



## Architectural analysis and synthesis of the plum tree root system in an orchard using a quantitative modelling approach

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### Abstract

A dynamic 3D representation of the root system architecture of plum is proposed by gathering quantitative and morphological observations of the tree root system in a model. The model includes two information levels: (i) a typology of root axes, based on morphological and developmental characteristics; (ii) a set of basic processes (axial and radial growth, ramification and reiteration, decay). The basic processes are qualitatively identical in space and time. An original approach was used to investigate these processes and to formalize them in the model. Concerning the main roots, a mechanism of reiteration is described that has a substantial influence on the structuring of the root system. Root mortality is assessed using the variation in branching density along the root axes. Radial growth is calculated from the ramification of root axes, using root section conservation properties. This model enables a link between static field observations and a dynamic simulation of the root system architecture. The architectural model allows examination of the global consequences of the basic processes at the level of the root system. The simulations provide useful output, from a simple root depth profile to a simulation of the dynamic 3D root system architecture, to investigate plant functioning and especially water and nutrient uptake.

### Introduction

Several research areas highlight the importance of the description of the root system architecture. The efficiency of belowground resource acquisition depends on the shape and structure of the root system (Clarkson, 1996; Fitter, 1996). Tree anchorage is determined by the geometry and the radial growth of the proximal part of the root system (Coutts, 1987). Traditionally, the root system has most often been characterized descriptively or by mapping of spatial root distribution (root depth or root density profile). However, the root architecture has several important characteristics that should be taken into account when dealing with resource acquisition.

Firstly, some studies have shown that roots tend to be highly clustered (Tardieu and Manichon, 1986). This root clumping has important consequences for water and mineral uptake (Tardieu et al., 1992). Secondly, different kinds of roots are observed in both annual and perennial plants (Jourdan and Rey, 1997b; Pagès and Serra, 1994; Pagès et al., 1993) and an ontogenetic gradient exists along roots. These differences are linked with wide variations in uptake and transfer capacity (Clarkson et al., 1968; Frensch et al., 1996; Steudle and Peterson, 1998). Finally, roots segments are connected to each other in a specific way. Evidence has been put forward on the substantial resistance to water flows throughout the root system (Tyree and Alexander, 1993) leading to non-uniform water potential within the root system (Nobel and Lee, 1991; Simonneau and Habib, 1994). Models that couple root system architecture with water and nutrient uptake are readily available. Such models provide

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a detailed picture of water uptake throughout the root system (Clausnitzer and Hopmans, 1994; Doussan et al., 1998; Kurth, 1994).

However, observation of the root architecture *in situ* is somewhat difficult, because of the opacity of the soil, the large volume of colonized soil and the extreme fragility of most roots. Consequently, practical observations of the root system are mainly discontinuous in time and, in addition, only part of the root system is observed.

Modelling could be a useful tool to characterize root system architecture. The analysis substitutes a set of basic developmental processes organized in time and space for the complexity of the global root architecture. Root architecture modelling is a frame based on the developmental processes that helps assemble scattered information about a system that is too large to be observed in its entirety. This approach was first developed for annual plants with limited spatial dimensions, that originated from seedlings (Clausnitzer and Hopmans, 1994; Diggle, 1988; Pagès and Aries, 1988). The processes described were root emergence and axial growth. However, tree root architecture presents some specific characteristics: (i) the root system is perennial and colonizes a very large volume of soil (a 3-year-old plum tree colonize more than 50 m<sup>3</sup>), (ii) radial growth can be very extensive, with main roots several centimetres in diameter (Coutts, 1987; Lyford, 1980), (iii) root mortality can be very high (Bloomfield et al., 1996), as has been shown in cherry roots where more than 40% of roots survived less than 14 days (Alexander and Farley, 1983), (iv) many roots are subject to reiteration, i.e. several axes could be emitted from one main root, these axes being of the same nature of the parent axis (Atger and Edelin, 1992; Coutts, 1987; Lyford, 1980).

Some studies have focused on certain aspects of this specificity. The explored volume of a tree root system has been investigated from a theoretical point of view using a fractal approach, but provided only a limited description of the developmental processes (Van Noordwijk et al., 1994). The diversity of the types of root and their respective properties has also been investigated in the oil palm root system (Jourdan and Rey, 1997a, b). However, the oil palm cannot be considered as a typical tree, nor does it show specific characteristics such as radial growth and reiteration. The purpose of this paper is therefore to attempt to model the architecture of the root system of the plum tree in an orchard, based on the description of basic developmental processes. Direct observations were

carried out of various parts of the root system. An original approach is proposed to quantitatively estimate and formalize root mortality and secondary radial growth, which are rarely depicted. The discussion then deals with the observed processes and their significance, and highlights the objectives and interest of root architecture modelling.

