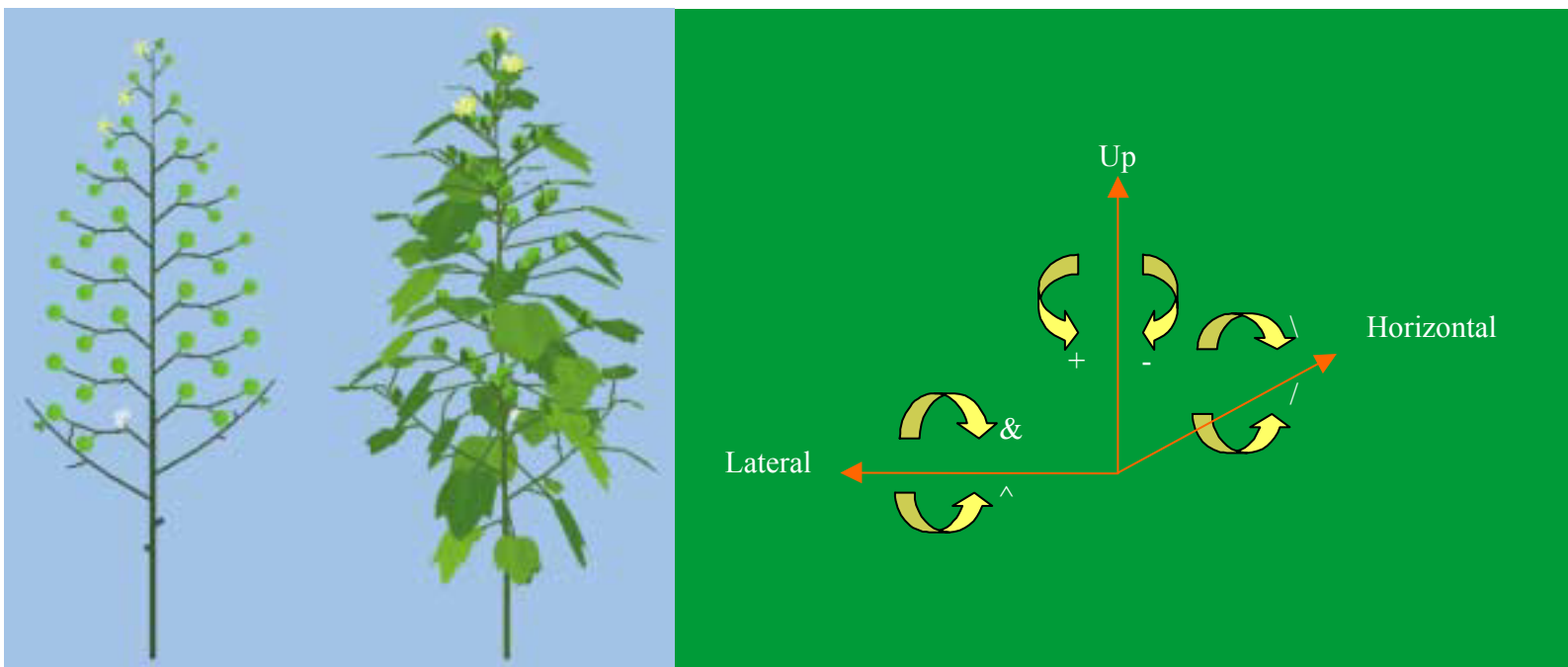


3D modelling of plants: a review

Report of the Virtual Plant Network Wageningen

P.H.B. de Visser, L.F.M. Marcelis, G.W.A.M. van der Heijden,
J. Vos, P.C. Struik & J.B. Evers





3D modelling of plants: a review

Report of the Virtual Plant Network Wageningen

P.H.B. de Visser¹, L.F.M. Marcelis¹, G.W.A.M. van der Heijden¹,
J. Vos², P.C. Struik² & J.B. Evers²

¹ Plant Research International

² Crop and Weed Ecology Group, Wageningen University

© 2002 Wageningen, Plant Research International B.V.

All rights reserved. No part of this publication may be reproduced, stored in a retrieval system or transmitted, in any form or by any means, electronic, mechanical, photocopying, recording or otherwise, without the prior written permission of Plant Research International B.V.

Copies of this report can be ordered from the (first) author. The costs are € 50 per copy (including handling and administration costs), for which an invoice will be included.

Plant Research International B.V.

Address : Droevendaalsesteeg 1, Wageningen, The Netherlands
: P.O. Box 16, 6700 AA Wageningen, The Netherlands
Tel. : +31 317 47 70 00
Fax : +31 317 41 80 94
E-mail : post@plant.wag-ur.nl
Internet : <http://www.plant.wageningen-ur.nl>

Table of contents

| | page |
|--|-------|
| 1. Introduction | 1 |
| 2. Structural models | 3 |
| 3. Functional Structural Models | 5 |
| 3.1 Introduction | 5 |
| 3.2 Process-based models with partial 3D functionality | 5 |
| 3.3 Pipe models | 6 |
| 3.4 L-systems | 7 |
| 3.5 Fractals | 9 |
| 3.6 Modelling light interception in canopies | 9 |
| 4. Modelling plant morphology on basis of genetic expression | 11 |
| 5. 3D visualisations of plants applying limited or no biological rules | 13 |
| 6. Other 3D approaches of interest | 15 |
| 6.1 Virtual reality | 15 |
| 6.2 Virtual life | 15 |
| 7. Software for the visual presentation of 3D objects | 17 |
| 8. Conclusions | 19 |
| 9. Summary | 21 |
| 10. Literature | 23 |
| Appendix I. Explanation of technical terms | 1 p. |
| Appendix II. 3D models: characteristics and origin | 1 p. |
| Appendix III. Research groups that use L-systems or comparable string notations | 3 pp. |
| Appendix IV. 3D imaging software | 3 pp. |

1. Introduction

The aim of this literature and software review is to identify and evaluate the most recent, state-of-the-art research on three-dimensional (3D) plant modelling and visualisation. The review has been prepared within the Plant Research International strategic research (SEO) project on Virtual Plants, which aims at an extension of our current plant growth models with 3D functionality and visualisation.

Recent developments in computer sciences and imaging tools have stimulated the research on 3D aspects of plant growth (Room *et al.*, 1996). These new tools will allow us to increase our understanding of plant form development in relation to its environment. The computer-simulated plant that interacts with its environment is frequently called the 'virtual plant'[#]. The growth and structure of such a plant responds to environmental conditions simulated in 3D space. This approach seems very promising, but requires a new and unique way of computer programming. Which new tools exist that can generate 3D plant structure and development correctly, and what are the possibilities to incorporate plant responses to environmental variations? Which processes can be dealt with in the models currently available?

Our review will focus on virtual plant models that incorporate environmental (either physical or biotic) influences. We are interested in 3D architectural models that simulate the topology and geometry of the plant as realistically as possible. Since these architectural characteristics are species- and even variety-specific, such models are rather detailed. We hypothesise that the plant's behaviour in a certain environment may differ between species or varieties which differ in 3D structure; the plant 3D model must therefore be botanically and architecturally correct. Some 3D plant models are used only for design purposes and may lack functionality and realism to address scientific questions. Yet these models may illustrate some of the techniques to visualise plant growth and structure. So, we will also shortly discuss these, mostly commercially available, software packages.

For what purposes should we apply virtual plant models and what is the additional information in comparison with non-3D plant models used up to now? If process-based models in three dimensions are technically possible, given the vast progress in computer sciences, which aspects are most important to focus on at this moment? To what depth do we require scientific knowledge to program a-biotic and physiological processes at the scale of individual plant organs? Are there any technical limits to measure, quantify and simulate the plant's structural components? These questions are condensed in the following three issues that will be treated in subsequent chapters:

- What are the existing approaches to quantify 3D plant structures? (Chapter 2).
- Which models are available that combine 3D structure and plant functioning, and to what extent do they incorporate growth in interaction with the plant's environment? (Chapter 3).
- Which approaches exist to simulate 3D plant morphology in response to genetic expression? (Chapter 4).

Additionally, we make an inventory of the current scanning techniques to create 3D digital images of plants (Appendix IV). If these techniques are readily available, do they produce data that are easy to use in 3D models?

[#] See Appendix I for explanation of the technical terms; they are only underlined the first time they are mentioned in this report.

The last three chapters give a review of methods to visualise plants and other objects in 3D. Chapter 5 deals with plant images that may look very realistic, but are merely illustrations or drawings without any mechanistic or architectural model behind it. Nevertheless, these techniques could be of use in presenting 3D illustrations of simulated plants. Chapter 6 deals with virtual reality, extending our review a little to other virtual objects and even virtual worlds, where every shape is described in 3D and where interactive features create special sensations and involvement. Chapter 7 gives a short overview of the current software tools that are commercially available for creation of artificial 3D objects.

The conclusions of this review are concisely listed in Chapter 8.

2. Structural models

Plant architecture can be interpreted in a number of ways that seem quite diverse. The different approaches will be categorised following the extensive review of Godin (2000) on plant architecture.

3D presentations of plant architecture can be categorised into:

- (a) global,
- (b) modular, and
- (c) multiscale representations (Godin, 2000).

In **global** representations plant architecture is considered as a whole, and the fact that plants do have different organs is not taken into account. Godin distinguishes two global representations. The **geometric global representations** focus mainly on the apparent shape of the main objects, like tree crowns that can be depicted as ellipses and trunks as cylinders. The other representation is the **compartment global representation**, where compartments are associated with specific functions or analogies, like compartments of carbon pools or blocks that represent resistances to water transport.

