

MSc Computer Games and Entertainment

Maths & Graphics Unit 2011/12

Lecturer: Gareth Edwards

Introduction to Morphogenesis

Presenting the work of Przemyslaw Prusinkiewicz, Mark
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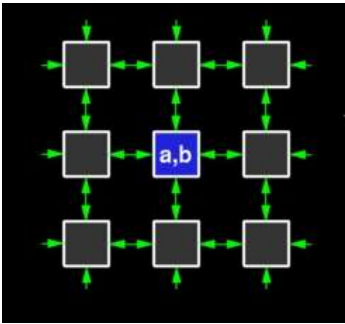
Morphogenesis

- In living organisms, complex forms and patterns result from development, and their emergence is traditionally referred to as *morphogenesis*.
- Rapid progress in the modelling of biological structures and simulation of their development has occurred over the last few years.
- It has been coupled with the visualization of simulation results, which has led to a better understanding of morphogenesis and given rise to new procedural techniques for realistic **IMAGE SYNTHESIS**.

Biological Structures

- Biological structures are interesting to model and visualize for several reasons.
 - *Database amplification*, a term coined by Alvy Ray Smith [Smi1984], is the process of creating complex images using small data sets.
 - *Emergence*, a term brought into prominence by the study of Artificial Life [Tay1992], means that the system as a whole acquires complex properties through the interaction, in space and over time, among its component modules. The modules themselves are usually fairly simple.
- By studying emergent processes in a biological context, we can gain a better understanding of the world around us.

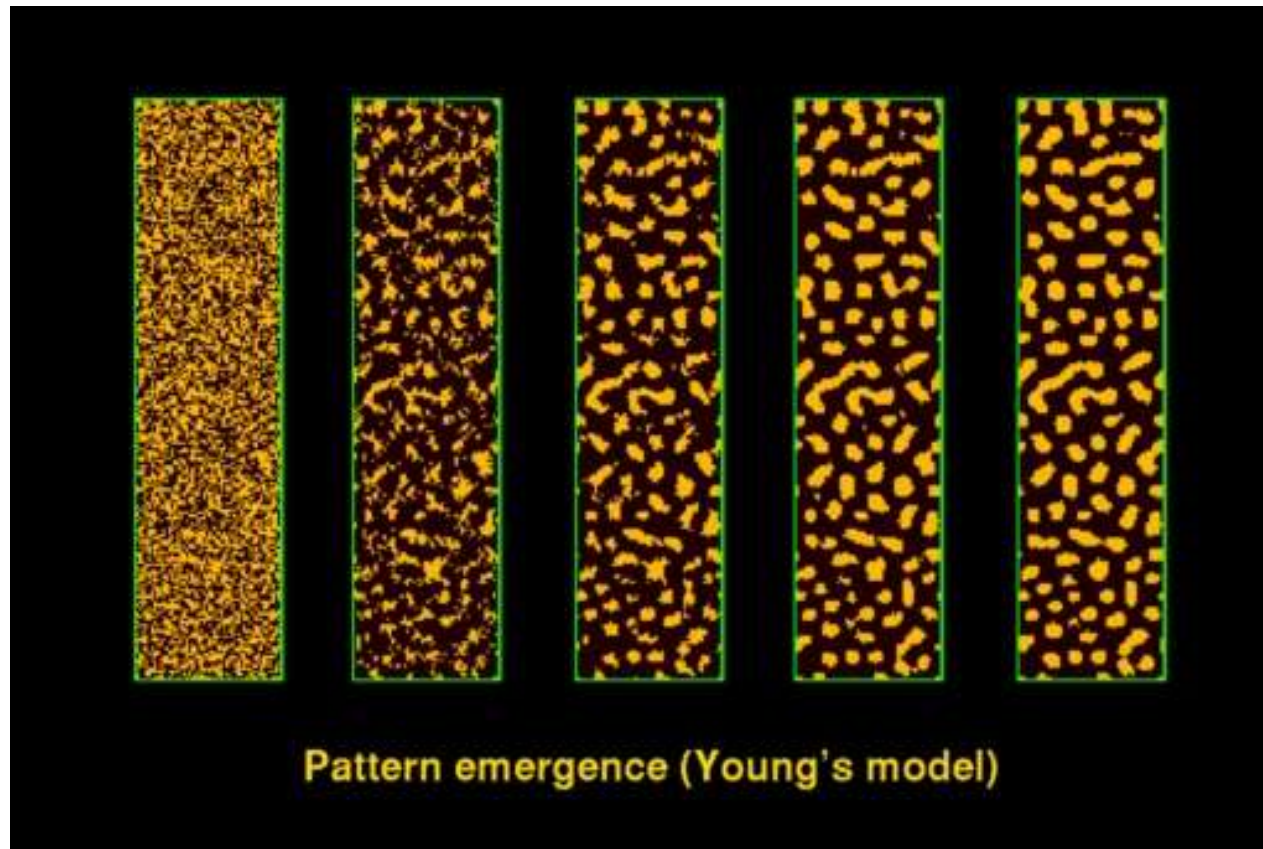
Reaction-Diffusion Model



- Historically, the first model of morphogenesis was proposed by Alan Turing [Tur1952], and is known as the reaction-diffusion model. The model operates in a plane.
- Each point of this plane is characterized by two numbers, representing concentrations of substances (morphogens) a and b .
- A system of coupled partial differential equations describes changes of these concentrations over time. The substances diffuse and react with each other.
- In the equations, the reaction components are captured by functions f and g , and the diffusion components are represented by the remaining terms. The original intent of the reaction-diffusion model was to explain the “breakdown of symmetry and homogeneity” or the emergence of a pattern in an originally homogenous medium.

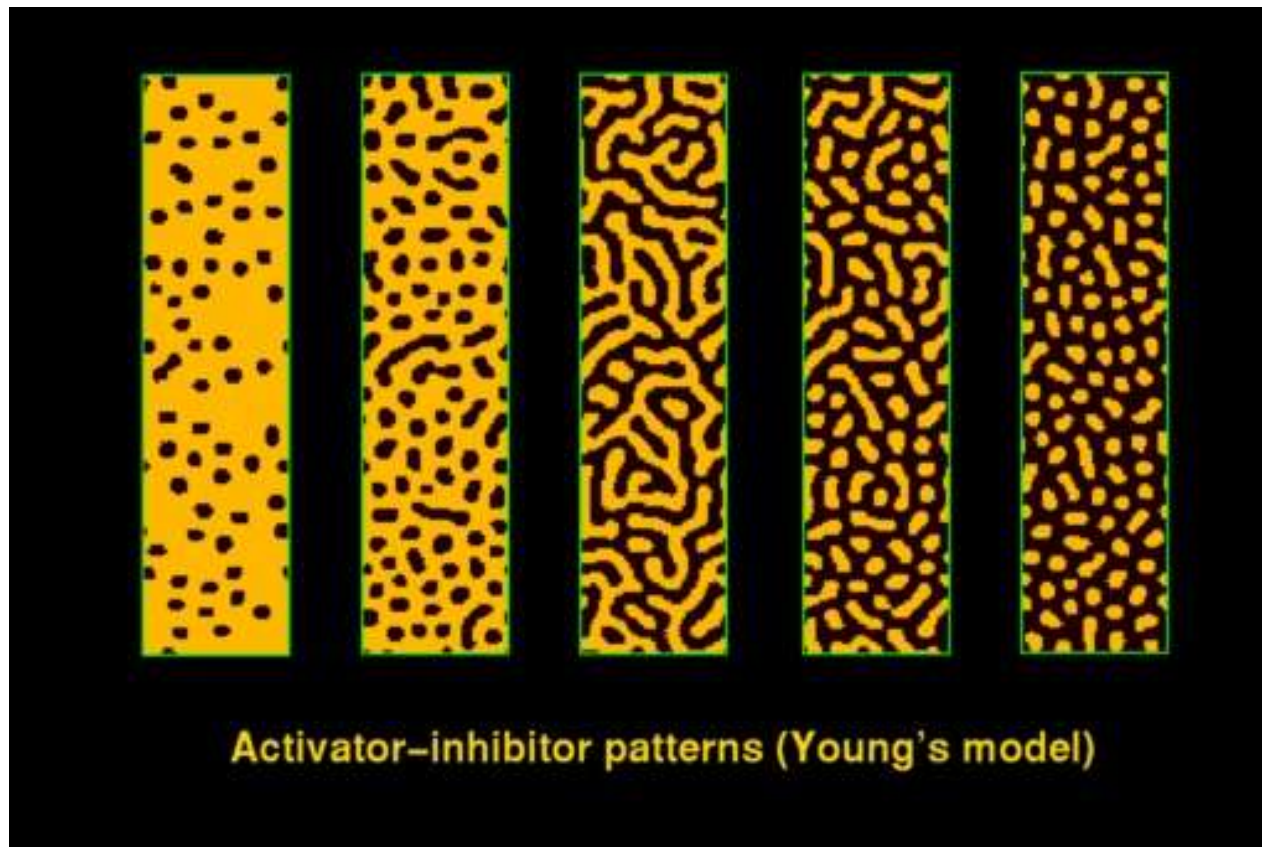
Pattern Emergence

- In a sequence of steps, the areas of high concentration (yellow) become clustered, producing a pattern of light blotches in a dark background.



Activator-Inhibitor Patterns

- In nature, the pattern on the right-hand side can be found, for example, in feathers of some birds, and the middle pattern can be found in the rabbit fish (as noticed and modeled by Camazine [Cam1993]).

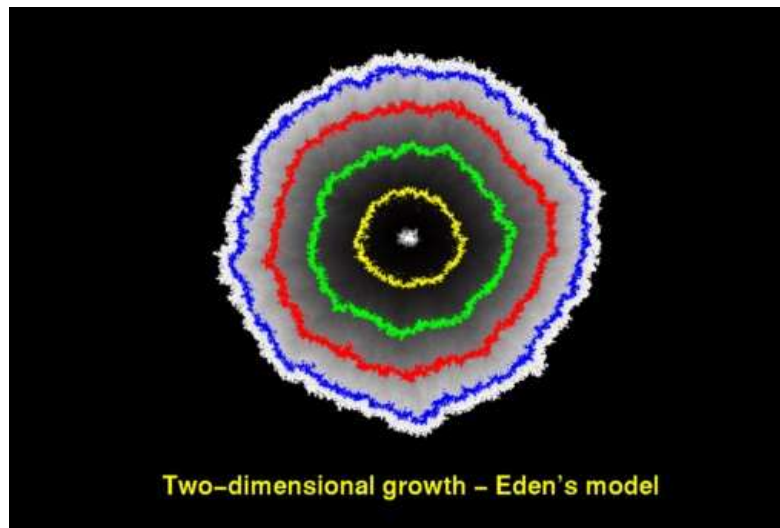


Eden's Model

- The application of reaction-diffusion models is limited by one key assumption originally made by Turing: the medium on which the reaction-diffusion takes place, be it a surface or a line, does not grow.
- One of the first computer models of growing biological structures was proposed by Eden [Ede1960].
- Eden's model is very simple.

Eden's Model

- The simulation takes place in a square grid. A single initial particle is placed in the centre of this grid. The subsequent particles are attached, one by one, to randomly chosen points on the border of the structure formed in the previous steps.



