Simulation Models of Plant Root System Architecture and Application: A Review

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Abstract: Quantification of root system architecture is essential for determining nutrient uptake by plant roots. Growing in opaque soils, roots are difficult to observe and interpret. This makes simulation modeling an attractive complementary approach. In this paper, root architecture models were reviewed and methods for constructing geometric models were introduced. *SIMROOT*, an important model for root architecture, was described as related to nutrient acquisition. By employing Extensible Tree data structure implemented on a SGI computer, this model provides vivid graphical visualization of root growing. Furthermore, the model can be developed to evaluate uptake of diffusive nutrients by plants. The application of these models was introduced. Modifications of the model to simulate competition for nutrient uptake within and between roots were also discussed.

Key words: simulation model; root architecture; data structure; diffusive nutrient competition
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Root architecture, defined as the explicit spatial configuration of a root system, determines the availability of plant to capture and transport soil water and nutrition resources[1~3]. The importance of root architecture in plant productivity stems from the fact that many soil resources are unevenly distributed, hence the spatial deployment of the root system determines the ability of a plant to exploit those resources. Root architecture is a fundamental aspect of plant productivity, especially in many environments characterized by low water and nutrient availability.

Because of the difficulty of observing and quantifying the architecture of actual roots, and the complexity and plasticity of roots as geometric objects, making reasonable estimates of the underground structure of plants, without causing much damage to the widespread root system, could be useful in root plant nutrition research[4]. This perspective approach is simulation modeling. Simulation modeling has heuristic value in helping modeler to define relevant process and interaction, and in suggesting issues and hypotheses for experimentation[5].

Pioneering researchers in numerical simulations of root systems used empirical growth rates and branching parameters to simulate the growth of a single root axis and second order branches in two dimension[6,7]. Crop models such as CERES-wheat[8], CERES-maize[9], and SOYGRO, PNUT-GRO, BEANGRO[10] considered root distribution in limited details.

The first model to explicitly consider root architecture in three dimension was ROOTMAP, which simulated the growth and structure for fibrous root systems[11]. And another three-dimensional model was used to simulate maize root system architecture[12]. Root system was a function of both root age and position along the axis.

Fitter et al[2] described a simulation model of root growth that simulated the development of root systems varying in several important architectural features, such as topology, branching angles, and link length. A dynamic root growth model was al-

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so developed to explicitly simulate the spatial root system architecture[13].

By using SGI computer and exploited Extensible Tree (ET) data structure, *SIMROOT*, a geometric simulation model of plant root systems, was developed to describe the three dimensional root architecture in details[14]. Research results showed that this model provided a strong universal platform for the implementation of root architecture studying.

According to the principle of root branching, all root system models reviewed above are geometric simulating models[15]. Another kind of root architecture modeling is based on fractal characteristics of root system[16]. Lindenmayer systems (L-systems) are good algorithms for biological development because of their potential to depict an intricate pattern by simple regularity[17]. Assuming that root branching pattern follows cross sectional area theory, a 'pipe stem' fractal root system model was used to simulate tree root[18]. Based on Leonardo da Vinci's cross section area tree branch-rule, another root architecture model ArtRoot was developed to simulate and visualize three dimension root systems[19]. Hierarchical modeling technique was also exploited to simulate fractal branching pattern of maize root growth[20]. A stochastic model considered growing roots and their microspore distribution[21]. Markov chain was used to simulate root branching[22].

Simulation of root system architecture is heuristic rather than predictive[4,5]. In general, the input parameters of root architecture model could be obtained by measuring empirical data in the field. A number of investigations provided important architectural parameters in soils[23]. These root growth and architectural studies in situ did make good approaches to developing root model.

1 Methods ot simulate root system architecture and diffusive nutrient competition

The essential problem in modeling root system architecture is to store all the information of shape and growth of the system. The methods of geometric simulation model will be described briefly.

1.1 Representation of root system

In most simulation models of root system, the three-dimensional architecture is simulated in discrete time steps. The model tracks each segment by recording its topological position within the root system and its spatial location with the model domain, as well as its age, mass and surface area[24]. When a root system is simulated, it is represented as a set of segments, each segment being the root part generated during one time step. For solid modeling of root system the additional information needed is root radius along the root axis.

