



Why are laterals less affected than main axes by homogeneous unfavourable physical conditions? A model-based hypothesis

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Abstract

When plants develop in strong soils, growth of the root system is generally depressed. However, branching and elongation of branches are often less affected than growth of the main axes, whenever the whole root system encounters even-impeded conditions. On the basis of a model simulating root growth and architecture as related to assimilate availability, we propose a simple hypothesis to explain such behaviour. In the model, growth of each root depends on its own elongation potential, which is estimated by its apical diameter. The potential elongation rate–apical diameter relationship is the same for all the roots of the system and is described by a monomolecular function. Our hypothesis is that the effect of soil strength can be simulated by introducing an impedance factor in the definition of root maximum potential elongation rate, common to the whole root system. When such impedance factor is applied, it affects more the potential of larger roots (main axes) than that of thinner roots (secondary and tertiary branches). Simulations provided in high impedance conditions led to root systems characterised by short taproots, whereas growth of secondary roots was unaffected and growth of tertiary roots was enhanced. Actual branching density was also higher, although branching rules have been unchanged. Such simulated systems were similar to that observed in strong soils. Friction laws or pore size can be involved in the larger reduction of the potential growth of main axes. Moreover, when growth of main axes is restricted, assimilate availability becomes higher for branches and that could explain that their growth could be increased in a homogeneous strong soil.

Introduction

When plants develop in unfavourable physical conditions, characterised by a high soil strength or impedance, growth of the root system is depressed, (Bengough and Mullins, 1990; Goss, 1977). However, the different root types and the different developmental processes seem to be differentially affected by soil strength. Branching (initiation and/or development of lateral meristems) is often enhanced (Goss, 1977) and elongation of branches is less affected than that of main axes (Misra and Gibbons, 1996) and could be sometimes enhanced (Goss and Scott Russel, 1980). Mechanisms relying mechanical impedance to the elongation of main axes have been studied by many authors (Wilson et al., 1977; review by Bengough and

Mullins, 1990): it is considered that physical constraints directly reduces cell elongation rate and/or division rate. On the other hand, explanations of the apparent increase in branch development in such conditions remain scarce (see, for instance, the review by Bennie, 1996). Competition for resources and active correlations (decrease of the inhibition exerted by main axes on the development of laterals) can explain the observed patterns when main roots encounter unfavourable conditions whereas laterals remain in better conditions (Riedacker et al., 1982) but such compensatory mechanisms are not likely to explain the relative, or even absolute, positive effects observed on laterals placed in the same environment than main axes. Some authors have proposed that growth of primary axes can induce horizontal ‘cracks’ in the surrounding

soil hence providing a local reduction in impedance that could be favourable to the growth of laterals (Barley et al., 1965; Misra and Gibbons, 1996). But such explanation seems limited to very particular conditions. A more suitable hypothesis is that pore size in the considered soils is such that main and larger roots are impeded, but not lateral, thinner roots (Bengough and Mullins, 1990). However, the penetration ability of roots is known to increase with root diameter (Materechera et al., 1992) and this should rather be favourable to the elongation of main axes.

The work presented herein is an analysis of the different responses of taproot and laterals facing a homogeneous constraining soil, on the basis of carbohydrate allocation within the root system. To this end, we used a specific model that describes rubber tree root system architecture and development as related to assimilate availability (Thaler and Pagès, 1998).

The model

Briefly, the model (Thaler and Pagès, 1998) developed for rubber tree (*Hevea brasiliensis*), considers each root to be a component of a system of axes – characterised by its spatial position and connections within the system – and as an individual sink competing for carbohydrates. Architectural bases of the model were developed by Pagès et al. (1989) and adapted to rubber tree by Pagès et al. (1995). At each time step, the root system, represented as a set of segments, is extended by the application of developmental processes: emission of new roots, growth and branching. The emission process generates the beginning of seminal (taproot and early secondary roots) and adventitious (late secondary roots) axes. Branching is assumed to occur accropetaly and is described by the inter-branch distance, which is specific to each root type. Root typology was established by Le Roux and Pagès (1994). The model developed by Thaler and Pagès (1998) differs with the previous architectural models by its way of simulating the growing process. In the present model, elongation and radial growth are no more simulated by typical growth functions of time, which parameters are fixed at the beginning of each root's growth. In order to rely root growth to assimilate availability, each root is assumed to be an individual sink competing for carbohydrates. The carbon requirements for growth are satisfied on the basis of the demand of the growing organs, which include the carbon involved in structural growth and the carbon used by growth respiration. Daily carbohydrate

