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MARSCHNER REVIEW

Assessing and analyzing 3D architecture of woody root systems, a review of methods and applications in tree and soil stability, resource acquisition and allocation

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Abstract In numerous studies dealing with roots of woody plants, a description of the root system architecture is needed. During the twentieth century, several manual measurement methods were used, depending on the objectives of study. Due to the difficulties in accessing the roots and the duration of measurements, the studies generally involved a low number of root systems, were often qualitative and focused only on one specific application. Quantitative methods in plant architecture were largely developed in the last 40 years for aerial architecture. However, root systems have particular features and often need specific procedures. Since the end of the 1990s, new devices and techniques have been available for coarse root architecture measurements including volume location techniques (non-invasive or destructive) and manual or semi-automatic 3D digitising. Full 3D root system architecture dynamics was also reconstructed from partial measurements using modelling procedures. On the one hand, non-invasive and automatic techniques need more development to obtain full 3D architecture, i.e. geometry and topology. On the other hand, both one inexpensive manual and one semi-automatic digitizing procedure are now available to measure precisely and rapidly the full 3D architecture of uprooted and excavated coarse root systems. Specific software and a large number of functions are also available for an in-depth analysis of root architecture and have already been used in a dozen of research papers including a fairly large sample of mature trees. A comprehensive analysis of root architecture can be achieved by classifying individual roots in several root types through architectural analysis. The objective of this paper is both to give a detailed overview of the state of the art techniques for 3D root system architecture measurement and analysis and to give examples of applications in this field. Practical details are also given so that this paper can be used as a sort of manual for people who want to improve their practice or to enter this quite new research field.

Keywords Architectural analysis · Tree root system architecture · Topology · Measurement method · Plasticity · Three-dimensional digitizer · Tree stability

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Introduction

Roots: function and structure

Two principal functions of root systems of terrestrial plants are the acquisition of soil based resources (mainly water and nutrients) and the provision of stability to maintain the plant's upright structure (Fitter 2002). The structure of the root systems also plays a major role in sink and storage functions, deposition and excretion of biochemical compounds and association with symbiotic organisms (Pagès 2002). In woody perennials, both fine and coarse roots contribute in their own way to the accomplishment of these functions. Soil based resources are absorbed by fine roots and transported to the shoots by coarse, woody roots supporting the network of fine roots. Stability is mainly provided by the coarse roots. The differentiation in coarse, woody roots and fine roots is mainly based on their diameter, with the corresponding limit generally being set to 2 mm (Böhm 1979). This classification must be regarded as arbitrary, and it would be wrong to identify root diameter with any particular kind of root function; it is only an aid to obtain information (Böhm 1979). Woody roots differ also from fine roots because their life span approaches the life span of the plant whereas fine roots generally have a rapid turn-over and a large seasonal variation.

Because of their functions and their more uniform distribution, fine roots of woody plants are often assessed using bulk root studies through soil monoliths, soil coring or impact counting. This usually provides root number, length, surface, volume, root tip number and biomass per unit soil volume (Böhm 1979). The spatial distribution of fine roots in a layer is often assumed to be homogeneous (Pagès 1999a). Fine root growth dynamics are also studied through bulk root studies such as repeated coring, ingrowth bags, minirhizotrons and rhizotrons. The latter two are transparent wall techniques that allow the researcher to observe on a serial basis particular plant roots while they are growing in soil (Gijsman et al. 1991; Pateña and Ingram 2000; Taylor et al. 1990; Vercambre et al. 2003).

Roots, like shoots, are dynamic branched structures originating from the collar of the plant. They really form a "system" in the sense that their components are connected in an organised network (Pagès 1999b). Their functioning seriously depends on the entire root system structure or architecture, being the three-dimensional (3D) structure of the belowground part of an individual plant, including both the topological arrangement of components and their coarse geometric characteristics. Topology deals with the physical connections between plant components, while geometry includes the shape, size, orientation and spatial location of the components (Godin et al. 1999a; Godin 2000; Gregory 2006; Reubens et al. 2007a). Geometry is mainly involved in plant-environment exchanges, anchorage and resource capture, while topology can be used to build up biological sequences embedded in axes or can be considered as the basis for internal fluxes of energy, mass and information (Godin et al. 1999a).

Data collection on root systems can be performed at different levels of detail, depending on the objective of the study. Each root system can just be weighed for biomass determination (e.g. Ritson and Sochacki 2003), or it can be cut into segments and sorted by diameter for bulk root length and biomass measurement (e.g. Le Goff and Ottorini 2001). It can also be used for more or less detailed architecture measurements, including only topology (Fitter 1987), only position of the root volume (e.g. Wilson 1975; Coutts 1983; Drexhage et al. 1999) or both topology and geometry (e.g. Henderson et al. 1983a; Danjon et al. 1999a; Oppelt et al. 2000).

Qualitative study of plant architecture was first developed by Hallé and Oldeman (1970) in tropical tree crowns and named "architectural analysis" (Barthélémy and Caraglio 2007). One of the aims of architectural analysis is to identify endogenous growth processes and to separate them from the plasticity of their expression resulting from external influences (Barthélémy and Caraglio 2007). It is based on studying how the meristem of each axis functions and how hierarchical relations are established between axes (Jourdan et al. 1995). The methodology was adapted to root systems by Atger and Edelin (1994, 1995). A differentiation can be made between qualitative and quantitative architecture measurements, or between partial determination of architectural parameters and full 3D architecture assessments. Although some methods are useful both for fine and coarse roots, in general methodology also depends on the dimensions of the roots to be measured. Full, detailed quantitative 3D plant architecture assessment was initiated by de Reffye (1979) and Fisher and Honda (1979). Several methods for description and modelling of 3D shoot and root architecture are reviewed in Godin (2000), Pagès et al. (2000a) and van der Heijden et al. (2007).

Traditional non-bulk methods for root architecture measurements are based either on photographs and drawings in plane and depth followed by qualitative analysis (McMinn 1963; Gray and Leiser 1982; Watson and O'Loughlin 1990), on topological measurements (Fitter 1987), on multiple 2D measurements such as root impact mapping on trench profile walls (Böhm 1979), or on partially quantitative measurements of root architecture [e.g. vertical and horizontal diameter, depth and orientation of all roots branching from the stump (Soethe et al. 2006)]. Using the latter in combination with modelling techniques allows 3D root system architecture characterization (e.g. Pagès et al. 2000a, b; Vercambre et al. 2003; Dupuy et al. 2005b; Collet et al. 2006). Such partial root architecture assessments aim at measuring only a limited set of architectural characteristics such as topology, interlateral length and branch angle, measuring a subsample of roots only (Collet et al. 2006), and/or studying root length and branching dynamics from field rhizotrons (Jourdan and Rey 1997a). Lastly, 3D cross-sectional area (CSA) root architecture manual measurements were used by e.g. Colin et al. (1995), Drexhage et al. (1999), Sundström and Keane (1999) and Nieuwenhuis and Wills (2002). This provides information mainly on root volume spatial distribution. With this method the growing space of a root system is spatially subdivided into concentric cylinders (see Fig. 1 in Nielsen and Hansen 2006). Where the roots intersect with one of the virtual cylinder walls, cross-section, vertical angle and azimuth are determined (Drexhage et al. 1999). This allows the measurement of root spread at different soil depths and radial distances from the tree. Major drawbacks of this technique is that the root and branching structure are only measured at certain points in space and no root descriptions are obtained in between the cylinder walls. Moreover, within one experiment, the diameter and bottom of the cylinder are fixed whereas the size of the tree varies (Danjon et al. 1999a). As experienced by the first author, 3D digitizing methods provide a lot more as well as more precise information, even though they do not require so much additional time (Danjon et al. 1999a).

Why measure 3D geometry in all coarse roots of a root system?

Shoot growth is generally fairly regular. Thus assessment of 3D shoot architecture has often been done by measuring topology, growth cycle lengths, diameters and branching angles in the stem and in a sample of branches (e.g. de Reffye et al. 1991; Heuret et al. 2006). For certain applications the 3D position of all leaves was required and mapped (Sinoquet et al. 1997). As the soil environment plays a decisive role in root system development, variation in environmental conditions often results in a highly heterogeneous distribution of coarse roots (Nicoll et al. 1997), which can also show a highly asymmetrical development relative to e.g. the slope direction, the dominant wind or crop lines in agroforestry (Salas et al. 2004; Danjon et al. 2005; Nicoll et al. 2006). Even for clonal plants of one age growing at the same spacing and under fairly uniform soil and site conditions, substantial variation in some root system characteristics does exist (Harrington and DeBell 1996). Simulations in *Picea sitchensis* (Bong.) Carr. have shown that root systems may be so variable that no reliable estimate can be obtained from measuring only one quarter (Henderson et al. 1983b). Despite the opportunities offered by the above-mentioned methods, a complete quantitative determination of 3D root system architecture is generally needed in order to fully understand coarse root system structure and functioning (Henderson et al. 1983a). Only in orchard trees which often have a more homogeneous root growth, partial measurement methods for coarse roots may be used (Vercambre et al. 2003).

Why record topology?

Studying topology, or the way in which root segments are connected to each other, offers the opportunity to understand the development of root system architecture in far greater detail. In their studies of the influence of wind and/or slope on root system architecture of trees e.g. Di Iorio et al. (2005), Tamasi et al. (2005) and Nicoll et al. (2006) mainly addressed the spatial distribution of root volume, i.e. radial, circular and vertical distribution. The topology data were only used to compute the distribution of volume, length and number of second order roots. However, using the same type of analysis, a much more detailed insight in the influence of dominant wind or planting methods on root system architecture was obtained by Danjon et al. (2005) and Khuder (2007). They considered together the root volume, length, and branching distributions in the different root compartments (see below) which compose a root system. Topology measurements are required for this latter way of analysis.

3D root system architecture assessment, including both geometry and topology

Assessment of 3D root system architecture of woody perennials is useful and important in many applications. Methods for this kind of measurements and analyses are quickly evolving and several procedures are being used by different applicants. Methods in plant architecture, largely developed on aerial parts (e.g. Barthélémy and Caraglio 2007; Godin 2000; Hanan and Hearn 2003; Prusinkiewicz and Rolland-Lagan 2006) could be applied to roots, of course. However, roots are functionally less differentiated, have a lack of morphological markers and a more irregular, opportunistic growth. Additionally, soil is generally a much more heterogeneous medium than air. Many aspects of the measurement and analysis procedures are therefore specific, even if the basis is the same. A clear overview of these methods, explaining the different steps to be made as well as discussing their advantages, drawbacks and application possibilities, would enhance making optimal choices, and defining standard approaches. However, such overview is currently unavailable.

The objectives of this paper are therefore (1) to give an overview of the state of the art techniques for 3D root system architecture description and analysis, pointing at knowledge gaps and advantages or drawbacks, highlighting what is specific to roots and focusing on methods already used on root systems; (2) to present recent developments and future challenges in this field; (3) to indicate the broad range of application possibilities from this kind of measurements and analyses.

Therefore, in what follows, the authors present a step by step overview of methods related to 3D root system architecture studies. First, different ways of getting to the roots are discussed, followed by a presentation of possible measurement methods as well as coding, sampling, and analysis procedures. Finally, possible outputs and applications are presented with the corresponding references.

Measurements

Getting to the roots

There are several ways to get to the roots, with excavation or uprooting as invasive methods.

Manual excavation using spades and hand tools is the most labor intensive and time-consuming method. To give an idea, full excavation of a root system in a 5 m^3 soil volume, recuperating all coarse roots, can take up to 8 man-days (Reubens et al. 2007b – see Fig. 1). Wet excavation has the advantage of being faster and, with low water pressure, breakage of the fine roots is much less severe. In sandy soils, wet excavation works much faster than dry excavation, but with increasing clay content, the advantage in time decreases (Stoeckeler and Kluender 1938). The main disadvantages of wet excavation are the amount of water needed (Böhm 1979) and the fact that the finer roots, when wet, tend to cling together, thus preventing the effective study of root branching or the relationship of the root to specific soil features. In recent years, the hydraulic soil excavation method has been refined (Gross 1995; Lindsey et al. 1995). Hydraulic soil excavation can result in minimal observable impacts on living roots and once excavated, the roots can be inspected if desired. The slurry removal requires additional equipment and it can result in additional clearance if landfill disposal is necessary (Gross and Julene 2002). High pressure air lances (Weir 1966 in Böhm 1979; Rizzo and Gross 2000) also do not wound the coarse roots, and do not require water or a system to get rid of the slurry. Excavation should be done progressively in layers or sectors, minimising corruption of architecture by securing roots in position using poles and pull ties or by suspending major roots from wooden planks spanning from the stump to the edges of the excavation (Edwards 2003; Danjon et al. 2007a, b). Once the root system is set free, there are two possibilities: either measuring the root system in its original position while it is still in the field (Oppelt et al. 2000; Danjon et al. 2007a, b), or taking the root system out of the soil and measuring it elsewhere (Di Iorio et al. 2005). An important factor for decision here will be the measurement method used (see next section). As for the first option, it is important to free the roots enough in order to be able to measure them appropriately. When the root system is taken out, measurements can be performed much more comfortably, e.g. on an appropriate height or under shelter in bad weather conditions. Furthermore, when the root system is taken away from the field, it is kept safe from human or animal disturbance if it is impossible to perform all measurements at once. On the other hand, it is much more difficult and often even impossible to keep the roots in their original position. The finer the roots to be measured, the more difficult this becomes.

