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A Method for Describing Plant Architecture which Integrates Topology and Geometry

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This paper presents a method for describing plant architecture using topological and geometric information. This method is based on the use of a multiscale model of plant topology—called multiscale tree graphs—which is extended to include geometry. The relationships between both multiscale topology and geometry are explicitly identified and topology and geometry are shown to contain redundant information. This redundancy is expressed as sets of constraints between the geometrical parameters of plant components that belong either to one scale or to different scales. These within- and between-scale constraints are used to reduce the number of measurements when digitizing plant architecture and to implement the geometrical parameters that are not specified. Different solutions for simplifying plant architectural descriptions are proposed. The method, implemented in software dedicated to plant architecture analysis (AMAPmod), does not depend on the plant species or on the geometric model used to describe the plant components. The multiscale approach allows plant architecture to be represented at different levels of accuracy. This method is illustrated on two plants, a 3-year-old apple tree and a 20-year-old walnut tree, which correspond to applications of different sizes and with different goals for the representation.

Key words: Plant architecture, digitizing, topology, geometry, multiscale tree graph, measurement, simplification schemes, 3D-reconstruction, AMAPmod.

INTRODUCTION

Plants are complex structures which can be described in many different ways depending on the requirements of the application, e.g. for bio-mechanics, hydraulic architecture or micrometeorology, or for simulation of plant growth. There is a general agreement that plants can be regarded as a collection of components having specific morphological characteristics, organized at several scales (White, 1979; Barthélémy, 1991). Plant architecture is a term applied to the organization of plant components in space which can change with time. At a given time, plant architecture can be defined by topological and geometric information. Topology deals with the physical connections between plant components, while geometry includes the shape, size, orientation and spatial location of the components.

Measuring plant architecture allows one to make a bridge between real and modelling worlds. Indeed, plant architecture is necessary input data for statistical and functional models of plants: geometry is mainly involved in plant-environment exchanges and resource capture, (e.g. light interception; Ross, 1981) while topology can be used to build up biological sequences embedded in axes (Costes and Guédon, 1997) or can be considered as the seat for internal fluxes for energy, mass and information (e.g. water transport; Dauzat and Rapidel, 1998; Sperry *et al.*, 1998). Plant architecture can also be the output of plant structure-function models dealing with the dynamics of growth and development (e.g. Takenaka, 1994; Mech and Prusinkiewicz, 1996; deReffye *et al.*, 1997; LeDizès *et al.*, 1997; Fournier and Andrieu, 1998).

Several methods have been proposed to measure either plant topology or geometry. For topological analysis, Godin and Caraglio (1998) developed a model of plant topological structure, called a multiscale tree graph (MTG). MTGs are suitable for representing plant topology with respect to scale and time. The multiscale nature of MTGs lies in the decomposition of the plant into larger or smaller components. At a given scale, topology expresses succession and branching relationships between plant components.

For geometric analysis, Sinoquet *et al.* (1998) proposed a method based on digital, three-dimensional measurements. This method was applied to analysis of leaves to derive attributes of the light microclimate from plant geometry. A geometric model, i.e. a shape, was associated with each component: for leaves, the geometric model was a set of triangles obeying leaf allometry. The geometric model was then scaled, rotated and translated according to the size, orientation and spatial location of leaves. Orientation angles and spatial co-ordinates were measured in three-dimensions with a digitizing device (Polhemus, 1993).

Recent works have used both topological and geometric information to describe plant architecture. Hanan and

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Room (1997) proposed a scheme based on a one-scale description of plant topology coupled with sonic digitizing, Godin and Costes (1997) proposed, as a first approach, the inclusion of 3D co-ordinates of entities in MTGs. Sinoquet *et al.* (1997*a*) took a symmetric approach and described a strategy for augmenting geometric information obtained from 3D digitizing with topological information. However, none of these works took advantage of the redundancy expressed by the combination of topological and geometric information, except in obvious ways (e.g. the bottom point of a successor is the same as the top point of its predecessor). Indeed integrating plant topology and geometry has mostly consisted of attributing spatial co-ordinates on plant topology descriptions. The first objective of this paper is to develop a comprehensive framework to represent plant architecture combining the MTG approach and 3D digitizing, to allow explicit identification of the relationships between both multiscale topology and geometry. Such a framework has been implemented in AMAPmod, i.e. software devoted to plant architecture analysis (Godin, Costes and Caraglio, 1997*a*). The second objective is to derive strategies for measurement of plant architecture using this framework. Special attention is paid to the possibility of using multiscale information to define simplified measurement protocols. Application of this framework to the measurement of a young apple tree and a 20-year-old walnut tree illustrates the method and emphasizes practical aspects of measuring plant architecture.

MATERIALS AND METHODS

A framework to integrate topology and geometry

Topological model. The topological model is a multiscale tree graph (Godin and Caraglio, 1998). This can be considered as a set of tree graphs which represent a plant at different levels of detail. By definition, scale 0 corresponds to the coarsest level of description. At any scale, s, the MTG appears as a simple tree graph which represents the set of plant components at this scale and their topological relationships. Only two kinds of relationships are used to describe the botanical nature of the links between plant components: succession and branching, denoted by operators $<$ and $+$, respectively. The succession relationship $x < y$ means that component y was created by the terminal bud of component x. Similarly the branching relationship $x + y$ means that y developed from an axillary bud of x. The integration of every tree graph at scale s ($s = 0, 1, \ldots, S$) in the MTG is achieved by introducing a decomposition relationship, denoted by the operator $/$. If a is a component from scale s-1, the relationship a/y means that component y defined at scale s is a component of a. Component a is called the complex of y. A detailed, yet simple, example of an MTG is depicted in Godin *et al.* (1997*a*).

Geometric model of a component. The geometry of a plant component refers to both its shape and its position in space. In an MTG, it can be defined in two different ways: (1) by a basic geometric model, i.e. a parametric model representing its external surface. Cone frustums, for example, are used as a basic geometric model to represent the shape of various types of plant components (e.g. deReffye *et al*., 1988; Prusinkiewicz and Lindenmayer, 1990; Weber and Penn, 1995) and are defined by a parametric model with multivariate parameter $\lambda = (b, t, h)$, where b is the bottom diameter, t the top diameter and h the height (Fig. 1A). Due to the widespread use of cone, this basic geometric model is used in the following sections for illustration. Each plant component has a specific position in space with respect to a global co-ordinate system. The position of a basic geometric model refers to its location and orientation with respect to this global co-ordinate system. For a cone frustum, the position is defined by the co-ordinates of the centres of

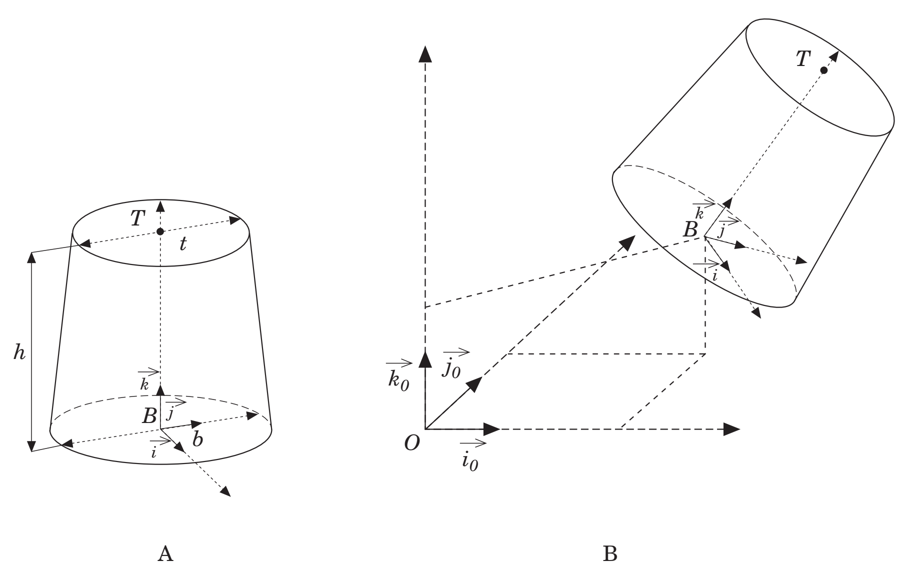

FIG. 1. A, A cone frustum is a basic geometric model with parameter $\lambda = (b, t, h)$, where b and t are the base and top diameters, respectively, and h is the height. B and T are, respectively, the base and top points on the cone symmetry axis and $(\vec{i}, \vec{j}, \vec{k})$ is the local reference system. B, Location and orientation of the surface with respect to a global reference system $(\vec{i_0}, \vec{j_0}, \vec{k_0})$ is part of the geometric model.

