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DIVISION S-2—NOTES

MODELING NUTRIENT UPTAKE USING A MOVING BOUNDARY APPROACH: COMPARISON WITH THE BARBER-CUSHMAN MODEL

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Abstract

Single nutrient uptake by a growing root system is often estimated by the Barber-Cushman model. The model solves the coupled equations of transport in the soil and absorption of nutrient by roots in fixed domains. This study was conducted to determine whether a moving boundary model that accounts for increasing root competition could improve predictions of nutrient uptake. Our model includes assumptions of the Barber-Cushman model and the moving boundary approximation. The model predicts nutrient uptake by coupling nutrient flux to roots and nutrient absorption on a variable domain in time. The model output was compared with measured uptake of Mg, K, P, and S by various crops and soils using experimental data obtained from the literature. Predicted Mg, K, and P uptake by pine seedlings was close to that observed for K and P, although for Mg the predicted uptake showed deviations similar to those of the Barber-Cushman model. Sulfur uptake by wheat in different soils was better predicted by the moving boundary model in at least 10 out of 18 measured cases. The model prediction was also compared with measured K uptake by three maize hybrids grown on typic Hapludult of Río Cuarto, Argentina, in a growth chamber. The moving boundary model appears to provide a better description of coupling between transport, absorption of nutrient, and root growth than the Barber-Cushman model, and it improves the prediction for nutrient uptake in some tests.

NUTRIENT UPTAKE has been evaluated through diffusive and mass flow models that are based on numerical approximation in fixed domains of differential transport equations in soils, coupled with absorption kinetics by roots (Cushman, 1979; Barber, 1995). These models estimate the nutrient concentration at the root-soil interface as well as the resulting nutrient uptake.

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Other models assume the root surface behaves like a zero-sink, whereby nutrient uptake is determined by the rate of nutrient supply to the root surface by mass flow and diffusion. In these models, the radius of finite cylindrical soil volume assigned to each root declines with increasing root density (Hoffland, 1990). In other models, analytical solutions (Nye and Tinker, 1977) were used for calculating the volume of the soil allocated to each root and the concentration at root surface, including a depletion zone that increased with time until it reached the non-transfer boundary (Smethurst, 1993). Recently, we have formulated free boundary models for root growth (Reginato et al., 1990, 1991, 1993a); i.e., analytical models through which it is possible to compute nutrient concentration at the root-soil interface and root growth rate (a priori an unknown function of time). This fact allows us to postulate a new model of nutrient uptake achieved through the transport and absorption of ions from a more dynamic point of view. This new model differs from our previous ones as the root growth rate is now plugged in as known function of time, just as in the Barber-Cushman model. Thus, the goal of the present work is to evaluate a moving boundary model for nutrient uptake that takes into account an increasing competition among roots for nutrient uptake from the soil by a growing root system that combines ion transport, absorption kinetics, and root growth simultaneously.

A one-dimensional model is considered here: i.e., a single cylindrical root in a soil where it is assumed that the conditions of moisture, light, and temperature are controlled (as in a growth chamber). With these assumptions, the following model of one-dimensional nutrient uptake through a moving boundary problem to one phase (the soil) (Crank, 1984; Tarzia, 1988) in cylindrical coordinates is proposed:

$$D \frac{\partial^2 C}{\partial r^2} + D(1 + \epsilon_0) \frac{1}{r} \frac{\partial C}{\partial r} = \frac{\partial C}{\partial t} \quad s_0 < r < R(t) \quad 0 < t < T \quad [1a]$$

$$C(r, 0) = \varphi(r) \quad s_0 \leq r \leq R_0 \quad [1b]$$

$$-Db \frac{\partial}{\partial r} C(R(t), t) + v_0 C(R(t), t) = 0 \quad 0 < t < T \quad [1c]$$

$$Db \frac{\partial}{\partial r} C(s_0, t) + v_0 C(s_0, t) = \frac{k_a [C(s_0, t) - C_u]}{1 + \frac{k_a [C(s_0, t) - C_u]}{J_m}} \quad 0 < t < T \quad [1d]$$