Root systems can also be directly uprooted. Uprooting of shrubs and saplings can be done by pulling the stump with a trestle, a mini-shovel or a lumbering crane (Danjon et al. 1999a, b). Large root systems can be uprooted with a mechanical shovel fitted with a large bucket or a long tooth (e.g. Colin et al. 1995). Danjon et al. (2005) described a study where five people could uproot and clean twenty-four 40 cm mean diameter at breast height (DBH) *Pinus pinaster* Ait. root systems in sandy spodosol within one day. Sandy spodosols are particularly well suited for excavation. For smaller trees (ca. 25 cm DBH) of the same species in the same soils, a combination of techniques is now used (Danjon et al. 2006a, 2007b). The stem is first cut at about one meter height and the ground cover removed with hand tools in a ca. 2-m radius around the tree. Alternatively chemical weeding can be carried out several months before. Then the upper soil layer is removed with a high pressure air lance so as to uncover most of the surface roots of the central part of the root system. A digital photo of each root system is then made, and used later when the root is repositioned for measurement. The soil is also loosened to 0.4 m depth, by driving the lance vertically and slowly into the soil. The stem is then carefully pulled vertically by a mechanical shovel, while the surface roots are dug out with hand tools by four people to approximately 4 m radial distance. Finally, root systems are cleaned with an air lance and hand tools. 2/3 man-day per 0.2 m DBH tree is required for this procedure. In the same way, 70 7 cm DBH *P. pinaster* root systems required 8 man-days to be uprooted (Khuder et al. 2007). When large roots were broken, the portion left in the soil was dug out with hand tools. Root systems should be immediately cleaned after uprooting to avoid rotting, and measured as soon as possible to avoid root shrinking and deformation due to drying.

Long horizontal surface roots reached more than 5 m horizontal extension in 5-year-old *P. pinaster* (Danjon et al. 1999b) and could reach more than 20 m extension in mature root systems (Stone and Kalisz 1991). Therefore, in the case of uprooting with a mechanical shovel or by vertically pulling the root system, roots belonging to the central part of the root system are generally easily loosened, but a substantial amount of horizontal surface root volume is lost during uprooting (more than 3% in Danjon et al. 2006a). A sample of long horizontal surface roots should be exposed before uprooting the tree by air lance and manual digging, followed by in situ measurement (see below and Danjon et al. 1999a, b).

When uprooting is used, a unique tree number, the north direction, the soil level and the horizontal plane have to be firmly marked in one way or another on the collar and the root system before uprooting. In *P. pinaster* (Danjon et al. 2005), a self-boring screw was driven horizontally with a cordless screwdriver at collar level to mark both the north and the soil level. Half a dozen of screws were also driven vertically in the main surface laterals near the stumps so as to have their top at the same level, defining a horizontal plane. These tags where then used to position the root system for measurement. Depending on the size of the root system and a balance between the sample size and the precision of geometric data, uprooted root systems can be positioned for measurement in various ways. Large root systems can be placed upside down with a crane on breeze blocks, attaching the largest roots with pull ties to wooden stakes driven in the soil (Danjon et al. 2005). Smaller root systems can be attached to a post or suspended (Danjon et al. 2007c).

The volume of roots lost during uprooting was estimated by Heth and Donald (1978) by measuring the terminal diameter of all broken roots larger than 20 mm and establishing a regression between the proximal diameter and the dry weight of a sample of intact branched sections of the root system. This allowed them to estimate the dry weight of the missing portions. In the same way, all terminal diameters and regressions between segment diameter and downstream root characteristics in hardly broken branched sections of the root system were obtained from 3D digitising data without extra measurements (Danjon et al. 2006a, 2007b). They were used to assess the volume of lost roots for each tree in several root classes (see below). In 12 cm mean DBH *P. pinaster* uprooted root systems, the estimation of the proportion of lost root volume averaged 2.6, 3.6 and 19.6% of the surface, sinkers and deep roots, respectively (Danjon et al. 2007c).

When invasive measurement techniques are used, only excavation permits a precise assessment of root geometry in both rigid and more flexible roots. However, it can not be used on large samples for which uprooting is required. Therefore there is a trade-off between sample size and precision in geometry assessment. When potted plants have to be measured, a 3D grid of nylon nets can be inserted into the pots before sowing or planting. Root architecture can then be measured after washing off the soil (Mou et al. 1997). In *P. pinaster*, the long surface roots with a diameter less than 1 cm are generally supple but straight and horizontal, bends are visible. They are therefore positioned for measurement in the most probable position (Danjon et al. 1999b, 2005). Deeper roots are more rigid. It may be more difficult to accurately position supple roots in heart-root systems (Köstler et al. 1968) like those of *Fagus sylvatica*. For smaller root systems, epoxy resin impregnation can be used to prevent serious changes in 3D geometry due to gravity (Commins et al. 1991). However, impregnation techniques should be improved, either by effectively displacing the water or using a dye to increase total matrix contrast. Moreover, this is only possible for potted plants.

Root architecture coding

Because of differences in the objectives and in the languages used in different studies, a wide variety of plant architecture representations have been proposed, using different formalisms and having dissimilar properties (Godin 2000). Two main categories of coding are used for plant architecture representation, the first including multi-scale representations and the second being based on L-systems.

A multi-scale representation developed by Godin and Caraglio (Godin et al. 1999a) is called multi-scale tree graphs (MTG's). At a given scale, it represents plant modularity by a directed graph, defined by a set of objects, called vertices, and a binary relation between these vertices, called edges (Godin et al. 1997). Multi-scale models of plants are a rather recent issue in plant architecture modelling (Godin 2000), but they offer certain flexibility for describing various types of plant structures in different ways. Also, they are known to have a high degree of robustness, offering the ability to adapt to objectives for which they were not initially designed (Godin 2000).

Other representations can be broadly classified as either global or modular representations, representing the plant as a whole or as made up by the repetition of certain types of components, respectively (Godin 2000). They differ from multi-scale representations in that plants are not described at different scales. An interesting group of modular representations are the ones based on L-systems, introduced by Lindenmayer (1968), for modelling plant architecture. They use a simple symbolic language to capture the basic structure of plants and exploit the repetitive nature of structure to recreate the evolving architecture over time (Prusinkiewicz 2004).

Shoots can generally be decomposed into a large number of components, e.g. entire shoot systems, axes, annual growth units, intra-annual growth cycles, internodes, leafs and reproduction organs, whose dynamics can be partly assessed by retrospective analysis. Due to the lack of morphological markers, growth flushes and growth units can hardly be identified in root systems. Topology coding with segments i.e. non-botanical entities can be exactly the same for the aerial system of large trees, where old growth units cannot be seen from scars on the bark.

In MTG coding, each axis base corresponds to the base of a segment and each branching point corresponds to the end of a segment. Additional segments are defined so as to represent changes in direction and taper in the best way. Therefore, components of root systems are generally roots and arbitrary segments defining a three scale representation: the entire root system decomposed into axes which are themselves decomposed into segments. This structure is the basis of the MTG files, where each line is a vertex, listed sequentially as a function of its position in the structure. Letters like “P”, “A”, “S” code for plant, axes and segments respectively, topological relationships are recorded with the “<”, “/” and “+” signs (Fig. 3). The first columns of the file code for the topology, columns in the middle for the geometry, which can be either 3D coordinates or lengths and branching angles. Finally, the last columns code for all additional information, e.g. cross sectional diameters, root graft, sample id. The name and format of the variables and the type of topological relationships is recorded in the header of the file. The MTG's used as input for the AMAPmod software (see below) are text files; they can be easily edited because of their simple structure. Any text, integer or real variable can be recorded by adding simply a column to the file. The most parsimonious way of coding (Godin et al. 1999a) is to capture *XYZ* coordinates, diameters and characteristics only at the insertion of all axes on the parent root and at the end of each segment (Fig. 3). In this way, in MTG files, the features of both elements can be represented in the same column, each axis and segment being coded on one line only. The characteristics of the proximal extremity of a segment are those of the end of the preceding segment, except for the first segment of an axis where it is that of the axis base.

The DTD format (see Kurth 1994 p 114) was used by Oppelt et al. (2000, 2001) to code root architecture. In DTD files, variables are pre-defined. Topology, geometry and additional information are mixed in several columns.

The Floradig software (see below – Hanan and Room 2002) exports a text data file in which a label is attached to every item of data. This label has a hierarchical, multi-level structure and lists all the elements connecting it to the base of the plant. This label can become very large in mature forest tree root systems (155,000 measurement points were recorded in the MTG data file used in Danjon et al. 2005). Additionally, each characteristic of an element is listed on a separate line. In both the Floradig and the DTD coding, it is not so easy to "see" the multi-scale structure for editing the files. Therefore, the MTG coding is certainly better adapted to code 3D root architecture than the DTD or Floradig code, which seem to be less flexible.

Sampling of measured roots

Generally, due to practical limitations, not all visible roots can be measured. Therefore a threshold has to be set, depending upon the objectives of the study, the sample size needed and the manpower available (Danjon et al. 2004). Henderson et al. (1983b) stopped measuring the roots when their diameter was less than 0.5 cm, and Oppelt et al. (2000) set 0.3 cm as lower limit. Alternatively, Danjon et al. (2005) measured only axes whose basal diameter was larger than 1 cm, measuring the other roots to their broken end. In this way, a better description of the main axes was obtained. The value of the threshold can dramatically change the time needed for measuring a root system and the number of roots measured. Measuring only the large roots (threshold set at 4 cm) on a mature *P. pinaster* root system may only take one day, whereas 10 days are required when the threshold is set to 0.5 cm (Fig. 4). It is recommended to prune all the roots which will not be measured, before starting digitizing (Danjon et al. 2005).

In studies where inter-lateral root length or fine root architecture is needed, the threshold can be lowered for e.g. one randomly chosen surface second order root or branched section and one sinker root per tree. Soethe (2006) excavated the root systems in half a circle of 1 m radius at one side of the stem, parallel to the slope direction, and carefully excavated one entire root of every tree. The geometry of the supple fine roots can rarely be measured, therefore Khuder (2007) only recorded the fine root number and mean length for each root segment, which enabled accurate analysis of root length and branching properties variability in seedlings.

Measurement techniques

3D-digitizing methods differ mainly in the degree of automation (manual, semi-automatic or automatic) and the way in which the geometry is assessed. For the latter, three main possibilities do exist:

1. Determination of the volume occupied by roots in the 3D space, also known as "non-contact point-cloud measurements" (van der Heijden et al. 2007). This category includes both all the non-destructive techniques and automatic destructive techniques like the 3D laser beam measurement.
2. Recording of *XYZ* coordinates or polar coordinates and depth of each root element.
3. Recording length, vertical angle and azimuth of each root element. The *XYZ* position is then computed recursively.

In all cases where the topology is described manually, root measurements should be taken starting from the collar and working progressively downwards and outwards, measuring each branch to its tip and then returning to the main root until its end is reached (Danjon et al. 2007a – Fig. 3). The topology is coded in this order in MTG files.

Automatic root volume location methods

Due to sample size constraints, non-destructive methods such as high resolution X-ray computed tomography (or "CT") scanning and nuclear magnetic resonance (NMR) imaging were used for small potted plants only. Lontoc-Roy et al. (2005) estimated the fractal dimension of four *Zea mays* seedlings at day 1, 2 and 3 using CT scanning. Except for this paper, only technical papers were published so far, in which the 3D root architecture was not examined, but only the spatial volume distribution (e.g. Heeraman et al.

1997; Kaestner et al. 2006) the fractal dimension (Lontoc-Roy et al. 2004) or root length and growth rate (e.g. Brown et al. 1991). X-ray tomography can become very expensive when studying larger root systems (Gregory et al. 2003) and not all soil conditions are practically suited for it, as soil density has to be different from that of roots for a clear observation (Lontoc-Roy et al. 2004).

