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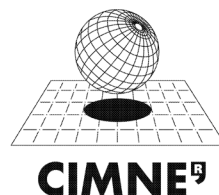
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CUMULATIVE NUTRIENT UPTAKE BY ROOTS OF CROPS AS SIMULATED BY FIXED AND MOVING BOUNDARY MODELS. CORRECTIONS AND IMPROVEMENTS

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Summary This work examines the relevance of physical models used to study the flux and nutrient uptake by roots of crops. The physical models studied are the one-dimensional fixed boundary model of Cushman-Barber [1] and an improved version of our one-dimensional moving boundary model [2]. The moving boundary model is solved by immobilizing the domain in dimensionless variables and computed by the finite elements method. To estimate the cumulative nutrient uptake a generalized and verified formula is used for both models. For simulations of nutrient uptake three datum sets extracted from literature were used. First, we compute the cumulative uptake of nutrient of low mobility as K and P by pine seedling in high soil concentrations. Second, we compute the K uptake by maize, wheat and sugar beet for low K soil and soil with K addition and finally we compute the P uptake by wheat to low concentrations. Third, we compute the P uptake for peanut for low, intermediate and high soil concentrations. For low concentrations, large variations of root density and low numbers of Peclet the moving boundary produces better predictions particularly for K. For P the moving boundary produces better predictions only at low concentrations being these predictions comparable to the obtained by 3D-dimensional architectural models [3]. Finally, in the light of these findings, conclusions drawn by previous papers [4] could be reinterpreted.

1 INTRODUCTION

Over the past four decades different mechanistic nutrient uptake models have been developed to simulate nutrient uptake.. Two categories of models have evolved: steady state and transient models. NUTRIENT UPTAKE [6] and NST 3.0 [7] are examples of a transient model with a numerical solution, while SSAND [8] and PCATS [9] are steady state models. The Barber-Cushman model [1] is a well-known and widely-used model in this category. The model treats the system as two concentric cylinders, where the inner is the root (with constant radius, and no extensions like branching, lateral roots, root hairs or mycorrhizal hypha), whose center is the spatial reference to the soil-root system, with radial orientation. The soil, (assumed homogeneous and isomorphic, with constant moisture content) forms an external

cylinder around the root, also with a constant radius. Movement of water and solutes in the soil system is radial to the root only, by mass-flow and diffusion, following Nye and Marriott 1969 [5]. Water flow, controlled by the transpiration demand (assumed constant with time), obeys the radial geometry of the system and mass conservation. Nutrient uptake rate is a function of concentration of the ion in question in the soil solution at the root surface, assuming that uptake occurs from a solution only, without interaction with other solutes. Updates to this basic feature include moving boundaries, the external radius (the available soil extent to each root) to account for root growth with time and consequent increase in root density [2]. NUTRIENT UPTAKE model and NST 3.0 are the personal computer version of the Barber-Cushman model. Further refinements of the Nye and Marriott derived models consisted to upscale from the root segment to the whole root system, and accounted for root growth. By using up scaling Roose et al. [10,11] provide a fully explicit ‘approximate’ analytical solution to the Nye–Tinker–Barber model and applied this solution to more complex root branching structure. Roose et al. showed that the method used to upscale may lead to substantial differences in the predicted uptake of nutrients between their models and NST 3.0 model. When applied to nutrients such as K and P, such models have generally proved quite efficient at predicting the acquisition over time scales of days or weeks for soils receiving high K or P inputs, but almost systematically failed in low input conditions [12,13]. Under such conditions, those models actually underestimate the observed uptake flux, which suggests that other processes than those accounted for by the models could be operating, and ultimately driving nutrient acquisition. However, a comparison of nutrient uptake predictions against experimentally measured values showed that the last version of three process-based models (NST 3.0, SSAND, and PCATS) largely underestimated P uptake for three woody plant species. This pattern showed that including mycorrhizal uptake in the simulations was not sufficient to predict accurately nutrient uptake under the low nutrient concentrations. These results suggested that rhizospheric effects, not yet taken into account in these models, could be carried out to improve their predictive ability. Further 3D root system architecture models were RootTyp, SimRoot, ROOTMAP, SPACSYS, R-SWMS, and RootBox [14] and they are being used to study how specific root traits affect the uptake of a variety of soil resources such as nitrogen, phosphorus, and water. From other point of view, heat and mass transfer with phase change problems such as evaporation, condensation, freezing, melting, sublimation, have wide application in separation processes, food technology, heat and mixture migration in soils and grounds, etc. This kind of problem are known in the literature as free or moving boundary problems depending if the interface is unknown or known a priori. A large bibliography and a review of explicit solutions on free and moving boundary problems for the heat-diffusion equation were given in [15]. The methodology of free and moving boundary problems have been also applied to agronomic problems. Thus, there are previous papers in this area for which the nutrient uptake has been implicitly modeled by moving boundary problems, for example, Abbes et al. [16], Huguenin and Kirk, [17]. Explicit one-dimensional moving boundary model applied to root growth and nutrient uptake was presented in Reginato et al.[2], Jonard et al.[18]. The goal of this paper is to consider an improved version of the moving boundary model applied to uptake of ions of low, medium and high availability by roots. In particular, we will revise and compare the uptake of ions through model NST 3.0, and the moving boundary model. For both models, we use a new generalized cumulative uptake formula and the moving boundary model is solved by the adaptive finite elements