## Materials and methods

### *Site and plant material*

Experiments were conducted at the Avignon INRA (Institut National de la Recherche Agronomique) research centre in southeastern France. The site is characterized by a north-Mediterranean climate, with wet winter and dry summer. The average annual precipitation is 700 mm. The monthly mean temperature ranges from 5 °C in winter to 23 °C in summer.

Peach tree scions (*Prunus Persica* L. Batsch), cv. 'Primerose' were grafted onto plum rootstocks of *Prunus* cv. 'Damas 1869'. In March 1994, grafted *Prunus* trees removed from the nursery at 1-year-old and planted in the orchard after the root system had been severely pruned. The transplanted root system is composed of about ten woody roots about 20 cm in length, originating from the stump. The trees were planted in a fluvisol (FAO), with soil material continuing to a depth of at least 3 m from the soil surface. The granulometric analysis gives clay (27.2%), loam (61.8%) and sand (11%). The tree density is 70 trees/ha, widely spaced to preclude both above- and belowground competition between trees. A thin compacted soil layer was observed at the base of the plough layer, 30 cm depth.

### *Observation of the root system*

Several root excavations were conducted in October 1996 and March–April 1997 (on 4 trees), to obtain information about the basal to the apical part of the root, in both shallow and deeper roots (until 2 m depth) in 3-year-old trees. Soil particles around the root system were carefully removed using a hand pick and a water-jet. Supplementary observations were made using cubic monoliths (17 samples) approximately 30 cm in width, from the soil surface to 1.5 m depth. These monoliths were immersed in a saturated salt-water solution, allowing easier soil removal. At transplantation time, a logarithmic spiral trench was

dug (Huguet, 1973) around 2 trees, and arranged as a field rhizotron. This experimental device allows direct observation of roots at different depths (down to 1.80 m) and at different distances from the trunk (up to 2 m). Dynamic observations were made through a transparent acrylic sheet along the wall. These observations were made at different dates from March to October.

These quantitative observations enabled the estimation of the length of the roots, variations in diameter and in branching density along the roots. Root cross-sections were made to determine root age by counting the number of annual rings. Qualitative observations such as the shape of the root tip, colour, suberisation, and lignification were also recorded (Le Roux, 1994).

### *Modelling of root architecture*

The model includes two information levels: a typology of root axes, and a set of basic processes. The root typology leads to the distinctions of the different root type, based on observation of morphological parameters such as the size and shape of the root tip, root length, root diameter and radial growth, colour, woody or not (Atger, 1992; Jourdan and Rey, 1997b; Pagès et al., 1993).

The root architecture modelling system is dynamic; the root system is represented as a set of root segments, with each segment representing the part of the root that was generated in one time step (Pagès and Aries, 1988). The roots are assumed to elongate according to the following mono-molecular time function:

$$L = A \left( 1 - e^{-\frac{bt}{A}} \right),$$

where  $L$  is the length of the root,  $t$  the time after emergence,  $A$  the asymptotic root length and  $b$  a rate parameter. Parameters are drawn from normal or lognormal distributions, leading to a stochastic representation of the axial growth.

Acropetal branching takes place on the young part of the root. The branches appear at a given distance from one another (inter-branch distance), and they can appear only on parts of the mother root that have reached a given age (duration of apical non branching). The inter-branch distance is defined for each root type.

Decay was modelled using the concept of time-lag necrosis. According to this model, a root is eliminated after a given period calculated from the moment when

it stops growing (time-lag necrosis) and when it no longer carries any living branch roots.

The extent of radial growth along roots is described using an adaptation of the pipe model (Coutts, 1987). According to this theory (Shinosaki et al., 1964; Van Noordwijk et al., 1994), the cross-sectional area of sapwood at any point in the root (or in the stem) is correlated with the sum of cross-sectional areas of sapwood of the branched roots (stems) distal to the main axis. The pipe model can be expressed as follows (Van Noordwijk et al., 1994):

$$A_M = \alpha \sum_{i=1}^n A_i,$$

where  $A_M$ , is the cross-sectional area of the main axis,  $A_i$ , is the cross-sectional area of the  $i$ th branch root axis, and  $\sum_{i=1}^n A_i$  is the sum of the cross-sectional areas of all axes after a branching event distal to the location of the main axis diameter measurement.  $\alpha$  is a proportionality constant between the cross-sectional area of the main axis and the sum of the cross-sectional areas of all axes. The increase in root diameter may be linked with the appearance of the branch roots.

### *Parameter estimation and fitting*

The parameters were adjusted following direct estimation or optimisation. With respect to axial and radial growth and branching, the parameters were directly determined following the field observations. The measured root length enabled estimation of the asymptotic value  $A$  and its variance, assuming a normal or lognormal distribution for each root type. The measured final root length was estimated on the proximal part of the parent roots, because in this zone the shape of the root tip indicates when no more growth will occur. A turgid tip with a long un-branched apical zone characterizes an active root, whereas a club-shaped or necrosed root tip indicates no root growth (Pagès et al., 2000a). Variations in the length of the branch root along the main roots gives an indirect estimation of the rate parameter ( $b$ ). The branching density was estimated near the root tip, where mortality has not yet occurred. Successive sections of plum roots were measured to determine the cross-sectional proportionality parameter  $\alpha$ .