Among the non-destructive geophysical techniques, the Ground Penetrating Radar (GPR) has the lowest wave length and resolution to detect small targets but also the highest wave attenuation that limits resolution and penetration in wet conducting media. A compromise between penetration and resolution must be made. An 800 MHz antenna represents a good balance between both constraints (Barton and Montagu 2004). Root diameter should be estimated from the waveform parameter which is independent of the root depth (Barton and Montagu 2004). Radar waves are very sensitive to moisture changes and may potentially discriminate healthy and decayed roots (al Hagrey 2007). The central part of larger root systems will produce a confusing profile because of interactions between the hyperbolas from all the closely spaced targets (Barton and Montagu 2004). GPR has been useful only for single root segments or biomass estimation so far, with a relatively low precision (Stokes et al. 1999; Butnor et al. 2001; Butnor et al. 2003; Barton and Montagu 2004; al Hagrey 2007). GPR was used to draw root architecture manually in plan and elevation from transects of soil made every 25 cm. However, results were unreliable (Stokes et al. 1999). Additionally, tap roots and sinkers could not be measured because the radar signal cannot identify objects running parallel to the scan properly. Three-dimensional root architecture may only be assessed with tomographic techniques similar to those used in medical imaging with an intensive mechanised scanning on tighter grid spacing, including scans at a range of angle toward soil surface to localize vertical roots (Barton and Montagu 2004). However, high soil water content, low root density or diverse terrain will prevent one using this technique (Butnor et al. 2001).

Further development of these systems is still needed using advanced data processing techniques developed for medical purposes (Barton and Montagu 2004). It is essential to invest time in getting good quality images and to use efficient 3D threshold and connectivity algorithms (Kaestner et al. 2006). Altogether, these methods offer opportunities, and advances in software and better object resolution could produce useful, non-destructive and rapid techniques essential to get directly the dynamics of 3D architecture.

Automatic destructive measurements such as 3D photogrammetry or 3D laser scanning (see van der Heijden et al. 2007) yield the same type of data. Their main drawback is that optical devices cannot capture data from branches hidden by another branch. In a technical paper, Gärtner and Denier (2006) described how they used a 3D laser scanning device to map the root surfaces of a large uprooted root system. Only the root surfaces visible from the position of the scanner are measured. Therefore, the root system had to be scanned from different positions, which was done within 1 1/2 h. Images were then merged using specific software. The measurement is automatic but can require a certain amount of manual intervention. It is certainly the best available technique to describe the shape of the root surfaces but it still needs development, evaluation and tools to extract information. As for other optical methods, it can be useful to measure simple root systems (Teobaldelli et al. 2007) but is certainly imprecise in complex and dense root systems where more roots are hidden from the beam. In the latter case, it may be necessary to cut the root system in several sectors and to scan them separately.

Except for the paper of Teobaldelli et al. (2007), in none of the technical papers we could find, reporting non-destructive or automatic methods, the topology was assessed. Although topology may be entered manually in the 3D structure displayed on the computer screen (Teobaldelli et al. 2007), an efficient measurement of root architecture requires an automatic assessment of the topology using a branch detection algorithm, but is not yet available (van der Heijden et al. 2007). A prototype program (part of the PointPicker program) has been developed for semi-automatic determination of topology based on previous work on human airways mapped through CT images (Hanan et al. 2004).

Manual measurements recording XYZ coordinates

Manual measurements are generally performed by recording the *XYZ* coordinates with a frame consisting of moveable rulers in *X* and *Y* direction. By shifting these rulers to the right position, coordinates of each root segment can be determined. Henderson et al. (1983b) used this method together with a plumb bob to get the vertical coordinates and measured eight 23 cm DBH *P. sitchensis* root systems. Khuder et al. (2006) and Khuder (2007) used a similar system on *Robinia pseudoacacia* seedlings grown in pots. A frame fitting the plant pot, with a vertical rod to measure the *Z* coordinates, was used to measure the progressively uncovered root systems. An average seedling with 43 segments, 24 coarse roots and 25 fine roots required one man/day measurement. The same method was followed by Reubens et al. (2007b) for in situ measurements of 1 year old field grown *Cordia africana* and *Olea europaea* seedlings. On average, measurement of one seedling took 5 h with two persons. Such techniques can be fairly efficient in small trees but require a lot of time for measurement in large root systems (Henderson et al. 1983b). Coordinates can also be assessed from a levelled *XY* grid constructed with strings (e.g. Puhe 1994; Mulatya et al. 2002).

Manual measurements recording length, vertical angle and azimuth of each root element

Dupuy (Dupuy 2003; Dupuy et al. 2003a, 2007; and http://www.archiroot.org.uk/) designed the ArchiRoot program to enter directly the length, vertical angle and azimuth of each root segment, the topology and root axis base and segment end diameter. These parameters are gathered with a simple compass, inclinometer and calliper. The *XYZ* coordinates are listed in a MTG file (see below). If a computer is available for immediate data entrance, validity of these data can be checked graphically during the measurement.

It was used on small potted *Quercus robur* and *R. pseudoacacia* seedlings (Reubens unpublished results) as well as large root systems measured in situ [Dupuy 2003; Reubens et al. 2007b (*C. africana*, *Acacia etbaica*, *Euclea racemosa* – see Fig. 1) and Dupuy et al. 2007 (26 cm DBH *Populus* root systems)]. This method turned out to be significantly more rapid than the frame method to measure large root systems, probably because the operator doesn't have to move a large frame. However, as experienced by the second author, for root structure measurements of small seedlings ($<50\times50\times50$ cm^3 soil volume), it turns out to be less efficient and less accurate than the frame method.

Semi-automatic digitising using a contact 3D digitizing device

XYZ coordinates of a point can be obtained with a contact 3D digitizing device. Such a device was first used by Lang (1973) to measure the 3D structure of aerial plant parts, studying the orientation of cotton leaves. Moulia and Sinoquet (1993) compared available devices to measure *Z. mays* aerial geometry. Semi-automatic measurement of 3D aerial tree architecture using a 3D digitizer was first proposed by Sinoquet and Rivet (1997) and Sinoquet et al. (1997), and was adapted to root systems by Danjon et al. (1999a).

Contact 3D digitizers are mainly used in virtual reality and biomedical applications. Alternative devices are available including articulated arms, electromagnetic tracking systems and acoustic (Hanan and Room 1997) devices. These devices were only compared by Moulia and Sinoquet (1993). Main conclusions of that comparison were that (1) articulated arms have a small active volume and cannot reach masked points; (2) acoustic devices should have a clear line of sight from all the microphones, are sensitive to echo and air motion, and they can therefore generally not be used in the field; and (3) electromagnetic devices are influenced by metal and electric equipment (Moulia and Sinoquet 1993). Moulia and Sinoquet (1993) obtained the best precision with the Polhemus 3D digitizer as compared to the sonic GP8-3D digitizer. However, when using a contact 3D digitizer, the main source of error generally doesn't come from the nominal accuracy of the device but from the manual operating process (Moulia and Sinoquet 1993). In the more than ten published research papers on coarse root system 3D architecture, only one model of contact 3D digitizer (Polhemus Fastrak, see below) was used so far. Therefore, mainly this semi-automatic technique is described in detail below.

The Polhemus "3Space Fastrack", manufactured by Polhemus (Polhemus, Colchester, Vermont), is an alternating current low frequency magnetic field digitizer, consisting of an electronic unit, a magnetic transmitter and a small receiver (pointer) fitted with a switch. The whole is connected to a computer (3SPACE FASTRACK user's manual, April 2005, 124pp). The "3Space Fastrack" provides 6-degree-of-freedom (*X Y Z* Cartesian coordinates and azimuth, elevation as well as roll orientation of the receiver) digitising of single points in a 1.5 m radius sphere. The size of the sphere can be extended to 5 m with the

"Long Ranger" option, providing the contact 3D digitizer with the largest range we could find. This range is appropriate for the measurement of larger tree root systems (Figs. 2 and 4). Metal can cause distortion within three times the distance between the transmitter and receiver (3SPACE FASTRACK user's manual).

When applied to root systems, semi-automated 3D measurements are most efficient when performed by two persons: one clicking the appropriate positions with the receiver and measuring the root diameters, and one person entering diameters and topological indications on the PC as well as controlling the measurement process with the aid of a table displayed or a root system image on the screen. Two perpendicularly taken diameters are generally measured at each point with a plastic dial calliper. The generation of driving software developed by Sinoquet and co-authors, i.e. Diplami (Sinoquet and Rivet 1997), Pol95 (Adam 1999), 3A (Adam et al. 1999) and PiafDigit (Donès et al. 2006), jointly capture topology and geometry and also allow the entry of other variables for each point. With PiafDigit, data can be visualized in 3D and corrected during measurement. Output files are coded in MTG format. The Polhemus Fastrak and Isotrak digitizers can also be driven with the Floradig software (Hanan and Wang 2004). Prior to architecture measurements, the accuracy of the digitizer has to be checked.

Very long and straight surface laterals can extend outside the active measurement volume. They can be measured by assessing their diameter every 0.5 m and the corresponding Euler angles in case of direction changes. The appropriate topology and geometry then has to be entered manually in the MTG file (Danjon et al. 1999a, b). Digitising can also be done in sections, requiring a labelling system. Files next have to be reassembled manually, adapting the topology and the geometry (Edwards 2003).

The main drawbacks of the Polhemus digitiser are the cost of the device (around 5,500 and 7,500 € for the standard and the long ranger digitizer, respectively), the technical skills needed to master the techniques, the duration of measurements, the difficulty of carrying the device to certain locations and to work in hard climatic conditions, and the influence of metal and electric equipment. This means that the measurement of uprooted root systems can generally not be done in existing buildings because the iron grids reinforcing concrete largely perturb the measurement. In mild climate it can be done outdoor, under a shelter in case of rain. However, in windy and wet climate like Scotland, the construction of a wooden shed may be required (Nicoll, personal communication).

On the other hand, digitizer drivers and analysis software are freely available. 3D digitising of sapling root systems can be learned within one day after a few hours of teaching. A standard 12 V car battery combined with a 220 V 1.1 A converter can be used to power the digitizer and a laptop more than 10 hours in the field. The manual method proposed by Dupuy et al. (2003a) can be performed anywhere with inexpensive tools, but is slower and less precise.

The Polhemus digitiser is highly versatile and can also be used for any measures where 3D coordinates are needed, including digitising aerial parts, stem shape, soil micro-topography, 3D root plate limit in uprooted trees, and motion tracking during tree pulling experiments.

Ultra-sound devices could certainly be used for uprooted root systems transported to the lab. Hanan and Room (1997) used the GTCO Freepoint 3D multiple sound-emitter sonic digitizer, which overpasses the masking problem, and the Floradig driving software to digitize shoots. However, the size and shape of the active volume (2.4×2.4×4.8 m) of this device may not be adapted to digitise larger root systems. The nominal resolution of this device is 0.01 cm. This device is not longer manufactured and we could not find another similar device. Hanan and Room (1997) also suggested to use a complementary voice synthetizer/recognition software (e.g. Dragon Naturally Speaking http://www.nuance.com/naturallyspeaking/professional/) to assist the data collection, and could easily correct their 3D data with the PointPicker program (Hanan et al. 2004).

Semi-automatic 3D digitising can reasonably be used in factorial experiments by measuring a hundred sapling's root systems. Seventy-six 7-year-old *P. pinaster* root systems of 7.6 cm mean collar diameter could be digitized within 25 days, yielding 12,000 measurement points corresponding to 2,800 individual roots. All roots with a diameter at origin larger than 0.2 cm were measured. One additional week was spent by one person to control and correct the data (Khuder et al. 2007).

Semi-automatic digitising using a digital compass and inclinometer

So far, this methodology was only used by Oppelt et al. (2000, 2001). They measured the 3D coarse root architecture of 20 tropical trees with an average root collar diameter of 6 cm with a program getting the data from a digital compass and inclinometer. The topology, length, vertical angle and azimuth of successive single segments were first measured with a digital compass (TECTRONIC 4000, Breithaupt, Kassel – Germany). Segment diameters were measured in a second step with a digital caliper (PM, 200, HHW Hommel – Switzerland), requiring the labelling of the measurement points. Data were recorded in the DTD format.

Reconstruction of 3D architecture using fractal branching and developmental models

3D root system architecture characterization can also be obtained from the measurement of a subsample of roots or branched sections of the root system only, followed by a reconstruction of entire root systems using static fractal branching models or dynamic developmental models (see below). This is a means to reduce the fieldwork needed to assess the root architecture (Pagès 1999b). The root system simulations can then be analysed with the same techniques and tools used to analyse 3D digitizing data. As mentioned before, these techniques may not be efficient in root systems with high heterogeneity of circular distribution for which a complete measurement is generally required. In the developmental model used by Vercambre et al. (2003), Pagès et al. (2004) and Collet et al. (2006), the following parameters determined the spatial distribution of the roots: primary growth rate, inter-lateral length, branching angle and geotropism, all influenced by soil mechanical constraints. In the fractal branching model used by Salas et al. (2004), the spatial distribution was determined by the inter-lateral length and by both horizontal and vertical bifurcation angles associated to each branching point.

Analysis

Software for analysis

3D root architecture data can be analysed with ordinary spreadsheets or statistical packages. A better analysis can however certainly be obtained using software devoted to plant architecture database analysis. Only the GROGRA (Kurth 1994) and AMAPmod (Godin et al. 1997; 1999a, b; Godin and Caraglio 1998) software were used on root systems so far. Floradig (Hanan and Room 2002) can only calculate parameters like length, area and angles of digitised points.

This fairly complex 3D data needs editing. Tools for visualizing the data in 3D are therefore needed both to check the data during and after the measurement and to analyse interactively the data.