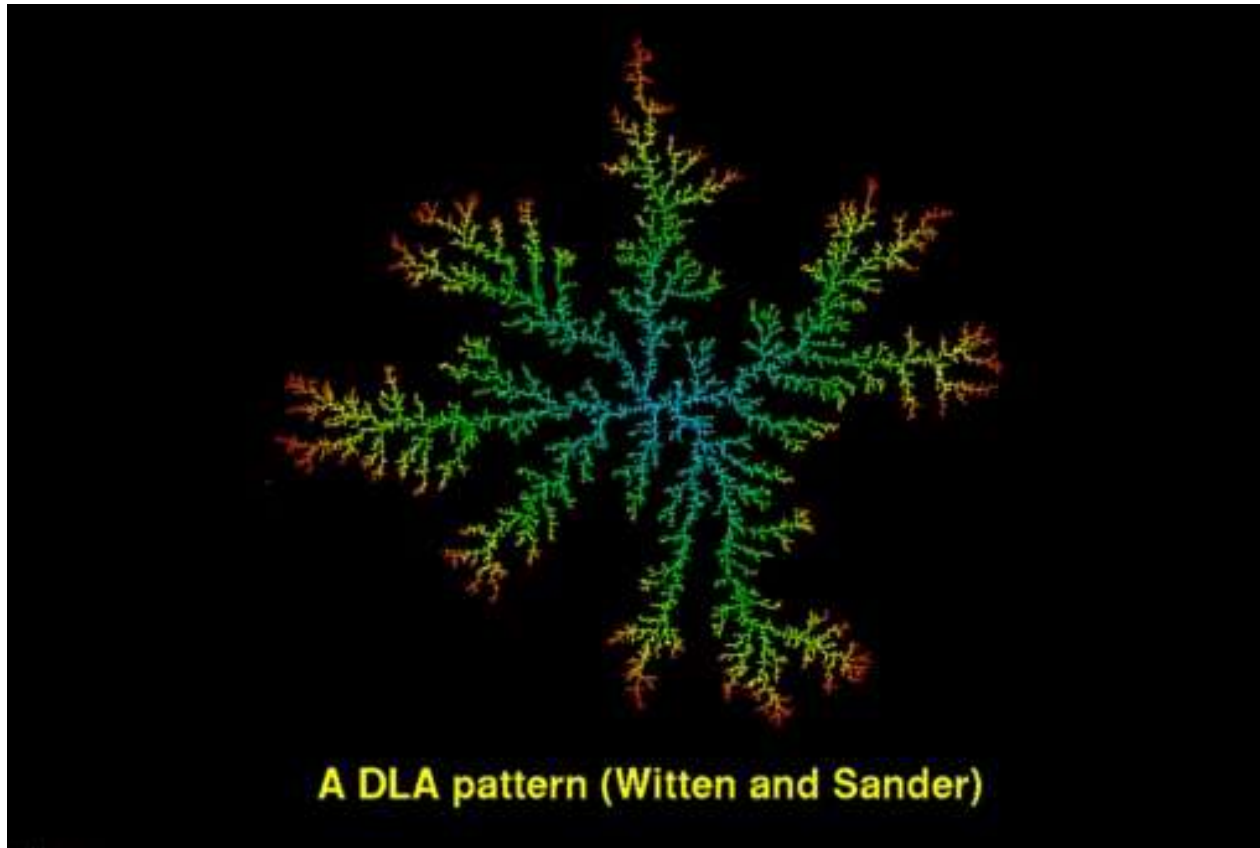
- A sample structure obtained this way is shown in above. The colours indicate the state of the structure at different points in time. A structure developing according to Eden's model is roughly circular.

Diffusion-Limited Aggregation

- In 1983 Witten and Sander [Wit1983] modified Eden's model by assuming that the particles originate far away from the developing structure, and perform a random walk in the surrounding space.
- Once a particle encounters the structure, it sticks to it.
- This model has been termed *diffusion-limited aggregation* (DLA for short), since the random walk of the particles can be viewed as a simulation of diffusion at the molecular level.
- Although the difference between the operation of Eden's model and diffusion-limited aggregation may seem rather minor, the difference in the resulting patterns is striking.

Diffusion-Limited Aggregation

- In contrast to Eden's approximately circular patterns, the DLA model produces fractal branching structures.



Diffusion-Limited Aggregation

- Mandelbrot and Evertsz [Man1990] proposed a visual explanation of this form [\[anim1\]](#).



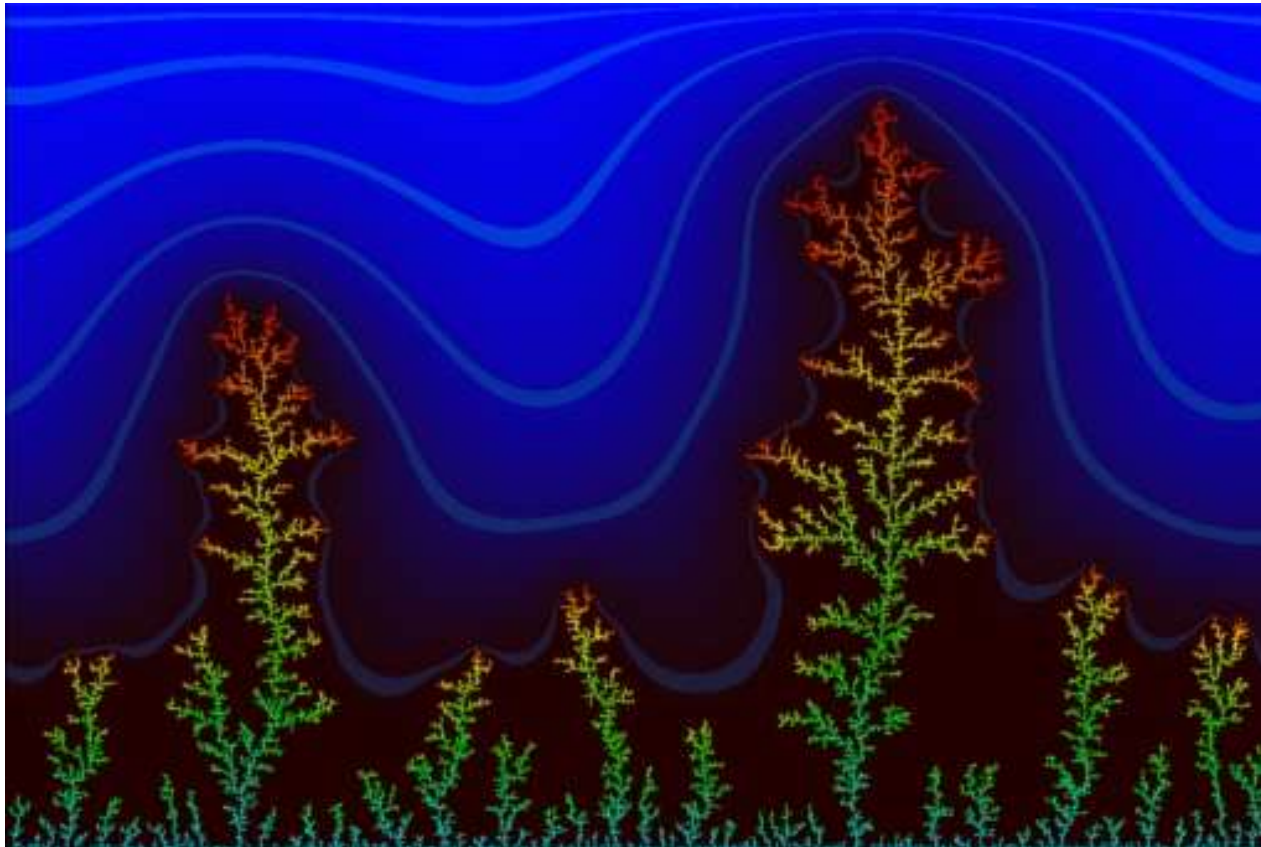
Diffusion-Limited Aggregation



- They depicted the average concentration of particles in the space surrounding the growing structure by solving Laplace's equation in this space.
- The boundary conditions imposed high concentrations of particles at the outer boundary of the space and zero on the boundary of the fractal.
- The green background colour indicates high concentration of particles in space, and black indicates low concentrations.
- It can be clearly seen that the concentration of particles between the branches is always very low, which is why the branches do not grow there; a bay remains a bay.
- On the other hand, the tips of the structure are very close to the areas of high concentration of particles, which is why the branches grow the fastest there [\[anim1\]](#).

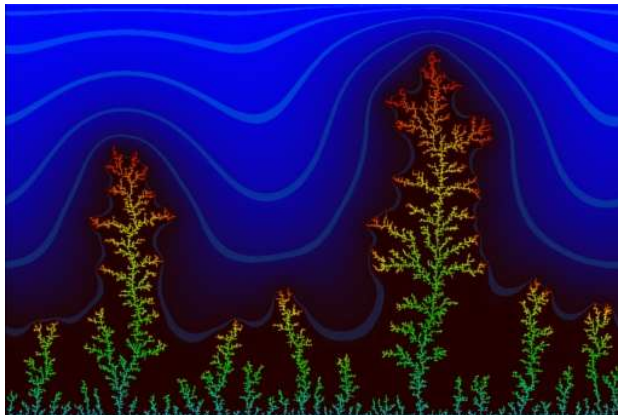
Diffusion-Limited Aggregation

- Here is a diffusion-limited aggregation process, in which the initial structure is a horizontal line, and particles come from above. A ``forest'' of branching structures is produced in this case



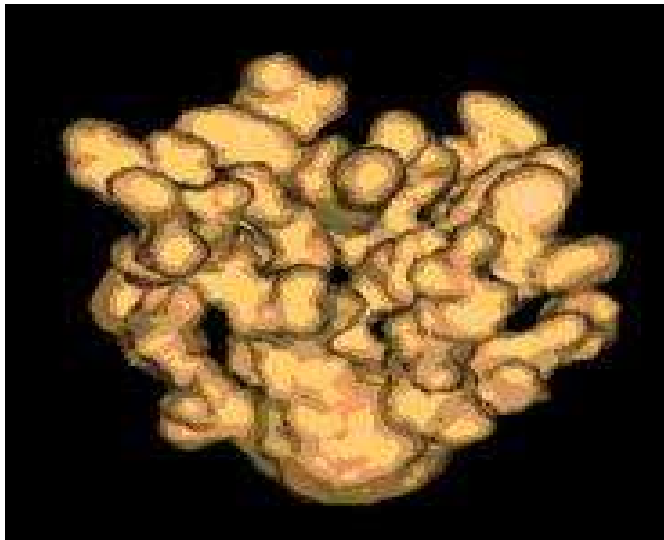
Diffusion-Limited Aggregation

- The travelling particles can be viewed as nutrients, used by a simple growing structure (such as a bacterial colony) to form its body.
- In this context, Eden's model can be viewed as describing the growth of a bacterial colony in an abundance of nutrients. The structure develops everywhere it has space to expand.
- In contrast, diffusion-limited growth occurs where nutrients are a scarce resource. The structure uses all nutrients in its proximity, and grows most vigorously in the directions exposed to the incoming nutrients.



Diffusion-limited growth of sponges

- A variant of the diffusion-limited growth model was proposed by Kaandorp [Kaa1992, Kaa1994] to simulate the growth of marine sessile organisms; namely corals and sponges.
- Both types of organisms develop by adding successive layers to the structure formed so far (*growth by accretion*). The layer size is determined locally by the availability of nutrients that diffuse in the water surrounding the organism [\[anim2\]](#).