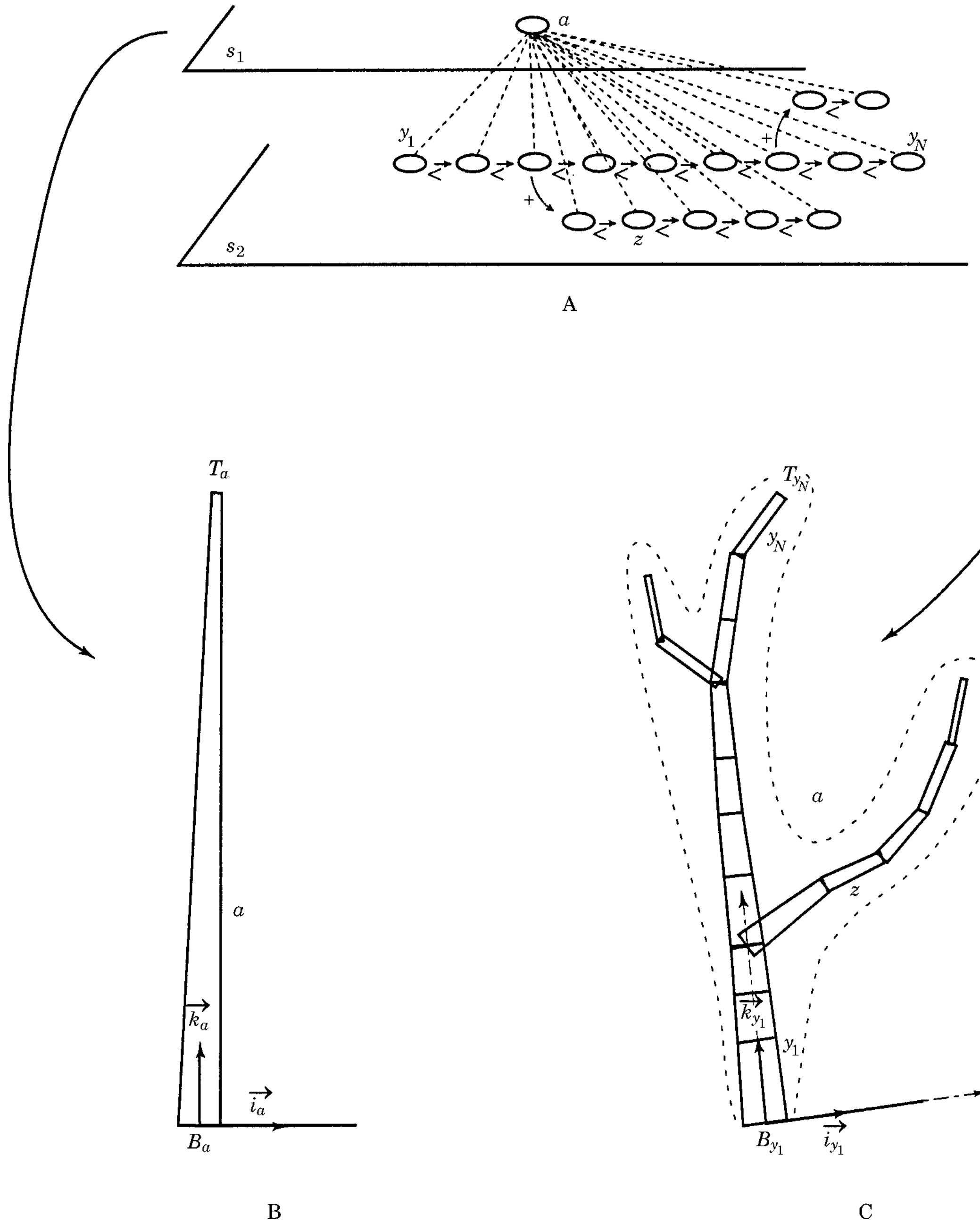

FIG. 2. Between scale constraints associated with multiscale representation of plant components. A, Multiscale graph representing a branching system at two scales, s_1 and s_2. Ovals represent plant components and arrows represent structural links between components. The dashed lines express the 'part of' relationship between component at different scales. B, Basic geometric model associated with the macroscopic component a representing the whole branching system at scale s_1. C, Compound geometric model representing the same branching system at finer scale s_2.

bottom and top sections (B and T), or by B and the axial direction $\vec{k}$ (Fig. 1 B). A geometric model for which some of its parameters or its position are unknown is called underspecified. (2) By a compound geometric model. The definition of a component's geometry can make use of the nested nature of the components of an MTG at different scales. Consider a plant component a at scale s_1 which is decomposed into components y_i $(i = 1, \ldots, N)$ at scale s_2 $(s_2 > s_1)$. If the geometric models of components y_i are known, the shape of component a can be defined as the combination of its component geometric models. The geometry of the macroscopic component a is thus represented by a compound geometric model. The geometric models associated with components y_i $(i = 1, \ldots, N)$ may themselves be either basic or compound.

Constraints induced by topology. Constraints induced by the topological arrangement of components on their geometric models at a given scale define within-scale constraints. They express redundancy between the information associated with the description of topology and geometry. In the case of cone frustums, if a component x precedes a component y $(x < y)$, this implies that the bottom of y, B_y, coincides with the top of x, T_x, and the continuity of diameters can be assumed between predecessor and successor:

$$B_y = T_x \text{ and } b_y = t_x \tag{1}$$

Similarly, if a component y is borne by a component x ($x+y$), the reference point of y is necessarily located somewhere within the volume delimited by the geometric model of x:

$$B_y \in [B_x, T_x] \text{ and } t_x > b_y \tag{2}$$

Equations (1) and (2), respectively, illustrate a case of equality between geometric parameters and a case where geometric parameters must be within a certain range of values.

Constraints induced by decomposition. Between-scale constraints express a redundancy in the information contained in the geometric descriptions of components at different scales. As previously mentioned, the geometry of a plant component a at scale s_1 which is decomposed into components $y_i (i = 1, \ldots, N)$ at scale $s_2 (s_2 > s_1)$ can be represented either by a basic or compound geometric model. Since the two representations are both geometric interpretations of the same component a, they must respect some consistency conditions, specified by between-scale constraints which are relationships that link the parameters of both geometric representations. In case of the branching system depicted in Fig. 2:

$$\begin{aligned} B_a &= B_{y_1} \\ h_a \vec{k}_a &= \overrightarrow{B_{y_1} T_{y_N}} \\ b_a &= b_{y_1} \\ t_a &= t_{y_N} \end{aligned} \tag{3}$$

Approximation of plant component geometry. The redundancy expressed by the within- and between-scale constraints can be used in two ways. If all the geometric parameters are known, the equations can be used to check the consistency of the corresponding geometric models. Alternatively, the equations can be used to compute the unknown parameters from those of other components.

Using within-scale constraints. For components at a given scale, the within-scale constraints can be used to compute part of the geometric parameters from those of the neighbouring components. Equation (1) for instance, can be used to compute the bottom points (B) and base diameters (b) of all the components of an axis (except for the first), provided the co-ordinates of the tips (T) and the top diameters (t) are known. This property is frequently used to simplify axis digitizing schemes (see below).

If the first component of an axis is connected to a bearing component, it is also possible to use within-scale constraints to infer its bottom point and diameter. However, the within-scale constraints expressed by eqn (2) need to be modified to compute the exact value of the bottom point since they specify membership to a domain of values. A good rule of thumb is to take the top point of the bearing component (u in the following) as a conventional insertion point and to make the approximation that the component borne on it is a cylinder. In this case, the insertion point and the diameter of component z can be computed using the following modified constraints:

$$\begin{aligned} B_z &= T_u \\ b_z &= t_z \end{aligned} \tag{4}$$

The maximum error made with such a systematic choice is bounded by the length of the bearing component. If the bearing component is an internode, its top corresponds to the insertion node of the axillary axis and the rule gives the exact insertion of the axillary axis. If u is at the same scale as z, eqn (4) defines new within-scale constraints. However, the bearing component u need not be at the same scale as z. The co-ordinates of the insertion point of each axis can be approximated for instance as the top co-ordinates of the finest component identified on the bearing axis (for example, z could be a growth unit and u an internode).