$$R(t) = R_0 \sqrt{\frac{l_0}{l(t)}} \quad 0 < t < T \quad [1e]$$

where r is the radial distance from the root axis (m), t is the time (s); T is the maximum time for which the system has solution (s); C_u is the concentration for which the net influx is null (mol cm^{-1}); v_0 is the mean effective velocity of soil solution at root surface [m s^{-1}]; b is the buffer power, D is the effective diffusion coefficient [$\text{m}^2 \text{s}^{-1}$], $k_a (= J_m/K_m)$ is the absorption power of nutrient [m s^{-1}]; J_m is the maximum influx at infinite concentrations [$\text{mol m}^{-2} \text{s}^{-1}$]; K_m is the concentration at which influx is $J_m/2$ [mol m^{-3}]; $R(t)$ is the variable half distance between root axes at time t (m), $\varphi(r)$ is the initial concentration defined in $[s_0, R(t)]$ (mol cm^{-1}), R_0 is the initial half distance between root axes (m), s_0 is the root radius (m), $l(t)$ is the root length as a function of time (m), and l_0 is the initial root length (m). The parameter ε_0 is given by $\varepsilon_0 = \frac{v_0 s_0}{Db}$ [dimensionless]. In our model, all coefficients are assumed to be constant. Equation [1a] represents the ion transport equation in the soil. Condition [1b] corresponds to the initial concentration, and Condition [1c] is the boundary condition representing null flux on the moving boundary $R(t)$ that is a priori a known function of time. Condition [1d] represents the mass balance at the root surface where the ions arriving are incorporated through absorption kinetics. Equation [1e] gives us the moving $R(t)$ as a function of the instantaneous root length $l(t)$, which is known a priori. Expression [1e] is obtained assuming a fixed volume of soil and relating $R(t)$ with the instantaneous root length (which is a special function according to method used to estimate longitudinal root growth: i.e., linear, exponential, sigmoid, etc.) (See Appendix A). Equation [1e] characterizes the moving boundary approximation and replaces a second equation in [1d], which was postulated in our previous free boundary models.

The model is solved by applying the integral balance method (Goodman, 1958; Reginato et al., 1993b). So, the partial differential equation [1a] is integrated in variable r on the domain $[s_0, R(t)]$. Moreover, by using an analogous methodology to that used in phase-change processes, the following expression for $C(r, t)$ is proposed:

$$C(r, t) = \varphi(r) \left[1 + \beta(t) \left(1 - \frac{r}{R(t)} \right)^2 \right] \quad [2]$$

with

$$\varphi(r) = C_R \exp^{-\varepsilon(R_0 - r)}, \quad \varepsilon = \frac{v_0}{Db} = \frac{\varepsilon_0}{s_0} \quad [3]$$

where C_R is the initial ion concentration in soil solution at $r = R_0$ [mol m^{-3}]. Expression [2] for the concentration verifies the initial [1b] by taking $\beta(0) = 0$ and boundary [1c] conditions. So, after some elementary and long manipulations, and taking into account the particular case of a linear root growth, the following differential equation for $\beta(t)$ was obtained (see Appendix B):

$$\frac{d\beta(t)}{dt} = \frac{F_2[R(t), \beta(t)]}{F_1[R(t)]}, \quad \beta(0) = 0 \quad [4]$$

$$\text{with: } R(t) = R_0 \sqrt{\frac{l_0}{l_0 + kt}}$$

The system [4] is solved through the Runge-Kutta method for ordinary differential equations, which was implemented in a FORTRAN program on a personal computer.

Total nutrient uptake can be obtained from the following formula, which can be considered a modified version of the Cushman formula (Claassen and Barber, 1976; Cushman, 1979).

$$U = 2\pi s_0 l_0 \int_{t=0}^{t=t_{\max}} J_c(t) dt + 2\pi s_0 \int_{t=0}^{t=t_{\max}} \left[\int_{t=t}^{t=t_{\max}} J_c(t) dt \right] \dot{l}(t) dt$$

$$J_c(t) = \frac{k_a [C(s_0, t) - C_u]}{1 + \frac{k_a [C(s_0, t) - C_u]}{J_m}} \quad [5]$$

where $J_c(t)$ is the influx, $\dot{l}(t)$ is the longitudinal root rate growth, and U is computed from $t = 0$ to $t = t_{\max}$.