In **modular representations** plants are decomposed into modules that may be organ-based or can simply consist of a spatial subdivision. The plant is made up of a repetition of modules. Most apparent modules are leaves, stems, buds, etc. Also the pipe model consists of a modular type, representing the plant as a set of similar pipes (for details see § 3.3).

Within the modular representations, three approaches can be distinguished:

- spatial (the 3D space is rigidly subdivided into cells or voxels),
- geometric (description of the geometry by digital scan or form functions), and
- topological. Topological representation seems the most promising and universal option. The plant is decomposed into its organs, which are connected in the 3D space. Pipe models and L-systems (see § 3.4) come into this category. The network of modules and their connections is depicted as a so-called tree graph (Figure 1).

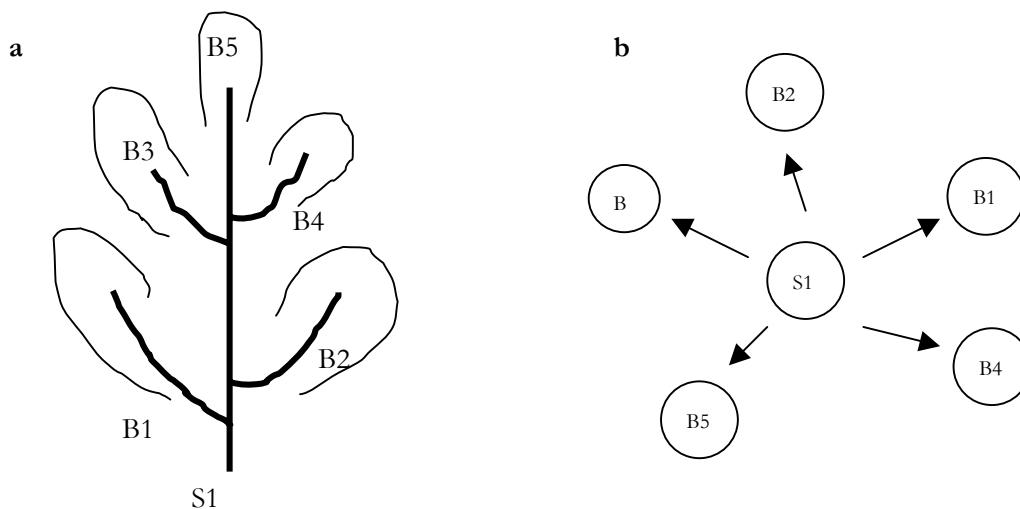


Figure 1. A tree (a) and the tree graph representation (b). *S*, main stem; *B*, branches.

The tree graph is a generic and universal plant representation. It has been customised for the various growth grammars, e.g. for L-systems the 'axial tree' is used. The computational representation of the tree graph can be categorised into:

- 1) chained lists of records,
- 2) matrices, written in tables, or
- 3) strings of characters, e.g. a computer program consisting of expressions with a specific (tree graph) hierarchy. Category 3 includes L-systems that efficiently describe the plant topology by giving vertices (= nodes) a character (mostly 'F') and branches between the nodes a bracket ('[]') notation.

In **multiscale representations** the plant is described at a number of scales or hierarchical levels. In contrast to the modular representation, the amount of data can be reduced since it does not require information on each individual organ's position and geometry. Less detail may sometimes suffice, at least in part of the plant (e.g. leaves in the treetop, or only first- and second-order branches). The plant structure contains details at different scales, and structures may be similar at these scales, implying self-similarity. Branching structures may be self-similar to a certain scale i , at the order $i+1$ branch. Sillion (1995) used the spatial multiscale representation to calculate radiosity in a tree canopy; geometric representations were used by Zeide (1991) for trees and Godin *et al.* (1999) for AMAP (see model description below). Also object-oriented programming has proven useful in the description of structures at multiple scales (Salminen *et al.*, 1994).

Plant architectural models mainly use empirical laws to simulate 3D development of the structure. These basically descriptive models do not incorporate effects of plant physiology and environmental conditions on morphogenesis. Recently, functional-structural models have been developed that combine the process-based non-architectural models with models of the plant 3D structure. These combined models will be discussed in the following chapter.

3. Functional Structural Models

3.1 Introduction

Functional Structural Models (FSM; see *e.g.* Sievänen *et al.*, 2000) combine quantification of the 3D structure of the plant with simulation of (a number of) physiological processes. The structural and functional parts of the model can be either integrated in one model or separated for parallel operation. Only in recent years, scientists started to work on coupling and integrating architectural models and functional, *i.e.*, mechanistic models. One of the apparent reasons for this belated interest is the inherent descriptive character of architectural modelling, thus not analysing and quantifying the mechanistic processes underlying the growth of the appearing plant structures.

With the aid of more powerful computers, the combination of detailed calculation of structures and simulation of complicated physiological processes in one model is now within reach. Since such models generate a complete plant, with all its structures and functions, in a computer, *i.e.* a virtual environment, such models are also called ‘virtual plants’ (Room *et al.*, 1996).

Below, we will discuss some FSM’s ranging from models with an emphasis on either structure or function, or with either general or only specific applicability. Together with a short description, the mentioned models will be classified according to their approach to model plant structure (global, modular, geometric, see Chapter 2) and biological functions (descriptive, mechanistic).

A rather large number of research groups applies L-systems or comparable string grammars. The modelling work of these groups is reported in Appendix III.

3.2 Process-based models with partial 3D functionality

Process-based models (PBM) incorporate mechanistic calculations of a number of growth-determining (a)biotic processes. PBM’s are generally validated for specific situations, making extrapolations to other plant-environment situations hardly feasible. Initially, PBM’s did not incorporate plant form but consisted of functional pools (*e.g.* Kropff & Van Laar, 1993). The COTONS model (Jallas *et al.*, 1998) is one of the first models to combine an architectural and a process-based (GOSSYM) model. The model could be classified as *modular & mechanistic model*. The extinction of light within the canopy is based on Lambert-Beer. The canopy is described by plant height, width and row spacing. Subsequently an age-related photosynthesis is modelled and carbohydrate production is calculated. These carbohydrates are allocated to the various organs, described in great detail. Emergence, growth and abscission of organs are depending on temperature and age. Effects of water and N are manifested by a change in an age threshold of the above processes. A morphology submodel, of which the output is comparable to that of L-systems, can visualise these organs. The visualisation model was based on Virtual Cotton (Room & Hanan, 1995), which, in turn, was based on L-systems (Prusinkiewicz & Hanan, 1989). Virtual Cotton, a *modular & descriptive* model, has shown to be a valuable tool to evaluate crop pests, compensatory growth and effects of pesticides in interaction with plant architecture (Room & Hanan, 1995). Yet, plant growth is controlled by morphogenetic rules and not by mechanistic processes.

A Dutch model for interspecific competition in row crops (Schnieders, 1999) was based on a SUCROS type of model, distinguishing a crop and a weed. It was calibrated for the crop witloof chicory and the weed *Senecio vulgaris*. It could be classified as *global & mechanistic*. Canopy geometry was dealt with in a module called INTERROW, which calculates light beams from a maximum of ten parts of the hemisphere.

The module INTERROW is a modified version of INTERCOM (Kropff & Van Laar, 1993), extended with a quantification of the three-dimensional structure of the canopy, being row height, row width, distance between and orientation of the rows. Light absorption is then calculated by a 3-point Gaussian integration (Goudriaan, 1977). The description of the model lacks a description of the vertical and horizontal distribution of leaf area within the row and is assumed homogeneous.

YPLANT, developed by Pearcy & Yang (1996) in California, calculates photosynthesis of trees and understorey vegetation. Light penetration of this *modular & partly mechanistic* model is simulated through a tropical forest canopy of *Clidemia octona* and understorey vegetation of *Conostegia cinnamomea*. Apart from the light regime, no other environmental variables are calculated. The 3D geometry of the canopy is simulated by calculation of all separate nodes and attached leaves, represented as vectors. The architectural construct is based on field measurements. The model shows a fairly good simulation of carbon assimilation and light competition between species. Unfortunately, YPLANT is not a dynamic but a stationary model, i.e., the model assumes a steady-state of the biomass parts and is not able to use the calculated carbohydrate production for growth. The YPLANT model is written in Pascal and can be obtained freely.

A multi-species, ecological and two-dimensional model was developed by Colosanti *et al.* (1997; 2001) in Great Britain. Plant growth modelling is general, deterministic, dynamic and mechanistic in nature. Its purpose is to investigate the extent to which morphology and function of the whole plant can be determined by resource acquisition and utilisation on the part of its components. There is an above- and a below-ground environment. The whole plant is represented by a branching structure made up from standard 'modules'. The behaviour of the complete plant is determined exclusively by a rule set that acts only at the level of the individual module. The model could be classified as *modular & mechanistic*, but without much detail. The simulations demonstrate the effectiveness of modular rule-based methods from which whole-plant behaviour can arise as an emergent property.

3.3 Pipe models

A pipe model describes a tree as consisting of unit pipes that connect each foliage element to the functional roots. In its original form, the pipe model is purely morphological (Shinozaki *et al.*, 1964). It can be seen as a *modular* description of plant topology. The theory predicts a linear relationship between foliage mass or area and the sapwood cross-sectional area below the crown. Non-functional pipes become part of the heartwood, which does not transport water and nutrients. Pipe models are partly process-based, given the fact that they quantify water and nutrient transport. The basic model can easily be extended with procedures for calculation of other growth processes. For example, the LIGNUM model (Perttunen *et al.*, 1996) uses the pipe model to partition carbon but calculates photosynthetic production in dependence of local climate of productive tree parts. LIGNUM combines a process-based model with a detailed description, using the pipe model, of the tree crown.