availability after maintenance respiration is calculated together with carbohydrate demand for the growth of leaf, stem and root. Growth occurs at potential rate for all sinks when sufficient carbon is available. If this is not possible, the fraction of potential growth that can be supported is calculated as the ratio of the carbon available after maintenance respiration to the sum of carbon requirements for potential growth of all the sinks. Since this fraction is the same for all sinks, variations in relative growth rates between organs depend on variations in the daily potential growth of each sink. Carbohydrate input is provided by seed reserves, photosynthesis and plant reserves. In the present version of the model, daily photosynthesis is proportional to leaf surface, specified by a specific rate which variations reflect light changes. The reserves are released according to constant rates. Empirical logistic relations fitted to observed growth describe stem potential elongation and leaf area potential growth. Stem potential radial growth and leaf specific mass potential growths are assumed to be constant.

The key point of the model is the determination of each root's growth potential. In most of allocation models, this potential is estimated by growth curves in conditions of non-limiting assimilate supply (Marcelis et al., 1989). But such a method is hardly suitable in our case since extensive variations in both growth rate and duration were recorded within root types (Le Roux and Pagès, 1994), so that growth curves for faster and longer-term growing roots are not likely to represent the growth potential for a given root type. Observed relationship between root elongation rate and apical diameter (Thaler and Pagès, 1996b) led us to consider the apical diameter of any root to be a convenient morphologic indicator of its elongation potential (Thaler and Pagès, 1998). The upper limit of the plot representing elongation rate versus apical diameter is considered to represent the potential elongation rate corresponding to each apical diameter. This relation is described by a monomolecular function which reflects the strong increase in potential elongation rate with diameter for low diameters (< 0.7 mm), and the lower increase for larger diameters (Figure 1).

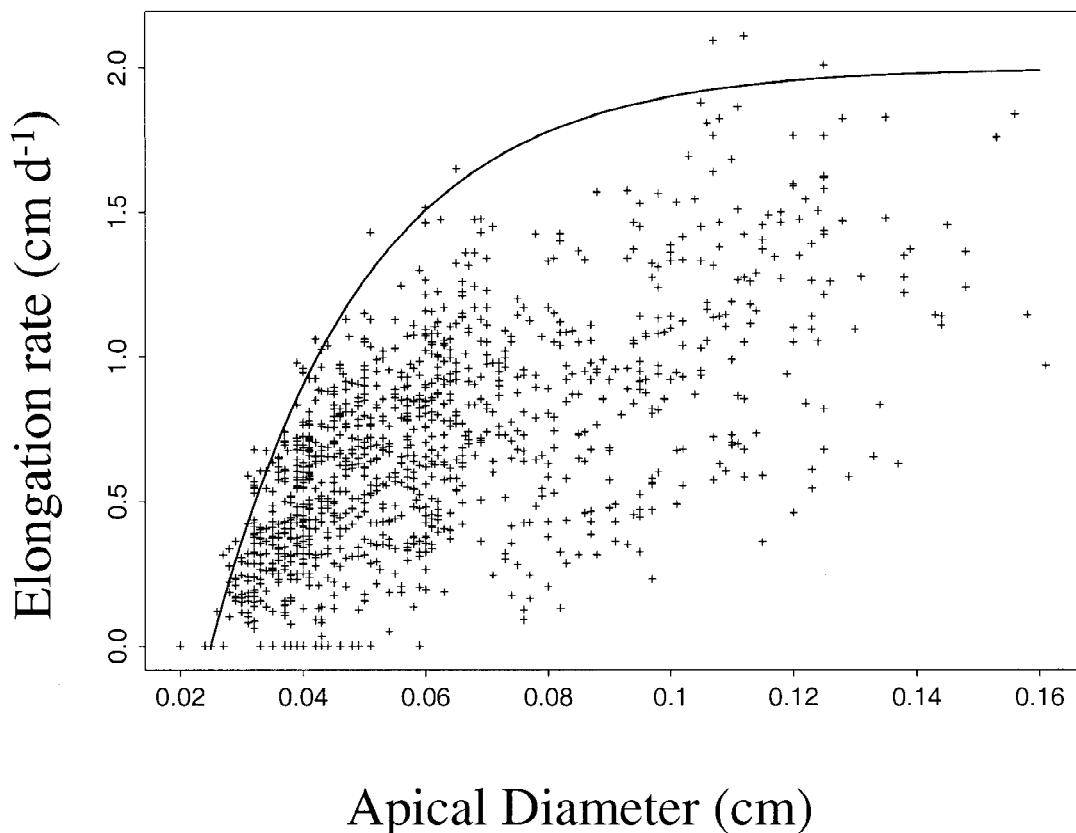
$$Ep = E_{\max} * (1 - \exp^{-b(D-D_0)/E_{\max}})$$

