

DigR: a generic model and its open source simulation software to mimic three-dimensional root-system architecture diversity

Jean-François Barczy^{1,2}, Hervé Rey^{1,2}, Sébastien Griffon^{1,2} and Christophe Jourdan^{3,4*}

¹CIRAD, UMR AMAP, F-34398 Montpellier, France, ²AMAP, Univ Montpellier, CIRAD, CNRS, INRA, IRD, Montpellier, France,

³CIRAD, UMR Eco&Sols, F-34398 Montpellier, France, and ⁴Eco & Sols, Univ Montpellier, CIRAD, INRA, IRD, Montpellier SupAgro, Montpellier, France

*For correspondence. E-mail christophe.jourdan@cirad.fr

Received: 19 October 2017 Returned for revision: 9 January 2018 Editorial decision: 22 January 2018 Accepted: 25 January 2018

- **Background and Aims** Many studies exist in the literature dealing with mathematical representations of root systems, categorized, for example, as pure structure description, partial derivative equations or functional–structural plant models. However, in these studies, root architecture modelling has seldom been carried out at the organ level with the inclusion of environmental influences that can be integrated into a whole plant characterization.
- **Methods** We have conducted a multidisciplinary study on root systems including field observations, architectural analysis, and formal and mathematical modelling. This integrative and coherent approach leads to a generic model (DigR) and its software simulator. Architecture analysis applied to root systems helps at root type classification and architectural unit design for each species. Roots belonging to a particular type share dynamic and morphological characteristics which consist of topological and geometric features. The DigR simulator is integrated into the Xplo environment, with a user interface to input parameter values and make output ready for dynamic 3-D visualization, statistical analysis and saving to standard formats. DigR is simulated in a quasi-parallel computing algorithm and may be used either as a standalone tool or integrated into other simulation platforms. The software is open-source and free to download at <http://amapstudio.cirad.fr/soft/xplo/download>.
- **Key Results** DigR is based on three key points: (1) a root-system architectural analysis, (2) root type classification and modelling and (3) a restricted set of 23 root type parameters with flexible values indexed in terms of root position. Genericity and botanical accuracy of the model is demonstrated for growth, branching, mortality and reiteration processes, and for different root architectures. Plugin examples demonstrate the model's versatility at simulating plastic responses to environmental constraints. Outputs of the model include diverse root system structures such as tap-root, fasciculate, tuberous, nodulated and clustered root systems.
- **Conclusions** DigR is based on plant architecture analysis which leads to specific root type classification and organization that are directly linked to field measurements. The open source simulator of the model has been included within a friendly user environment. DigR accuracy and versatility are demonstrated for growth simulations of complex root systems for both annual and perennial plants.

Keywords: DigR, AMAPstudio, root architectural model, root types, structural model, simulation platform, functional plugins, *Elaeis guineensis*, *Eucalyptus* sp., *Cicer arietinum*, *Beta vulgaris*, *Lupinus* sp.

INTRODUCTION

Two main approaches are currently used to represent the root systems of plants and their development through time. These representations are based on two different formalisms, (1) continuous representation of root systems through time and space using partial derivative equation (PDE) sets with time and space as state variables that produce dynamic density maps and (2) discrete time event formalism based on explicit structure root system development that takes into account structural meristem production and that leads to an explicit output of the root system.

(1) Continuous models generally simulate root apex density and interactions of the roots through time and space through classical advection, diffusion and reaction PDEs. They do not explicitly deal with root architecture (Dupuy *et al.*, 2005, 2010; Bastian *et al.*, 2008; Bonneau *et al.*, 2012). This type of model caters for large-scale use, for example for individual plot or field scales.

Continuous models can also be coupled with other models that generally use the same formalism such as water transport (Doussan *et al.*, 1998), or nutrient uptake competition (Mayer *et al.*, 1999, 2012; Bonneau *et al.*, 2012), or rhizospheric pH (Kim and Silk, 1999). Another root system modelling based on voxel automata has also been proposed (Mulia *et al.*, 2010) that provides a 3-D root system structure interacting with soil water content represented into voxels. Nevertheless, this model uses an approximate root system representation with too few parameters to be able to accurately simulate the organ types and the overall system architecture.

Generally speaking, these continuous models are difficult to calibrate and their use at large scales requires parameter homogeneity assumptions that most of the time are incorrect or inconsistent. Indeed, most root functioning rules that are applied do not take environment heterogeneity into account. It is thus necessary to cater for the diversity of apex functioning

depending on the type of environment. For instance Guo *et al.* (2008) introduced vertical and horizontal spatial diversity and Baddeley and Watson (2005) took time of development into account. It is well known that root branching order and diameter are parameters that are strongly correlated to root lifespan (Eissenstat *et al.*, 2000). Roots belonging to the same branching order and diameter class may have different lifespans within the same root system. This functional heterogeneity may come from different topological positions within the root system structure (e.g. in terms of distance from the stem) or different trophic status (Hodge, 2004; Pregitzer *et al.*, 1993). Root apices belonging to the same type may also have heterogeneous functioning (Jourdan and Rey, 1997a) due to either their mycorrhizal fungal colonization status (Eissenstat *et al.*, 2000; Resendes *et al.*, 2008), or their association with bacterial nodules that fix atmospheric nitrogen (Hirsch *et al.*, 1997) or with blue-green algae (Cyanophyceae) or Cycadaceae (Spratt, 1911; Nathanielsz and Staff, 1975).

Architectural analysis combined with root type classification (typology) that characterizes the root system and its spatial distribution is therefore a suitable approach for precisely identifying the heterogeneity of root functioning. Roots are produced by meristems functioning in response to the environment as well as endogenous properties of a given species. These properties express the morphological, anatomical and physiological characteristics that combine to construct the root-system architectural unit (Atger, 1992; Jourdan and Rey, 1997a; Barthélémy and Caraglio, 2007).

To identify typology into a root system, meristem behaviour has to be classified taking into account processes that may belong to the structure (branching order, reiteration capabilities, branching quality and density), or to the growth and development (growth time, rest duration, mortality frequency) of roots during the entire ontogeny of the plant (Jourdan and Rey, 1997a).

(2) Several discrete event models that describe root architecture are available. They describe more-or-less detailed components of the system including the root system itself, edaphic environment and their coupling. Depending on the background of the modellers, models may be more focused on the biological object or on the mathematical formalism. For instance, some models based on root typology have been developed from a classification based on growth, branching and death processes measured on real plants (Lungley, 1973; Diggle, 1988; Pagès *et al.*, 1989, 2004; Jourdan and Rey, 1997b, c) or using morphological markers (Pagès *et al.*, 2014). On the other hand, other researchers put more focus on the mathematical approach applied to the root system using L-systems (Leitner *et al.*, 2010) or fractals (Van Noordwijk *et al.*, 1994; Ozier-Lafontaine *et al.*, 1999), or using combination of the two (Shibusawa, 1994).

Some models describe 3-D root system architecture well in a simplified environment with a more-or-less accurate typology most of the time based on apex diameter and proposing root-soil interaction functions (functional-structural root architectural models) such as ‘RootTyp’ (Pagès *et al.*, 2004), ‘SimRoot’ (Nielsen *et al.*, 1994; Lynch *et al.*, 1997) and ‘Rootmap’ (Diggle, 1988) (reviewed by Dunbabin *et al.*, 2013). Other models are more approximate regarding root system accuracy (typology coming only from apex diameter)

but offer sub-models to describe water and nutrient uptake, i.e. ‘SPACSYS’ (Wu *et al.*, 2007), ‘R-SWMS’ (Javaux *et al.*, 2008) and ‘RootBox’ (Leitner *et al.*, 2010), or provide specific ecosystem management applications such as thinning due to root pathogen propagation in forest tree plantations (Brown and Kulasiri, 1994; Brown *et al.*, 1997). The recent development of the OpenSimRoot model (Postma *et al.*, 2017), an open source model derived from SimRoot, will provide new insights and improvements as it can be used and expanded by both modellers and non-modellers to simulate root system architecture with water and nutrient uptake functions in different crop management scenarios and for large range of species and environments.

Nevertheless, all these models are mainly focused on annual crop and herbaceous plant simulation with a lifespan limited to a maximum of several months and are generally aimed at one or several species (grasses and herbs; reviewed by Dunbabin *et al.*, 2013). Few examples exist dealing with perennials (Jourdan and Rey, 1997b, c) and these can grow for decades, involving senescence and reiteration processes (Atger, 1992; Atger and Edelin, 1994).

The goal of this paper is to present a root architectural model that takes structural and functional heterogeneity into account. It is also able to cover intra- and inter-species diversity. We aim to model root systems of both perennial and annual plants, whether herbaceous or ligneous, belonging to either monocot or dicot clades and up to plant senescence. It is thus necessary to be able to model the diversity of roots such as primary or secondary taproots, fasciculate roots, plagiotropic roots, tuberous roots, nodule roots and cluster roots. To do so, we used our knowledge of root architecture to build a dedicated root system model inspired by the approach that has been applied to the shoot system in the model AMAPsim (Barczy *et al.*, 2008).

We assume that it is possible to build a discrete generic model using parameters that are directly measured in the field and avoiding proxy functions such as advection or transition age between types. It will be based on root typology taking into account growth, branching, mortality, self-pruning, reiteration and geometry features. To take account of this assumption we propose a parsimonious model called DigR, which is accurate enough to account for diversity and morphological variability through time. DigR parameters are defined as close as possible to what is measured on the actual root system. These will be calibrated using values derived from field measurements.

This model is provided with its open-source simulation software (DigR). The software proposes a user-friendly interface to input parameter values. The software architecture will be designed to be easily linked to other models dealing with physiological root functioning and edaphic environment interactions (both biotic and abiotic) and also with the shoot compartment. This software will be improved, maintained and distributed from a permanent software environment. The output is root system hierarchical mock-ups ready to be displayed and to be processed for sophisticated filtering and extraction of root traits such as root length, average diameter, biomass, specific root length (SRL), specific root area and root mortality rate.

METHODS

Root observation data

The DigR model is built from measurements of root systems taken after partial or total field excavations or in controlled environments. Classic root traits include length, diameter and branch density. These root traits may be measured through time with a diachronic approach or with synchronous root growth monitoring. Root trait values are measured directly over time through (mini)rhizotrons or scanners or measured indirectly by sequential coring or ingrowth core methods.

Architectural analysis (Jourdan and Rey, 1997a) ultimately leads to root type identification and classification and to design of the architectural unit that consists of the root-type and its structural hierarchy and topology resulting from plant ontogeny.

Examples shown in this paper came from measurements on (1) oil palm trees (*Elaeis guineensis*) carried out in the Ivory Coast (Jourdan and Rey, 1997a), (2) cuttings of eucalyptus (*Eucalyptus grandis* × *urophylla*) measured in the Congo (Thongo M'Bou, 2008; Thongo M'Bou et al., 2008) and (3) seedlings of eucalyptus in Brazil (Jourdan, unpublished data). We also show some examples of annual plants derived from unpublished data.

