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Links between root developmental traits and foraging performance

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Summary

We designed a simple dynamic and stochastic architectural model with six parameters to link the foraging performance of root systems to their developmental processes. Soil foraging was quantified by the volume enveloping the roots until a given uptake distance. Many simulated architectures were obtained by combining four different values for each parameter.

The rate of soil colonization was mainly defined by individual root elongation rates and inter-branch distances. Less intuitively, we showed that differentiation of elongation rates among the roots increased this colonization rate. Uptake efficiency - the ratio of the actual colonized volume to the volume of a unique cylinder with the same length and a radius corresponding to the uptake distance- declined with root system size. Nevertheless, large variations in efficiency existed among root systems for a given size, typically in a 4 to 10-fold range. Therefore, the “efficiency gain” was defined as the deviation from the average trend in efficiency versus size. Between-root differentiation in elongation rates increased this gain. The level of hierarchy between mother and lateral roots as well as the variation of elongation rates among lateral roots were also shown to contribute to this optimization. Several parameter combinations could lead to similar efficiency gains.

Key words: Root uptake; Root system architecture; Virtual plants; Water and nutrients;

Introduction

Water and nutrient uptake is a major function carried out by plant root systems. The development and specialization of root systems allowed plants to colonize many environments in which water and nutrient resources can be scarce and variable in space and time.

At the plant and population levels, this uptake function is affected by both the uptake capacity of individual roots or root parts and by the entire root system architecture (structure and shape) including its dynamics (Lynch, 2007).

The relationship between the architecture and the uptake capacity of root systems has often been considered from a spatial point of view using a number of criteria focusing on the root system shape, particularly extension and distribution. Thus, root depth and root length density distribution are the most common descriptors used as inputs to quantify water and nutrient uptake in crop models (Asseng et al., 1997). Predicting uptake from the spatial distribution of roots relies on the implicit assumption that transport from the soil to the root is the bottleneck in the whole uptake process. Even though one can assume this shortcut in many situations, especially when soil resources are scarce, the quantification of the colonized soil volume and the root length density distribution raises questions. Root length density is generally estimated through measurements on soil samples at a given scale (typically decimeter scale), and is extrapolated at other scales -particularly smaller scales (some millimeters)- for predicting uptake of resources with a low or intermediate mobility (Barber, 1995). Moreover, since observation methods do not preserve the spatial structure of root networks in the soil, we tend to have a biased vision of the actual root distribution and even to ignore it.

Another view on the relationships between root system architecture and uptake capacity was developed by Fitter et al. (2D approach by Fitter, 1987; 3D approach by Fitter et al., 1991) and Berntson (1994). In these approaches, not only was the spatial distribution of roots considered, but also the topological characteristics of root systems. The root system was considered as a binary tree with nodes (branching points) and links (root segments connecting the nodes or apices). These trees were characterized by topological indexes to quantify their overall size and the hierarchy between mother and lateral roots, with two extreme branching patterns (herringbone and dichotomous tree). In addition to topology, metric characteristics were given through internode lengths and branching angles. These studies showed that the foraging efficiency of root systems depends on their topological

characteristics: herringbone systems are more efficient at colonizing the soil and capturing nutrients but more expensive and less efficient at transporting these nutrients to the shoot system. Some experimental data validated the hypothesis that one or the other system (herringbone or dichotomous) could be favored by some plastic plant species, which, depending on the resource availability in the soil medium, tended to fit the root system to the situation (Fitter, 1986). Berntson (1994) underlined the necessary trade-off between two antagonistic properties: uptake potential (related to root system size) on the one hand, and uptake efficiency on the other hand. By studying the carbon cost variation of individual root pieces associated with growth and maintenance, Nielsen et al. (1994) advocated the use of architectural models for integrating cost and benefit aspects at the root system level, and made some illustrative calculations. Beyond their specific results, all these studies demonstrated that an important characteristic of roots is that they are linked in a structured branching system and that it is important to consider this in models. In addition, Grabarnik et al. (1998) pointed out that the spatial aggregation of individual roots is a direct consequence of the branching pattern of root systems.