Using between-scale constraints. For components at different scales, two types of inference can be carried out depending on whether the geometry is scaled up or down. Scaling up the geometry applies to plant components a (at scale s_1) whose basic geometric model is under-specified and whose components y_i ($i = 1, \ldots, N$) (at scale $s_2, s_2 > s_1$) are associated with fully specified geometric models. In this case, between scale constraints apply and allow us to compute all of the parameters of a's basic geometric model. Conversely, scaling down the geometry applies to plant components y_i (at scale s_2) whose complex a (at scale $s_1, s_2 > s_1$) is associated with an entirely specified geometric model. The geometric model of a is not, in general, sufficient to determine the geometry of its components. If under-specified basic geometric models are defined for each component y_i, it is possible to determine some of the missing geometric parameters at the highest scale (s_2) from those at the lowest scale (s_1), using between-scale and within-scale constraints. However, most of the parameters at the greater scale s_2 are left unspecified. Additional within or between-scale constraints have to be defined to infer the missing geometric data.

Scaling down axis component geometry. Let us consider an axis a whose geometry is represented by a basic geometric model (as in Fig. 2B), but the geometry of its components $y_1, y_2, \ldots, y_N$ is not specified. To approximate the geometry of the n components, the simplest assumption is that the component geometric models are pieces of the coarse geometric model. The geometry of each y_i is thus a cone frustum with parameters ($B_{y_i}, \overrightarrow{k_{y_i}}, b_{y_i}, t_{y_i}, h_{y_i}$) which can be simply computed from the parameters of the coarse model:

$$\begin{aligned} \overrightarrow{k_{y_i}} &= \overrightarrow{k_a} \\ \text{For each } i \text{ in } [1, N],\ h_{y_i} &= \frac{\|\overrightarrow{B_a T_a}\|}{N} \\ t_{y_i} - b_{y_i} &= \frac{b_a - t_a}{N} \end{aligned} \tag{5}$$

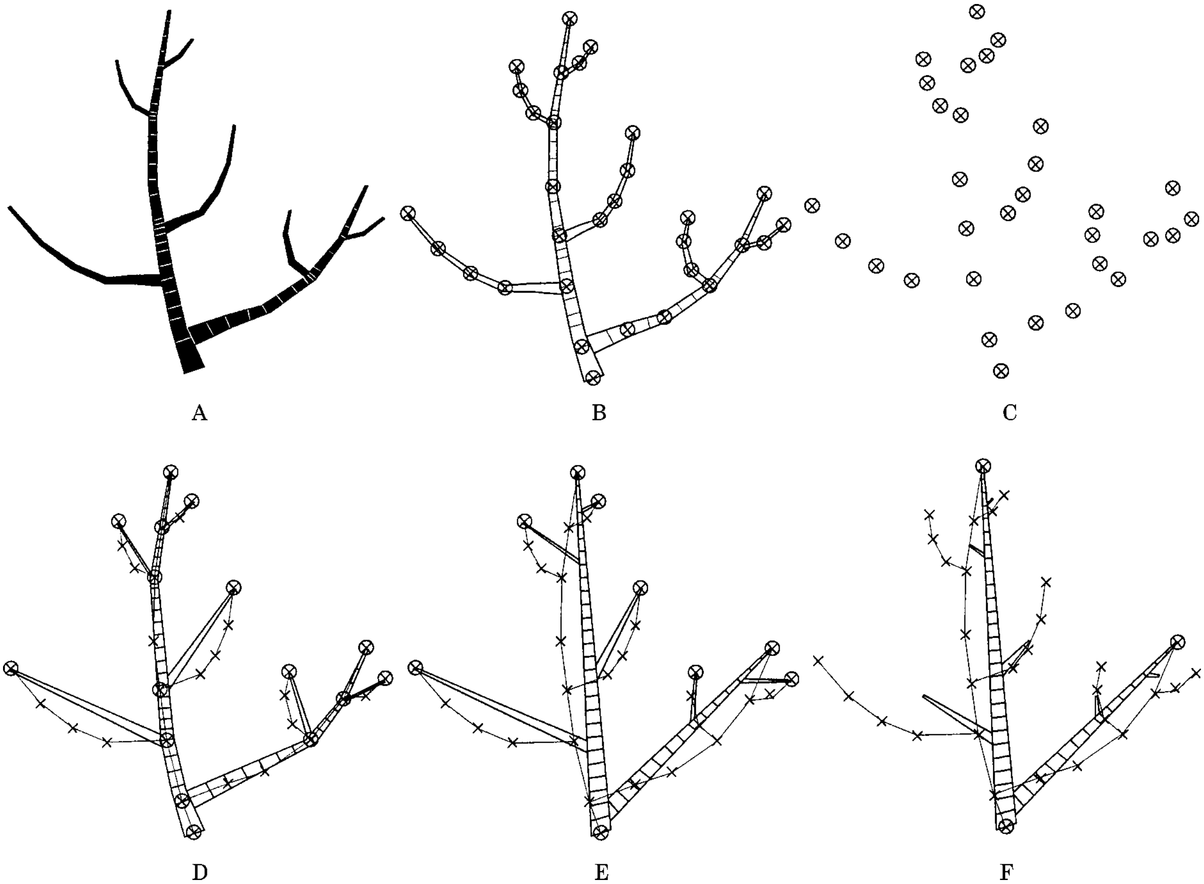

FIG. 3. Approximation strategies for digitizing a monopodial branching system. A, A monopodial branching system. Two axes have been decomposed into sub-components (e.g. internode units). B and C, Precise modelling of the branching system geometry would require recording all the 3D points (denoted by ⊗). D, Digitized points not corresponding to branching points have not been recorded (×). E, Only the extremities of the branching system axes have been recorded. F, Only the extremities of the two major axes have been recorded.

This equation corresponds to new between-scale constraints deriving from the above additional geometric assumptions. They express, respectively, the co-linearity of the axis segments, the homogeneity of the length of the components and the linear decrease of the top diameter. For each $i > 1$, the other geometric parameters, B_{y_i}, b_{y_i}, are determined using the within-scale constraints due to topological connections [eqn (1)]. B_{y_1} and b_{y_1} are determined according to the between-scale constraints from eqn (3).

If the considered axis is a sympodial branch, i.e. a branch made up of a series $y_1, y_2, \ldots, y_N$ of modules (Bell, 1991), then the previous strategy still applies using the same additional geometric eqn (5). However, within a sympodial branch, the within-scale constraints expressed in eqn (1) needed to be extended to successive modules, i.e. related by the + operator.

Scaling down branching system component geometry. These simple schemes for approximating axis geometry and location can be extended to approximate the geometry of any branching structure. To represent a branching system (containing either monopodial or sympodial branches), we may approximate its bearing axis geometry by some basic geometric model and scale down its component geometry using additional between-scale constraints as described above. This provides an estimation of the insertion points of its axillary branches [e.g. using eqn (4)]. Then, an approximation of the axillary branches can be carried out recursively. The direction of the second order axes is determined from the spatial co-ordinates of their extremities. Similarly, the geometry of their components can be estimated.

Measurement of plant architecture

Topological recording. Most scales currently used in topological descriptions are based on botanical principles which allow us to make hypotheses concerning plant growth dynamics, the stage of differentiation of axes, and reiteration processes. The scales are based on plant decompositions into either metamers, growth units, annual shoots, axes, branching systems or plants. At any given scale, different morphological types of components and different types of topological connections can be defined.

Once suitable decompositions have been defined, the plant components must be described in a certain order. A 'depth first order' is often convenient, i.e. components are described from the base to the top of the plant and each axillary branch is entirely described before resuming description of the bearer. The components of a component are described immediately after the component has been identified. This strategy ensures that no components are forgotten (Godin *et al.*, 1997*a*).

Digitizing strategy. In order to represent plant geometry, each component must be associated with a geometric model, either basic or compound, which has to be estimated from field measurements. However, in actual digitizing applications, geometric information is not necessarily collected at scale *s* for all components. Depending on the desired accuracy for a given part of the plant, geometry may be measured locally at scales that are different from *s*. Where greater accuracy is required, components at scale *s* may be decomposed into finer components. The geometry of components at scale *s* is thus represented by compound geometric models. On the contrary, where limited accuracy is required, it is possible to measure more macroscopic components at a scale less than *s*, and then scale down to infer geometric information at scale *s*.

For a branching system, different approximation strategies can be used to obtain a satisfactory balance between the number of measurements and geometric accuracy. Figure 3 illustrates these approximation strategies for representing the geometry of a monopodial branching system at the internode scale (Fig. 3A). Since it might be unrealistic to digitize every internode, a first approximation strategy can be used. Points are sampled on the plant structure so that segments between any consecutive two points are straight (Fig. 3B and C). Internode geometric parameters that were not measured can then be scaled down from the geometry of these straight segments using eqn (5) (whereas *a* is now a segment) (Fig. 3B).

