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How to include organ interactions in models of the root system architecture? The concept of endogenous environment

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Abstract – A first generation of models describing the development of the root system architecture did not include explicitly the allocation of resources. These models aimed to mimic the morphogenetic programme, by translating the developmental events into a set of formal production rules. The major strength of these models was their ability to simulate simply the relevant topological characteristics of the root systems. However, the root system development is known to be highly sensitive to carbon limitations. These effects appear first at the root system level, whose global size can be greatly affected by the amount of carbohydrates which are available for the root system development (depending on the carbon budget within the whole plant). Moreover, competition for carbohydrates within the root system accounts for multiple architectural variations which appear in the heterogeneous soil environment. For example, compensatory growth is a common behaviour within root systems. These phenomena can be described by merging “source-sink models” to “morphogenetic rule models”. The morphogenetic rule model simulates the topology of the system (between root connections), whereas the source-sink model simulates the size (growth rate) of the different organs, and allows the definition of an endogenous environment. But in these source-sink models, the definition of the sink strength is a crucial point, which has received only very little attention for the roots. As an alternative to pre-defined potential growth functions, we suggest to use an instantaneous sink strength of each meristem, related to its size. After having justified this approach by experimental data, we show how this sink strength indicator can vary along time, according to the time-dependent availability of carbohydrates. Thus, the sink strength of each axis can be quantified independently, according to its temporal and spatial position within the whole architecture. Although more buffered than the growth rate of the axis, its sink strength can vary during its development course. This very simple model allows the simulation of various growth patterns. It gives an interesting plasticity to the simulated root systems.

architecture / carbon allocation / model / root system / sink strength

Résumé – Comment inclure des interactions entre organes dans les modèles d'architecture du système racinaire ? Le concept d'environnement endogène. Les premiers modèles décrivant le développement de l'architecture des systèmes racinaires ne prenaient pas en compte explicitement la répartition des ressources. Ces modèles avaient pour but de reproduire un programme morphogénétique, en traduisant les processus de développement par un jeu de règles formelles de production. La force principale de ces modèles est leur capacité à simuler les caractéristiques topologiques majeures des systèmes racinaires. Cependant, le développement racinaire est connu pour être très sensible aux restrictions de fourniture en carbone. Ces effets apparaissent premièrement au niveau du système racinaire entier, dont la taille peut être largement affectée par la quantité de glucides disponible durant son développement. De plus, la compétition pour les glucides au sein du système racinaire rend compte de multiples variations architecturales qui apparaissent en sol hétérogène. Ces phénomènes peuvent être décrits en couplant des « modèles source – puits » avec des « modèles de règles morphogénétiques ». Le modèle fondé sur des règles morphogénétiques simule la topologie du système (branchements entre racines), tandis que le modèle source – puits simule la taille des différents organes, et permet la définition d'un « environnement endogène », qui évolue au cours du temps. Dans ces modèles, la définition d'une force de puits est un point central, qui a été

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peu étudié sur les racines. Comme alternative à l'utilisation de courbes de croissance potentielles, fixées à l'avance, nous suggérons d'utiliser une force de puits instantanée pour chaque méristème, liée à sa taille. Cet indicateur peut lui-même varier au cours du temps, de manière tamponnée, en fonction de la disponibilité en glucides. Le modèle très simple qui est ainsi proposé permet de générer des patrons de croissance variés, et donne ainsi une plasticité intéressante aux systèmes racinaires simulés.

architecture / répartition du carbone / modèle / système racinaire / force de puits

1. INTRODUCTION

Modelling the root system architecture is a recent idea, since most models appeared during the last 10 years [6-13].

At the beginning, those models were mostly devoted to the simulation of root spatial distribution in the soil, as inputs for models of water and nutrient uptake. Compared to models dealing with root length density (e.g. [9]), considering the architecture allowed the simulation of new aspects of the root system morphology: spatial structure with local clumping due to the branching system, and between-root connections. Both aspects are considered as very important for a more reliable representation of the uptake system.