In order to build a more dynamic and developmental point of view, it is worth starting from the elementary building processes which make sense for those who study root development, give constraints to the spatial structure of root systems and contribute to their originality. For example, it is rather trivial to assert that root system extension proceeds at precise locations -near the apex of existing roots- and exhibits local variations which are dependent on the apical characteristics of these roots (e. g. size and age of their meristem). Therefore, the elongation process induces, at a given time, a spatial distribution of new root pieces which is far from random. Likewise, branching is also an important and highly organized process which results in the generation of new lateral meristems at specific locations along their mother roots. Variations in their growth potential and orientation will have further consequences. Therefore, it is clear that elementary developmental processes have an impact on root distribution and dynamics, but their relationships with the integrated performance of root systems are not straightforward. We need tools like simulation models to bridge the different scales and viewpoints. Making these connections is also an important challenge to link studies on the genetic and environmental control of developmental figures made at the root level with studies on integrated functioning at the plant and population level (de Dorlodot et al., 2007). It should also help in the search for relevant developmental

traits for an integrated view at the ecosystem level that could be observed on samples of growing roots (Hummel et al., 2007; Roumet et al., 2008).

The present work aims to contribute to this investigation, by revealing in a more general and dynamic way the links between the developmental traits of root systems and their foraging performance. For that, we use a simplified architectural model of the root system which allows a dynamic and three-dimensional representation based on developmental rules simulating elongation and branching of individual roots. This model includes stochastic processes, because random variations in development, called developmental instability by Forde (2009), could play a specific role in uptake functions, as speculated by Forde (2009) and Pagès et al. (1993). In this study, the foraging performances of the simulated root systems are also modeled via several dynamic criteria to account for various possible plant strategies and the capture of various soil resources.

Modeling approach

Root system development and architecture

For this study, we built a very simple dynamic model of the three-dimensional root system architecture, based on previous experiences in root system modeling (Pagès and Aries, 1988; Pagès et al., 2004; Leitner et al., 2010). This model was designed to integrate the major developmental processes (elongation and branching) in the simplest way, while using a reduced number of parameters whose values can be estimated from data in the literature.

In this model, time was divided into one day steps during which existing axes (roots) are virtually elongated, and new lateral axes can appear by branching.

Fitter (1987) highlighted that diameter is one of the major morphological characteristics on which roots exhibit variations. Moreover, several authors (e. g. Wilcox, 1962; Hackett, 1973; Coutts, 1987; Cahn et al., 1989; Pagès, 1995; Lecompte et al., 2005) showed a clear relationship between root tip diameter and elongation rates on various species. Root tip diameter reflects meristem size, as well as the ability of the meristem to use photo-assimilates and produce new elongating cells which contribute to root elongation. In the model, elongation rate was assumed to be a linear function of the tip diameter, with a given slope (E). This parameter E represents the global sink strength of root meristems, i. e. the

general propensity of the plant to allocate photo-assimilates to its root system. We used several references (Wilcox, 1962; Hackett, 1973; Coutts, 1987; Cahn et al, 1989; Pagès, 1995; Lecompte et al., 2005) to extract parameter values for E .

In the model root system, tip diameter is assumed to vary within a defined range, between two threshold values (D_{min} and D_{max}). The minimal diameter (D_{min}) is the value under which no elongation is possible. Therefore, it is estimated as the diameter of the finest roots that the plant is able to develop and elongate. The maximal value (D_{max}) is attributed to the first (primary) root. Similarly, it can be estimated by the diameter of the thickest roots.

Thus, elongation (L) of any root is calculated at each time step from its tip diameter (D) using the following equation:

$$\begin{aligned} \text{If } (D < D_{min}) \quad & L = 0; \\ \text{else } (D \geq D_{min}) \quad & L = E * (D_{max} - D_{min}) \end{aligned} \quad [1]$$

Values for D_{min} and D_{max} were mainly extracted from the review of Fitter (2002).

In order to render the winding character of root trajectories, and to improve estimates of colonized volumes (see below), the direction of root elongation was noised by a small random angle every 5 mm. The amount of this noise was calibrated visually using pictures and drawings from Kutschera (1960).

During root elongation, each tip was also assumed to initiate lateral primordia which are regularly spaced along the root. The distance between successive primordia is given by the parameter IBD (inter-branch distance). Primordia become meristems and start elongating their branch roots five days after initiation. As in other models (Leitner et al., 2010), the initial growth direction was defined by two angles. The radial angle, in the plane perpendicular to the mother root, is drawn at random. The insertion angle, in the plane containing both the mother and daughter roots, was fixed at 80 degrees. This value was estimated from Kutschera's pictures (Kutschera, 1960) and personal unpublished data.