method. Moreover, we also compare the cumulative uptake predicted by a more complex root branching system model with ones obtained by our moving boundary model.

2 THE MOVING BOUNDARY MODEL

This model is based on the same assumptions formulated by the Barber-Cushman model but, now, the model incorporates a new boundary condition for root competition (among roots of root system) which represents the net flux on the moving boundary $R(t)$. This moving boundary is given by the instantaneous half distance between roots axis which is the result of the root length variation. Thus, moving boundary $R(t)$ is a function of the instantaneous root length $\ell(t)$ which is a known function of time. A representation of the new condition can be visualised assuming a fixed volume of soil in which the root system is distributed like a homogenous piling up by roots, i.e., we propose an idealized total root system submerged in a fixed volume of soil (pots) instead of a single root in an infinite volume of soil. The conditions of humidity, light and temperature are assumed to be controlled (as in a growth chamber). Based on these assumptions and using root length density as a function of t , $R(t)$ (the moving boundary), the following set of equations and boundary conditions in cylindrical coordinates are used:

$$(\phi + b) \frac{\partial C}{\partial t} = \frac{\phi D}{r} \frac{\partial}{\partial r} \left(r \frac{\partial C}{\partial r} \right) + \frac{vs_o}{r} \frac{\partial C}{\partial r}, \quad s_o < r < R(t), \quad t > 0 \quad (1)$$

$$C(r, 0) = C_o(r), \quad s_o < r < R_o \quad (2)$$

$$D\phi \frac{\partial C(s_o, t)}{\partial r} + vC(s_o, t) = \frac{J_m [C(s_o, t) - C_u]_+}{K_m + [C(s_o, t) - C_u]_+}, \quad t > 0 \quad (3)$$

$$D\phi \frac{\partial C(R(t), t)}{\partial r} + \frac{vs_o}{R(t)} C(R(t), t) = 0, \quad t > 0 \quad (4)$$

where the moving boundary is given by:

$$R(t) = \sqrt{\frac{\ell_o}{\ell(t)} (R_o^2 - s_o^2) + s_o^2}, \quad t > 0 \quad (5)$$

where r is the radial distance from the axis of the root [cm]; t is the time [s]; b is the buffer power [dimensionless]; D is the diffusion coefficient in soil [$\text{cm}^2 \text{s}^{-1}$] ($= D_f f$, where D_f is the diffusion coefficient in free liquid and f is a tortuosity factor); s_o is the root radius [cm]; v is the effective velocity of flux solution [cm s^{-1}]; R_o is the initial half distance among root axis [cm]; J_m is the maximum influx [$\text{mol cm}^{-2} \text{s}^{-1}$]; K_m is the concentration for which the influx is $J_m/2$ [mol cm^{-3}]; C_u is the threshold concentration below which influx stops [mol cm^{-3}]; $R(t)$ is the half distance among roots axis [cm]; $C_o(r)$ is the initial concentration profile in $[s_o, R_o]$ [mol cm^{-3}] and $\ell(t)$ is the known root length as a function of time [cm] (the known law of root growth which can be linear, exponential or sigmoid; in the computed results we have used for some case the linear growth $\ell(t) = \ell_o + kt$ with units of k in [cm s^{-1}] and the exponential growth defined by $\ell(t) = \ell_o e^{kt}$ with units of k in [s^{-1}]. We denote x_+ as the part positive of x defined by $x_+ = \text{Max}(0; x)$. Equation (1) is the equation of diffusive and convective transport of ions in soil and condition (2) corresponds to the initial profile of