On the other hand, with respect to root mortality, a direct estimation is very difficult to assess. No method is available to distinguish a functional root (efficient in absorption and/or transfer) from others. Root growth is not continuous and the end of the root growth does not mean its death (Bloomfield et al., 1996). Morphological parameters (colour, elasticity) are neither

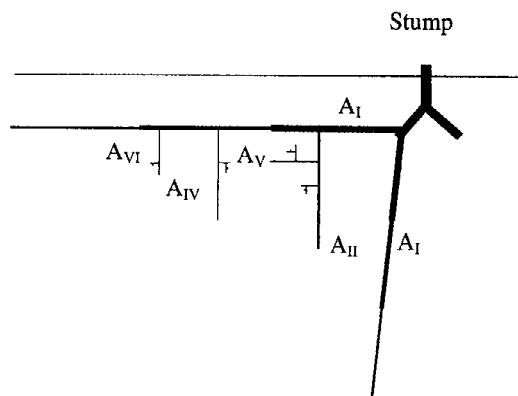


Figure 1. Schematic representation of the plum root system, with the different root types and their characteristics.

sufficient nor reliable. The mortality study was consequently based on the observation of the variation in branching density along the axes, on the assumption that the density of root emergence is constant over time. This assumption has been confirmed for several species (Jourdan and Rey, 1997a; Pagès and Serra, 1994). Root decay can only be considered as a marker by default (Le Roux, 1994). The necrosis time lag of the different root types was fitted by minimizing the difference between variations in the actual and simulated branching density along the axes.

## Results and discussion

### *Classification of root types*

Six categories of roots were identified and a simplified representation of the root system is shown in Figure 1. Table 1 presents a summary of the characteristics of the different root types from type  $A_I$  to type  $A_{VI}$ . Woody roots are stiffened and thickened by secondary xylem. Woody roots are generally 2 mm or more in diameter, and have distinct annual growth rings in the xylem. The non-woody roots are thin, flexible, lack secondary growth and are generally less than a few millimetres in diameter. Various other parameters enable us to distinguish the different root types, especially apical diameter and root length. Very striking differences appear between root types from the  $A_I$  type, with roots several meters long and a large apical diameter (1.25 mm), to  $A_{VI}$  fine roots (0.18 mm) less than 10 mm in length. The  $A_I$  root type presents two main growth directions, nearly vertical and horizontal, and these determine the volume of explored soil. In a

3-year-old root system, the large woody roots colonize a half sphere with a radius of 3 m. The fine roots develop from this perennial structure.

The root vigour, which could be expressed via the maximal root length, decreases according to the root type. This property seems to be a characteristic of many root systems (Eshel and Waisel, 1996; Fitter, 1996) and is well documented for numerous annual and perennial species (Atger and Edelin, 1992; Jourdan and Rey, 1997a; Le Roux, 1994; Pagès and Serra, 1994). Between the two extreme root types ( $A_I$  and  $A_{VI}$ ), the root system appears as a broad continuum. Each root type presents large variability, especially in its growth. This may make root distinction seem a little arbitrary. However, even if the distinction is difficult to assess, these morphological variations overlap with differences in functional characteristics. Woody roots have been shown to present lower uptake capacities (Clarkson, 1996; Steudle and Peterson, 1998). This has direct implications for the functioning of the root system at the levels of both a single root and the entire root system.

### *Measuring process parameters*

#### *Acropetal branching and reiteration*

The branching process occurs with the classical acropetal branching pattern, i.e. the emergence of new branches follows the growth of the axis. No late emergence outside the acropetal sequence was observed in the older part of the root system. Classical acropetal branching leads to subordination of the ramification to the parent axis. On the other hand, reiteration leads to axes that are of the same nature as the parent axis. Reiteration gives rise to axes that repeat the structure of the system bearing them (Atger, 1992; Coutts, 1987; Lyford, 1980). Several roots take over from the parent axis, which results in root forks located along the axis. The insertion angle of the reiterated axes and of classic branched roots, defined as the angle between the mother root and its branch, is very different. Acropetal branches appear with an open angle ( $70-80^\circ$ ) inducing a typical fishbone branching pattern, whereas the growth direction of reiterated axes is much closer to the direction of growth of the parent root. In the plum root system observed in the orchard, reiteration occurs regularly in the whole root system. The distance between the first reiteration and the base of the plant corresponds to half a year of growth, and the distance between two successive reiterations is nearly 1 year of growth. Moreover, the number of annual rings of the

Table 1. Root typology based on morphological characteristics of the plum root system

