

The modelling of growing natural forms

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Abstract

The tutorial introduces a variety of ways of modelling branching biological structures. Methods for generating plant like images, such as Diffusion Limited Aggregation and Iterated Function Systems are briefly discussed. The main concentration is on two methods that can be used to model the growth of such structures. The powerful L-systems method gains explanatory power by use of parameters, context and environmental sensitivity, enabling natural features such as leaf drop, self-pruning and self-seeding. The method of Kaandorp for modelling marine sessile organisms such as sponges and corals, in which geometric features are “grown” directly, is compared for veracity with observed organisms in different physical environments.

1. Introduction

This tutorial is structured in three parts. Part one describes a variety of methods for producing images of plant like forms. This discusses the natures of various types of depiction, gives a historical overview of specialised studies and examples of Iterated Function Systems (IFS) and Diffusion Limited Aggregation (DLA). Part two concentrates on L-systems. Refinements to the basic method that enable modelling of growing structures are described and the section ends with two case studies of fungus and tree growth. References for parts 1 and 2 (by Jones) appear at the end of part 2. Finally, the modelling of growing marine sessile organisms using geometric transformation rules which relate to environmental factors is described in part three (by Kaandorp). This technique is shown to have close similarities with observations from nature.

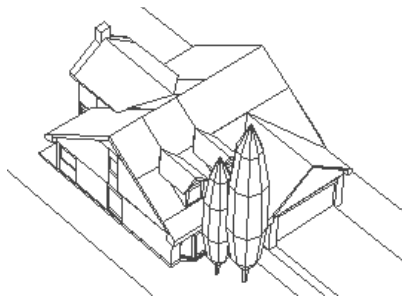


Figure 1.1: Polygonal trees in an architectural drawing

1.1. Realism or not?

The style of depiction should depend on the potential use of the image. In flight and driving simulators, movement may mask inadequacies. Many systems use “billboarding” to represent trees as one or more intersecting scanned planar images rotated always to face the location of the observer (as by Visual Environments Inc. ¹). Architectural line drawings may depict trees as simple polyhedral structures, to match the complexity of other features (fig. 1.1) (by the late John Lansdown ²). The rough cross-hatched texture of computer generated trees by Campa ³ looks natural in particular types of architectural illustration (fig. 1.2).

Poynter ⁴ developed a scheme for rapid production of images as interpretations of cartographic data sets (fig. 1.3). Terrain is depicted from height information. Individual fields are delineated and texture mapped according to their crops,

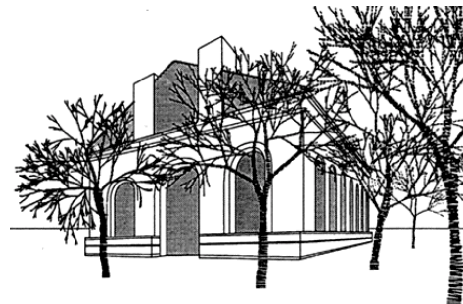


Figure 1.2: Campa's sketchy trees in an architectural illustration



Figure 1.3: *Fields, trees, hedgerows and a forest*

with hedgerows, trees and forests shown in a stylised way, using level of detail variation,

Synthesised images that directly model the appearance of specific trees can achieve high levels of photo-realism, both structurally and through the use of texture mapping. The maple (fig. 1.4) created by Thum is an example. Thum also generated models of other tree forms⁵.

These examples from Middlesex University and other methods discussed below show a wide range of styles of plant depiction. By “plant” we implicitly include other branching growing structures. The variety reflects different needs, from quick spatial impressions to photo-realism, from simple shape models to interpretation of underlying biological principles. Each of the illustrations shown can be considered successful in its own right. In all cases, fitness for purpose is a criterion in deciding on a successful method.



Figure 1.4: *A maple, modelled by Thum. The close up (lower image) shows detailed bark, leaf texture and shape.*

1.2. Some historical developments

Computer models of growing processes should be soundly based in biology. Classics by Thompson⁶ and Stephens⁷ and web sites^{8, 9} are useful and readable. The Register of Ecological Models¹⁰ lists downloadable ecological modellers.

Honda¹¹ gives a parametric description of tree skeletons. He distinguishes monopodial branching (in which one sub-branch continues in the same direction as the originating branch) from dichotomous branching. He influenced the work of Aono and Kunii¹², which preceded the popularisation of and is similar to the well known L-systems method, described in detail later. They model a variety of genuses of tree, and give data that enables the results to be duplicated. Smith¹³ describes the method of “graftals”, also an independently developed method related to L-systems. The name he chose connects the near fractal structure of trees to their graphic depiction. Trees are fractal¹⁴ to the extent that they display “statistical self similarity”, with branches and sub-branches having scaled down structural likeness to the tree as a whole. However, this is seen in nature to be limited to about seven levels of sub-copies, rather than the infinitesimal subdivision allowed in fractal theory. This observation can be useful in limiting tree models based on fractal methods. Estvanik¹⁵ gives detailed information on implementation of graftals.

Bloomenthal¹⁶ models tree branches as generalised cylinders whose axes follow spline curves. Control points for branches are created by a recursive algorithm. A high degree of realism is achieved by texture mapping of bark and leaves, and level-of-detail features are included for viewing at different distances.

Reeves and Blau¹⁷ illustrate collections of trees using particle systems to add leaves to an underlying branch structure. The structure is generated recursively, with separate algorithms applied to affect growth by features such as gravity, prevailing wind and sunlight. A typical forest image requires of the order of one million particles, which are sorted and rendered with colours taking into account sunlight and shade. The emphasis is on creating an effective image rather than directly modelling botanical data.

De Reffye et al.¹⁸ describe what is now known as the AMAP method (Atelier de Modélisation de l’Architecture des Plantes)¹⁹. Françon and Lienhardt²⁰ describe its goal as:

the definition of a rigorous and faithful model of plants and plant growth, for botanical and agronomical purposes. The method is based on botanical knowledge, and is validated through observations and measures on natural plants (p 27).

The method takes account of whether growth is continuous or not, how branches develop, whether branches have a tendency to grow towards the horizontal (plagiotrop) or vertical (orthotrop), and is based on tropical tree data collected by Hallé, Oldeman and Tomlinson²¹.

Holton²² models a tree structure as a collection of unbroken strands running from the tree base (or root) to terminate at a leaf or branch. The thickness of a structural element depends on the numbers of strands passing through it. Gravity and nutrition supply are also taken into account.

Weber and Penn²³ use curved and tapering cones for the trunk, with branching structures defined recursively. They list 80 parameters used to control structure in their system for each of four different tree types. These govern features such as overall tree shape, size, levels of recursion, angles of branching and number of leaves per shoot. They also list the following features of a “good” tree modelling and rendering system, which they claim are achieved by their method:

- an appropriate level of resolution and quality;
- three dimensional modelling to enable realistic animation;
- accurate branching structure;
- capability of modelling a wide variety of tree types;
- random variations;
- time-dependent variability due to natural forces;
- concise and easily understandable modelling structure;
- models of different resolution to be viewed at different distances;
- stable and easy-to-use system.

Cellular automata, in which the contents of pre-defined cells change at regular clock ticks using functional rules dependent on the contents of neighbour cells, have been used in a number of plant studies. Arvo and Kirk²⁴ and Greene²⁵ use them to “train” climbing plants against existing structures. In particular, Greene uses strands, as Holton did later, to give varying thickness in roots negotiating their way around rocks. Colasanti and Hunt²⁶ create a 2D growing environment through cellular automata, in which the contents of cells change at regular clock ticks depending on the contents of neighbouring cells. The above ground cells are initially loaded with a parameter representing sunlight energy, which subsequently “seeps” down through cells, with cells in shade when growing structures cells above them absorb light. Below ground cells are loaded with soil nutrient levels, which are absorbed by growing roots, to be replenished in a simulation of natural processes. Branching Benes uses location information and the equivalent of a shadow buffer algorithm to assess the amount of light received structures grow to seek appropriate resources. Stuart uses cellular automata to model the spread of forest fires²⁷, cells are defined to contain trees, shrubs, rock or bare soil with given levels of moisture. Fire affects these levels and spreads in a way controlled by local terrain slope and strength and direction of the wind.

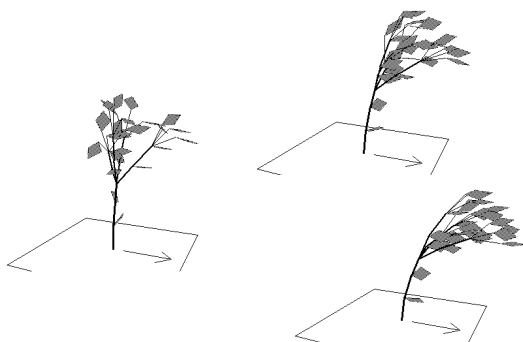


Figure 1.5: Stills from animations of wind-blown trees, in a light breeze, medium and strong wind (clockwise from the left)

Benes uses location information and a shadow buffer to assess the amount of light received by growing parts of an L-system structure²⁸. This is applied to structures after the method of de Reffye et al.¹⁸ to influence growth rates and to bend structures towards sources of light²⁹.

The movement of plants affects the realism of a display, even in still images, where distortion due to wind affects plant geometry. Stösser et al.³⁰ show animations of weeping willows in the wind. Jones and Aitken³¹ use a wind-tree model to animate simple stick and leaf representations of trees (fig. 1.5). Their model uses pseudo physics to allow elastic recoil and twisting of branches, fluttering of leaves, wind attenuation for segments in the lee of others and varying wind forces. Wu et al.³² build their models of trees by user interaction to create outlines of and give three dimensional depth to selected branches of a photographic image, which is then animated. Ono³³ animates deformation and destruction of trees under severe wind forces. Although the method is simplified, there is no branch twisting, wind attenuation nor collision detection, Ono states, “visually satisfying results do *not* depend on physical accuracy”. The results were shown to be “perceptually realistic” in the 1996 film *Twister*³⁴. The Tree Storm system³⁵ animates trees at varying levels of wind stress.

This is a selective choice of important or original work in the modelling and rendering of plant growth. Other papers worthy of note cannot be discussed in detail due to limitations of space. They include the work of Honda et al.³⁶, the pioneering work of Kawaguchi³⁷, Erickson³⁸ on the geometry of phyllotaxis, Gardner³⁹ on textured quadric surface representation of trees and later⁴⁰ fractal ellipsoids in a paper that concentrates mainly on representation of smoke, Viennot et al.⁴¹ on ramifying patterns, Sakai⁴², Castéra and Morlier⁴³ on structural influences, de Leon’s branching structures⁴⁴, Fournier et al.⁴⁵, Takenaka’s consideration of light sensitivity⁴⁶, Farnsworth and van Gardingen’s study of the Sikta spruce⁴⁷, Deussen et al.⁴⁸ give an important review of the state of the art in plant modelling, discussing ways of achieving memory and time efficiency. Products, such as Tree Professional³⁵, Virtual Forest⁴⁹, PlantStudio⁵⁰ and xfrog⁵¹ offer high quality tree modelling, with tree features input and controlled interactively. Before considering the two main themes of this tutorial in detail, we first look at two other methods used for depiction of plant like forms.

1.3. Iterated Function Systems

Iterated Function Systems (IFS) are described here as they are commonly used to depict plant like forms. These are images without any descriptive power in terms of growth, so only a brief description is given. IFS were largely developed and publicised by Barnsley⁵² and his collaborators as a technique for generating fractal forms and for image compression^{53,54}. There are two main methods for generating an image of an IFS.