The tip diameter of lateral roots was attributed at emergence, during the branching process. It was drawn at random in a distribution defined by two parameters ($MRDB$ and V , see below). For each lateral root, we calculated its tip diameter (D_l) from the mother root diameter (D_m) according to the following equation:

$$D_l = D_m * MRDB * \exp(V * \mathfrak{R}) / \exp(V) \quad [2]$$

$\mathfrak{R}$ is a random number from a uniform distribution between 0 and 1. Parameter *MRDB* represents the maximal diameter of the branch root relatively to its mother. Values for *MRDB* were obtained from the compilation of Lecompte et al. (2005) and from Pagès and Serra (1994). Parameter *V* modulates the variance of the distribution. Examples are given in Figure 1 to illustrate the effect of these parameters on the branching pattern.

Parameter names, abbreviations and values are presented in table 1.

Foraging criteria: definition and calculation

Like root system development, we modeled soil colonization in a very simple way.

We calculated the soil volumes enveloping the root system at three different distances ($d_1=3$ mm; $d_2=12$ mm; $d_3=50$ mm). This enveloping volume is a rough representation of the rhizospheric soil volume that is exploitable by the root system during its development, as suggested by Ge et al. (2000) or Hinsinger et al. (2005). The closest volume (closer than d_1) was assumed to be correlated with the amount of poorly-mobile resources, like phosphate, that can hardly diffuse on some millimeters whilst the distant volume (within d_3) was assumed to be correlated with the amount of mobile resources (like nitrate or water) that can move on several centimeters (Barber, 1995). The intermediate volume (within d_2) is devoted to resources with an intermediate mobility (like potassium).

These volumes were estimated numerically. The soil volume was divided into conveniently sized voxels (typically 4 to 20 mm in order to obtain a correct accuracy). We calculated the minimal distance from the center of each voxel to the root system. When this distance was smaller than one of the threshold distances, the voxel was considered to be inside the corresponding volume. The product of the number of voxels by the volume of voxels gave an estimate of the enveloping volume. This calculation algorithm allowed us to take overlaps between the rhizospheres of individual root into account.

Time dependent variations in these volumes were considered by repeating the calculations for each time step.

The accuracy of the volume estimation was tested and it was shown to depend both on the root system size and the voxel size. From simulations, we showed that a voxel size of 5 mm was satisfactory for obtaining an error below 10 % for the d_1 volumes, at least for root systems with a total length greater than 80 cm. This error decreased very quickly for longer root systems and was lower for d_2 and d_3 volumes (data not shown).

In order to compare the foraging performance of root systems, we defined “efficiency” as the ratio of the colonized volume to the volume of a virtual cylinder with the same length as the whole root system and a radius equal to the considered threshold distance (d_1 , d_2 , d_3). This was given by the following equation:

$$e = EV / (\pi * TL * d_i^2) \quad [3]$$

where e is the efficiency, EV the estimated d_i volume and TL is the total length of the root system.

Data analysis

Basically, our strategy was to study the relationships between the six developmental parameters and the foraging criteria defined previously.

For this purpose, we made a large number of simulations combining different values for each parameter (Table 1), and for each simulated root system, we calculated the foraging criteria (volumes and efficiencies as a function of time, as explained above). We considered four different values for each parameter, giving a total of 4096 (i.e. 4^6) different simulations. For each simulation, each parameter was drawn at random around a central value X , in the interval $[X-10\%; X+10\%]$. This choice allowed us to systematically sample a large range for each parameter and avoid the drawback of being restricted to a limited number of prefixed values (Saltelli et al., 2008). Within the dataset, each line represented a simulated root system. Columns were: (i) parameter values; (ii) d_1 , d_2 and d_3 volumes at three dates (20, 40 and 60 days); (iii) corresponding efficiencies.

For an overall exploration of this large data set, we graphed and smoothed the main trends between parameter values and foraging variables. We also used quantiles to study the envelopes of the scatter plots more specifically. Envelopes were interesting for highlighting

the potential values that can be obtained with some parameter values. Regressions and correlation analyses were used to test our visual impressions during data exploration.

Simulations were made by running a home-made C++ program, and data analyses were carried out with the R free software (R Development Core Team, 2010; <http://www.R-project.org/>).

Results

Colonization dynamics

Very large variations were observed between the dimensions that were reached by the simulated root systems, as shown in table 2. The total root length in the longest root system was 12.7 km. The largest volume closer than 50 mm to the root system reached 2.64 m³. The minimal length values (only some cm) were less interesting and probably not very realistic. The minimal values for colonized volumes were obviously very small as well, but these values should be considered with care, since the estimation method is not suitable for obtaining accurate data on such small root systems. Median values showed that the distributions were skew, with many more small than large root systems.