MATERIALS AND METHODS

Three maize hybrids (Dekalb 762, Capitán Ciba, and Tilkara Funks) were grown in cylindrical pots with 1.6 kg of Typic Hapludult from Río IV, Córdoba, Argentina, in a growth chamber at 26°C. The whole-pot experiment consisted of four replicates with 15 plants in each pot for the three hybrids. At emergence, 5 days after germination [DAG], plants were harvested to determine initial K and root length. The plants were harvested 11 DAG, dried at 70°C, digested by wet combustion and analyzed for K by flame photometry (Jackson, 1964).

Determination of Model Parameters

Soil and plant parameters for K uptake simulation were estimated as follows:

Soil parameters. Values of C_R (initial soil solution concentration of K) were obtained by analyzing aliquots of displaced solution from soil columns equilibrated at field capacity for 24 h (Adams, 1974). Buffer power b and diffusion coefficient D were determined as described by Kovar and Barber (1990). Flux velocity v_0 was determined by dividing the total water uptake of the plant in each pot within a given time by the mean root surface area within the same given time: $v_0 = W / (\ln S - \ln S_0) / (t - t_0) (S - S_0)$. Total water uptake W was obtained by subtracting the water loss due to evaporation from the total water loss due to evapotranspiration.

Root parameters. The exponential root growth rate k was calculated from root length as a function of time by $k = (\ln l(t) - \ln l_0) / (t - t_0)$. The linear growth rate was calculated from the relation $k = (l(t) - l_0) / (t - t_0)$. The mean root radius s_0 was calculated from the root length and fresh weight by: $s_0 = [\text{fresh wt.} / \pi (\text{root length})]^{1/2}$ assuming a root tissue density of 1 g cm^{-3} . Half distance between roots' axes, R_0 , was calculated by: $R_0 = [\text{soil volume} / \pi (\text{root length})]^{1/2}$. Root length, l , was measured by the line-intersect method (Tennant, 1975).

Kinetics uptake parameters. J_m , K_m , C_u , and k_a were deter-

Table 1. Soil and plant parameters used in the moving boundary model.

	Hybrid		
	Capitán Ciba	Dekalb 762	Tilkara Funks
Exponential root growth rate k , s^{-1}	1.066×10^{-6}	9.63×10^{-7}	8.59×10^{-7}
Mean water influx rate at root surface v_0 , $m\ s^{-1}$	1.26×10^{-8}	2.24×10^{-8}	1.15×10^{-8}
Mean root radius s_0 , m	5×10^{-4}	3.8×10^{-4}	3.4×10^{-4}
Initial root length l_0 , m	1.8	2.41	2.05
Initial half distance between roots axes R_0 , m	1.27×10^{-2}	1.14×10^{-2}	1.24×10^{-2}
Soil buffer power b , dimensionless	11.6	11.6	11.6
Effective diffusion coefficient for the ion in soil D , $m^2\ s^{-1}$	6.827×10^{-12}	6.827×10^{-12}	6.827×10^{-12}
Maximum influx rate at high concentrations J_m , $mol\ m^{-2}\ s^{-1}$	1.316×10^{-6}	6.752×10^{-6}	4.744×10^{-6}
Absorption power k_a , $m\ s^{-1}$	1×10^{-6}	3.57×10^{-6}	2.584×10^{-6}
Ion concentration in soil solution below which influx ceases C_0 , $mol\ m^{-3}$	2.183×10^{-2}	1.5×10^{-3}	9.9×10^{-4}
Initial concentration of ion in the soil solution C_R , $mol\ m^{-3}$	8.4	8.4	8.4

mined by analysis of K depletion curves in a nutritive solution from which roots absorb nutrients (Claassen and Barber, 1974).

Soil and plant parameters used in the moving boundary model are listed in Table 1.

RESULTS AND DISCUSSION

The results obtained for the K uptake of the three maize hybrids are presented in Table 2. The values obtained represent good results.

