected for plants that grew in optimal conditions at all times in our experiment. Thus approach can be used for two- and three-dimensional simulations of root growth in concert with soil water and nutrient transport that is described by similar transport equations.

© 2001 US Government

ACKNOWLEDGEMENTS

We appreciate the useful comments of Drs F. D. Whisler and J. Euphrath on an early version of this manuscript.

LITERATURE CITED

- Acock B, Pachepsky Y. 1996. Convective-diffusive model of two-dimensional root growth and proliferation. *Plant and Soil* **180**: 231–240.
- Acock B, Reddy VR, Whisler FD, Baker DN, McKinion JM, Hodges HF, Boote KJ. 1983. *The soybean crop simulator GLYCIM. Number 002 in series: Responses of vegetation to carbon dioxide*. Eashington, USA: Dept. of Energy and Dept. of Agriculture.

- Ares J, Singh JC. 1974. A model of the root biomass dynamics of a short grass prairie dominated by blue grama (*Bouteloua gracilis*). *Journal of Applied Ecology* 11: 727–743.
- Bar-Yosef B, Lambert JR, Baker DN. 1982. Rhizos: a simulation of root growth and soil processes, sensitivity analysis and validation for cotton. *Transactions of the ASAE* 25: 1268–1273, 1281.
- Bengough AG, Mackenzie CJ, Diggle AJ. 1992. Relations between root length densities and root intersections with horizontal and vertical planes using root growth modelling in 3-dimensions. *Plant and Soil* 145: 245–252.
- Brugge R. 1985. A mechanistic model of grass root growth and development dependent upon photosynthesis and nitrogen uptake. *Journal of Theoretical Biology* 116: 443–467.
- Brugge R, Thornley JHM. 1985. A growth model of root mass and vertical distribution, dependent on carbon substrate from photosynthesis and with non-limiting soil conditions. *Annals of Botany* 55: 563–577.
- Chen DX, Lieth JH. 1993. A two-dimensional, dynamic model for root growth distribution of potted plants. *Journal of the American Society for Horticultural Science* 118: 181–187.
- Chopart JL, Vauclin M. 1990. Water balance estimation model: field test and sensitivity analysis. *Soil Science Society of America Journal* 54: 1377–1384.
- Clapp RB, Hornberger GM. 1978. Empirical equations for some soil hydraulic properties. *Water Resources Research* 14(4): 601–604.
- Clausnitzer V, Hopmans JW. 1994. Simultaneous modeling of transient three-dimensional root growth and soil water flow. *Plant and Soil* 164: 299–314.
- Diggle AJ. 1988. ROOTMAP—a model in three-dimensional coordinates of the growth and structure of fibrous root systems. *Plant and Soil* 105: 169–178.
- Gerwitz A, Page ER. 1974. An empirical mathematical model to describe plant root systems. *Journal of Applied Ecology* 11: 773–781.
- Grant RF. 1993. Simulation model of soil compaction and root growth: I. Model structure. *Plant and Soil* 150: 1–14.
- Hanks RG. 1994. Model for predicting plant yield as influenced by water use. *Agronomy Journal* 66: 660–665.
- Hansen GK. 1975. A dynamic continuous simulation model of water state and transportation in the soil-plant-atmosphere system. I. The model and its sensitivity. *Acta Agriculturae Scandinavica* 25: 129–149.
- Hayhoe H. 1981. Analysis of a diffusion model for plant root growth and an application to plant soil-water uptake. *Soil Science* 131: 334–343.
- Hillel D, Talpaz H. 1976. Simulation of root growth and its effect on the pattern of soil water uptake by a nonuniform root system. *Soil Science* 121: 307–312.