Since potential uptake is first determined by the dynamics of the colonized volumes, we focused further investigations on these variables.

Some of the variations observed for colonized volumes were clearly related to parameter values. Figure 2 illustrates some of the relationships. In the graphs both the individual data points were plotted (one per root system) as well as the trends for the upper envelope, joining the 98% quantiles for eight classes of parameter values. A more systematic presentation of the linear trends is given in table 3 where correlation tests between the parameter classes and these quantiles are shown.

Table 3 shows that the extreme diameters had a clear influence on the colonization potentials. Both extremes were important for the d₁ volume, while only the maximal diameter was significant for the d₃ volume. Overall, the larger the diameter range, the higher the colonization potential.

The slope of growth rate versus diameter was also strongly and positively correlated to the volumes, confirming the importance of plant resource allocation to the roots and differentiation of growth rates (through diameter).

Branching density (inverse of inter-branch distance) also had a clear positive influence on the d_1 volume, but not on the d_3 volume where it was counterbalanced by overlapping effects.

Neither the hierarchy between mother and daughter roots nor the variations among daughter roots had a clear effect on the colonized volumes.

Relationship between colonization potential and efficiency

It is worth noting that the estimated efficiency (from equation 3) was sometimes greater than 1, especially in the case of very small root systems, because the colonized volume includes both a cylinder volume around the root axis and hemispheric volumes at root ends. It became generally lower than 1 in the case of branched root systems, because of volume overlapping which tended to reduce its value.

As a more general feature, negative correlations between colonization potential and efficiency were systematically observed, as shown in figure 3 for the three distances. Efficiencies tended to decrease with root length, because overlapping increased. As expected, this decreasing trend was more pronounced as the distance increased. These figures revealed that total root length became less and less efficient as the considered distance from the roots increased, and as the root system extended during plant growth. For 2 km long root systems, the median efficiency values were about 0.67, 0.17 and 0.025 for d_1 , d_2 and d_3 respectively, showing the important effect of overlapping.

Nevertheless, there were large variations in efficiency for each size of root system. For example, efficiency varied typically from 0.2 to 1.0 for the d_1 volume, and relative variations were even higher for larger distances. For 2 km long root systems, the most efficient ones reached values of approximately 1.0, 0.6 and 0.12 for d_1 , d_2 and d_3 respectively.

Efficiency gain

From these general trends of efficiency versus total length, it was possible to calculate what we can call an “efficiency gain” for each root system as the difference between its observed value and the trend value for the same length. In other words, the “efficiency gain” was a residual from the central trend, used as a measure of the relative performance of each root system in reference to what could be expected, given its size. In the following, the smallest root systems (those under the 10 % length quantile) were discarded because such small root systems were less relevant to our study, and estimates of their efficiency gain could suffer from a lack of accuracy (see material and methods).

The relationship between efficiency gain and age was analyzed by scatter plots (Figure 4) and correlation tests (Table 4) considering values at three dates: 20, 40 and 60 days. Correlations were high, especially between days 40 and 60 and for the biggest distances. The points were distributed around the bisecting line. These results showed that efficiency gains were stable with age, at least after a sufficient growth period. They legitimated our focus on later dates in the following analyses.

Next, efficiency gains (at day 60) were plotted against parameter values together with trend lines (graphs not shown). The correlation coefficients are shown in Table 5. All coefficients were highly significant for the three distances, and there were also significant differences between the considered parameters. In the following, these results are discussed from the highest to the lowest correlations. Inter-branch distance was the most important parameter for the three distances, with its influence increasing with increasing distance. These correlations point out the importance of overlapping between rhizospheres, which increased with branching density. Less intuitive are the positive correlations between efficiency gain and maximal diameter on one hand and efficiency gain and slope of growth rate versus diameter on the other. We interpret these correlations together, because both parameters contribute to increase the between-root differentiation within the root system. Furthermore, both correlations tended to increase with the considered distance (from d_1 to d_3). A closer examination between maximal diameter and efficiency gain showed that the relationship was not linear: the increase in efficiency gain was more pronounced for diameters between 0.5 and 1.8 mm. The maximal relative diameter of daughter roots correlated negatively with efficiency gain, showing that the hierarchy between mother and daughter roots was an important determinant for efficiency. When lateral roots were given about the same growth potential as their mother roots ($MRDB=0.9$), the efficiency gain

