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MATHEMATICAL MODEL FOR POLLUTANT UPTAKE BY MULTIPLE ROOT BRANCHING STRUCTURE OF A PLANT

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ABSTRACT:

Aim : To develop a mathematical model for dependence of rate of pollutant uptake by the cylindrical root on the length and density of root hairs.
Method: Specific geometrical properties of root hairs, in particular their radius and density in order to approximate their influence on pollutant uptake, are considered for development of the model.
Result: A mathematical expression is derived for the pollutant uptake. The analytical solution of the model with some specific boundary conditions is compared with numerical results.
Conclusion: It is estimated that there is a linear relationship between the increase in root surface area and the pollutant flux.

Key Words*:* uptake parameter, asymptotic matching, van Genuchten formula, relative water content

Introduction

Multiple root branching structure of any plant is the part of the root surface cells and it is considered for the mechanism of pollutant uptake. However, due to their small radius and high density it is thought that their presence can increase the pollutant uptake by up to 78% [5]. The number of root branches varies with the levels of nutrients in the soil. For example, at high phosphorus concentrations the number of root branches per centimeter of root length (for maize) is approximately 500, but at low phosphorus concentration this number can increase up to 2000 [6]. The development of root branches is therefore thought to be an adaptive plant response to the deficiency of nutrients in the soil. In addition to the number of root branches varying with the pollutant status of the plant, their length can also increase with nutrient deficiency. This effect has been measured in rape, where the root branch length can vary between 0.3 and 3 mm depending on the level of nitrogen and phosphorus in the soil [6].
Root branches extend the total root surface area quite considerably. For the average maize root with radius 2×10^{-2} cm, and root branches with length 0.1 cm, radius 10^{-3} cm, and number density of 1000 root branches per centimeter of root length, the increase in the total root surface area is approximately 500%. At the same time the increase in the volume of root tissue is 25%. This implies that with the relatively small increase in the volume, i.e., the increase in pollutant absorbing root surface area is large.
The contribution of the uptake by the root branches has been formerly calculated merely by using the cylindrical root model, with the root radius taken to be the root radius plus the root branch length. It is by the fact that the concentration of pollutants or nutrients in the root branch region is relax rapidly to the time equilibrium [7]. This would lead, in the case of root branch length 10 times the radius of the root, to 10 times increase in the dimensionless pollutant uptake coefficient λ. However, this method does not take into account the dramatic increase of root surface area and the experimental observations also contradict this approach [9,10].
Another popular approach in modelling root branch uptake is to consider them to be a volume sink with infinite thickness extending from the root surface [5,12]. Calibration of those models is usually very complex, since in general they contain large numbers of independent parameters (in some cases up to 16-20 different parameters) [11, 13].
Another possible way of tackling the modelling of root with multiple branches may be to calculate an effective root radius corresponding to the total root surface area including the contribution from root branches [3], i.e., given a root radius a, branch radii a_h, with length l, and the number of root branches per unit length of the root n, the *effective root radius* r_e is calculated as $r_e = a + a_h nl$.
One of the first mathematical models for the growth of root branching structure was proposed by Edelstein [1]. Here a growth model for plant multiple root branching structure based on the original model of Edelstein [1]

developed and its both analytical and numerical solutions are determined. This provides the basis for testing the fungal growth model against experimental data [6,8].

In this paper we aim to establish a detailed dependence of the rate of pollutant uptake by the cylindrical root on the length and density of root branches. The specific geometrical properties of root branches, in particular their radius and density are considered in order to approximate their influence on pollutant uptake.

Mathematical model

Root branches can be considered to be cylinders that extend perpendicularly from the root surface. The root branches density n is the number of root branches per unit length of the root and it varies from species to species. For maize plants a typical range is from 100 to 2000 root branches per centimeter of the root [5,6,14].