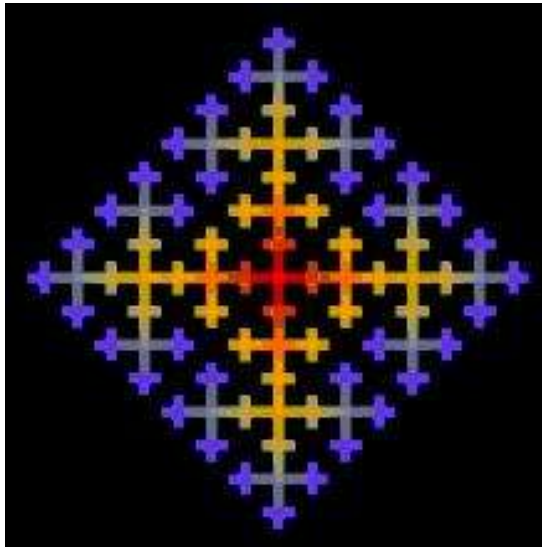


Cellular Automata

- Diffusion-limited aggregation and growth represent one extension of Eden's model explaining the formation of branching patterns.
- Another extension was proposed by Ulam [Ula1962], the co-inventor of cellular automata.
- A cellular automaton consists of cells, arranged in a (usually) square grid, and communicating with each other.
- Ulam assumed that new cells can be added on the border of the structure formed so far only if these cells do not collide with each other or with the previously added cells.

Cellular Automata

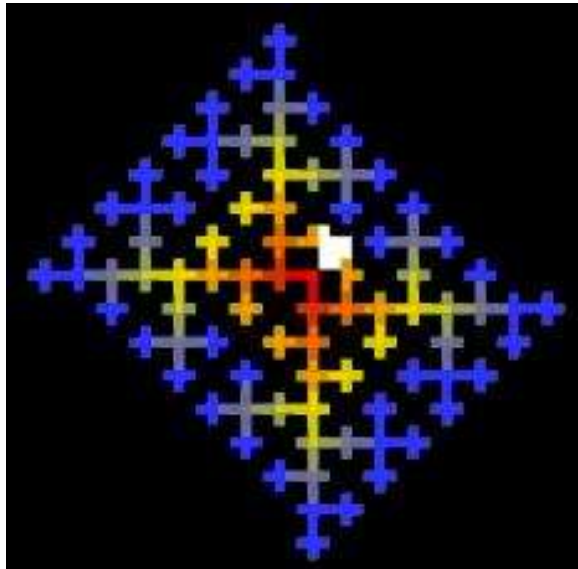
- The development of the resulting branching structure, which he called *Maltese crosses*.



- An interesting feature of this model is its sensitivity to the environment (note that DLA models are also sensitive to the environment) [\[anim3\]](#).

Cellular Automata

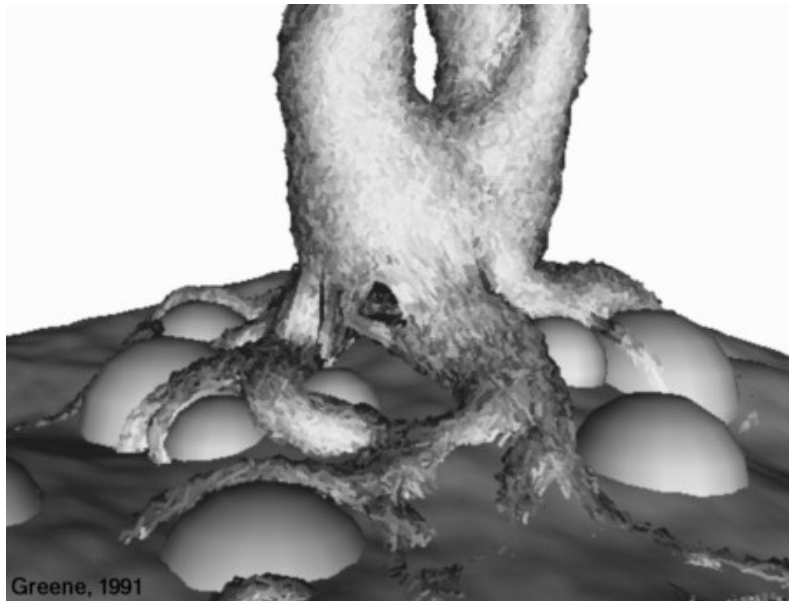
- The image below the development of a Maltese cross affected by an obstacle (shown in white).



- Although the structure is somewhat distorted, it accommodates the presence of the obstacle and grows around it without losing its branching character [\[anim4\]](#).

Cellular Automata

- A three-dimensional extension of this basic concept was applied by Greene [Gre1991] to model the development of tree roots around the stones in the ground



- A similar concept was applied in [Gre1989] to simulate the development of vines around a house.

L-Systems

- In the domain of plants, the models discussed up to this point have two limitations.
- First, they are extremely opportunistic: the growth of a structure is controlled almost exclusively by the environment.
- In reality, plant structures are determined to a large extent by genetic factors.
- Secondly, all models described so far represent accretive growth; that is, a process in which a structure develops by the progressive addition of new material.
- The developmental patterns of higher organisms are often much more complicated.

L-Systems

- For example, during the development of the compound leaf shown below, the apex produces a succession of leaflets that grow in size while the internodes elongate and the branching angles increase.
- The changes of the branching angles and the elongation of the internodes are non-accretive components of this process [\[anim5\]](#).



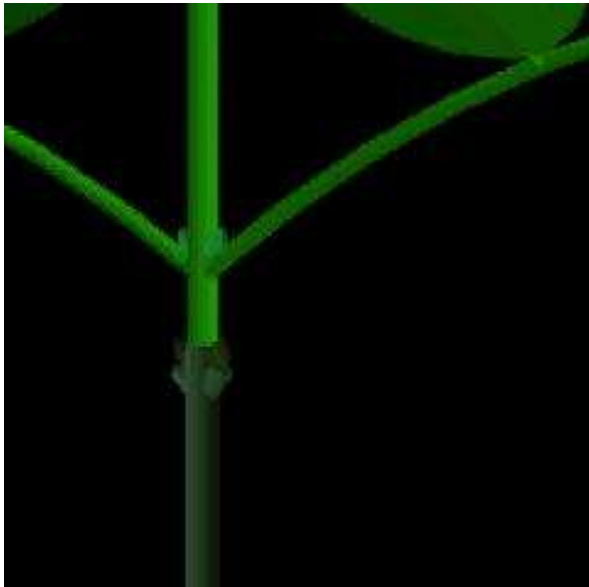
L-Systems

- Similar phenomena can be observed in the development of shoots of *Fraxinus pennsylvanica*, or green ash [Pru1994b] [\[anim6\]](#).
- The first image below illustrates this development from a fixed viewpoint, while the second and the third shows the same simulation from the viewpoint of a camera focused on the shoot apex [\[anim7\]](#).



L-Systems

- Note the gradual elongation of internodes and changes in branching angles [\[anim8\]](#).

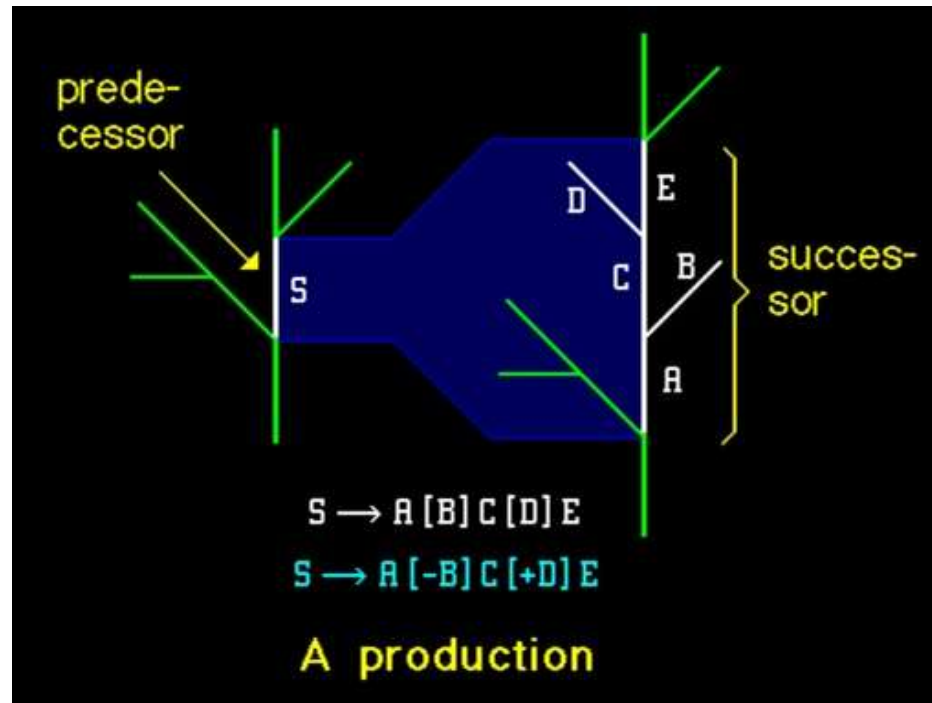


L-Systems

- To capture such non-accretive, internally driven processes, Lindenmayer [Lin1968] proposed a model of development based on *rewriting rules* or *productions*.
- This model, known as *L-systems*, originally provided a formal description of the development of simple multicellular organisms and was later extended to higher plants.

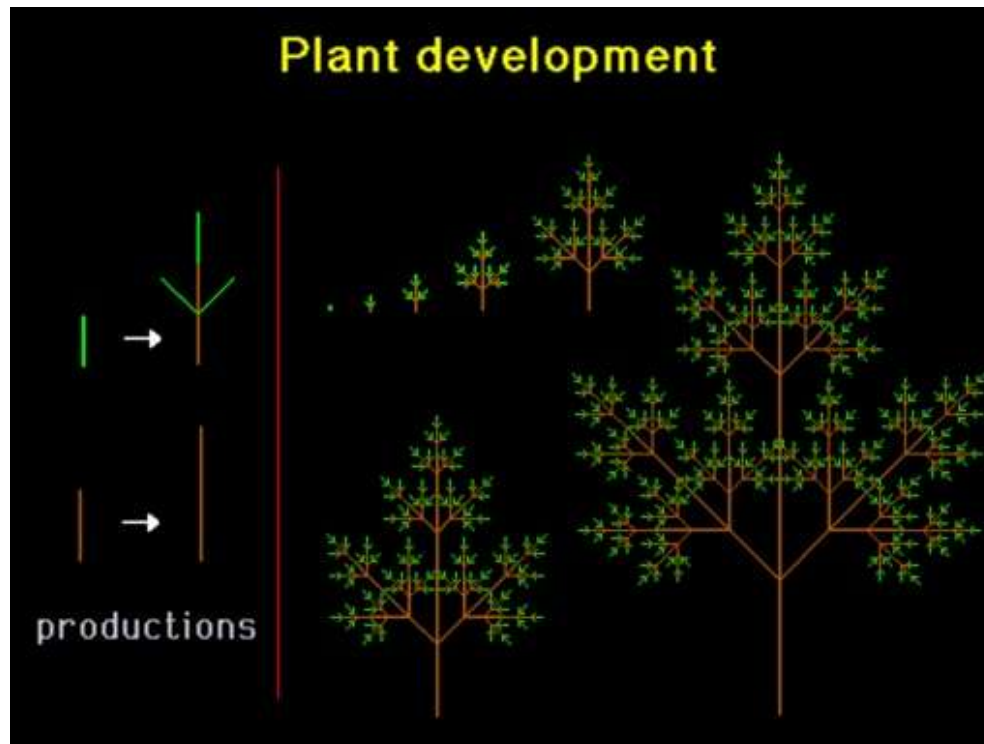
L-Systems

- The rewriting rules operate on entire modules of a plant; for example an apex, an internode, or a leaf.
- Each rule consists of two components, a predecessor and a successor, as shown below:



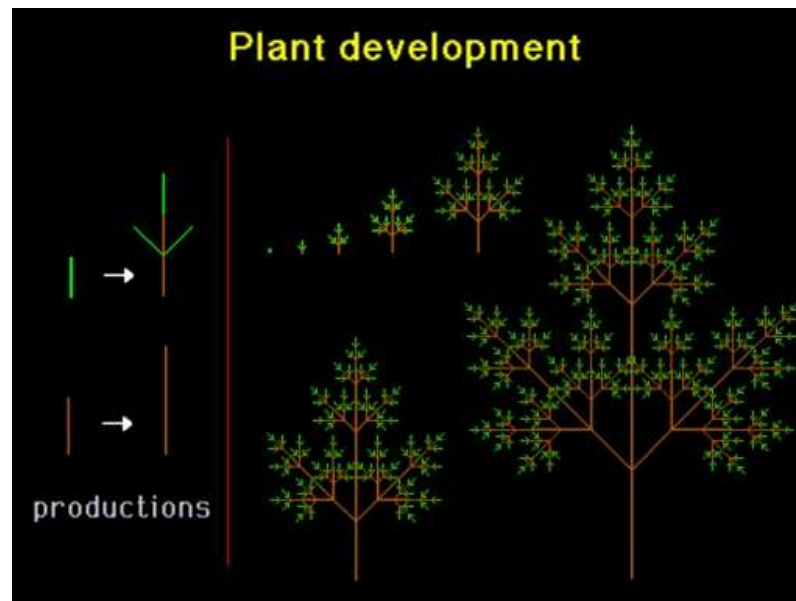
L-Systems

- During a derivation step, the predecessor (identified by its label) is replaced by the successor. Lindenmayer developed a string notation that makes it easy to specify productions and carry out simulations. Even very simple L-systems can produce plant-like structures. The image below shows an L-system with two productions.