The pipe model is particularly useful for woody plant species to model the distribution of resources between foliage and woody structures. Despite the wide use of pipe models in tree research, its emphasis on the relationship between foliage and sapwood restricts its applicability to annual crops.

3.4 L-systems

The Algorithmic Beauty of Plants (Prusinkiewicz & Lindenmayer, 1990) focuses on algorithms that describe plant development over time through the use of L-systems. L-systems (Lindenmayer systems) were developed by the botanist A. Lindenmayer in the 1960s (Lindenmayer, 1968). L-systems are a mathematical tool to model plant development and structure that are derived from formal grammars for string generation. These basic generation algorithms produce output that can be graphically displayed by 3D rendering engines such as VRML or ray tracers (thus introducing yet a third discipline, computer graphics, into this multidisciplinary area of research). L-systems permit the modelling of the influence of outside environmental forces, such as moisture, wind, and sunlight through input parameters. Plant modelling is *modular & descriptive* in closed L-systems, and partly *mechanistic* in Open L-systems. The decomposition rule in the latest version of vlab and L-studio (commercially available L-systems software) allows for certain multiscale features. For description and further details on L-systems grammar, we refer to Prusinkiewicz & Lindenmayer (1990) and Prusinkiewicz & Hanan (1989).

Syntax of L-systems

L-systems allow specification of how an object transforms from one state to another, sometimes adding new parts, during an interval of time. Particular plant parts in particular states are represented by symbols and the process of transformation is expressed in the form of morphogenetic rules or 'productions' which resemble equations. An example is given by the rule below, using symbols A for an apical bud, B for axillary bud, L for a leaf, F for a unit length of internode and '[']' to enclose a branch.

We start with an apical bud A. The following productions are then implemented in each time step:

A -> FL[B]A each apical bud becomes an internode+leaf+axillary bud+apical bud

B -> A each axillary bud becomes an apical bud

F -> FF each internode doubles in length

In successive time steps, the virtual plant is represented by:

Step 1: FLA

Step 2: FFLFL[B]A

Step 3: FFFFLLFFL[A]FL[B]A

Step 4: FFFFFFFFFFFFFL[FL[BA]

Extra symbols can be added to describe branch angles, colours and branch width. In essence, apex A grows in 3D space in analogy to a turtle moving forward, giving a so-called 'turtle interpretation' of the string, generated in successive time steps. The turtle movements in 3D are described at each time step by a vector, of which the direction is controlled by the symbols +, -, %, ^, \, / (see Figure 2).

Plant species models described as L-system

The list of species being described by L-systems grammar is vastly increasing. Models have been made for cucumber (Higashide *et al.*, 2000), pea and bean (Gould *et al.*, 1992; Diaz-Ambrona *et al.*, 1998), palm tree (Chazda, 1985), barley (Buck-Sorlin, 1999), sunflower (Prusinkiewicz & Lindenmayer, 1990; see Figure 3), cotton (Room *et al.*, 1996), white clover (Gautier *et al.*, 2000), and sorghum (Kaitaniemi *et al.*, 2000).

L-systems were also applied to describe specific processes, like root architecture (Shibusawa, 1992), plant diseases (Wilson & Chakrabarty, 1998), and insect herbivory (Room *et al.*, 1996).

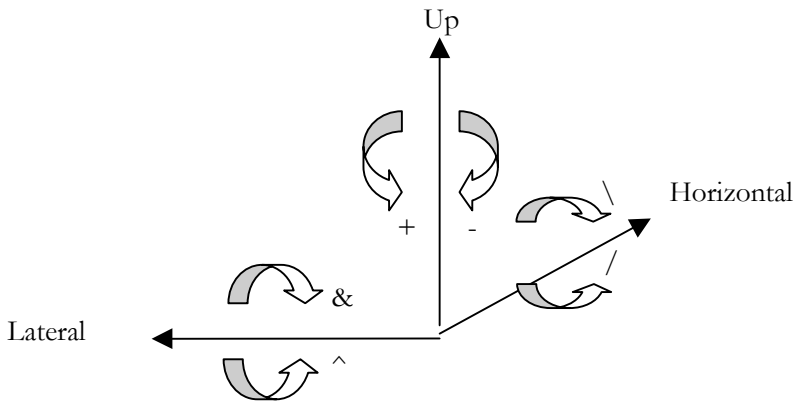


Figure 2. Symbols are used to describe the direction of the moving turtle in 3D.

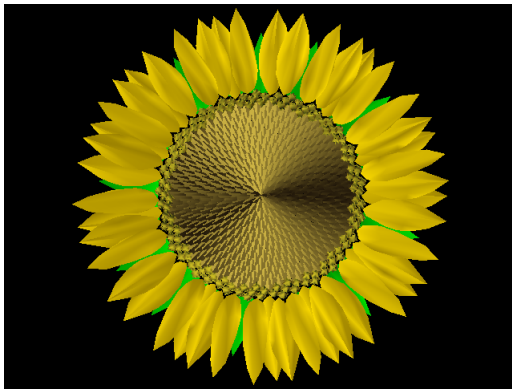


Figure 3. The famous sunflower of Prusinkiewicz & Lindenmayer (1990), described by an L-system of only 8 lines of source code.

L-systems in interaction with the 3D environment: Open L-systems

In the Open L-system the voxels in the 3D space (i.e. smallest units having x,y,z co-ordinates) contain information on, e.g., the presence of a plant organ or soil water content. This information is 'read' by the apices of the growing plant, which will process these data according to given programming rules. In this way the apex can avoid collisions with neighbouring apices, leaves or roots, or properties of the newly formed plant part can be altered. Mech & Prusinkiewicz (1999) (Figure 4) show a nice example for root water uptake, hampered by soil water content and water uptake by neighbouring roots, on the basis of water diffusion between voxels (numerical solution on the basis of finite differences). The root architecture is similar to that proposed by Diggle (1988) in his 3D ROOTMAP model.

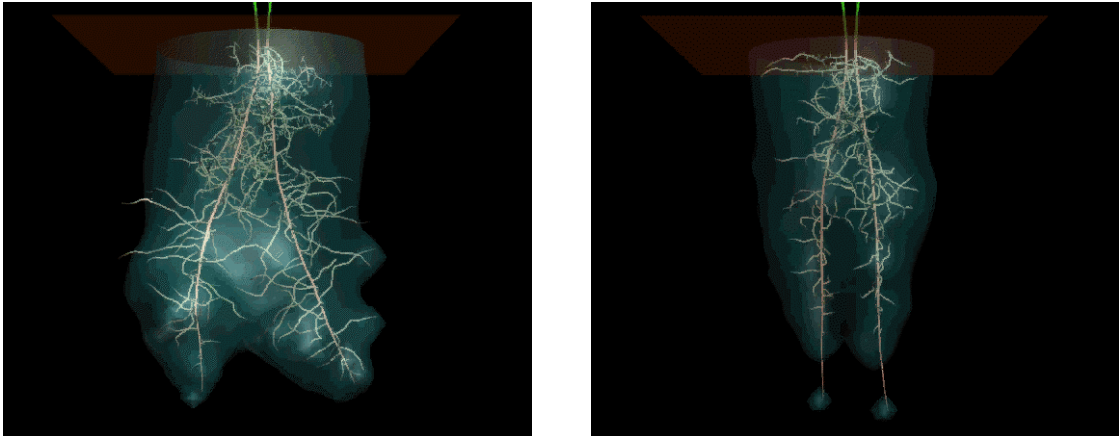


Figure 4. Root systems responding to their own uptake of water or nutrients. A high water uptake rate (left) promotes divergence of roots in comparison with a low uptake rate (right).

3.5 Fractals

A fractal object has two important properties: it is characterised by irregularities at every scale and has a homogeneous mass distribution. In fractal objects, the structure contains details at different scales. In this sense, fractal structures have an infinite length: a famous example is the fractal structure of the British coastline, which seems infinitely long giving its new details each time when zooming in. Fractal structures may be similar at these scales we zoom into, implying self-similarity. Also branching structures are self-similar for a number of scales, yet not to infinity. Therefore, when using fractal geometry to describe plant structure, a certain range of scales has to be defined. The scales may, for example, range from the whole plant to the tiling of objects in annual shoots at the smallest scale. The fractal approach has predominantly been used to describe multiscale architecture of tree crowns (e.g. Viennot *et al.*, 1989), and is already in use since the 1980's.

3.6 Modelling light interception in canopies

Quite a number of physiological models use ray tracing to estimate light adsorption in a 3D canopy. Ray tracing follows the track of light, being direct or diffuse, from a specific part of the hemisphere to the plant surface. The first ray tracing techniques were used by Honda *et al.* (1981) and Chazda (1985), still on two-dimensional plant structures. Later, 3D models were developed, e.g. by Niklas (1988), but his PHYLO model was applicable only to relatively simple shoots and direct light only. ECOPHYS (Dickmann *et al.*, 1990) was developed for poplar trees only. In the model YPLANT (Percy & Yang, 1996) the light that reaches the understorey vegetation is calculated by the module CANOPY; this is calibrated by photographs of the canopy from a ground perspective, and is less accurate at low light intensities.

The current radiation models mostly apply the rendering equation of Kajiya (1986) to trace the rays in a 3D continuum. The rays from the hemisphere and from ray-reflecting leaf patches arrive at N patches, giving N rendering equations to solve.