tended to decline. Variation among daughter roots (though V parameter) was also positively correlated to efficiency gain, regardless of the distance considered. These correlation coefficients (with V) were not significantly different, although they increased slightly with distance. Finally the smallest effect (due to minimal diameter) was more difficult to interpret, because it could have two counterbalancing origins which we verified on the simulated root systems (data not shown). A high minimal diameter tended to cause a slight decrease in the overall diameter range. At the same time, a higher minimal diameter led to a reduction in branching density due to the abortion of lateral roots that had not reached the minimal diameter. The first effect was slight but rather negative on efficiency gain, the latter effect was stronger and positive. The overall correlation resulting from these two opposite effects was low.

Differences between distances for the efficiency gains

In order to examine the differential impact of parameters on the efficiency gains for the different distances, we calculated the differences between efficiency gains for the extreme distances (d_1 and d_3) and explored their relationships with parameter values.

This investigation confirmed some points that we perceived in the previous correlation analysis. Firstly, the growth rate differentiation (through parameters D_{max} and E) was much more important for increasing efficiency at large compared to short distance. Secondly, an increase of inter-branch distance above 6 mm had a higher impact on the efficiency gain observed for large distance.

Root system size and “optimal” parameters

Since parameter values for the most efficient root systems may depend on their size, we selected the root systems with the highest efficiency gain in each class of root system size, defined by their total length. In order to retain the same number of root systems in each class, we divided the population of root systems using quantiles with class breaks as the quantile values: 0.5, 0.6, ..., 1.0. Thus, once again we have excluded the small root systems (under quantile 0.5). The most significant results are presented in figure 5. From the trends in figures 5A and 5B (relative to d_1 volume) it is clear that maximal diameter was an

important parameter for determining the size of efficient root systems, as well as elongation rates (via E). The trends observed with other parameters were less clear (not shown). Regarding the d_3 volume (figures 5C and 5D), the minimal diameter decreased with size, whereas the maximal diameter stayed close to the maximal values (systematically higher than for d_1 volume). The values for elongation rates (E) also remained near the maximal values (not shown).

Interactions between parameters

In addition to these analyses, focused on individual parameters, we studied correlations between parameters among large and efficient root systems, in order to detect possible combined effects for pairs of parameters. For this, only root systems above both the 0.8 quantile for total length and efficiency gain were selected. This generated a sub-population of 162 individuals on which the highly significant correlations ($p < 0.001$) between parameters are reported in table 6. These correlations were very similar for the three distances d_1 , d_2 and d_3 . They reveal that some parameters act in association and highlight possible combined strategies for reaching both high colonization volume and efficiency gain. Thus, the positive correlation between IBD and $RMDB$ showed that the higher the growth rate of laterals, the higher their spacing along the mother root. Complementarily, the negative correlation between IBD and V indicates that small spacing between laterals was associated with high growth rate variations among laterals. The negative correlation between D_{max} and $RMDB$ reflects that a strong hierarchy between mother and daughter roots (low $RMDB$) required thick roots (high D_{max}).

Figure 6 illustrates that similar characteristics for total length and efficiency were obtained with different parameter associations. Parameters for these two root systems are shown in table 7.

Discussion and conclusion

This *in silico* study demonstrated the quantitative effects of individual root developmental processes on the global foraging performance of root systems. The models and simulations allowed part of the complexity to be elucidated and provided a general framework for such a study, by taking into account a large part of the diversity of plants and soil resources. The root architecture model that was used was a sort of synthesis or summary of previous models developed over the last 20 years, among which some have been tested in field conditions (Pellerin and Pagès, 1996). The number of parameters (six in this case) was very low in order to allow systematic tests of their effects by crossing their values (Saltelli, 2008). Unlike previous work, we used developmental parameters characterizing different processes instead of morphological (and static) characteristics because we thought that it was important to clearly separate the processes. For example, the length of internal links (or internodes) is the result of both the branching process (with inter-branch distance parameter) and the growth process (selection of growing roots beyond the minimal diameter). On real root systems, it is also modified by root shedding. Several processes were stochastic in this model, such as the emergence direction of lateral roots, their trajectory, and the growth rate of lateral roots. We considered that random aspects of development should be included, since stochasticity can make sense on several aspects of root system functioning and is not the sole result of environmental variations (Forde, 2009). Regarding soil resources, it was assumed that the amount of resources that can be acquired by the plant is, on average, approximately proportional to the soil volume enveloping the roots. The distance from the roots of the volume contour was considered as essentially dependent on the soil-to-root transport capacity of these soil resources. This model was deliberately very simple, because our aim was not to quantify uptake for a given soil, but to compare a large number of architectures under average conditions. Specific cases of soil heterogeneity (far from randomness, or predictable) are beyond the scope of this general approach.