An IFS is defined by a set of contractive transformations, $\{T_1, T_2, \dots, T_n\}$, often affine transformations that may be constructed by combinations of the translations, scalings and rotations familiar to computer graphics experts⁵⁵. These result in simple linear equations. If all scale factors lie

between -1 and 1, the transformation is contractive in that distinct points will be moved closer to each other under transformation. There are two methods for generating images or objects of an IFS. The first involves applying the transformations to a raster image, starting with an arbitrary neutral image I.

```

Given arbitrary images I, J
Repeat
  Copy I into J and clear I
  Loop for k = 1 to n
    Draw  $T_k(J)$  into I
  End k loop
Until I and J are similar
Display I
    
```

The sequence of composited images stabilises after some iterations to the 'attractor' of the IFS, regardless of the form of the neutral starting image, just as the "steady state" solution of a differential equation can eliminate the memory of the "initial conditions".

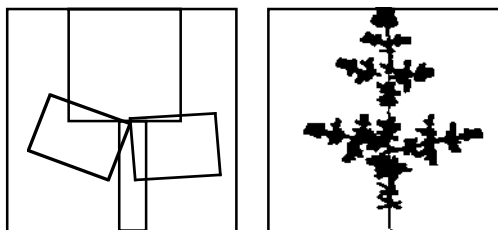


Figure 1.6: A simple IFS example after four iterations

Figure 1.6 shows how a simple IFS can be related to the image or attractor, which has become relatively stable after four iterations from an initially all black image. The left part of fig. 1.6 shows an image region (outer square) and four affine transformations as interior rectangles. The transformed image is created by overlaying the scaled, translated and rotated versions of the original image that fill these four regions. Comparison with the IFS attractor identifies transformations corresponding to the lower trunk, lower left branch, lower right branch and upper part, each a contracted copy of the whole "tree".

Generating an image from an IFS is easy, the inverse problem of finding the IFS that represents an image is not so simple. Although the process can be automated, its relative slowness due to complexity has been one of the major drawbacks of IFS as an image compression system. The 'collage theorem' is useful in identifying component transformations. If the image can be recreated by overlaying copies of itself, each of these copies represents a component transformation of the IFS. Figure 1.6 illustrates this, the location of sub-copies of the object itself relating to the positions of transformed rectangles.

The alternative image generation method is known as the 'chaos game'.

```

Given arbitrary point  $P_0$ 
Loop for k = 1 to a large number
  Select  $T_k$  at random from  $T_1, \dots, T_n$ 
  Find point  $P_k = T_k(P_{k-1})$ 
  Plot point  $P_k$ 
End k loop
    
```

A Markov chain⁵⁶ of points eventually fills the attractor that comprises the image, provided enough iterations are allowed. The image is more evenly filled if transformations are selected with probability proportional to their area contraction ratios, thus generating more points in large compared to small regions. This merely affects the speed of achieving a steady solution, in any case a deterministic object results from a random process. The fundamental theorem of IFS is that one and only one image is generated from this algorithm. By looping enough times, both algorithms produce identical images of the same IFS.

The illustration of fig. 1.6 is based in two dimensions, tree like objects occupying 3D space can be created by three dimensional transformations (fig. 1.7). Clearly, this method mimics appearance and has no information on growth characteristics. Local changes to an image or object are difficult to achieve, as the result of a change to one of the transformations will be distributed throughout the whole structure due to the fractal self-similar property of the IFS.

Colour as well as position may be transformed, and can be made dependent on the transformation selected, for example, brown for a 'trunk' transform, green for a 'foliage' transform. In 'distributed IFS', the probability of selection of transformations is dependent on the previous selection.

Several authors use non-affine transformations to extend modelling options. Gröller⁵⁷ adds tapering and twisting functions, Frame and Angers⁵⁸ use higher level polynomials, Jones and Campa⁵⁹ use randomised functions and Jones and Moar⁶⁰ use functions involving moduli (fig. 1.7). Branches are flattened and folded by a modulus function to mimic the features of a naturally occurring tree. 3D rendering of random points uses z-buffer and shadow buffer. Hart⁶¹ states that, 'even the contractivity condition can be weakened to so called eventual contractivity'.

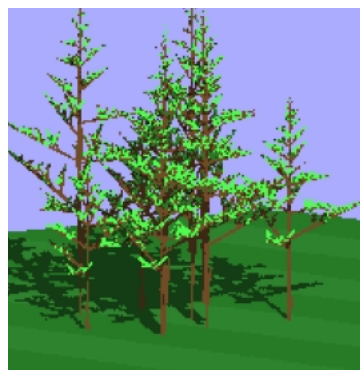


Figure 1.7: A 3D IFS using non-affine transformations

1.4. Diffusion Limited Aggregation

Diffusion Limited aggregation (DLA) generates branching structures using a stochastic algorithm^{62, 63, 64}. This represents structures that grow by accumulating particles, which "stick" to parts of the existing structure. Aharony⁶⁵ gives electrodeposition, growth in aqueous solutions, dielectric breakdown and viscous fingering in porous media as

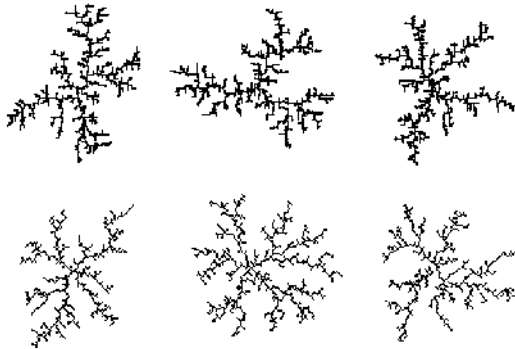


Figure 1.8: Examples of diffusion limited aggregation with different walk and aggregation rules

examples. These non-botanical features are mentioned here as physically growing branching structures. Guyon and Stanley⁶⁶ give several illustrations of natural and synthetic examples.

A starting structure (often a single pixel) is defined as occupied. A particle is set off in a random walk from a randomly specified origin, typically at a set radial distance from the original particle. If the particle moves too far from start pixels, it is discarded and a new one created. If the particle lies adjacent to an occupied pixel, it is aggregated to the structure, and its pixel is labelled as occupied. The process continues until the structure reaches a given size, often defined by a maximum distance from the original particle (the diffusion limitation). The process produces branched clusters (fig. 1.8).

In the three top illustrations of fig. 1.8, the aggregation rule is four-connected, a pixel is only absorbed to the structure if it lies alongside an edge of an occupied pixel. The lower row uses an eight-connected aggregation rule, allowing edge and corner connections. The columns have different walk characteristics, the leftmost has a four-connected walk, with equal probabilities for up, down, left or right moves. The middle column uses an equal probability eight-connected walk, with diagonal moves also allowed. Noting that diagonal steps are longer by a factor of $\sqrt{2}$, the rightmost column “weights” the probability of a diagonal step by $1/\sqrt{2}$ to make the expected length (probability times distance) of a step in any direction the same. This attempts to compensate for grid dependency, which is visible in the general vertical/horizontal or diagonal tendency of growth

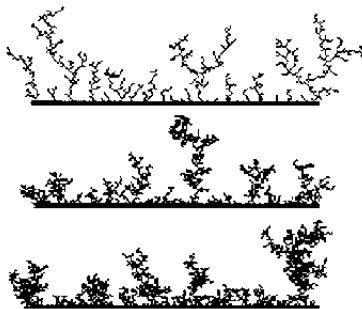


Figure 1.9: Line attracted DLAs. From top to bottom, particles are accumulated after one, five and ten visits

directions in some images. It would be useful to test this compensation statistically rather than visually.

Rules can be varied in several ways. Objects may be grown outwards from inside the occupied cells. If the initial attractor is a row of cells with the start of the random walk at another parallel row, plant like growths from the “ground” attractor are achieved. Figure 1.9 shows this effect in the upper illustration, where lower growths appear stunted by overshadowing of more successful structures. The other images are similarly set up with aggregation inhibited until a particle has been in an “aggregating position” five (middle) or ten (lower) times, as though it is accumulating stickiness. Increasing the number of required visits gives greater bulk to the aggregation.

Batty and Longhurst^{67, 68} model the growth of cities using a “dielectric breakdown model”, in which walk probabilities are affected by a field function which takes account of terrain slopes and natural barriers such as rivers, and accumulation is delayed until receptor sites have achieved a number of visits. Stanley shows how the field itself can be affected by the current state of the aggregate⁶⁹. Roberg and Abbess use DLA within a Manhattan grid road layout to model the accretive growth of traffic jams⁷⁰. Figure 1.10 shows a large traffic jam simulation created by a blockage at one intersection of a Manhattan grid road layout, which shows oddly plant like growth features.

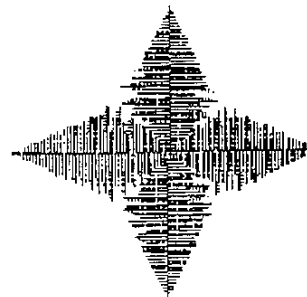


Figure 1.10: A large traffic jam simulation

1.5. Summary

This concludes a brief review of various methods of modelling the appearance and growth characteristics of growing objects. The main methods of L-systems and the modelling of marine sessile organisms are explored in greater depth in the two following parts.

2. L-Systems

Lindenmayer devised L-systems as a set of mathematical construction rules for describing plant forms as character strings⁷¹. They may also be used to construct regular fractal forms. Levy⁷² describes how two of Lindenmayer’s students, Hogeweg and Hesper⁷³, generated computed images of L-systems which Lindenmayer considered ‘charming but inconsequential’. Smith, stimulated by a Lindenmayer talk at a conference in Holland, subsequently developed his related method of graftals¹³. Lindenmayer was convinced of the value of visual interpretation of L-systems through his collaboration with Prusinkiewicz from the mid 1980s⁷⁴.

Their influential and beautifully illustrated book ⁷⁵ was published shortly after Lindenmayer's death in 1989. Readers who wish to develop L-systems for themselves are recommended to use this book as an essential reference (a soft cover version was published in 1996). The method has subsequently been considerably developed by Prusinkiewicz and others ^{76, 77, 78, 79, 80, 48}.

The three essential features of L-systems are *an alphabet*, *an axiom* and *a set of productions*. The alphabet is the set of characters allowed within the specific system. The axiom is a starting string that is recursively converted by productions, rules for converting single characters to other characters or strings. At a sequence of finite clock ticks, productions are applied to all characters of the existing string, enabling "growth". The method is similar to Chomsky's transformational grammars ⁸¹ but L-systems apply productions *simultaneously* to all characters at each clock tick, rather than serially.

An L-systems string can be illustrated by relating the alphabet to the turtle graphics commands of the Logo language ⁸². The position of a "turtle" that moves around the drawing surface is controlled by string characters. The position of a turtle is given by its location and the direction it faces, (x, y, θ) and moves are made relative to this position. The command "F" for "move forward" is enabled by changing the turtle definition to

$$(x + d \cos(\theta), y + d \sin(\theta), \theta),$$

where d is a set distance for the move — d may be associated with F as a parameter, $F(d)$. Logo also includes the commands "pen down" and "pen up" to enable drawing of lines or position change without drawing, some systems use "f" for the "pen up" version of "F". Direction change is created by "+" for turn left, "-" for turn right (many authors use these in the opposite sense). These may be defined to have a set angle, or may be parameterised, so $+(\alpha)$ and $-(\theta)$ change the turtle definition to $(x, y, \theta + \alpha)$ and $(x, y, \theta - \alpha)$ respectively.