The mechanism of pollutant uptake at the root branches surface is thought to be the same as on the root surface, and hence the model derived for single cylindrical root can be extended for root branches. By modifying the boundary surface to include root branches we can have the following form of dimensional model from the conservation law

$$\left(b+\phi_l\right)\frac{\partial c}{\partial t}+\nabla.(cu)=D\phi_l\nabla^2 c, \qquad (1)$$

with boundary conditions

$$n.(D\phi_l\nabla c)=\frac{F_m c}{k_m+c}-E \qquad on\ \partial H, \qquad (2)$$

Where b is soil buffer power, ϕ_l is the soil porosity, c is solute is present in the liquid, D is the diffusion coefficient of the solute in free water, u is the Darcy flux of water, F_m (μ*mol cm*$^{-2}$ *s*$^{-1}$) is the maximal root uptake rate and K_m (*μmol cm*$^{-3}$) is the Michaelis Menten constant, $E=\frac{F_m c_{\min}}{k_m+c_{\min}}$, ∂H is the root and root branch surface. The root surface is defined by $r=\sqrt{x^2+y^2}=a$, with a being the dimensional root radius. Any particular root branch surface is given by $\rho=\sqrt{y^2+z^2}=a_{h,d,}$ where $a_{h,d,}$ is the dimensional radius of the root branch, i.e., the root branch is placed along the x-axis. r and ρ are radial coordinates associated with the root and root branch respectively. The corresponding angle variables for root and root branch are θ*=arctan(y/x)* and ϕ = *arctan(z/y)* (Figures 1 and 2). n is the unit normal to the root and root branch surface. In order to include inter root branch competition in the model, a zero flux boundary condition at the half way distance between two neighboring root branches will be imposed. Hence we require

$$\frac{\partial c}{\partial \theta}=0\ at\ \ \theta=\pm\frac{d_d}{a},\ \ and\ \ \frac{\partial c}{\partial z}=0\ \ at\ \ z=\pm d_{d,} \qquad (3)$$

where d_d is the dimensional half distance between the two root branches and the far-field boundary condition is,

$$c\to c_0\ \ as\ r\to\infty, \qquad (4)$$

with the initial condition

$$c=c_0\ \ at\ \ t=0. \qquad (5)$$

Non-dimensionalising the model by

$$t=\frac{a^2(\phi_l+b)}{D\phi_l}t^*,\ \ r=ar^*,\ \ c=K_m c^*. \qquad (6)$$

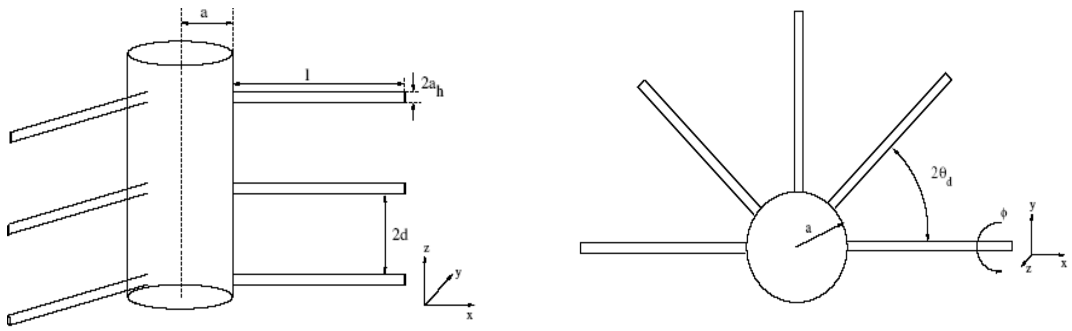

Figure 1: Root with root branches. Parameter d is the half distance between the root branches, a_h is the root branch radius, a is the root radius, l is the length of the root branch, and θ_d = d_d/a is the angle corresponding to the half distance between the root branches.

The dimensionless model, dropping *s , is given by

$$\frac{\partial c}{\partial t} = \nabla^2 c, \tag{7}$$

With the boundary condition is given by $n.\nabla c = \frac{\lambda c}{1+c}$ on ∂H, (8)

where n is the unit outward normal to surface ∂H. The far-field boundary condition is

$$c \to \infty \text{ as } r \to \infty, \tag{9}$$

and the initial condition is $c = c_\infty$ at $t = 0.$ (10)