Figure 3D shows a second level of simplification: points that are not branching points or axis terminal points have been discarded from the sampling strategy. The axis segments between consecutive digitized points are assumed to be straight segments whose geometry can be used to scale down the geometry of their internodes. By contrast with the previous digitizing scheme, the total number of points in this example has been reduced by half.

Figure 3E shows a third level of simplification where branching points have also been removed from the set of digitized points. In this case, the direction of the axis bearing the whole branching system is determined by digitizing its endpoints. If this axis geometry is assumed to be a straight segment, its component geometry can be determined by scaling down. From the topological information contained in the MTG, we know which of these components are bearing second order branches. Then, recursively, the direction of the second order branches are determined from the previous estimates of their insertion points and their digitized extremities. In turn, the location and geometry of their components can be estimated by scaling down, etc.

This scheme can be further simplified when the overall geometry of a branching system can be approximated by the geometry of its principal axes (Fig. 3F). As in the previous scheme, the geometry of the principal axes is determined by a recursive scaling down. Since no points have been digitized on the other axillary branches, their global direction is unknown. Hence, the geometry of these axillary branches can only be approximated using default rules and values. For example, the length of such an axillary branch can be approximated by a mean component length multiplied by its number of components, the insertion angles can have a constant value, etc. (Fig. 3F).

Figure 4 illustrates a similar approximation strategy for a sympodial branching system (Fig. 4A). This branching system can be approximated as discussed above by digitizing the extremity of each module (Fig. 4B). However, it is not possible to further simplify this digitizing scheme as in the monopodial case. Indeed, if intermediate points at the extremities of the modules are not recorded (points 2, 3, 5), the first bearing module (axis 1–2) has no defined extremity since point 2 is not recorded. Hence, its geometry must be approximated using default rules (that define its overall direction and the mean length of its components) as well as the geometry of axes 2–3 and 2–5, leading to a wrong geometric interpretation (Fig. 4C).

To further simplify the digitizing of this sympodial branching system, it is necessary to take into account the multiscale topological information that describes how modules are grouped into sympodial branches (Fig. 4D). Digitizing points 1 and 4 determines the basic geometric model that represents sympodial branch a_1. It is then possible to scale down the geometry of a_1 components using eqn (5) (Fig. 4E). For the same digitized points (i.e. 1, 4, 6), a different multiscale topological description (Fig. 4F) would lead to a different geometric representation of the branching structure at the internode scale (Fig. 4G).

All these strategies may be applied to simplify measurements of both moderate-size plants—in which the detailed geometry of small branching systems is unnecessary and expensive to measure—and large trees which contain so many components that not all could be described geometrically. The resulting digitizing method is flexible: it allows several levels of geometric simplification and it does not depend on a predetermined scale of description.

Recording spatial co-ordinates. In the following applications spatial co-ordinates were measured with an electromagnetic 3D digitizer Fastrak (Polhemus, 1993). The digitizer includes a pointer (i.e. which shows the point to be measured) and gives the spatial co-ordinates and orientation angles which are simultaneously recorded (Raab *et al.*, 1979). In the field, the error in measuring spatial co-ordinates is about 1 cm, because of plant movements due to the wind and operator error (Thanisawanyangkura *et al.*, 1997). Additional error can be expected in the presence of metallic objects which disturb the magnetic field. Further information about the 3D digitizing technique may be found in Moulia and Sinoquet (1993) and Sinoquet *et al.* (1998).

Spatial co-ordinates measured on the plants were the tips of the plant components abstracted by cylinders or cone frustums. The pointer was held parallel to the component surface, so that the pointer's normal direction intersected the central axis of the component. This made it possible to compute the spatial co-ordinates of the central axis from pointer co-ordinates, pointer orientation angles and the component diameter t_z. The latter was measured with a

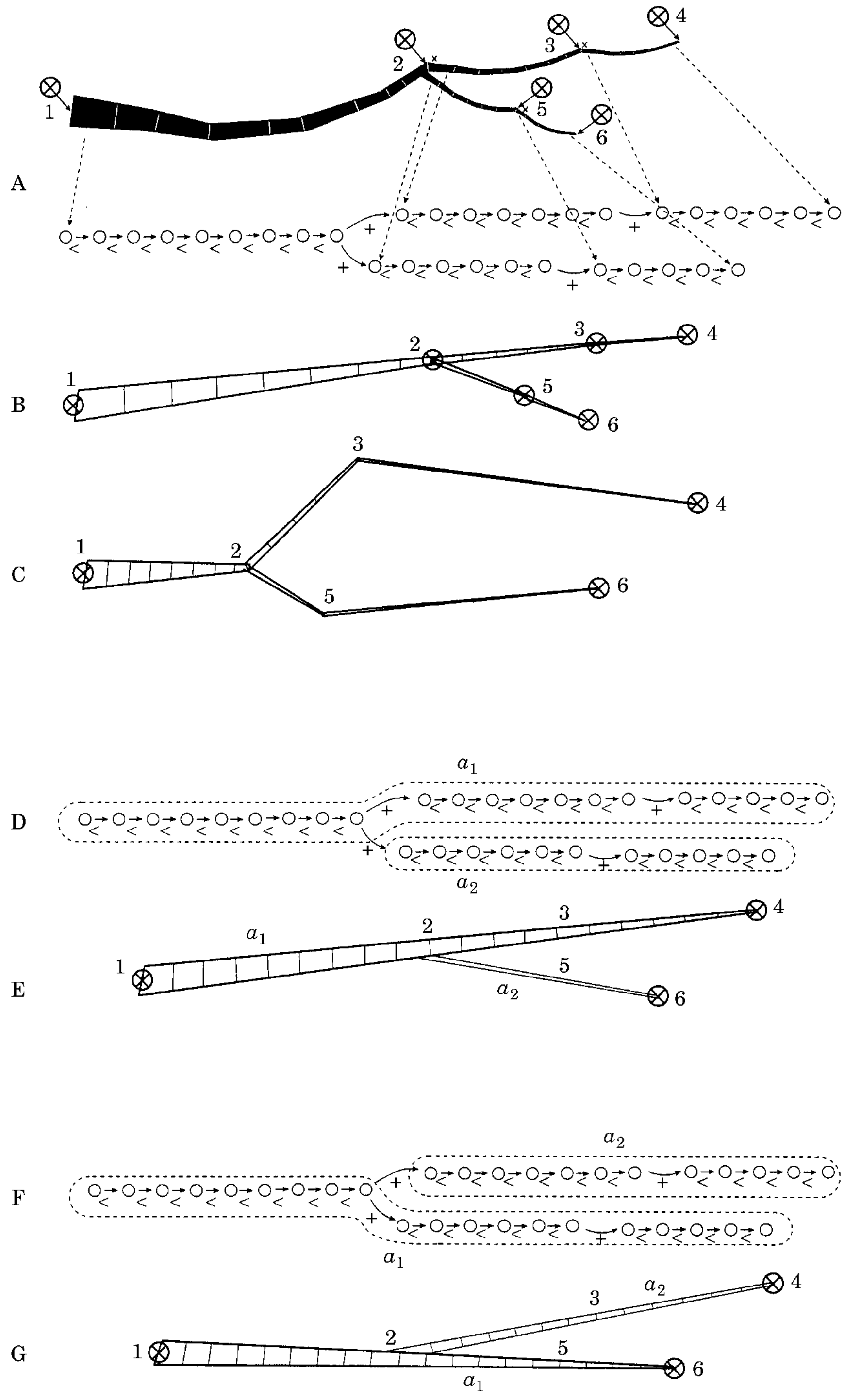

FIG. 4. Approximating the geometry of a sympodial branching system. A, Six points are digitized corresponding to the base and to the extremity of each axis. B, A reconstitution using linear interpolation between digitized points. C, Resulting geometric model if points 2–4 are not digitized: only the branching system extremities have been considered. D, Multiscale topological information is added so that a better approximation can be made. Alternative multiscale topological information (F) could result in a relatively biased geometric reconstruction (G).

calliper at the same time as digitizing. The digitizer was not used to measure the diameter because of measurement error.

Data encoding and analysis. Code files. Plant descriptions are encoded in a textual form, using a specific code for topology in which each component is represented by a label and its topological relations by specific symbols (Godin *et al*., 1997*a*). Each label is made up of a letter and an index. The letter represents the component class, i.e. the type of component. The index is an integer that locally allows us to identify the component among its immediate neighbours (e.g. the rank or the year of growth of the corresponding component). The index meaning is necessarily the same for all the components of a given class. The information relative to the scales, classes and topological relations allowed between components is summarized in the header of a code file which is input in a spreadsheet-like format. All the measurements that can be carried out on plant components as well as spatial co-ordinates are attributed to plant components, at a given scale. The multiscale description can be used to attribute the variables at adequate scales.