Model description

Root system analysis allows classifying root types that share homogeneous structural and dynamic features. The number of types that may be identified depends strongly on the accuracy of knowledge and on the goal of the study. The finer the knowledge and accuracy of the modelling, the higher the number of different root types. All roots belonging to the same root type will share the same properties with some variability.

Formalism

The DigR model is based on this structural and typological formalism. Classification will rely on the main growth processes for each root type (apical growth, branching, death and pruning) and geometry (secondary growth, growth direction). Branching representation will introduce the architectural root unit (Fig. 1A), which explains the basic organization patterns of root types (Jourdan and Rey, 1997a). The repetition and setup of these patterns will construct the whole root system structure through time (Fig. 1B).

Given the typology for a particular species, measurements show that meristem behaviour is changing through time. For instance, growth rate or branching density may vary homogeneously at different growth stages of axes belonging to a particular root type. Because measurements are made according to position along roots, it is convenient to express root functioning according to position indices.

For a given species, meristem production may vary due to specific variability. To accommodate this, simple stochastic functions that will be applied on default processes through a value for standard deviation were used.

Finally, the resulting topology will be improved based on geometry to provide correct diameters and positions in 3-D space. The output is a 3-D mock-up containing the average shape of a root system through its life and associated with a topological hierarchy of its components.

Processes and parameters

Every root type will be described through the same processes and the same set of parameters. Only the parameter values will make a given behaviour different between two separate root types. The main processes that will be described are apical growth, death and pruning; branching and reiteration; diameter growth and geometrical features (angles and growth directions). A particular focus will be put on finding a formulation that will remain as close as possible to what is measured in real root systems. Because observations show that root behaviour may change through their life, DigR manages parameter values that may change according to position along roots of each type. This position is measured directly on (mini)rhizotrons for fine roots or *a posteriori* after soil excavation for coarse roots.

Apical growth. Compared to aerial parts, there are no obvious morphological markers (scars, nodes, growth endpoints) to describe the development of root axes. Researchers usually measure the length increase per time unit. For each root type this elongation rate will be represented according to a value that may vary at different root lengths. After initial formation, each apical meristem of lateral roots remains dormant a few days before emerging; this phenomenon builds up the unbranched apical zone of the bearing axis. To model this feature, we defined a time delay before a root type begins its apical growth. To model this process, two parameters are defined, DelayBeforeGrowth and GrowthSpeed (Table 1). To obtain the time delay value, the length increase of each root type can be directly monitored through minirhizotron or rhizotron observations. It can also be estimated through sequential excavations on different roots with time.

Death and pruning. An important feature of root systems is the mortality rate that mainly, but not always, occurs in fine roots. For this, a DeathProbability (Table 1) will be tested along each root type with a value that may vary along the root. When the probability test is positive the root will stop its growth. Root self-pruning will occur after a delay that depends on the root type (LagBeforePruning, Table 1). This delay is difficult to estimate and is commonly estimated *a posteriori* from a comparison of branching densities between roots belonging to the same type and measured a different time of their life. Death is tested at the end of each growth time unit. To obtain the death probability value, we measure total length of dead roots belonging to the same root type. We then compute a root death probability to fit the total root length distribution.

Branching. For each type, branching is represented as a mix (BranchingSet) of different branching types (BranchingType, Table 1), each of them with its frequency within the mix (BranchingTypeFrequency, Table 1), and an average distance between laterals (InterBranchDistance, Table 1). The Interbranching distances may vary along a bearing root. If a

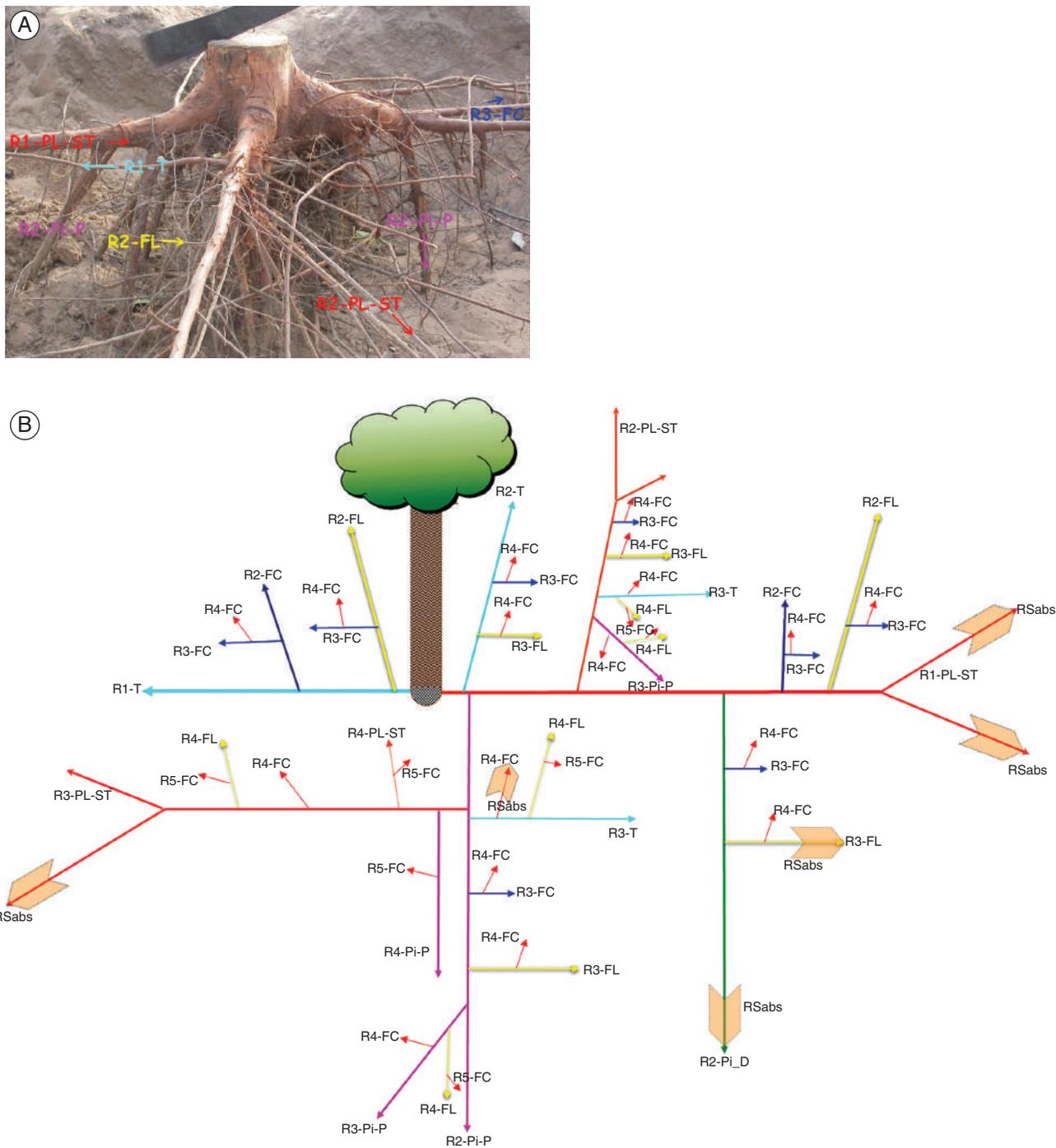


FIG. 1. Cutting eucalypt (*Eucalyptus urophylla* × *grandis*) architectural units. (A) Diagram of the root types and their topological links. (B) Picture of a part of a 4-year-old eucalypt root system in Congo Benin showing the main root types coming from architectural analysis. Eucalypt root typology is composed of coarse roots such as plagiotropic delayed roots (PL-ST); proximal (Pi-P) and distal delayed sinker roots (Pi-D); cable-like delayed roots (T); and fine roots such as long (>10 cm, FL) and short roots (<10 cm, FC). The root tip zone of each root, comprising very thin, short-lived and small (<3 cm long) roots which make up the absorbing system, is not taken into account. The index on R (R1, R2 to R5) accounts for branching order for observation convenience. Note that the same root type may appear at different branching orders, for instance the root system may contain R2-FL, R3-FL and R4-FL that share the same properties.

mix consists of more than one lateral type, the positions of laterals of one type are dependent on the positions of those of other types. It is also possible to define different mixes (many BranchingSets) that will be borne by roots belonging to the same root type and which are independent. To simulate the particular

case of whorl or cluster roots, it is possible to declare a potential number of lateral roots at each position along the bearing root (MaxBranchNumber, Table 1) and a probability for each of these lateral roots to begin their growth (BranchingProbability, Table 1). To obtain branching values, for each mother root type

TABLE 1. List of processes and associated parameters of the DigR model; index and mean values of parameters for taproot of sugar-beet root system are given in the two right-hand columns as an example

Process	Parameter name	Meaning	Unit or value	Index*	Value†
Apical growth	DelayBeforeGrowth‡	Time a new axial meristem will wait before starting to grow	Time unit	0	0
	GrowthSpeed‡	Root length that a meristem will produce per time unit	cm time unit ⁻¹	0	30
				29	30
Death	DeathProbability‡	Probability that an apical meristem will die	[0, 1]	30	1
				0	0
Pruning	LagBeforePruning	Time a root will stay in structure before pruning after death	Time unit	–	999
Branching (BranchingSet)	BranchingType‡§	Type of axial meristem that will be borne in this branching set	Label	1	1
	BranchingTypeFrequency‡§¶	Frequency of this type in this branching set	[0, 100]	1	100
	InterBranchDistance‡§¶	Distance between two axial meristems in this set	cm	0	30
				30	1.7
	MaxBranchNumber	Maximum number of roots at the same position (whorl, cluster roots)	Number	–	1
Diameter growth	BranchingProbability‡	Probability of birth for each root at the same position	[0, 1]	0	1
	InitialDiameter¶	Diameter of apical meristem	cm	–	0.1
	DiameterIncreaseRatio‡¶	Ratio to apply to initial diameter to reach final diameter	[0, ∞]	0	1
				30	1
				31	80
				33	100
				60	10
Direction of growth	DiameterIncreaseTime‡¶	Time to reach final diameter	Time unit	0	28
	DiameterIncreaseDelay‡¶	Time a root will wait before diameter growth	Time unit	0	20
	InsertionMode	Initial growing direction policy	Rhizotaxy, to vertical	–	Rhizotaxy
	InsertionAngle¶	Branching angle on bearer according to Insertion Mode	Degree	–	60
	RhizotaxyAngle‡¶	Helicoid angle between successive roots along bearer	Degrees	0	180
	ConstraintHorizontalAngle	Horizontal opening angle of the conic part of the constraint shape	Degrees	–	45
	ConstraintVerticalAngle	Vertical opening angle of the conic part of the constraint shape	Degrees	–	45
	ConstraintConeLength	Beginning conic part length of the constraint shape	cm	–	99999
	ConstraintConeDirection‡	Direction of the constraint shape along root	Degrees	0	0
Tortuosity	TortuosityAngle¶	Random deviation angle along apical growth	Degrees	–	1
Reiteration	ReiterationFrequency‡	Frequency for each position to reiterate	[0, 1]	0	100
	ReiterationDistance‡	Distance between reiteration along bearing root	cm	0	47
	ReiterationBranchingAngle	Angle between reiteration and bearing root	Degrees	–	10
	ReiterationRhizotaxyAngle	Spiral angle between successive reiterations	Degrees	–	180
	MaxReiterationOrder	Maximum topological order for reiterations along bearing root	Number	–	1

*Position along the root axis.