AMAPmod includes a utility to control the structure of the input file, numerous built-in functions which can be assembled in user-made functions to compute parameters, a program to display 3D graphics of various elements of the root system (see Fig. 1, 2, 3, 4, 5, 6) and functions required for advanced statistical analysis in plant architecture. In AMAPmod, lacking information such as coordinates of long surface laterals (Danjon et al. 1999a, b) are inferred from default values.

Danjon et al. (1999a, b, 2005, 2007a), Di Iorio et al. (2005), Tamasi et al. (2005), Nicoll et al. (2006) and Khuder et al. (2006, 2007) used the AMAPmod software to compute matrices of root segments and axes characteristics. AMAPmod was also used for specific purposes like the computation of topological indices (Danjon et al. 2004; Khuder 2007) or characteristics of root impacts on planes parallel to the soil surface (Danjon et al. 2007a, b). Software devoted to plant architecture analysis like AMAPmod generally does not include tools for ordinary statistical analysis and plotting. Further analyses were therefore developed by Danjon and co-workers for the R open software (www.r-project.org). Codes for AMAPmod and R can be reused on similar studies and are freely available. Both software packages are programming software requiring time and skills for learning the programming language (amap-e-learning.cirad.fr, cran.r-project.org) but they are highly multi-purpose and adaptable. AMAPmod uses the same coding of data as the AMAPsim architecture simulation program and other companion software. AMAPmod is now part of the OpenAlea *open source* project running both under Linux and windows (Pradal et al. 2007; http://openalea.gforge.inria.fr). OpenAlea integrates programs developed by the functional-structural plant models community, i.e. programs for MTG visualization, statistical analysis, fractal analysis, computer graphics, biophysics and functional-structural models (Pradal et al. 2007). Alternatively,

Fig. 1 Graphical reconstruction of a mature *Euclea racemosa* root system in Tigray (Northern Ethiopia) using the AMAPmod software. Full manual excavation using spade, pickaxe, shovels and spoons, and taking care to maintain all root segments >3 mm in their original position takes about 6 man days. Measurement performed within 2 days using a simple compass, inclinometer, measurement tape and calliper. Data entered in the ArchiRoot program prior to analysis in AMAPmod and R. Root segments coloured as a function of their branching order: *black* taproot, *blue* order 2, *red* order 3, *green* order 4. Root system with a total length of 3,462 cm, a total volume of 4,641 cm^3, consisting of 63 roots or 280 segments

Di Iorio et al. (2005) analysed the AMAPmod output file in an excel spreadsheet.

The GROGRA software (Kurth 1994) was initially developed for simulation of plant growth and architecture using L-systems (Lindenmayer 1968) and an associated stochastic growth grammar. With its companion programs it can also be used to check, edit and analyse 3D architecture data files, for graphical

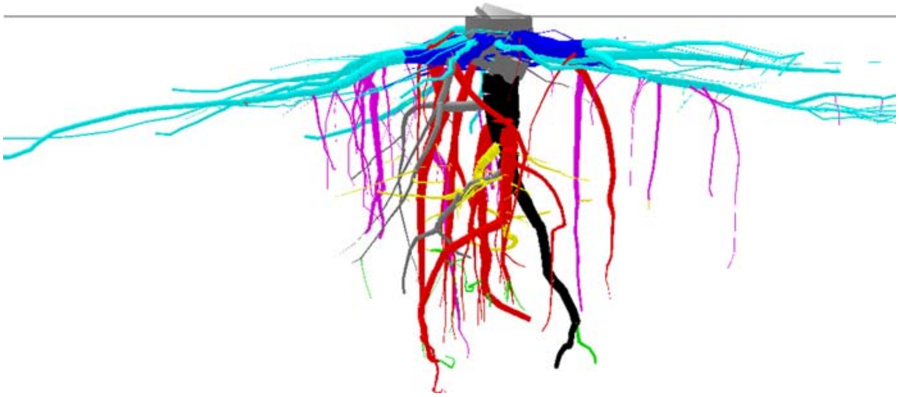

Fig. 2 Graphical reconstruction of a root system of a 27-years-old *P. pinaster* tree in sandy spodosol with deep water table in the South-West France "Landes de Gascogne" forest. "Vielle Bas" stand, tree no. 9. Installed and measured within 8 hours by two people using the Diplami software. Grayscale or color as a function of the compartment after Danjon et al. (2005): *grey* stump and oblique roots, *black* taproot, *blue* ZRT, *light blue* horizontal surface beyond ZRT, *red* sinker beneath ZRT, *violet* sinkers beyond ZRT, *yellow* intermediate depth root, *green* deep roots. Root system with a total length of 13,335 cm, a total volume of 103,270 cm^3, consisting of 183 roots and 1,610 segments. Measurement F. Lagane, B. Issenhuth, INRA

display of the structures, to determine fractal dimensions and to run functional-structural plant models. Oppelt et al. (2000, 2001) used GROGRA for analysing 3D architecture data of tree root systems.

Details concerning both measurement and analysis

Root architecture data are complex, analyses can be made in several ways, and results will largely depend on the way the analysis is made. It should start with an exploratory data analysis, first checking the root systems one by one for error. When several treatments are compared, one interesting way to detect differences is to over-plot all root systems of each treatment (Fig. 5 and Khuder et al. 2006). Analysis should be tree size independent and interactive. Interactive analysis can be made with software including graphical tools like AMAPmod. Assumptions and limits can be adapted and changed during analysis, checking part by part the results on 3D representations of the root system coloured as a function of corresponding values of variables. Such an interactive analysis was done by Danjon et al. (2005) and Khuder et al. (2007 – Figs. 2, 4 and 5), defining the limit between root categories by examining 3D images of root systems where segments were coloured according to their category. Alternative ways to take into account several fundamental features of root systems in the analyses are described hereafter.

Defining the measurement points

Measurements have to be made to match the goal of the study and the expected digital representation. The topology is generally recorded by defining arbitrary segments coded in the output file as oval cylinders (Fig. 3). For root systems of mature trees or shrubs, it is recommended to define segments longer than 3 cm, especially on tap roots. Defining very short segments will result in an overestimation of root length and volume because of proportionally large imprecision in *XYZ* pith position. In the same way, when a 3D digitizer is used, in large axes, digitising should be made with the same receiver direction, for example clicking all the time on the tap root from the north direction. As the taproot is generally highly branched near the collar, in larger trees, it should be virtually divided into segments of about 3 cm length bearing each several second order roots which originate approximately at the same level, like branch whorls.

Certain root system features need specific coding techniques. In mature *P. pinaster* root systems on spodosols, when the sinkers reach a hard pan, they produce several dozens of horizontal roots joining on their first 10 to 50 cm. These structures were considered as large flat roots with branches; the topology could not be retrieved (Danjon et al. 2005).

It is recommended to progressively cut and remove each large arborescence after measurement, to get closer to the roots and to avoid double measurements

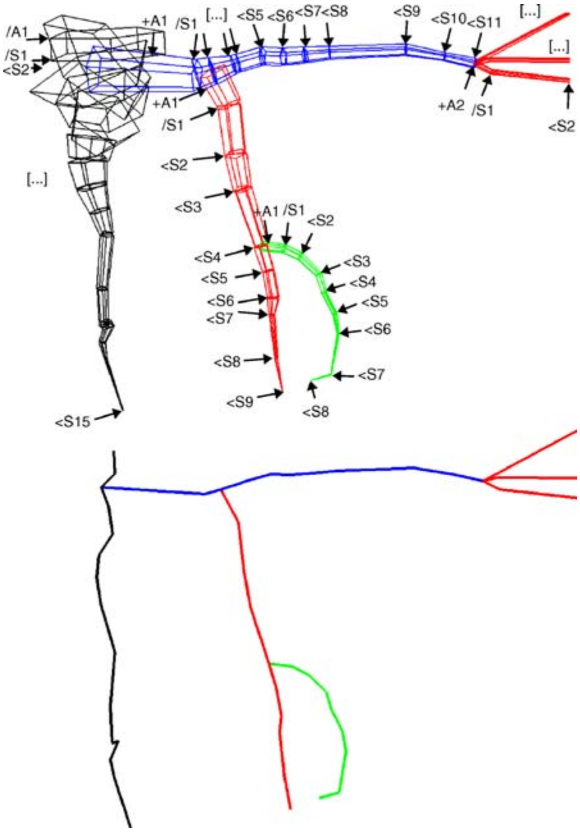

Fig. 3 *Top* Schematic representation of the measurement procedure using a 6 degree of freedom digitizer and coding in the MTG format. Same color code as for Fig. 1b. Digitising starts at the collar with 3 points on the tap root, then clicking the 3 first points of the second order root, 5 points on the third order root, the whole green fourth order root, then back to the third order root to its end, and so on. Topological code is *A* for axes and *S* for segments, *slash* means the vertex is nested within a vertex at larger scale; *less than symbol* means "succession" and *plus symbol* means "is branching" (see Table 1 in Danjon et al. 1999b). For each point, the position and orientation of the receiver is indicated by an arrow. *Bottom* Same root structure, plotting only the main axis of each segment, i.e. root diameters are not represented

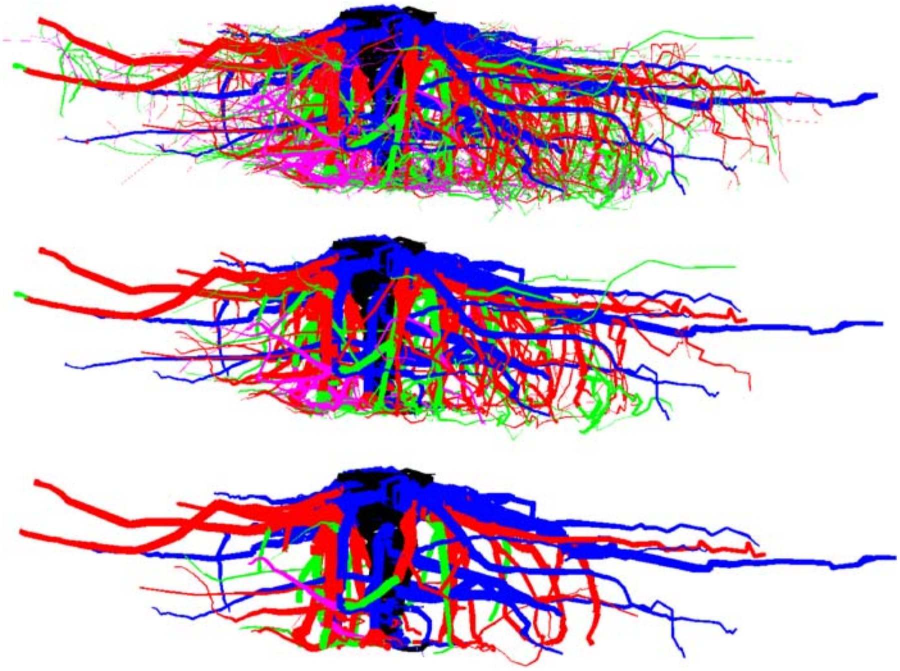

Fig. 4 Graphical reconstruction of a mature *P. pinaster* root system, showing how the sampling threshold affects the measurement. *Top* Original MTG where all root axes with basal diameter larger than 0.5 cm were measured. *Middle and bottom* Threshold set to 2 and 4 cm, respectively. The number of root segments decreases from 6,700 to 4,000 and to 1,600. Same color code as for Fig. 1. Dataset from Danjon et al. (2005)

(Henderson et al. 1983b). Measured roots can also be labelled, as was done in Danjon et al. (1999a, b).

The coordinates of a given cross section are generally measured at the external surface of the bark. As the coordinates of the centre of the cross section are generally needed, they can be computed from the roll and attitude of the receiver in case of a measurement with a 6th degree of freedom digitizer (performed in this way by Danjon et al. (1999a) and in all papers using the Polhemus digitizer). In case of manual measurement, these coordinates may also be computed if for example all coordinates from horizontal cross sections are measured at the top of the cross section and the coordinates for vertical sections on the outer side.