Reconstruction of plant architecture. These code files can then be read by the AMAPmod software (Godin *et al.* 1997*a*, *b*). Data exploration and analysis is then performed interactively, using the AMAPmod Language (AML), which allows computation on topological locations, multiple-criteria selections of plant components, and graphical and statistical analysis of the results—including fitting of statistical models. A specialized module has been designed to reconstruct the geometry of a plant from the measured spatial co-ordinates according to the principles described in previous sections, i.e. fully or under-specified geometric models and making use of within- and between-scale constraints.

Analysis of plant architecture. Using AMAPmod software allows one to define *a posteriori* different types of variables from the data contained in the plant architecture database, since the plant architecture was preserved by the measurement process. Topological, geometric or biological variables corresponding to measured values, called raw variables, can then be extracted from the database. From these raw variables, new variables, called synthesized variables, can be constructed in AML using variables associated with components at the same scale or at other scales. The extracted data can be plotted in different ways and further investigated using AMAPmod modelling tools (Godin *et al.*, 1997*b*).

RESULTS

Digitizing of a young apple tree

The method was applied to study development of fruit quality in apple trees (*Malus x domestica* Borkh), by comparison of two cultivars trained in two different systems. Both the topological and geometric location of fruits within the canopy were assumed to be key factors for fruit quality. Topological location in relation to surrounding vegetative components was assumed to be important for two main physiological functions: (1) assimilate supply or competition for sugars between organs; and (2) water flow related to transpiration of leaves.

Cultivars 'Fuji' and 'Braeburn' were planted at the INRA Laboratoire d'Arboriculture experimental station, near Montpellier (France) in 1995, after 1 year's growth in a nursery. A block of 20 trees was trained in each system. The first training system relied mainly on systematic bending of the laterals during summer and of the central axis when it reached 3 m in height. In the second training system, the laterals were left to develop even in an erected position and bending occurred in a natural way with fruiting. Two trees from each system (i.e. eight trees in total) were chosen for the following descriptions.

TABLE 1. *Topological relationships between classes used to describe apple tree architecture*

Scale	Classes	/	<	+
1	J	R,W,S		
1	N	R,W,S		
2	R	U,B,D,I		R,W,S
2	W	B,D.I		W,S
2	S	D,I		S
3	I	E		D,B,U
3	D	E	I,D,B,U	I,D,B,U
3	B	E	I,D,B,U	I,D,B,U
3	U	E	I,D,B,U	I,D,B,U
4	E		E	E,F
4	F			

Each line represents a type of plant component and specifies its scale, the possible types of its components (column /) and the type of component that can follow it (column <) or be borne by it (column +) at the same scale. See text for details.

Topological description. Four scales were used to describe plant topology (Table 1). At plant scale 1, two classes of components were used to distinguish the two cultivars (J for 'Fuji' and N for 'Braeburn') and the index represented the rank of the tree on the row. At branch scale 2, three classes were considered: R for branches (i.e. contain at least one long growth unit), W for brindles and S for spurs. At scale 3, four classes of growth units (GUs) were considered according to their floral or vegetative character and their length: I for inflorescences; D for GU less than 5 cm; B for GU from 5 to 20 cm; and U for GU more than 20 cm. GU indexes represent their year of growth (from 1994, year of growth in the nursery, to 1997, year of digitizing). For example, U94 denotes a growth unit grown in 1994 (Table 2). At metamer scale 4, we measured those metamers whose leaf (E) was sufficiently developed to make a photosynthetic contribution, and did not measure metamers whose leaf was reduced. The index in this case indicated the rank of the metamer within the GU. Fruits (F) were considered as components from scale 4, like metamers. They were indexed after thinning so that each fruit could be identified up to harvest.

Since inflorescences in apple trees are terminal on the axes and are followed by a sympodial and immediate branching (Crabbé and Alvarez, 1991) no succession relationship was allowed after an I symbol. The other GUs, i.e. D, B, and U were allowed to follow and to bear each other. At scale 4, metamers followed each other and could be followed by fruits if they were components of an I (F, like I, does not have a successor).

Description method. Each tree was digitized in spring and autumn to quantify changes in 3D co-ordinates during the growth and fruiting period. We precisely located shoots and fruits by describing their insertion at node level. This was possible since the trees were sufficiently young (4-year-old) and morphological marks were still visible. Nevertheless, it was necessary to compromise between the time devoted to recording *vs*. the precision, since leaves and spurs (short

TABLE 2. *Code representing the digitized branch*

ENTITY-CODE					XX	YY	ZZ	TopDia	Blush
/J1									
^/R1/U94					0	0	0	375	
^/E1 < < E35									
^ < E39					2·1	1·3	90·3	307	
	+R1/D94/E1							179	
		< 195/E1			−2·1	1	94·3	179	
		^ +U95							
		^/E1 < < E15			−18	−4·2	103·7	147	
		^ < E16 < < E22							
			+S1/196/E1+D96/E1 < < E6		−26·4	−6·7	104·4	50	
		^ < E23 < E24							
			+S1/196/E1+D96/E1 < < E4		−31·9	−5·5	105·1	46	
		^ < E25			−32·8	−6·6	103·6	144	
			+S1/196/E1+D96/E1 < < E4		−33·8	−6·4	103·8	57	
		^ < E26							
			+S1/196/E1+D96/E1		−34·5	−4·3	102·6	36	
		^ < E27							
			+S1/196/E1+D96/E1 < E2		−37·3	−5·1	104	53	
		^ < E28							
			+S1/196/E1+D96/E1 < < E3		−37·6	−4·8	101·2	50	
		^ < E29							
			+S1/196/E1+D96/E1 < < E4		−39	−3·9	102·7	50	
		^ < E30			−41·1	−6·2	102·2	136	
			+S1/196/E1		−41·4	−6·1	102·7	62	
				+S1/D96/E1	−42·5	−6·2	102·8	35	
			^ < E2		−42·5	−6·2	102·8	35	
				+D96/E1 < < E6	−41·7	−11·5	103·1	62	
		^ < E31							
			+S1/196/E1+D96/E1 < < E4		−42·4	−4·4	100·3	43	
		^ < E32							
			+S1/196/E1		−44·9	−4·8	102·1	43	
				+S1/D96/E1	−45·8	−4·2	103·4	40	
			^ < E2		−46·1	−4·4	103·2	43	
				+D96/E1 < E2	−48·2	−4·4	104·8	43	
		^ < E33							
			+S1/196/E1		−47·2	−5·3	100	45	
				+D96/E1 < < E5					
			^ < F1						0·75
		^ < E34							
			+S1/196/E1+D96/E1 < < E4		−51·3	−3·3	100·4	47	
		^ < E35			−51·8	−4·8	101·1	136	
			+R1/196/E1		−52·1	−4·1	101·8	82	
				+U96					
				^/E1 < < E5	−55·5	−9	104·3	82	
				^ < E6 < < E10	−60·1	−16	109·7	82	
				^ < E11 < < E15	−64·5	−23	116·6	82	
				^ < E16 < < E20	−68·6	−28·7	125	82	
				^ < E21 < < E25	−70·9	−30·7	132·7	82	

The first 5 columns contain topological codes (one column per order). One column may contain more than one component. The notation E1 < < E5 is a shorthand for E1 < E2 < E3 < E4 < E5. Columns 6 to 10 are used to attach attributes to the last component defined on a line: columns XX, YY, ZZ contain the x, y, z co-ordinates of the tip of this component, TopDia contains its top diameter and Blush contains the percentage of blush of a fruit. See Godin *et al.* (1997) for more details about the coding strategy.

axillary shoots) were very numerous. Considering that it would be unrealistic to digitize each leaf, and too coarse to digitize at the GU scale, not all the geometric information was recorded at the leaf scale. Long shoots were decomposed into straight segments containing at most five internodes (Fig. 5). Then, to represent the plant at the scale of internodes, the geometry of each internode was scaled down from these segments.

A particular strategy was applied to sample short laterals. When less than 5 cm long, they were not decomposed into internodes and the 3D co-ordinates were only recorded at their extremities. Five centimetres was chosen as the threshold because this length is often used to distinguish the presence/absence of elongation on twigs and because the distance between two successive points needs to be greater than the expected digitizer precision (which is 1 cm). When these short laterals contain a floral GU, the branching system is sympodial (Fig. 5A). Approximation strategies described above were used to reconstruct these branching systems.