1.2 Primary root emission

Different plants have different root emission patterns. The root system models vary with different plants. A maize plant consists of elementary units. The stem base is assumed to be cone-shaped. The roots are emitted from the base to the top of the phytomeres. A common bean plant has four kinds of root type: tap, basal, adventitious and lateral root. If the morphology of root system is taken into account, fibre roots can grow out off all these four types of root.

1.3 Root growth

The length and direction of each growing axis must be evaluated in order to generate a three-dimensional object. The program function that computes axis elongation processes the following inputs: axis order (root type), inter-node rank, location of the axis apex, and root age[12].

The root growth direction can be computed from several directional components. If both root physiological and soil mechanical aspects are taken into account for simulated root system, the root growth can be dissected into three directional components, which are represented by mathematical vectors[13] (Fig. 1).

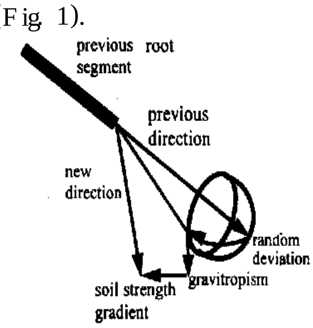

Fig. 1 Components of the growth direction vector

Gravitropism, defined here as root growth under a preferred vertical angle, was attributed to various causes. Genotype soil temperature and light were shown to affect gravitropism.

1.4 Root branching

In terms of geometry, two parameters are sufficient to determine the new direction of the branching root: the axial and radial branching angle, respectively[12]. But unlike the mean frequency of lateral roots which was commonly used to characterize the root branching process in many models[12, 14, 19], this model developed a root branching process which can be more accurately estimated by segmenting roots into length classes in which branching density is computed by Markov chain. As a result the model can be used to account for the distribution of inter-lateral root lengths on the radical[21].

1.5 Data structure-description and algorithm

The data structure is the conceptual object in which data are stored and also referred to as the organization of such objects. To achieve linear growth, the system is traversed at each time step and each root axis is incremented in length. The length increment generated at each time step is stored as a separate segment. The algorithm used to perform the length increment operation computes the growth increment as a function of the root growth parameters for the current root.

Volume and surface area are two important parameters for calculating correlates of root system efficiency. A single axis root may be approximated by a series of truncated cones. Then the volume of a root system is simply the summation of all volumes of these truncated cones in the system. With L as the segment length, R_1 the radius at the beginning of the segment, and R_2 that at the end, the volume of the root system can be computed as

$$V = \sum_{roots}\left(\sum_{segments}\frac{1}{3}\pi\cdot L\,(R_1^2 + R_2^2 + R_1R_2)\right) \quad (1)$$

The surface area can be similarly computed

$$S = \sum_{roots}\left(\sum_{segments}(R_1 + R_2)\sqrt{(R_1 - R_2)^2 + L^2}\right) \quad (2)$$

1.6 Visualization of root system growth

In order to compare a system model to a real root system, graphic visualization can be used as the most straightforward means. The methods used to visualize the model must provide basic geometrical information[25]. The data structure and the visualization code provide continuous viewing of the axial (wireframe) structure of the root as well as continuous solid representation of the root as it grows. For the wireframe rendering mode the tree is recursively traversed, drawing all segments of a root. The routine then proceeds to call itself for the child and right sibling in turn. The concept of the truncated cone is carried into the routines which render the three dimensional solid image of the root system. The routine for rendering a shaded image is identical in layout to that for the wireframe. Instead of a single line, however, each segment is rendered as a truncated cone using a collection of shaded polygons in the form of a triangular mesh[26].

Similar to *SIMROOT*, Program ArtRoot can visualize three-dimensional root system structure associated with another computer program PLUTON[27] that was developed for drawing three-dimensional molecular structures.

1.7 Relationship between data structure and root system topology

In general, utilizing the ET data structure any branching pattern which occurs in nature can be simulated on the *SIMROOT* platform presented here. Because of the amorphous nature of the ET it often takes forms similar to other well-known data structures. Note in particular the case of purely dichotomous branching where the ET degenerates to a form very similar to that of a binary tree. The ET data structure had demonstrated the ability to handle single axis or multiple axe roots as well as a purely dichotomous branching pattern.

