Splitting advection, diffusion and reaction processes in a continuous model of root growth

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Introduction

Modeling and simulating plant root growth in connection with soil water and nutrient transfer is an important challenge that finds applications in many fields of research. Density based models, which are often represented under the form of partial differential equations (PDE), aim in integrating root characteristics through time and spatial dependant density functions (Bastian *et al*., 2008; Dupuy *et al*., 2010). PDE models are useful when it is difficult to track all individual components in a root system. In addition, they are low CPU time consuming, which can be very powerful when applied at a large scale.

The aim of this paper is to propose a single generic PDE for modeling the growth of a large diversity of dense root networks. The model includes three main physical phenomena, namely advection, diffusion and reaction, which both aggregate different aspects of plant architecture and development rules, e.g. elongation, ramification and mortality. This formulation can be generalized to any unknown density functions, e.g. biomass, root and tip diameters, length, orientation angles. A numerical scheme based on splitting operators is proposed to solve the problem, separating between these three different processes. This splitting approach has three main advantages. It is first a powerful and consistent numerical method that allows the use of appropriate numerical scheme for each kind of process and its related equation. Second, it can help to analyze the relative importance of these processes at a given scale for different root architectures and the evolution of their respective weight regarding to plant ontology. Lastly, it makes easier the parameterization of the growth model. The application of the splitting method is shown and discussed for different root system types.

Theoretical Framework

The fundamental PDE equation of the root dynamical model is given by:

$$\partial_t n = \mathcal{A}(n) + \mathcal{D}(n) + \mathcal{R}(n) \qquad (1)$$

where ∂_t corresponds to the partial derivative in time. As in Bastian et al. (2008), the unknown function of equation (1) is the total root tips cross section area per unit of volume n (x,y,t), ($m^2.m^{-3}$). The soil is supposed to be a square domain $\Omega \subset \Re^2$.

The three semi-group operators are defined by:

- $\mathcal{A}(n) = \vec{v}.\nabla(n)$: the advection operator corresponds to the system displacement with a velocity $\vec{v}$ (x,y,t), where C is a coefficient of soil fertility.
- $\mathcal{D}(n) = \nabla.(D\nabla n)$: the diffusion operator allows the whole system to spread out in space. Both isotropic or anisotropic diffusion strategies can be considered through the expression of the diffusion coefficient D(x,y,t,C). The advection and diffusion phenomena implicitly integrate the primary growth process of all root types and their corresponding growth velocities.
- $\mathcal{R}(n)$ = f(C,n,d): the reaction operator, represents root branching and root mortality, d is the root mortality rate and f is a nonlinear function.

Matlab software was used to solve the model, based on the discretization of equation (1). A single numerical scheme is not always efficient to simulate the three different phenomena simultaneously. The splitting method was then used as an alternative approach. This approach allows reliable numerical schemes to be developed for each operator (Hundsdorder et al., 2003). Let Δt be the time step, and $t_k = t_0 + k\Delta t$. Then, if we note n^k an approximation of n at time t_k, the formal algorithm leads to

Formal algorithm:
For k = 0:T

1. Solve $d_t n_A = \mathcal{A}(n_A)$ with $n_A(0) = n^k$ on $[0, \Delta t]$;
2. Solve $d_t n_D = \mathcal{D}(n_D)$ with $n_D(0) = n_A(\Delta t)$ on $[0, +\Delta t]$;
3. Solve $d_t n_R = \mathcal{R}(n_R)$ with $n_R(0) = n_D(\Delta t)$
4. Set $n^{k+1} = n_R(\Delta t)$;

end

Numerical Results

The AMAPsim software (Barczi et al., 2008) was used to generate root systems at different times based on architectural models. Aggregated data extraction was then performed using PlantXtract (RACINES software in Jourdan and Rey, 1997b). This tool returns the values of generalized density functions, e.g. root length, apexes number, in each cell of a meshed domain. The dynamic density maps can then be plotted with Matlab and can be used for model parameterization and evaluation.

Operators in equation (1) are linked with different growth strategies. If only transport and reaction are considered, the root system grows and ramifies according to direction and norm of transport velocity, describing a dichotomic system for example. If diffusion and reaction are considered, simulation results are in agreement with density maps of homogeneous herringbone root systems for instance.

Considering the combination between the three phenomena, the root growth dynamics are more complex depending on which term of equation (1) is favored and on the velocity and diffusion coefficient expressions. Observed and simulated dynamic data of eucalyptus root systems were also considered for evaluating our PDE model (Figure 1). Simulation results are shown only considering one part of the whole root system, i.e. a single horizontal root bearing a dense network of fine roots (Figure 1B). The density map of apex number per volume unit were extracted from these data (Figure 1C) and compared to the numerical approximation performed by the model (Figure 1D). An early stage of the root development, i.e. before the first self-pruning of lateral roots, is presented in figure 1D, considering only diffusion and reaction operators with Dy = 0,15 $m^2.month^{-1}$, Dx = 0 $m^2.month^{-1}$ and C(t) constant. These coefficients were estimated using the total and local apices number provided by the architectural model.