Ep: potential elongation rate (cm d^{-1})

E_{\max} : maximum potential elongation rate (cm d^{-1})

D: apical diameter (mm)

D_0 : threshold diameter under which the root does not elongate (mm)



$$Ep = Emax \times (1 - \exp(-b(D-D0)/Emax))$$

Figure 1. Apical diameter (cm)–elongation rate relationship for taproots and secondary roots. Each point represents data for one root at a given date. At each date 6 roots were measured on each plant (10) of the experiment. The envelope curve (—) is a monomolecular function adjusted to 95% quantiles.

b: initial increase in elongation rate with diameter (slope at threshold diameter, cm d^{-2}).

Moreover, the potential growth itself is controlled by the supply/demand ratio. For a given root, the apical diameter is not constant, but increases when this ratio is high and decreases when it is low (Thaler and Pagès, 1996b). Variations in apical diameter are simulated by successive functions:

During primordium development: for each root type, a potential initial (at emergence date) diameter and a daily potential diameter increment are defined. When assimilate supply is higher than demand, the primordium grows at its potential rate. When demand is higher than supply, a proportion of the potential increment is achieved. If the diameter at the emergence

date is lower than a fixed threshold, the root fails to emerge.

After emergence: from its value at emergence, the diameter for each root will increase when the supply/demand ratio is higher than a given threshold, or decrease when this ratio is lower than another threshold. These thresholds and the (constant) increasing and decreasing rates are input parameters of the model. The elongation rate–apical diameter relationship and the rule describing the evolution of the apical diameter are common to all the root types described by Le Roux and Pagès (1994) on rubber tree: taproot, early secondary roots (ESR), acropetal secondary roots (ASR), late secondary roots (LSR), tertiary roots for all secondary root type, and quaternary roots.

However, each root type has a specific initial (at emergence) potential diameter: 2.0 mm for the taproot, 0.8 mm for the ESR, 0.5 mm for the ASR and 0.37 mm for tertiary roots. Thereby, starting from an initial value depending on root type, the potential elongation rate for all roots within the system will vary following a unique rule. Growth dynamics of any root is so controlled daily by a two step variation according to assimilate availability:

- variation in the proportion of potential growth actually achieved
- variation in the potential growth itself.

(Variation in apical diameter for the next time step.) We used this model to study the effects of uniform mechanical constraints on the development of a root system. We have considered that, from an intrinsic potential, external factors such as soil strength determine a conditional potential, as proposed to model the influence of temperature in classical growth models (Grossman and DeJong, 1994). We made the hypothesis that the variation induced by soil impedance affects the maximum potential elongation rate (E_{max}) defined for all the roots of the system. Introducing an impedance factor (I) to the definition of the potential elongation rate simulates such variation.

$$E_{max} = I * E_{max}$$

$$Ep = I * E_{max} * (1 - \exp^{-b(D-D_0)/I * E_{max}})$$

We made no additional hypotheses on possible active correlations or specific effects on branching or any different behaviour between the different root types in response to the level of mechanical impedance.

Methods

Materials and methods used to establish the model and its parameters were described in Thaler and Pages (1996a,b, 1997).

We have simulated root systems developing with different impedance factors (I), using a set of default values for the other parameters of the model (Thaler and Pagès, 1998), except for E_{max} which was chosen as 2.0 cm d^{-1} (default value: 1.7 cm d^{-1}). Three impedance factors were considered: 1.0 (low impedance), 0.75 and 0.5 (high impedance). Duration of the simulation was 77 days. The model displays graphs representing the kinetics of mass, length, diameter for individual organs or per root type, but also the structure of modelled systems, i.e. the position of the

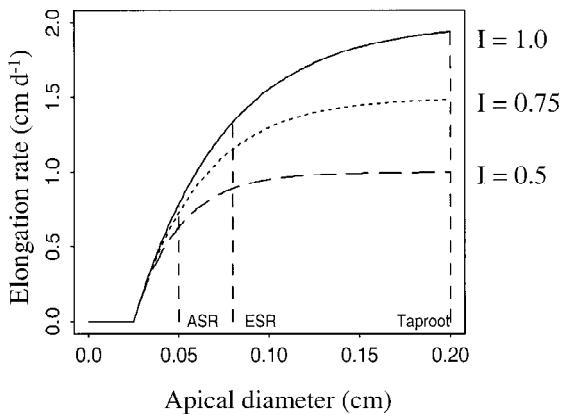
different axes and the connections between them. Geometrical parameters (growth and branching angles) were not taken into account in the present work. Analyses rely on the examination of these graphs.