	$A_I$	$A_{II}$	$A_{III}$	$A_{IV}$	$A_V$	$A_{VI}$
Nature	woody	woody	woody	non-woody	non-woody	non-woody
Axial growth	indeterminate	indeterminate	determinate	determinate	determinate	determinate
Radial growth	high	intermediate	low	no	no	no
Range of length (cm)	> 1000	> 10	> 5	> 1	> 0.5	< 1
Apical diameter	1.25	0.90	0.40 ( $\pm 0.16$ )	0.29 ( $\pm 0.1$ )	0.21 ( $\pm 0.04$ )	0.18
Mortality	perennial	abscission	abscission	abscission	abscission	abscission
Carried types	$A_{II}, A_{III}, A_{IV}$	$A_{III}, A_{IV}, A_V$	$A_{IV}$	$A_V$	$A_{VI}$	–

xylem before and after a reiteration event is identical, i.e. the two segments are of the same age. These different elements indicate a typical summer reiteration. The reiteration process concerns only root type  $A_I$ . Each  $A_I$  root can die or give rise to 1 to 3 replacement members in such a way that the root shows a fork composed of several branches. The determinism of reiteration could be of traumatic or endogenous origin. Traumatic origin may result from pronounced drought stress in summer, from spring regrowth or from injury (Lyford, 1980). The frequency of the reiteration, i.e. its regular occurrence cannot be explained only by traumas whose necessarily random character does not agree with our observations. Such a regular reiteration has already been described for tree root systems (Atger and Edelin, 1992). Reiteration is not separable from the strategy of root development. This study emphasizes the importance of reiteration for the development of root architecture, allowing a better exploration of soil volume with several axes developing after the decay of the main root tip, but further study is necessary to investigate the determinism of this process in the plum tree in orchards.

The acropetal branching density was estimated along the root using the decile 9 (Figure 2). Measured root density from the monoliths and from the rhizotron are close to this decile. This choice is based on the possible underestimation of the observed branching density resulting from the direct excavation. A large variation in branching density is observed along the roots, varying from 0 to 4 roots per cm. The branching density follows a regular pattern. Beyond the un-branched apical part, a rapid increase in branching density is observed near the root tip. Branching density is maximal some centimetres from the root tip. Next, branching density decreases due to mortality. The emergence branching density is estimated using

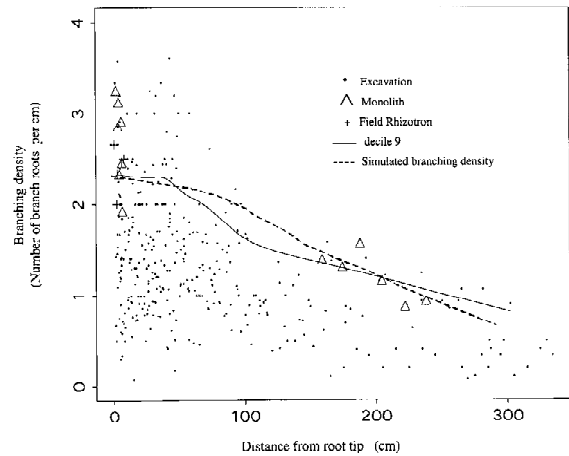


Figure 2. Variation in the branching density along  $A_I$  axes. The branching density is maximal near the apex, and slowly decreases with increasing distance to the root tip. The line is fitted to the decile 9.

the observed maximal branching density, giving 2.4, 2.4, 3.3, 3.2 and 3.2 roots per cm from root type  $A_I$  to  $A_V$ , respectively.

#### Axial growth

Acropetal branching on the larger roots (type  $A_I, A_{II}$ ) is complicated, as the root axis carries several root types ( $A_{II}, A_{III}$  and  $A_{IV}$ ). During the excavations, only root density was measured with no quantification of the proportion of each type of root. On each segment on the main root, the root length distribution of the ramifications results from the proportion of the three populations, and of their respective length distribution. In order to determine the proportion of the different root types at emergence, it is necessary to estimate both the root growth characteristics of types  $A_{II}, A_{III}$ , and  $A_{IV}$  and the proportion of these different root types along the axes. As the root growth

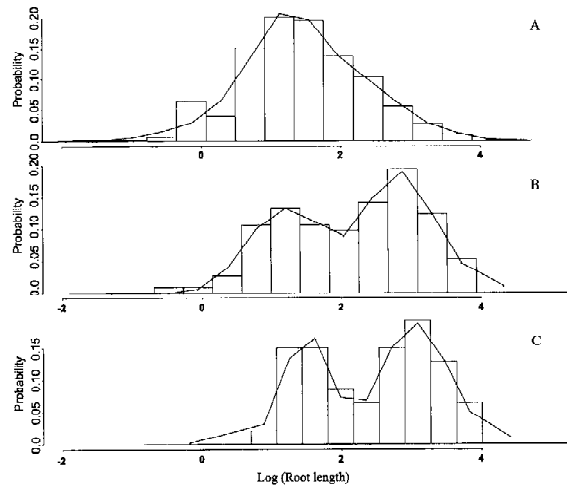


Figure 3. Observed and adjusted root length distribution of the branched roots on the main axes (root type  $A_I$ ) on different zones of the main axes: (A) on the apical part corresponding to branched roots younger than 1 year old, (B) intermediate part of the axes corresponding to branched roots between 1 and 2 years old, and (C) proximal part of the main axes with branched roots over 2 years old. The line is the fitted distribution.