For a more exhaustive analysis, the model was also tested with experimental data extracted from the literature. Thus, uptake of Mg, K, and P for loblolly pine seedlings during 180 days in a modified A horizon soil mesic Typic Hapludult (Kelly et al., 1992) was estimated. The comparison between the Barber-Cushman prediction using the NUTRIENT UPTAKE program (Oates and Barber, 1987) and the estimation of the present moving boundary model that assumes a linear root growth with time is shown in Table 3. Predicted uptakes improved in all cases, although for Mg uptake the same deviations showed by the Barber-Cushman model persisted, probably because high J_m values obtained from solution studies are responsible for underprediction of Mg uptake by crops (Rengel et al., 1990). Thus, both models can be improved taking into account J_m values obtained from soil studies. The nutrient uptake predicted by our model can be improved in its theoretical aspects. In this respect, the limitation of these models is that both consider the absorption of only one nutrient explicitly without taking into account the simultaneous absorption of ions and the possible coupling with other ions in the absorption. This last fact suggests the need for a model that simultaneously takes into account the interactions among nutrients, as for example, by using competitive kinetic absorption.

The model is further tested with data of S uptake by wheat grown on Norwood silt loam (Typic Hapludalf)

Table 2. Potassium uptake by three maize hybrids: observed vs. predicted uptake by the moving boundary model.

Hybrid	K uptake	
	Observed	Predicted
	mmol pot ⁻¹	
Dekalb 762	0.1685	0.213
Tilkara Funks	0.293	0.325
Capitán Ciba	0.304	0.287

and Mhoon silty clay loam (Typic Fluvaquent) for a period of 24 and 17 d, respectively, under glasshouse conditions (Delgado and Amacher, 1997). The NUTRIENT UPTAKE program (Oates and Barber, 1987) and the present model were used for the input data. The predicted uptakes using a linear root growth are shown in Table 4. The moving boundary model provides a better prediction in 10 cases for a total number of 18 predictions. We remark that for Norwood soils the comparison between the predicted uptakes by the Barber-Cushman model and the predicted uptakes by our model shows that our model overpredicts 1.27 times the observed uptakes, while the Barber-Cushman model overpredicted 1.72 times the observed values. This fact is shown in Fig. 1. For the Mhoon soils, the predictions are poor. On the other hand, when accounting for K, P, and Mg for long periods of time our model makes better predictions. We remark that the validity of the root competition assumption for the soils considered in the tests is justified because the depletion radius ($r_D = s_0 + 2\sqrt{Dt}$; following Baldwin and Nye [1974]) equals the instantaneous half distance between root axes $R(t)$ in 3 to 4 d for the soils considered. Thus, the moving boundary model may be a good alternative method for the prediction of nutrient uptake.

Appendix A

The expression [1e] is obtained assuming that the available soil volume at time t results from the difference between the available soil volume at initial time $t = 0$, and the grown root volume at time t : i.e., if R_0 is the initial half distance between roots, l_0 is the initial root length, and $l(t)$ is the root length at

Table 3. Magnesium, potassium and phosphorus uptake by pine seedling: observed vs. predicted by Barber-Cushman and moving boundary models.

Nutrient	Observed uptake	Predicted uptake			
		Barber-Cushman model†		Moving boundary model‡	
	mmol pot ⁻¹	Error§		mmol pot ⁻¹	Error§
Mg	1.617	0.625	61.3	0.680¶	57.1
K	6.663	6.285	5.6	6.653¶	0.15
P	1.332	1.185	11	1.302¶	2.25

† Kelly et al. (1992).

‡ As described in present paper.

§ Relative error = [(Observed uptake – predicted uptake)/Observed uptake] × 100.

¶ The value obtained by the moving boundary model represents a better prediction.

Table 4. Sulfur uptake by wheat: observed vs. predicted by Barber-Cushman and moving boundary models.

Crop (soil)	Observed uptake	Predicted uptake			
		Barber-Cushman model†	Moving boundary model‡	Error§	Error§
	mmol pot ⁻¹		mmol pot ⁻¹		
Wheat (Norwood +)	0.02557	0.004678	0.00749¶	81.7	70.7
	0.0287	0.02969	0.02684	3.4	6.5
	0.0452	0.05925	0.0532¶	31	17.7
	0.06923	0.09355	0.0746¶	35.1	7.75
	0.08358	0.1294	0.099¶	54.8	18.4
Wheat (Norwood)	0.01091	0.004678	0.00822¶	57.1	24.6
	0.0234	0.03119	0.02966¶	33.3	26.7
	0.0452	0.0701	0.06599¶	55	46
	0.0561	0.106	0.08624¶	88.9	53.7
	0.0977	0.145	0.1141¶	48.4	16.8
Wheat (Mhoon +)	0.08576	0.09048	0.01247	5.5	85.3
	0.1356	0.2089	0.01383	54	89.8
	0.229	0.3071	0.01477	34	93.5
	0.2426	0.4288	0.01577	76.7	93.5
	0.0555	0.02807	0.01913	49.4	65.5
Wheat (Mhoon)	0.08358	0.05519	0.03627	33.9	56.6
	0.0764	0.08731	0.05137	14.3	32.7
	0.08358	0.1185	0.06883¶	41.8	17.6