The rendering equation is: $I(x, x') = g(x, x') \left[\varepsilon(x, x') + \int_S \rho(x, x', x'') I(x', x'') dx'' \right]$

The equation simply balances energy exchanges between surfaces. The intensity $I(x, x')$ is equal to the sum (integral) of the light intensity $\varepsilon(x, x')$ emitted from a surface at point x' towards x and the total light intensity $I(x', x'')$ coming from all points x'' on all surfaces (S) to the point x' and scattered by the surface at point x' (as defined by the scattering coefficient $\rho(x, x', x'')$). The factor $g(x, x')$ is a 'geometry' term expressing the visibility of point x from x' .

The calculation of rendering requires much computer processing time and internal memory. These technical problems can be avoided by simplifying the canopy by artificially creating elementary cells (EC, Wernecke *et al.*, 2000), nested canopies (Chelle & Andrieu, 1998) or multiscale-voxel spaces (Sillion, 1995). The model of Chelle & Andrieu (1999) calculates multiple scattering of radiation of a user-defined selection of wavelengths, enabling the calculation of red/far red ratios within the canopy. Further simplifications use Monte Carlo techniques (Wernecke *et al.*, 2000) or radiosity in turbid media (an approach Chelle adopted from Verhoef, 1985) and are said to promote calculation speed.

The 3D structure of the canopy can also be interpreted from its reflectance characteristics. Lewis (1999) constructed a canopy reflectance model, the Botanical Plant Modelling System (BPMS), which simulates the structure of individual plants in a canopy and/or underlying soil/topography from remote sensing data. The canopy radiation regime is simulated from the definition of the illumination conditions, camera imaging properties and plant and soil radiometric attributes using Monte Carlo ray tracing. The model is aimed at simulating the canopy short-wave radiometric regime and its component parts to allow studying the effect of plant geometry and other factors on the remote sensing signal.

4. Modelling plant morphology on basis of genetic expression

So far, only a few studies are reported on 3D modelling of growth and morphology of plants as influenced by genetic expression. This rather new research area will probably expand quickly, since the software tools to link genetic information to 3D visualisation are rapidly developing. A range of applications is possible, given the vast amount of data on genetic control of plant development. Especially for model plants in genetics like *Arabidopsis thaliana* (see <http://www.arabidopsis.org>) and barley the genetic basis of the morphology of plant organs is known. In the last few years most research focused on *Arabidopsis*, while some decades ago barley used to be the most important plant species in genetic research (e.g. Smith, 1951).

A private initiative of Laurens Lapré resulted in the C programme Lparser, which simulates plant growth with L-systems, with the option to create other genotypes by changing the projection rule before or during animation. Information at: <http://www.xs4all.nl/~ljlapre/main.htm>.

At the Institute of Plant Genetics and Crop Plant Research (Institut für Pflanzengenetik und Kulturpflanzenforschung, IPK) at Gatersleben, Buck-Sorlin linked the morphology of barley spike phenotypes to genetic markers (Buck-Sorlin & Bachmann, 2000). He used L-systems software to incorporate genetic information on expression of alleles into grammar rules which control growth and morphology (on basis of eight genes you can animate your own variety at: <http://taxon.ipk-gatersleben.de/homepage/index.html>).

A PhD research at Rijksuniversiteit Utrecht (RUU) will start this year to model pattern formation of *Arabidopsis* roots by combining genetic and bioinformatics research. Cell division and formation are measured as well as modelled. The effect on pattern formation of genetic expression and of the root's environment, mediated by growth hormones, especially auxin, will be studied. The Chair of Theoretical Biology has expertise in evolution of morphogenesis by gene networks, cell-to-cell signalling and physical cell interactions, preferably studied on *Dichtyostelium discoideum* (Marée & Hogeweg, 2001). Lindenmayer was head of this research group when he published his famous work on cellular automata (1968), that formed the basis of L-systems grammar.

5. 3D visualisations of plants applying limited or no biological rules

Since the technical possibilities to visualise virtual 3D objects became available world-wide, graphic designers have been applying a range of software tools for plant visualisations on internet sites, in musea, folders, gardening software, etc. For L-systems as well as other simulation tools, the technique to present the virtual object on screen or printer is similar. The shape of the object is determined by a set of polygons that are again determined by their cartesian x,y,z-co-ordinates in 3D space. Any software package that is able to produce these polygons is capable of presenting 3D objects. Software to construct 3D objects (e.g. Coreldraw, 3D Studio Max, Maya, VRML) and make visualisations (a feature available in Windows or Unix software) is commercially available (see Chapter 7 for a short overview).

The plant simulation software to produce the input for the virtual plant image is not always based on L-systems. Although L-systems are elegant mathematically, they were not universally adopted as a solution for the computer graphics community. Specialised software for the creation of plants, landscapes and worlds was created:

Plant Studio

3D visualisation of distinct species, mutants and crossings can be done with PlantStudio of Kurtz-Fernhout (<http://www.kurtz-fernhout.com>). This software does not manipulate the actual gene expression, but solely an empirical growth parameter that may originate from (multi)genetic control, environmental effects, or both. No interaction with the environment is computed. Growth and development per species solely depends on the time elapsed since emergence. The PlantStudio database consists of ca. 80 plant species, mainly garden flowers and some commercial crops (corn, sunflower, onion, cabbage, tomato, carrot).



Lace

Lace is a programme, based on Java applets that generate 3D plants according to properties that are typed in by the user using the Java interface. It is present on the Internet: <http://www.verio.com/claurel/lace/index.html>.

XFROG

Software for virtual plants that is strongly competitive to L-systems is the work of B. Lintermann and O. Deussen from University of Karlsruhe in Germany. Their software, called *xfrog*, is described in Lintermann & Deussen (1996). The best features of their approach to plant modelling are the interactive nature of *xfrog*, and the animations that could be played of plant development. In the animation web page that accompanies their 1996 paper, they showed a fern developing, an ivy plant growing around a stick, and a tree growing, blooming, and shedding its leaves (complete with colour changes). Their continued emphasis is on creating elegant models instead of true-to-nature development modelling. They emphasise getting 'visually correct shapes of plants' (Lintermann & Deussen, 1998) in an easy-to-use software package (Lintermann & Deussen, 1999).

Xfrog is easy to use, can produce beautiful images, and is able to show users the results of their changes instantaneously. *Xfrog* breaks down the parts of a plant into components according to required geometrical detail (not topological, i.e. leaves, branches, etc.), which seems to make the task easier. In *xfrog*, components such as leaf, tree, stems, wreathes, and balls are connected into a graph, which is traversed in order to draw a wireframe model of the plant. Some of the components (e.g., tree and leaf) have parameters that correlate to a plant's response to its environment, like phototropism and gravitropism. The virtual plants are 'bred' under the influence of moisture, soil chemistry, temperature, and neighbouring plants (effects are predefined in nine genotype-environment combinations). *Xfrog* first produces a wireframe model of the geometry, which is later processed using certain textures.

Perceptually realistic flower generation is claimed by Lu *et al.* (2001), who improved the description of flower form during its development and at the appropriate scale. L-systems have no way to simulate detailed flowers, except for an add-in that calculates bicubic surfaces with the aid of many parameters. Lu *et al.* used a simple patch surface description, requiring three basic factors (petal length, width and curvature).

6. Other 3D approaches of interest

6.1 Virtual reality

VRML (Virtual Reality Modelling Language) is the generally accepted standard tool to build and explore virtual worlds. VRML is a tool that extends the World-Wide Web with 3D visualisations. The major impulse for VRML was given at the First and Second World-Wide Web International Conference, leading to VRML 1.0 in 1994 and to WebSpace in 1995, produced by SGI (Silicon Graphics Int.). Following VRML 1.0, in January 1996 VRML 2.0 proposals were submitted: Moving Worlds (SGI), Dynamic Worlds (GMD), HoloWeb (Sun), Active VRML (MS), Out of this World (Apple), Reactive VE (IBM). By vote on the [www.vrml](http://www.vrml.org) web site, 70% chose for Moving Worlds, which formed the base for VRML 2.0, to be finalised in August 1996 after 74 revisions at the Siggraph Conference. At this moment, virtual world designs can be enhanced: by sound, movie texture, elevation grid, extrusion, background, etc. The behaviour can be simulated by use of sensors, collision detection, and interpolation. The scripting used is Java, VRMLScript/JavaScript or Java EAI.

VRML browsers (Cosmo/Live3D, Community Place, Liquid Reality, VRwave, Casus Presenter, WorldView, Toolbar) are mostly freely available. VRML code can be written in simple text editors and shows many similarities to the language C. VRML-files have a *.wrl extension. Manuals on the internet: <http://www.tecfa.unige.ch/guides/vrml/vrml97/spec/index.html>.

Some applications on the web:

- The application of L-systems modelling with VRML has resulted in Nervegarden ([link on biota.org](http://link.biota.org)), a virtual world consisting of a number of islands where user-made plant species are growing. Users can admire the other user's artificial plants, by walking or flying around on a bee!
- A multitude of virtual worlds has been created on the web. Good portals to start an inventory are: www.ccon.org, www.digitalspace.com, and www.biota.org.

Some interesting initiatives:

- A company in Wageningen that produces 3D applications from objects to the landscape scale is called *Green Dino* (<http://www.virtual-reality.nl>). It offers real time 3D viewers, scenario editors and PC-based modular virtual reality systems. Its object-oriented software is compatible with CAD, GIS and multimedia data. Green Dino is one of the suppliers of SGI equipment like multi-channel display systems upon 360 degrees field of view and a multi-user collaborative working system.
- CAVE Amsterdam: CAVE is the acronym for Cave Automatic Virtual Environment. A CAVE consists of a room of 3 x 3 m that exists of three walls and a floor which show the projections of a virtual world. Together with special glasses, the user views a world in 3D that seems very realistic, also because head movements result in a change of the projected images and sounds of the scene are incorporated.