Colonization dynamics

The first important criterion for evaluating the virtual root systems was their ability to colonize the soil volume as quickly as possible. Berntson (1994) used the term “potential” to qualify this prime characteristic. The dynamics of this potential are obviously important

aspects of fitness because of inter-plant competition and the necessary dynamic adaptation of uptake to requirements and environmental changes. Among real plants, this criterion is known to vary greatly, but quantifications are lacking, as discussed by Ryser (2006). We obtained a large range in the results of our simulations due to parameter variations. For example, total root length varied from some centimeters to more than 12 km. Root depth and lateral extensions reached several meters. Our strategy to run the simulation using all combinations of parameters without any selection led to a large number of very small root systems, but we eventually selected the not trivial extended and branched root systems in subsequent analyses.

In this population, fast growing root systems were obtained by two -non exclusive- ways. The first one was to develop individual fast growing roots by increasing meristem size (D_{max}) and plant resource allocation (E). The second way was to increase the number of roots growing simultaneously, either by reducing the inter-branch distance (IBD), allowing the growth of very fine roots (D_{min}), or giving branch roots a high growth rate ($MRDB$, V).

In any case, all these strategies for increasing the overall growth rate are faced with the limited amount of photo assimilates that the plant can supply to its root system. Therefore, it was important to include efficiency considerations in the analysis.

An intrinsic negative correlation between size and efficiency

Efficiency was defined as a dimensionless coefficient calculated by the ratio of the colonized volume (enveloping volume at a given distance d_i from the roots) to the volume of a unique virtual cylinder having the same length as the root system and a radius d_i .

Thus, we could characterize the link between root system size and root system efficiency. Very important and general, this relationship is a direct consequence of the spatial organization of roots. A branching system has aggregated roots in space, because of their connections (Grabarnik et al., 1998), which induce overlaps between the rhizospheres of individual roots. Larger root systems gave more overlaps. Berntson (1994) underlined this fundamental relationship between potential and efficiency, and discussed the necessary trade-off between these two characteristics. Although quantitatively important, this aspect is generally neglected in uptake models in which root length density measurements are used without quantifying aggregation. The relationship between size and efficiency was also

dependent on the colonized volume that was considered, since overlaps are more frequent and important for large rhizospheres. In our population, it typically decreased down to 0.6 for the small enveloping volume (3 mm distance), and down to 0.02 for the largest (50 mm distance).

Efficiency for a given size was highly sensitive to developmental parameters

Interestingly, we also showed that the size - efficiency relationship was not as tight as assumed by Berntson (1994), and that there was room for root systems to enhance their efficiency regardless of size. Efficiency varied typically in a 4 to 10-fold range for a given size. This fact led us to study more thoroughly the difference between the expected efficiency (approximated by the average trend) and the “actual” efficiency of each individual root system. This difference, called the “efficiency gain”, was a very interesting performance criterion, since it was size independent (by construction) and was shown to be almost age independent.

The differentiation of root growth rate was an important aspect of efficiency gain, on which several parameters contributed (maximal diameter, minimal diameter, slope of elongation rate versus diameter). This differentiation always appeared to favor efficiency gain, especially for the largest enveloping volume, and the largest root systems. This finding may be linked to the important notion of heterorhizy. Instead of developing one single type of roots, with approximately the same morphogenetic potentials, many plant species have evolved developing differentiated roots (Waisel and Eshel, 2002). Thick roots (macrorhizae) extend the external boundaries of the colonized volume, while fine roots (brachyrhizae) can colonize and exploit the intermediate spaces. Nevertheless, root differentiation is constrained by biophysical limitations. The thickest roots (3.3 mm in this study) are expensive to build, they have a low surface to mass ratio, and their growth cost is high, especially in strong soils. The majority of soil pores are much smaller than their tip, so to penetrate their environment they must push large volumes of soil. Root fineness is also limited, as discussed by Fitter (1987), by the structural organization of individual roots and their resistance to water transport. Increasing the specific root length by diminishing root diameter is a common response of root systems in the case of nutrient shortage, with an obvious effect on the global carbon cost of the root system (Comas and Eissenstat, 2004;

447 Comas and Eissenstat, 2009). However this strategy is likely to reduce diameter
448 differentiation in the whole root system. The lower diameter limit that we used (0.045 mm)
449 is probably not far from the absolute limit, but it is worth noting that many plants, especially
450 among dicotyledonous trees, do not grow such thin roots, maybe because of their
451 vulnerability to drought or grazing. Root hairs and mycorrhizae are probably efficient
452 alternatives for increasing the very local soil-plant exchanges.