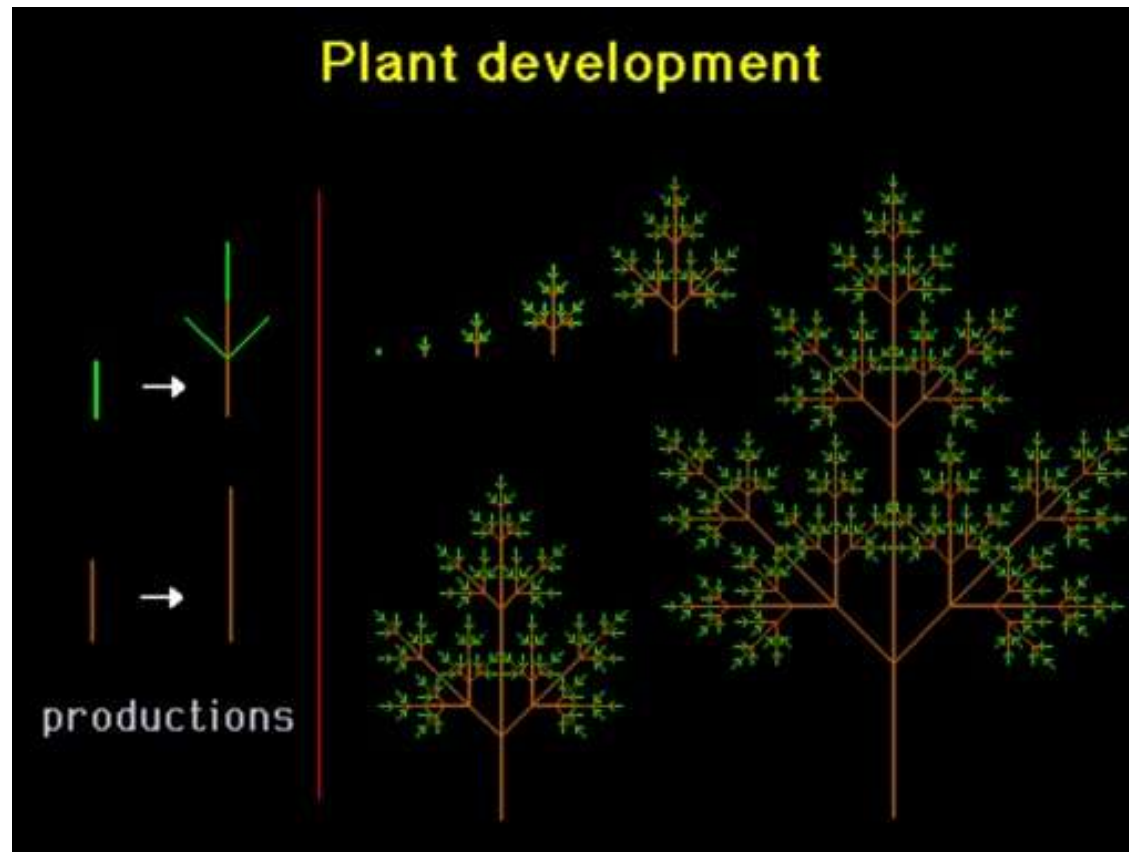
L-Systems

- The first production specifies that the apex, shown in green, creates a branching substructure with three apices and an internode. The second production increases the internode length. Productions are assumed to be invariant with respect to scaling, which means that if we change the length of the predecessor by factor r , we should rescale the successor by the same factor. The developmental process starts with an apex and yields a compound leaf structure, resembling those found in some fern fronds



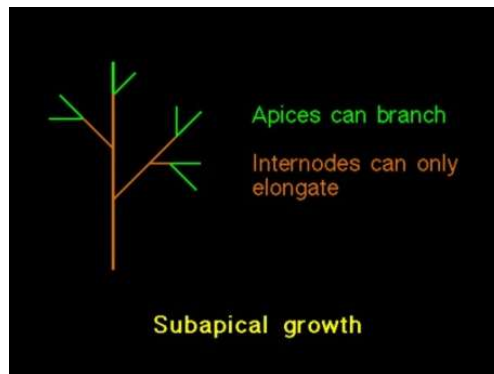
Branching patterns of herbaceous plants

- In spite of its simplicity, the simple model of a compound leaf shown in in the image below properly reflects one of the general principles of the development of higher plants.



Branching patterns of herbaceous plants

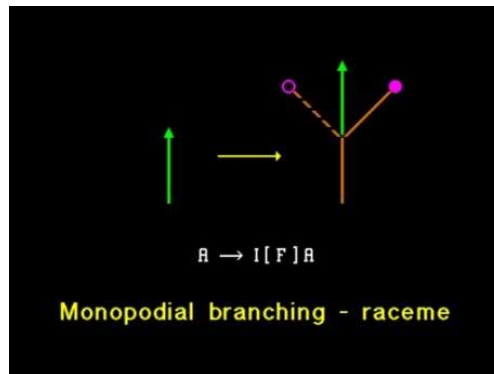
- It is called the principle of *subapical growth*, and means that only apices can create new branches. Internodes may elongate, but cannot initiate branches. These rules are illustrated schematically in the image below.



- A variety of structures can be produced through subapical growth, depending on which apices remain active and initiate new branches, and which ones do not. In line with the research interests of Lindenmayer and other biologists using L-systems, this section focuses on the modelling and simulation of the inflorescences of herbaceous plants. For a more complete description see Chapter 3 of [Pru1990].

Branching patterns of herbaceous plants

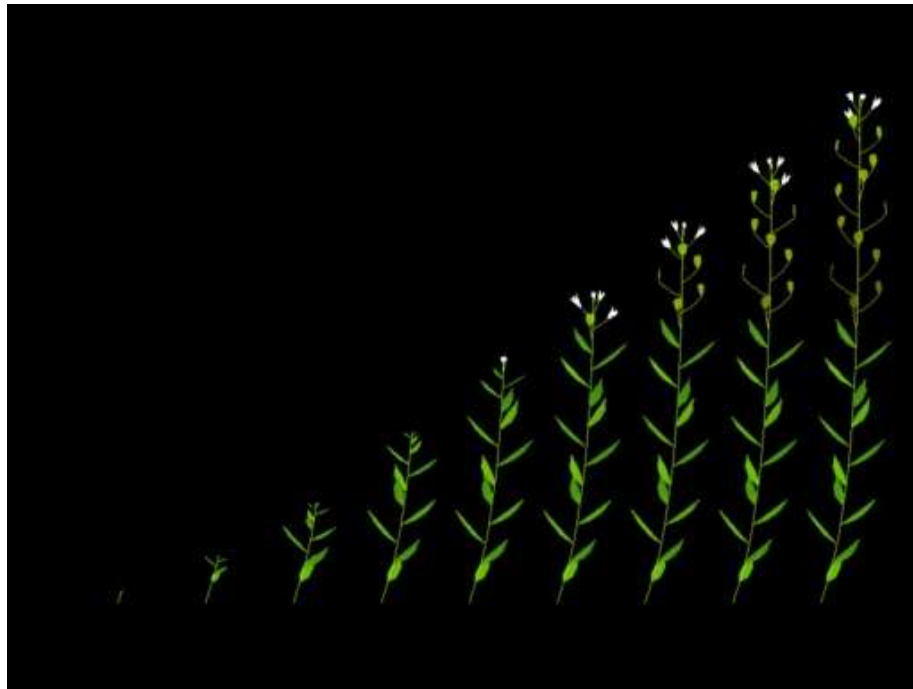
- The simplest case occurs when only the apex of the main axis of the growing plant produces new branches, as shown below.



- These lateral branches carry buds and then flowers, but do not branch any further. The resulting structure is called a *monopodial* branching structure, and the corresponding inflorescence is called a *raceme*.

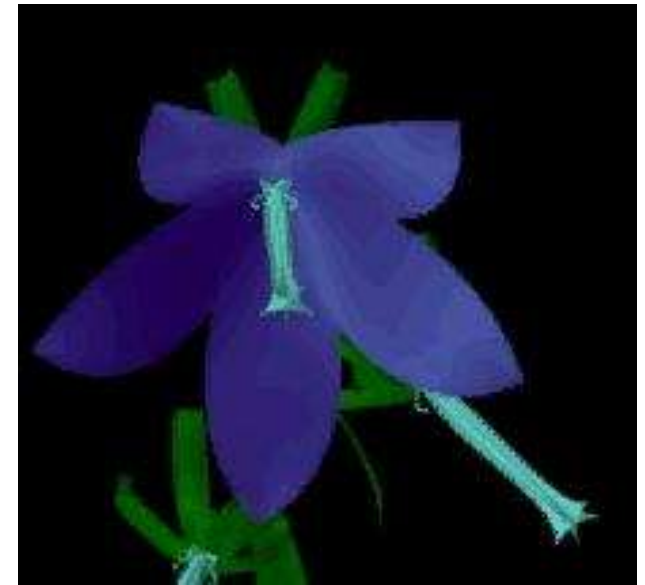
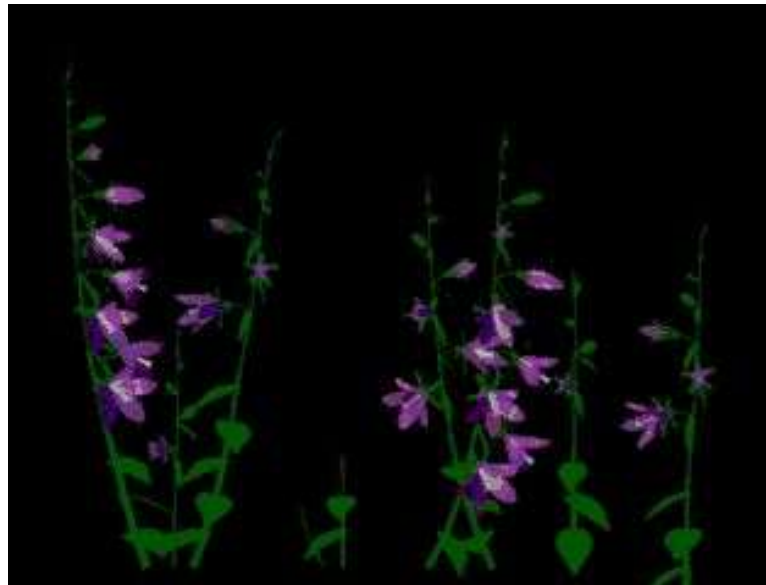
Branching patterns of herbaceous plants

- The image below illustrates the development of a common weed *Capsella bursa-pastoris*, or shepherd's purse, following this principle.