1.8 Mathematical formulation of diffusive nutrient movement in soil

We may illustrate the principle of nutrient solute movement by considering a movement of a solute through soil (e.g. by diffusion) in the direction of x axis. If there were two imaginary planes of unit cross-section normal to the axis, and distance δx apart. The volume enclosed is $\delta x \times 1 = \delta x$. Within this volume

$$\left(\delta x\,\frac{\partial C}{\partial t}\right)_x \approx (F_x - F_{x+\delta x})_t \approx \left(-\frac{\partial F}{\partial x}\delta x\right)_t \quad (3)$$

where F_x, $F_{x+\delta x}$ = flux of solute at x, $x+\delta x$; C = amount of solute per unit volume of soil. If movement of solute is by diffusion alone, D is the coefficient of diffusion

$$\text{then} \quad F = -D\frac{dC}{dx} \tag{4}$$

As $\delta x \to 0$, we have Fick's law in one dimension,

$$\frac{\partial C}{\partial t} = -\frac{\partial}{\partial x}\left(D\frac{dC}{dx}\right) \tag{5}$$

Or expressed in cylindrical co-ordinates for a root,

$$\frac{\partial C}{\partial t} = -\frac{1}{r}\frac{\partial}{\partial r}(rF_r) \tag{6}$$

where r is the radial distance from the axis of the cylinder.

2 Manipulation of root architecture modeling and nutrient uptake simulation

2.1 Manipulation of geometric modeling of root architecture

2.1.1 Simulation of the gravitropism of root system

In soil, nutrients have heterogeneous distribution, and show differences in mobility. Also soil mechanical strength and temperature are unevenly distributed[13]. The effects of soil environment on root system architecture and plant genotype adaptability to soil condition can be simulated by the geometric model. By changing root system gravitropism (Fig. 2a) the model was used to study effects of deficiency of soil nutrients on root system architecture. Similarly, by changing directional bias (Fig. 2b), the root growth model can be used to simulate effects of water gradient in soil and mechanical soil strength on root system architecture.

2.1.2 Simulation of root system with different growth rates, internode lengths and the effect of random variation on root system

Root system architecture varies with different genotypes and plant growth conditions. The variation of root growth rates could be easily simulated by the geometric model. Internode length is one of the root branching patterns, whose variation can also be simulated by the geometric model.

When plant roots grow in a soil with different mechanical strength distribution or hard particles like stone, the root elongation trajectories of root growth will change according to heterogeneous soil condition. In root system architectural model, this effect can be expressed as a mechanical vector, or a random deviation. This random variation of root system can also be simulated by geometric model (Fig. 2c).

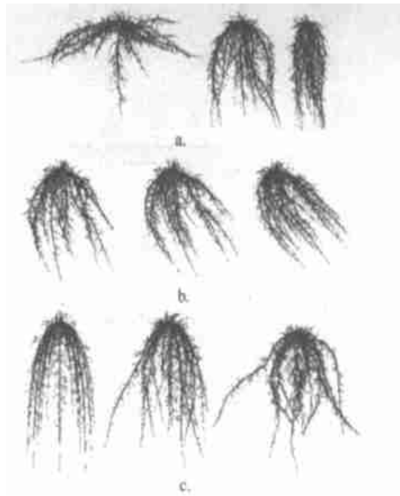

Fig. 2 Visualization of root system depicted different effects of root physiology and soil condition on root architecture

2.1.3 Simulation of multiple root system

Plants always grow in field as a group, and compete for nutrients with the neighboring plants. Simulation of nutrient uptake by root systems is necessary to facilitate quantitative understanding of these processes, to predict the consequences of competition for nutrients, and to prioritize future research on the mechanisms of nutrient competition. By modifying *SimRoot* graphics subroutine with duplicating transformation algorithm, the multiple root systems can be visualized as two or three root systems (Fig. 3).

2.2 Manipulating root morphology

The *SIMROOT* platform has the ability to drastically change the geometric aspects of a simulated root system by changing the functional form of the growth model or simply the parameters of that model. For root morphology modeling, it was regarded as the basic herringbone branch structure. The fiber roots are simply straight branching components that connect to root. This structure is similar to that of lateral roots growing on basal root But the fibre roots are much thinner than roots Therefore the model of root morphology can be simulated as thick root axis surrounded by a lot of very thin fibre roots

Fig 3 Visualization of multiple root system

2 3 Simulating nutrient uptake by single or competing root systems

Most of the nutrient uptake models rely on solute-transport theory as shown in Equation 5 or 6 A major dichotomy in the evolution of these models is that some depend on an accurate numerical method for determining the concentration at the root surface, while others depend on a less accurate, but faster, analytical method