concentrations. Condition (4) represents a null flux on the moving limit of not-transference or instantaneous half mean distance between roots $R(t)$. We remark that the null flux condition imposed in this paper by equation (4) is a more realistic condition and a corrected version with respect to the similar one used in our previous model [2]. Condition (3) represents the mass balance on the root surface and the expression (5) represents the moving boundary $R(t)$ as a function of the instantaneous root length $\ell(t)$. Expression (5) for the moving boundary is an improved version of a similar condition used in our previous model and introduces minor error in the computational algorithm designed to solve the problem. Unlike the expression proposed for $R(t)$ in the previous version of our model which was based on considerations of constant volume of soil including roots (If the total volume of root plus soil remains constant then the amount of soil available to root will not be constant over time, i.e., the root grows at the expense of the decrease of the volume of soil), is now considered a constant volume of soil. The solution of problem (1) - (5) is obtained by the application of the adaptive finite element method (Schnepf et al. [19]) by using a dimensionless formulation through the following change of variable (similar to the one proposed by Roose, [10]), but now scaling the difference of coordinates $(r-s_0)$ by the difference of coordinates $(R(t)-s_0)$, i.e., transforming the variable interval $(s_0, R(t))$ in a fixed interval $(0, 1)$ for all $t > 0$:

$$C^*(r^*, t^*) = \frac{C(r, t)}{K_m}, \quad r^* = \frac{r - s_0}{R(t) - s_0}, \quad t^* = \frac{D\phi}{(\phi + b)R_0^2} t \quad (6)$$

Once the influx values on the root surface are obtained we estimate the cumulative nutrient uptake by our growing root system by the following generalized formula valid for any range of concentrations (Reginato and Tarzia, [20]):

$$\Delta U = U(t_f) - U(t_i) = 2\pi s_0 \int_{t_i}^{t_f} J(t) \ell(t) dt \quad (7)$$

where J is given in $\text{mol cm}^{-2} \text{s}^{-1}$, in cm and U in moles. The influx $J(t)$ is given by:

$$J(t) = J_m [C(s_0, t) - C_u] / [K_m + (C(s_0, t) - C_u)] \quad (8)$$

Moreover, and based in this generalized formula; we define a weight averaged influx which is consistent with the experimental William's formula [21]. This averaged influx is given by:

$$\bar{J} = \frac{\int_{t_i}^{t_f} J(t) \ell(t) dt}{\int_{t_i}^{t_f} \ell(t) dt} \quad (9)$$

where $\bar{J}$ is given in $\text{mol cm}^{-2} \text{s}^{-1}$. This weight averaged influx is more realistic because takes into account the temporal contribution of root length to the influx. In the case of constant influx $J(t) = J$, the averaged influx given by (9) coincides with the temporal averaged influx.

3 THE SIMULATIONS

For comparison of simulations of influx on root surface and cumulative uptake versus observed data we use six set of input data sets extracted from literature. From now on, we denote the simulations as:

FB-NST 3.0: Original fixed boundary model NST 3.0,

FB-NST 3.0*: Fixed boundary model NST 3.0 with generalized nutrient uptake formula (7), MB-FE: Moving boundary model solved by finite element method with generalized nutrient uptake formula (7).

First, we compute the influx on root surface of Cd by maize, sunflower, flax and spinach for two levels of concentration [3] and the results are shown in Table 1

Table 1. Observed and predicted Cd influx by different crops to different soil Cd concentrations.

Plant	Soil Conc. ($10^{-3} \mu\text{mol cm}^{-3}$)	Influx of Cd ($10^{-16} \text{ mol cm}^{-2} \text{ s}^{-1}$)					
		Observed	Pred. NST 3.0	Pred./ Obs.	Pred. MB- FE	Pred./ Obs.	Pred. Cum. Uptake MB-FE (μmol)
Maize	0.22	0.25	2.45	9.8	0.81	3.68	10.5
Sunflower	0.38	2.12	6.11	2.9	3.29	1.55	9.89
Flax	1.19	3.54	24.40	6.9	10.78	3.04	10.29
Spinach	0.48	7.55	12.00	1.6	9.78	1.29	4.72
Maize+	0.74	1.64	7.73	4.7	1.9	1.16	22.73
Sunflower+	1.80	5.56	25.90	4.7	10.2	1.83	32.42
Flax+	4.59	10.98	82.20	7.5	44.87	4.08	33.18
Spinach+	3.07	42.11	75.00	1.8	61.13	1.45	16.91

The influxes obtained by our MB-FE model are averaged by using the formula (9).

Second, we compute the influx on root surface and cumulative K uptake by maize, wheat and sugar beet for low K soil and soil with K addition [13] and the results are shown in Tables 2 and 3.