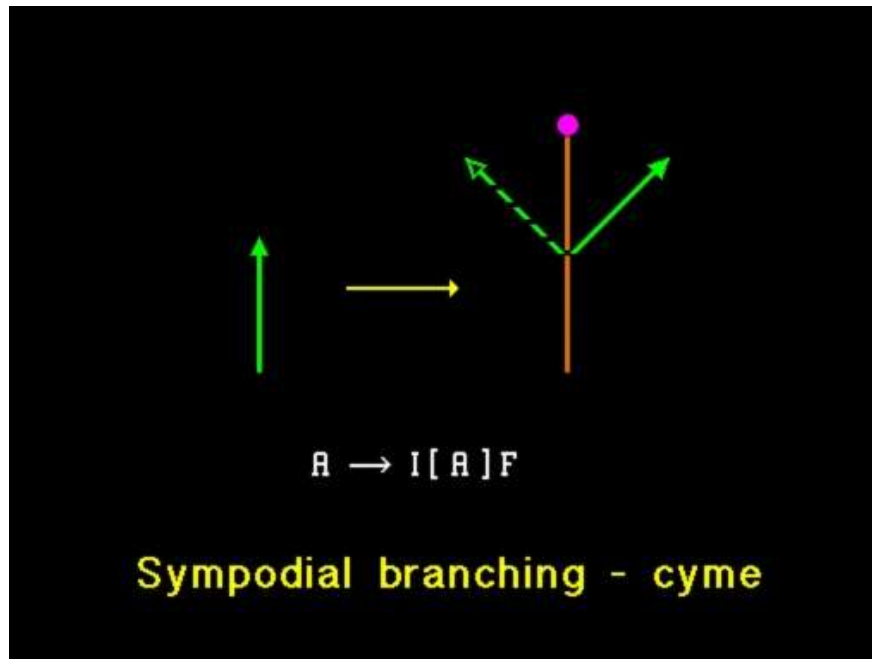
Branching patterns of herbaceous plants

- The creeping bellflower *Campanula rapunculoides* shown below develops in the same manner [\[anim9\]](#) [\[anim10\]](#) [\[anim11\]](#).



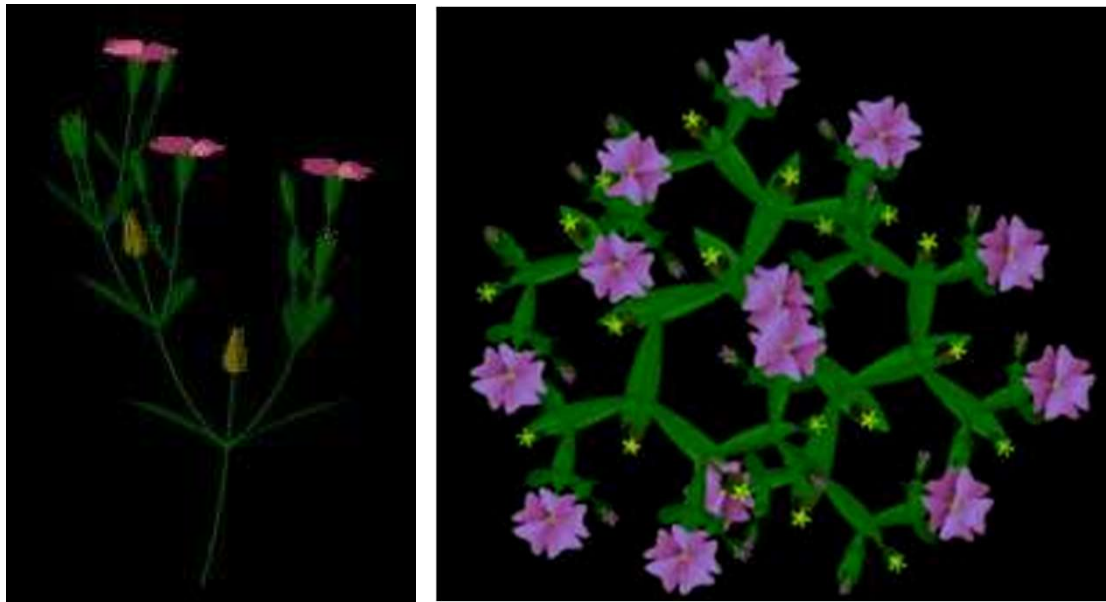
Branching patterns of herbaceous plants

- The image below shows a form of branching which, in a sense, is opposite to the previous one. In this case, called *sympodial* branching, the apex produces a flower bud terminating the development of the current axis, but in addition produces one or more active lateral apices. This process repeats recursively, with the main thrust of the development always going into the lateral branches.



Branching patterns of herbaceous plants

- The resulting inflorescence type is called a *cyme*. The development of *Lychnis coronaria*, or rose campion, shown below in the two separate images, provides a good example of the process [\[anim12\]](#) [\[anim13\]](#).



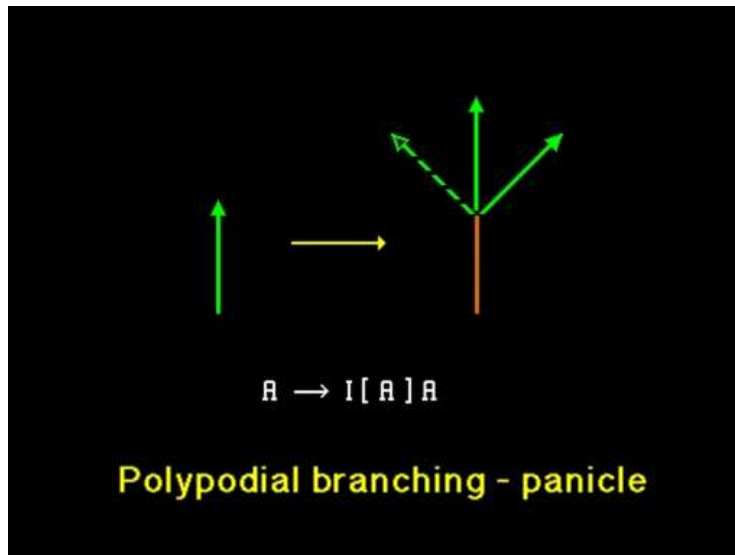
Branching patterns of herbaceous plants

- A view of the development of a single flower [\[anim14\]](#).



Branching patterns of herbaceous plants

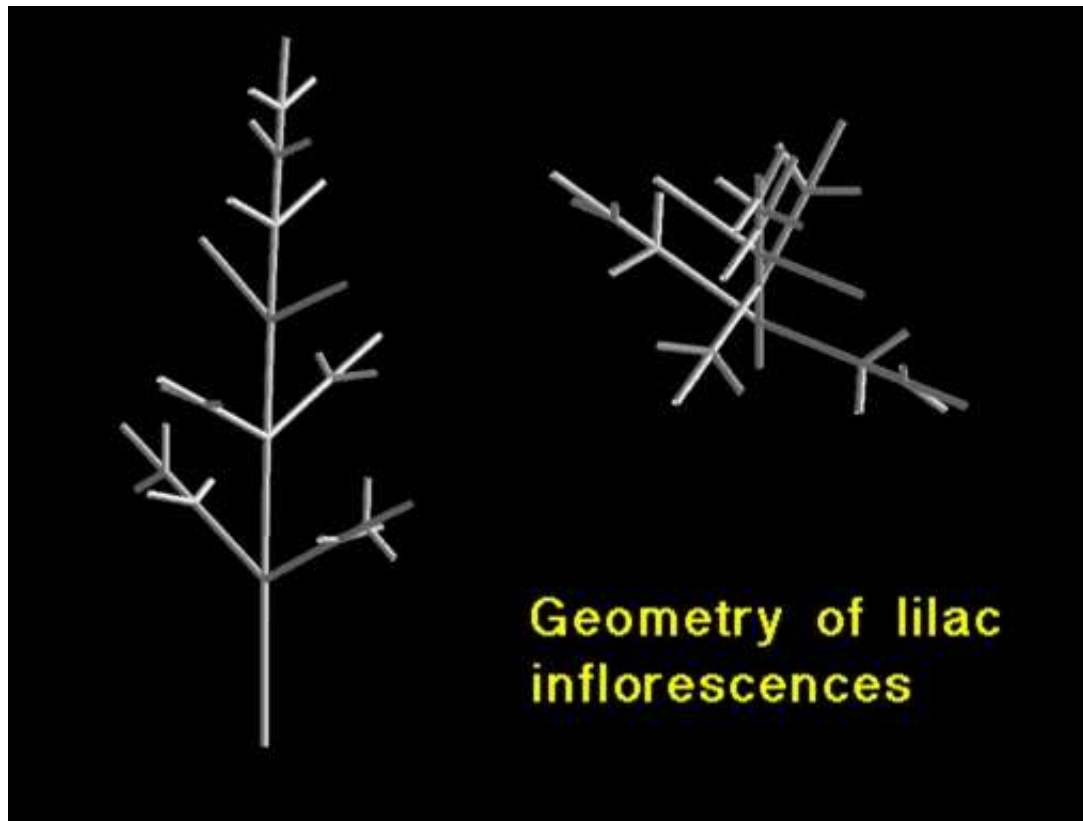
- Yet another branching type, called *polypodial* branching, is shown schematically below



- In this case, both the apex of the main axis and the lateral apices produce new branches until, at some point in time, the apices undergo a developmental switch and are transformed into flower buds. The resulting inflorescence, called a *panicle*, may adopt various forms depending on the geometric parameters.

Branching patterns of herbaceous plants

- The image below shows a so-called *decussate* branching pattern, in which pairs of lateral branches are arranged in mutually perpendicular planes.



Branching patterns of herbaceous plants

- By terminating each of these branches with a flower we can model lilac inflorescences, as shown below.



Signals In Plants

- We might think that we are now able to model all possible inflorescences, since we have considered all possible branching types.
- This is not quite true – we are only half way through the lecture!

Signals In Plants

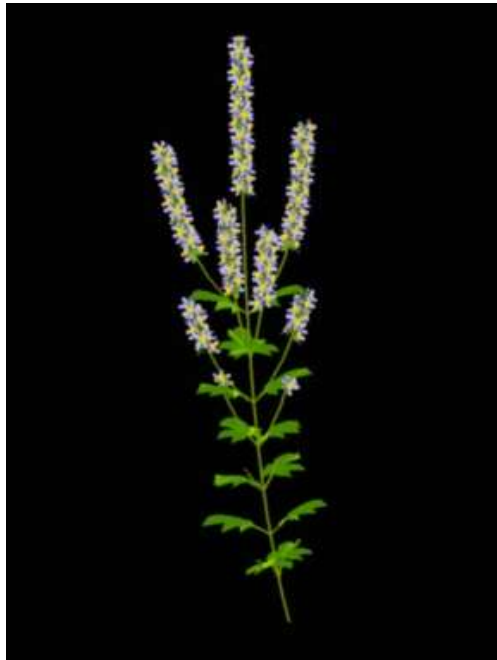
- One problem is related to the flowering sequences. For example, in wild carrot, shown below, flowers first appear at the top of the structure and the flowering zone progresses basipetally (downwards).



- As plants develop from the bottom up and not from the top down, the basipetal flowering sequence is opposite to the order in which the buds were originally formed.