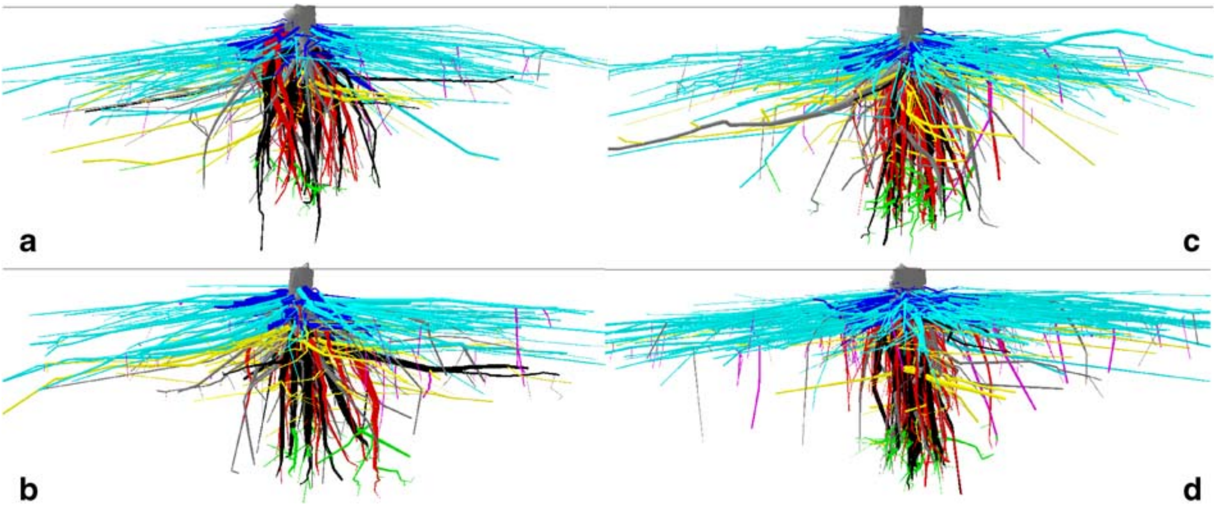

Fig. 5 Overplotting of all 19 root systems of a treatment for exploratory data analysis. Colour or greyscale as a function of the root compartment (see Fig. 2). **a** Control trees, **b** pruned taproot, **c** and **d** cuttings. Seven-years-old *P. pinaster* trees. Dataset from Khuder et al. (2007). Only few differences between the treatments were found

Fig. 6 Stump (*grey*) and taproot (*black*) in 22 12-years-old *P. pinaster* first order roots. The limit between stump and taproot was determined during measurement and recorded in the MTG file (Measurement: F. Lagane, B. Issenhuth - INRA, dataset from Danjon et al. 2007c)

Recording additional information

Any information concerning individual root segments, for example root grafts, root rot, dead roots, cluster roots, reiteration or large changes in soil profile, can be recorded by entering an extra code during digitising (Danjon et al. 2005). In the same way, the topological and geometric position of specific root segments or cross sections sampled for any purpose, e.g. density (Danjon et al. 2006b), bark thickness, vessel diameter and density (Nygren et al. 2004), age (Di Iorio et al. 2007) and carbon content (Bert and Danjon 2006), can be recorded. The limit of the sampled segments should be marked e.g. by two saw cutting lines and the segment tagged before starting the measurements. The position of any measurement device e.g. sap-flow sensors, micro-dendrometers, 3D motion captor or strain gauges can also be recorded.

Root grafts can be of primary importance in plant stability, fungal infection dynamics, and carbon dynamics through stump survival. Grafts can be measured on one root by defining a segment from the origin to the end of the graft. A specific code (one for self-grafts and one for between trees grafts) is then recorded in the file for this segment. At tree level, the intensity of each type of grafting can then be taken into account by computing the number of grafts, the ratio of the graft surface (half of the external surface of each grafted segment) to the total external root surface, or by pooling the volume of all grafted segments (Danjon et al. 2005).

Assessing root biomass from 3D digitizing

Digitizing provides root volume. Root dry weight per segment can be obtained in three ways from a sample of root segments:

1. By root diameter classes in a random sample of root segments (Danjon et al. 2007a)
2. Only establishing a regression between root diameter and root density, or
3. From the characterisation of the distribution of root density in the root system assessed by drying and weighing segments recorded in the database (Bert and Danjon 2006; Danjon et al. 2006b).

Measuring the soil surface

As the vertical root distribution is one of the important characteristics of root systems, the soil level limit should be defined precisely and in the same way for all sampled trees. In natural environment, the soil surface is often not flat and uniform. Additionally, the soil surface often changes position during the life of a tree through erosion or deposition in many forms (Tobin et al. 2007). Danjon et al. (1999a, b, 2005) removed the litter and determined the soil level limit visually, as the mean position around the stump. In the corresponding intensively managed stands, the soil surface in the inter-rows was generally 0.1 to 0.4 m lower, which resulted in an overestimation of the computed root depth in inter-row roots. The status of buttresses and aerial adventitious roots also has to be assessed in the analysis.

Determining branching orders and the taproot

In root system architecture analysis it is common to consider the main root arising from the seed as the first order root (Barthélémy and Caraglio 2007). A root originating or branching from this first order root is hence considered as a second order root, and so on. However, even in young trees, it is generally difficult to determine the original branching order of every root, because the meristem of a root can die and be replaced by another meristem with similar properties. For example, the tap root of *Quercus petraea* Matt. Liebl. seedlings shows a high reiteration capacity leading to the formation of a root system with successive substitutive tap roots (Collet et al. 2006). Such a substitution is often invisible externally, especially on the taproot. Therefore "apparent branching orders" (Barthélémy and Caraglio 2007) are generally recorded. The probable function of the root can also be taken into account in determining the branching order. In Khuder et al. (2007), the largest vertical root originating from the stump was coded as a tap root, even in cuttings. In the same way, forks were generally recorded when a root split into two equally sized roots subtending equal angles to the parent root (Danjon et al. 1999a). When the morphology of the fork indicates that it originates from a death meristem or from pruning, this should be recorded in the data file.

The stump

The stump can be defined as the portion of the first order root with a large diameter from where most of the large surface roots branch (Danjon et al. 2005). Especially in older, mature trees, it generally constitutes a large portion of the coarse root biomass and plays a specific role in stability and sap flow conduction. Therefore it is generally recommended to examine the root or taproot volume or biomass excluding the stump (Nicoll et al. 1997). The stump lower limit can be defined in several ways:

1. Defining a standard, fixed stump depth (Danjon et al. 1999a, b) or length (when the tap root is not perpendicular to the soil surface, as in the case of slope/non-slope treatments – Khuder et al. 2006)
2. Defining a relative stump depth per tree, e.g. as a percentage of the maximal depth of the root system
3. Subjectively defining the limit during the measurement, and recording the last segment composing the stump in the data base (Danjon et al. 2005 – see Fig. 6).

The zone of rapid taper (ZRT)

The ZRT (Eis 1974) is the proximal part of shallow horizontal roots near the stump, showing an oval, I-beam or T-beam shaped diameter reinforcement in response to wind movement (Coutts et al. 1999). The ZRT is of major importance to anchorage (Coutts 1987) and includes a substantial amount of coarse root biomass in older trees (Danjon et al. 2005). In the same way as for the stump, the limit for the ZRT can be defined in three ways:

1. Defining a standard, fixed radial distance of the main tree axis or of the stump bark (e.g. Danjon et al. 1999a, b)
2. Defining the ZRT by a radial distance function of the tree size. In Danjon et al. (2005), this limit was set to 2.2*DBH to determine which sinkers where beneath the ZRT
3. Directly from the definition of the ZRT, as function of root taper or ovality. In Danjon et al. (2005), the ZRT included the last segment of each axis for which the taper from axis origin was larger than 1.25% per cm and all segments located between the axis origin and this last segment (see Fig. 2, ZRT is in dark blue). This value was set to 2.5% in smaller trees (Khuder et al. 2007).

Additionally, the vertical limit for the ZRT is generally the same as the limit chosen for the horizontal shallow root compartment, i.e. it can be either the same as for the stump, or a fixed or relative depth.

Scaling the depth and the radial distance to the root system size

The classification of a root segment as a function of its vertical and/or radial position or within a sequence of compartments (see below) requires setting limits. These limits should generally be scaled as a function of the tree size or/and the tree maximal rooting depth. In *P. pinaster* saplings Danjon et al. (1999a, b) set two fixed spatial limits for shallow and deep roots when studying the vertical distribution of rooting. In mature *P. pinaster* trees, Danjon et al. (2005) scaled the lower limit for the shallow and upper limit of deep roots to 33 and 75% of the maximum rooting depth beneath the zone of rapid taper (ZRT) for each tree, respectively. Because the maximum tree rooting depth ranged from 0.74 to 1.28 m due to various soil limitations.

When trees have grown on a slope and the analysis is made using a reference frame parallel to the slope, the taproot is generally inclined. In the compartment and circular distribution computations, radial distance and azimuth of a segment has then to be computed relative to the end of the taproot segment which bears the corresponding root arborescence (Khuder et al. 2006, 2007).

Volume and length of the first segment of an axis

The volume and length of the first segment of an axis is required to compute the volume and length of this axis, respectively. The volume of the proximal segment of a root should be computed using its proximal and distal diameters and the length between its origin and the end of the segment. Root system volume is only poorly affected by the threshold set to sample the roots.

Conversely, to assess the coarse root length produced by the tree from the seed, the length between the end of the segment of the mother axis which bears the axis A and the base of the first segment of axis A should be used in computation. Additionally, including all information available on fine root length will improve the estimation of total root length.

Precise volume distribution

In spatial root distribution computations, the length or volume of all segments whose centre is located in a given elementary surface is generally simply pooled (Danjon et al. 1999a, 2005; Di Iorio et al. 2005; Tamasi et al. 2005; Nicoll et al. 2006). A more precise repartition of length and volume may be obtained from software which could segment the truncated cones in the 3D space. Alternatively, Khuder et al. (2006) and Danjon et al. (2007a, b) simply divided all segments into 1 cm long virtual segments using the AMAPmod software and used the parameters of this new set of segments instead of the original segments in their spatial analyses.

Further refinements

Further refinements are often necessary, especially in complex root systems or complex soil conditions. For example, in Danjon et al. (2005), the growth direction of several horizontal surface roots changed to become oblique or vertical at distance from their origin, and some sinkers grew horizontally when they reached the hard pan. For the classification of roots in horizontal, oblique and vertical roots, the vertical angle for horizontal shallow roots and sinkers was therefore computed from their origin to the point were they reached the ZRT limit or the deep root limit, respectively.

Possible outputs of the data

When a nearly full description of the coarse root system 3D architecture is reconstructed from measurements or modelling, most of the parameters listed in Table 1 from Reubens et al. (2007a) can be computed. Analyses can also be grouped in the following main types.

Summary characteristics of the root system

Most papers published so far first present simple summary characteristics at the root system level including e.g. total root volume and biomass, length, number, biomass ratios, mean inter-lateral length, number of forks, maximum rooting depth and radial extension (e.g. Danjon et al. 1999a, b).

Bulk 1D, 2D or 3D continuous spatial distributions

The most common use of 3D root architecture data is to compute the continuous spatial distribution of coarse root volume, biomass, external surface, specific root length or length.

The spatial distribution of branching or root orientation characteristics, including e.g. root number, fork number, branching points and bend number, mean branching angles, mean root vertical angle, root graft number and surface, and % of root rot, can also be examined (Danjon et al. 2005; Khuder et al. 2007).

Finally, the spatial distribution of any property of the root cross sections, root segments or root axes can be inferred from the measurement of samples localized during digitizing. Bert and Danjon (2006) measured the wood density and root carbon content in a sample of root segments. The parameters of a regression between root wood C content and root diameter were used to compute the weighted mean carbon concentration (WMCC) at root system level from the diameter and volume of the 44,000 digitized segments.

The horizontal and vertical (radial distance × depth) 2D distribution were generally displayed using isocontour graphs (e.g. Danjon et al. 1999a, b). Because of the continuous measurement, statistical distributions can be fit to the distributions (Henderson et al. 1983a) and thresholds in distributions can be detected [see Figs. 1 and 2 in Danjon et al. 1999a; Figs. 4, 5, and 6 in Danjon et al. 1999b; and Fig. 5 in Jourdan and Rey (1997c)]. 1D circular distributions are of particular interest to assess the reaction of the root system to a directional stimulus (e.g. dominant wind and/or a slope – Danjon et al. 2005; Nicoll et al. 2006). The effect of directional stimuli can be tested in the same way as for dominant wind, comparing the windward, leeward and perpendicular to wind sectors (Danjon et al. 2005). It can also be done using various circular statistics tests and indices (Di Iorio et al. 2005; Nicoll et al. 2006). However, the latter are generally not so powerful because they just test if the distribution is uniform or not, whereas the sector method directly takes into account the a priori information concerning the direction of the stimuli. Danjon et al. (2005) excluded the taproot and the root segments located within half of the DBH radial distance because their contribution to each sector could not be determined. Alternatively, as mentioned above, the sector of a segment should be determined from the azimuth computed relative to the end of the taproot segment which bears the corresponding root arborescence (Khuder et al. 2006, 2007). It should be noted that defining sectors as a function of the cardinal points has generally no meaning and that the sectors should be centered on any heterogeneity like e.g. tree lines, slope, dominant wind.

When the distribution of fresh root properties such as nitrogen or carbohydrates content, mechanical properties, vulnerability to xylem cavitation or precise fresh volume of root segments is studied, the sampling of root segments for analysis has to be performed immediately after felling the tree. Root system excavation and measurement should then start with the parts of the root system where the samples are taken. When the root system is lifted, the sampled branched section of the root system can be extracted and cut-off before or just after uprooting, stored in a cold room, pasted to the root system just for measurement and immediately treated (Lagane, personal communication). Root systems can also be stored in a natural water body (e.g. a lake) to avoid dehydration until root measurements are carried out (Khuder et al. 2007).