† Delgado and Amacher (1997). We have extracted their predicted S uptake by using J_m obtained from soil studies.

‡ As described in the present paper.

§ Relative error = [Observed uptake – predicted uptake]/Observed uptake] × 100.

¶ The value obtained by the moving boundary model represents a better prediction.

time t , then we have

$$V_{\text{soil}}|_{t=t} = V_{\text{soil}}|_{t=0} - V_{\text{root}}|_{t=t}$$

that is

$$\pi l(t)[R^2(t) - s_0^2] = \pi l_0[R_0^2 - s_0^2] - \pi s_0^2[l(t) - l_0]$$

Thus, after elementary manipulations, the condition [1e] is obtained.

Appendix B

Integral balance method (Reginato et al., 1993b). The functions F_1 and F_2 are given by

$$F_1(R(t)) = C_R \exp^{-\varepsilon R_0} \left\{ \frac{[\exp^{\varepsilon R(t)} - \exp^{\varepsilon s_0}]}{\varepsilon} - \frac{2}{R(t)} \right. \\ \left. \frac{[\exp^{\varepsilon R(t)}(\varepsilon R(t) - 1) - \exp^{\varepsilon s_0}(\varepsilon s_0 - 1)]}{\varepsilon^2} + \frac{1}{R^2(t)} \right. \\ \left. \frac{[\exp^{\varepsilon R(t)}(\varepsilon^2 R^2(t) - 2\varepsilon R(t) + 2) - \exp^{\varepsilon s_0}(\varepsilon^2 s_0^2 - 2\varepsilon s_0 + 2)]}{\varepsilon^3} \right\}$$

$$F_2(R(t), \beta(t)) = G_1 + G_2 + G_3 + G_4 + G_5$$

where

$$G_1(R(t), \beta(t)) = D\varepsilon C_R \exp^{-\varepsilon(R_0 - R(t))} + D\varepsilon C(s_0, t) \\ - \frac{k_a}{b} \frac{[C(s_0, t) - C_u]}{1 + \frac{k_a[C(s_0, t) - C_u]}{J_m}}$$

$$\text{with } C(s_0, t) = C_R \exp^{-\varepsilon(R_0 - s_0)} \left[1 + \beta(t) \left(1 - \frac{s_0}{R(t)} \right)^2 \right]$$

$$G_2(R(t), \beta(t)) = D(1 + \varepsilon_0) \frac{2\beta(t)}{R(t)}$$

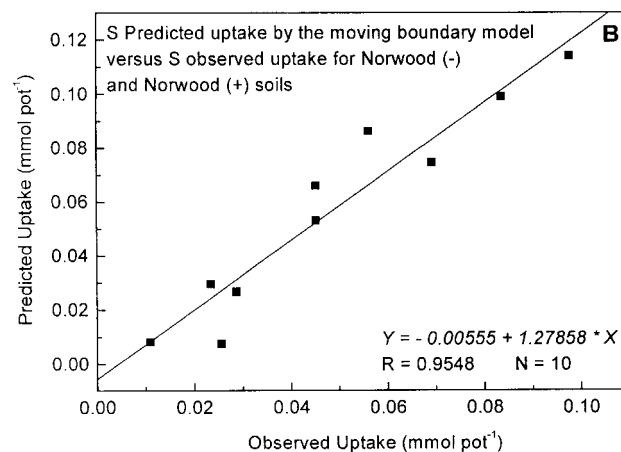
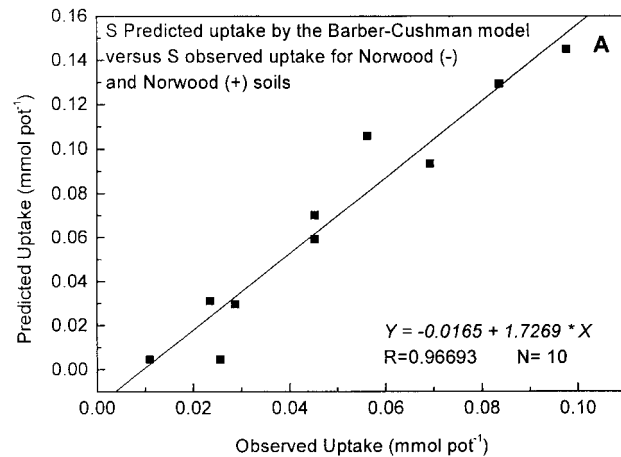