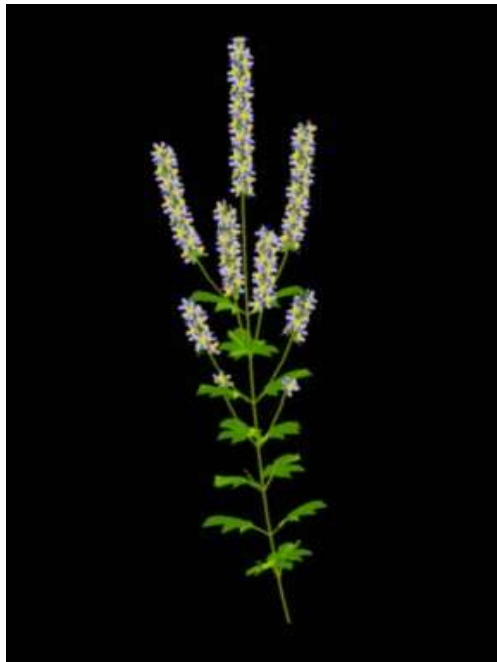
Signals In Plants

- The mint plant shown below illustrates the same point. Again, the top group of flowers was created last, yet opens first.



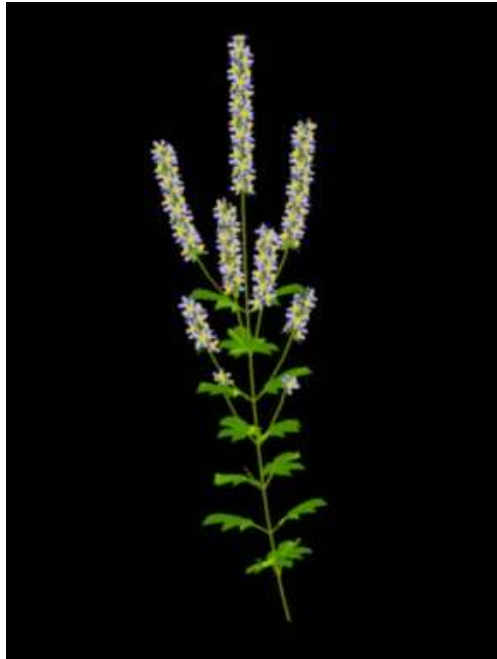
Signals In Plants

- In order to capture such processes, it is necessary to consider various forms of information flow in a developing plant. The L-system rules outlined in earlier represent information transfer by *lineage*, or from the mother module to the daughter modules.



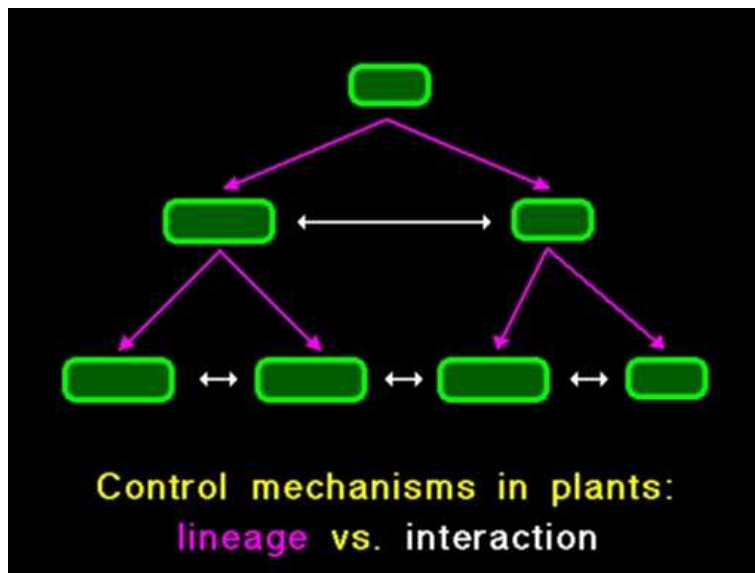
Signals In Plants

- They are called *context-free* rules in formal language (L-system) terminology. In many plants the *interaction* between coexisting modules also plays an important role. Such interaction may have the form of a flow of nutrients, water, or hormones between the modules of a developing plant.



Signals In Plants

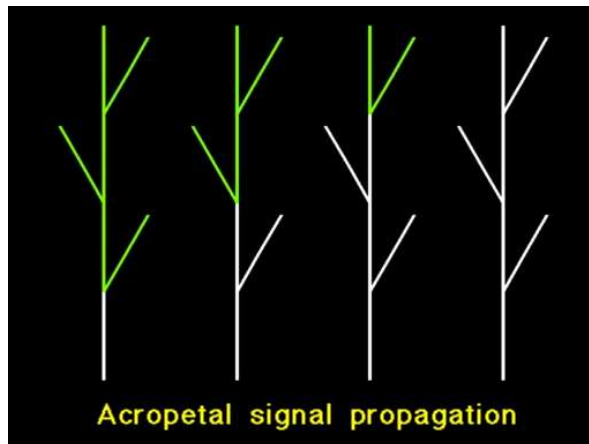
- The relationship between information transfer by lineage and interaction is shown schematically below. A cell (module) divides, producing two new cells that subsequently divide as well. Information can be transferred by lineage (diagonal arrows) or by interaction (horizontal arrows).



- Interactive processes can be captured by *context-sensitive* L-systems. In the context-sensitive case, a rule is applied to a particular module only if this module has some specific neighbours.

Signals In Plants

- For example, in the image below, a green module becomes white if and only if there is already a white module directly below it. Thus, context sensitivity makes it possible to simulate propagation of a signal.



- The flow of information in a static structure is of some interest, but even more interesting phenomena occur in growing structures. For example, consider a flower-inducing signal, corresponding to the hypothetical hormone *florigen*, which is sent from the bottom of the growing plant towards the apices. An apex reached by this signal is transformed into a flowering bud, then a flower, and finally a fruit.

Signals In Plants

- Depending on the relative growth rates of the main axis and the lateral branches, and on the respective ratios of signal propagation, the flowering zone may progress acropetally (upwards) as shown in the first image below, or basipetally (downwards) as shown in the second image [\[anim15\]](#) [\[anim16\]](#).



Signals In Plants

- The two images below illustrate a basipetal flowering sequence using a schematic and a realistic model of hawkweed (*Hieracium umbellatum*). Once the apex of the main axis has been transformed into a flowering bud, flowers on the lower branches are formed one after another in a basipetal sequence [\[anim17\]](#) [\[anim18\]](#).



Signals In Plants

- And a close-up of the development of a single flower from the bud to an open flower to a fruit [\[anim19\]](#).



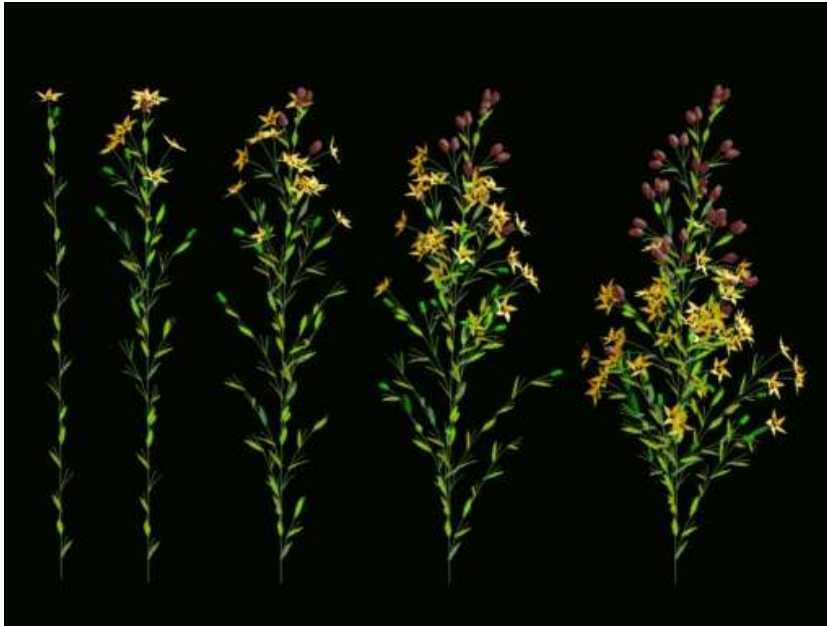
Signals In Plants

- Some models may require several signals. This occurs, in particular, when the flowering sequence progresses from the top down, and in some stages the plant is more extensively developed near the top than near the bottom. *Mycelis muralis*, or wall lettuce, shown schematically below, provides an example [\[anim20\]](#).



Signals In Plants

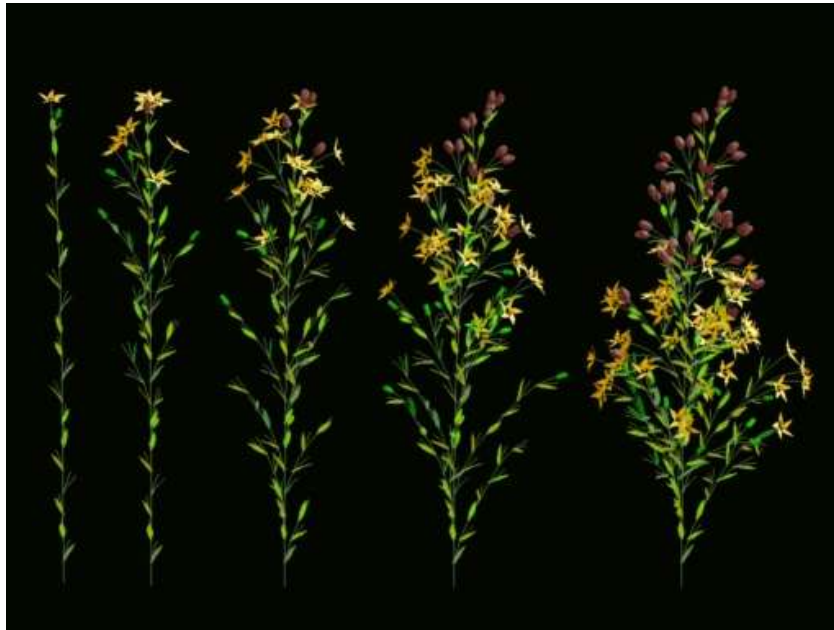
- Initially, the apex of the main axis produces a sequence of lateral branches.



- At this stage, their further development is inhibited. At some point in time, florigen is induced near the base of the plant and propagates upwards. When it reaches the apex of the main axis, the apex is transformed into a bud, and then a flower.

Signals In Plants

- Shortly afterwards, another signal is sent from the apex and propagates downwards.



- This signal lifts the apical dominance, allowing the lateral branches to grow. As this enabling sequence proceeds from the top down, the top part of the structure can be more developed than the bottom part.

Signals In Plants

- A three-dimensional rendering of this developmental sequence is shown below [\[anim21\]](#).



Exogenous Control Of Plant Development

- Diffusion-limited aggregation and cellular automata provide models of *exogenous* mechanisms of branching pattern formation. In this case, components of the growing structure communicate through the surrounding space.
- In contrast, L-systems simulate *endogenous* control mechanisms, which rely on information flow within the developing structure. Both lineage and interaction between adjacent modules are forms of endogenous control.
- In nature, endogenous and exogenous control mechanisms are often combined.
- For example, the development of a tree is affected by the genetically controlled formation of meristems (apices), the flow of water, nutrients, and phytohormones through the branching structure, and the plant response to environmental factors, such as the shading and crowding of branches.

Exogenous Control Of Plant Development

- *Environmentally-sensitive* L-systems represent one of the approaches proposed to create comprehensive models integrating endogenous and exogenous phenomena [Pru1994c].
- In this case, development is assumed to take place in a space characterized by a scalar or vector field.
- Modules of a growing plant test values of this field at points of interest.