†Observed or modelled values of the parameter according to its relative position along root axis

‡Mean parameter values depending on position along root.

§Mean parameter values depending on branching set.

¶Mean stochastic variability values.

and according to mother root length, we count the number of lateral roots and label their type. We compute the average and standard deviation of spacing and root type distribution of laterals on a set of measurements.

Geometry. The main features for geometry are generated by controlling the diameter, the position and the growth direction of roots in 3-D space depending on their type.

Diameter growth. Diameter is controlled through a simple linear law with an initial meristem diameter (InitialDiameter, Table 1), a diameter increase ratio (DiameterIncreaseRatio, Table 1) and a time to reach the maximum diameter (DiameterIncreaseTime, Table 1). In addition, it is possible to define a delay before starting secondary growth (DiameterIncreaseDelay, Table 1). To determine initial diameter values, for each root type, we measure the apex diameter. To obtain the diameter increase values, for each root type, we measure diameter of roots with time. This allows us to compute values for diameter increase ratio, diameter increase time and lag before diameter increase.

Direction of growth and tortuosity. To control the geometrical shape of a root of a given root type it is necessary to compute its growth direction from birth to death (Fig. 2). Initial growing direction (InsertionMode, Table 1) may be computed according to the current bearer direction or according to the vertical through an initial insertion (InsertionAngle, Table 1) and a rhizotaxy angle (RhizotaxyAngle, Table 1). Depending on root type, the growth direction may have to be forced. For instance, plagiotropic roots tend to grow in a horizontal plane while orthotropic root tends to grow in a vertical direction. Therefore, a constraint cone (Fig. 2) is defined with a horizontal and a vertical opening angle (ConstraintHorizontalAngle and ConstraintVerticalAngle, respectively, Table 1), a cone length (ConstraintConeLength, Table 1) and growth direction angles (ConstraintConeAngle, Table 1). To take into account root tortuosity within the soil, a random local deviation angle with a maximum value may apply along the root (TortuosityAngle, Table 1). To obtain values for the initial direction of root growth, rhizotaxy angle, we directly observe it after excavation. We

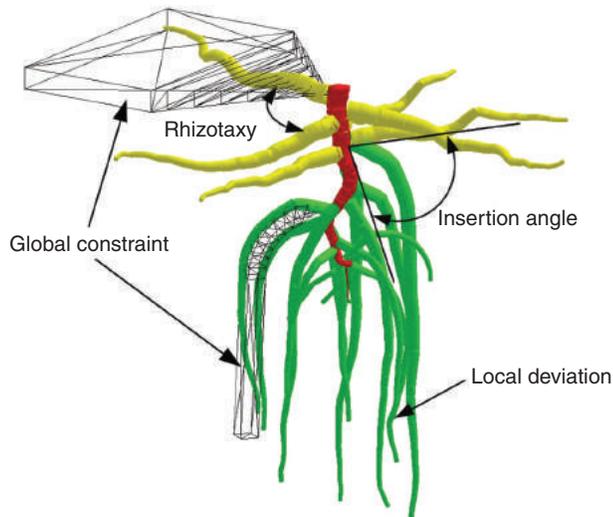


FIG. 2. Root system simulation showing geometrical features to control root shape in terms of rhizotaxy angle (helicoïd angle between two successive lateral roots) and insertion angle (angle between bearing root and laterals), root deformations (local deviation and tortuosity) and root direction within global constraint cones.

adjust tortuosity angle and constraint cone shape to fit observed general root shape.

Reiteration. Reiteration is the capacity of a particular root type to divide and self-reproduce. Reiteration is characterized by its probability (ReiterationProbability, Table 1), inter-reiteration distance (ReiterationDistance, Table 1), and branching and rhizotaxic angles along their position on the bearer axis (ReiterationBranchingAngle and ReiterationRhizotaxyAngle, respectively, Table 1). The maximum branching order limits the number of reiterations (MaxReiterationOrder, Table 1). Observations and architectural analysis allow us to identify where reiteration takes place. Their position and number are measured on field excavations. The parameter values (probability, initial angle, rhizotaxy) are computed in the same way as for branching process.

Toward a new paradigm to make DigR functional

DigR is a purely structural model. To be able to change the paradigm and take account of functional considerations with root–environment interactions, we set up a software interface that allows linking to external functional models which simulate these processes and which influence the default DigR behaviour.

For instance, to simulate root growth and functioning (absorption, excretion, water and nutrient balance, root branching, etc.) taking into account edaphic properties (water and nutrient content, soil density, porosity, temperature, etc.), we need to define a formal framework consisting of:

- Geometrical space discretization Δl that defines a minimum voxel in which environmental conditions are assumed to be homogeneous. Voxel size is a parameter with a value fixed by the user.
- Time discretization Δt that defines a minimum time step when the environment remains stable. The environment will be re-evaluated at this time step.

We define software external plugins that will both evaluate edaphic properties and compute their influence on root system growth. For instance, we may need to modify growth speed according to soil water content. To do so, we need to establish a default growth speed for each root type and a function reflecting the influence of water content on this default value. On the other hand, we may also want to simulate water content evolution due to water uptake from roots. To do so, we will need a function that will re-evaluate water content of soil voxels (Δl) at every time step (Δt) and depending on RLD (root length density) into the voxels. This knowledge may come from experiments or from observations in different soil water and root growth conditions. Given the steady water content of voxels during Δt , DigR will compute meristem growth during this time step with locally modified growth speed according to meristem position. The simulation can then loop at this time step. It is important to make a distinction between the time unit which is the interval between two observations on the real root system or the simulation time when an output may be requested, and between the time step at which the environment may update, and between the time events that allow every meristem to synchronize along a single time unit and that may occur at any time regardless of any time unit or time step.

Software implementation

DigR simulator was implemented in a software architecture in which every current living meristem of the simulated plant is simulated in quasi-parallel and running the same discrete event algorithm (<http://amapstudio.cirad.fr/soft/digr/start>). Every meristem will have a production value according to the parameter values that are attached to its current type. A parameter manager is able to return the parameter values according to the type of the current meristem for the simulated species.

This collection of meristems is synchronized through the same time scale thanks to a scheduler that is able to record, order and run events from every meristem. During simulation, meristem events are recorded at every branching time or time unit. After running its current event, a meristem computes its next event and records it into the scheduler's time-ordered events stack. This allows meristems to grow together along the same time scale, thus generating a quasi-parallel computing. This means that the simulation can be stopped at any time while keeping a homogeneous structure of the current simulated root system. Each meristem sets up a new root segment between its two consecutive events.

The scheduler is also able to record and run events coming from other additional plugins. A plugin can register events at any time. At the time this event is run by the scheduler, it has access to the current plant structure and can interact with it. A plugin can also register to the parameter manager so that it will be able to modify parameter values before they are used by meristems. The functioning part of the root system can be simulated then through external plugins.

Another software feature is an observer design pattern (Gamma, 1995) that will affect the parameter value access mechanism. Simulated meristem objects are not assigned to their growth parameter values directly. They obtain them by asking a function (accessor) that fetches the values from the

default parameters of the simulated species. This accessor also has code that raises a software signal before it returns the requested parameter value. Any other object of the simulator may subscribe to accessor signals. Upon receiving an accessor signal, subscriber objects will be run and will be given two arguments, the requested parameter value and the meristem object that tried to get this parameter value. According to these arguments, the subscriber object algorithm may modify the parameter value before it is returned to the accessor. Every DigR parameter has its own signal so that subscribers can listen only to the parameters that they are able to manage.

The general flowchart for this observer pattern is as follows: (1) a root meristem object requests a particular parameter value from the accessor, (2) the accessor fetches the default parameter value and raises a parameter signal, (3) any subscriber object for this parameter signal is run with the parameter value and the root meristem object as arguments. The subscriber object computes the correct value for the parameter and returns this value to the accessor. (4) The accessor returns the final parameter value to the meristem object.

A DigR simulator was implemented in Xplo, which is a software part of the AMAPstudio environment (Griffon and De Coligny, 2014).

Moreover, the DigR simulator is natively hosted into the Xplo platform, which is a part of the AMAPstudio framework (Griffon and De Coligny, 2014). This software suite is written in java, aimed at plant modelling, and free to download (under Lesser General Public Licence, see <http://amapstudio.cirad.fr>). Xplo allows users to interactively load empty parameter files or is already filled with parameter values obtained from root systems previously modelled. These values can be modified according to the user's observations. Xplo runs simulations and obtains outputs as 3-D objects, plots or tables. Moreover, a user can explore and make root trait extractions from the current output, i.e. sum of root length, average diameter, total biomass, necromass, etc., for each root type or for the whole root system. Parameter files of the plant root system models detailed in the Results section are available in the Xplo installer that can be freely downloaded from the AMAPstudio website.

RESULTS

Some outputs of the model

Fasciculate root system with development over time. We have chosen the oil palm tree (*Elaeis guineensis*) to illustrate fasciculate or fibrous root system modelling. This tree may live for some decades. The root architecture has six root types at the juvenile stage (from germination to 1 year old, Fig. 3A). It then sets up two new root types over the next 2 years (Fig. 3B; Jourdan and Rey, 1997a). At 10 years old, the oil palm tree is in its adult stage with maximum potential yield. The root system reaches about 6 m horizontal radius and 5 m depth on average in the tertiary sandy soil of the Ivory Coast (Fig. 3C; Jourdan and Rey, 1997b, c).

Primary (seedling) and secondary (cutting) taproot systems. We chose eucalyptus to illustrate primary taproot (seedling, *Eucalyptus grandis*, Fig. 4A) and secondary taproot (cutting, *Eucalyptus urophylla* × *Eucalyptus grandis*, Fig. 4B)

root systems. They show separate soil exploring strategies. *Eucalyptus* seedlings consist of an orthotropic taproot having positive geotropism, lateral plagiotropic roots, late lateral plagiotropic roots, a distal secondary taproot and various fine roots with variable lifespans. Main and distal taproots and plagiotropic roots may reiterate. The cutting is made up of a dominant plagiotropic system which bears proximal and distal secondary taproots, lateral plagiotropic roots and various fine roots with variable lifespans.