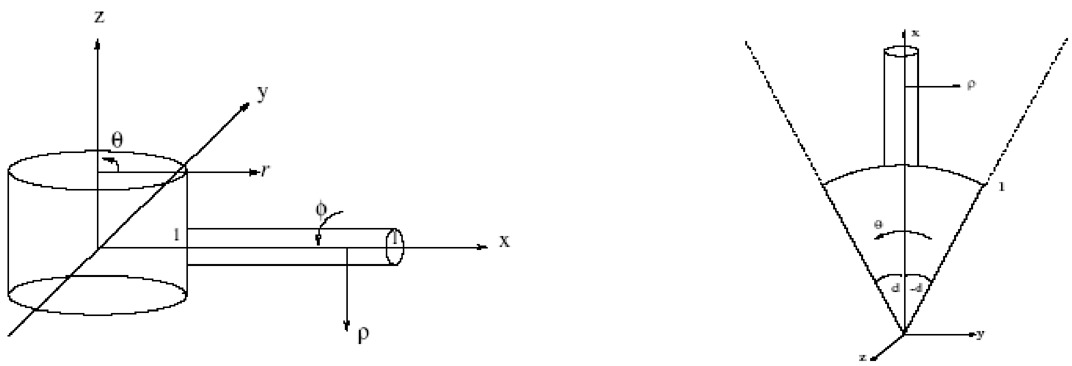

Figure 2: Dimensionless root and root branch surface. ∂H is given by r = 1 and ρ= a_h, where r and θ are the radial root surface coordinates, and ρ and ϕ are the radial coordinates associated with the root branch. $r^2 = x^2 + y^2, \tan(\theta) = y/x,$ *and* $\rho^2 = y^2 + z^2, \tan(\phi) = z/y$

The boundary surface ∂H is given as a combination of two intersecting cylinders (Fig. 2) characterized with corresponding cylindrical coordinate systems. Here the root surface is characterised by $r = \sqrt{x^2 + y^2} = 1$, and θ= *arctan(y/x)* and root branch surface is characterized by $\rho = \sqrt{y^2 + z^2} = a_h$, where $a_h = a_{h,d} / a$ is the dimensionless root branch radius, with $a_h d$ [cm] being the dimensional root branch radius, and a [cm] the dimensional root radius. Similarly the angle variable ϕ = *arctan(z/y)* associated with the root branch, and the root branch length variable x. Zero flux boundary conditions at the halfway distance between the two neighboring root branches are given by

$$\frac{\partial c}{\partial \theta} = 0 \text{ at } \theta = \pm d, \text{ and } \frac{\partial c}{\partial z} = 0 \text{ at } z = \pm d, \tag{11}$$

where d is the dimensionless half way distance between the root branches.

Non-dimensional Parameter Estimation

As reported in [6] there are approximately 500 to 2000 root branches per cm of root length. Hence, the average distance between the root branches can be calculated in following way: if the number of root branches per unit length [cm] of the root is n, then the number of root branches per unit root surface area is $n/(2\pi a),$, where a is the radius of the root [cm]. Thus, the average half distances d [cm] between the root branches at the root surface is $\sqrt{\pi a/(2n)}$ [cm].

The dimensionless distance between the root branches are given by $d = d[cm]/a[cm] = \sqrt{\pi(2na)}$.

In the following sections we will use this parameter estimation to derive an approximation to the root branch pollutant uptake. The dimensionless parameters are presented in Table 1

Parameter	Dimensional	Dimensionless
Root radius (a)	$2x10^{-2}$ [cm]	1
Root branch radius (a_h)	$2.5x10^{-4}$-10^{-3} [cm]	(1-5)$x10^{-2}$
Length of the root branch (l)	10^{-2}-$3x10^{-1}$ [cm]	0.5-10

Number of root branches per unit of root length (n)	500-2000 [cm^{-1}]	10-40
Number of branches per unit root surface area (m)	3978-15915 [cm^{-2}]	1.59-6.39
Half distance between root branches (d)	3.9×10^{-3}-10^{-2} [cm]	0.19-0.39

Table 1: Root and root branch dimensional and dimensionless parameters.

The same parameter ranges for maize are also applicable for wheat, paddy, tomato, onion, and carrot ([4],[6]). As one can see the distance between root branches is at least one order of magnitude larger than the root branch radius, i.e., $d >> a_h$.