Characters "[" and "]" mean "start a branch" and "end a branch". When the string is interpreted as a drawing, the character "[" does not affect the turtle, but pushes its current state onto a stack data structure. Drawing continues until the corresponding "]" is reached, the turtle is moved in "pen up" mode to the location popped from the stack, then it is returned to "pen down" mode to continue drawing from the location where the branch emanated. The stack ensures proper nesting of branches, so sub-branching is achieved to the required level.

Suppose the alphabet consists of characters:

- F: forward drawing step,
- +: left turn of 45°,
- : right turn of 45°,
- <: left turn of 30°,
- [: initiate a branch,
-]: end a branch.

Let the axiom be "F" and establish the single production

$$F \rightarrow F [+ F] [< F] F [- F] F,$$

which means that character "F" is changed to the string to the right of the arrow. By convention, when a character has no defined production, it is left unchanged, it is subject to the production $* \rightarrow *$.

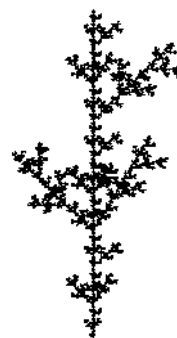


Figure 2.1: A simple L-systems construction

A little thought should give some sense of the structure described. Assume the axiom 'F' is drawn vertically upwards. The structure then has three main stem 'F' segments, as seen by eliminating all bracketed branch parts. After the first stem segment, there are one segment branches 45° to the left ([+ F]) and 30° to the right ([< F]), with a similar one segment branch 45° to the right ([- F]) after the second stem segment. The first two iterations create strings from the axiom as:

- 0 F
- 1 F [+ F] [< F] F [- F] F
- 2 F [+ F] [< F] F [- F] F [+ F [+ F] [< F] F [- F] F] [< F [+ F] [< F] F [- F] F] F [+ F] [< F] F [- F] F [- F [+ F] [< F] F [- F] F] F

This illustrates the string generation process as far as stage 2. The string gets very complex after relatively few iterations, so no more are written down. However, fig. 2.1 shows the drawn interpretation of this process after six levels of recursion, the original overall branching structure as described above still being apparent.

There are at least two ways of interpreting this developing string as a drawing. Each stage of iteration can be considered to add finer detail to the structure of an established plant. For this interpretation, the length of each drawing stage should be reduced by a factor of one third in this particular case. We have noted that the overall structure has three main stem parts at the first iteration, so these three will each be replaced by three at the second and so on. Adjusting the length of a drawing step by a factor of one third keeps the overall structure the same size, each iteration adding extra detail. Alternatively the created object can be considered to be growing with the drawing step kept the same length. The 'growing' object then increases in length by a factor of three at each clock tick. This unrealistic feature can be overcome using parametric L-systems as discussed later.

Prusinkiewicz and Lindenmayer call 'the simplest class of L-systems, those which are deterministic and context free' DOL-systems' ⁷⁵. Tree generation systems, as that of fig. 2.1, are known by them as 'bracketed OL-systems'.

This simple example has some characteristics of natural plants, greater realism can be achieved by including specific characters to represent leaves and flowers. We note some other un-plant like features:

- all lines are straight,
- there is exact self similarity in structural terms,
- the 'object' is two dimensional,
- the level of detail in each section is the same,
- plant structure and geometry are independent.

Specialist features can be added to the basic system to overcome the problems identified above. These include stochastic drawing and productions, context sensitivity, query modules, parametric L-systems and three dimensional L-systems.

2.1. Stochastic drawing and productions

Randomness is used to give natural irregularity to physical location and structures, to geometry and topology. The former is achieved by subjecting the turtle state to random change, affecting length and angle of drawing elements, giving the kind of variability created by natural causes in real plants.

This is not straightforward in implementation. Suppose we want to draw the 'tree' of fig. 2.1 with increasing levels of detail by reducing the drawing length by one third at each stage, but also to include some stochastic angle variation. At stages 1 and 2, the string to be drawn is

- 1 F [+ F] / < F] F [- F] F
- 2 F [+ F] [< F] F [- F] F [+ F] [< F] F [- F] F] / < F [+ F] [< F] F [- F] F] F [+ F] [< F] F [- F] F [- F [+ F] [< F] F [- F] F] F

The bracket before the second branching section is italicised, it is at string position 6 at stage 1, at position 32 in stage 2. When the branch angle is implemented, it will be given some random deviation from 30°. If successive stages are to look like the same plant with increasing levels of detail, the angle of this branch should not change from. At subsequent stages, the same sequence of random numbers can be generated by seeding the random number generator with the same value⁸³. However, the identification of the same structural object to receive this random deviation, when its location in the list is varied, is not straightforward. The random value allocated can be stored as a parameter pointed at from the character when it is first generated in the list. However, the starting location (turtle position) of this branch will be changed when subsequent intermediate random values are allocated. We content ourselves here with noting the complexity of the issue, the method is adequate for producing one off images that have more plant-like features than the deterministic method.

It is relatively easier to implement topological or structural change. Not all oak trees are identical, although they are recognisably of the same genus. Structures of the same type should have some identifiable physical similarities, but allow variability between examples. This is achieved by applying stochastic production rules, where different rules are applied with given probabilities. Still based on the example of fig. 2.1, we can apply the transformation

$$F \begin{cases} \xrightarrow{0.95} F [+ F] [< F] F [- F] F \\ \xrightarrow{0.05} \% \end{cases}$$

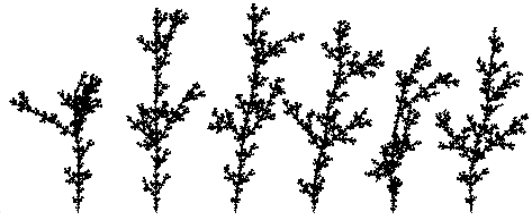


Figure 2.2: Seven examples of stochastic L-systems

meaning that with probability 0.95, F is transformed in the same way as previously, but with probability 0.05, F is replaced by a null segment, which terminates drawing of the particular branch and subsequent segments, as discussed later. Figure 2.2 shows seven examples of this effect, allied to random angle deviations for each F stage of -2°, 0° and 2° applied with equal probability. The 'plants' now have irregularity both in location and form.

This was the first run of the programme, readers may believe there are only six examples shown. The small speck to the left is the first example, killed off by random chance, the L-systems equivalent of a late frost. This effect has never subsequently occurred in any run of the programme. Figure 2.3 shows instances from a similar L-system, the left/right turn directions are selected at random and there is a slight tendency for branches to turn towards the upward vertical, simulating the orthotropic growth of some plants (those that tend to the horizontal are plagiotropic)²¹. The effect is to produce plant like images that differ from each other but could be from the same genus. These examples show more natural features than the deterministic methods of fig. 2.2.

2.2. L-systems in three dimensions

Simple extensions of the alphabet and its interpretation allow generation of L-systems in 3D, allowing a greater degree of realism. For a 3D turtle, location is given by position vector $\mathbf{r} = (x, y, z)$ in a 3D Cartesian space. Orientation is given by three mutually orthogonal unit vectors, \mathbf{h} defining heading, \mathbf{u} for the "up" direction and \mathbf{l} for the "left" direction fig. 2.4). When you sit in an aircraft, your location is (x, y, z) , you face the direction \mathbf{h} with the top of your head pointing towards \mathbf{u} and the craft's left wing pointing towards \mathbf{l} . (For those not familiar with vectors, a 3D Cartesian vector $\mathbf{v} = (v_x, v_y, v_z)$ represents displacements v_x, v_y, v_z respectively in the x, y and z directions. A unit vector represents a displacement of overall unit length, which

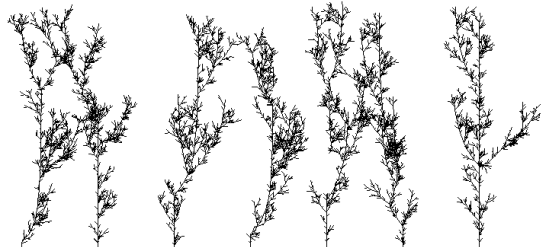


Figure 2.3: L-systems plants with orthotropic tendency and other random features

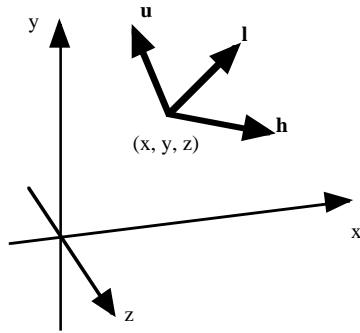


Figure 2.4: The components of a 3D turtle

occurs when $\sqrt{v_x^2 + v_y^2 + v_z^2} = 1$.) A forward drawing step 'F' of length d (like the craft leaving a smoke trail in the sky) is performed by changing the position vector \mathbf{r} to $\mathbf{r}' = \mathbf{r} + d\mathbf{h}$, and joining the points \mathbf{r} and \mathbf{r}' . To create solid objects, the join can be created as a cylinder, conical frustum or other solid form with axis along the line of generation from \mathbf{r} to \mathbf{r}' .

After the method of Prusinkiewicz and Lindenmayer⁷⁵, control of direction uses three operations of roll (represented by string symbols '/' for a positive rotation and '~' for a negative rotation), pitch ('&' for a positive rotation, '^' for a negative rotation) and yaw ('+' for a positive rotation, '-' for a negative rotation), with rotations implemented by standard computer graphics matrix methods⁵⁵. The use of \mathbf{h} , \mathbf{u} and \mathbf{l} to define the turtle orientation has considerable redundancy, as it could be defined by the three "Euler" angles, representing the rotation operations required to rearrange the coordinate axes in the turtle orientation (Euler was a prolific 18th Century Swiss mathematician). However, by holding this extra information, redirection of the turtle is simplified, so this is one of the many examples in computer graphics when memory is traded for speed and simplicity of operation.

Suppose matrix \mathbf{M}_v represents a composite rotation aligning a general unit vector \mathbf{v} with the z-axis, \mathbf{I}_v is the inverse of this (realigning the z-direction with \mathbf{v}) and \mathbf{R}_z is a rotation of given angle about the z-axis. We are already using a Cartesian coordinate system to represent position (x, y, z) , so the z-axis is properly defined. These standard operations are easily implemented in a 3D computer graphics system, and can be concatenated, or combined to make a single operation⁵⁵. For example, to rotate of a vector \mathbf{w} by a given angle about a general vector direction \mathbf{v} , the sequence

- use \mathbf{M}_v to align \mathbf{v} with the z-axis,
- use \mathbf{R}_z to rotate by the required angle about the z-axis,
- use \mathbf{I}_v to realign the z-axis with the direction of \mathbf{v}

is applied to \mathbf{w} . Using the standard methods of matrix operation, the order of application is important. Thus, applying \mathbf{M}_v to \mathbf{w} is done by the matrix multiple $\mathbf{M}_v\mathbf{w}$. Applying \mathbf{R}_z to the vector result of this, we get $\mathbf{R}_z\mathbf{M}_v\mathbf{w}$. Finally, the application of \mathbf{I}_v gives the final direction as vector $\mathbf{I}_v\mathbf{R}_z\mathbf{M}_v\mathbf{w}$.

Combinations of matrices, such as $\mathbf{I}_v\mathbf{R}_z\mathbf{M}_v$ can be pre-computed, so that only one standard operation needs to be applied to all features of an object to be reoriented. Using them

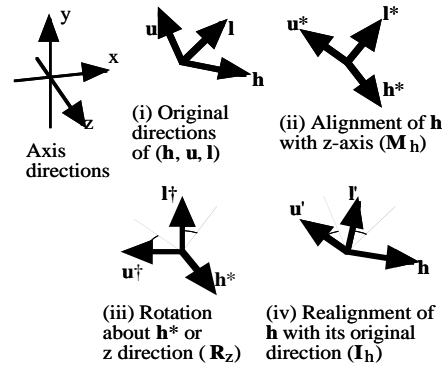


Figure 2.5: The roll operation in four stages

as building blocks, the required direction changes of roll, pitch and yaw can be performed as follows.