Another example shows the ability of DigR to express species variability on eucalyptus root systems (Fig. 4C) using the standard deviation associated with each of the model parameters. Each simulation corresponds to particular individuals belonging to the same distribution.

Finally, the dynamic 3-D growth process may be simulated with time unit defined by the user. An example of growth from zero to 5 years old at monthly time unit is illustrated in Supplementary Data Fig. S1.

Particular cases. DigR allows the use to simulate root system features such as specific storage organ (tuberous roots), nitrogen-fixing organs through symbiosis with bacteria (nodule roots) and proliferation of proteoid roots (cluster roots). We present some cultivated annual plants in the next examples.

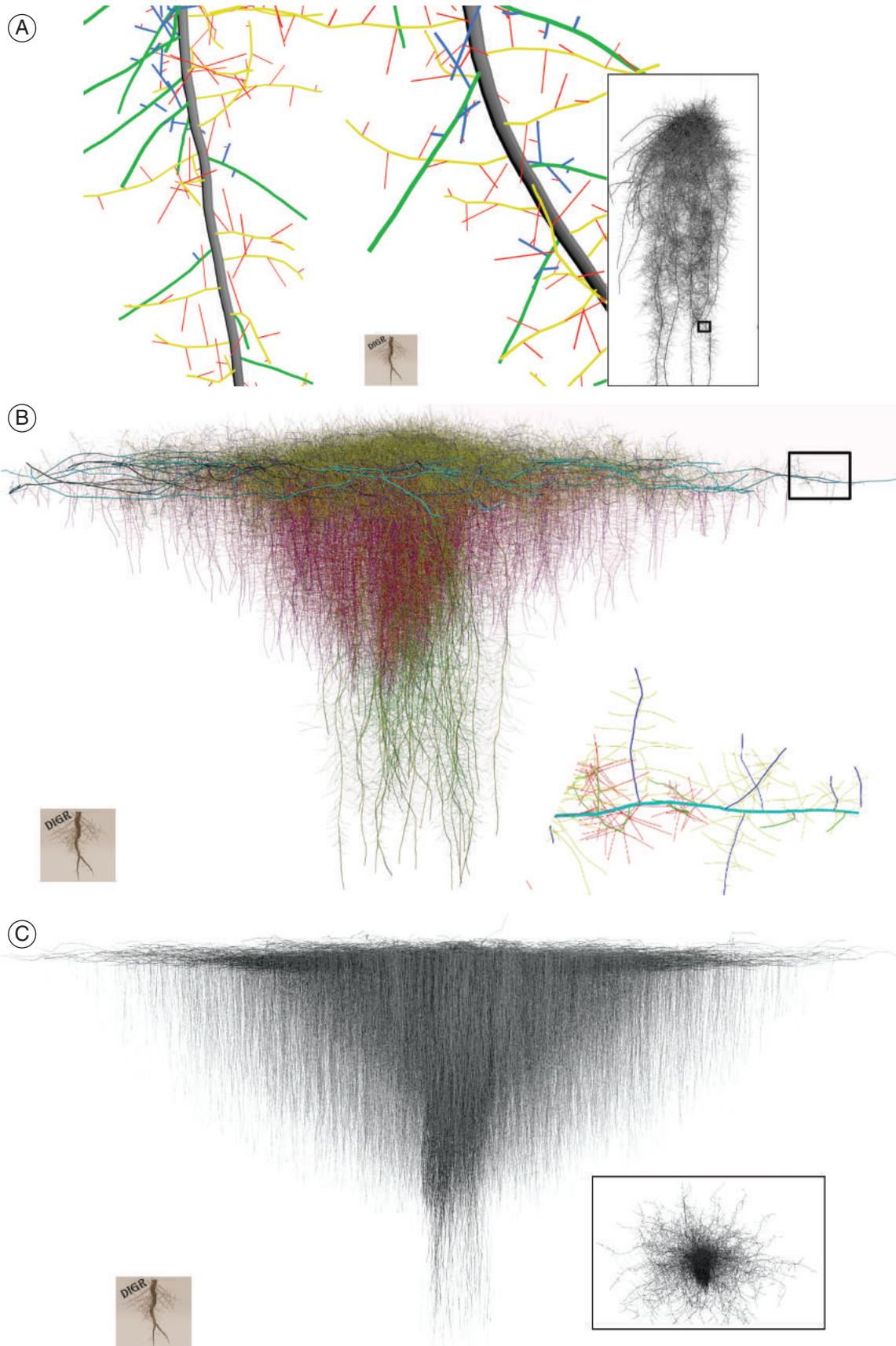
Tuberous root system. Sugar beet (*Beta vulgaris*, Fig. 5A), just like carrot, uses the primary taproot to store carbohydrates and nutrients. This taproot can reiterate and bears two different fine root types. One has a diameter which can increase and the other one retains a constant diameter and absorbs water and nutrients. Tuberous root systems may also be found within Convolvulaceae such as sweet potato (*Ipomoea batatas*), Euphorbiaceae such as cassava (*Manihot esculenta*) and Asteraceae (*Dalhia*). A detailed description of how parametrization of processes was made for this example is given in Table 1.

Nodulated root system. Chickpea (*Cicer arietinum*) is one of several species with root systems bearing nitrogen-fixing nodules that contain bacteria such as *Rhizobium*. These organs are mainly distributed near the collar on the primary taproot and on first-order laterals of large and small diameter (Fig. 5B). This behaviour is common within Fabaceae and also in some Betulaceae (*Alnus*) that are associated with *Frankia*.

Cluster roots. Lupin (*Lupinus* sp.) has cluster roots (Fig. 5C). This particular root type is made up of fine roots of the same length and diameter gathered into clusters, located on first-order laterals mainly near the collar. They enhance nutrient uptake by modifying solubilization in nutrient-poor soils. This kind of root system is common within Proteaceae, but also in some Fabaceae and Moraceae.

Root trait extraction

The simulation examples shown above are numerical objects written in native Xplo format, which provides a strongly topological and hierarchical graph structure. Each component of the simulated system belongs to a particular type, is linked to its bearer and has its own particular geometrical dimensions. It is thus possible to use an Xplo extraction feature on these objects (extraction view, Fig. 6) to obtain quantitative root trait data at different scales both in space and in time.



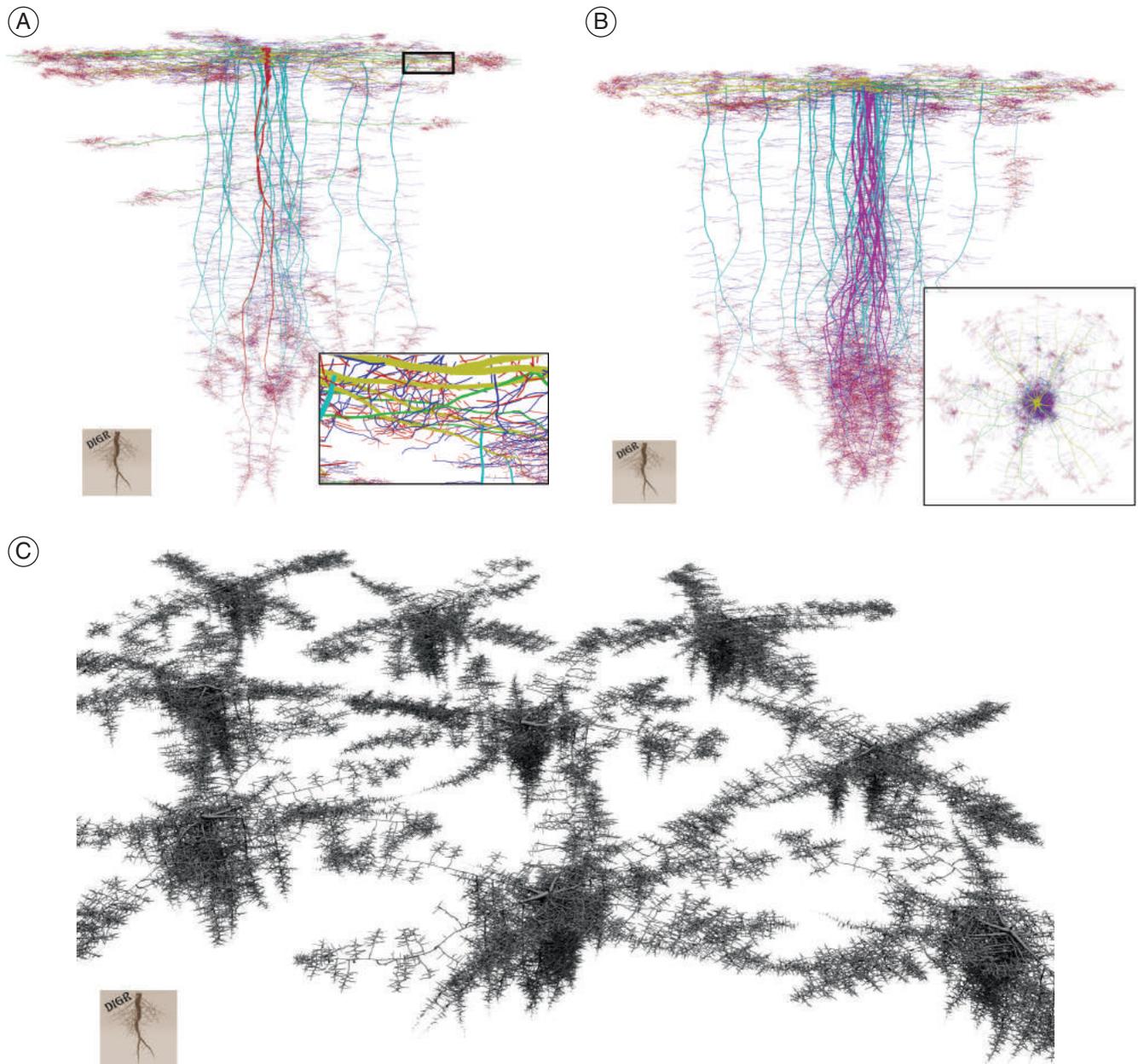


FIG. 4. Simulations of eucalypt taproot systems depending on their primary (seedling) or secondary origin (cutting). (A) Side view of a 5-year-old seedling (main) and detail (black rectangle) of plagiotropic secondary roots (yellow) and their laterals (bottom right). (B) Side (main) and top views (bottom right) of a eucalypt cutting at the same age. (C) Perspective view of intra-specific variability with six individuals at same age (2 years old). Different root types are shown: taproot (red); distal secondary taproot (light blue); proximal secondary taproot (pink); plagiotropic secondary root (blue); cable-like root (yellow); long fine root (blue); medium fine root (purple); short fine root (red). DigR logo represents 2×2 m scale for (A) and (B), and 1×1 m for (C) main windows.