characteristics of type  $A_{IV}$  had already been adjusted (see below), a theoretical distribution was then fitted by varying the proportion of the different populations, as well as the root growth characteristics for root types  $A_{II}$  and  $A_{III}$  (Figure 3). On 1-year-old segments on the main axis, the proportion of different root types is respectively 35, 60 and 5% for types  $A_{II}$ ,  $A_{III}$  and  $A_{IV}$  respectively. This branching density was used as emergence proportions on root types  $A_I$  and  $A_{II}$ . On the 2-year-old segment, all the  $A_{IV}$  roots and some of the  $A_{III}$  roots have disappeared. The mean length of the branched roots increases as a result of root growth as well as lopping off, which occurs especially in higher root types ( $A_{III}$  and  $A_{IV}$ ). The variation in mean root length gives an estimation of the annual growth of the different root types. The final root length of each root type is then adjusted on the proximal part of the main axis. Root type  $A_{III}$  shows typically determinate growth, i.e. the growth duration is finite in time, and a low growth rate, contrasting with root type  $A_{II}$ .

For the higher root types ( $A_{IV}$ ,  $A_V$ ,  $A_{VI}$ ), the observed distribution of final root length is highly asymmetrical, a large number of roots are short, and only a few are long (Figure 4) and can be fitted by a lognormal distribution. This asymmetrical distribution is often linked to the opportunistic growth behaviour of the roots. Soil conditions (water and minerals avail-

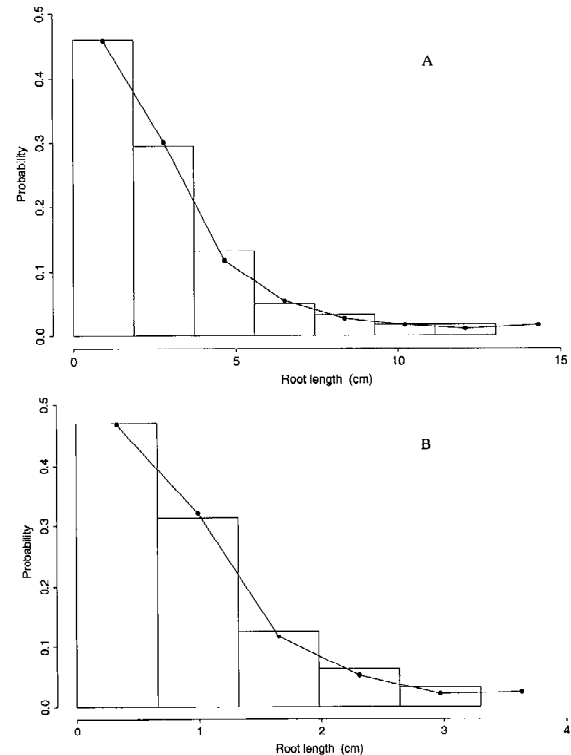


Figure 4. Observed and adjusted final root length distribution of the root type  $A_{IV}$  (A) and  $A_V$  (B). The adjusted distribution is assumed to be log-normal.

ability, oxygen concentration, etc.) greatly affect root growth, and root plasticity allows better colonization of the heterogeneous soil volume (Granato and Rapper, 1989).

A previous study has shown that the growth of the main root is typically indeterminate, i.e. the growth could potentially continue indefinitely, and linear over time (Pagès and Serra, 1994). The plum trees used in these studies were not fruit bearing, consequently axial growth was assumed to occur throughout the growing season (Glenn and Walker, 1993; Williamson and Coston, 1989). We assumed that the measured length results from 3 years of growth, with annual growth being constant. This assumption is a crude simplification of actual growth, but is sufficient to model the root architecture in large time steps, typically at a scale of several weeks. The mean of the main root growth deduced from field measurements based on these assumptions is about 1 m per year, with a standard deviation of  $0.2 \text{ m yr}^{-1}$ . Whereas root plasticity is rather high in the higher root types, root length distribution of the main roots is much more symmetrical.