Roll rotates by a given angle about the heading \mathbf{h} , resetting left vector \mathbf{l} and up vector \mathbf{u} to

$$\mathbf{l}' = \mathbf{I}_h\mathbf{R}_z\mathbf{M}_h\mathbf{l} \quad \text{and} \quad \mathbf{u}' = \mathbf{h} \times \mathbf{l}'$$

Figure 2.5 illustrates the four stages starting with the original location, subsequently applying rotations \mathbf{M}_h , \mathbf{R}_z and \mathbf{I}_h in turn. Note that in this case it is slightly less efficient to apply the matrix rotation method for \mathbf{u}'

$$\mathbf{u}' = \mathbf{I}_h\mathbf{R}_z\mathbf{M}_h\mathbf{u}$$

as even after pre-computation of $\mathbf{I}_h\mathbf{R}_z\mathbf{M}_h$ used for \mathbf{l}' this takes 9 multiplications, whereas the cross product $\mathbf{u}' = \mathbf{h} \times \mathbf{l}'$ takes 6 multiplications. Cross multiplication also ensures that \mathbf{u}' and \mathbf{l}' are orthogonal, avoiding possible drift due to rounding error after repeated calculations. However, we note that the levels of branching in trees seldom exceeds seven, so the rounding errors are unlikely to accumulate significantly.

The operations of pitch and yaw are achieved in equivalent ways.

Pitch (tilting the aircraft nose downward from a normal flight position) rotates by the given angle about the left vector \mathbf{l} , resetting \mathbf{h} and \mathbf{u} to

$$\mathbf{h}' = \mathbf{I}_l\mathbf{R}_z\mathbf{M}_l\mathbf{h} \quad \text{and} \quad \mathbf{u}' = \mathbf{h}' \times \mathbf{l}$$

Yaw (turning to the left) rotates by the given angle about the up vector \mathbf{u} , resetting \mathbf{h} and \mathbf{l} to

$$\mathbf{h}' = \mathbf{I}_u\mathbf{R}_z\mathbf{M}_u\mathbf{h} \quad \text{and} \quad \mathbf{l}' = \mathbf{u} \times \mathbf{h}'$$

Repeated applications of such sequences could cause rounding errors in lengths of the 'unit' vectors, as well as the angle drift mentioned above. However, this is unlikely to cause significant problems if the level of branching is no greater than 7.

Combinations of roll, pitch and yaw can orient tree branches in any desired direction. The symbols representing these can be included in the L-systems alphabet, and appropriately used in productions to mimic the characteristics of existing trees, for example the numbers of branches emanating at each branching point and the angles at which these branches occur.

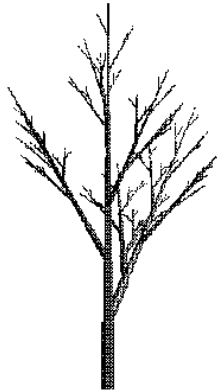


Figure 2.6: A 3D tree structure generated by Briggs

Figure 2.6 shows an example of a 3D tree generated by Briggs⁸⁴, using conic frusta to represent forward 'drawing' steps. This has growth simulation features to be discussed later.

2.3. Context sensitivity

Further modelling complexity is introduced by context sensitive L-systems. Productions are applied dependent on the string characters that occur to the left or right of the subject. The 'context' here is restricted to the character string, effects of the larger geometric context in which the structure is situated are discussed later.

Representation of a context sensitive production is in the form

$$L < C > R \rightarrow \text{Word}$$

The character 'C' is changed to 'Word' if 'L' appears to its left in a string and 'R' appears to its right. Prusinkiewicz and Lindenmayer⁷⁵ call this a 2L-system. Systems which use only one sided context sensitive productions, of form

$$L < C \rightarrow \text{Word}$$

or

$$C > R \rightarrow \text{Word}$$

are called 1L-systems, and the concept can be widened further to iL-systems, in which the left and right contexts can be strings of defined length rather than just single characters.

Care must be taken in defining the left and right contexts in the case of bracketed L-systems. If a closing bracket immediately precedes the subject character or an opening bracket immediately succeeds it, the bracket and its possibly nested contents, are ignored in determining the right or left context. This associates the character with the main branch of which it is a part or from which it emanates. Thus, in the string

$$A B [C D [E]] F [G H] I J,$$

the character 'F' has left context 'B' and right context 'I'. 'C', also, has left context B. This technique is used by Prusinkiewicz and Lindenmayer to propagate signals along the structure, from root to tips (acropetally) using the left context, from tip to roots (basipetally) using the right context. As a simple example, suppose we have an alphabet of two characters, • and -. With one axiom

$$\bullet \bullet \bullet \bullet \bullet \bullet \bullet -,$$

and productions

$$\bullet > - \rightarrow -,$$

$$- \rightarrow \bullet,$$

The dash character is passed along the row of symbols from right to left in the sequence,

$$\begin{array}{l} \bullet \bullet \bullet \bullet \bullet \bullet \bullet -, \\ \bullet \bullet \bullet \bullet \bullet - \bullet \bullet, \\ \bullet \bullet \bullet - \bullet \bullet \bullet, \\ \bullet \bullet \bullet - \bullet \bullet \bullet, \end{array}$$

and so on. A dash is always changed to a dot, a dot is changed to a dash whenever it has a dash to its right. Some examples given below combine context sensitivity with other features.

2.4. Parametric L-systems

Since Lindenmayer proposed the association of numerical parameters with alphabetic characters⁸⁵, the method has been highly developed. In most computer languages, it is relatively easy to create structures that define each character with one or more parameters. At the simplest level, these can represent obvious characteristics of the structural segment, such as its age (by incrementing time steps) or its length (perhaps scaled depending on the level of recursion at which it is generated). This is a possible method to increase realism. Lansdown² urges caution, discussing a study⁸⁶ which suggests internodes (distances between successive branching sections) are 'more or less of fixed length'. Lansdown also cites a rule of McMahon, that the widths of a branch is proportional to its length to the power 3/2⁸⁷. Many such empirical studies are useful in relating models to real structures.

Productions now take two forms. Some affect parameters without changing the structure of the character string and thus the object structure. Structural change is made dependent on the values of certain parameters, for example a leaf may be discarded if its age reaches a threshold, a branch may be formed if the accumulation of nutrient in its parent branch is adequate to trigger new growth.

Several examples are discussed in more detail later, just one simple illustrative case is shown here. Suppose a leaf with character L is to disappear after 20 developmental stages, and that it is created with initial 'age' 0, represented as L(0). A composite production to generate this effect is

$$\begin{array}{l} L(t) : t = 20 \rightarrow \text{null}, \\ L(t) : t < 20 \rightarrow L(t-1). \end{array}$$

The condition appears after the colon and before the arrow. Age can be used to affect size for growing features and to affect colour for decaying features, leaves give an example in both cases.

2.5. Environmental sensitivity

Now we look at the final bullet point of section 3, the separation of topological structure from geometric information. The simple L-system method is: "create a string,

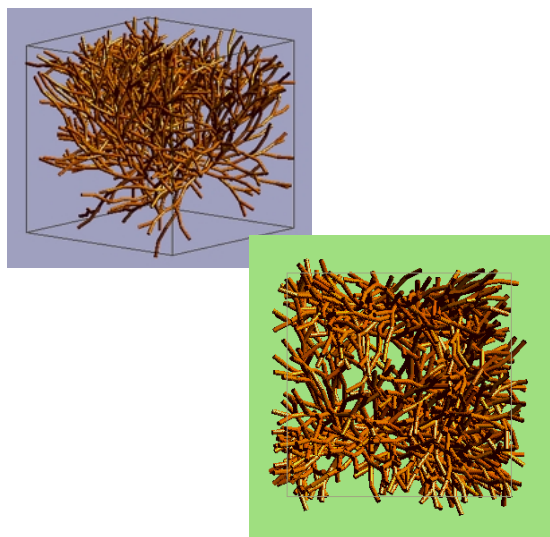


Figure 2.7: Side and top view of L-systems pruned against a surrounding cube (programmed by Briggs⁸⁴ after the method of Prusinkiewicz et al.⁷⁷)

then draw it". There is a systematic driving set of rules that creates the object regardless of its location. This is clearly unrealistic in terms of growing plants, where environmental considerations can have considerable influence from the major effects of climate to the localised effects of the plant's geometry itself. For increased explanatory power, the topological structure has to be made responsive to the location of plant elements.

Use of "query modules" was explained by Prusinkiewicz et al.⁷⁷ in an elegant paper describing synthetic topiary.

... the generated string is interpreted after each derivation step, and turtle attributes found during the interpretation are returned as parameters to reserved *query modules* in the string. Each derivation step is performed as in parametric L-systems, except that the parameters associated with the query modules remain undefined. During the interpretation, these modules are assigned values that depend on the turtle's position and orientation in space. (p 352).

The locations of structural elements are made available via query modules as parameters at the time productions are applied, and thus may be used to affect the production as do other parameters. Similar results can be achieved by making the location values direct parameters of the structural element itself. Note that it is not necessary to 'draw' each developmental stage, recursion can continue for the required number of stages before drawing is performed, but locations are evaluated at at each stage.

In their 1994 paper, Prusinkiewicz et al.⁷⁷ use the query module to simulate topiary. One or more tree growths are initiated inside the reference structure of a geometric model, either a simple shape such as a cube (fig 2.7) or cylinder or an isosurface model⁸⁸ of a more complex shape such as a dinosaur. The latter method creates a particular function of

position $\phi(x, y, z)$, defining the surface as the implicit solution of the equation

$$\phi(x, y, z) = \text{constant.}$$

The apical or growing tip of each branch is queried at each stage of development to identify its position. This is then tested

against the reference structure to determine if it lies inside or outside. In the case of an isosurface model this is simply done by evaluating the field function at the point and comparing it with the field constant. When the tip lies outside the structure, its branch is pruned and grows no more. The structure grows until it reaches or just passes the object's surface, gradually filling the structure in a simulation of topiary. By making the growth sensitive to an environmental feature, the plant structure is affected by location.

In a subsequent development, M ech and Prusinkiewicz⁷⁸ use the query module to affect growth dependent on plants' own structures and the structures of other objects in the neighbourhood. Again, a query module is used at growing parts of branches. This time the location is tested against shadows cast by the tree itself and other neighbouring trees that are themselves growing. Rays are cast in general sun directions through the growing object and its environment to estimate part or full shadow volumes. The method is similar to that used independently by Aitken^{31, 89} to identify branches in the lee of the wind from others in animating wind blown trees. If a branch section is not in total shadow, a signal is propagated back down the branch using context sensitive productions. Any branch section that does not receive such light energy for a given number of time periods is deemed to have died out, and is removed or culled from the structure — a counting parameter is used to determine the time since energy was received. The effect is to thin out overshadowed parts of the structure by self-pruning while allowing those that receive full sunlight to grow unhindered. This is a natural feature observed in forests, where interior trees develop into 'canopy' growths with the remains of stunted branches seen on otherwise bare trunks, full foliage only achieved where the canopy reaches clear sunlight. At the edge of the forest, individual trees have asymmetric growths, with leaves proliferating on the unshaded side.