Approximate solution

Far away from the root and root branches, i.e., in the outer region, the model of pollutant uptake by root and root branch is expected to be the same as in the absence of root branches. This is because far away from the root the influence from the root and root branch length scales can be considered negligible. Hence, far away from the root the concentration profile is given by the similarity solution

$$c(r,t) = c_\infty + BE_1(\frac{r^2}{4t}), \tag{12}$$

where $E_1(x) = \int_x^\infty e^{-y} \frac{dy}{y}$ is the exponential integral, and B is the matching constant, $B'(t)B(t) << 1$, and it is to be determined by matching the outer solution with the inner solution that is valid near the root surface. The variable r is the radial distance from the root centre, i.e., the radial coordinate associated with the root. Given a particular position (r,θ,z) associated with the root, the corresponding Cartesian coordinates are $x = r\cos\theta$, $y = r\sin\theta$, and z. Equivalently, in terms of radial coordinates (x,ρ,ϕ) associated with the root branches, these are x, $y = \rho\cos\phi$, and $z = \sin\phi$.. Hence, we can write $r^2 = x^2 + \rho^2\cos^2\theta$, which implies that using root branch coordinates the outer solution becomes

$$c(x,\rho,\phi,t) = c_\infty + BE_1(\frac{x^2 + \rho^2\cos^2\phi}{4t}) \tag{13}$$

Near the root and root branch surface the diffusion profile clearly has quite a complex structure. There is a diffusion gradient in the direction of the root surface at $r = 1$ and also in the direction of the root branch surface $\rho = \sqrt{y^2 + z^2} = a_h$. However, we can approximate the solution when the inter root branch distance is much bigger than the root branch radius, $d >> a_h$, and the root branch radius is very small, $a_h << 1$

First we look for the solution near the root branch surface. The solution in this region can be calculated using an appropriate rescaling of the space variable. We introduce the space variable $\hat{\rho} = \rho / a_h$ (where $\rho = \sqrt{y^2 + z^2}$ is the radial coordinate associated with root branch), and then the diffusion equation written in the radial coordinates $(x,\hat{\rho},\phi)$, associated with root branches, becomes

$$\frac{\partial^2 c}{\partial \hat{\rho}^2} + \frac{1}{\hat{\rho}}\frac{\partial c}{\partial \hat{\rho}} + \frac{1}{\hat{\rho}^2}\frac{\partial^2 c}{\partial \phi^2} = a_h^2(\frac{\partial c}{\partial t} - \frac{\partial^2 c}{\partial x^2}) \tag{14}$$

in which $a_h << 1$, At the leading order this reduces to

$$\frac{\partial^2 c}{\partial \hat{\rho}^2} + \frac{1}{\hat{\rho}}\frac{\partial c}{\partial \hat{\rho}} + \frac{1}{\hat{\rho}^2}\frac{\partial^2 c}{\partial \phi^2} = 0 \tag{15}$$

The solution of (14) independent of φ is $c = A_1(x) + A_2(x) ln\,\hat{\rho}.$ (16)

where A_1 and A_2 depend on the distance from the root surface along the x -axis. The root branch surface boundary condition is $\frac{\partial c}{\partial \hat{\rho}} = \frac{a_h \lambda_c}{1+c}$ on $\hat{\rho} = 1$ (17)

However, $x^2 = r^2 - a_h^2\hat{\rho}^2\cos^2\phi$, i.e., $A_1(x) = A_1(\sqrt{r^2 - a_h^2\hat{\rho}^2\cos^2\phi}) \approx A_1(r)$ since $a_h << 1$. Hence,

$A_2 = \partial c / \partial \hat{\rho}$ and $A_1 = c$ at $\hat{\rho} = 1$, which implies that $A_2 = a_h \lambda A_1(r)/[1 + A_1(r)]$. Therefore the solution near the root branch is in the form

$$c = A_1(r) + \frac{a_h \lambda A_1(r)}{1 + A_1(r)} ln \hat{\rho}. \tag{18}$$

When $a_h \lambda << 1$ (our estimated parameters show that this is mostly the case) the root air influence on the general diffusion profile around the root is small, which implies that the diffusion profile around and between the root branches is flat. In [10] Itoh and Barber concluded the same, but their justification is inaccurate. They thought that the diffusion profile around the root branches is flat because of the small distance between the root branches. In fact the distance between the root branches compared to their radius is large, $a_h << d$. However, we have shown that the concentration profile around the root branches is flat because the dimensionless root branch pollutant uptake coefficient $a_h \lambda$ for root branches is small, i.e., root branches are very weak sinks in the soil because of their very small radius.