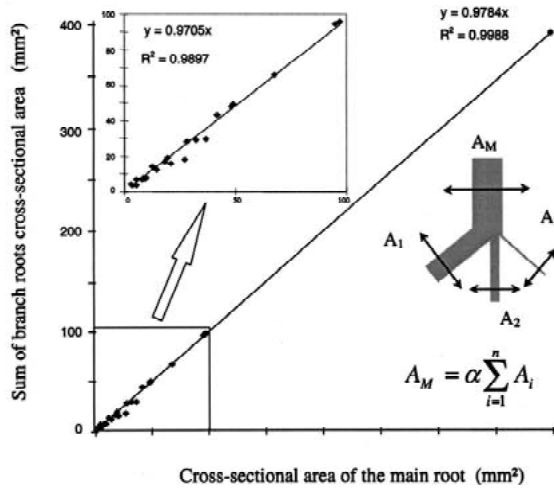


Figure 5. Relation between the root section and the sum of the sections of daughter roots for type  $A_I$  and  $A_{II}$ .

The perennial roots are less sensitive to variations in soil conditions.

#### Radial growth

As a result of the cyclic activity of vascular cambium, some roots show marked radial growth (type  $A_I$ ,  $A_{II}$  and to a lesser extent  $A_{III}$ ), whereas others show suberisation but no lignification. Radial growth is rarely depicted, even if this process is essential when investigating water uptake by the root system. Investigating rubber tree architecture, Le Roux (1994) formalized variations in the root diameter in relation with time, but independently of other processes such as branching or axial growth.

We investigated the relation between the root section before and after branching or a reiteration event (Figure 5). The relation is linear and closely follows the bisector (the slope is 0.97,  $n = 25$ ), i.e. the root section is conserved before and after a branching event. As a consequence, the cross sectional area of the main axis is nearly equal to the sum of the cross-sectional areas of all axes after a branching event distal to where the main axis diameter was measured. From the root tip, the increase in the root diameter could then be assessed for each root by calculating the sum of the branch root sections. The cross sectional area is therefore related to the amount of root tip attached to each root. As long as the secondary thickening is governed by transport requirements as suggested by the pipe model (Coutts, 1987; Shinosaki et al., 1964), the derived relations can potentially be

used independently of the way the branching pattern developed.

#### Mortality

Technical difficulties and limitations prevented accurate quantification of root mortality. These practical difficulties were overcome by observing the variation in branching density along the axis and allowed estimation of root mortality. Indeed, root lopping is a direct consequence of root mortality, even if it is only a marker by-default. Root type  $A_I$  is perennial, and the necrosis time lag adjustment gives 500, 220, 100, 60 and 30 days for root types  $A_{II}$ ,  $A_{III}$ ,  $A_{IV}$ ,  $A_V$  and  $A_{VI}$ , respectively. The simulated branching density along the main axis is shown in Figure 2. The simulated branching density is a little higher on the intermediate old segment, but the trends are similar, with a gradual decrease in branching density along the axes. The estimated range of time-lag necrosis is the same as that described in previous more classical observations. Considerable variations exist in the longevity of plum roots as in other plant species, from less than 10 days to several years (Alexander and Farley, 1983; Bloomfield et al., 1996; Jourdan and Rey, 1997a; Marshall and Waring, 1985).

#### Simulations

The root typology and the fitted parameters are brought together to allow for simulation of the architecture of the tree root system. This model aggregates several models that formalize root development (Table 2). For estimating the actual root development of the *Plum* tree root system under given soil conditions, three different methods were combined – excavation, monolith and field-rhizotron. These observations enable estimation of actual root development taking into account potential root development affected by soil constraints. Consequently, the effect of soil constraints on root development is introduced indirectly. Only a thin compacted soil layer was observed at the base of the plough layer. Except in this zone, where the roots were more tortuous and less branched, no major difference in root development appeared within the root system.

As the model aggregates several sub-models, the validation of the model is indirect. The model contains phenomenological parts that are not really refutable (Pagès et al., 2000a), except in the way the parameters were adjusted. An overall visual evaluation of the models can be obtained through pictures of the

Table 2. Model parameters adjusted for the different processes and for the different root types

	$A_I$	$A_{II}$	$A_{III}$	$A_{IV}$	$A_V$	$A_{VI}$
Insertion angle (rad.)	0.7	1.3	1.3	1.3	1.3	1.3
Distance between branched roots (cm)	0.4	0.21	0.15	0.15	0.15	–
Model of axial growth	$L = A \cdot (1 - e^{-b \cdot t / A})$ with $L$ = length (mm) and $t$ = time (day)					
a (cm): maximal length	1100.0	21.5	4.4	2.0	0.7	0.1
b (cm/day): growth rate	0.60	0.20	0.08	0.05	0.03	0.025
Model of radial growth	$A_M = \alpha \sum A_{Fi}$			No radial growth		
$\alpha$	0.97			–		
Time necrosis (days)	$\infty$	500	220	100	60	30