Continuous 3D mapping of biological properties and their variation in time (e.g. root volume, length or number of root branches) could be achieved using general density functions (Dupuy et al. 2005c). This approach is a good way for modelling root/soil interaction as it provides a local root morphological characterization aggregated in a given unit of soil volume. In the same way, the soil is often also characterised by continuous variables and equations (Tobin et al. 2007). This density based approach was implemented and tested by Dupuy et al. (2005a, b) using the 3D architecture data from Danjon et al. (2005). Brown et al. (1997) suggested using density functions in simulations of interactions between tree roots and fungi.

Distributions in several classes

The distribution of most of the aforementioned parameters over e.g. segment diameter or depth classes, axis angle toward soil surface and branching order can also be computed (see Fig. 1 in Danjon et al. 1999b). For *P. pinaster* saplings, Danjon et al. (1999b) computed the correlation between the proportion of roots by depth, angle toward soil surface and diameter on the one hand, and several other tree characteristics on the other hand. Di Iorio et al. (2005) computed volume, length, number of roots and circular distribution indices in each branching order. It might be important to remark here that the branching order is just one easy way to categorize roots (Doussan et al. 2003; Pagès 1999a), and is often not sufficient to describe the fairly complex structure of tree root systems (Jourdan and Rey 1997b). Root order is in that context not really of functional importance: a second order root originating from the stump can fork at 20 cm from its base into two third order roots which will have the same morphological type as the second order root, forming a reiteration (Doussan et al. 2003). In many species e.g. *P. sitchensis* (Henderson et al. 1983b), *Platanus hybrida* Brot. (Atger and Edelin 1995) and *Prunus* (Vercambre et al. 2003), reiteration deeply affects the architecture of the root system (Doussan et al. 2003). In the same way, a third order root can both be a large sinker or a small surface root. A classification in root types (see below) is generally more appropriate to describe the root system structure and functions.

Individual root characteristics

The architecture of a fully established branched system, whatever its complexity, can be summarized in terms of a very simple sequence of axes which represents its fundamental organisation (Barthélémy and Caraglio 2007). Root systems of woody species follow an inherent growth pattern called "architectural model" or "morphogenetic program" which is divided in successive architectural phases, resulting in a strong topological structuration as a function of time (Barthélémy and Caraglio 2007; Pagès 1999a). Different models can be represented by closely related species (Barthélémy and Caraglio 2007). This fundamental growth program determines a morphological differentiation of axes. Individual roots can be grouped in several distinct root types by a qualitative architectural analysis, according to their morphological, anatomical or functional distinctive features (Pagès 1999a; Atger and Edelin 1994 and 1995; Barthélémy and Caraglio 2007). Quantitative characteristics of each category can then be measured (Jourdan et al. 1995; Colas 1997; Pagès et al. 2004). Jourdan, Pagès and co-workers used this classification to implement developmental models. In this way, Collet et al. (2006) defined five classes of roots (taproot, large lateral with reiteration, large lateral without reiteration, small lateral and fine root) in young *Q. petraea* seedlings. Eight qualitative and nine quantitative parameters for each class were then defined. The standard deviation of 3 of these parameters was used to obtain stochastic simulations of root growth of the seedling. This stochastic approach permits to take into account the transition between root types, which was often rather continuous.

Root classes can also be defined as a function of their location and potential contribution to mechanical stability of the tree. In this way, Danjon and co-workers defined "root compartments" in 3D digitizing data by setting thresholds between categories using both topology and geometry and checking for consistency on graphs where the segments were coloured as a function of their category (Danjon et al. 2005; Khuder et al. 2006, 2007). Classes may also be obtained by multivariate or cluster analysis. Danjon et al. (2005) defined nine root compartments in mature *P. pinaster* trees, sub-dividing the first order root, the surface roots and the sinkers each in two compartments (e.g. the first order was divided in "stump" and "taproot" – see Fig. 6). The biomass allocation and spatial distribution in each compartment is of primary interest for assessing the effect of a directional stimulus on the root system development (Danjon et al. 2005). A classification should also differentiate roots specialized in a particular function (storage roots, aerial roots, air roots, proteoid or cluster roots – Gregory 2006).

Most of the properties listed in "Measurements" can be computed per root type or root compartment. The directional root deviation can be computed for each root according to Nicoll et al. (2006) as being the absolute change in root azimuth angle between a point at a small distance from the root origin on the mother root and the root tip.

Topology and fractal analysis

Fitter (1985, 2002) proposed the computation of topological indices, which have so far largely been used in annual plant root systems for which it is difficult to determine the geometry. From a topological point of view one could rank root systems between two extremes: on the one hand the herringbone system with a maximum external path length and altitude, most efficient in soil exploration, and on the other hand the dichotomous branching system, with a minimum external path length and altitude, more efficient to exploit a restricted soil volume, and most efficient at transporting materials to the shoot system (Fitter 1987 – see Fig. 7).

Fractal analysis, introduced by Mandelbrot (1975), has provided a powerful approach for an integrated quantification of topology and geometry of complex shapes and objects (Foroutan-Pour et al. 1999). Fractal objects and processes are said to display self-invariant properties including scale independence, self-similarity, complexity, and infinite length or detail. Although nature adds an element of randomness to its structures (Kenkel and Walker 1996), many natural structures and phenomena have fractal properties (Fitter and Stickland 1992a, b). The principles of fractal geometry seem appropriate for the description of root systems because

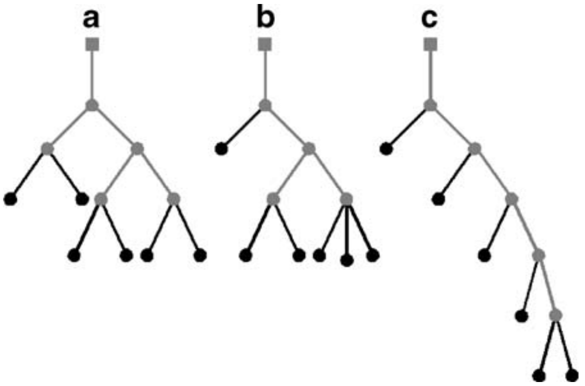

Fig. 7 Diagram of root systems topology with **a** dichotomous and **c** herringbone branching pattern. Diagram **b** represents the root system of Fig. 4. Each segment between dots is a link, exterior links are in *black*, the *grey square* is the collar of the plant. All root systems have the same (n=6) "number of exterior links", often referred to as the "magnitude" of the tree (after Oppelt et al. 2001)

the repetitive branching of roots leads to a certain degree of self-symmetry, which is a fundamental characteristic of fractal objects (Eshel 1998). Fractal theory is used in two ways, describing fractal geometry and fractal branching of root systems.

Fractal geometry offers a parameter FD known as the fractal dimension, which can be viewed as a relative measure of complexity, or as an index of the scale-dependency of a pattern (Berntson 1994; Tatsumi 1995; Berntson and Stoll 1997). Da Silva et al. (2006) proposed and tested a new way to estimate the 3D fractal dimension in plant architecture using the box counting method (Kenkel and Walker 1996). Walk et al. (2004) suggested to use also the two other parameters, 'fractal abundance' (FA) and "lacunarity" (F) which can be computed jointly with FD. They tested the relationship between these parameters and soil depletion and root competition using the SimRoot 3D geometric root model on *Phaseolus vulgaris* (Lynch et al. 1997) producing a total of 1,080 simulations. Fractal dimension was most closely correlated with competition between roots, while fractal abundance was more closely correlated with depletion volume. Combined with FD, Lacunarity correlates with measures of soil exploration.

Biological scaling, or the change of e.g. exchange surfaces or transport distances in a branching system, can be described by allometric equations, frequently scaling plants on the basis of stem or proximal root diameter following the principle of the "constant cross sectional area' or 'pipe-stem model' (Shinozaki et al. 1964). West et al. (1997) suggest for example to scale the proximal diameter "d" of a supplying vessel to the mass "m" of the organ to be fed by the following equation: $d=lme$, where "l" is a constant and e=3/8 the scaling exponent. The pipe model theory is a special case with scaling factor 1 of a more general fractal scaling pattern of various biological transport systems (West et al. 1997). This principle has mainly been used for modelling tree structure and dry matter allocation. However, the pipe model relationships seem to be species and site-dependent, and the hydraulic structure of stem, branches and roots to be different in many species (Van Noordwijk and Mulia 2002). To limit these problems, the application of fractal theory together with the classical models offers the opportunity to develop consistent and transparent models for describing trees in terms of branching properties and for deriving allometric equations (e.g. Collet et al. 2006). Therefore fractal branching analysis is a means to estimate global variables like root system volume, length or biomass from data of easily measurable parameters and simplifying hypotheses based on fractal theories. In other words, characteristics of the entire root system can be modelled without measuring the whole root system. Major applications were the development of e.g. the fractal allocation models by Van Noordwijk et al. (1994) and West et al. (1999). A computational method to quantify the similarity between different branching structures within a plant, represented as rooted tree graph, was proposed by Ferraro et al. (2004). This method is based on the more general procedures developed by Ferraro and Godin (2000) and has been included in AMAPmod to analyse MTG coded data.

However, as for Fitter's topology, current models may not be adapted to large and complex root systems which are composed of different root types (Oppelt et al. 2005; Danjon et al. 2005). In current fractal branching models only the parameter variation by branching order (Salas et al. 2004), or in two root classes (horizontal and vertical – WanFBA – van Noordwijk and Mulia 2002) is taken into account, not the root type. It may explain why some fractal branching parameters showed a considerable variability, hence affecting the precision of the root length and biomass estimates and the architecture generated by the model (van Noordwijk and Purnomosidhi 1995; Ozier-Lafontaine et al. 1999; Oppelt et al. 2001). Danjon et al. (2006a) have shown that the mean volume of root born by a given root section varies as a function of its root compartment. Additionally, stability and strength requirements are as relevant as water transport capacities in determining root diameters (Coutts 1983). Actually, fractal branching studies in woody root systems often only take into account the tapering of roots by branching and not the tapering between branching points (Soethe 2006). Even though, in tropical mountain species, between-branch tapering is often larger than within-branch tapering. Therefore, excluding the tapering between branching points from computation may overestimate root volume estimations in fractal branching models. Additionally, this tapering can increase with branch diameter (Soethe 2006; Soethe et al. 2007).

3D architecture data is well suited to compute fractal dimension and topological indices, and it can also be used to establish the parameters required for fractal allocation models. It should be noted that measurements of diameter generally have to be made at a certain distance (5 cm for large roots in mature trees in Richardson and zu Dohna 2003) above and below the point of bifurcation, to avoid the swelling that often accompanies branching. As a rule of thumb, the diameter may be measured at a distance approximately 1/2 of the diameter before branching. Topological indices and fractal branching parameters were computed from 3D digitizing data by Oppelt et al. (2001) for 20 tropical fruit tree root systems and by Danjon et al. (2004) for a *P. pinaster* chronosequence.

Root systems can be compared using algorithms computing distances between graphs, calculating the minimum cost of edit operations needed to transform one tree graph into another (Ferraro and Godin 2000, 2003; Segura et al. 2007).

All these techniques could be used on a portion of a root system, computing for example topological indices of second order surface roots and their branches, or topological indices of branched sections of the root system branching from the taproot near the soil surface, at intermediate depth or deep (Khuder 2007). Fractal dimension analysis can be performed using root volume location measurements without assessing the topology (Lontoc-Roy et al. 2005).

Root architecture dynamics

In small root systems, 3D growth dynamics may be assessed by non-invasive techniques (e.g. Kaestner et al. 2006), in aeroponic chambers (e.g. Eshel et al. 2001) or in transparent media (Jourdan 1995). In larger woody plant root systems, the short term root growth dynamics can only be assessed in 2D through rhizotrons, field rhizotrons or mini-rhizotrons (e.g. Jourdan and Rey 1997a; Vercambre et al. 2003). It should be noted that, in order to get spatial dynamics of root development in rhizotrons, the position of the root segments should be mapped in 2D, and the topology can in certain cases be measured as done by Khuder (2007) using the rhizodigit software (Jourdan 2005).

Root dynamics at a larger time scale can be assessed in two ways, which can be combined:

1. By retrospective architectural measurements, using traditional dendro-ecology techniques (e.g. Fayle 1968; Coutts and Lewis 1983; Richardson 2000; Plourde 2007) in root sections tagged in the 3D data file (Di Iorio et al. 2007). Root sample age, CSA growth curve and eccentricity dynamics can be measured from the annual growth rings if these are present.
2. By the means of a chronosequence, i.e. sampling trees at different ages. Intra-annual growth dynamics of *Q. petraea* seedlings were characterised partly through a chronosequence by Collet et al. (2006). Several characteristics of *P. pinaster* root systems were computed from a chronosequence (Danjon et al. 2004).