Fig. 1. Comparison between predicted and observed S uptakes by (A) the Barber-Cushman model and (B) the moving boundary model.

$$\left(\frac{1}{R(t)} - \varepsilon \right) C_R \exp^{-\varepsilon R_0} \frac{[\exp^{\varepsilon R(t)} - \exp^{\varepsilon s_0}]}{\varepsilon} \\ G_3(R(t), \beta(t)) = \frac{\beta(t)}{R^2(t)} \left[D(1 + \varepsilon_0)\varepsilon - 2\dot{R}(t) \right] \\ C_R \exp^{-\varepsilon R_0} \frac{[\exp^{\varepsilon R(t)}(\varepsilon R(t) - 1) - \exp^{\varepsilon s_0}(\varepsilon s_0 - 1)]}{\varepsilon^2} \\ G_4(R(t), \beta(t)) = \frac{2\beta(t)\dot{R}(t)}{R^3(t)} C_R \exp^{-\varepsilon R_0} \\ \frac{[\exp^{\varepsilon R(t)}(\varepsilon^2 R^2(t) - 2\varepsilon R(t) + 2) - \exp^{\varepsilon s_0}(\varepsilon^2 s_0^2 - 2\varepsilon s_0 + 2)]}{\varepsilon^3}$$

$$\text{with } \dot{R}(t) = \frac{-kR(t)}{2(l_0 + kt)}$$

$$G_5 = \left[D(1 + \varepsilon_0) \left(\varepsilon + \varepsilon\beta(t) - \frac{2\beta(t)}{R(t)} \right) \right] C_R \exp^{-\varepsilon R_0} \\ \left[\ln \frac{R(t)}{s_0} + \varepsilon[R(t) - s_0] + \frac{\varepsilon^2}{4}[R^2(t) - s_0^2] \right. \\ \left. + \frac{\varepsilon^3}{18}[R^3(t) - s_0^3] + \frac{\varepsilon^4}{96}[R^4(t) - s_0^4] \right. \\ \left. + \frac{\varepsilon^5}{600}[R^5(t) - s_0^5] + \frac{\varepsilon^6}{4320}[R^6(t) - s_0^6] \right]$$

$$+ \frac{\epsilon^7}{35280}[R^7(t) - s_0^7] + \frac{\epsilon^8}{322560}[R^8(t) - s_0^8] + \frac{\epsilon^9}{3265920}[R^9(t) - s_0^9]$$

The solution is found integrating the partial differential equation [1a] in variable r over the domain $[s_0, R(t)]$ with $C(r, t)$ given by the expression [3]. Thus, for linear root growth rate, $l(t) = l_0 + kt$, the problem [1] reduces to

$$\int_{s_0}^{R(t)} C_t(r, t) dr = D \int_{s_0}^{R(t)} C_{rr}(r, t) dr + D(1 + \epsilon_0) \int_{s_0}^{R(t)} \frac{C_r(r, t)}{r} dr$$

$$R(t) = R_0 \sqrt{\frac{l_0}{l_0 + kt}}, \quad \beta(0) = 0$$

Computing the following integrals, $\int_{s_0}^{R(t)} C_t(r, t) dr$, $\int_{s_0}^{R(t)} C_{rr}(r, t) dr$, and $\int_{s_0}^{R(t)} \frac{C_r(r, t)}{r} dr$ and taking into account that the integral for e^{er}/r is approximate by a Taylor polynomial of nine's order in variable r (Abramowitz, 1972), after elementary manipulations we obtain system [4].

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