Results

When I varied between 1.0 (low impedance) and 0.5 (high impedance), curves representing the elongation rate-apical diameter relationships diverged more markedly for diameters larger than 0.5 mm. Therefore, the elongation potential for roots with large diameter, like taproot, was more sensitive to impedance variations than the elongation potential for thinner roots like ASR and tertiary roots (Figure 2).

The overall growth of the root system, characterised by its dry weight, was slightly affected by variations in I (data not shown). On the other hand, Figure 3 shows that the different root types had various reactions to changes in this parameter: elongation of taproot was strongly depressed when impedance increased, secondary roots were slightly affected, whereas elongation of tertiary roots was enhanced (temporal fluctuations in root growth rates were due to variations in assimilate availability consecutive to the rhythmic development of the shoot) Thaler and Pagès, 1996a. Conditions that lead to a decrease of the maximum potential elongation of roots thus resulted in root systems with a relative (secondary roots) or absolute (tertiary roots) enhancement of the growth of branches.

Figure 4 shows the structure of the root systems resulting from simulations with impedance factor of 1.0 and 0.5. Tertiary roots were not shown. Differential responses of secondary roots and taproots resulted in clearly different root structures. When impedance was low ($I = 1.0$), the root system was characterised by a long taproot bearing short branches, whereas higher impedance ($I = 0.5$) resulted in a shorter taproot bearing a larger proportion of longer laterals. Length of the longest lateral roots, the ESR, was similar in both cases, so that the horizontal expansion/vertical expansion ratio was largely higher with higher impedance. Moreover, when impedance was low, some segments of the taproot were unbranched (the branches failed to emerge since assimilate availability was too low during the development of their primordium, as a result of high demand exerted by taproot and by the rhythmic growth of shoot). While such bare segments were very short with higher impedance as a result of lower de-



$$Ep = I \cdot Emax \cdot (1 - \exp(-b(D-D0)/I \cdot Emax))$$

Figure 2. Evolution of simulated potential elongation rate (cm d^{-1}) as a function of apical diameter with three impedance factors: 1.0 (—, low impedance); 0.75 (- - -, moderate impedance); 0.5 (---, high impedance).

mand exerted by taproot. Higher impedance can so result in root systems with a higher overall branching density, although the process of branching has been unchanged.

Discussion

Simulations produced with a model merging allocation and architectural features, showed that root development patterns encountered in uniform constraining soils can be reproduced by introducing an impedance factor which reduces the maximum potential elongation rate common to all the roots of the system.

Such factor induces larger variations in the potential and actual growth for larger, fast growing roots – as taproots – than for thinner, slow growing roots as ASR and tertiary roots. Such behaviour of the model resulted from the observed differences between the initial apical diameter of the different root types (Le Roux and Pagès, 1994).

By this way, we can reproduce root development patterns encountered in impeded soil: decrease in the elongation of main axes, increase in the branching density and increase in elongation of branches, leading to less hierarchized root systems (Misra and Gibbons, 1996). It was not necessary to introduce hormonal correlations or to suppose differences in the impedance faced by main axes versus laterals.