Models of 3D root architecture

As aforementioned, static or dynamic root system models can be derived from 3D digitising data and complementary root growth dynamics measurements (e.g. Henderson et al. 1983b; Colas 1997 and Jourdan and Rey 1997b, c using AMAPsim; Collet et al. (2006) using Root Typ). They are very useful for summarising all available knowledge, to obtain entire root systems from partially measured root systems, to get root system structures at any age, to test hypotheses (Henderson et al. 1983a), to assess relative importance of parameters and to provide a sample of mock-ups as input in any application requiring a detailed representation of the structure. The latter include e.g. structural-functional uptake and carbon allocation models (Pagès et al. 2000b), models of slope stability (Kokutse et al. 2006; Danjon et al. 2007a, b), or biomechanical models (Dupuy et al. 2003a, b, 2007).

All root developmental models include one or several stochastic processes because almost all growth parameters have certain variability in each root type (Pagès 1999a). Including an effect of soil properties on root growth requires a map of the soil properties (e.g. soil temperature or soil bulk density – Pagès 1999a). Relationship within the root system should also been taken into account, because roots compete for carbohydrates. When the growth of a root is stopped by a stone, some laterals generally increase their growth (Pagès 1999a). Developmental models generally have a large number of parameters, because each root type has its own set of characteristics. However, many parameters are independent and have a straight biological meaning (Pagès 1999a).

A dynamic 3D model of root system development was adapted to *Q. petraea* seedlings, in order to evaluate the effects of grass competition on seedling root system development. The model is based on root typology and the implementation of a series of developmental processes (axial and radial growth, branching, reiteration, decay and abscission). The initial diameter of a root is generally used to define its root type. A detailed description of parameters needed for 3D models of root system growth dynamics can be found in Jourdan and Rey (1997b) and Pagès et al. (2004).

The model of Jourdan and Rey (1997b) takes into account morphogenetic gradients by assigning a physiological age to each meristem at a given stage of its development (Barthélémy and Caraglio 2007). The physiological age depends upon the location of the meristem in the structure and upon the stage of development of the plant. Eight types of roots were defined.

Functional-structural growth models

Root systems and shoots can be linked using functional-structural plant models (FSPM's) through allocation of assimilates and nutrient and water uptake and transport. FSPM are either based on an architectural model and add functional details to it, or begin with a process-based physiological model and extend it with structural details (Perttunen and Sievanen 2005). Roots are often treated as an aggregate sink of carbon having neither spatial structure nor architecture (e.g. Lo et al. 2001). They can also be described very coarsely by several compartments (e.g. taproot, coarse root and fine roots in the SIMWAL model – Balandier et al. 2000).

Classical water and nutrient uptake models represent the root system by a vertical distribution of root length density only. They are fairly well adapted to cereal or grass crops which have homogeneous dense and continuously recolonizing root systems (Pagès et al. 2000a, b). However, even for crop plants, including details of root architecture permits a sharper insight into the soil exploration/utilization process (Doussan et al. 2003). This holds even more for trees, having much more heterogeneous root systems, often highly structured in several root types (Pagès et al. 2000a, b). Therefore, to correctly model their nutrient and water absorption as well as association with symbiotic organisms, a realistic modelling of the 3D development of the root system is needed (Balandier et al. 2000). However, modelling water and nutrients acquisition requires linking coarse and fine root architecture, taking into account physiological heterogeneity that exists along a single root axis in relation to ageing (Doussan et al. 2003), and modeling the hydraulic architecture and the root/mycorrhiza system (Sievanen et al. 2000). Models of interaction between root systems and their environment are reviewed by Doussan et al. (2003).

Using the AMAPpara software, de Reffye et al. (1995) and Blaise et al. (2000) simulated simultaneously root and shoot growth using very simple theoretical architectural models and simple functions for water transport and carbon assimilation and allocation. They could test hypotheses concerning the interactions between structure and function at the whole tree level and effect of pruning the shoots or coppicing.

The generic FSPM GRAAL model (Drouet and Pagès 2003, 2007) integrates at the whole plant level (i.e. shoot and root systems) organ production and carbon partitioning processes described at the organ level. Shoot and root organs are initiated as a function of temperature. Their potential growth in size (length, width, diameter) and dry mass depends on temperature and carbon availability. GRAAL was used on *Z. mays* assuming that roots do not exhibit radial growth and defining three root types (first, second and third order roots) with specific properties. GRAAL-CN (Drouet and Pagès 2007) focuses on carbon and nitrogen assimilation and partitioning.

In the ALMIS FSPM model simulating *Alnus* growth (Eschenbach 2005), roots are also composed of both root segments and root tips. Each root segment or root tip is described by its dimension, topology and geometry and is sensitive to its single neighbouring environment (state variable of the corresponding soil voxel). The formation of a new root or a new segment depends on the local availability of assimilates and nutrients. Carbon and nutrient fluxes are modelled by carbon gain and nutrient uptake, by transport and demand. Very different root architectures were obtained by changing the nutrient transport or nutrient uptake parameters. However, in this model, root architecture simulations are apparently not based on an architectural analysis nor include radial growth.

Using the SimRoot FSPM root model, Walk et al. (2006) showed that there is a high interaction between 3D root architecture and phosphorus acquisition in *Phaseolus vulgaris*. They ran precise spatial and temporal patterns of root deployment, using eight distinct root types, showing each specific phosphorus acquisition and respiration property. More generally, the SimRoot model was used intensively to test hypotheses concerning nutrient uptake, carbon allocation, fractal analysis and gravitropism (see Walk et al. 2004, 2006), which was not done with woody plant root models so far.

One challenge in 3D tree root system growth models is to include the effect of mechanical stimulation from the shoot into primary and secondary root growth and carbon allocation. It should be noted that no verbal model description in the literature is complete (Kurth 2000).

Connection between fine and coarse roots

The spatial distribution of fine roots is of huge importance for soil resource capture. As they are branching from the coarse roots, the relationship between the spatial distributions of both types of roots can be assessed. This was done on an individual tree basis on isolated trees by Oppelt et al. (2005), by a combination of full coarse root architecture 3D digitizing and the sampling of 75 soil cores per tree on a grid for fine root measurements. The spatial distribution relative to the depth and the distance to the tree can also be obtained at the stand level by comparing the fine root content in cores and the spatial distribution of the coarse roots obtained by 3D digitizing (see the 2D plot in Danjon et al. 1999a, b).

As aforementioned, the topological and geometric relationships between coarse and fine roots can also be assessed on a subsample of coarse roots by recording the position, number and/or mean length in the digitizing file (Khuder 2007). Sap-flow measurements provide information concerning functional relationships between coarse and fine roots (Coners and Leuschner 2002). In small, carefully excavated root systems, the topological position of mycorrhizae or nodules may also be recorded (Khuder 2007).

Examples of applications

The above mentioned techniques for 3D root architecture analysis were combined in the following research fields.

Genetic determinism of architectural development and plasticity in species, populations or varieties

Genetic determinism and structural plasticity of root system structure has been studied before using topological and architectural analysis or by comparing distributions. Oppelt et al. (2000, 2001, 2005) compared root architecture for four tropical fruit tree species grown under arid conditions using 3D digitising data. Root length and volume, mean inter-lateral length, topological, fractal dimension and fractal branching parameters were computed for each root system. Rooting patterns were analysed from root length distribution profiles and qualitatively from a graphical reconstruction of root systems. The two species more specifically adapted to extreme drought showed a herringbone pattern and large apical unbranched lengths, indicating an explorative strategy in root development. Herringbone root pattern had a lower fractal dimension i.e. spatial filling potential. A preservation of the CSA in the branching nodes was observed.

Interaction between root development and soil profile type was studied by Danjon et al. (2005). *P. pinaster* trees adapted their root architecture to the soil depth wich was determined either by a hard pan or a deeper water table. On more shallow soil, the ZRT and sinkers were reinforced at the expense of the taproot. Root systems on hard pan developed “hard pan shields” and dense root mats of fine roots just over the pan, which may certainly improve their stability and nutrient and water uptake.

The distribution by root angle toward soil surface or by root compartment can be used to characterize the type of root system (tap-, sinker- or heart-root system – Köstler et al. 1968). Danjon et al. (1999a, 2005) and Khuder et al. (2007) observed that *P. pinaster* grown in spodosols first develop a strong taproot and long surface roots, and progressively grow towards a structure organized in a kind of rigid 'cage' composed of a taproot, the zone of rapid taper of horizontal surface roots an numerous sinkers and deep roots, guyed by long surface roots. The proportion of oblique roots in the root volume was always small indicating that *P. pinaster* is a tap or sinker root system.

Tree stability and anchorage

Anchorage is mainly function of root/shoot ratio, vertical root distribution, radial symmetry, as well as spread and shape of lateral roots (Stokes 2002). Relationships between root architecture and tree stability were established by comparing wind thrown vs. control trees (Mason 1985; Harrington and De Bell 1996; Danjon et al. 2005). This can also be done by correlating architectural parameters to stem straightness (Danjon et al. 1999b) or pulling tests parameters. In mature *P. pinaster*, wind thrown trees differed from undamaged trees by their resource allocation to several root compartments defined by a quantitative architectural analysis (Danjon et al. 2005). They also differed by their root circular distribution. Influence of artificial wind on 3D root system architecture was examined by Berthier (2001) and Tamasi et al. (2005) on tree seedlings. Wind loading resulted in increased growth of lateral roots at the expense of the tap root and in more numerous and longer windward roots than leeward roots. Khuder (Khuder 2007; Khuder et al. 2007) showed from an in-depth analysis of root architecture that a non-directional mechanical perturbation applied to the shoots of *Robinia pseudoacacia* seedlings influences largely their root architecture. The stump and taproot thicken and get shorter, and are fully guyed by straight fine roots.

Finite elements models were used on 3D *P. pinaster* root architecture data to compute force vs. displacement curves to get the stiffness and the strength of the structure (Fourcaud et al. 2003, 2004). However, root–soil interaction in large entire root systems turned out to be too complex; hence Fourcaud and co-workers further examined root–soil interaction at a small scale on simple root models. They first studied the influence of the topology and geometry of small virtual branched sections of the root system on pull-out resistance as a function of soil type by 2D mechanical modelling (Dupuy et al. 2005a). In a second paper, Dupuy et al. (2005b) examined the influence of entire root system morphology and soil type on the mechanical behaviour of tree anchorage by 3D numerical modelling on schematic and simplified MTG coded root systems. Lastly, Fourcaud et al. (2007) determined the role of individual roots by 2D modelling the uprooting and the stress distribution in the soil and the roots in saturated soft clay and loamy sand-like soils. Very simple root models were used; individual roots were removed to determine their contribution to anchorage. In the three papers, a strong interaction between root arborescence or root system morphology and soil type was observed. In saturated soft clays for example, only the most peripheral root elements were involved in the formation of the circular root soil plate and the rotation axis was located close to the center of the plate (Fourcaud et al. 2007). These simulations could explain some of the features observed in real root system 3D architecture by Danjon et al. (2005) and Khuder et al. (2007). Dupuy et al. (2007) showed how experimental winching test data can be compared to the uprooting resistance values obtained by finite element modelling with a generic 3D uprooting mechanic model. The model was tested using two digitized 24 cm DBH *Populus* root systems and still requires a large CPU time.

Slope stability and soil erosion control

The stability of a grassed slope is generally estimated in 2D assuming that the additional cohesion provided by roots is homogeneous in soil layers. This approach is not suitable for forested slopes because of the heterogeneous distribution of woody roots (Kokutse et al. 2006). Although the architecture of a root system greatly influences its soil fixing efficiency, limited architectural work was done in a context of slope stabilization and erosion control, and hence a lot of uncertainties concerning which characteristics are important do remain (Reubens et al. 2007a). Therefore, contribution of tree structural roots to soil reinforcement and slope stability may be better understood by taking into account 3D architecture (Achim et al. 2003; Van Beek et al. 2005; Reubens et al. 2007a, b).

In a technical paper, Danjon et al. (2007a, b) showed how 3D measurements of root architecture could be used to compute more accurately the level of safety of a forested slope, using the spatial distribution of a large number of root architectural parameters. In particular, they produced parallel and perpendicular to the slope 2D maps of additional cohesion provided by roots, and computed factors of safety. In a preliminary study, Kokutse et al. (2006) used a numerical model to test the slope reinforcement provided by three geometrical approximations corresponding to simple tree root morphologies (heart-, tap- and plate-like root system). The taproot system provided the best slope reinforcement because it was the deepest.

The adaptive growth response of trees to wind and slope was studied by Nicoll et al. (2006) by digitising 24 *P. sitchensis* root systems in both flat and 30° inclined stands. The prevailing wind was across slope. Trees on the flat area had more root mass in the leeward sector whereas trees on the slope had more root mass in the windward sector than the other sectors. Khuder (Khuder 2007; Khuder et al. 2007) showed that in *R. pseudoacacia* seedlings grown in a greenhouse, trees on slope develop a vertical taproot, a larger ZRT, a more superficial root system and more roots perpendicular to the slope. Interaction between slope and the above mentioned non directional mechanical perturbation was rarely significant (Khuder et al. 2007). Trees with slope and mechanical perturbation showed more surface root length and volume in the upslope sector at the expense of the downward sector. The reverse was observed in deeper roots.

