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A density-based approach for the modelling of root architecture: application to Maritime pine (*Pinus pinaster* Ait.) root systems

L. Dupuy^{a,b,*}, T. Fourcaud^{a,c}, A. Stokes^a, F. Danjon^d

^aLaboratoire de Rhéologie du Bois de Bordeaux, (Mixed unit: CNRS, INRA, Université Bordeaux I),

Domaine de l'Hermitage 69 route d'Arcachon 33612 Cestas Cedex, France

^bInstitut pour le Développement Forestier, 23 avenue Bosquet, 75007 Paris, France

^cAMAP CIRAD - AMIS, TA 40/PS2 cedex 5, 34398 Montpellier, France

^dEphysE - INRA - 69 route d'arcachon 33612 Cestas Cedex, France

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Abstract

Root morphology influences strongly plant/soil interactions. However, the complexity of root architecture is a major barrier when analysing many phenomena, e.g. anchorage, water or nutrient uptake. Therefore, we have developed a new approach for the representation and modelling of root architecture based on branching density. A general root branching density in a space of finite dimension was used and enabled us to consider various morphological properties. A root system model was then constructed which minimizes the difference between measured and simulated root systems, expressed with functions which map root density in the soil. The model was tested in 2D using data from Maritime pine *Pinus pinaster* Ait. structural roots as input. We showed that simulated and real root systems had similar root distributions in terms of radial distance, depth, branching angle and branching order. These results indicate that general density functions are not only a powerful basis for constructing models of architecture, but can also be used to represent such structures when considering root/soil interaction. These models are particularly useful in that they provide a local morphological characterization which is aggregated in a given unit of soil volume. © 2005 Elsevier Ltd. All rights reserved.

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1. Introduction

Plant anchorage, water and nutrient uptake depend largely on root growth and architecture. A description of spatial distribution and root morphology is usually needed to represent such phenomena (Fitter et al., 1991). It is hence of great interest to develop suitable methods for the representation, analysis and modelling of root growth.

E-mail addresses: lxd20@cam.ac.uk (L. Dupuy), fourcaud@cirad.fr (T. Fourcaud).

Traditionally, the study of root architecture has focused on the understanding of growth processes from a physiological point of view (Coutts, 1989; Puhe, 2003). As a consequence, previous mathematical descriptions have all been based on the functioning of apices, in terms of branching and orientation in space (Henderson et al., 1983; Diggle, 1988; Pagès et al., 1989; Fitter et al., 1991; Jourdan and Rey, 1997). It is possible to reconstruct entire root systems from these models by using simulation programs. However, the complexity of root growth through time makes it difficult to parameterize such models in relation to nutrient uptake, soil mechanical impedance or plant physiology. In addition, the collection of appropriate root data generally requires excavation of the complete root system through the use

^{*}Corresponding author: Department of Plant Sciences, University of Cambridge, Downing Street, Cambridge CB2 3E4, England. Tel.: + 44 1223 7 66545.

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Nomenclature

- *CV* log likelihood determined using a cross-validation procedure
- d(x) the density function generalized in a space of finite dimension $x \in \mathbb{R}^d$
- E^k error between the target density function and the simulated density function at increment k
- $f^k(t)$ continuous function determining the properties of the *k*th root
- P_N () canonical projection on the subspace that is defined by the variables whose indices belong to the finite set of integers N
- R^k kth root in the root system S

r radial distance

of time-consuming and difficult techniques, e.g. air spade excavation (Rizzo and Gross, 2000) or digitizing (Danjon et al., 1999). As a consequence, there has been an increasing interest in the development of new concepts for the analysis of root architecture using global properties, e.g. fractal geometry (Oppelt et al., 2001; Berntson, 2002) and fractal branching analysis (van Noordwijk et al., 2000). Geostatistical methods have also been found to give good results for descriptions of root distribution in soil (Bengough et al., 2000). Nevertheless, none of these approaches are general enough to consider any given root morphological property in an aggregated way. The use of different types of density, e.g. biomass, volume, length or branching density, can be employed to describe locally the distribution of roots in soil (Danjon et al., 1999). When using different kinds of morphological variables in the calculation of density (other than spatial coordinates), it is possible to consider various properties exhibited by real root systems. Such representations are very promising, as they can exploit fast sampling methods (Pierret et al., 2000) and would be well adapted to problems concerning root/soil interactions (Persson and Jansson, 1989; Wu et al., 1988; Dupuy et al., 2005).

In this paper, we have developed a new modelling approach using general density functions. This approach is based on the mathematical representation of the distribution of root properties in soil, e.g. number, angle or diameter. The method was tested on 50 year old Maritime pine *Pinus pinaster* Ait root systems data. The structural components of these root system had been measured previously. This study case aimed at demonstrating the ability of density functions to represent real root system complexity using a limited number of morphological variables.

S_k root system \hat{S}^k simulated root

simulated root system at increment k variance of the normal probability distribu-

- v variance of the normal probability distribution
- $x^k \in \mathbb{R}^b$ kth branching in a space of finite dimension d. The spatial coordinates represent the properties used to describe the branching at this point
- *z* depth in the soil
- α root angle from the horizontal
- $\Omega, \widetilde{\Omega}$ the set of associated properties; i.e. variables other than spatial coordinates; in a continuous and discretized form
- symbol indicating an output from a simulation process
- $\|\| \qquad \text{Euclidian norm on } \mathbb{R}^n$

2. Materials and methods

2.1. Definition of the root system

In order to use density functions for root architecture modelling, we need to mathematically define root systems as well as single roots and root topology.

We aim to represent a root system S at target time T, as a set of single roots R^k connected together according to a set of relationships τ , called topology, that are inherent to the root architecture. The final root system results from a construction process through time and S(t) defines the root system at each time t of its development ($t \in [0, T]$). S(t) may represent a model of real plant root growth, or may simply be an artificial method resulting at time T in a realistic final root system.

A single root was usually considered as a wire-like object, characterized by additional properties such as diameter, age or branching order (Jourdan and Rey, 1997; Godin et al., 1999; Oppelt et al., 2001). Using the same hypothesis, we considered a root as a trajectory R(t) in an extended space \mathbb{R}^s , where *s* is the number of properties associated to the root model. By convention, $\mathbb{R}^s = \mathbb{R}^q \times \mathbb{R}^{s-q}$, where the *q* first variables are the spatial coordinates (usually q = 1...3 for one-, two-and three-dimensional representations) and the next s-q variables are called the associated variables.

The kth root \mathbb{R}^k of the root system S is then a continuous set of points of \mathbb{R}^s , defined (Fig. 1a) as

$$R^{k}(t) = \{f^{k}(u) \in \mathbb{R}^{s}, u \in [t^{k}, t]\}$$
(1)

where t^k is the date of initiation of the root and f^k is a continuous function of $[t^k, T]$ to \mathbb{R}^s . This function determines the evolution of properties along the root. At time *t*, the complete root system (Fig. 1b), S(t), is then

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