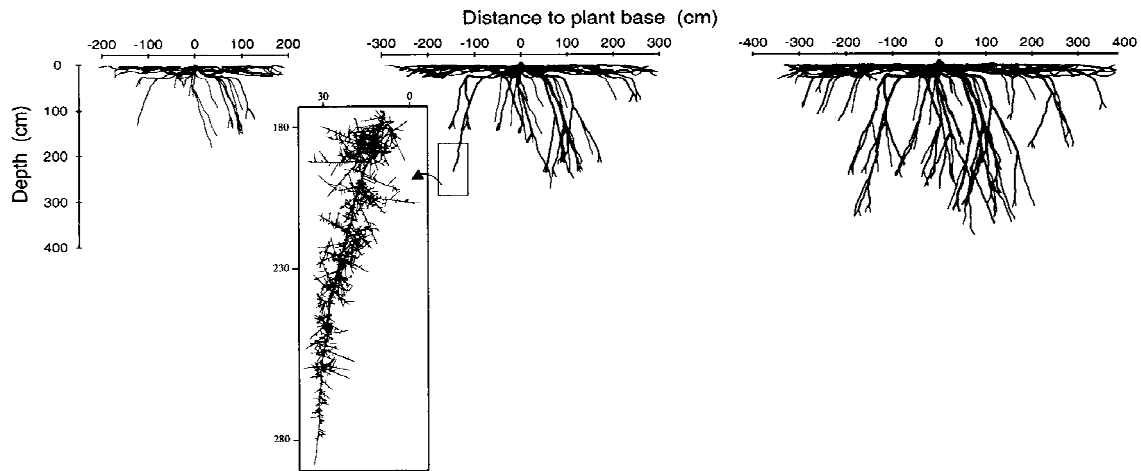


Figure 6. Projection of the perennial structure of a simulated 3-dimensional plum root system of 2, 3 and 4-year-old trees with a detailed view of the branched roots.

simulated architecture. Figure 6 presents a simulation of the perennial structure of 2, 3 and 4-year-old plum root systems. The root system colonizes a large volume of soil, with some roots showing marked horizontal growth, whereas others are nearly vertical. The maximum root depth is close to 3 m. Figure 7 is a simulation of a 3-year-old root system seen from above. Seen from various angles, the soil volume is quite well colonized. The architecture of the root system shows quite evenly spaced forking, allowing a finer net exploration of the soil volume. The bases of the old perennial axes gradually become bare as a result of root mortality. This global visual observation leads only to a qualitative appreciation of the architectural model.

Direct comparisons between the actual and simulated root architecture are a tremendous job, due to

the large volume of colonized soil and to the variability of the spatial root distribution. Model outputs can be used to quantify model predictions for some global criteria, such as some classical parameters describing root development. The simplest descriptions of root systems are models that calculate the distribution of roots with depth. The simulated root length profile is presented in Figure 8. Nearly 30% of the root length is located within the first 30 cm of soil. In deeper layers, the vertical growing main roots lead to nearly uniform root length distribution. Geometrical aspects of the model can also be tested using 2D summaries of global outputs, such as vertical or horizontal root maps (Figure 9). Some large areas show no root impact whereas others are intensively colonized. The branch roots arising from the large main roots lead to a highly clustered root distribution. Such



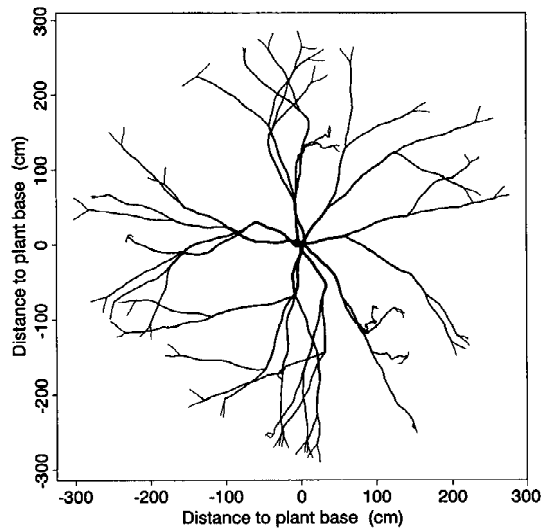


Figure 7. Projection of a simulated 3-dimensional root system of a 3-year-old plum root system seen from above, revealing the root mapping of the soil volume.

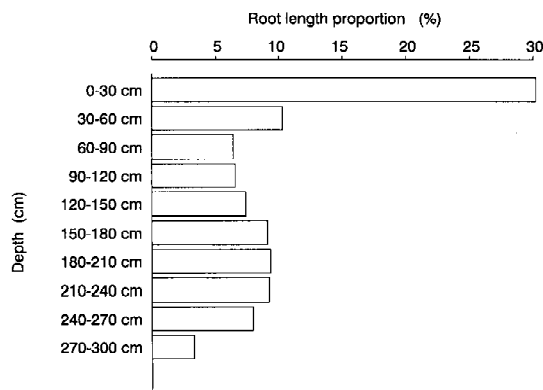


Figure 8. Percentage of roots contained in a soil layer, for a simulated 3-year-old plum root system.

root distributions have been observed in some annual plants (Tardieu et al., 1992) and to a lesser extent in orchard trees (for apple tree see Levin et al., 1979). The irregular pattern of the root colonization could be magnified in the case of uncultivated trees, growing in soils of natural ecosystems characterized by a highly heterogeneous distribution of the resources.