Table 2. Observed and predicted cumulative K uptake for maize, wheat, and sugar beet grown on a low K soil with (+K) and without (-K) fertilization using data extracted from literature (Samal et al., 2010 [13])

Cumulative Uptake (μmol)	Maize				Wheat				Sugar beet			
	-K	U_p/U_o	+K	U_p/U_o	-K	U_p/U_o	+K	U_p/U_o	-K	U_p/U_o	+K	U_p/U_o
Observed	678		1633		524		759		434		1035	
FB-NST 3.0	3180	4.7	2410	14.7	5410	10.3	7600	10.0	449	10.3	44900	43.4
FB-NST 3.0*	1421	2.1	1844	11.3	2657	5.1	7412	9.8	317	7.3	30968	30
MB-FE	380	0.56	1563	0.95	443	0.84	1769	2.3	464	1.1	1809	1.7
R.L.D	0.9→22 (21 days)				0.4→27 (26 days)				0.1→18 (26 days)			

Table 3. Observed and predicted root K influx on root surface for maize, wheat, and sugar beet grown on a low K soil with (+K) and without (-K) fertilization using data extracted from literature (Samal et al., 2010 [13])

Influx on root surface ($10^{-7} \mu\text{mol cm}^{-1} \text{ s}^{-1}$)	Maize				Wheat				Sugar beet			
	-K	J_p/J_o	+K	J_p/J_o	-K	J_p/J_o	+K	J_p/J_o	-K	J_p/J_o	+K	J_p/J_o
Observed	1.99		3.87		2.39		3.22		8.45		19.0	
FB-NST 3.0	1.27	0.64	4.33	1.12	1.77	0.68	3.9	1.21	2.64	0.31	15.1	0.8
MB-FE	1.67	0.84	2.48	0.64	1.52	0.58	8.28	2.6	2.7	0.31	7.1	0.38

Third, we compute the influx on root surface and cumulative P uptake by peanut for low, intermediate and high soil concentrations [22] and the results are shown in Tables 4 and 5.

Table 4. Observed and predicted cumulative P uptake by peanut without root hairs at different soil levels using data extracted from literature (Singh et al., 2003 [22]).

Cumulative Uptake (μmol)	Peanut									
	0 P	U_p/U_o	+50 P	U_p/U_o	+100 P	U_p/U_o	+200 P	U_p/U_o	+400 P	U_p/U_o
Observed	540		640		900		1060		1320	
FB-NTS 3.0	1180	2.2	6230	9.7	18000	20	39900	37.6	44500	33.5
FB-NTS 3.0*	708.4	1.3	3704	5.8	11856	13	39922	37.6	43841	33.2
MB-FE	468.8	0.9	2211	3.4	5395	6	13338	12.6	42169	32
R.L.D.(72 days)	0.9→85		0.9→100		0.9→100		1→107		0.8→75	

Table 5. Average predicted/observed ratio for influx of P by peanut on root surface and cumulative uptake obtained by NST 3.0, NST 3.0* and MB-FE using data extracted from literature (Singh et al., 2003 [22]).

Influx on root surface ($10^{-8} \mu\text{mol cm}^{-1} \text{s}^{-1}$)	Peanut									
	0 P	J_p/J_o	+50 P	J_p/J_o	+100 P	J_p/J_o	+200 P	J_p/J_o	+400 P	J_p/J_o
Observed	3.44		3.59		5.15		6.13		10.11	
FB-NTS 3.0	0.29	0.08	1.33	0.37	3.65	0.7	7.5	1.2	10.9	1.08
MB-FE	1.15	0.33	4.53	1.26	10.83	2.1	25.75	4.2	105.3	10.4

Finally, in order to verify the reliability of our moving boundary model and a 3D-dimensional architectural model we compute the P uptake by wheat to low concentrations [3] and the results are shown in Figures 1, 2 and 3.

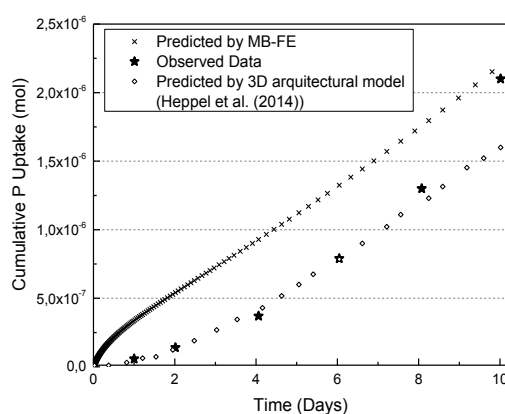


Figure 1. Observed, MB-FE and Heppel predicted values for the cumulative uptake of P by wheat seedlings over a 10 days period when grown in and low-P soils.