6.2 Virtual life

Apart from the initiatives on plants, there are also many initiatives on virtual animals and hypothetical creatures. The international community of scientists and software developers on virtual life meet annually at the International Conference on Artificial Life (ALIFE). An internet portal to this community can be found at www.biota.org. It is beyond the scope of this review to elaborate on virtual animals, but the software tools and paradigms may be very similar to those of virtual plants.

The connection between virtual plants and animals may be at least two-fold:

- (1) multiple plants can interact and compete with each other at the scale of an ecosystem (Firbank & Watkinson, 1985), and animals compete for a certain fitness and reproduction as well (Sims, 1994), and
- (2) these interactions depend on the geometry of the virtual life form, which is generally described as a wireframe in cartesian space.

The well-known example of virtual creatures by Karl Sims is illustrated below:

Evolved virtual creatures by Karl Sims

Sims (1994) developed a system for the evolution and co-evolution of virtual creatures that compete in physically simulated 3D worlds. Pairs of individuals enter one-to-one contests in which they contend to gain control of a common resource. Realistic dynamic simulation, including gravity, collisions and friction, restrict the actions to physically plausible behaviour. A grammar related to L-systems and graftal is used to 'build' the creatures, and evolve them on the basis of the contest outcome. The best creatures are selected for further reproduction on the basis of a genetic algorithm, either by combination or mutation. The contest for best swimming capacity resulted in the creature in Figure 5.

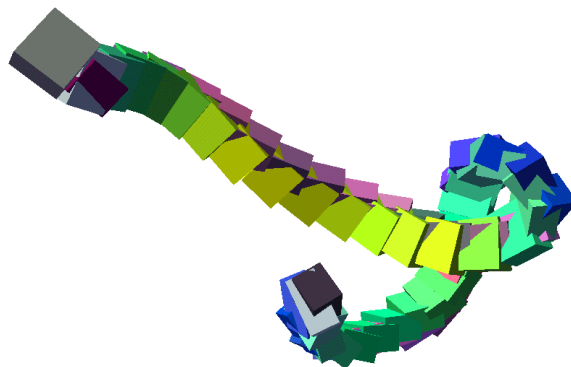


Figure 5. *Evolved swimming creature simulated by Sims (1994).*

7. Software for the visual presentation of 3D objects

In the 1980's computer aided design (CAD/CAM-software) was introduced in engineering and architecture. Since then a range of software packages was developed enabling 3D visualisation of objects on computer screens. Nowadays many packages are commercially available at an affordable price. Most basic programming languages like Delphi, C++ and JAVA have 3D functionality, but further processing to create animations, ray shading and other design features are easier and better done with specialised packages. For that purpose, 3D Studio Max, Maya and Lightwave are the most common and useful tools. Other advanced features can be found in Adobe Photoshop, Wirefusion, and Corel.

In general, graphic object modelling software first produces a wireframe model (Figure 6) of the object, to describe the structure. The second step, done with a rendering tool, is to put texture and shading on the wireframe. Sometimes, the modelling process is combined with natural objects, such as when leaves are scanned in to provide textures and to make the drawing of the whole tree simpler. (If the leaf were made up of many little polygons, it would take too long to draw the thousands that must be modelled on a fully grown tree). Mostly, several options for the format of the output file are available: DXF (for CAD), WRL (for VRML), OBJ (for WaveFront), LWO (for LightWave), etc., and appear mostly as polygons with their co-ordinates and texture.



Figure 6. *A wireframe model of a rose, scanned with 3D scanning equipment.*

The OpenGL software renders and visualises the constructed image. OpenGL is a cross-platform standard for 3D rendering and 3D hardware acceleration. The software runtime library comes with all Windows, MacOS, Linux and Unix systems. Its hardware acceleration facilitates geometry, real-time lighting, clipping, transformations, rendering and special effects (real-time fog, anti-aliasing, volume shadows, bump mapping, motion blur, transparency, reflections, 3D textures, volume rendering). OpenGL is the 3D power behind all professional 3D graphics and effects in movies. It is used in broadcasting, CAD/CAM/CAE, entertainment, medical imaging and virtual reality. OpenGL is designed to support future innovations in software and hardware.

8. Conclusions

The models that claim to have partial or full 3D functionality range from purely descriptive, focusing on graphic design, to process-based, simulating growth processes using in-depth knowledge of plant physiology. The choice for a descriptive or a process-based model depends on its specific purpose. This review gives an overview of both types of models, since 3D functionality as well as 3D visualisation is aimed. We list the conclusions on the basis of both types of models and their possible combinations, i.e. descriptive, process-based and coupled or functional-structural models (FSM).

- A first group of descriptive models was noticed that solely produces 3D illustrations. The models of this type currently are quite advanced in their computer graphics output (e.g. AMAP Genesis). Depending on their computer language, these models may be coupled to modules that calculate growth processes. The most prominent example is L-systems modelling (Lindenmayer & Prusinkiewicz, 1990), which was first used to simulate complicated plant forms but which later showed to be very useful in 3D simulation of growth processes.
- A second group of descriptive models visualises a hypothetical plant for further processing. This 3D image of the plant can be used to calculate processes that follow from its 3D structure, e.g. light interception, adsorption of pesticides, or transpiration. Probably the coupling of architectural and physiological models started here. A good example is the AMAPsim model, which simulates light interception and CO₂ assimilation on the basis of a fixed 3D structure (Barczy *et al.*, 1997).
- 3D models based on genetic expression are rather scarce. Such models are not necessarily process-based or descriptive, but have the functionality to change growth rules to obtain a 3D morphology in accordance with a specific genotype. No model seems to exist yet that simulates the complete sequence from gene expression, hormone metabolism, sink-source relations to plant growth.
- Process-based models (PBM) show an enormous range in their spatial resolution and their amount of incorporated mechanistic processes. Although PBM have always been quite successful in simulation of crop or forest yield, these models in first instance do not incorporate 3D structures of plant and/or crop. Yet, a limited number of PBM are now extended with (partial) 3D functionality, making simulation of 3D processes as well as visualisations possible. The coupling of the process-based and architectural parts of the models is still rather provisional (Hanan, 1997). The use of the available models for other crops or climates is very limited, urging for a more generic approach to coupling physiology and structure: FSM.
- Functional-structural models (FSM), also referred to as 'virtual plants', have been developed rather recently. They are mostly based on object-oriented programming, pipe models or Open L-systems. These models prove that coupling of architecture and physiology is possible with the current, powerful computer systems. The models up to now have only a limited number of process-based calculations at organ level (root or leaf), thereby averaging the other physiological processes at the plant or crop level. At this moment, only a few publications are available that incorporate all major plant processes like light interception, photosynthesis and transpiration at the organ level (Dauzat *et al.*, 2001; Hanan & Hearn, 2002). The latter models show significant improvements in the fits between measured and simulated values relative to their non-3D ancestors. However, the scientific knowledge to parameterise such complicated 3D models, i.e. the programming of a-biotic, morphogenetic and physiological processes at the scale of individual plant organs, requires a huge investment in research. Only larger research groups or co-operative initiatives are able to assemble all required data.

L-systems are the most frequently applied and most realistic approach to construct the architecture of (sets of) individual plants. It has proven to be a fast and flexible method to create all kinds of 3D images. The software package L-studio has the possibility to let the L-system communicate with the plants' 3D virtual environment, using C++ (Mech & Prusinkiewicz, 1999). It illustrates the possibility to combine a flexible, realistic structural model with a powerful computer language that can easily simulate processes like light interception, assimilation, transpiration, water uptake (roots), etc.

9. Summary

The aim of this literature and software review was to identify and evaluate the most recent, state-of-the-art research on three-dimensional (3D) plant modelling and visualisation. Recent developments in computer sciences and imaging tools have stimulated the research on 3D aspects of plant growth. A very diverse range of models exists that describe 3D architecture of plants. The architectural models range from global representations to very detailed models using multiple scales. The modelling languages based on string generation seem to be the most promising ones to incorporate 3D properties of plants in a biologically realistic way. Many commercial software packages exist that produce 3D visualisations of plants, yet most of them lack the possibility to calculate environmental effects on growth.

Models that combine 3D architecture and process-based simulation in relation to the plants' environment are often called functional-structural models or 'virtual plants'. Such models have been developed recently at a number of research institutes around the world. The architectural part of these models is mostly rather detailed, yet the physiological processes are only occasionally calculated at the detailed, i.e. the organ level. The most promising 3D modelling language is based on L-systems. This language uses the calculation of strings of symbols in a recursive (i.e. repetitive) way and also enables the incorporation of environmental effects.

Although computer techniques to model plant growth in 3D have developed rapidly, the scientific knowledge to program a-biotic, morphogenetic and physiological processes at the scale of individual plant organs is still very limited. International collaborations will facilitate the increase in knowledge on 3D processes in the development of plants.