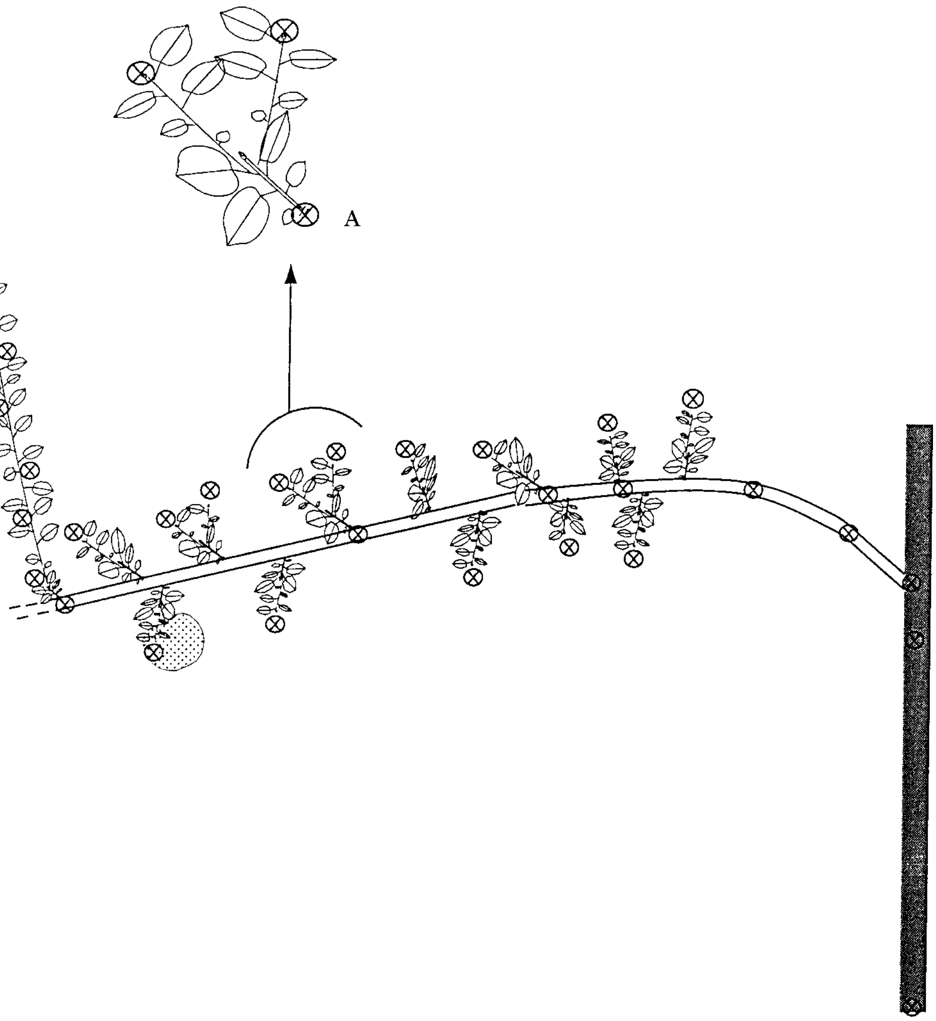

FIG. 5. Part of a fruiting branch described in Table 2 showing the digitized points. A, How a short branching system is simplified in the digitizing process.

'Fuji' trees were described in 1 d by two workers while 2 d were necessary to describe each 'Braeburn' tree, since these had more branches. Finally, 24 worker-days were used in the field to digitize eight trees. An excerpt of the code file resulting from the description of the part of the tree represented in Fig. 5 is given in Table 2.

Using the apple tree database. Figure 6 shows a visual comparison of a photograph of the real apple tree with the 3D geometric reconstruction from digitized measurements, which indicates the method precision. The axes are not perfectly smoothed on the 3D reconstruction, but the general geometric aspect of the plant is reasonably accurate. The effect of the presence of a metallic wire in the neighbourhood of a digitized point can be observed on the trunk immediately above the first branches. Branch movements due to wind explains the sudden changes of direction at the end of some lateral branches.

Figure 7 gives a polygonal representation of the geometric model associated with the branch whose code is described in Table 2. Because of the approximation schemes, a branch containing approx. 200 components may be digitized with only 28 clicks of the digitizer (detailed in Fig. 5). The method was used to analyse the development of this branch through time. To do this, the branch was digitized at the beginning of the vegetative period and then at the end. It should be noted that in such applications, the integration of topology and geometry is absolutely necessary since, as the geometry of the components changes, topology is the only means to identify components through time. Figure 8 illustrates the bending of the same branch under the weight of its fruits. Such data can be used, for example, to quantify the relative change in spatial position of the different branch components. These changes influence the location of regrowth during 1997, the spatial location of the fruits and their light environment. A study of the balance between growth and fruiting within the canopy was reported by Costes *et al.* (1999).

Digitizing of a 20-year-old walnut tree

This application was aimed primarily at providing input parameters for simulation models to compute the dis-

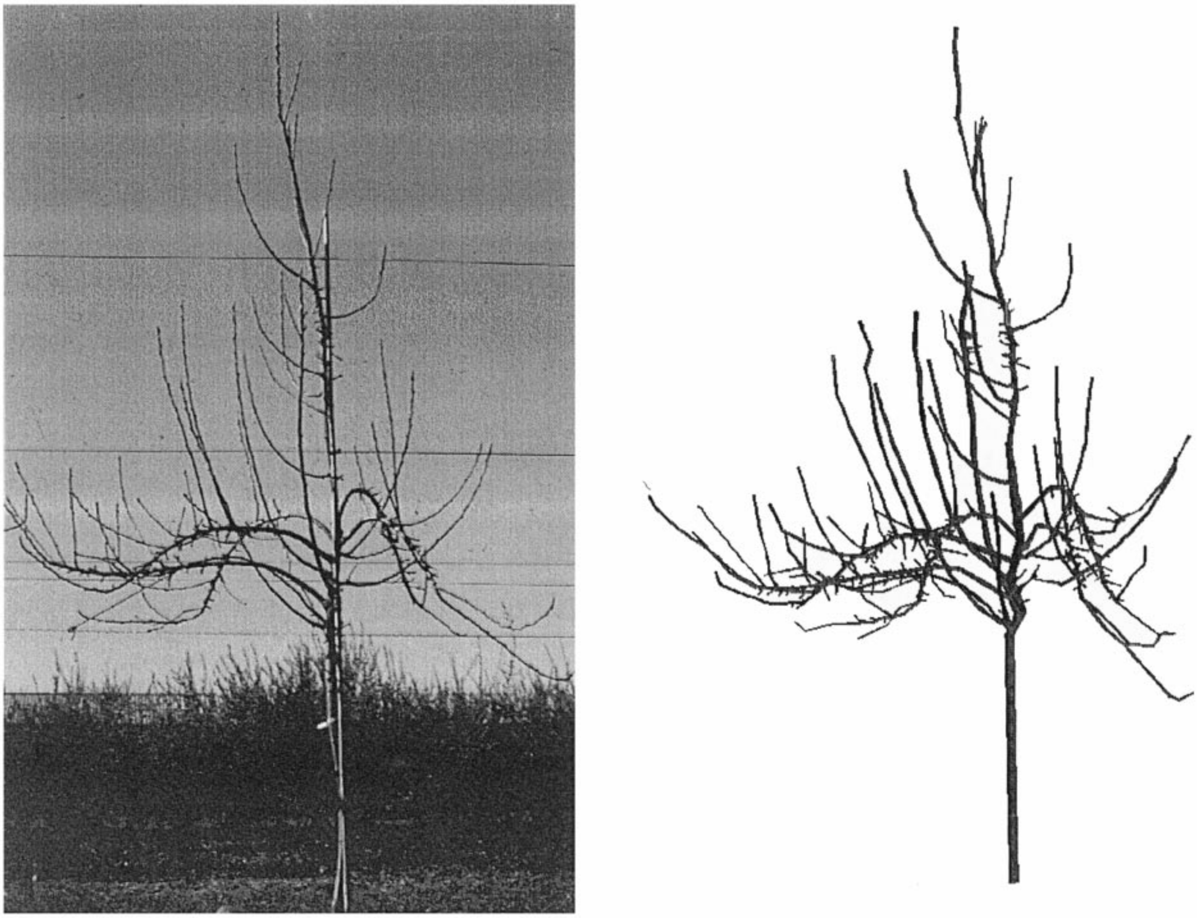

FIG. 6. Visual comparison of the original plant and its 3D geometric reconstruction.

tribution of light interception, transpiration and photosynthesis in the tree crown, i.e. at the scale of the current-year shoot. A secondary purpose was to identify the determinants of current-year shoot morphology, mainly shoot vigour as expressed by basal shoot diameter. For this, parameters of shoot morphology, shoot location in both the tree topology and geometry, and shoot environment were correlated.