From these first models, based essentially on rules which mimic the main features of the morphogenetic phenomena, various improvements have been proposed. Among them, a special effort has been made to include sub-models describing the interactions between the roots and their exogenous environment, the soil. However, the organs of the plant, especially the roots, do not interact only with their exogenous environment, but also with what could be called an "endogenous environment". This endogenous environment is the result of the whole plant processes and interactions between the different organs. In this sense, it is closely related to both structure and function. In order to improve the architectural models of the root system, and to enlarge their scope of interest, a next step in their development would be to account for this endogenous environment.

In this paper, we intend to present very briefly the historical background of these architectural models, which defines a common basis for most of the present developments. Then, we shall discuss why the concept of endogenous environment is important, and how it can be formalised.

2. RULES FOR PREDICTING THE TOPOLOGICAL STRUCTURE OF A ROOT SYSTEM

Root systems are known to exhibit large variations in their shape, if one considers descriptive variables such as

depth, colonised volume, or density. At the same time, root systems are very highly organised structures, from a topological point of view. For example, many authors (reviewed by Coutts [4]) have shown that the tree root systems are made up of very distinct types of roots, and these roots are not connected to each other in a random way. The observation of this strict organisation has motivated modellers to describe the root system development as the result of the combination of local developmental processes that occur in a regular pattern in space and time. These developmental patterns can be formalised by a number of specific rules applying along time on the different parts of the structure.

In order to illustrate this point, we can take two examples: the emergence of seminal and nodal roots on cereal root systems, and the acropetal emergence of branch roots on a given root (acropetal branching).

On the maize root system for instance, the major roots appear sequentially, firstly from the embryo (seminal root), and then from the successive basal nodes, upwards along the shoot. This pattern of emergence is highly organised, since the roots on a given node appear only when the roots of the node just beneath have completed their emergence. Furthermore, the rank of the node where emergence takes place at a given moment is tightly correlated to the phyllochron or cumulated thermal time experienced by the plant [14]. Thus, this pattern of emergence can be translated by a simple rule specifying that each node can develop roots during a given time (age) window.

Regarding branching of existing roots, a very common process occurring in almost all root systems is acropetal branching, in which lateral roots emerge in a restricted region along the root, at a given distance behind the apex. This phenomenon is well mimicked if one considers that root meristems are initiated as primordia in very young parts of the roots (age window for initiation on the root segment), and then the primordium will develop and emerge as a new lateral root after a given duration (developmental time).

Both processes are examples of stable processes, which occur in a large range of growing conditions, and lead to highly determined topological structures. Thus, they are worth formalising through morphogenetic rules,

such as production rules translated with the L-System language [16]. These rules are probably an economic way for simulating the organogenetic processes at this organisation level (organ level), processes which involve multiple interactions at lower levels (e.g. cell level).

Applying these very simple production rules with different sets of parameters allow the simulation of very different shapes, as shown by Pagès and Aries [13] in the case of root systems.

3. INCLUSION OF SUB-MODELS FOR DESCRIBING THE SOIL-ROOT INTERACTIONS

Since the soil is a very heterogeneous medium, and it is well known that this heterogeneity in physical and chemical properties can have heavy consequences on root development, the simulation of the root system architecture requires the use of sub-models relating the application of developmental rules to the most influential soil properties. This approach has been developed by Diggle [6] and Pagès et al. [14] concerning the soil temperature, which affects directly the root growth rate. More recently, other environmental variables, such as the soil bulk density and the soil matric potential have been used to model the local growth rates [5].

These models assumed that the global architecture of the root system can be described as the result of local and independent influences. This approximation is probably valid in some situations, depending on the required precision and the level of heterogeneity.

4. EVIDENCE FOR DEVELOPMENTAL CORRELATIONS

It is quite obvious that the different parts of the plant do not grow independently, even though these interactions result in an equilibrium between plant organs and a well-defined morphology in a large range of situations.

Without reviewing the literature, we can take three examples which reveal different aspects of these correlations.