Exogenous Control Of Plant Development

- For example, the image below shows the operation of an environmentally-sensitive L-system simulating the response of a simple two-dimensional branching structure to pruning. The developing structure is confined to a square, and the apices test whether they are within or outside this area. During the initial phase of development the apex of the main axis creates a sequence of internodes and dormant buds [\[anim22\]](#) .



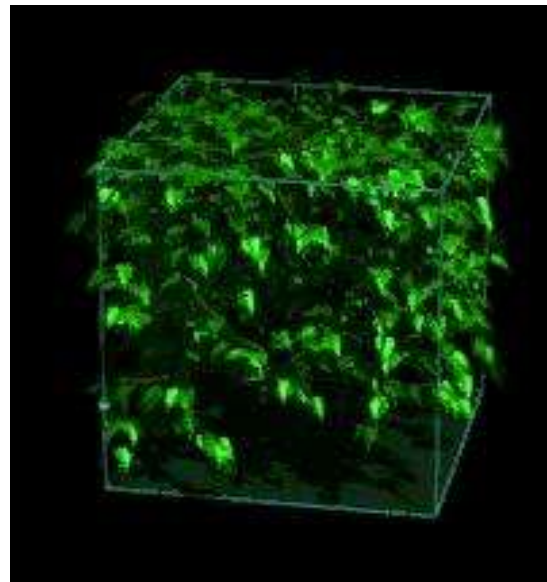
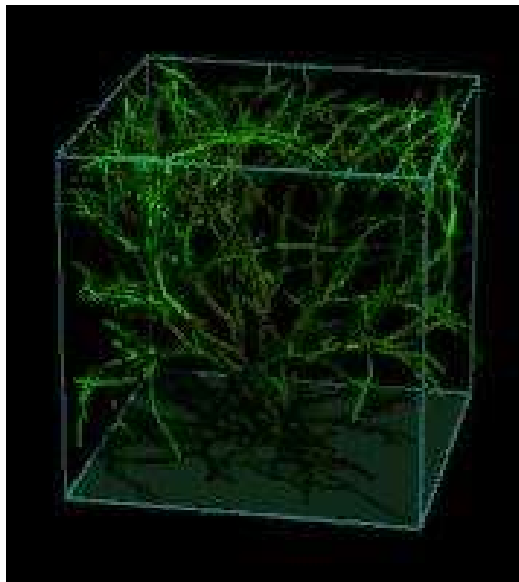
Exogenous Control Of Plant Development

- After crossing the bounding square the apex is pruned and a signal activating the nearest dormant bud is sent basipetally. The activated bud initiates a lateral branch, which grows in the same manner as the initial structure (*traumatic reiteration*). After crossing the bounding square, the apex of the reiterated branch is also pruned, and the bud-activating signal is generated again. The final structure results from the repetition of this process [\[anim22\]](#) .



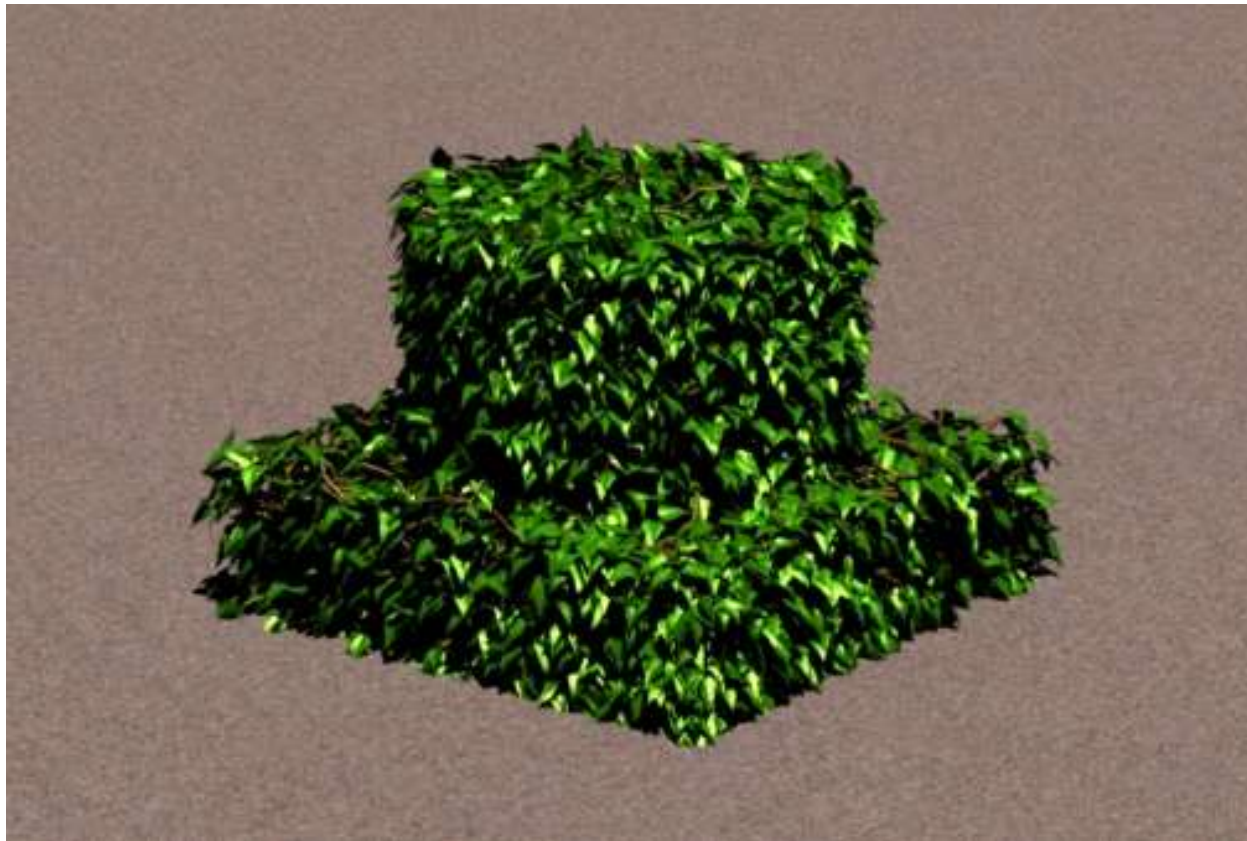
Exogenous Control Of Plant Development

- Three-dimensional extensions of the above model are shown below.
- In both cases, some of the newly created buds initiate new branches spontaneously, yielding tree-like structures. Pruning constrains the outline of the growing plants to a cubical bounding box, and increases the density of branches and leaves near the box boundaries [\[anim23\]](#) [\[anim24\]](#).



Exogenous Control Of Plant Development

- The pruning of plants to elaborate ornamental shapes is termed *topiary*. For example, the image below shows a plant confined to a bounding volume defined as the union of parallelepiped and a cylinder.

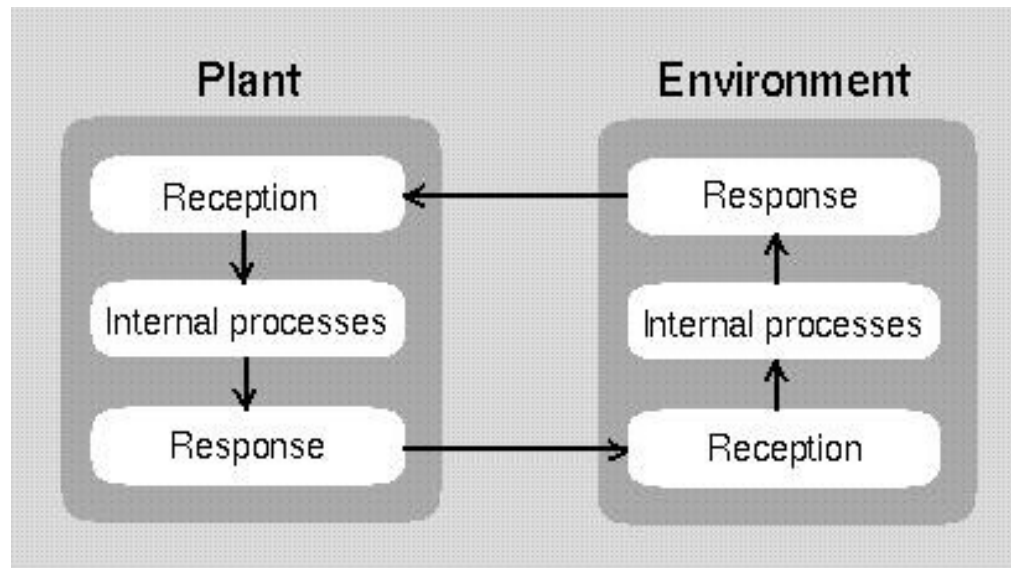


Interaction Between Plants and their Environment

- We know that despite the described systems and strategies that there is still much missing.
- The Big Picture.
- Plants don't grow up or outwards or downwards...
- They grow into and around, competing for resources, for sunshine, for space.

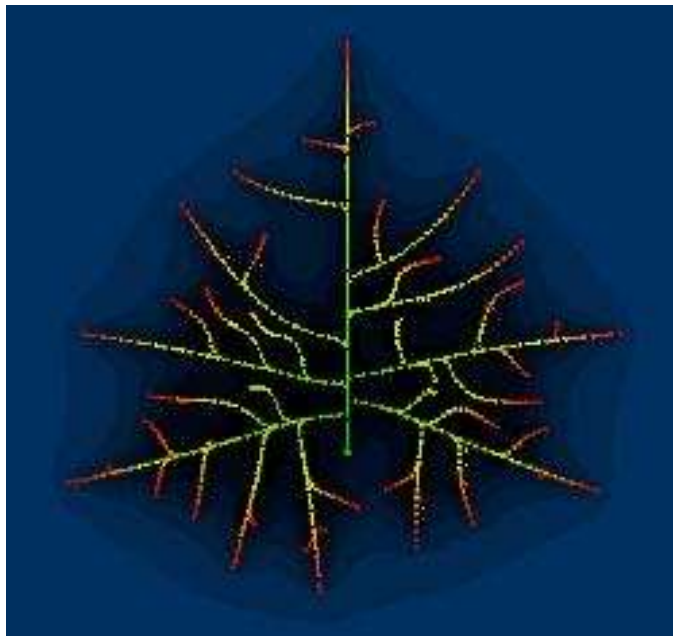
Interaction Between Plants and their Environment

- Innature, interactions between a plant and its environment have often a more complicated character, with the environment affecting the plant and the plant reciprocally affecting the environment. This bi-directional information flow can be conceptualized as the feedback loop shown below.