2.6. Continuous time methods: Differential L-systems

Prusinkiewicz et al.⁷⁶ defined differential L-systems (dL-systems) to cope with continuous and discrete developmental aspects of growth. Leaves and new branches lengthen and thicken in continuous time, the development of a bud into a flower or branch is a discrete action. In discussing parametric L-systems above, it was noted that some productions change parameters such as lengths, others affect structure. Three points are made in favour of this new method.

- In principle, the time interval can be made arbitrarily small, but once chosen it is part of the model and cannot easily be changed. From the viewpoint of computer animation, it is preferable to specify the time interval as an easy to control parameter that is not implicit in the underlying model.

- The continuity criteria for the smooth progression of shapes during animation can be specified more easily in a continuous time domain.
- It is conceptually elegant to separate this model of development in the continuous domain from its observation, which takes place at discrete times.

In dL-systems, productions affect discrete changes to structures, with continuous change controlled by differential equations. Elements grow according to the continuous time differential equations until a threshold is achieved. At the precise time this occurs, it triggers a production to cause a structural change. Thus, the productions do not all occur at regular clock ticks, but are controlled by a continuous growth process. The discrete time method effectively approximates differential equations by their discrete time equivalent difference equations.

Lindenmayer's botanical/mathematical theory, its visual interpretation as well as further development by Prusinkiewicz and others has been most fruitful (the word is apt) in generating a rich set of models of developmental phenomena. For this tutorial, the extensive work of Prusinkiewicz and his collaborators is left now, but readers are encouraged to explore references for themselves. Further information can be obtained from extensive web sites maintained at the University of Calgary⁹⁰, the University of Queensland⁹¹ and California State University⁹².

As with the IFS method discussed earlier, L-systems provide very compact rule sets for generating complex objects. Unlike IFS, they have considerable potential for describing developmental or growing forms, a particular method for this is presented in the remainder of this section. Given the fundamental elements of an L-system, methods for depicting the generated structure are relatively straightforward. As for IFS, the inverse problem is the difficulty, that of devising rules that will generate specific plant like forms. Considerable ingenuity is used in matching rule sets to observed structures. Some help may be available from interactive methods, such as those of Lintermann and Deussen⁹³. They show an interactive method for creation of geometric replacement rules in an L-systems type environment with structures subject to free form deformations, and demonstrate the modelling of a dandelion and animations of growth. Kaandorp⁹⁴ also uses geometric construction rules, his work is described in considerable detail later in this tutorial.

2.7. Modelling of Nutrient Distribution in a fungus

The remainder of this section describes two case studies in modelling of developmental growth by simulating features of natural development. Tunbridge and Jones⁹⁵ used the method of parametric L-systems to model a specific form of fungal growth, *Aspergillus Nidulans*, which develops as a set of filaments or growing tubes.

Their "bio-mechanistic" method involves direct modelling of the biological processes underlying the growth of the plant, showing that methods already used to model flowering plants, sponges and algae can be extended and adapted to the modelling of fungal growth.

Prosser and Trinci⁹⁶ contains a comprehensive review of early work on mathematical models describing the growth of filamentous fungi or moulds, but there have been few computer

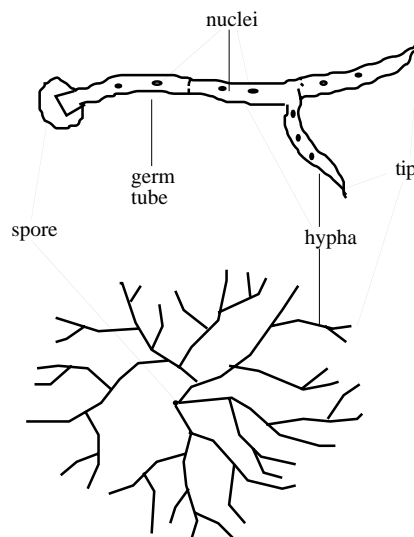


Figure 2.8: Close up of a small mycelium (above) and a larger one (below)

graphics simulations of such growths. Two examples are based on empirical models. The fungus *Mucor hiemalis* is modelled by Hutchinson et al⁹⁷ using a frequency distribution approach to model branching frequencies, angles and lengths. A computer model realistically determines colony morphology, but images produced use straight lines to represent curved filaments. Quinn and Fujimoto⁹⁸ use a similar method for the fungus *Erysiphe polygonii*, giving more realistic images through randomly determined angle changes in filaments. Liddell and Hanson⁹⁹ use an L-systems like model to produce images of growth of a fungus using an empirical 'environmental diffusion rule'. This controls a diffusion limited aggregation growth taking nutrient levels in the surrounding medium into account.

There are few realistic computer graphics simulations based on a mechanistic model of fungal growth, one based on the underlying biological growth processes. Other mechanistic models include those of DeCosta and Lindenmayer, modelling growth of blue-green algae using rules based on the biological processes of cell division and the internal movement of metabolites¹⁰⁰, Jansen and Lindenmayer for flowering plants¹⁰¹. Prusinkiewicz and others also model growing cellular structures⁷⁵, including the structures of sea shells¹⁰². Meinhardt¹⁰³ models growth of patterns on the surfaces of sea shells using differential equations for the distribution of pigments, effectively reducing them to cellular automata by the discretisation of continuous spatial variables to a growing front of cells.

Many fungi grow through their propagating medium in the form of moulds as branching networks of fine threads. These are 3 dimensional but can be visualised as overlapping curves. A whole network is called a *mycelium* with individual threads called *hyphae* (fig. 2.8). A simple model of a hypha is of a fine tube filled with a liquid (the *cytoplasm*), comprising all the chemicals and structures needed to sustain and

develop the fungus. Such microscopic structures include *nuclei*, important 'control centres' for growth processes. Hyphae extend by growing at their *tips*. Branch hyphae are usually originated some way behind the tip. Hyphal tubes are divided, in some types of fungus, by walls called *septa*. A septum may form a complete barrier or may allow some cytoplasm to flow through a *septal pore*.

A new mycelium typically starts with the germination of a spore to form a single hypha or *germ-tube*. By a process of elongation and branching a colony is formed, generally lying roughly within a circle. Radial colony extension rate is approximately constant, whilst the total length of the mycelium increases exponentially.

The comprehensive mathematical model of fungal growth developed by Prosser and Trinci⁹⁶ fits well into the formalism of context sensitive parametric L-systems. It is based on the underlying biological processes that support growth. This mechanistic model is summarised below and is used to develop the L-systems implementation of this study.

2.7.1. Cytoplasm formation and distribution

The cytoplasm contains *vesicles*, cytoplasmic structures containing nutrients necessary for extension of the hyphal or axial tip, which can be considered as tiny spheres suspended in the cytoplasm. They are produced throughout the hypha and flow towards the hyphal tip. It is believed that vesicles fuse with the hyphal tip when they reach it, their contents being used to fuel the extension of the tip. There are alternative theories¹⁰⁴, but the method used here still holds as a valid model of the distribution of 'nutrients' within the cytoplasm.

Trinci¹⁰⁵ describes the formation of new septa (cross walls). The *apical compartment*, that portion of hypha that lies between the tip and the next septum, contains four nuclei. As the tip extends, the volume of cytoplasm contained in this compartment increases. When the volume of cytoplasm per nucleus in an apical compartment reaches a critical value, the four nuclei divide to form eight nuclei. When this division is complete, a new septum is formed across the apical compartment, separating the nuclei into two clusters of four. The septum gradually grows to its maximum size, giving increased resistance to the flow of vesicles.

2.7.2. Branching

When the number of vesicles in part of a hypha between two septa reaches a critical concentration, vesicles fuse with part of a side-wall of the hypha causing it to swell and eventually branch at that point. Septa have a constraining effect on the flow of vesicles, so this usually occurs in the part of a hypha just behind a septum. Flow of vesicles through the hypha before the branch is divided so that some flow into the branch, the remainder flowing in the original direction.

2.7.3. Spore germination

The growth of a colony in this model starts from a spore. The spore produces vesicles at a constant rate until their concentration reaches a critical level, when the spore germinates by producing a hyphal tip. In the model, only one hyphal tip is produced by an individual spore, but this can be modified to suit different circumstances.

2.7.4. The mathematical model

This has two main elements, to control production of hypha and vesicles and to control the hyphal extension through absorption of vesicles. The former considers the hypha as consisting of tips and segments. Segments have no biological analogue, being used purely for modelling purposes except in the case of apical segments, which are collectively equivalent to an apical compartment. General hyphal segments have constant length L_h and produce vesicles at a constant rate R_p .

Tips increase in length as they absorb vesicles, being initially of negligible length. When the tip length reaches that of a hyphal segment, a new hyphal segment is created behind it, reducing the tip to negligible length. Vesicles, produced at a constant rate by each hyphal segment, flow at a constant rate towards the tip. The presence of a septum inhibits flow. The number of vesicles absorbed by a tip in one standard time interval is functionally dependent on the number of vesicles in the tip, as well as the preset saturation constant for absorption and maximum rate of absorption. Elongation of the tip in the time interval is proportional to the number of vesicles absorbed

Values of relevant constants are taken from observations by Prosser and Trinci⁹⁶ as specified in⁹⁵, which contains detailed descriptions of the L-systems productions, only qualitative descriptions are given below to describe the nature of the processes involved.

2.7.5. L-systems implementation

The L-systems representation of *Aspergillus Nidulans* has sixteen context sensitive parametric productions (five of which affect structural change, the other eleven affect parameter values) on an alphabet containing nine characters, listed below.

- P : ungerminated spore,
- G: germinated spore,
- T: tip,
- A: apical segment,
- S: normal segment,
- M: segment with a septum
- B: segment from which a branch is produced,
- [: branch start,
-]: branch end.

Figure 2.9 shows a small part of a mycelium represented as

... S S B [S S B [A A A T] M A T] M A A T.

All characters except brackets '[' and ']' have associated parameters, from one for P up to six for T.

P(0) is the axiom, an ungerminated spore with no vesicles. A parametric production increases vesicle level at a constant rate up to a threshold, when P is changed to a germinated spore G and a growing tip with appropriate parameters. P takes no further role, G continues to generate and export vesicles.

None of the parameter changing productions is stochastic, the model could be improved by allowing some random variation in vesicle production. Most characters have parameters representing their current vesicle content and the number of vesicles to be exported to the right context (T does not have the latter). The character list is scanned from the

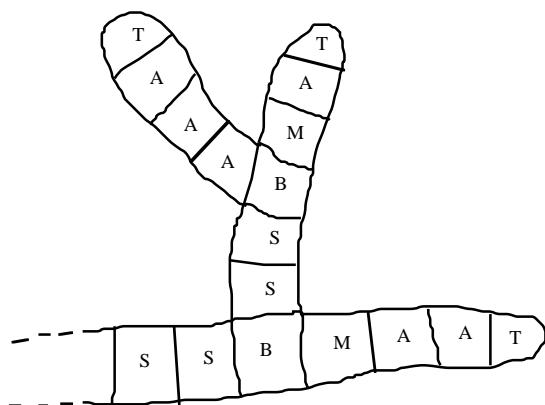


Figure 2.9: A small part of a mycelium represented by L-systems characters

left, imports from the left context being added to the current content by context sensitive productions, calculating the amount to be exported as a fraction of the current content. This simulates the motion of vesicles towards the growing tips according to Prosser and Trinci's model⁹⁶. For a branch base B, the export is divided proportionately into two parts, one to pass into the right context septum (M), the other to continue into the branch (S or A). It should be clear that context sensitivity is an important aspect. Structure affecting productions are (ignoring parameters for simplicity):

- $P \rightarrow GT$
an ungerminated spore germinates and grows a tip when its vesicle content achieves a threshold;
- $T \rightarrow AT$
a tip grows, leaving an apical segment behind it when it achieves a certain size;
- $A \rightarrow M$
an apical segment becomes a septum on a signal that its right context has achieved a certain size;
- $A \rightarrow S$
an apical segment becomes a normal segment when its right context has changed to a septum;
- $S \rightarrow B[T]$
a normal segment becomes a branch segment with a growing tip when its parameter value achieves a threshold.