In this example (Fig. 6), a 1-year-old oil-palm root system was simulated. A selection of a tertiary roots was made in the 3-D view with the mouse (red rectangle in lower right window). The corresponding object is automatically highlighted in the

browser view and its attached variables are displayed (lower left window). All roots belonging to the same type may then be extracted and some simple calculations (length, death time, diameters) may be carried out (upper left window). Extracted

FIG. 3. Simulations of fasciculate oil-palm root systems that show different root types at three different ages. (A) Side view of 1-year-old oil-palm root system (bottom right) and detail of two primary order roots (black rectangle) with colour related to root architectural unit (main). (B) Side view of a global oil-palm root system at 3 years old (main) and top view of a detail (black rectangle) of a horizontal primary root and its laterals (bottom right). (C) Side (main) and top view (bottom right) of an oil-palm root system at 10 years old. The complete root system is made up of eight root types: primary vertical roots (grey in A and B); horizontal primary roots (light blue); vertical secondary roots growing downward (pink); vertical secondary roots growing upward (dark blue); horizontal secondary roots (light green); tertiary surface roots (yellow); tertiary deep roots (blue) and quaternary roots (light red). DigR logo represents 2×2 cm scale for (A), 50×50 cm for (B) and 1×1 m for (C) main windows.

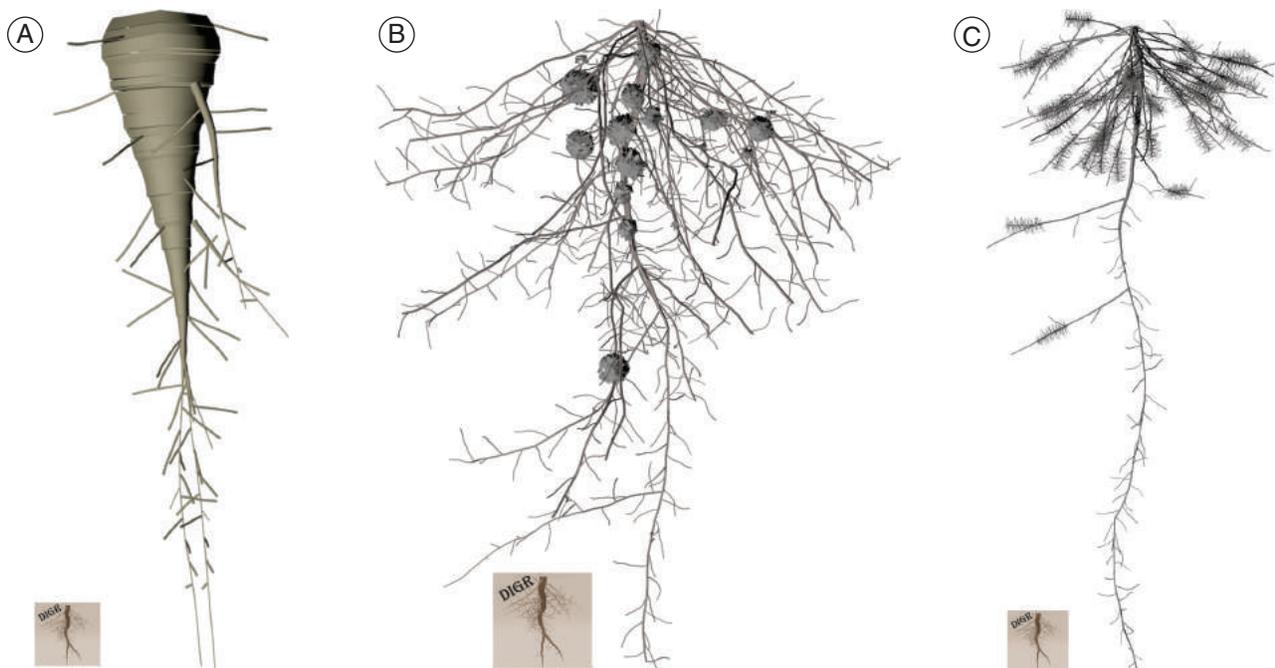


FIG. 5. Simulation examples of particular root systems with (A) sugar beet (*Beta vulgaris*) illustrating tuber roots, (B) chick pea (*Cicer arietinum*) illustrating nodule roots and (C) lupin (*Lupinus* sp.) illustrating cluster roots. These root systems are simulated at 50 d (A) and 60 d (B, C) old respectively and grew in homogeneous edaphic environment. DigR logo represents 5 × 5 cm scale for (A), 3 × 3 cm for (B) and 2 × 2 cm for (C).

values may be displayed in plot windows (upper right window), where a length histogram of tertiary root is displayed. Extractions may be refined according to topological criteria or according to any combination of variables attached to each object.

Table 2 shows root traits that were extracted for a 1-year-old oil-palm root system for each root type that was modelled. This root system is made of 116 722 roots with 0.03 % being primary roots, which contain 40.3 % of the total root dry mass and 52.9 % of the total root dry biomass. The root system is made of living roots (76.2 % of the total mass) and dead roots not already self-pruned (23.8 % of the total mass). Moreover, there are 115 040 fine roots (RT3 and RT4, distinguished by their diameter and topological branching order) that contain 39.8 % of the total dry mass equivalent to the mass of the primary roots. Total root length is 3044 m with 47.6 % of RT3 fine roots and 45.7 % of RT4 fine roots. Structure roots (RT1 and RT2) respectively contain 1.1 % and 5.6 % of the total length. With regard to mortality, we can extract the number of dead roots, their length and their time of death. Extraction of the monthly dry mass of dead roots (necromass) allows computation of the evolution of the ratio between necromass and biomass for consecutive simulation outputs, which is the evolution of the monthly mortality rate at the plant level. This figure is globally 31 % with a high variability depending on root type. For instance, it is 0 for primary roots (that never die) and 116 % for fine roots (RT3 and RT4 together).

Reaction to soil compaction

To test the plugin feature of the simulator, we have developed a very simple soil model that has a uniform and compacted soil

layer below a depth of 50 cm as an example (Fig. 7). The compact layer is parameterized to slow down the root elongation rate, to increase root diameter and tortuosity and to increase the branching density for each root meristem that is in the compacted layer. The soil plugin supplies different parameter values to DigR when meristem depth is more than m. The results are shown in Fig. 7.

DISCUSSION

DigR is a structural model that is able to dynamically simulate the architecture of many contrasting plant root systems, big or small, young or old, among taproot or fasciculate systems. It relies on root typology to account for differences in behaviour among all roots constituting plant root systems. Some architectural root models are already described in the literature, such as Rootmap (Diggle, 1988), SimRoot (Lynch *et al.*, 1997), AMAPsim (Jourdan and Rey, 1997b, c), RootTyp (Pagès *et al.*, 2004), SPACSYS (Wu *et al.*, 2007), R-SWMS (Javaux *et al.*, 2008), RootBox (Leitner *et al.*, 2010) and OpenSimRoot (Postma *et al.*, 2017). These models differ in their simulation paradigm, software language and running environment. They also differ in their parametrization and their aim. For instance, Rootmap focuses more on root system plasticity by simulating root proliferation whereas SimRoot and its extended version OpenSimRoot target resource acquisition. AMAPsim is very accurate in its simulation of growth and development of root meristems and produces very realistic root systems. RootTyp is equivalent to DigR in that it relies on root typology and takes into account many species as well as allowing it to be connected to soil models for detailed studies of root–soil interactions. SPACSYS is more focused on crop modelling

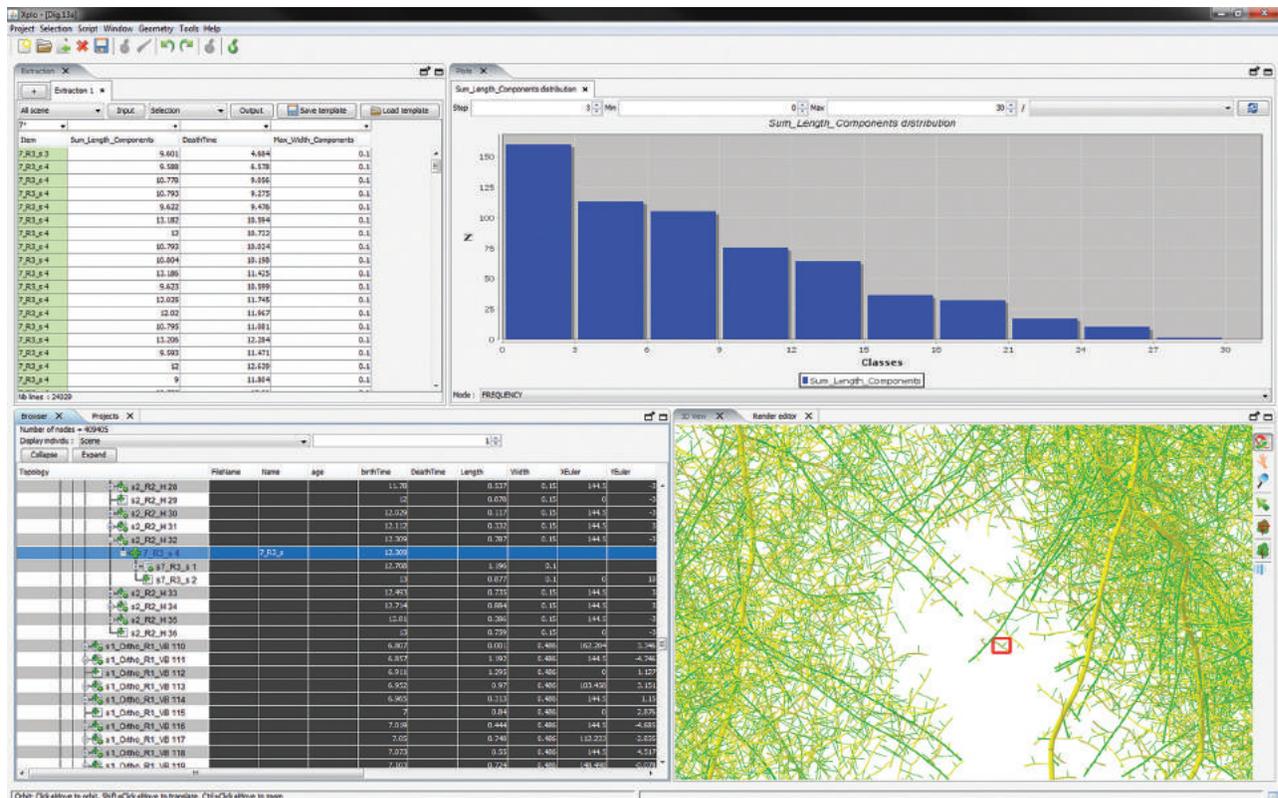


FIG. 6. Snapshot of Xplo software running DigR model with a 1-year-old oil-palm simulation. The lower left window (topological view) exhibits the structure of the root system through a graph representation, which details topological relationships between root segments of different root types (left column) and the associated root parameter values (other columns). The lower right window shows the 3-D mock-up display (geometrical view) which highlights the selected root segment (red square) of R3 type whose characteristics are selected (in blue) within the topological view. In the upper left window, all roots belonging to the same R3 root type are extracted (extraction view, left column) and root traits are computed (other columns). The upper right window (plot view) displays, here as an example, the root length distribution of the R3 root type previously extracted.

and predicts yield according to dynamic root–soil interactions. R-SWMS is dedicated to the modelling of root hydraulic architecture and to estimate root water uptake efficiency. RootBox is a root growth and development model based on the L-System paradigm. It is open source and offers a software environment where algorithms may be easily shared and adapted for specific applications.