For $a_h << 1$, the diffusion profile in r is the same as in absence of root branches, i.e., $A_1 (r)$ is given by the uniform approximation as

$$A_1(r,t) = c_\infty - \frac{F(t)}{2} E_1\left(\frac{r^2}{4t}\right), \tag{19}$$

where F(t), the pollutant uptake by the root, is given by equation [2] :

$$F(t) = \frac{2\lambda c_\infty}{1 + c_\infty + \frac{\lambda}{2} ln(4e^{-\gamma} t + 1) + \sqrt{4c_\infty + [1 - c_\infty + \frac{\lambda}{2} ln(4e^{-\gamma} t + 1)]^2}} \tag{20}$$

The pollutant uptake by the root branches, $F_h (t)$, will be given by integrating the diffusion profile over the root branch length, i.e., from $r = 1$ to $l + 1$, and around it, times the number of root branches per unit root surface area. Hence we have

$$F_h(t) = 2\pi a_h \lambda m \int_1^{l+1} \frac{A_1(r,t)}{1 + A_1(r,t)} dr, \tag{21}$$

where m is the number of root branches per unit of dimensionless root surface area. Taking $A_1 (r)$ to be given by the inner approximation, i.e., $A_1 (r,t) = c(1,t) + F(t) ln r$ by expanding (19) for small r, and $m = n/2\pi$ (n is the number of root branches per unit of dimensionless root length), we get

$$F_h(t) = n a_h \lambda \int_1^{l+1} \frac{c(1,t) + F(t) ln r}{1 + c(1,t) + F(t) ln r} dr. \tag{22}$$

This gives, using the fact that $c(1,t) = F(t)/(\lambda - F(t))$, the expression for $F_h (t)$:

$$F_h(t) = a_h n \lambda \left[1 + \frac{e^{-\frac{\lambda}{F(\lambda - F)}}}{F} \left\{ E_1\left(ln(\frac{1}{1+l}) \right) - \frac{\lambda}{F(\lambda - F)} - E_1\left(-\frac{\lambda}{F(\lambda - F)} \right) \right\} \right] \tag{23}$$

This solution is valid for the times $t >> (l + 1)^2/4$ such that $\eta = r^2/(4t) << 1$ in the root branch region so that the approximation of the exponential integral $E_1(\frac{r^2}{4t})$ for small argument is valid. This corresponds to dimensional time more than 2 hours. When $\eta = r^2/(4t) >> 1$ in the root branch region, i.e., $t << (l + 1)^2/4$, we can approximate the exponential integral using Watsons Lemma [15] and find that at the leading order $E_1(\eta) \sim e^{-n}/\eta$, when $\eta >> 1$.

Hence the integrand in (21) becomes, using the binomial expansion,

$$\frac{A_1}{1 + A_1} = \frac{c_\infty - \frac{F}{2\eta} e^{-\eta}}{1 + c_\infty - \frac{F}{2\eta} e^{-\eta}} \approx \frac{c_\infty - \frac{F}{2\eta} e^{-\eta}}{1 + c_\infty} [1 + \ldots], \tag{24}$$

and the uptake of pollutant by root branches is given by

$$F_h(t) = a_h n \lambda \left\{ \frac{c_\infty}{1 + c_\infty} l + \frac{2tF(t)}{2(1 + c_\infty)} \left[\frac{e^{-(1+l)^2/4t}}{1 + l} - e^{-1/4t} + \frac{1}{2}\sqrt{\frac{\pi}{t}} \left(erf\left(\frac{1+l}{2\sqrt{t}}\right) - erf\left(\frac{1}{2\sqrt{t}}\right) \right) \right] \right\} \tag{25}$$

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For root branches with length 14 mm, this solution is valid for times of order 2 hours to 1 day or less. However, the vegetative time-scale of the roots and root branches is of order 10 days or more. Hence, except in very short time experiments, the use of (25) are appropriate.