The model was checked against the experimental observations of Prosser and Trinci⁹⁶, and gave a high level of agreement with the number of growing tips and the overall length of hypha generated over a range of growing times. both differed by less than 10% from observed values up to 16 hours simulated growth⁹⁵.

2.7.6. The drawing stage

The method is of the limited form in which the character string is created independently of the geometric location of the structure. This is unrealistic, in that the growth probably develops to seek nutrient in, for example, a Petri dish. An enhancement of the method would be to 'grow' the mycelium in a culture of nutrient, possibly represented as cellular automata with nutrient content being diminished by the

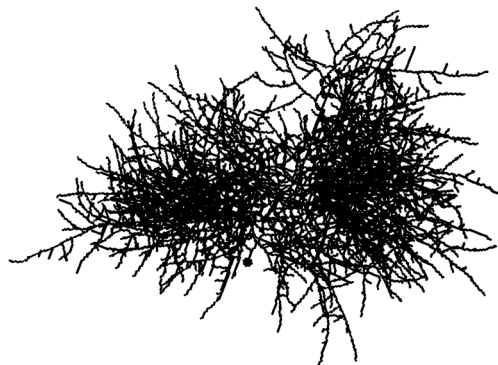


Figure 2.10: Simulated growth of *Aspergillus nidulans*

presence of hypha in a cell. The mycelium could then be given a tendency to grow towards levels of higher nutrient, and vesicle production could be made environmentally sensitive. This should achieve the relatively circular nature of such structures in reality. In the absence of this, a number of pragmatic random drawing rules are adopted to give a reasonable visual interpretation.

A spore, P or G, is drawn as a small circle. Structural characters representing hyphal segments are drawn as forward turtle lines. A, S, M and B, have fixed length, T has length proportional to its vesicle content, which is held as one of its parameters. Stochastic drawing elements include

- random branching direction (right or left);
- Normally distributed branching angle;
- randomly deviated turtle direction for segment drawing, with a bias towards the radially outward direction.

The last condition is a pragmatic attempt to simulate the outward search for nutrient, that is only partly successful as can be seen in fig. 2.10. However, the model is successful in simulating many of the features of a natural form of growth using parametric and context sensitive L-systems.

2.8. A tree growth simulation

The work developed by Tunbridge is extended by Briggs,^{84, 106, 107} to the modelling of growing trees using context and environmentally sensitive L-systems. This study does not attempt to generate a particular genus of tree, but creates a general tree-like growth, with many naturalistic features. Further work is needed to fine-tune the model to specific tree types.

A fungus grows by outward distribution of cytoplasm. A growing tree distributes nutrient absorbed from the soil by its roots. This depends on soil water saturation and chemical content. It also generates and distributes energy in the form of sugars and starches formed by photosynthesis. This is dependent on the time span and intensity of sunlight received at leaves and, to a lesser extent, the trunk and branches. Growth is powered by nutrients and energy. Leaves, when they age, discolour and fall. New trees are propagated from seeds that fall from the original plant. All these features are included in the model, in which trunk and branch segments

grow thicker by absorbing nutrients and energy distributed about the structure. (fig 2.11).

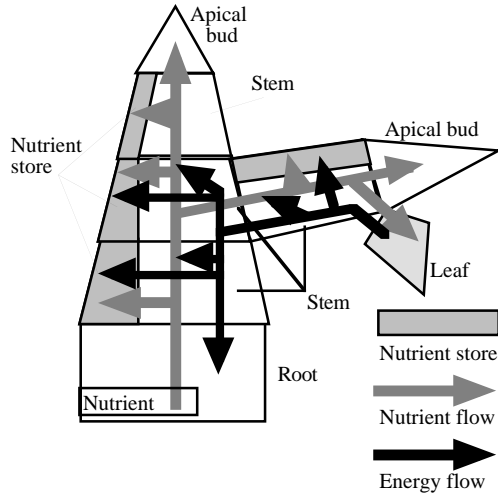


Figure 2.11: Conceptual illustration of nutrient and energy flow in the L-system model

2.8.1. The L-systems specification

Branching and direction changes are enabled by the usual symbols. Other characters (listed below) represent root R, stem S, apical (or growing) bud A, leaf L (fig 2.11), G (ground), p (query module) and % (prune). Their parameters and associated productions are given below, all structural changes are triggered at a parameter threshold ^{84, 106}. The axiom is essentially

$$R S [L] A,$$

a root and one stem segment with an apical bud above them and a leaf emanating from the top of the stem segment. The full specification is

$$R(1) S(1, 0, 0, 0) [-L(1, 0, 0)p(0, 0, 0)] A(0).$$

Each leaf has a query module p associated with it. This is loaded with the (x, y, z) location of the leaf's base when the system develops, but is initiated with a zero value.

- Root R(export nutrient)

The root could be the base of a second L-system representing root structure, but this has not been implemented. The root exports nutrients to its right context, which must be a stem segment S. The thickness of a stem segment is related to Holton's strands ²², its first parameter being the number of "strands". The number of strands (like a bundle of strings) is proportional to the cross sectional area, so S has diameter proportional to the root of its strand number. The amount of nutrient passed is proportional to the number of strands in the S segment at the root's right context. There is just one production,

$$R(n)>S(s, \dots, \dots, \dots) \rightarrow R(W*s),$$

where W is a constant of proportionality, often set to 1.

- Stem S(strand, nutrient, export nutrient, export energy)

A stem segment imports nutrient from its left context (root or stem), imports energy from its right context (when it is a stem) and any subsequent branch section (leaf or stem), exports nutrients to its right context (apical bud or stem) and to any existing branch segment (leaf or stem) and exports energy to its left context (stem or root). It has no structure changing productions; once created, it remains in place. The simplified production

$$S(s, n, e_n, e_c) \rightarrow S(s + n, \text{importNutr}*N + \text{importEnergy}*E, (1 - N)*\text{importNutr} + D*\text{importEnergy}, (1 - D - E)*\text{importEnergy})$$

represents twelve context sensitive productions which evaluate the effects of nutrient imported from the left context (importNutr) and energy imported from the right context (importEnergy) for all combinations of left and right contexts of character S. Parameters n, e_n and e_c represent the nutrient store, nutrient for export and energy for export.

Proportions N of imported nutrient and E of imported energy are absorbed, enabling thickening. Parameters E, D (a fraction of imported energy converted into nutrient for development) and N affect the general tree shape. Each stem section is depicted as a frustum of a cone, base radius proportional to the square root of its number of strands, upper radius equal to the base radius of the right context. At branches, the passage of nutrients is divided in proportion to the number of strands in the main stem and branch section.

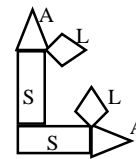


Figure 2.12: An apical bud converts to this structure

- Apical Bud A(nutrient)

An apical bud is the growing tip of a branch or trunk. It is depicted as a cone whose height is proportional to its nutrient content, with base width of one strand. It accumulates imported nutrients from the left context until a threshold, g, required for growth is achieved.

$$S(s, n, e_n, e_c) < A(v): (v \leq g) \rightarrow A(v + e_n).$$

When g is passed, the apical bud is converted to the structure of fig. 2.12, creating a new branch and two leaves. It is depicted as a cone whose height is proportional to its nutrient content, with base width of one strand. When v > g, the production is essentially (ignoring parameters)

$$A \rightarrow [S [L] A] S [L] A,$$

adding one forward stem segment with branching leaf and apical bud, with an equivalent side branch structure.

$$S(s, n, e_n, e_c) < A(v): (v > g) \rightarrow / (90) [+(24) S(1, 0, 0, 0) [-(90) L(0.5, 0, 0)p(x, y, z)] A(0)] -(20) S(1, 0, 0, 0) [-(90) L(0.5, 0, 0)p(x, y, z)] A(v + e_n - g),$$

Is the full rule for this production, showing angle change and initial parameter values allocated in the 3D model, showing that new stems have one strand.

This production can be changed to match characteristics of specific tree types to model particular species, it is the “engine” that drives the tree’s topological structure.

- Leaf L(scale, age, export energy)

The leaf is the important photosynthetic element, importing nutrient from and exporting energy to its left context. Exported energy is the product of imported nutrient and a sun factor H, which can be dependent on time, leaf age and on the location given in the leaf’s query module for shading effects. In practice, the energy produced diminishes with age of a leaf, and apical buds and other features of growing plants have a relatively minor photosynthetic effect. These features are not implemented, but the data structure allows for such developments in future implementations. The leaf is aged by a set amount D each stage. When the age of the leaf reaches 70% of its optimum, it falls to the ground. This is implemented by replacing string element L by GL, where G is a “ground” character, reducing the y-coordinate of the turtle location to zero for drawing of the next leaf element. When the leaf reaches twice its optimum age (by this stage, it is lying on the ground and coloured black), it is pruned from the string. The character ‘%’ indicates that the character G to which it is applied and all subsequent characters up to the end of the current branch level (which can only be a leaf structure in this case) are eliminated. The leaf could be scaled dependent on a size parameter s (variation of s is not shown below) and its colour varies with age. The current implementation ranges through light to dark greens, browns, then red and black after falling to the ground. The following four productions create these effects.

$$S(\dots, \dots, e_n, \dots) < L(s, a, n): (a \leq 0.7 - D) \rightarrow L(s, a+D, e_n * H);$$

$$L(s, a, n): (0.7 - D < a \leq 0.7) \rightarrow G L(s, a+D, 0),$$

$$L(s, a, n): (0.7 < a < 2) \rightarrow L(s, a+D, 0),$$

$$G > L(s, a, n): (a \geq 2) \rightarrow \%$$

A basic leaf is pre-defined as a simple closed shaded kite. Size change for growing leaves has not been implemented, but would not be difficult. With symbol F(d) depicting a forward drawing edge of length d, the leaf boundary is

$$\{-(40) F(0.25) + (60) F(0.47) + (320) F(0.47) + (60) F(0.25)\}.$$

2.8.2. Examples of modelled trees

The OpenGL¹⁰⁸ ancillary library is used to depict trunk sections as interpenetrating truncated cones with base radius and upper radii related to the strand parameter as described above.

Figure 2.13 shows two views of a tree that has grown for 100 cycles, with the constant settings N = 0.02, E = 0.01, D = 0.01, H = 1, W = 1 (these are defined within section 2.8.1).

Branching angles are subject to stochastic variation to give naturally irregular appearance. No clash detection has been implemented, so some branches may be seen to pass through



Figure 2.13: View of a modelled tree from the side (top) and below (bottom)

each other on close scrutiny. It is worth reiterating that this feasibility study does not attempt to model a particular type of tree and that structural, as opposed to visual, effect is of major importance.

Different effects are produced by changing constants. With nutrient flow parameter N increased from 0.02 to 0.05, more nutrient is absorbed within stem segments, which grow more thickly. Less nutrient is available for leaf development, so the photosynthetic effect is diminished, producing a structure with thicker trunk and less foliage (fig. 2.14), which has parameters as for fig. 2.13 except for the change of N and the number of growth stages set to 120.