10. Literature

- Barczi, J.F., P. de Reffye & Y. Caraglio, 1997.
Essai sur l'identification et la mise en oeuvre des paramètres nécessaires à la simulation d'une architecture végétale : le logiciel AMAPsim. In: *Modélisation et simulation de l'architecture des végétaux*. J. Bouchon, P. de Reffye and D. Barthélémy (Eds). *Science Update*. INRA Editions, Paris, France, pp. 205-254.
- Buck-Sorlin, G.H., 1999.
Barley Modelling and Simulation (*Virtual Barley*). WWW-document (<http://mansfeld.ipkgatersleben.de/bucksorlin/>).
- Buck-Sorlin, G.H. & K. Bachmann, 2000.
Simulating the morphology of barley spike phenotypes using genotype information. *Agronomie: Plant Genetics and Breeding* 20: 691-702 (also available online under www.edpsciences.org).
- Cellier, P., Ruget, F., Chartier, M., Bonhomme, R., 1993. Estimating the temperature of a maize apex during early growth stages. *Agric. For. Meteorol.* 63: 35-54.
- Chazda, R.L., 1985.
Leaf display, canopy structure and light interception of two palm species. *Am. J. Bot.* 72: 1493-1502.
- Chelle, M. & B. Andrieu, 1998.
The nested radiosity model for the distribution of light within plant canopies. *Ecol. Modelling* 111: 75-91.
- Chelle, M. & B. Andrieu, 1999.
Radiative models for architectural modelling. *Agronomie* 19: 225-240.
- Colasanti, R.L. & R. Hunt, 1997.
Resource dynamics and plant growth: A self-assembling model for individuals, populations and communities. *Funct. Ecol.* 11 (2): 133-145.
- Colasanti, R.L., R. Hunt & A.P. Askew, 2001.
A self-assembling model of resource dynamics and plant growth incorporating plant functional types. *Funct. Ecol.* 15 (5): 676-687.
- Dauzat, J. & M.N. Eroy, 1997.
Simulating light regime and intercrop yields in coconut based farming systems. *European Journal of Agronomy* 7: 63-74.
- Dauzat, J., B. Rapidel & A. Berger, 2001.
Simulation of leaf transpiration and sap flow in virtual plants: model description and application to a coffee plantation in Costa Rica. *Agr. For. Meteorology* 109: 143-160.
- Díaz-Ambrona, C.H., A.M. Tarquis & M. Inés Mínguez, 1998.
Faba bean canopy modelling with a parametric open L-system: a comparison with the Monsi and Saeki model modelling. *Field Crops Research* 58: 1-13.
- Dickmann, D.I., D.A. Michael, J.G. Isebrands & S. Westin, 1990.
Effects of leaf display on light interception and apparent photosynthesis in two contrasting *Populus* cultivars during their second growing season. *Tree Physiology* 7: 7-20.
- Diggle, A.J., 1988.
ROOTMAP - a model in three-dimensional co-ordinates of the growth and structure of fibrous root systems. *Plant and Soil* 105: 169-178.
- Drouet, J.-L. & R. Bonhomme, 1999.
Do variations in local leaf irradiance explain changes to leaf nitrogen within row maize canopies? *Annals of Botany* 84: 61-69.
- Firbank, J. & A.R. Watkinson, 1985.
A model of interference within plant monocultures. *J. of Theoretical Biology* 116: 291-311.

- Fournier, C. & B. Andrieu, 1998.
A 3D architectural and process-based model of maize development. *Annals of Botany* 81: 233-250.
- Fournier, C. & B. Andrieu, 1999.
ADEL-maize: an L-system based model for the integration of growth processes from the organ to the canopy. Application to regulation of morphogenesis by light availability. *Agronomie* 19: 313-327.
- Fournier, C. & B. Andrieu, 2000.
Dynamics of the elongation of internodes in maize (*Zea mays* L.): analysis of phases of elongation and their relationship to phytomer development. *Annals of Botany* 86: 551-563.
- Gautier, H., R. Mech, P. Prusinkiewicz & C. Varlet-Grancher, 2000.
3D Architectural modelling of aerial photomorphogenesis in white clover (*Trifolium repens* L.) using L-systems. *Annals of Botany* 85: 359-370.
- Godin, C., E. Costes & Y. Caraglio, 1997.
Exploring plant topology structure with the AMAPmod software: an outline. *Silva Fennica* 31: 355-366.
- Godin, C., Y. Guédo & E. Costes, 1999.
Exploration of plant architecture databases with the AMAPmod software illustrated on an apple tree hybrid family. *Agronomie* 19(3-4): 163-184.
- Godin, C., 2000.
Representing and encoding plant architecture: A review. *Ann. For. Sci.* 57: 413-438.
- Goudriaan, J., 1977.
Crop meteorology: a simulation study. Simulation Monographs, Pudoc, Wageningen, 249 pp.
- Gould, K.S., J.P.W. Young & E.G. Cutter, 1992.
L-systems analysis of compound leaf development in *Pisum sativum* L. *Annals of Botany* 70: 189-196.
- Hanan, J.S., 1997.
Virtual plants - integrating architectural and physiological models. *Environmental Modelling & Software* 12: 35-42.
- Hanan, J. & A.B. Hearn, 2002.
Linking physiological and architectural models of cotton (submitted to *Agricultural Systems*).
- Hanan, J.S. & P.M. Room, 1997.
Practical aspects of virtual plant research. In: M.T. Michalewicz (Ed.), *Plants to ecosystems. Advances in Computational Life Sciences*, pp. 28-44.
- Higashide, T., M. Takaichi & H. Shimaji, 2000.
Modelling of cucumber growth using the L-system. *Acta Horticulturae* 519: 43-51.
- Honda, H., P.B. Tomlinson & J.B. Fisher, 1981.
Computer simulation of branch interaction and regulation by unequal flow rates in botanical tress. *Am. J. Bot.* 68: 569-585.
- Jallas, E., R. Sequeira, P. Martin, S. Turner & M. Cretenet, 1998.
COTONS, a cotton simulation model for the next century. Seminar proceedings of l'Unité de Biométrie et Intelligence Artificielle du centre INRA, Toulouse, France.
- Kaitaniemi, P., J.S. Hanan & P.M. Room, 2000.
Virtual sorghum: visualisation of partitioning and morphogenesis. *Computers and Electronics in Agriculture* 28: 195-205.
- Kajiya, J.T., 1986.
The rendering equation. *Computer Graphics* (SIGGRAPH '86 Proceedings) 20(4): 143-150.
- Kropff, M.J. & H.H. van Laar (Eds.), 1993.
Modelling Crop-Weed Interactions, CAB International, Wallingford, 274 pp.
- Kurth, W., 1994.
Growth Grammar Interpreter GROGRA 2.4: A software tool for the 3-dimensional interpretation of stochastic, sensitive growth grammars in the context of plant modelling. Introduction and Reference Manual, 190 p. *Berichte des Forschungszentrums Waldökosysteme der Universität Göttingen*, Ser. B, Vol. 38 (1994).

- Kurth, W. & B. Sloboda, 1997.
Growth grammars simulating trees - an extension of L-systems incorporating local variables and sensitivity. *Silva Fennica* 31: 285-295.
- Lewis, P., 1999.
Three-dimensional plant modelling for remote sensing simulation studies using the Botanical Plant Modelling System. *Agronomie* 19: 185-201.
- Lindenmayer, A., 1968.
Mathematical models for cellular interactions in development, Parts I and II, *J. Theor. Biol.* 18: 280-315.
- Lintermann, B. & O. Deussen, 1996.
Interactive modelling and animation of branching botanical structures. In: R. Boulic and G. Hegron (Eds.), *Seventh International Workshop on Computer Animation and Simulation* (EGCAS'96). New York, NY: Springer-Verlag Wien, pp. 139-151.
- Lintermann, B. & O. Deussen, 1998.
A modelling method and interface for creating plants. *Computer Graphics Forum* 17 (1) (March).
- Lintermann, B. & O. Deussen, 1999.
'Interactive Modelling of Plants' IEEE Computer Graphics and Applications 19 (1) (January/February). (see: <http://www.computer.org/cga/cg1999/g1toc.htm>)
- Lu, Z., Cl. Willis & D. Paddon, 2001.
Perceptually realistic flower generation. *Computer Graphics Forum* 20: 1-8.
- Marée, A.F. & P. Hogeweg, 2001.
How amoeboids self-organise into a fruiting body: multicellular co-ordination in *Dicthyostelium discoideum*. *Proc. Natl. Acad. Sci. USA* 98 (7): 3879-3883.
- Mech, R. & P. Prusinkiewicz, 1999.
Visual models of plants interacting with their environment. Proceedings of SIGGRAPH 96 (New Orleans, Louisiana, August 4-9, 1996). In: *Computer Graphics Proceedings, Annual Conference Series, 1996*, ACM SIGGRAPH, pp. 397-410.
- Niklas, K.J., 1988.
The role of phyllotactic pattern as a 'development constraint' on the interception of light by leaf surfaces. *Evolution* 42: 1-16.
- Pearcy, R.W. & W. Yang, 1996.
A three-dimensional crown architecture model for assessment of light capture and carbon gain by understorey plants. *Oecologia* 108: 1-12.
- Perttunen, J., R. Sievänen, E. Nikinmaa, H. Salminen, H. Saarenmaa & J. Väkevä, 1996.
LIGNUM: a tree model based on simple structural units. *Ann. Bot.* 77: 87-98.
- Prusinkiewicz, P. & J. Hanan, 1989.
Lindenmayer Systems, Fractals, and Plants, Lecture Notes in *Biomathematics* 79, Springer-Verlag, Berlin.
- Prusinkiewicz, P. & A. Lindenmayer, 1990.
The Algorithmic Beauty of Plants. Springer-Verlag, Berlin.
- Room, P. & J. Hanan, 1995.
Virtual cotton: a new tool for research, management and training. In: G.A. Constable & N.W. Forrester (eds.), *Challenging the Future: Proceedings of the World Cotton Research Conference - 1*; Brisbane. CSIRO Publishing, Melbourne, pp. 40-44.
- Room, P., J. Hanan & P. Prusinkiewicz, 1996.
Virtual plants; new perspectives for ecologists, pathologists and agricultural scientists. *Trends in Plant Science*, Elsevier Trends Journals 1 (1): 33-38.
- Salminen, H., H. Saarenmaa, J. Perttunen, R. Sievänen, J. Väkevä & E. Nikinmaa, 1994.
Modelling trees using an object-oriented scheme. *Math. Comp. Model.* 20 (8): 49-67.
- Schmieders, B.J., 1999.
A quantitative analysis of inter-specific competition in crops with a row structure. PhD thesis, Agricultural University Wageningen, 165 pp.