The first example is on the developmental response of young oak root systems where the taproot growth has been hindered by an obstacle. In this case [15], there was both a direct response of the taproot to the obstacle, since its growth was blocked or decreased, and an indirect response of some lateral roots near the taproot tip whose growth was promoted (*figure 1*). Thus, lateral roots could exhibit a developmental response to a stimulus, which did not relate to their exogenous environment,

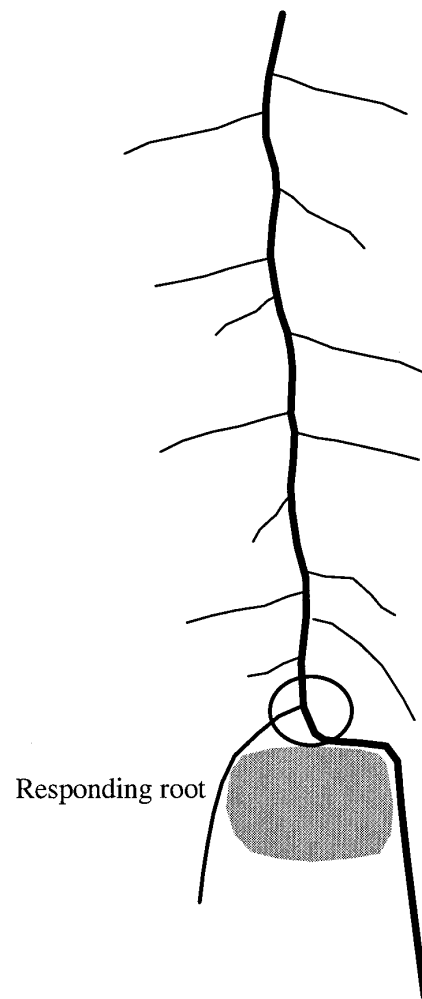


Figure 1. Growth correlations at short distance in an oak tree seedling, between the taproot and its most distal lateral roots (after Pagès et al. [15]). The growth of the most distal lateral root was promoted after the taproot has been hindered by an obstacle. The circle represents the apparent extension of the interaction zone.

but only to that of their mother root. The global response was essentially local, since only the laterals close to the tip of the mother root responded.

In the second example [7], the growing medium of the root system was artificially made heterogeneous by the means of a hydroponics system, in which the major part of the root system bathed in a nutrient solution without nitrogen, whereas a smaller part bathed in a nitrogen-enriched nutrient solution. The roots growing in this enriched medium exhibited a clear direct response to their environment with a higher growth rate, whilst the

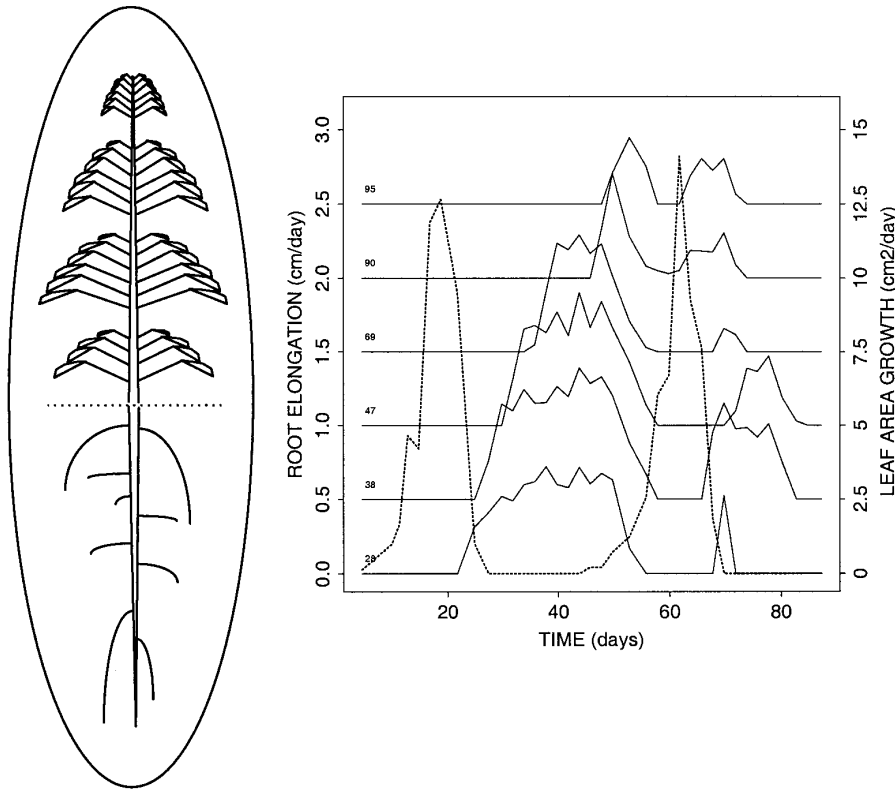


Figure 2. Growth correlations at the global plant level in a rubber tree seedling, schematically represented in the left part of the figure. On the right, relationship between cumulated leaf area growth (dotted line) and individual root growth (solid line) for several lateral roots along the taproot. The numbers correspond to their rank, from the base to the apex (after Thaler and Pagès [19]).