E, representing energy absorption within stem sections, is increased from 0.01 to 0.04 in fig. 2.15, giving increased thickening of stems compared to fig. 2.13, this occurring more evenly from the leaves down in comparison with the ‘root up’ effect of fig. 2.14. In fig. 2.15, the number of stages is 120 and other parameters except E are as for fig. 2.13. This includes drawing parameters, such as lengths of cylinder

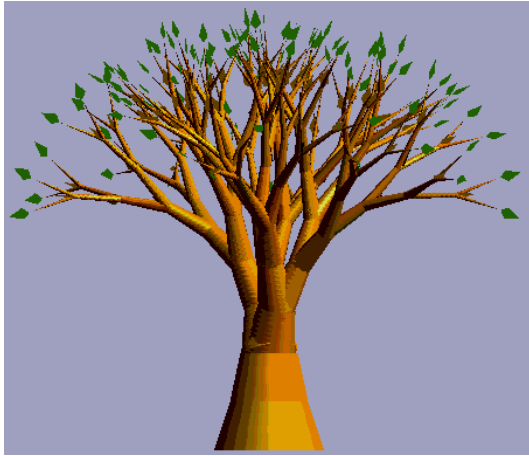


Figure 2.14: A tree with increased nutrient absorption

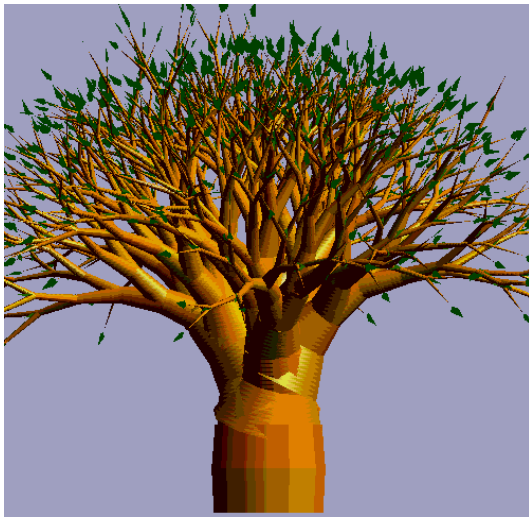


Figure 2.15: A tree with increased energy absorption

sections and random angle variations, so it is clear that N and E have a considerable influence on tree shape.

By associating a query module ⁷⁷ with each leaf, the effect of having part of the structure in shade can be simulated. In fig. 2.16, the sun energy factor H for leaves to the left of the tree trunk (where $x < -1$) is diminished to one tenth of the used for leaves to the right. The structural effect is clearly visible, with the left side being less well developed with thinner branches. Real tree branches in shade may develop to be long and thin in a “search” for light. Figure 2.16 does not show this characteristic, but it does show how growth is affected by environmental factors. This could be fine tuned to make length as well as thickness dependent on energy content. Leaf colours change with age and those older than 70% of the optimum age detach from the tree using the ‘ground’ symbol G. Real plants re-seed through the germination of fallen seeds. Flower, fruit and seed characters have been implemented in an incomplete study, but to simulate the effect of plant redevelopment, a



Figure 2.16: A tree shaded on the left side, showing leaf drop and colouring with age



Figure 2.17: Re-seeding is also shown in this image

randomly selected small proportion of the fallen leaves have been allowed to behave as seeds, generating new plant growths. Several leaves close to the trunk in fig. 2.17 have re-seeded. Figures 2.16 and 2.17 are developed over 90 stages, with parameters as for fig 2.13.

2.9. Summary

These case studies demonstrates the potential of parametric L-systems for modelling nutrient and energy flows in plant growth. There is potential for further development of the model. It would be relatively easily to include stochastic variation of growing parameters and use of observed day by day rainfall and sunshine data to simulate changing nutrient uptake from the soil and photosynthetic energy production. Other environmental data could be used to affect productions, adjusting formulae to take account of seasonal

factors, the age of the plant, and features such as temperature and wind speed to affect leaf fall rate and parameter passing rates, for example. No attempt has yet been made to model realistic trees, but a study to 'fine tune' parameters and productions to match real tree observations is needed. There is no clash detection between branches, and no attempt is made to create realistic impressions of tree bark and leaf structure. The "self-pruning" system of Mech and Prusinkiewicz⁷⁸, allowing branches constantly shaded by other features of the structure to wither and die, could be implemented using the 'G' ground character, with self shading also affecting rate of structural growth through the photosynthetic effect. The effect of self-shading could be made more realistic by allowing energy intake to affect the length of new segments as well as the thickness of developing segments. A flower/fruit/seed character should be developed — the potential for this has been demonstrated by subverting the characteristics of leaves to allow self-seeding in section 2.8.2.

In spite of these limitations, the result demonstrates the potential of the method; a simplistic interpretation of the mechanisms of nutrient and energy flow through the structure produces controllable life like features. The discrete time model should be adequate to model long term tree variations across a cycle of seasons and years, relating the number of generation steps to the season and year. The effects of leaf aging and detachment and the potential for flower, fruit and seed generation within a more complex model have been shown. By combining studies such as the root modelling, self shading and pruning methods of Prusinkiewicz et al.⁷⁷ and Mech and Prusinkiewicz⁷⁸, the phototropism of Benech²⁹, the tree-wind animation of Jones and Aitken³¹ and the realistic tree interpretations of others with parametric L-systems, convincing models and depictions of plant growths could be achieved. The ultimate would be a garden modelling system, where a variety of plants could be allowed to "grow" together under varying climatic and environmental conditions.

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References

¹ URL <http://www.visenv.com/3dtrees/3dtrees.htm>. Visual Environments Inc, active May 2000.

² J. Lansdown. *Modelling Living Forms*, Research Report, Centre for Electronic Arts, Middlesex University, 1996.

³ A. Campa. *Images from Chaos, a personal view*, MSc Computer Graphics Dissertation, Middlesex University, 1990.

⁴ S. Poynter. *An Efficient Countryside Model*, MSc Computer Graphics Dissertation, Middlesex University, 1994.

⁵ J. Thum. *Jon's Trees*, MSc Applied Computing Technology Dissertation, Middlesex University, 1993.

⁶ D.'A.W. Thomson. *On Growth and Form*, Cambridge University Press, 1942.

⁷ P.S. Stevens. *Patterns in Nature*, Penguin, 1974.

⁸ URL <http://charlotte.anu.edu.au/Forestry/mensuration/>. Australian National University, active June 2000.

⁹ URL <http://www.cof.orst.edu/cof/fr/research/organon/>. Oregon State University, active June 2000.

¹⁰ URL <http://www.ag.iastate.edu>. The Register of Ecological Models, active May 2000.

¹¹ H. Honda. Description of the form of trees by the parameters of the tree like body. *Journal of Theoretical Biology*, 31: 331-338, 1971.

¹² M. Aono and T. Kunii. Botanical tree image generation. *IEEE Computer Graphics and Applications*, 4(5): 10-34, 1984.

¹³ A.R. Smith. Plants, fractals and formal languages. *ACM Computer Graphics*, 18(3): 1-10, July 1984.

¹⁴ B.B. Mandelbrot. *The Fractal Geometry of Nature*, W.H. Freeman, 1983.

¹⁵ S. Estvanik. From fractals to graftals. *Computer Language*, 3(7): 45-58, 1986.

¹⁶ J. Bloomenthal. Modeling the mighty maple. *ACM Computer Graphics*, 19(3): 305-311, 1985.

¹⁷ W.T. Reeves and R. Blau. Approximate and probabilistic algorithms for shading and rendering structured particle systems. *ACM Computer Graphics*, 19(3): 312-322, 1985.

¹⁸ P. deReffye, C. Edelin, J. Françon, M. Jaegger and C. Puech. Plant models faithful to botanical structure and development. *ACM Computer Graphics*, 22(4): 151-158, 1988.

¹⁹ URL www.cirad.fr/presentation/en/program-eng/amap/archit.shtml. AMAP, active June 2000.

²⁰ J. Françon and P. Lienhardt. Basic principles of topology based methods for simulating metamorphoses of natural objects. In N. Magnenat-Thalmann and D. Thalmann (Eds.), *Artificial Life and Virtual Reality*, 23-44, Wiley, 1994.

²¹ F. Hallé, R.A.A. Oldeman and P.B. Tomlinson. *Tropical Trees and Forests: an architectural analysis*, Springer, 1978.

- 22 M. Holton. Strands, gravity and botanical tree imagery. *Computer Graphics Forum*, **13**(1): 57-67, 1994.
- 23 J. Weber and J. Penn. Creation and rendering of realistic trees. *ACM Computer Graphics*, **18**: 119-128, 1995.
- 24 J. Arvo and D. Kirk. Modeling plants with environment-sensitive automata. *Proceedings of Ausgraph '88*, 27-33, 1988.
- 25 N. Greene. Detailing tree skeletons with voxel automata. *ACM SIGGRAPH '91 Course Notes on Photorealistic Volume Modeling and Rendering Techniques*, 1991.
- 26 R.L. Colasanti and R. Hunt. Real botany with artificial plants. In P. Husbands and D. Harvey (Eds.) *Fourth European Conference on Artificial Life*, MIT Press, 1997.
- 27 M. Stuart. *Diary of a Forest Fire*, MSc Computer Graphics Dissertation, Middlesex University, 1994.
- 28 B. Benes. An efficient estimation of light in plant development. In R. Boulic and G. Hégron (Eds.), *Computer Animation and Simulation '96*, 153-165 and 225, Springer, 1996.
- 29 B. Benes. Visual model of plant development with respect to influence of light. In D. Thalmann and M. van de Panne (Eds.), *Computer Animation and Simulation '97*, 125-136 and 199, Springer, 1997.
- 30 A. Stösser, A. Schmitt, B. Neidecker, H. Müller, T. Maus and W. Leister. Tools for efficient photo-realistic computer animation. *Proceedings of EUROGRAPHICS '88*, 31-41 and C-1, 1988.
- 31 H. Jones and M. Aitken. Modelling the effect of wind blown trees. *Eurographics UK Chapter Annual Conference*, University of East Anglia, 245-254, March 1997.
- 32 E. Wu, T. Yan, Y. Chen and J. Feng. Reconstruction and physically based animation of trees from static images. In N. Magnenat-Thalmann and D. Thalmann (Eds.), *Computer Animation and Simulation '99*, 157-166 and 229, Springer, 1999.
- 33 H. Ono. Practical experience in the physical animation and destruction of trees. In D. Thalmann and M. van de Panne (Eds.), *Computer Animation and Simulation '97*, 149-159 and 201-203, Springer, 1997.
- 34 Industrial Light and Magic. *Twister*, Jan de Bont (director), produced by Amblin Entertainment, distributed by Warner Brothers, 1996.
- 35 URL <http://www.onyxtree.com>. Tree Professional, active June 2000.
- 36 H. Honda, P.B. Tomlinson and J.B. Fisher. Computer simulation of branch interaction and regulation by unequal flow rates in botanical trees. *American Journal of Botany*, **68**: 569-585, 1981.
- 37 Y. Kawaguchi. A morphological study of the forms of nature. *Computer Graphics*, **16**(3): 223-232, 1982.
- 38 R.O. Erickson. The geometry of phyllotaxis. In J.E. Dale and F.L. Milthrope (Eds.), *The Growth and Functioning of leaves*, 53-88, Cambridge University Press, 1983.
- 39 G.Y. Gardner. Simulation of natural scenes using textured quadric surfaces. *ACM Computer Graphics*, **18**(3): 11-20, 1984.
- 40 G.Y. Gardner. Modeling amorphous natural features. In *ACM SIGGRAPH '94 Course Notes on Modeling Natural Phenomena*, 24 pp., 1994.
- 41 X.G. Viennot, G. Eyrolles, N. Janey and D. Arquès. Combinatorial analysis of ramified patterns and computer imagery of trees. *ACM Computer Graphics*, **23**(4): 31-40, 1989.
- 42 S. Sakai. Sympodial and monopodial branching in Acer. *Canadian Journal of Botany*, **68**(7): 1549-1553, 1990.
- 43 P. Castéra and V. Morlier. Growth pattern and bending mechanisms of branches. *Trees Structure and Function*, **5**(4): 232-238, 1991.
- 44 M.K. de Leon. Branching object generation and animation system with cubic Hermite interpolation. *Journal of Visualisation and Computer Animation*, **2**: 60-67, 1991.
- 45 M. Fournier, H. Bailleres and B. Chanson. Tree biomechanics: growth, cumulative prestresses, and reorientations. *Biometrics*, **2**(3): 229-251, 1994.
- 46 A. Takenaka. A simulation model of tree architecture development based on growth response to local light environment. *Journal of Plant Research*, **(107)**1087: 321-330, 1994.
- 47 K.D. Farnsworth and P.R. van Gardingen. Allometric analysis of Sikta spruce branches: mechanical versus hydraulic design principles. *Trees Structure and Function*, **10**(1): 1-12, 1995.
- 48 O. Deussen, P. Hanrahan, B. Lintermann, R. Mech, M. Pharr and P. Prusinkiewicz. Realistic Modelling and Rendering of Plant Ecosystems. *Proceedings of ACM SIGGRAPH '98*, 275-286, 1998.
- 49 URL <http://www.innovativegis.com>. Virtual Forest, active May 2000.
- 50 URL <http://www.kurtz-fernhout.com/PlantStudio/>. Plant Studio, active June 2000.
- 51 URL <http://www.greenworks.de>, xfrog, active June 2000.
- 52 M.F. Barnsley. *Fractals Everywhere* (2 ed.), Academic Press, 1992.
- 53 Y. Fisher. *Fractal Encoding – Theory and Applications to Digital Images*, Springer, 1994.
- 54 N. Lu. *Fractal Imaging*, Academic Press, 1997.
- 55 J.D. Foley, A. van Dam, S.K. Feiner, J.G. Hughes. *Computer Graphics: principles and practice*, Addison-Wesley, 1990.