More generally, the root architectural model can be used as a tool to investigate the consequences of various combinations of parameters (typology and/or process parameters) for global root architecture or to estimate certain specific data from a local to a global level. The model also allows retrospective analysis of root development, assuming that the processes are qualitatively and quantitatively identical during the

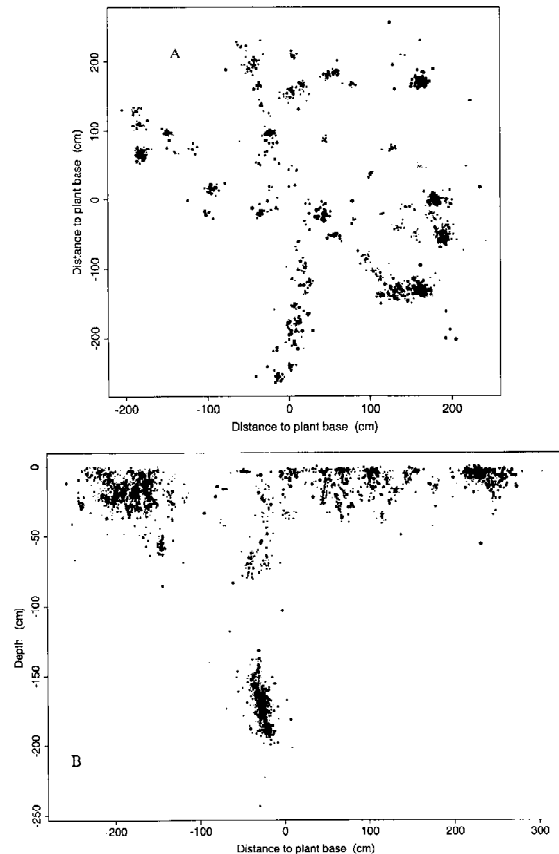


Figure 9. Simulated root contact map for a 3-year-old plum root system. (A) horizontal root map contact at depth of 50 cm, and (B) vertical at 100 cm from the plant base. Size of dots is proportional to the root diameter.

root development period. For example, analysis of the growth of the main root can give an estimation of the variation in the volume of the explored soil with age, as well as an appreciation of the fineness of the root mesh throughout this soil volume. The explored soil volume expands from  $2 \text{ m}^3$  for a 1-year-old Plum root system to more than  $100 \text{ m}^3$  for a 4-year-old. An indicator of the fineness of the root mesh is the ratio of the total length of the main roots ( $A_I$ ) to the explored soil volume. This ratio decreases rapidly with the age of the root system to reach a stable value close to 2.5, i.e. one cubic meter of soil contains nearly 2.5 m of larger roots from which the fine roots develop. The spatial expansion of the root system is linked with the reiteration process to allow for a constant fineness of the main root mesh.

Finally, this study: (i) highlights processes that are not generally studied in root development, such as reiteration, (ii) presents some unusual ways to investigate

and assess these processes, such as root mortality, and (iii) proposed original ways to formalize basic process, such as the radial growth process. Moreover, the formalization of the different processes is usually done without any interaction between the processes. Root development has been considered to be the result of several independent processes that contribute to building up the root system (Diggle, 1988; Pagès and Aries, 1988). However, these different processes are largely inter-related. In this study, the modelling approach is an attempt to link the different processes. As described above, radial growth depends directly on the branching process. Root decay is linked with both the end of the growth and the presence of branched roots. Consequently, even if axial and radial growth are defined independently, these processes are linked via the branching process and root decay. The longer the root, the more branched roots appear – with few being pruned – leading to a substantial increase in root diameter. Links between processes point to relations at a larger scale. The proximal root diameter and the total length of the root have been shown to be correlated, especially in the main roots. This information provides another way to validate the architectural model.

## Conclusion

Architectural analysis and modelling of the plum tree root system in an orchard using a quantitative modelling approach proved to be a useful tool. The tree root system is difficult to study, because of its belowground nature and its size. Different experimental designs are needed to investigate the organization of the root system architecture in an orchard: excavation, monolith, rhizotron, etc. These methods of observation can only partially explore the whole root system. With only a few basic assumptions, the architectural model framework helps to focus specific observations on various part of the root system, from the proximal to the distal part, and from the main to the fine roots. It also allows integration of various kinds of information from various points of view: static–dynamic, local–global, quantitative and morphological observations.

Root function now needs to be investigated in more detail, with special emphasis on possible variations between root types. This work would combine structural and functional characteristics resulting in an integrated approach to understand belowground resource acquisition at the scale of a root segment up to the entire root system (Pagès et al., 2000b).

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