DigR is a purely structural model and the simulator provides output corresponding to what was measured. Nevertheless, there may be interactions between a root system and its environment during its growth or at different geometrical positions that may contribute to explaining differences between individuals belonging to the same species. For instance, season cycles may induce variability in soil water content, thus making root growth behave differently from the default (different branching densities or growth speed), or soil texture may change from one place to another thus changing the fate of root meristems (tortuosity, root diameter, growth speed, etc.). Because we often do not have expert knowledge of these interaction processes and consequently may not want to estimate them, this software architecture makes it possible to test different hypotheses and compare them. This feature is implemented through default DigR parameter values that may be changed according to external knowledge described in software plugins.

The software mechanism that has been implemented has three major notable features

The first feature is a quasi-parallel computing algorithm. This allows all meristems to grow at the same time along the same time scale, keeping a global homogeneous growing structure during the simulation. This feature opens the opportunity to dynamically couple with other algorithms that may interact with roots along their growth and is a key point toward functional simulation. On the other hand, it makes simulation much heavier and time consuming. Nevertheless, computing time remains within an affordable range. For instance, simulation of a eucalypt root system described with seven root types up to 5 years old using a computer with a 2.4-GHz processor will take 3 min. The simulated mock-up is made of 300 000 components (plus all the short root axes that were simulated with time and that do not appear in the final mockup because they were self-pruned after their death).

The parameter observer mechanism has two main advantages. First, the meristem objects receive a parameter value without knowing the way it was computed (possibly coming from subscribers). Second, it is possible to plug in different subscribers to test and compare different external effects on meristem behaviour without changing the default meristem algorithm. The combination of more than one subscriber during

TABLE 2. Example of root trait values extracted from Xplo software (extraction view, Fig. 3A) of a 1-year old oil-palm root system simulated through DigR

Root traits	Root types				Root system
	RT1	RT2	RT3	RT4	Total
Total root number (%)*	40 (0.03)	1642 (1.4)	24 329 (20.8)	90 711 (77.7)	116 722
Total root length (m, (%)*)	34.3 (1.1)	169.8 (5.6)	1448.7 (47.6)	1391.3 (45.7)	3044.2
Average root length (cm)	85.8 ± 71.6	11.7 ± 9.6	6.0 ± 4.0	1.5 ± 0.7	
Average root diameter (mm)	5.0 ± 0.3	1.5 ± 0.2	1.0 ± 0.1	0.5 ± 0.1	
Total number of dead roots†	0	66	5804	51280	57 150 (49 %)
Proportion of dead root (%) on live+dead root number	0	4.0	23.9	56.5	
Average lifespan (months)	3.64 ± 3.09	2.5 ± 2.44	1.9 ± 1.22	0.8 ± 0.33	
Average dead root length (cm)	-	31.6 ± 6.3	11.0 ± 5.8	2.0 ± 0.9	
Total dead root length (m)	0	20.8	638.6	1025.6	1685.1 (55 %)
Proportion of dead root (%) on live+dead root length	0	12.3	44.1	73.7	
Number of live roots	40	1576	18525	39431	59 572 (51 %)
Proportion of live root number (%)	100.0	96.0	76.1	43.5	
Total live root length (m)	34.3	149.0	810.1	365.7	1359.1 (45 %)
Proportion of live root length (%)	100.0	87.7	55.9	26.3	
Total root dry biomass‡ (g, (%)*)	65.2 (52.9)	28.3 (23.0)	24.3 (19.7)	5.5 (4.4)	123.3 (76.2)
Total root dry Necromass‡ (g, (%)*)	0 (0.0)	4.0 (10.3)	19.2 (49.8)	15.4 (40.0)	38.5 (23.8)
Total root dry mass§ (g, (%)*)	65.2 (40.3)	32.3 (19.9)	43.5 (26.9)	20.9 (12.9)	161.8
Monthly mortality rate (%)	0	14.0	78.8	280.5	31.2

Some root traits are presented for each root type such as root (or root tip) number, root length (m), root diameter (mm), root mortality characteristics, root dry bio- and necromass (g) and monthly mortality rate (%).

*Percentages of the total root system value, the other percentages are in relation to each root type value.

†Dead roots here are those still attached to the root system before pruning.

‡The total root biomass (mass of live roots) was calculated through a linear biomass value, which was similar for each root belonging to one type and was measured from field observations (Jourdan and Rey, 1997a). This value was 1.90, 0.19, 0.03 and 0.015 g m⁻¹ for primary (RT1), secondary (RT2), tertiary (RT3) and quaternary (RT4) roots, respectively. For the necromass (mass of dead roots) calculations, we used this same value as we considered necromass to be the sum of dead roots still attached to root system prior to pruning.

§Total root dry mass is the sum of total root dry biomass and total root dry necromass.

a simulation would result in unpredictable behaviour if they modify the same parameter.

The third feature of DigR simulator plugins is that they may register to the event scheduler at specified simulation times. At these times, plugins are run and they can both re-evaluate their own status and modify the current root system structure. The running order of plugins that have to be activated at the same time is computed according to a priority level associated with each plugin. It is the responsibility of the user who runs simulation to check that there will be no conflict between plugins that may be used during a single simulation.

The result is that, like RootTyp, DigR is ready to host sub-models that account for root–soil interactions (Fig. 7). The main difference is that in DigR, no predefined choice is made to model these interactions whereas in RootTyp soil modelling choices are fixed. A software interface exists to plug external functions into the default simulation kernel (Griffon and De Coligny, 2014). Different functions may simulate the same processes in different ways so that they may be compared by plugging them in alternately to the default kernel. These functions may account for physical values (soil density, porosity, water content, etc.) or chemical composition (nutrient content) of the soil. They also define the way that these values will influence the default DigR parameter values, thus changing the default root system growth. We chose to illustrate this feature (Fig. 7)

with a soil with very high penetration resistance below 50 cm depth. The associated plugin changes some parameter values for meristems growing below 50 cm. Growth speed is divided by 2, tortuosity is 30 % higher, branching density is doubled and lateral diameters are 30 % bigger. All these values are fixed arbitrarily. Calibration using data from experiments under controlled situations would be necessary to get accurate values for particular cases. Similar procedures could be applied to simulate interactions with physical and chemical soil conditions (water, nutrients) or biological conditions (fungal symbiotic associations). The functions can also register for calls at predefined times. For instance, a soil could re-evaluate its water content according to a time specified by a meteorological file or a soil nutrient uptake protocol. Simulation of pruning due to external intervention could also occur according to the timing of some agronomic procedures (e.g. ploughing).

The DigR simulator has been developed using the java language. Java programs are run in a Java Virtual Machine (JVM) that can use an amount of memory that is limited to the physical Read Access Memory (RAM) of the machine that is running the simulation. This automatically restricts the size of the root system that will be simulated. With 15 Gb of RAM dedicated to the JVM, it is possible to simulate root systems that consist of more than 1 million roots. This kind of simulation may take more than 1 h on a normal desktop PC.

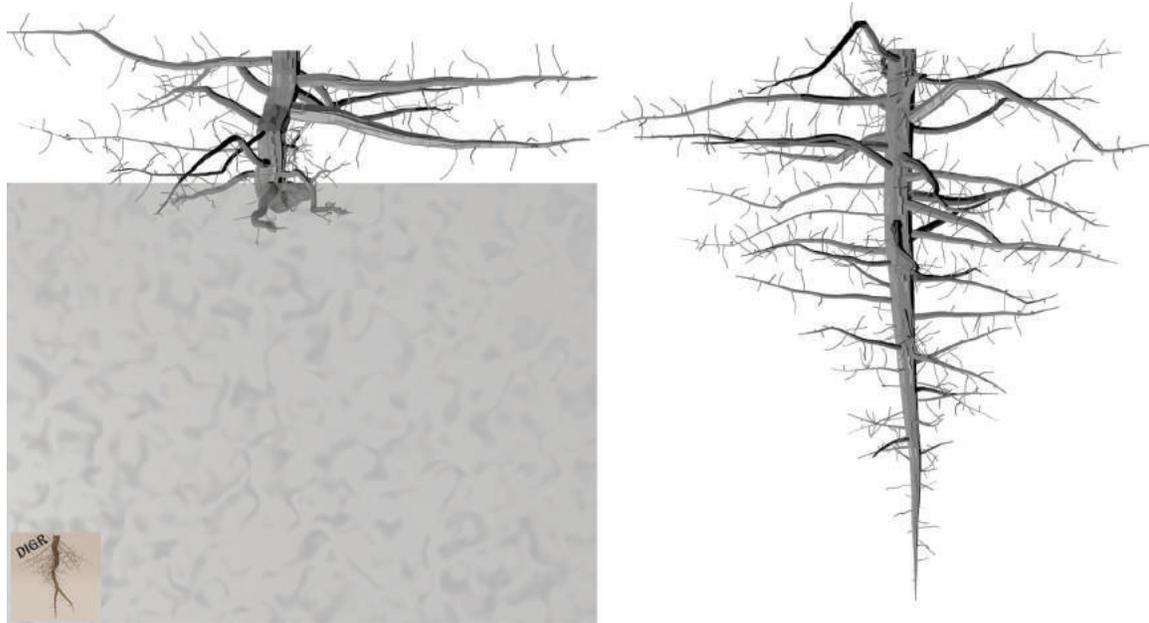


FIG. 7. Simulation of a theoretical perennial plant tap-root system without edaphic constraint (right) and with a virtual strong soil compaction located at 50 cm depth (left). Root growth speed and unbranched apical zone are strongly reduced while branching density, root diameter and tortuosity angles are increased. DigR logo represents 40 × 40 cm.

Root architecture models generally do not take into account plant shoots (RootBox, AMAPsim), or if they do, the shoots are considered to be a black box that provides a continuous C flux to roots (ROOTMAP, RootTyp). Alternatively, the shoot system may be considered to be carbon-balanced fluxes ruled by costs and gains (SimRoot, OpenSimRoot). For some shoot system models, a very simplified root system is used (GreenLab, Kang *et al.*, 2008; Jullien *et al.*, 2011), or simulation is dedicated to very small plants or plants at the juvenile stage (SPACSYS). In our case, accounting for shoots could take place through external plugins in the same way that has been described for soil plugins. It would then be possible to moderate root compartment growth, for instance according to overall root–shoot partitioning or intra-root system balance. In the same way it would be possible to account for the root system as a contributing factor for sugar production via water uptake and redistribution in combination with photosynthate production.