- 56 D.R. Cox and H.D. Miller. *The Theory of Stochastic Processes*, Methuen, 1965.
- 57 E. Gröller. Modeling and Rendering of Nonlinear Iterated Function Systems. *Computers & Graphics*, **18**(5): 739-748, 1994.
- 58 M. Frame and M. Angers. Some Nonlinear Iterated Function Systems. *Computers & Graphics*, **18**(1): 119-125, 1994.
- 59 H. Jones and A. Campa. Abstract and natural forms from iterated function systems. In N. Magnenat Thalmann and D. Thalmann (Eds.). *Communicating with Virtual Worlds*, 332-344, Springer, 1993.
- 60 H. Jones and M. Moar. Iterated Function Systems and Non Affine Transformations: Examples in 2D and 3D, *15th Spring Conference on Computer Graphics*, University of Bratislava, 201-209, April-May 1999.
- 61 J.C. Hart. Iterated Function Systems and Recurrent Iterated Function Systems. In Fractal Models for Image Synthesis, Compression and Analysis, *ACM SIGGRAPH '96, Course 27*, New Orleans, August 1996.
- 62 T. Witten and L. Sander. Diffusion limited aggregation. *Physics Review Letters*, **47**: 1400-1403, 1981.
- 63 L.M. Sander. Fractal growth processes. *Nature*, **322**: 789-793, 1986.
- 64 D. Stauffer. Cellular automata. In A. Bunde and S. Havlin (Eds.). *Fractals and Disordered Systems*, 294-321, Springer, 1991.
- 65 A. Aharony. Fractal growth. In A. Bunde and S. Havlin (Eds.). *Fractals and Disordered Systems*, 150-173, Springer, 1991.
- 66 E. Guyon and H.E. Stanley, *Fractal Forms*. Elsevier/North Holland, 1991.
- 67 M. Batty. Cities as fractals: simulating growth and form. In A.R. Crilly, R.A. Earnshaw and H. Jones (Eds.). *Fractals and Chaos*, 43-69 and plates 5-11, Springer, 1991.
- 68 M. Batty and P. Longhurst. *Fractal Cities: a geometry of form and function*. Academic Press, 1994.
- 69 H.E. Stanley. Fractals and multifractals: the interplay of physics and geometry. In A. Bunde and S. Havlin (Eds.). *Fractals and Disordered Systems*, 1-49, Springer, 1991.
- 70 P. Roberg and C.R. Abbess. Fractal structure of traffic jam images. *Proceedings of Stochastic Systems and Engineering, IMA*: **54**, 251-281, 1993.
- 71 A. Lindenmayer. Mathematical models for cellular interactions in development, Parts I and II. *Journal of Theoretical Biology*, **18**: 280-315, 1968.
- 72 S. Levy. *Artificial Life*, Jonathan Cape, 1992.
- 73 P. Hogeweg and B. Hesper. A model study of biomorphological description. *Pattern Recognition*, **6**: 165-179, 1974.
- 74 P. Prusinkiewicz, A. Lindenmayer and J. Hanan. Developmental models of herbaceous plants for computer imagery purposes. *ACM Computer Graphics*, **22**(4): 141-150, 1988.
- 75 P. Prusinkiewicz and A. Lindenmayer. *The Algorithmic Beauty of Plants*, Springer, 1990.
- 76 P. Prusinkiewicz, M.S. Hammel, E. Mjolsness. Animation of plant development. *Proceedings of ACM SIGGRAPH '93*, 351-360, 1993.
- 77 P. Prusinkiewicz, M. James and R. Mëch. Synthetic topiary. *Proceedings of ACM SIGGRAPH '94*, 351-358, 1994.
- 78 R. Mëch, P. Prusinkiewicz. (1996) Visual models of plants interacting with their environment. *Proceedings of ACM SIGGRAPH '96*, 397-410, 1996.
- 79 P. Prusinkiewicz, M. Hammel, J. Hanan and R. Mëch. Visual models of plant development. In G. Rozenberg and A. Salomaa (Eds.). *Handbook of Formal Languages Vol. 3*, 535-597, Springer, 1997.
- 80 P. Prusinkiewicz, J. Hanan, M. Hammel and R. Mëch. L-systems: from the theory to visual models of plants. In M. Michalewicz (Ed.). *Plants to ecosystems. Advances in Computational Life Sciences Vol. 1*, 1-27, CSIRO, 1997.
- 81 N. Chomsky. Three models for the description of language. *IRE Transactions on Information Theory*, **2**(3): 113-124, 1956.
- 82 H. Abelson and A.A. diSessa. *Turtle Geometry*, MIT Press, 1982.
- 83 H. Jones. Stochastic methods and non-fractal applications. In S. Coquillart, W. Strasser and P. Stucki (Eds.). *From Object Modelling to Advanced Visual Computing*, 140-165, Springer, 1994.
- 84 P. Briggs. *Plant Growth Simulation using L-systems*, MSc Computer Graphics dissertation, Middlesex University, 1995.
- 85 A. Lindenmayer. Adding continuous components to L-systems. In G. Rozenberg and A. Salomaa (Eds.). *L-Systems*, 53-68, Springer, 1974.
- 86 R. Bochert and N. Slade. Bifurcation ratios and adaptive geometry of trees. *Botanical Gazette*, **142**(3): 394-401, 1981.
- 87 T.A. McMahon. The mechanical design of trees. *Scientific American*, **233**(1): 92-102, 1975.
- 88 G. Wyvill, C. McPheeters and B. Wyvill. Data structures for soft objects. *The Visual Computer*, **2**(4):227-234, 1986.
- 89 M. Aitken. *Modelling the Effect of Wind on Tree Forms Generated using L-Systems*, MSc Computer Graphics Dissertation, Middlesex University, 1993.
- 90 URL <http://www.cpsc.ucalgary.ca/projects/bmv/vmm/title.html>. University of Calgary, active June 2000.

- ⁹¹ URL <http://www.ctpm.uq.edu.au/virtualplants/ipirefs.html>. University of Queensland, active June 2000.
- ⁹² URL <http://life.csu.edu.au/complex/tutorials/tutorial2.htm>. Charles Sturt University (© D.G. Green 1993), active June 2000.
- ⁹³ B. Lintermann and O. Deussen. Interactive modelling and animation of branching botanical structures. In R. Boulic and G. Hégron (Eds.). *Computer Animation and Simulation '96*, 139-151 and 223-224, Springer, 1996.
- ⁹⁴ J.A. Kaandorp. *Fractal Modelling: growth and form in biology*. Springer, 1994.
- ⁹⁵ A. Tunbridge and H. Jones. An L-Systems approach to the modelling of fungal growth. *Journal of Visualization and Computer Animation*, **6**(2): 91-107, 1995.
- ⁹⁶ I. Prosser and A.P.J. Trinci. A model for hyphal growth and branching. *Jou. Gen. Micro.*, 111: 153-164, 1979.
- ⁹⁷ S.A. Hutchinson, P. Sharma, K.R. Clarke and I. MacDonald. Control of hyphal orientation of *Mucor hiemalis*. *Trans. Brit. Mycol. Soc.*, **75**(2): 177-191, 1980.
- ⁹⁸ J.A. Quinn and T.T. Fujimoto. Computer graphics simulation of growth and sporulation of *Erysiphe polygonii*. *Phytopathology*, **76**: 883-888, 1986.
- ⁹⁹ C.M. Liddell and D. Hansen. Visualizing complex biological interactions in the soil ecosystem. *Journal of Visualization and Computer Animation*, **4**(1): 3-12, 1993.
- ¹⁰⁰ C.G. deKoster and A. Lindenmayer. Discrete and continuous models for heterocyst differentiation in growing filaments of blue-green bacteria. *Acta Biotheoretica*, **36**: 249-273, 1987.
- ¹⁰¹ J.M. Janssen and A. Lindenmayer. Models for the control of branch positions and flowering sequences of capitula in *Mycelis muralis* (L.) Dumont (Compositae). *New Phytologist*, **105**: 191-220, 1987.
- ¹⁰² P. Prusinkiewicz and D.R. Fowler. Shell models in three dimensions. In H. Meinhardt. *The Algorithmic Beauty of Sea Shells*, 162-181, Springer, 1995.
- ¹⁰³ H. Meinhardt. *The Algorithmic Beauty of Sea Shells*. Springer, 1995.
- ¹⁰⁴ I.B. Heath, *Tip Growth in Plants and Fungal Cells*. Academic Press, 1990.
- ¹⁰⁵ A.P. Trinci. Wall and hyphal growth. *Science Progress*, **65**: 75-99, 1978.
- ¹⁰⁶ H. Jones, A. Tunbridge and P. Briggs. Modelling of growing biological processes using parametric L-systems. In R.A. Earnshaw, H. Jones and J. Vince (Eds.). *Visualization and Modeling*, 303-317, Academic Press, 1997.
- ¹⁰⁷ H Jones and P Briggs. Modelling the growth processes of trees. *Eurographics UK Chapter Annual Conference*, University of Leeds, 97-106, March 1998.
- ¹⁰⁸ J. Neider, T. Davis and M. Woo. *OpenGL Programming Guide*, Addison-Wesley, 1993.