Measurements were made on a walnut tree (*Juglans regia* L.) grown for timber in an orchard located near Clermont-Ferrand (45° N, 2° E), France. Trees were planted staggered at a density of 100 plants ha^{-1}. All were 20-year-old and about 7·5 m high. The measured tree was 7·9 m high. Crown radius and height were 5·5 and 5 m, respectively. The estimated crown volume was approximately 95 m^3.

Description method. The strategy for describing the architecture was based on the following: the tree was sufficiently large to include many components (6837 leaves attached to 1729 current-year shoots), and the tree was sufficiently old so that most leaf and bud scars were indistinct. These two features prevented tree architecture from being measured at the internode or the growth unit scale.

The primary purpose of this application was to accurately describe the spatial distribution of foliage within the tree canopy as this was the main determinant of the distribution of light, and consequently transpiration and photosynthesis within the crown. This meant defining leafy shoots, i.e. current-year shoots, as tree components and measuring their spatial location within the crown. Topological positions of current-year shoots also had to be taken into account since photosynthesis and transpiration rates at the interface between the plant and the atmosphere were to be coupled to fluxes within the plant, i.e. assimilate partitioning and water transport in the hydraulic architecture, respectively. Topology therefore was described to account for transport and storage capacity of the tree components that connect each pair of current-year shoots.

For the secondary purpose of this application, current-year shoots had to be defined as tree components since we were assessing their variability. Only the topological location of current-year shoots was required to identify the hierarchical position of the shoot (e.g. terminal shoot *vs.* axillary shoot) or to compute the path length from collar to the shoot. Additional information concerning the topology of units grown during previous years was unnecessary. By contrast, the spatial location of the shoot had to be accurately described to simulate its environmental properties, especially light microclimate. For both purposes, the branching points of the shoots on the tree structure had

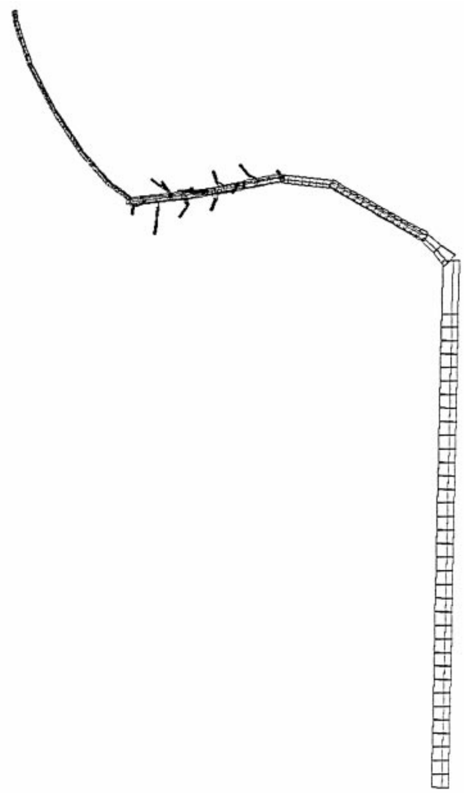

FIG. 7. Geometric reconstruction of the branching system described in Table 2, performed at the internode scale with AMAPmod.

to be identified and every branching point in the tree had to be measured in order to accurately compute topological distances between shoots or the path length from any shoot to the collar.

Given the above constraints, the tree was topologically described at two scales (Table 3). At scale 1, the tree was split into axes A. The axis of order 1 was the trunk, axes of order 2 were the branches connected to the trunk, and so on. At scale 2, axes were split into segments S and current-year growth units U. Segments accounted for the woody structures set during the previous years, i.e. leafless parts. Any number of segments might be used to render branch curvature and changes in diameter, but a segment limit must be defined at every branching point. Segments were thus used to accurately describe the geometry of the woody structure but they did not have any botanical significance. Leafy shoots, i.e. set during the current-year, were described as one growth unit, or several in cases of polycyclism or sylleptic growth. Topological relationships between tree components are shown in Table 3. The combination $S < U$ means that U is a terminal shoot while the combination $S + U$ means that U is an axillary shoot. The combinations $U < U$ and $U + U$ account for polycyclism and sylleptic growth, respectively.

In addition to the spatial co-ordinates, measured attributes of the tree components included the basal diameter of axes and growth units and the top diameter of the segments. All diameters were measured using a Vernier calliper at the same time as digitizing. The number of leaves on the growth units was also recorded to provide a bulk description of shoot morphology: this prevented us from decomposing growth units into internodes. As in the apple tree case, all this information was recorded in a code file.

Using the walnut tree database. The walnut tree database illustrates aspects of the use of the variables extracted from digitized plant architecture. Figure 9A shows the spatial distribution of the current-year shoots located in a 1 m thick vertical plane orientated south-north and centred on the tree trunk. Small shoots (i.e. with diameter less than 5 mm) tended to be located in the lower part of the tree canopy, whereas large shoots (i.e. with diameter greater than 10 mm) were only located in the very outer canopy. Basal diameter was used to estimate leaf area of current-year shoots from an allometric relationship established from a sample of shoots. This allowed us to assess the spatial distribution of leaf area in the crown volume (Fig. 10). This information was thus derived from two independent geometric variables, namely shoot diameter and spatial co-ordinates. According to the first purpose of the application to walnut, the spatial distribution of leaf area was then used as an input parameter of a simulation model computing light interception at the current-year shoot scale (Sinoquet *et al*., 1997*b*). Simulated daily irradiance for an overcast sky (i.e. for which the ratio of diffuse to global radiation equals 1) was finally included in the database as an attribute of current-year shoots. Figure 9B shows the spatial distribution of current-year shoot irradiance in the same 1 m thick vertical plane as in Fig. 9A. Shoots receiving low irradiance ($< 20\%$) were mostly found in the inner canopy. In the periphery of the crown, shoot irradiance was higher, although dense foliage at the top of the crown reduced the irradiance on most shoots (i.e. $< 40\%$). For the second purpose of the application to walnut, an attempt to identify the determinants of shoot morphology was made from a correlation analysis between basal diameter and other shoot variables: the best correlation was then found for shoot irradiance and bearing diameter while other topological variables did not show any correlation with shoot diameter (Sinoquet *et al*., 1997*b*). This walnut tree application illustrates how information can be extracted from the database to determine input parameters for simulation models (here, a light interception model) of plant function, and how information on plant architecture can be used together with additional information on plant components (in this case, morphological and environmental attributes of the growth units).

DISCUSSION

This paper presents a method for describing plant architecture, including topological and geometric information at several scales. The multiscale representation of topology is a crucial choice in three basic respects. First, the method relies on a very general model of plant topological structure which guarantees its applicability to a wide range of plant species, application goals and modelling contexts. Second, it