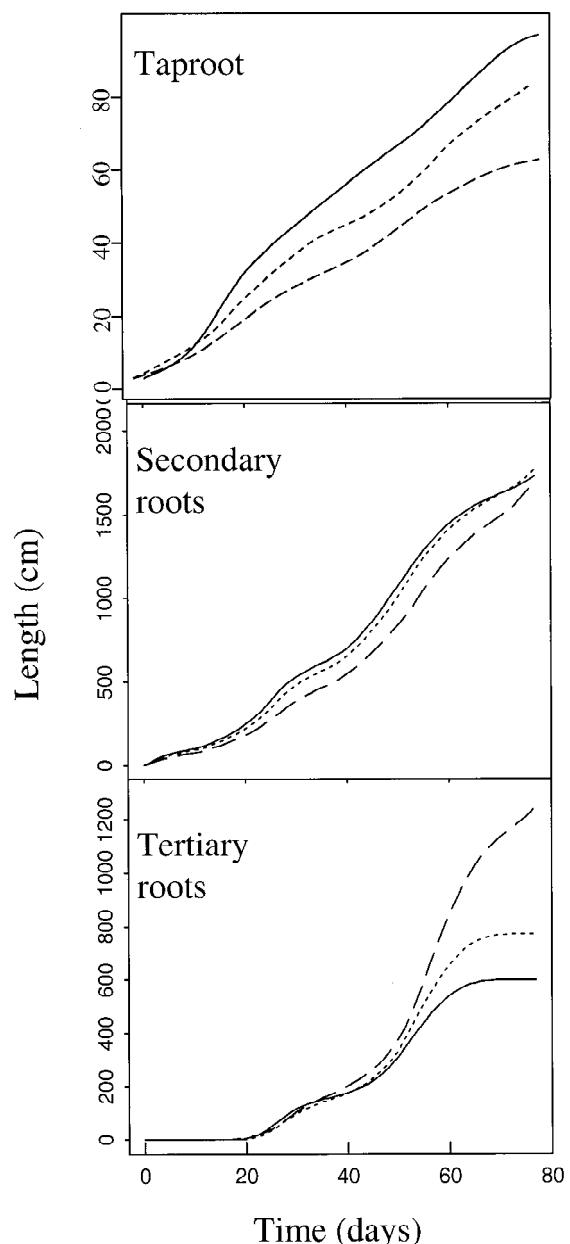


Figure 3. Evolution of cumulated length for the taproot, secondary roots and tertiary roots of root systems simulated with three impedance factors: 1.0 (—, low impedance); 0.75 (- - -, moderate impedance); 0.5 (---, high impedance).

An explanation of the higher decrease recorded for main axes could be that the friction encountered by a given root is proportional to its elongation rate, so that fast growing roots could be more affected by soil strength. In the same way, pore size in the con-

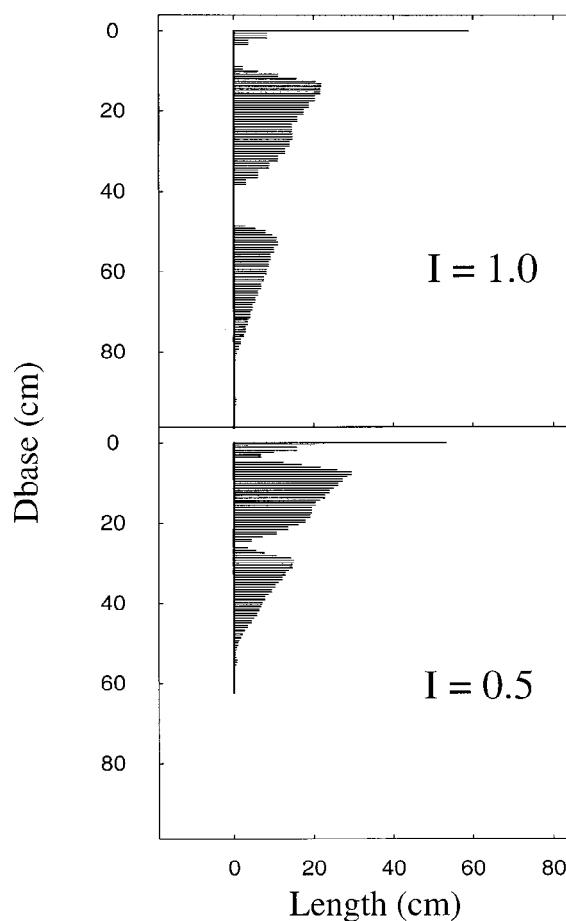


Figure 4. Simulation of root development with two impedance factors: 1.0 (low impedance) and 0.5 (high impedance). Horizontal lines represent the final length (cm) of each secondary roots as a function of its insertion position (Dbase, cm) along the taproot, shown by the vertical line.

sidered soils could be such that main and larger roots are impeded, but not thinner roots.

Moreover, in our model, consequences of such limitation of taproot growth potential will result in a decrease of its carbohydrate demand also. Therefrom, the availability of carbohydrates is likely to become higher for the growth of secondary and tertiary roots. This results in the absolute increase in the length of laterals that can be observed in a homogeneous unfavourable environment (Goss and Scott Russel, 1980). Such behaviour is reinforced since we consider sink strength of the different roots to be controlled by assimilate availability: taproot lower demand induced by high impedance will result in an increase in the potential growth for its branches, without explicit in-

vovement of hormonal correlations. Since the growth of lateral primordia also depends on assimilate availability, a decrease in taproot demand allows a larger number of lateral primordia to reach the threshold diameter which is required to the emergence of the root, thus increasing the actual branching density, as observed in media with high mechanical impedance (Goss and Scott Russel, 1980; Misra and Gibbons, 1996).

Generally speaking it can be supposed that axes with high growth potential are likely to be dependent on external conditions, which could limit the achievement of such potential, while thinner roots are not or few dependent on soil conditions, but are limited by their own growth potential, dependent on meristem size, estimated by the apical diameter (Thaler and Pagès, 1997).

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