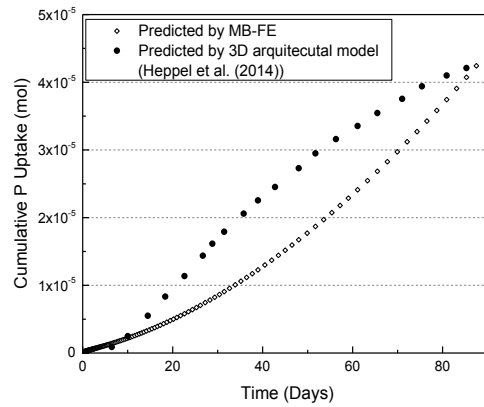


Figure 2. Predicted cumulative plant P acquisition by the MB-FE and the Heppel et al. model with an exponential branching distribution over a 90 days period when grown in and low-P soils.

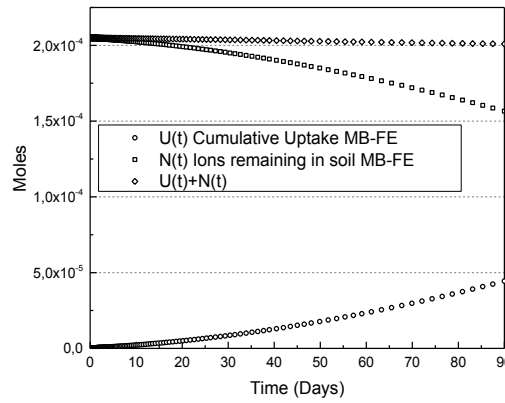


Figure 3. Mass balance for the cumulative P uptake and the P ions remaining in soil with data of Heppel obtained by the moving boundary model.

4 RESULTS AND DISCUSSION

From Table 1, we conclude that MB-FE model predicts the average influx on root surface better than the FB-NST 3.0 always for different plants for two levels of concentrations. From Table 2, we conclude that for ions as K the MB-FE model is the best numerical method to compute the cumulative K uptake on a low K soil with K addition and without K addition for all cases. From Table 3, we conclude that in almost all cases, FB-NST 3.0 produces better predicted influxes except for maize without K addition. From Table 4 for low and increasing level of P concentration the fixed (original NST 3.0 and NST3.0*) and moving MB-FE models over predicting always except in the soil without P addition (low concentrations). In this last case, MB-FE under predict with an acceptable error. From Table 5, we conclude that to low concentrations both models FB-NST 3.0 (with temporal average influx) and MB-FE (with weight average influx) under predict the average influx. For increasing level of P addition both models over predict the average influx. From Figure 1, we conclude that our MB-FE model predict better the final cumulative P uptake at 10 days. Although cumulative uptake predicted by the 3D model best fit to the experimental data we remark that this setting is obtained by choosing the best branching mode that fits to the experimental curve. Thus, the

The reason for which the MB-FE model is better than the other schemes (FB-NST 3.0 and FB-NST 3.0*) is that these last methods do not satisfy the mass balance among the ions taken by root and the ions remaining in soil. The ions remaining in soil were calculated by the following expression:

$$N(t) = 2\pi(1+b)\ell(t)\int_{s_0}^{R(t)} rC(r,t)dr \quad (10)$$

The mass balance for the program NTS 3.0 is not considered here because, obviously, to compute the ions remaining in soil, the operation must be done with concentration profiles as a function of time which has been calculated in fixed domain, but this result must be compared with the cumulative uptake by a growing root, i.e., which has been calculated by integration in a variable. Figure 3 show the mass balance for the results obtained by the finite elements method. The calculus was done with data extracted from [3] for the P uptake by wheat to low concentration. The obtained improvements by our model are mainly due to three factors: a) the use of a generalized formula for the cumulative nutrient uptake, b) the influxes obtained by the moving boundary model and the cumulative uptake, which are obtained through integration in a variable domain, while for the fixed boundary model the influxes are obtained in a fixed domain and the cumulative uptake by integration is on a variable domain, c) the use of a numerical method (finite element method) that ensures the balance of mass among the absorbed ions and the remaining ions in soil while the finite difference method does not satisfy it. Finally, in the light of these findings, conclusions drawn by previous papers [4] could be reinterpreted and our model could be included in larger field/catchment/climate scale models something which is not practically possible with the 3D numerical simulations due to their high computational burden.

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