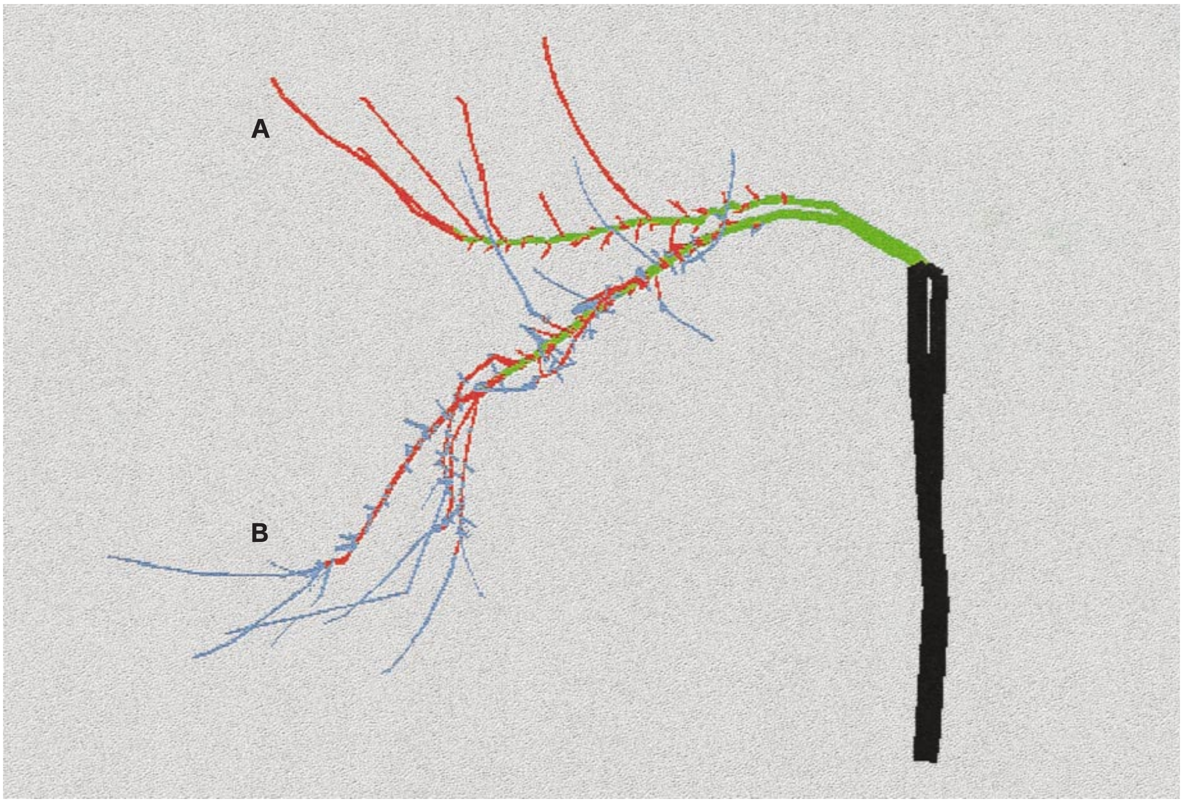

FIG. 8. Branch digitized at the beginning (A) and end (B) of the vegetative period. GUs created during years 95, 96 and 97 are respectively green, red and blue.

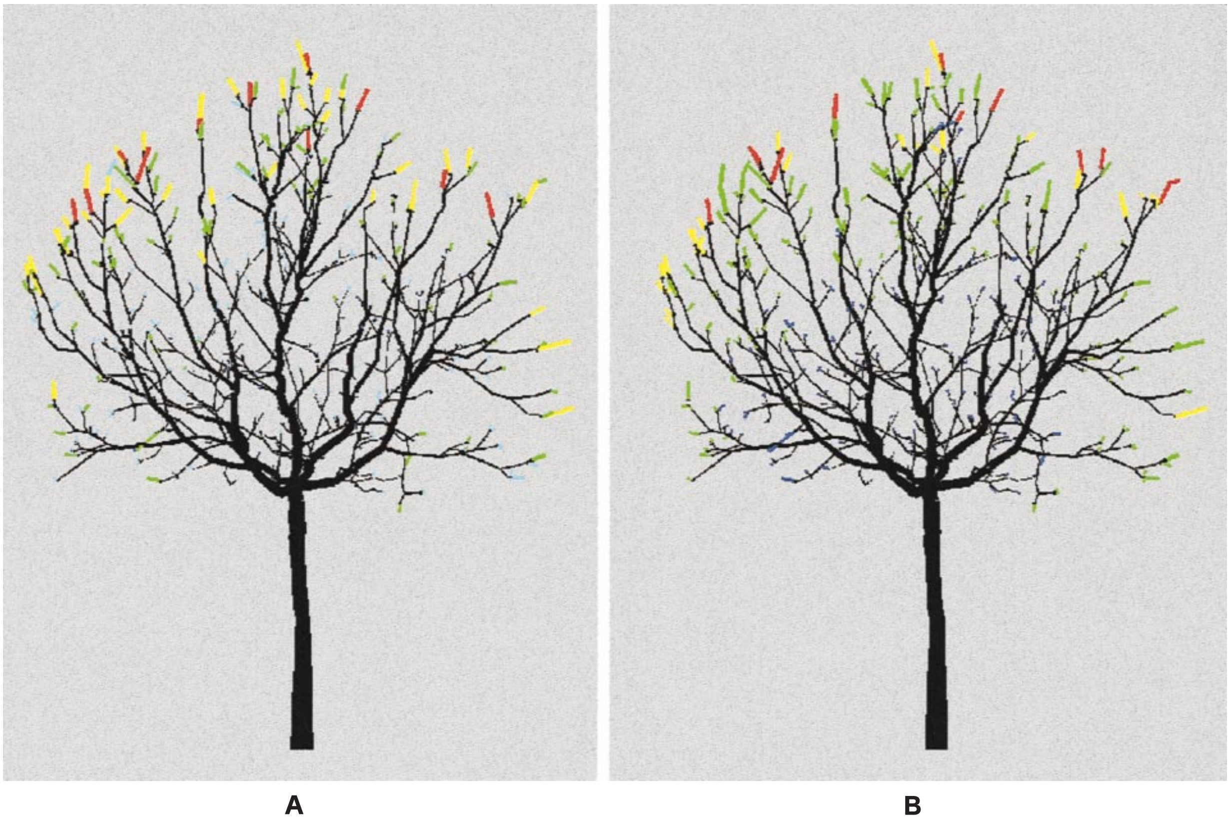

FIG. 9. A, Distribution of shoot (measured) diameters in the digitized walnut-tree. The following colour codes have been used: blue, diameters < 5 mm; light blue, 5–7·5 mm; green, 7·5–10 mm; yellow, 10–12·5 mm; red, > 12·5 mm. B, Distribution of (simulated) shoot irradiance above the tree on a horizontal plane. Colour codes used for shoot irradiance: blue, < 20 %; green, 20–40 %; yellow, 40–60 %; red, 60–80 %.

TABLE 3. *Topological relationships between classes used to describe walnut tree architecture*

Scale	Classes	/	<	+
1	A	S,U		A
2	S		S,U	S,U
2	U		U	U

See Table 1 for details.

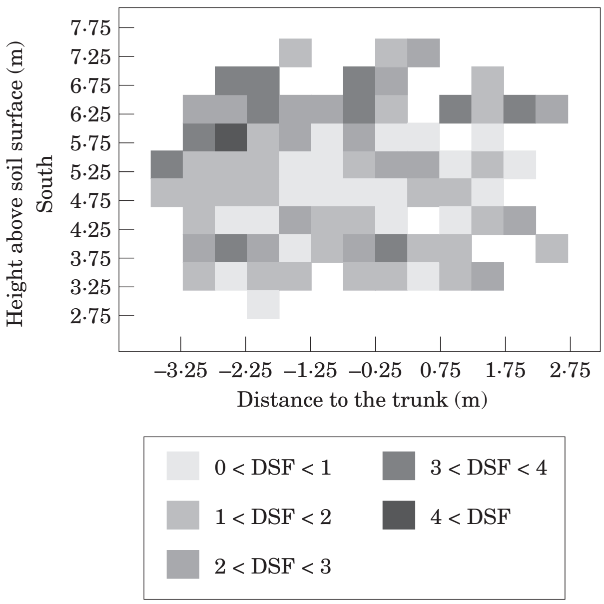

FIG. 10. Spatial distribution of leaf area density (DSF, m^2m^{-3}) in a 1 m thick vertical plane oriented north-south and centred on the tree trunk.

enables us to design approximation schemes to simplify measurements that do not depend on a specific scale. These schemes simplify the geometry of branching systems to varying degrees and can be used to simplify the geometry of small as well as large plants. This is particularly useful in adapting the sampling strategy for different applications. Finally, the integration of multiscale topology and geometry defines a new framework to deal with the changing nature of plant geometry with respect to scales and application goals. This framework may be used in other applications, e.g. simulation of plant growth.

To represent plant components, cone frustums were the basic geometric model. Nevertheless, the complexity of the surface shape to be modelled can, in some cases, justify more complex basic geometric models. For example, if an axis (or a portion of axis) is not straight, its overall geometry can be modelled by an adequate basic geometric model, such as a spline (e.g. Bloomenthal, 1985). Many other types of surface, such as ellipsoids, (e.g. Norman and Welles, 1983; Cescatti, 1997), polygonal envelopes (Cluzeau, Dupouey and Courbaud, 1995) for trees, or kiwi vines (Buwalda, Curtis and Smith, 1993), or more complex parametric models (e.g. Prévot, Aries and Monestiez, 1991) for maize leaves, were used to represent basic geometric models of plant components. The digitizing method described does not depend on the choice of a given basic geometric model. It can be tuned to account for other geometric models by changing within- and between-scale constraints.

The proposed description method, however, shows some limitation in its application. Data acquisition in the field is tedious. Indeed, given the current technology, neither topology recording nor spatial co-ordinate measurements can be automated. Even if automated plant digitizing is presently impossible, the proposed method is being improved by developing software for the simultaneous acquisition of multiscale topological and geometric information. For instance, Room, Maillette and Hanan (1994) suggested the use of voice recognition for automated code acquisition so that digitizing could be carried out by one person working alone dictating into a microphone. Such software would considerably ease the detection of inconsistent measures and the practical construction of plant architecture databases.

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