453 Another important characteristic, not unrelated to differentiation, was the hierarchy
454 between mother and daughter roots. This property was quantified using the *MRDB*
455 parameter. Fitter et al. (1991) found that a pronounced hierarchy between a root and its
456 laterals (herringbone pattern) was favorable for exploration efficiency, in comparison to a
457 dichotomous pattern. Our study confirms this point, and also provides several nuances. It is
458 especially true for the high distance volume, and for low inter-branch distances. When inter-
459 branch distance was higher than 10 mm, intermediate and low hierarchies resulted in the
460 best efficiencies.

461 Interestingly, our study highlights the role of growth rate variation among laterals, qualified
462 as “good noise” by Forde (2009). Efficiency was increased when lateral roots of various
463 growth rates were alternated along the mother root. Among these laterals, the shortest
464 exploit the local space, whilst the longest can deplete farther sites and are complemented by
465 their own laterals. Thus, we confirmed that not only deterministic processes should be
466 considered in such an approach, but also the stochastic ones. It is probable that stochasticity
467 would also improve the global efficiency of a plastic response to heterogeneity. The
468 amplitude of these types of variations and their origin remains to be studied.

469 The role of inter-branch distance is also decisive for shaping the root system. Typical
470 observed values of inter-branch distance (say from 2 to 10 mm) are rather under valued
471 compared to the most efficient found in our study (from 6 to 24 mm). We have seen that
472 branching density is central for multiplying the number of growing roots, and is therefore a
473 major factor for speeding up colonization. Meanwhile, we found that it is unfavorable for
474 efficiency gains if the inter-branch distance is lower than the radius of the considered
475 rhizosphere. This can be linked to the interior links as defined by Fitter (1987). Some trade-
476 off must be found by the growing plant on this adjustment, since several more or less mobile
477 resources must be taken. This trait should be analyzed in relation to the most limiting
478 resources in the plant environment (Lynch, 2007). Moreover, since lateral roots appear

along defined rows around the mother root, the within row spacing of lateral roots (as defined and studied by Draye, 2002) might be a developmental way for diminishing overlaps. In addition, self-pruning of those small roots, which have exploited the non-mobile resources of the very local environment, could return inter-branch distance to higher values.

Perspectives

This work is an introduction towards more detailed and realistic models for understanding how developmental processes contribute to shape efficient root systems. To further improve our capacity to simulate realistic root systems, several new approaches could be taken. As a first step additional developmental processes could be included whose importance should not be underestimated: orientation via tropism, production of adventitious roots on shoot axes, decay and reiteration (Vercambre et al., 2003). Another important way forward would be to consider the interactive and dynamic plasticity of the growing roots in response to a heterogeneous and changing environment. Recent progress in modeling could allow this approach to be merged with a more realistic transport and uptake model, as well as a dynamic carbon model, for refining benefit and cost evaluations, and maybe defining idéotypes of root systems.

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Table 1: Names, units and central values of model parameters. For each simulation, a particular value was drawn at random uniformly in the interval $[X-10\%;X+10\%]$, where X is a central value. All combinations of values were used, giving a total of 4096 simulations (i.e. 4^6).

Parameters	1	2	3	4
Minimal diameter D_{min} (mm)	0.05	0.10	0.20	0.30
Maximal diameter D_{max} (mm)	0.5	1	1.8	3
Slope of growth rate versus diameter E (day ⁻¹)	8	12	18	28
Inter-branch distance IBD (mm)	3	6	12	24
Maximal relative diameter of branch root $MRDB$ (–)	0.3	0.5	0.7	0.9
Variation diameter branch root V (–)	0.5	1	2	3

Table 2: Range of values obtained for the 4096 simulated root systems (“ d_i volume” denotes the soil volume closer than distance d_i to the root system).