Dynamics of carbon stocks and resource allocation to coarse roots

Carbon stocks in coarse roots are generally assessed at the stand level by extracting and weighting the root system and all coarse roots located in an elementary area of the stand around each tree of a sample. The boundaries between these subplots are mid-way between the sample tree and the adjoining trees. Representative samples were then taken for dry weight and carbon content estimation (e.g. Ritson and Sochacki 2003). However, it is often not easy to get really representative samples in this way. Le Goff and Ottorini (2001) additionally sorted the root segments by diameter and got root length, biomass and carbon content estimations by root diameter class.

Carbon stocks in coarse roots were precisely estimated at the individual tree level by Bert and Danjon (2006) in 50-years old (clear cut age) *P. pinaster* trees, using three-dimensional digitizing. Digitizing was therefore combined with sampling of root segments localised in the structure for wood and bark carbon content and density measurements, as aforementioned. In the lateral root wood, the C concentration was related to the segment diameter through a negative exponential function. Conversely, no trend was found neither for the lateral root bark nor for the taproot wood and bark C concentrations. The weighted mean carbon concentration of taproot, lateral root and stem wood reached 51.7, 51.3 and 53.3% respectively. The expansion factor converting the stem biomass into total biomass was also computed. The amount of root biomass lost during uprooting was not estimated, it could have been computed without extra measurement according to Danjon et al. (2006a, b, 2007b).

Root decomposition varies as a function of soil depth and aeration, decomposition of deep roots generally being slower (Kramer et al. 2004). If a relation between basic density loss and root segment diameter or depth is available, this kind of data could also be use in combination with 3D architecture data to estimate the rate of decay of woody roots at the single tree or at the stand level.

Water and nutrient uptake, hydraulic architecture

The potential resource uptake by a root system is partly determined by its 3D structural root architecture through the support provided for fine roots. Considering the water and nutrition absorption capacity only through a mapping of root length density is misleading because it takes into account neither the between-root connections and the between- and along-root variations in uptake capacities (Pagès 1999a).

Clausnitzer and Hopmans (1994) combined a detailed 3D root growth model for crop species and a 3D transient water flow model. In this model, the root apices growth is a function of current local soil conditions. It includes growth of the shoots and dynamic assimilate allocation to roots and shoots. The spatial distribution of structural root systems was assessed by Oppelt et al. (2005) from 3D coarse root architecture data. They computed an "exploration index" which is the proportion of 1 dm^3 voxels occupied by any root and an "exploitation index" which is the proportion of voxels occupied by an amount of roots larger than a given threshold. The "exploitation index" was divided by the total root volume to yield a "generalized efficiency of exploitation" (GEE). The main differences between the four studied species were found for the exploration index. Oppelt et al. (2005) found also a good correlation between coarse root and fine root length and volume at tree level, but only when they considered the fine root cores sampled in the voxels occupied by coarse roots.

Monitoring of sap-flow in woody roots (e.g. Green and Clothier 1995) can be analysed in relation to the 3D structural root architecture, comparing the seasonal changes in sap-flow with the structure and spatial distribution of roots upstream of the gauges. Coners and Leuschner (2002) studied in situ water absorption by fine roots in different parts of the root system using miniature sap-flow gauges. Once the measurements were finished they extracted all the upstream absorbing fine roots with root tips for root surface determination, examining relationships between both fine and coarse roots. Topological indices could be correlated with the volume of soil explored by coarse roots (Fitter 2002).

Oliveira et al. (2005) monitored the sapflow in root systems of amazonian trees exhibiting a very simple root architecture: a single several meters long vertical taproot and many surface roots. They showed that the coarse root system is the seat of nocturnal transfer of water by root, i.e. both (upward) hydraulic lift and (downward) hydraulic redistribution, influencing largely the ecosystem productivity.

The influence of machinery load on root system water transport was studied by Nadezhdina et al. (2006) from the monitoring of sap flow gauges. Only the roots located above 10 cm depth were influenced by loading.

Chopard (2004) proposed a model simulating water transfer in the soil and the root system, based on the architecture of main roots coded as MTG structures, taking into account the within-plant transfer. Fine roots were averaged in absorptive volumes related to the main roots. This model was used to simulate the interaction between root structure and water availability in the soil, mainly for individual trees and strips of underlying crops.

Doussan et al. (1999) combined knowledge about water uptake and distribution of hydraulic conductance in root systems and the above-mentioned 3D *Prunus* root system developmental model (Vercambre et al. 2003) to model the water absorption and conduction through the root system. The root segments each had a specific axial conductance, radial hydraulic conductance governed water transport from the soil into the root. Two logarithmic relationships between axial conductance and root diameter were used, one for fine roots, the other for coarse roots. The main result is that in 1-year-old trees in non-limiting and uniform soil conditions, (1) roots located in the proximal part of the root system contribute largely to the total uptake (2) absorption capacity is greatly overestimated with respect to their transfer capacity.

Fungal infection dynamics

Coarse root architecture and spatial distribution play a predominant role in root rot contamination processes, and propagation inside a contaminated root system (Brown and Kulasiri 1994). Brown et al. (1997) showed how the 3D spread of *Armillaria* fungal infection in a *Pinus radiata* stand can be simulated using a 3D root system model. They adapted the 3D *P. sitchensis* root architecture model of Henderson et al. (1983b), root segments were associated to a fungal load (e.g. mm of hyphae per mm^2 of root surface) and a physiological phase. Infection was simulated by "sliding" the fungal nodes up and down the roots. The distance between healthy and the nearest infected segment and a probability to be infected completed the model. Root systems from thinned or dead trees and biological control techniques were included in the modelling, but not root grafts.

Evaluation of nursery, planting and management practices

Influence of establishment techniques on root architecture, and later growth and stability, can be studied by examining e.g. the distribution in several types of roots, the root deformations or the spatial distribution. In a study performed by Danjon et al. (1999a), a high variability in deep rooting was found in paper pot planted *P. pinaster* saplings, mean root volume percentage located below 30 cm depth was 6%, and two thirds of the trees could not regenerate a strong taproot. The correlation between stem straightness and proportion of deep root volume reached 0.43 ($p < .01$).

When compared to naturally regenerated trees, 15-years-old planted *P. banksiana* showed a poorer development of tap and sinker roots and a preferential development of the surface roots along the furrows (+50% – Plourde 2007). Khuder et al. (2007) observed from a detailed analysis of their architecture that the root systems of 7-years-old *P. pinaster* cuttings differed from normal seedlings mainly because the former only had half the number of second order roots branching from the stump and half the root length when compared to the seedlings. It indicates that the architectural pattern of maritime pine is stable and that the proximal part of the taproot grown from the seed has a very high branching rate. In the same way, Danjon et al. (2007c) compared the root systems of intensively fertilised vs control trees of 12-years old *P. pinaster*. Root systems of both treatments were similar, they differed only marginally in circular distribution of root characteristics relative to the dominant wind.

Collet et al. (2006) showed that grass competition considerably reduces *Q. petraea* seedling size. However, nor root branching density neither the scaling coefficient between cross sectional area before and after a branching point, which was close to 1 as predicted by the pipe model theory, differed. Seedlings with grass competition showed also a larger proportion of short roots and a smaller number of roots.

Choosing a set of procedures

In order to finally assess full 3D root system architecture, several options were presented for each of the different process steps, i.e. getting to the roots, sampling, measuring, coding and analysing. It is not always easy to compare the options because only very few comparisons have been actually published. One can imagine that different combinations of methods from each of these categories can be made in order to establish an optimal working procedure adapted to specific research needs, constraints and circumstances. However, certain steps are structurally linked. Using the AMAPmod software e.g. requires an MTG coding. A filter to get MTG files from DTD coded data is available under the GROGRA family of programs (Kurth 1994), but data captured with the FloraDig software cannot actually be converted in MTG files (Hanan, personal communication). Other options are linked for practical reasons, e.g. digitizer driving programs able to produce an MTG file do only exist for a certain model of digitiser.

Moreover, except for Oppelt et al. (2000, 2001), all research papers published in this field used the MTG coding, the Polhemus Fastrack digitiser and most of them AMAPmod for analysis. Both a driver for an efficient 3D digitising device (Donès et al. 2006) and a program to assist manual measurement exist, and many functions for analysis are freely available for open software (AMAP and R, Danjon et al. 2005; Khuder et al. 2007). It should be noted that several years were spent to establish all the presented procedures including measurement methods, software for measuring and analysing, framework and code for analysing. Danjon and co-workers spent actually more time to establish new analysis procedures than to measure root systems. We therefore strongly suggest using these existing versatile and efficient methods more than creating new measurement and analysis chains which will require writing new driving software and new procedures. It will save a lot of time and will allow comparisons to be made between different studies within the small community of 3D root architecture researchers.

Existing methods for full 3D data capture and automatic feature extraction still show many problems, manual or semi-automatic measurement methods are often laborious to use but have the important advantage of direct human interpretation (van der Heijden et al. 2007). Single root segments can be accurately detected by GPR in ideal conditions (damp and uniform pure sand, low density of segments, segments parallel to the soil surface, high infradensity of root wood – Barton and Montagu 2004). However, establishing efficient GPR measurement procedures for root architecture will certainly require a large amount of work. In all cases they may certainly yield precise data in a fairly low range of natural circumstances. Once software reconstructing the topology from non-destructive or automatic methods is available, it should also code the topology in one of the existing codes, enabling the analysis to be made with the existing tools.

Assessment of 3D root architecture is a must in certain applications, such as tree stability, while it is only optional in other applications, such as carbon stocks estimations. When it is optional, classical measurement methods are generally used, although 3D digitizing of root architecture may provide much more information for comparatively a small amount of additional work. In a review on representations of plant architecture, Godin (2000) defined three main types of plant architecture representations, namely the global, modular and multiscale representations, which correspond to an increased degree of robustness. Non robust models work solely for the goal they are initially designed. In the same way, measurement procedures can be more or less "robust". For example, the biomass and carbon content assessment in 148 *P. pinaster* trees made by Ritson and Sochacki (2003) could only be used for estimation of carbon stocks in stem, crowns, and roots as a function of tree DBH and stem height. In the same way, the measurements made by Richardson and zu Dohna (2003) in 14 *Pseudotsuga menziesii* root systems could only be used to estimate their fractal branching properties. On the other hand, the full 3D digitizing of coarse root architecture in 24 mature *P. pinaster* trees reported by Danjon et al. (2005) have already been used for (1) a description of root architecture of *P. pinaster* grown in sandy spodosols, (2) an in depth assessment of the adaptation of the root systems to dominant wind and to the soil profile, (3) the determination of the key features for stability (Danjon et al. 2005), (4) for topology and fractal branching assessment (Danjon et al. 2004), and (5) a study on carbon concentration variations and carbon stocks in coarse roots (Bert and Danjon 2006). This "robust" measurement method used by Danjon et al. provided really a comprehensive overview of quite all aspects of coarse root architecture. Moreover, limits as well as hypotheses to be tested can be changed once the measurements are done: e.g. root diameter classes, circular sectors and compartments definitions were only defined during the analysis and can be very easily changed.

Conclusions

Root system architecture is an important characteristic in tree structure. Efficient measurement and analysis techniques are now available for 3D root architecture studies, including even a measurement procedure requiring very simple equipment (Dupuy et al. 2003a). They are now used by several research groups, mainly in Europe. Some of these groups are working on e.g. riverbank or slope stabilization as well as erosion control, including eco-engineering applications for prevention. However, publications in this field are still sparse and up to now, the number of technical papers certainly exceeds the number of research papers. One of the future needs of tree-root research is to improve and standardize methods (Hendricks et al. 2006; Brunner and Godbold 2007; Noguchi et al. 2007). We hope that this review will help developing this quite new research field and encourage establishment of standard measurement and analysis procedures.

From the examples of applications we gave at the end of this review, one can see that 3D root system architecture studies largely improved our understanding of tree stability and of the way several tree species adapt their root architecture to mechanical stimulations. However, in other fields like fungal infection dynamics or carbon stocks and cycle, very few papers were published.

In the last years, progress in 3D root architecture research in woody plants was made in three quite separate approaches: (1) Pagès, Collet, Vercambre and co-workers on developmental modelling of coarse root dynamics, root types and fine roots, (2) Ozier-Lafontaine, Nygren and co-workers on fractal branching analysis, and (3) Danjon, Oppelt and co-workers, focussing on 3D full digitizing integrating spatial heterogeneity and root compartments (in particular directional effect like dominant wind or slope) or soil resource exploitation. Challenging studies have applied these techniques on fairly large samples, exploring new fields such as the effect of root structure on erosion control in the presence of cattle browsing (Reubens et al. 2007b). In the coming years, root research may benefit from these three approaches, as it was partly done by Collet et al. (2006).

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