The results for calculating the pollutant uptake by root and root branches (given by equation (25)) are shown on Figure 3, up to time $t = 10^4$, which in dimensional terms corresponds to a time of order 20 days. As we can see, the pollutant uptake in this regime is strongly dominated by the presence of root branches. The pollutant uptake by the root branches is approximately 5-6 times that of the root. With the root branch parameters $a_h = 0.01$, $l = 10$, and $n = 40$ the total root surface area has also increased by 5 times [16].

This result suggests that it would be instructive to revise the estimates of pollutant uptake parameters F_m and K_m derived from experiments which omit the effect of pollutant uptake by root branches. As we can see from Fig. 4

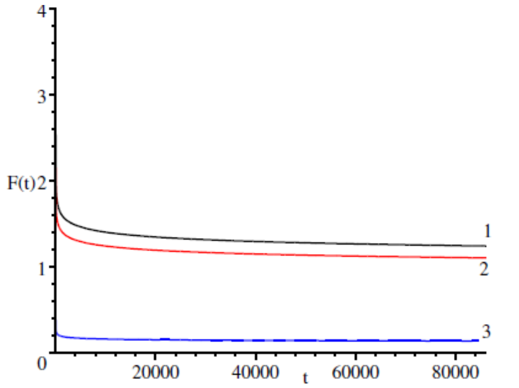

Fig 3: The dimensionless pollutant uptake by the root and root hair. The line 2 shows the uptake of salts by the root hair given by (23), the line 3 shows the uptake by the root, and line 1 shows the total uptake by the plant. Parameters are $\lambda = 1$, $c_\infty = 1$, $n = 40$, a_h = 0:01, and l = 10. t = 105 corresponds to ≈ 20 days.

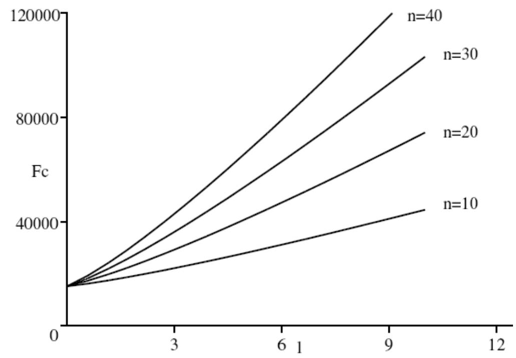

Fig 4: The cumulative uptake $F(c)=\int_{t_1}^{t_2} F(t)+F_h(t)dt$ with $t_1=50$ and $t_2 = 10^5$ (corresponding dimensionally approximately to 1-20 days), depending on the root branch length l for different numbers of root branches, n, per unit (non-dimensional) root length (typically n ranges from 10 to 40). Cumulative uptake is calculated using the trapezoidal rule and graph shows the cumulative uptake F_c as a function of root branch length.

the length of the root branches influences the cumulative pollutant uptake by the root almost linearly. The number of root branches has a similar effect on the pollutant uptake.

Conclusion

There are two main conclusions we can derive from the study. Firstly, the influence of root branches can be, divided into two different situations. When root branch length is of the order of the root radius or less, their effect is purely to extend the root surface area. This can be seen in Figure 3 where in the region of $l < 1$, F_c/S is approximately constant indicating the linear relationship between the increase in root surface area and pollutant flux. Longer root branches however, can take up substantially more pollutants since they extend into soil with higher concentration.

Secondly, in the current parameter estimation the roots are considered to be smooth cylinders, however, in experiments roots clearly do have root branches. The neglect of root branches in the parameter estimation results in higher values of F_m and also K_m. The adjustment of the estimation procedure to include root branches would lead to smaller values of F_m and K_m, and hence also, making the current calculation applicable for most of the parameter ranges

The volume of root branches compared to the root volume differs by a factor of up to 4 or 5. Hence, it is natural to expect that it is more beneficial for a plant to produce more root branches, since the upkeep of the root branch tissue is probably as costly as that of the root tissue (since the root branches are basically part of the root surface epidermal cells anyway).

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