In applying an analytical solution, the zone of nutrient depletion around a root was defined as the radial distance coincident with a 5% decease in the initial concentration This modification was particularly important during the early stages of uptake Nye and Tinker[28] described this modification as an option This model presented a mathematical and conceptual basis for simulating uptake by competing roots These concepts utilized an analytical solution to determine the position of the no-transfer boundary between two competing roots Practically, we can simply calculate the nutrient competition by eliminating the overlap depletion zone volume between two adjacent roots

In order to calculate nutrient uptake of root system, the information needed includes soil depletion zone volume and the nutrient concentration in depletion zone Diffusive nutrients such as phosphorus are generally immobile The availability of these nutrients is typically highest in the topsoil Therefore the nutrient uptake by same volume of depletion zone in topsoil is obviously higher than that in subsoil The total nutrient uptake of root system can be obtained by accumulating all nutrient uptake dispersed in stratified soil A recursive algorithm based on traverse is used to perform calculation for actual depletion zone volume in different layers and multiply with the nutrient concentration in corresponding layers

3 Application of root architecture models

Unlike those models used to generate botanical tree image for exhibiting tree appearance[29], the objectives of root architecture modeling are to simulate the relationship between root architecture and plant physiology, soil property, and acquisition of nutrients and water Practically all root architecture models were developed as platforms for analyzing the plant nutrition processes For example, the root architecture simulation model was employed to evaluate parameters describing the root system architecture of field grown maize plant[30]. Then the model was used to compare simulated and observed horizontal and vertical root map for maize The model was also exploited to study the interaction between rubber seedling root development and assimilate availability[31].

The model developed by Clausnitzer and Hopmanns[13], was initially used to associate plant root growth with soil water potential Late on, this model was expanded to simulate solute transport and nutrient uptake and interactions between plant growth and nutrient concentration[24].

The root architecture simulation model described by Fitter et al [2] also demonstrated the potential utility of geometric models in analyzing the functional implications of root architecture The simulation result of this model showed that changing root architecture would lead to varying root exploitation efficiency[32].

Similar to Fitter's model, a reconstruction model of root architecture based on digitized actual root systems excavated the soil and used growth rules to simulate the native architecture prior to excavation[33]. This model was particularly useful in evaluating root system topology, which would not be changed by excavation

By using *SIMROOT*, nutrient acquisition efficiency of root system was estimated based on carbon rather than root volume[34]. Biomass deposition and rates of root respiration and root exudation were measured along a root axis and the spatial distribution of these carbon costs was used as input functions for the model. *SIMROOT* was applied to fractal analysis of bean roots[4]. The result demonstrated that the true three-dimensional fractal dimension (D3) was significantly correlated with planar (D2) and linear (D1) fractal dimension.

We also modified *SIMROOT* to investigate the effect of root gravitropism on inter-root competition and nutrient uptake for P. The result shows that altered gravitropic sensitivity in P-stressed roots, resulting in a shallower root system, is a positive adaptive response to low P availability by reducing inter-root competition within the same plant and by concentrating root activity in soil domains with the greatest P availability[35]. When plants grow in group, competition for soil nutrient not only occurs within but also between root systems. The result of simulation shows that distance between roots, root shallowness and soil diffusion coefficient have significant effects on multiroot competition, and consequently affect nutrient uptake[36].

In a recent study, the effects of root architecture on P acquisition efficiency of plant by computer simulation together with biological experiments were quantitatively assessed, in order to determine an ideal root architecture for efficient P acquisition under water and P coupled stresses[37].

To sum up, root architecture modeling proved to be an effective method to study plant nutrition problem related to root system architecture.

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根构型模拟模型及其应用

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摘　要: 根构型定量表述是确定植物根系养分吸收的基础。因生长在不透明土壤中的根系难于被观测和分析解释, 这就使得模拟模型成为研究相关问题的一种重要的补充方法。本文对根构型模型作了综述, 介绍了根构型的几何模拟方法, 评述了作为根构型与养分吸收主要模型的 *SIMROOT* 平台。通过采用"扩展树"数据结构并在 SGI 工作站上操作, 这一模型能展现根系生长的生动图形。进而还可将此模型进一步开发用于评价扩散性养分的吸收。根构型模型的应用, 包括我们改进模型对根系内及多根系间的养分竞争进行的模拟, 也作了介绍。

关键词: 模拟模型; 根构型; 数据结构; 扩散性养分竞争