- Shibusawa, S., 1992.
Hierarchical modelling of a branching growth root system based on L-system. *Acta Horticulturae* 319 (2): 649-664.
- Shinozaki, K., K. Yoda, K. Hozumi & T. Kira, 1964.
A quantitative analysis of plant form - the pipe model theory. I: basic analyses. *Jpn. J. Ecol.* 14: 97-105.
- Sievänen, R., E. Nikinmaa, P. Nygren, H. Ozier-Lafontaine, J. Perttunen & H. Hakula, 2000.
Components of functional-structural tree models. *Ann. For. Sci.* 57: 399-412.
- Sillion, F.X., 1995.
Hierarchical solution techniques for realistic rendering. In: State of the Art Report - Graphicon '95 Conference, St. Petersburg, Russia.
- Sims, K., 1994.
Evolving 3D morphology and behaviour by competition. *Artificial Life IV Proceedings*, R. Brooks and P. Maes (eds.), MIT press, pp. 28-39.
- Smith, L., 1951.
Genetics and cytology of barley. *Bot. Rev.* 17: 1-51; 133-202; 285-355.
- Verhoef, W., 1985.
Earth observation modelling based on layer scattering matrices. *Remote Sensing of Environment* 17: 164-178.
- Viennot, X.G., G. Eyrolles, N. Janey & D. Arquès, 1989.
Combinatorial analysis of ramified patterns and computer imagery of trees. In: SIGGRAPH '89, ACM, Boston, USA, pp. 31-40.
- Wernecke, P., G.H. Buck-Sorlin & W. Diepenbrock, 2000.
Combining process- with architectural models: The simulation tool VICA. *SAMS (Systems-Analysis-Modelling-Simulation)* 39: 235-277.
- Wilson, P.A. & S. Chakrabarty, 1998.
The virtual plant: a new tool for the study and management of plant diseases. *Crop Protection* 17 (3): 231-239.
- Zeide, B., 1991.
Fractal geometry in forestry applications. *For. Ecol. Manag.* 46: 179-188.

Appendix I.

Explanation of technical terms

The terms, listed below, are underlined the first time they are mentioned in the report.

| | |
|-----------------------|---|
| Axial tree | Scheme of plant structure consisting of vertices connected by edges, used in L-systems topology |
| Cartesian space | 3D continuum described by an X,Y,Z co-ordinate system |
| Edge | Connection between vertices or border of a module or basic element |
| Fractal | Mathematical construct of a structure that is self-similar at an infinite number of scales (when zooming in/out) |
| FSM | Functional Structural Model |
| Geometry | Quantitative description of an object by the position of its outside boundaries in 2D or 3D (not a vector approach) |
| L-system | Formal grammar for string generation to model growing or static objects in 2D or 3D |
| Morphogenesis | Development of the form of a plant organ |
| Multiple scattering | Light beams are scattered in all directions due to reflection from and transmission through objects |
| PBM | Process Based Model |
| Polygon | Triangle or quadrangle described by its corners |
| Topology | Description of an object (plant, landscape) on the basis of its functional components and their connections |
| Turtle interpretation | Direction of growth or movement in 3D space, modelled in analogy to a turtle moving forward |
| Radiosity | Radiation of one object on the other, consisting of reflected light having an object-dependent spectrum |
| Ray tracing | Calculation of the tracks of light beams in a 3D scene; enables shadows, transparency, reflection, refraction |
| Rendering | Making a 2D image of a 3D scene using given structure, colour, texture and light conditions |
| Tree graph | Plant description based on a network of components and their connections, representing plant topology |
| Vertex | Top of a vector, module or basic element in 3D space |
| Virtual plant | Simulated plant in 3D, which structural dynamics respond to environmental conditions |
| Voxel | Pixel in a 3D image |
| VRML | Virtual Reality Modelling Language |
| Wireframe | Frame of wires that connect points (vertices) of a geometric 3D model |

Appendix II.

3D models: characteristics and origin

| | Functionality | Structure /Function* | | Language | Origin |
|----------------|--|----------------------|-----------|-----------------------------------|--|
| AMAP | | mod | mech | C++ | CIRAD-France |
| AMAP Genesis | Creates state-of-the-art 3D scenes and animations of plants, ecosystems, etc. Purely illustrative | mod | descr | Combination of L-systems and Maya | Commercially available, see www.bionatics.com |
| ADEL Maize | Maize crop growth is simulated to the organ detail on the basis of temperature-related development and local light-controlled photosynthesis | mod | mech | L-systems | INRA-Grignon (Fournier & Andrieu) |
| COTONS | Cotton growth simulation similar to ADEL Maize, and including water and N relations | mod | mech | - | INRA-Toulouse (Jallas <i>et al.</i> , 1998) |
| Virtual Cotton | Growth of cotton on basis of temperature dependent morphogenesis | mod | desc | L-systems | CPAI (Room & Hanan, 1995) |
| GROGRA | Generic models based on string generation | mod | mech | Grogra | Göttingen-Germany (Kurth, 1994) |
| INTERROW | Carbon-based model, uses simple 3D structures of the crop canopy for photosynthesis and transpiration | glob | mech | Fortran | Wageningen (Schmieders, 1999) |
| Lace | Generation of plant images by tuning allometric parameters | mod | desc | JAVA | Internet (C. Laurel) |
| LIGNUM | Pipe model allocates assimilates, photosynthesis at organ level. For woody species | mod | mech | - | Finland (Perttunen <i>et al.</i> , 1996) |
| Lstudio/VLAB | Generic models based on string generation | mod | desc/mech | L-systems | Univ. Calgary (Prusinkiewicz) |
| Plant Studio | Generation of plant growth by empirically tuning allometric parameters | mod | desc | C++ | Internet (www.kurtz-fernhout.com) |
| XFROG | Illustrations of growth by empirical string generation | mod | desc | Xfrog | Univ. Karlsruhe (Lintermann & Deussen) |
| YPLANT | | mod | mech | Pascal | UK (Percy & Yang, 1996) |

* mod, modular; glob, global; mech, mechanistic; desc, descriptive

Appendix III.

Research groups that use L-systems or comparable string notations

1. CIRAD in France

At CIRAD a group of scientists has combined plant development research with bioinformatics. The work on plant growth simulation and synthetic 3D images actually started with the modelling of palm tree architecture in Africa (Chazda, 1985). This modelling expertise of CIRAD has been assembled in the AMAP™ software (Atelier de Modelisation et d'Architecture des Plantes or Plant Modelling Programme) (Godin *et al.*, 1997; 1999). In conjunction with INRA and in relation with the national and international scientific community, AMAP designs and develops the necessary methods for measuring, analysing and simulating the architecture, functioning, growth and production of plants, crops and plant stands, be they annual or perennial, tropical or temperate. Its research involves a wide range of expertise: biology, botany, ecology, applied mathematics, information technology. AMAP™ consists of a number of tools:

- (a) AMAPmod is software to systematically organise measurement data on plant architecture, explore the database and perform statistical tests.
- (b) AMAPsim (Barczi *et al.*, 1997) simulates light interception and/or ground cover of the plants, having a fixed 3D architecture that has been derived from AMAPmod or directly from measurements. AMAPsim can also simulate plant growth by interpolation between fixed stages of plant growth, and can supply 3D visual output. AMAPsim is written in C++ and has been applied to tobacco, pine, pea, cotton, etc.
- (c) AMAPpara simulates the tree growth within a forest stand.
- (d) AMAPmeca simulates biomechanical constraints.
- (e) AMAPfysio, simulating plant physiological processes, consists of:
 - (f) PlantFlow, calculates the carbon balance, transpiration flow and phloem flow.
- (g) AMAPlux simulates the radiation exchange at the leaf surface (Dauzat & Eroy, 1997), using the modules (h) and (i):
 - (h) MIR/MUSC: calculates incoming radiation (MIR) and multiple scattering (MUSC).
 - (i) ART calculates the transfer of light beams within the 3D canopy.

AMAPlux is able to simulate the energy balance of the leaf as well as stomatal conductivity. At CIRAD L-system software is also used to simulate 3D plant architecture: a recent paper (Dauzat *et al.*, 2001) describes the current possibilities to couple L-system modelling and mechanistic modelling of transpiration for coffee plantations.

The commercial software package *AMAP Genesis*

The new simulation technology, called AMAP™, has a strong scientific basis. On the basis of AMAP, commercial software packages of AMAP Genesis were developed:

- *natFX* delivers an advanced solution for 3D plant modelling and animation. Derived from AMAP® technology and integrated into the Maya® environment (currently using Maya 3.0). *natFX* enables 3D artists to model, with only a few mouse clicks, realistically textured plants.
- *REALnat* meets the growing industry demands required to populate 3D realtime visual simulations with virtual plants.