roots growing in the poorer medium, especially at the vicinity of the enriched zone, showed a restricted growth. Here again, the environmental heterogeneity resulted not only in a direct response to the environment, but also in a more global response within the root system, via the alteration of an endogenous environment.

In the third example [19], the heterogeneity of the endogenous environment was revealed by temporal variations of the leaf growth rate, in a typically rhythmic species, the rubber tree (*Hevea brasiliensis*). In young seedlings of this species, the individual root growth rates were highly restricted while the leaves were growing (figure 2). Thus, in this third example, growth correlations manifested at the plant level, inducing a synchronism in root growth.

Therefore, these three examples show the existence and various aspects of an “endogenous environment” of the organs, which may vary in space and time according to the structure and function of the global plant. Heterogeneity in environmental conditions usually reveals these correlations, but they may also manifest through temporal variations in the organ functioning. These correlations have heavy consequences in architec-

tural modelling. In particular, it is not possible to extrapolate direct local relationships between developmental behaviours of the plant organs and environmental characteristics, since the behaviour is sensitive to the status of the global plant. It also raises the question: how to represent such a concept in future models?

5. MERGING PREVIOUS MODELS WITH A SOURCE-SINK APPROACH

In addition to the previous modelling approaches, which are based on morphogenetic rules extended by sub-models describing the local interactions between the organs and their environment, a representation of the endogenous environment is required to account for growth correlations.

The general principle is to simulate a dynamic topological network of organs at various stages using morphogenetic models, and to simulate the growth of these organs (and eventually their dimensions) using the source-sink concepts [8]. Several attempts to simulate such processes have been presented during the last years ([2, 11, 17, 18]).

The carbohydrate resource is the major substrate for energy and material requirements, for which root systems are entirely dependent on shoot systems. Furthermore, root systems are known to be very sensitive to carbohydrate restrictions, regarding both growth and functioning [4]. Therefore, the carbohydrate resource availability is particularly interesting to consider in a first step, as a main determinant of the endogenous environment.

The source of carbohydrates can be considered as unique, located at the collar, if one considers only the root system development. Conversely, the sinks are distributed throughout the root system, considering that each root segment is a sink for maintenance respiration and possibly for radial growth, and each meristem is a sink for axial growth (structure and associated energy). In source-sink models, such as TOMGRO [10], maintenance respiration is generally considered as a sink with highest priority, and its demand is satisfied first, by subtracting the total maintenance respiration cost from the total pool of carbohydrates.

Regarding growth, the sink strength is a key point in those source-sink models. It determines largely the simulated allocation rules. It relies generally on potential growth curves, which allow the calculation of a potential growth rate at each time step, and so a carbohydrate demand. This approach is very suitable for organs with a determinate growth pattern, such as fruits or leaves,

which are known to stop growing after a time duration, whatever the conditions. The potential growth curve can be estimated by the actual growth curve of the largest organs, which are assumed to grow without carbohydrate limitation. In the case of root elongation, the problem is more complex, because roots cannot be considered as determinate growth organs, even though most of them eventually exhibit a determinate growth pattern. The problem is that their growth pattern is not so strictly defined as those of fruits and leaves. Thus, a predefined growth curve would lead to underestimate their growth plasticity. For these reasons, Pagès [12] and Thaler and Pagès [20] suggested to define an instantaneous growth potential, related to the apical diameter of the root (*figure 3*). This diameter, measured at the distance from the tip corresponding to the meristem level, is a good external indicator of the meristem size, and particularly of its number of meristematic cells [1]. From this instantaneous potential growth rate, it is possible to calculate a corresponding carbohydrate demand, taking into account both the amount of structural carbohydrate and the energy cost. The global demand of the root system, calculated as the sum of all root individual demands, can be compared to the carbohydrate availability, and a satisfaction coefficient (value between 0 and 1) is calculated for the given time step (ratio total availability/global demand). In this model, the apical diameter of the roots, and thus their sink strength for the next time step, is modified according to the value of the satisfaction