	Minimum	Median	Maximum
Length at day 40 (m)	0.0349	4.34	1924
Length at day 60 (m)	0.0554	14.76	12710
d_1 volume at day 40 (dm ³)	0.00	0.12	35.11
d_1 volume at day 60 (dm ³)	0.00	0.41	137.0
d_2 volume at day 40 (dm ³)	0.021	1.61	170.7
d_2 volume at day 60 (dm ³)	0.032	5.13	654.6
d_3 volume at day 40 (dm ³)	0.791	15.51	746.9
d_3 volume at day 60 (dm ³)	0.948	41.53	2638

Table 3. Correlation coefficients between parameters and the 0.98 volume quantile (calculated at day 60). For each parameter, eight classes were defined for which the 0.98 quantiles were calculated. Coefficients in bold characters are significant at the 5% level (df = 7).

	D_{min}	D_{max}	E	IBD	$MRDB$	V
d ₁ volume	-0.966	0.825	0.995	-0.964	0.359	-0.785
d ₂ volume	-0.919	0.956	0.989	-0.877	0.236	-0.584
d ₃ volume	-0.663	0.993	0.994	0.576	0.180	0.342

Table 4: Correlation coefficients between efficiency gains at three dates: day 20, 40 and 60.
All coefficients were highly significant (df = 3686).

Distance	Dates	Correlation coefficient
d_1	day 20 – day 40	0.671
	day 40 – day 60	0.785
d_2	day 20 – day 40	0.790
	day 40 – day 60	0.940
d_3	day 20 – day 40	0.893
	day 40 – day 60	0.969

Table 5: Correlation coefficients between model parameters and efficiency gains for the three distances d_1 , d_2 and d_3 . All coefficients were highly significant ($df=3686$).

	Efficiency gain for distance d_1	Efficiency gain for distance d_2	Efficiency gain for distance d_3
Minimal diameter (D_{min})	0.0930	0.141	0.208
Maximal diameter (D_{max})	0.124	0.408	0.479
Slope of growth rate versus diameter (E)	0.203	0.394	0.387
Inter-branch distance (IBD)	0.341	0.488	0.533
Maximal relative diameter of branch roots ($MRDB$)	-0.323	-0.240	-0.260
Variation of diameter of branch roots (V)	0.242	0.253	0.309

Table 6: Correlation coefficients that were highly significant between parameters among large and efficient root systems. The selection method led to a sub-population of 162 root systems (see the text).

Correlation coefficients for d_1 volume (df = 161)		
	<i>RMDB</i>	<i>V</i>
D_{max}	-0.481	
<i>IBD</i>	0.434	-0.384
Correlation coefficients for d_3 volume (df = 161)		
D_{max}	-0.317	
<i>IBD</i>	0.540	-0.373

Table 7: Parameter values for the two root systems presented in Figure 6.

Parameters	Root system Fig 6A and 6B	Root system Fig 6C and 6D
Minimal diameter D_{min} (mm)	0.203	0.188
Maximal diameter D_{max} (mm)	2.93	3.08
Slope of growth rate versus diameter E (day ⁻¹)	26.6	25.5
Inter-branch distance IBD (mm)	23.5	23.8
Maximal relative diameter branch root $MRDB$ (--)	0.489	0.881
Variation diameter branch root V (--)	0.528	2.95

Figure captions

Figure 1: Visual illustration of various branching patterns obtained by varying the *RMDB* and *V* parameters. A: *RMDB*=0.3 and *V*=0.5; B: *RMDB*=0.3 and *V*=3.0; C: *RMDB*=0.9 and *V*=0.5; D: *RMDB*=0.9 and *V*=3.0.

Figure 2: Scatter plots illustrating some of the relationships between the colonized volume and developmental parameters. Each point represents a simulated root system. The lines connect the 0.98 quantiles calculated on eight different classes of each parameter.

Figure 3: Relationships between root system size (total root length) and efficiency for the three distances d_1 , d_2 and d_3 . The lines connect the median values calculated for classes of root system sizes.

Figure 4: Relationships between values of efficiency gain for the d_3 distance and the three dates: day 20, 40 and 60. The bisecting lines are shown.

Figure 5: Relationship between parameter values and size for optimal root systems. A and B are for the d_1 volume, C and D for the d_3 volume. Symbols represent the average value for the most efficient root systems in each class of total length. Bars represent the standard deviation.

Figure 6: Examples of efficient root systems for mobile resources (distance d_3). A and C are side views, and B and D are top views. These two root systems were the same age (40 days), the same length (100 m) and were approximately as efficient (0.5). They differ in their *RMDB* and *V* values. Length units are meters. Parameter values are given in Table 7.

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662

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