The company put a lot of effort into making the *REALnat* interface intuitive, allowing developers to efficiently generate simple geometric plant shapes such as trees, bushes, buds and flowers. *REALnat* equally disposes a wide array of graphic options that facilitate integration into real-time environments. The program is therefore capable of producing many textures that are all visually coherent.

2. INRA in France

ADEL Maize, developed at INRA-Grignon, is an L-system based model that considers the canopy as a set of individual plants (Fournier & Andrieu, 1999). It combines a 3D model of maize development with physical models computing the light distribution in the 3D structure. The growth model is based on CERES-Maize. Phytomer development is based on temperature, calculated for the apices, i.e. at the outer boundaries of the plants, using energy balance calculations from Cellier *et al.* (1993). The temperature-based growth sets the sink strength. Dry matter production is calculated using the light use efficiency concept. PAR (photosynthetically active radiation) is calculated locally on individual leaves, receiving PAR from a limited set of parts of the hemisphere (multiple scattering calculations were judged unnecessary and are not incorporated in this model version). The modelling results were satisfying, although the model did not incorporate photomorphogenesis. A new version incorporates sink-source dynamics at the level of individual organs instead of sink at plant level. More information on the data used for the model can be found in Drouet & Bonhomme (1999) and Fournier & Andrieu (1998; 2000).

ADEL Wheat simulates wheat growth in 3D, is less far developed than ADEL Maize, but also uses temperature sums to calculate development of each plant organ separately.

3. Institute of Forest Biometry and Informatics, Göttingen, Germany

For more than a decade scientists in Göttingen have been developing models for the architecture of trees. In coupling these models to environmental variables, especially the work of Wilfried Kurth (e.g. Kurth & Sloboda, 1997) is of interest. He developed the grammar language GROGRA (Kurth, 1994), not basically different from the concept of L-systems. GROGRA was developed by extending the classical parametric L-systems by (1) declaration of stochastic parameters, (2) global sensitivity (enabling e.g. reactions on external stimuli like overshadowing or contact from neighbouring plants), (3) a two-phase rule application concept, (4) nested grammar construction (inclusion of one grammar as submodule of another).

Recently, the group of Kurth has coupled models on microclimate from CIRAD (Dauzat & Eroy, 1997), GROGRA, the hydraulic model HYDRA, and AMAP. This activity is done within the PhD work of G. Jürgenson, who aims at linking existing process-oriented and structural models. Process-related information and structural information actualise each other by application of computer science approaches like rule-based systems, object-oriented simulation and communicating processes. The application prototype will be model-intercepted radiation, transpiration and architectural development of trees. Three basic models will be coupled together: a structure-oriented growth model of tree crowns, a model of microclimate inside the crown, and a model of water flow in the tree. The technical realisation will be carried out in a generic way, i.e., each of the used basic models can be substituted by another one which simulates the same phenomenon (although possibly in another way, or at a differing level of detail). With this linkage of models, Jürgenson hopes to contribute to a better understanding of the influence of spatial heterogeneity in forest stands on transpiration dynamics.

Tree growth is simulated with AMAPsim as well as with GROGRA (Kurth, 1994). In interaction with canopy structure, spatially heterogeneous transpiration rate will be calculated with the models MIR and MUSC from CIRAD.

4. University of Halle, Germany

The group around Prof. Wulf Diepenbrock has intensified research on 3D plant modelling the last two years. Especially the work of Wernecke on light interception of canopies, using the modelling tool VICA (VIRtual CANopies) based on Monte Carlo ray tracing techniques (see Chapter 5), and Buck-Sorlin on L-systems of several barley varieties (see also Chapter 4), is noteworthy.

5. University of Calgary, Canada

A vast amount of 3D plant models is developed on the basis of L-systems at the department of Computer Science at the University of Calgary, as is shown in e.g. *The Algorithmic Beauty of Plants* (Prusinkiewicz & Lindenmayer, 1990). These plant models are endogenous and do not interact with the plant's environment. Yet, these so-called closed L-systems can incorporate effects of temperature (given by the modeller per time step) on the plant's development, but this is a unidirectional process and not an interaction. The endless possibilities of L-systems to create plant structures and their 3D visualisation on computers has promoted its distribution over the world. In some way the architectural information of the model can very easily be transferred to a visual format. In recent years, more attention is being paid to the possibilities to have the virtual plants interact with their environment:

Mech & Prusinkiewicz (1999) (Univ. Calgary), as well as Hanan & Hearn (2002) (from CPAI and Australian Cotton Research Institute, respectively), extensively reviewed the possibilities of Open (environmentally-sensitive) L-systems. Open L-systems are an extension of L-systems, using constructs for modelling the bi-directional information exchange between plants and their environment. The authors apply L-systems in combination with simulation of the plant's environment (light, collision detection, soil water content).

6. Centre for Plant Architecture and Informatics (CPAI), Brisbane, Australia

Research at CPAI focuses on 3D biological dynamics at the spatial scale of individual plants, their organs, and their immediate neighbours. The Centre is helping to fill knowledge gaps between developmental biology, ecology, and the agricultural sciences, by forming new links between them and computer science. A major goal is to enhance and make available to biological scientists new tools and techniques for collecting and handling dynamic spatial information. Prototype tools have been developed by the Centre's scientists and their international collaborators (Room *et al.*, 1996). For example, FLORADIG is software to automate 3D-digitiser measurement of plant architecture and locations of insects on plants (Hanan & Room, 1997). The Virtual Laboratory in Botany (vlab, predominantly constructed in Calgary but with help of Hanan) is a software environment for 3D modelling and simulation of plant morphogenesis and insect activity. Current research focuses on combining architectural models with physiological models (M. Renton), incorporating genetic and hormonal signals (C. Beveridge), optimising production rules using genetic algorithms.

Appendix IV.

3D imaging software

Information on the architecture of the actual plant is required for any 3D-plant model that aims at realistic simulations. The spatial properties of the plant, geometrical as well as topological, are required to parameterise and validate 3D plant models. Such models simulate the 3D position and size of each individual organ within a given plant. These organs, i.e., stems, leaves, flowers, etc., have distinct colour and surface properties, which may be essential for a given species, variety or even mutant. Which methods exist that can acquire organ-specific 3D geometry, colour and texture, and how do they process and store the 3D information?

In the past, manual measurements and manual input into a database were used. Nowadays, imaging equipment is commercially available which is to a certain extent automated and stores the 3D data in a digital format. Below, we list a number of 3D imaging systems that generate 3D images of objects. These systems are evaluated for their capabilities to acquire 3D information of growing plants.

1. Laser scanner

A laser beam scans the object, typically like the electron beam within a television, i.e. from left to right, down from the top. Major advantages of this method are its high accuracy and its robustness to measure local objects. Disadvantages are the fixed resolution (depending on the thickness of the laser beam), which may be crucial for scanning small flowers, and scattering as a result of the translucent character of some objects, like thin leaves.



Hand-held laser scanner (left) and the produced image (right). Notice the different positions of the light source and the receptor, in order to detect laser shifts by the triangulation method.

2. Touch probes

A hand-held probe touches a specific point of an object, and when the user presses a button the touch probe transmits a signal to a receiver. The receiver calculates the 3D co-ordinates of the 'touched' point by synchronously receiving information from two other, fixed points (3-point measurement). The method is very robust and errors can be corrected instantaneously. However, the method is very time-consuming and the resulting 3D image is only very schematic.

3. Profiling

The silhouette of an object is isolated from a mono colour background by chroma-keying of its digital picture. From a number of viewing angles, realised by turning the object on a turning table, the silhouette is created. The total of silhouettes is used to calculate the 3D geometry of the object. The software describes the 3D data in the format of a wireframe. The colour and texture of the different object parts is available in the taken pictures. This texture information is mapped onto the polygons that form the 'building blocks' of the wireframe. The method is rather robust, but concavities can not be handled.

Concavities occur when holes in a surface, or empty spaces behind parts that are situated in front, are not seen in the silhouette profile, and thus lead to amorphous 'blobs'. Removing these artefacts by 3D editing software is very time-consuming. Another disadvantage of the profiling method is its difficulty to register thin objects like twigs and petioles. The final 3D image may not show the twigs if the twig silhouettes do not match between the different viewpoint images and subsequent merging may not produce a shape but only emptiness.



Scanstation for the profiling method (left) and one of a serie of pictures of Arabidopsis (right).

4. Structured light

A light pattern is projected onto an object and deformation of the pattern renders 3D information. This method functions reasonable for relatively large, solid objects. It has been used regularly for human faces. The method can hardly distinguish thin structures like stems and twigs. The method only renders a 2.5 D image, and images of the back of the object have to be collected separately and should be merged with those of the front image, which may result in loss of information and can be time-consuming. No specific results are reported for plants.

5. Photogrammetry

This method extracts 3D information from a large number of images, taken from various positions. On each image, specific spots like edges or ridges have to be highlighted and tagged manually by mouse clicking. The shifts in space, of all highlighted structures between the different pictures, brings about the 3D shape of the edited object. The method is not reliable, error prone and only works well for simple, large objects. It is not recommendable for plants, with their complex structures and lack of contrast.

In conclusion, the best methods for 3D imaging of plants seem to be (1) laser scanning and (2) profiling. The laser method is rather expensive and does not produce texture and colour. The profiling method is not so expensive, captures texture and colour as well, is basically simple and can easily be adjusted to the user's wishes. In the case the optimised set-up still leads to loss of 3D information, in both methods the 3D images can be corrected afterwards using commercially available editing software.