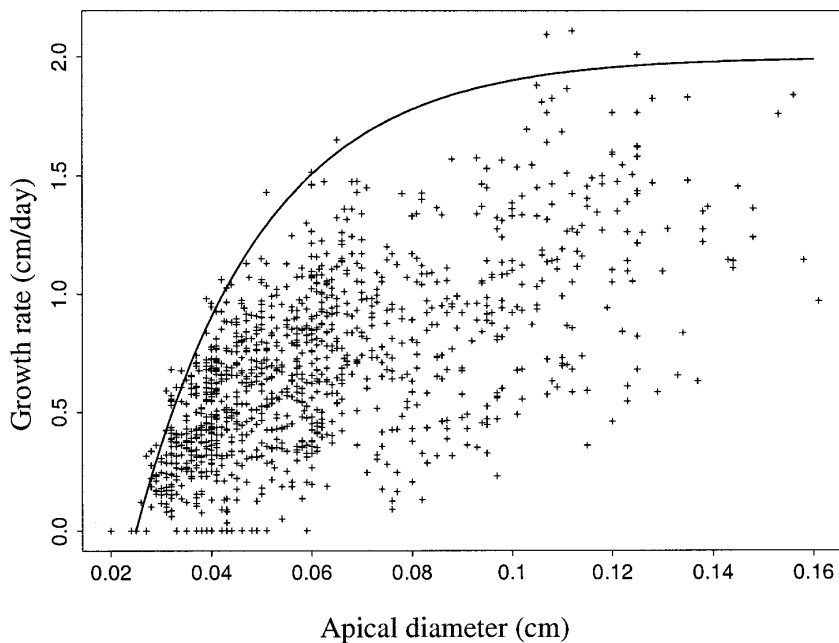


Figure 3. Relationship between root apical diameter and root growth rate in rubber tree seedlings. Each dot represents a root at a given time. The curve represents a theoretical potential growth rate function (after Thaler and Pagès [19]).

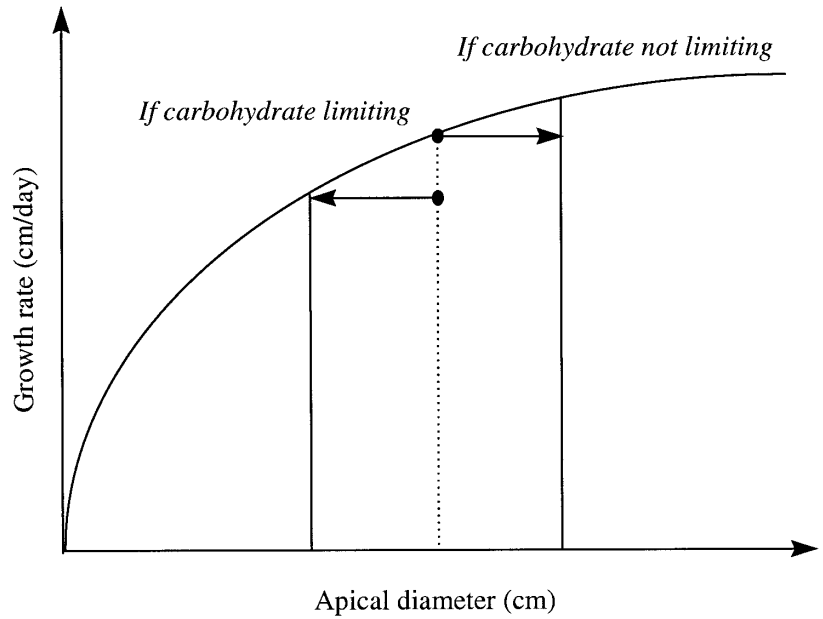


Figure 4. Modelling the time-dependent variations of apical diameter. At a given time step, a demand is calculated from the present apical diameter. When the demand is satisfied (carbohydrates not limiting) the potential curve is reached and the diameter increases. Conversely, when carbohydrates are limiting, the potential curve is not reached and the apical diameter decreases (after Thaler and Pagès [20]).