The previous models are mainly dedicated to small structures of annual plants (wheat, maize, peas, lupin, etc.) or juvenile perennials with a complex root system consisting of tens of thousands of roots but with a global radius or depth of usually less of a few decimetres. Nevertheless, some models such as RootTyp are able to simulate perennial structures like tree root systems because they take reiteration processes into account. However, most of the time, simulated plants remain young. From a computer point of view, modelling plant at young ages or annual plants may come from different choices of the simulation algorithm or structural representation into memory. These choices may exclude computing for old ages for reasons of simulation time or memory overflow. From a modelling point of view, modelling young plants may come from choices that do not take into account the change of root behaviour depending upon their own age (organ's age) or plant age. To take plant age into account, in DigR, most of the parameters of the different processes (growth speed, branching, mortality and

reiteration) have values indexed according to position along the root type (equivalent to root age). Compared to previous architectural root models such as RootTyp or ROOTMAP, this feature makes it possible to accurately simulate root growth through the entire life of the plant independently of root system age. Combinations of root types with flexible parametrization allow root system growth to be simulated through young, adult and old plant ages with a single set of parameter values. For instance, root growth rate (indexed on root length) can change with the age of plants, which is usually observed in perennial plants (Jourdan and Rey, 1997a), even in herbaceous plants (Watson *et al.*, 2000).

DigR does not account for temporary growth pauses that may come from external environmental factors (biotic or abiotic). Such phenomena would come from external plugins.

DigR has 23 parameters, a large number compared to similar architectural models such as RootTyp (19 parameters) or Archisimple (eight). However, the increased number of parameters gives increased accuracy of the model in the simulation of features such as the characterization of root geometry (essential for a realistic root distribution in the soil), and also the characterization of the processes of root senescence and delayed root reiteration to model root systems of adult trees. It is also important to keep in mind that all parameters have default values. Depending on the specificity of the root system being simulated, not all parameters require specific values to be input by the user.

DigR is a generic structural model that can simulate plant root architecture and development of broad plant diversity in size, age and type (herbs, shrubs or trees), within monocots and dicots, but also in gymnosperms (including Cycads and *Ginkgo*) or groups of pteridophytes. Root form diversity is also taken into account with DigR. Not only can cylindrically shaped roots be simulated but also tuberous root (Fig. 5A), or the presence of root nodules, represented by protrusions of roots (Fig. 5B),

or the particular case of cluster roots (Fig. 5C). These simulations may find practical applications in plant experiments such as distribution and estimation of rhizosphere volume for nutrient uptake (Fig. 8) at root, plant or plot levels, for each root type and each nutrient within the soil profile. A first application was made with the former AMAPsim model (Jourdan and Rey, 1997c). Through the Xplo environment (Fig. 8), it is now possible with DigR to apply this more easily thanks to custom post-processing scripts. Specific uptake and soil diffusion rates for nutrients depend on soil availability and can be modelled through a reactive transport model such as MIN3P (Mayer et al., 1999, 2012) which can be coupled with DigR as was done for the Archisimple–MIN3P coupled model (Gérard et al., 2017). Moreover, in simulating useful soil volume related to each root type, it can be convenient to take into account any specialized functions of deep roots compared to shallow roots as shown by da Silva et al. (2011) for a eucalypt plantation in deep Ferralsol soil of Brazil. These deep roots provide a safety-net service by taking up nutrients, principally nitrogen, leached from the topsoil. For phosphate acquisition with a reduced rhizosphere volume, DigR coupled with a reactive transport model could estimate P uptake at a fixed simulation time unit, and could be compared to other models dedicated to P uptake such as SPACSYS or RootBox.

DigR uses the AMAPstudio framework and more specifically the Xplo platform to host the root growth editor and simulator. The DigR editor interface is user-friendly and allows input of the values of observed root parameters analysed from field measurements of each root type. The DigR editor provides main tables in which values of root apical growth, root death and pruning, root branching, root diameter, direction of growth and reiteration processes are input (Table 1).

In Xplo, users can make an initial examination of simulated shape through the 3-D view, then can use the data extraction

features to measure the simulated system to check if they match field observations. With Xplo, users can design and run their own measurements, without programming, and can visualize results in tables and graphs (Fig. 6, Table 2).

The root traits directly extractable from Xplo software are root number, root length, root diameter, root lifespan (birth and death ages) and root branching density. Through additional data sets, such as root mass density, it is possible to compute other root traits such as biomass for living roots and necromass for dead roots still present in the system before pruning. As DigR is a dynamic model, root systems can be simulated from germination to death, on any time unit interval (day, month and year depending on the species), which allows computation of root production, root mortality rate and root turnover. Furthermore, complex root traits such as specific root length (SRL), specific root area (SRA), root area ratio (RAR) or cross-sectional area (CSA) can also be computed as an output of DigR simulations, by root type, by soil depth and by root location, and for each simulation age. Finally, these outputs can be used as inputs in eco-engineering models for soil stability for example (Mao et al., 2012, 2013, 2014) or as values used in analyses of root economics spectrum (Prieto et al., 2015; Roumet et al., 2016).

CONCLUSIONS AND PERSPECTIVES

The DigR model is a new root model that includes architectural concepts and relies on root typology. The root architectural unit is a key feature of the root modelling process in representing root system organization. Basic functions that explain root system growth (apical growth, branching, death and pruning) are adapted to our specific field knowledge and experimental measurements. The DigR simulator is based on 23 parameters whose

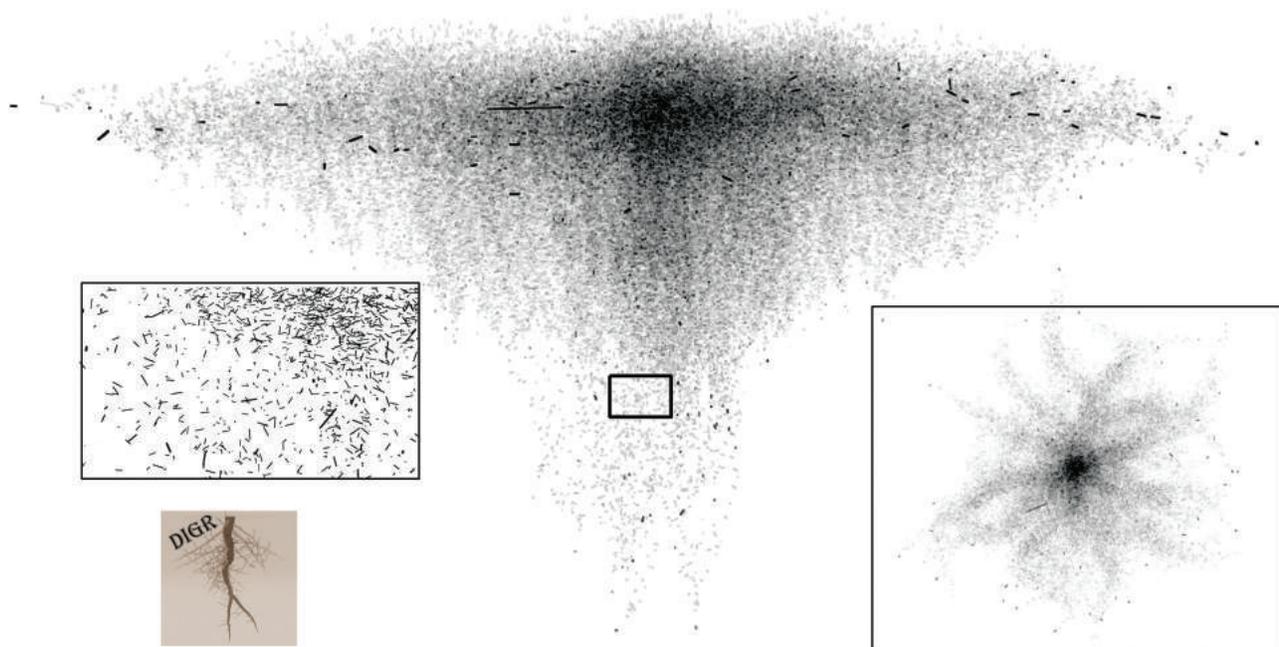


FIG. 8. Simulation of a 3-year-old oil-palm root system exhibiting uptake zones located behind each root tip. Global view (main window), top view (bottom right) and detail view (bottom left). DigR logo represents 1 × 1 m scale (main window), 2 × 2 m (bottom right) and 50 × 50 cm (left).

values are indexed based on root type and length position along the roots.

This model is implemented using the free AMAPstudio framework (<http://amapstudio.cirad.fr>) and is hosted in the Xplo platform. It includes a friendly user interface to input parameter values, to run simulations, and to control the output through 3-D visualization and topological display. Moreover, it allows filtering and extracting data from simulation to control the accuracy of the simulations and obtain root trait values that could not be directly measured on real root systems. The software simulator is written in a way that makes it ready to be connected with external plugins that can interact with the default kernel behaviour. These plugins can host knowledge about the mutual influence between roots and soil or shoot compartment, making DigR, which is a pure structure model, a functional one.

Examples of the capabilities of DigR are shown through simulations of contrasted plant architectures of either annuals or perennials. The extraction of root traits from simulations was demonstrated on a 3-year-old oil-palm root system and an example of root–soil interaction is also proposed.

Test results show that fine roots are the major part of root global number within root systems. In our model, each fine root is individually simulated and becomes a heavy burden for simulation of the large root system. Because this compartment is homogeneous, it would be a challenge to represent them with sets of PDEs, which are very accurate for this kind of object (Dupuy *et al.*, 2010). An interesting improvement of the model would be to make it a hybrid combination with a discrete structural part and a fine root compartment using PDE formalism. This is a theoretical and technical challenge. Further investigation of the model would be to apply it to different species and to collaborate with soil and shoot specialists to develop new plugins that would link their knowledge of root systems and thus to upscale towards a more integrated modelling and simulation approach.

SUPPLEMENTARY DATA

Supplementary data are available online at www.aob.oxford-journals.org and consist of the following. Fig. S1: Simulation of the growth of an oil-palm root system.

ACKNOWLEDGEMENTS

We thank Armel Thongo and technical staff of CRDPI (Pointe-noire, Congo) for measurements on the *Eucalyptus* root system, and technical staff of CNRA (La Mé, Ivory Coast) for measurement on oil-palm root system. We also thank Nick Rowe for his kind help with the English text and two anonymous reviewers for providing helpful comments and suggestions that greatly improved the manuscript. This work was supported by the ‘Centre International de Recherches en Agronomie pour le Développement’ (CIRAD, Montpellier, France).

Conflict of Interest: none declared.