- Hoogenboom G, Huck MG. 1986. *ROOTSIM V.4.0.—a dynamic simulation of root growth, water uptake, and biomass partitioning in a soil-plant-atmosphere continuum: Update and documentation*. Alabama: Alabama Agricultural Station, Agronomy and Soils Department, ser. 109.
- Hoogenboom G, Huck MG, Peterson CM. 1988. Predicting root growth and water uptake under different soil water regimes. *Agricultural Systems* 26: 263–290.
- Huck MG, Hillel D. 1983. A model of root growth and water uptake accounting for photosynthesis, respiration, transpiration and soil hydraulics. In: Hillel D, ed. *Advances in irrigation, Vol. 2*. New York: Academic Press, 273–333.
- Jaffe MJ, Takahashi H, Biro RL. 1985. A pea mutant for the study of hydrotropism in roots. *Science* 230: 5–447.
- Johnson IR, Thornley JHM. 1985. Dynamic model of the response of a vegetative grass crop to light, temperature and nitrogen. *Plant, Cell and Environment* 8: 485–499.
- Jones CA, Bland WL, Ritchie JT, Williams JR. 1990. Simulation of root growth. In: Ritchie JY, Hanks RJ, eds. *Modelling plant and soil systems*. Madison, USA: American Society of Agronomy, 91–123.
- Klepper B, Rickman RW. 1990. Modelling crop root growth and function. *Advances in Agronomy* 44: 113–132.
- Marani A, Cardon GE, Phene CJ. 1992. CALGOS, a version of GOSSYM adapted for irrigated cotton. I. Drip irrigation, soil water transport and root growth. Beltwide Cotton Conference Proceedings, 1992. 1352–1357.
- Narda KN, Curry RB. 1981. SOYROOT—A dynamic model of soybean root growth and water uptake. *Transactions of the ASAE* 24: 651–656.
- Page ER, Gerwitz A. 1974. Mathematical models based on diffusion equations, to describe root systems of isolated plants, row crops and swards. *Plant and Soil* 41: 243–254.
- Pages L, Jordan MO, Picard D. 1989. A simulation model of the three-dimensional architecture of the maize root system. *Plant and Soil* 119: 147–154.
- Pollard JT. 1977. *A handbook of numerical and statistical techniques with examples mainly from the life sciences*. Cambridge: Cambridge University Press.
- Porter JR, Klepper B, Belford RK. 1986. A model (WHTROOT) which synchronizes root growth and development with shoot development for winter wheat. *Plant and Soil* 92: 133–145.
- Press WH, Teukolsky SA, Vetterling WT, Flannery BP. 1992. *Numerical recipes in Fortran 77: The art of scientific computing*. Cambridge: Cambridge University Press.
- Robertson MJ, Fukai S, Hammer GL, Ludlow MM. 1993. Modeling root growth of grain sorghum using the CERES approach. *Field Crops Research* 33: 113–130.
- Rose DA. 1983. The description of the growth of root systems. *Plant and Soil* 75: 405–415.
- Shein EV, Pachepsky YA. 1995. Influence of root concentration on the critical soil water potential. *Plant and Soil* 171: 351–357.
- Shibusawa S. 1992. Hierarchical modelling of a branching root system based on L-system. *Acta Horticulturae* 319: 659–664.
- Subbaiah R, Rao KA. 1993. Root growth simulation model under specified environment. *Journal of Irrigation and Drainage Engineering* 119: 898–904.
- Timlin JD, Pachepsky YA, Acock B. 1996. A design for a modular generic soil simulator to interface with plant models. *Agronomy Journal* 88: 162–169.
- Van Genuchten MT. 1981. Non-equilibrium transport parameters from miscible displacement experiments. Research Report No. 119. Riverside, USA: US Salinity Laboratory, USDA-SEA-ARS.
- Whisler FD, Acock B, Baker DN. 1986. Crop simulation models in agronomic systems. *Advances in Agronomy* 40: 141–208.
- Whitmore AP. 1991. A method for assessing the goodness of computer simulation of soil processes. *Journal of Soil Science* 42: 289–299.