coefficient (*figure 4*). When the value equals 1 (the root meristem is entirely provided), the apical diameter increases, and so the sink strength will become higher next time. Conversely, when the satisfaction coefficient is lower than a given threshold, the root meristem is considered as poorly supplied, and the apical diameter decreases, inducing a decrease of the sink strength for the next time. This feedback effect of the carbohydrate supply on root meristems allows the simulation of various root growth patterns, which depend on the location of the root within the architecture (both in space and time). Moreover, this simulation system allows the representation of nearly similar behaviours between root elongation and root apical diameter, as observed in both oak [12] and rubber [19] trees. It allows also the representation of spatial rhythmic variations that can be observed within the root system (*figure 5*).

In this type of model, the endogenous environment is represented in a very simplified way, by a global and time-dependent carbohydrate availability. This environment is the result of (1) the source functioning, (2) the morphogenetic programme which generates continuously new sinks, (3) the response of these sinks to carbohydrate availability, and (4) the response of the sinks to the exogenous environment.

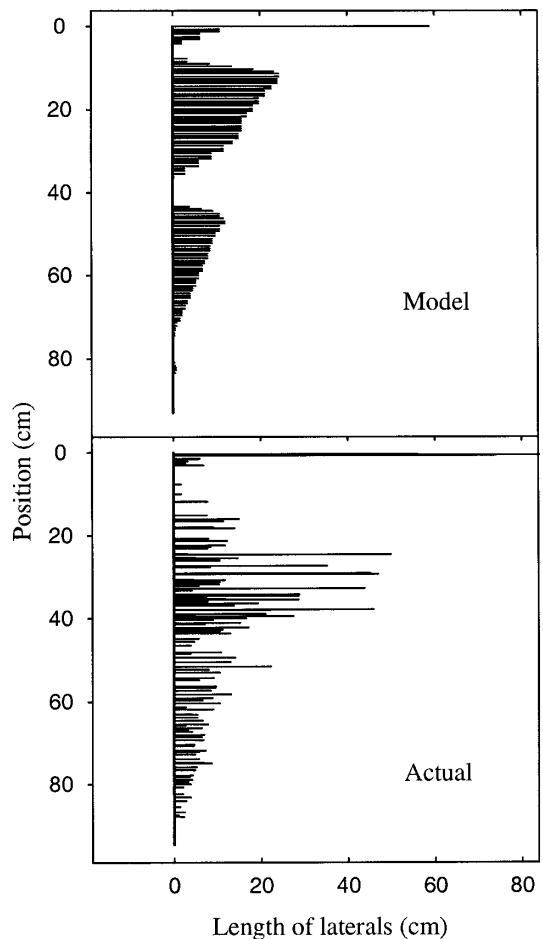


Figure 5. Comparison of simulated and actual distributions of lateral root length along the taproot for rubber tree seedlings (after Thaler and Pagès [20]).

6. CONCLUSION AND PERSPECTIVES

During the last ten years, the models of root system architecture have been improved largely. They are becoming helpful tools for studying the root system development thanks to the simultaneous simulation of organogenetic processes, interactions between the organs and their environment, and more recently interactions between these organs.

The representation of the interactions between these organs is probably one of our challenging tasks during the next years. For that, we think that it is promising to formalise further the concept of endogenous environment as a complement of the more classical concept of exogenous environment, which most of the works have focused on to this date. This endogenous environment has to be related to the so called "complexe corrélatif", which Champagnat et al. [3] defined as the result of the multiple and changing influences of the organ network within the plant.

A part of this environment is determined by the competition for the necessary resources, especially carbohydrates in the case of root systems. No doubt that other resources and signals can play a substantial role.

The current attempts have considered a global endogenous environment, which is shared by all organs at the same time, whatever their position within the architecture. This is a completely opposite direction to most structure-based models in which all organs are assumed to be independent [6]. Some compromises should be found probably between these two extreme modelling approaches. Experiments have shown that growth interactions operate at variable distances [15-19]. The topological network is an important information for such simulations, since we can observe for instance some particular relationships between a mother root and its young laterals.

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