Conclusion and Perspectives

This work aimed to show that a single PDE can be generic enough to simulate the growth of dense root networks that follow different modes of development. Beyond its interest for solving numerically the problem, the splitting method also constitutes a powerful approach to separate growth and development into different physical processes, which can be more or less relevant according to the expected output. For instance, Dupuy *et al.* (2010) pointed out that transport equations are sufficient to simulate the wave displacement of root tips.

Application of such PDE model to more complex tree root systems can be also performed at different scales. It is for instance possible to consider the whole root system as an assembly of multi-sources of dense roots borne by a skeleton of coarse roots. In this case, a hybrid approach can be used that make the coupling between EDPs at different points of fine root emergence and an architectural model (Jourdan and Rey, 1997a; Pagès *et al*., 2004). It will be also interesting to test further the model in non-homogeneous conditions making the coupling with other transfer equations commonly used to calculate nutriment concentration and water movement within the soil. Our approach has been designed to address such kind of issues.

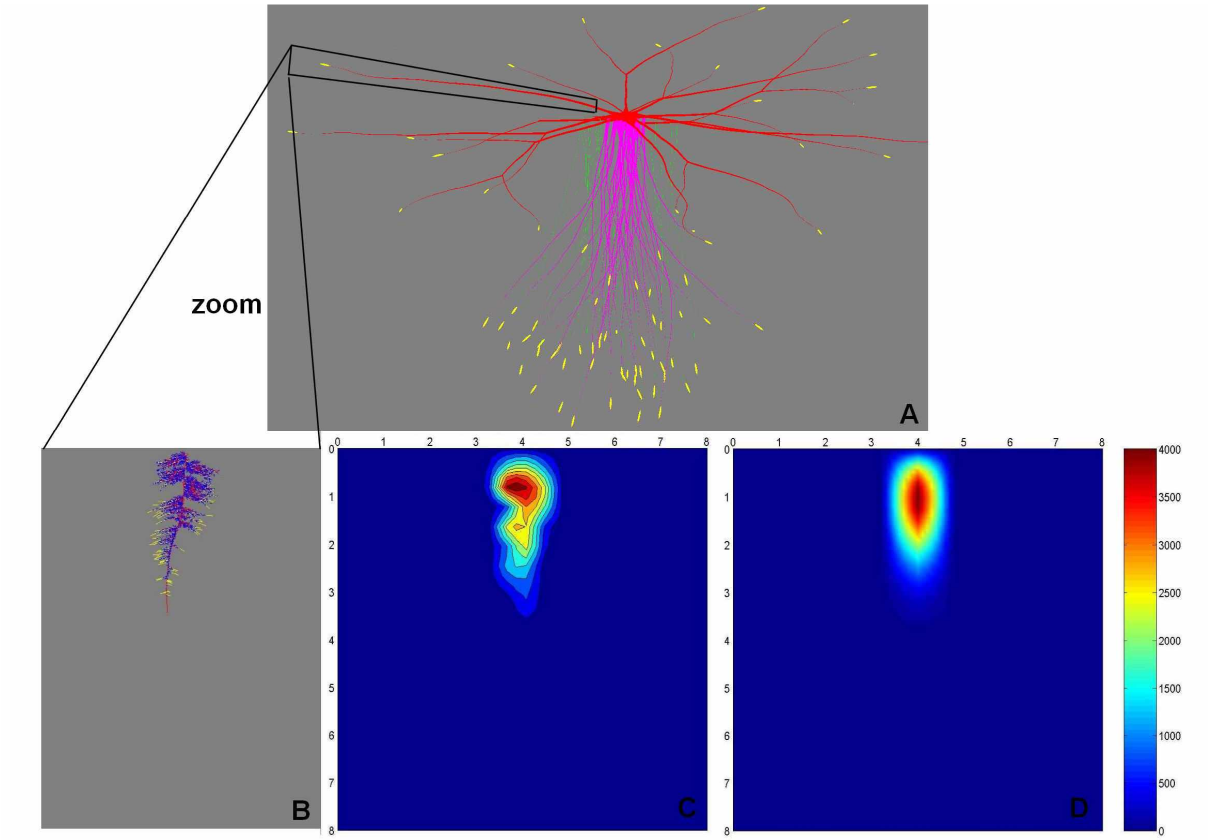

Figure 1: (A) Eucalyptus root system simulated by AMAPsim; (B) A single horizontal exploring root bearing fine roots, after 10 months of growth; (C) Density map of apex number per volume unit extracted from root architecture (B); (D) Density map of apex number per unit volume predicted by the PDE model; the domain units are in m.

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