LITERATURE CITED

Atger C. 1992. *Essai sur l'architecture racinaire des arbres*. PhD thesis, University of Montpellier II.
 Atger C, Edelin C. 1994. Stratégies d'occupation du milieu souterrain par les systèmes racinaires des arbres. *Revue d'écologie* **49**: 343–356.

Baddeley J, Watson C. 2005. Influences of root diameter, tree age, soil depth and season on fine root survivorship in *Prunus avium*. *Plant and Soil* **276**: 15–22.
 Barczy JF, Rey H, Caraglio Y, *et al.* 2008. AmapSim: A structural whole-plant simulator based on botanical knowledge and designed to host external functional models. *Annals of Botany* **101**: 1125–1138.
 Barthélémy D, Caraglio Y. 2007. Plant architecture: a dynamic, multilevel and comprehensive approach to plant form, structure and ontogeny. *Annals of Botany* **99**: 375–407.
 Bastian P, Chavarría-Krauser A, Engwer C, Jäger W, Marnach S, Ptashnyk M. 2008. Modelling in vitro growth of dense root networks. *Journal of Theoretical Biology* **254**: 99–109.
 Bonneu A, Dumont Y, Rey H, Jourdan C, Fourcaud T. 2012. A minimal continuous model for simulating growth and development of plant root systems. *Plant and Soil* **354**: 211–227.
 Brown TN, Kulasiri D. 1994. Simulation of *Pinus radiata* root system structure for ecosystem management applications. *Simulation* **62**: 42–57.
 Brown TN, Kulasiri D, Gaunt RE. 1997. A root-morphology based simulation for plant/soil microbial ecosystem modelling. *Ecological Modelling* **99**: 275–287.
 da Silva EV, Bouillet JP, de Moraes Gonçalves JL, *et al.* 2011. Functional specialization of Eucalyptus fine roots: contrasting potential uptake rates for nitrogen, potassium and calcium tracers at varying soil depths. *Functional Ecology* **25**: 996–1006.
 Diggle AJ. 1988. Rootmap, a model in three-dimensional coordinates of the growth and structure of fibrous root systems. *Plant and Soil* **105**: 169–178.
 Doussan C, Pagès L, Vercambre G. 1998. Modelling of the hydraulic architecture of root systems: an integrated approach to water absorption-model description. *Annals of Botany* **81**: 213–223.
 Dunbabin VM, Postma JA, Schnepf A, *et al.* 2013. Modelling root–soil interactions using three-dimensional models of root growth, architecture and function. *Plant and Soil* **372**: 93–124.
 Dupuy L, Fourcaud T, Stokes A. 2005. A numerical investigation into the influence of soil type and root architecture on tree anchorage. *Plant and Soil* **278**: 119–134.
 Dupuy L, Gregory PJ, Bengough AG. 2010. Root growth models: towards a new generation of continuous approaches. *Journal of Experimental Botany* **61**: 2131–2143.
 Eissenstat DM, Wells CE, Yanai RD, Whitbeck JL. 2000. Building roots in a changing environment: implications for root longevity. *New Phytologist* **147**: 33–42.
 Gamma E. 1995. *Design patterns: elements of reusable object-oriented software*. Delhi: Pearson Education India.
 Gérard F, Blitz-Frayret C, Hinsinger P, Pagès L. 2017. Modelling the interactions between root system architecture, root functions and reactive transport processes in soil. *Plant and Soil* **413**: 161–180.
 Griffon S, De Coligny F. 2014. AMAPstudio: an editing and simulation software suite for plants architecture modelling. *Ecological Modelling* **290**: 3–10.
 Guo D, Li H, Mitchell RJ, *et al.* 2008. Fine root heterogeneity by branch order: exploring the discrepancy in root turnover estimates between minirhizotron and carbon isotopic methods. *New Phytologist* **177**: 443–456.
 Hirsch AM, LaRue TA, Doyle J. 1997. Is the legume nodule a modified root or stem or an organ sui generis? *Critical Reviews in Plant Sciences* **16**: 361–392.
 Hodge A. 2004. The plastic plant: root responses to heterogeneous supplies of nutrients. *New Phytologist* **162**: 9–24.
 Javaux M, Schröder T, Vanderborght J, Vereecken H. 2008. Use of a three-dimensional detailed modeling approach for predicting root water uptake. *Vadose Zone Journal* **7**: 1079–1088.
 Jourdan C, Rey H. 1997a. Architecture and development of the oil-palm (*Elaeis guineensis* Jacq.) root system. *Plant and Soil* **189**: 33–48.
 Jourdan C, Rey H. 1997b. Modelling and simulation of the architecture and development of the oil-palm (*Elaeis guineensis* Jacq.) root system. I. The model. *Plant and Soil* **190**: 217–233.
 Jourdan C, Rey H. 1997c. Modelling and simulation of the architecture and development of the oil-palm (*Elaeis guineensis* Jacq.) root system: II. Estimation of root parameters using the Racines postprocessor. *Plant and Soil* **190**: 235–246.
 Jullien A, Mathieu A, Allirand J-M, *et al.* 2011. Characterization of the interactions between architecture and source–sink relationships in winter oil-seed rape (*Brassica napus*) using the GreenLab model. *Annals of Botany* **107**: 765–779.
 Kang MZ, Cournède PH, de Reffye P, Auclair D, Hu BG. 2008. Analytical study of a stochastic plant growth model: Application to the GreenLab model. *Mathematics and Computers in Simulation* **78**: 57–75.

- Kim T, Silk W. 1999.** A mathematical model for pH patterns in the rhizospheres of growth zones. *Plant, Cell & Environment* **22**: 1527–1538.
- Leitner D, Klepsch S, Bodner G, Schnepf A. 2010.** A dynamic root system growth model based on L-Systems. *Plant and Soil* **332**: 177–192.
- Lungley DR. 1973.** The growth of root systems. A numerical computer simulation model. *Plant and Soil* **38**: 145–159.
- Lynch JP, Nielsen KL, Davis RD, JablOKow AG. 1997.** SimRoot: Modelling and visualization of root systems. *Plant and Soil* **188**: 139–151.
- Mao Z, Saint-André L, Genet M, et al. 2012.** Engineering ecological protection against landslides in diverse mountain forests: choosing cohesion models. *Ecological Engineering* **45**: 55–69.
- Mao Z, Jourdan C, Bonis M-L, et al. 2013.** Modelling root demography in heterogeneous mountain forests and applications for slope stability analysis. *Plant and Soil* **363**: 357–382.
- Mao Z, Bourrier F, Stokes A, Fourcaud T. 2014.** Three-dimensional modelling of slope stability in heterogeneous montane forest ecosystems. *Ecological Modelling* **273**: 11–22.
- Mayer K, Benner S, Blowes D, Frind E. 1999.** The reactive transport model MIN3P: application to acid mine drainage generation and treatment-nickel rim mine site, Sudbury, Ontario. *Mining and Environment* **1**: 145–154.
- Mayer K, Amos R, Molins S, Gerard F. 2012.** Reactive transport modeling in variably saturated media with min3p: Basic model formulation and model enhancements. *Groundwater Reactive Transport Models*: 186–211.
- Mulia R, Dupraz C, van Noordwijk M. 2010.** Reconciling root plasticity and architectural ground rules in tree root growth models with voxel automata. *Plant and Soil* **337**: 77–92.
- Nathanielsz CP, Staff IA. 1975.** A mode of entry of blue-green algae into the apogeotropic roots of *Macrozamia communis*. *American Journal of Botany* **62**: 232–235.
- Nielsen KL, Lynch JP, JablOKow AG, Curtis PS. 1994.** Carbon cost of root systems: an architectural approach. *Plant and Soil* **165**: 161–169.
- Ozier-Lafontaine H, Lecompte F, Sillon JF. 1999.** Fractal analysis of the root architecture of *Gliricidia sepium* for the spatial prediction of root branching, size and mass: model development and evaluation in agroforestry. *Plant and Soil* **209**: 167–179.
- Pagès L, Jordan MO, Picard D. 1989.** A simulation model of the three-dimensional architecture of the maize root system. *Plant and Soil* **119**: 147–154.
- Pagès L, Vercambre G, Drouet J-L, Lecompte F, Collet C, Le Bot J. 2004.** Root Typ: a generic model to depict and analyse the root system architecture. *Plant and Soil* **258**: 103–119.
- Pagès L, Bécel C, Boukcim H, Moreau D, Nguyen C, Voisin A-S. 2014.** Calibration and evaluation of ArchiSimple, a simple model of root system architecture. *Ecological Modelling* **290**: 76–84.
- Postma JA, Kuppe C, Owen MR, et al. 2017.** OpenSimRoot: widening the scope and application of root architectural models. *New Phytologist* **215**: 1274–1286.
- Pregitzer KS, Hendrick RL, Fogel R. 1993.** The demography of fine roots in response to patches of water and nitrogen. *New Phytologist* **125**: 575–580.
- Prieto I, Roumet C, Cardinael R, et al. 2015.** Root functional parameters along a land-use gradient: evidence of a community-level economics spectrum. *Journal of Ecology* **103**: 361–373.
- Resendes ML, Bryla DR, Eissenstat DM. 2008.** Early events in the life of apple roots: variation in root growth rate is linked to mycorrhizal and nonmycorrhizal fungal colonization. *Plant and Soil* **313**: 175–186.
- Roumet C, Birouste M, Picon-Cochard C, et al. 2016.** Root structure–function relationships in 74 species: evidence of a root economics spectrum related to carbon economy. *New Phytologist* **210**: 815–826.
- Shibusawa S. 1994.** Modelling the branching growth fractal pattern of the maize root system. *Plant and Soil* **165**: 339–347.
- Spratt ER. 1911.** Some observations on the life-history of *Anabaena cycadeae*. *Annals of Botany* **25**: 369–380.
- Thongo M'Bou A. 2008.** *Etude du système racinaire de l'Eucalyptus en plantation tropicale: analyse architecturale, croissance et respiration*. Ph.D Thesis, Univeristy of Nancy 1, France and University of Brazzaville, Congo.
- Thongo M'Bou A, Jourdan C, Deleporte P, et al. 2008.** Root elongation in tropical *Eucalyptus* plantations: effect of soil water content. *Annals of Forest Science* **65**: 609–609.
- Van Noordwijk M, Spek LY, Willigen PD. 1994.** Proximal root diameter as predictor of total root size for fractal branching models. 1. Theory. *Plant and Soil* **164**: 107–117.
- Watson CA, Ross JM, Bagnaresi U, et al. 2000.** Environment-induced modifications to root longevity in *Lolium perenne* and *Trifolium repens*. *Annals of Botany* **85**: 397–401.
- Wu L, McGechan MB, McRoberts N, Baddeley JA, Watson CA. 2007.** SPACSYS: Integration of a 3-D root architecture component to carbon, nitrogen and water cycling – Model description. *Ecological Modelling* **200**: 343–359.