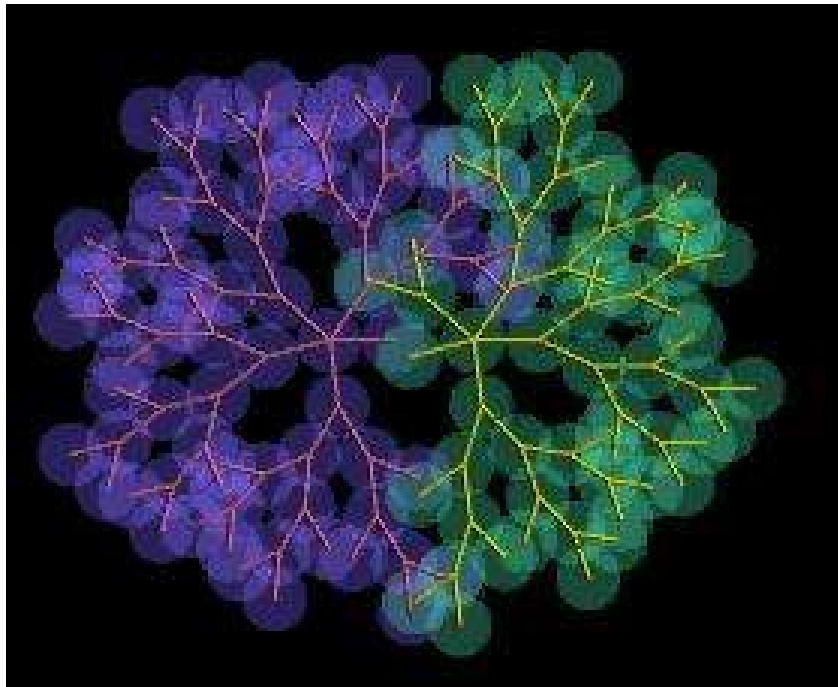
Interaction Between Plants and their Environment

- Simulation of plants interacting with their environment can be carried out within the general framework of *open L-systems* [Mec1996]. The development is assumed to take place in a space characterized by a scalar or vector field. Modules of a growing plant can test values of this field at points of interest, and send values that affect the field at specific locations. Sample models constructed according to this scheme are shown below [\[anim25\]](#).



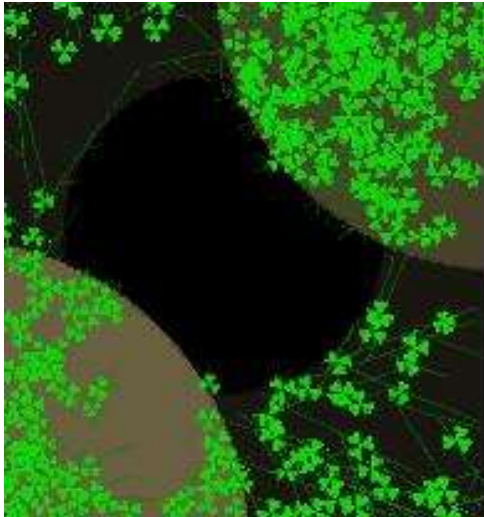
Interaction Between Plants and their Environment

- The model is sensitive to the local density of the growing structure. The gradient of the density function is used to select the least crowded areas available for the further development of each branch. In very dense areas, the growth stops altogether. In this way, the resulting geometry is determined by interactions between the branches, mediated by the environment .



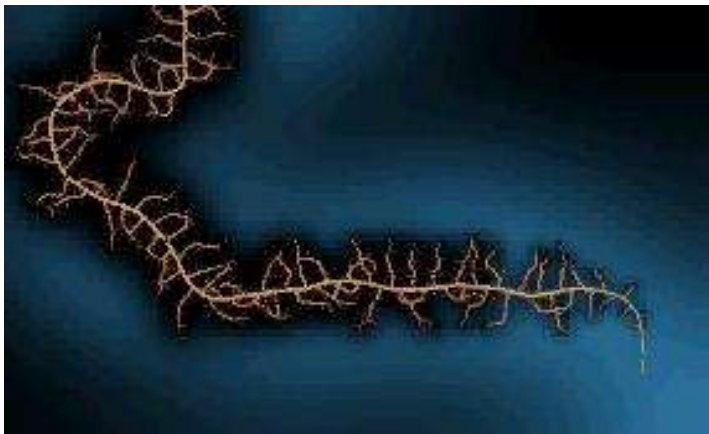
Interaction Between Plants and their Environment

- The image below shows the development two planar branch tiers competing for space. The underlying model, based on the observation of the tropical tree *Terminalia catappa*, was proposed by Honda, Tomlinson, and Fisher [Hon1981]. The circles represent leaf clusters, located at the nodes. The endpoint of each branch, or apex, produces new branches, unless they would fall into an existing cluster. This interaction limits the extent of branching, and adapts the shape of each tier to the presence of its neighbour [\[anim27\]](#).



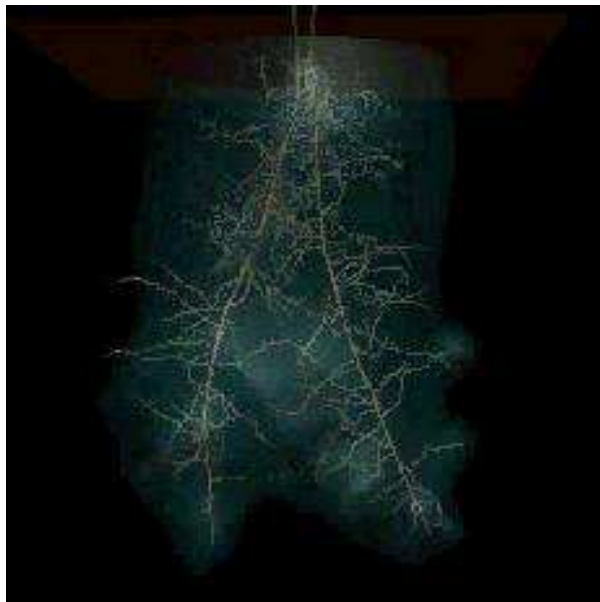
Interaction Between Plants and their Environment

- The image below shows the top view of a ground area with different intensities of incoming light. A hypothetical clonal plant inspired by clover propagates by means of horizontal stem segments (*spacers*) which connect individual plants (*ramets*). Old spacers and ramets die. The clone takes advantage of high light intensity by increasing the frequency of branching and decreasing the length of the spacers. Collisions are avoided. After colonizing the most favourable bottom left patch, the plant reinvades the top right patch. Light conditions in that patch are not sufficient to continuously sustain the plant. The colony disappears until the patch is reached again by a new wave of propagation. The dynamics of propagation reflects the plant's adaptation to its environment [\[anim28\]](#).



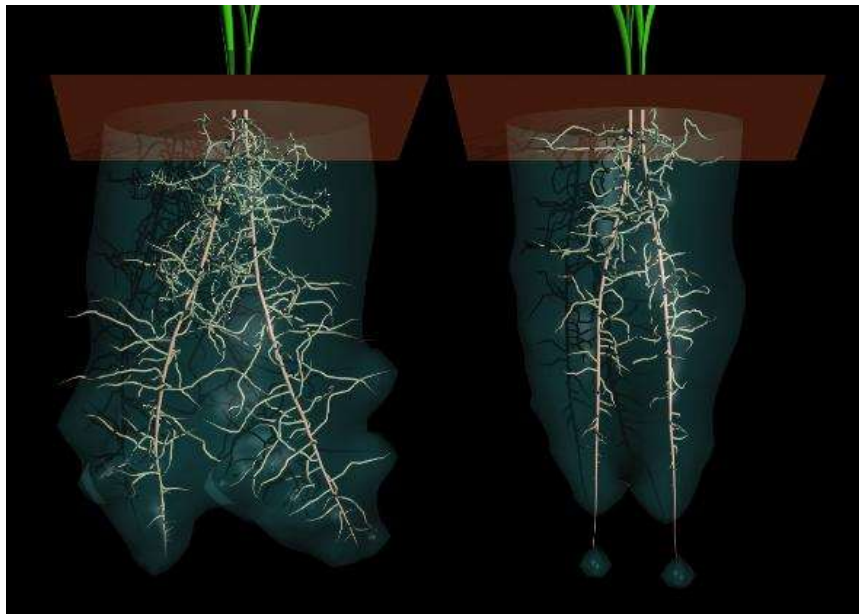
Interaction Between Plants and their Environment

- The image below shows a two-dimensional model of a root seeking water in the soil during its development. The initial water distribution has been predetermined, forming an S-shaped zone of high concentration indicated by the light colour. The growing tips of the main root and rootlets absorb water that diffuses in the soil. The decreased water concentration is indicated by dark areas that emerge around the root system. In areas with insufficient water concentration the rootlets cease to grow before they have reached their potential full length [\[anim29\]](#).



Interaction Between Plants and their Environment

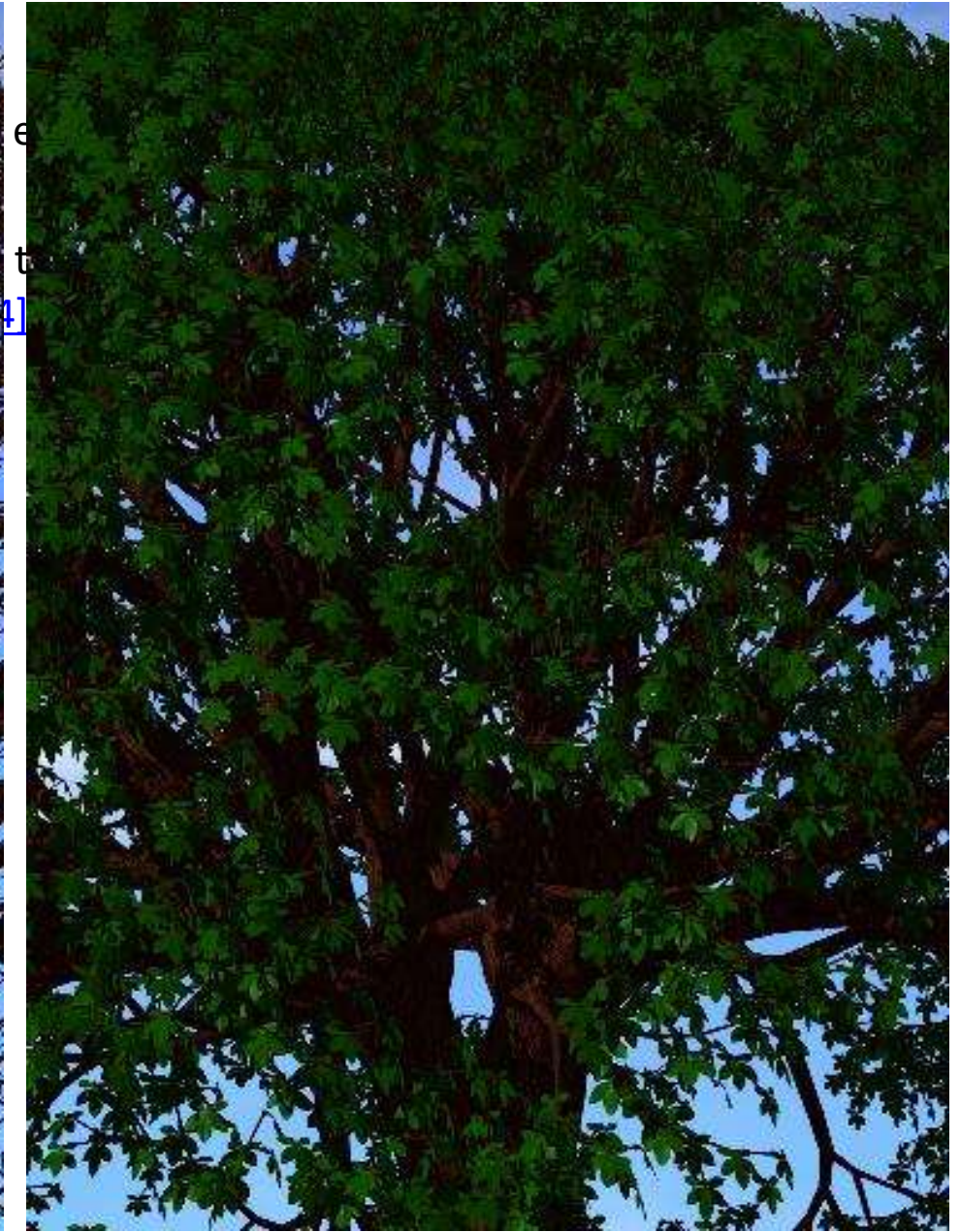
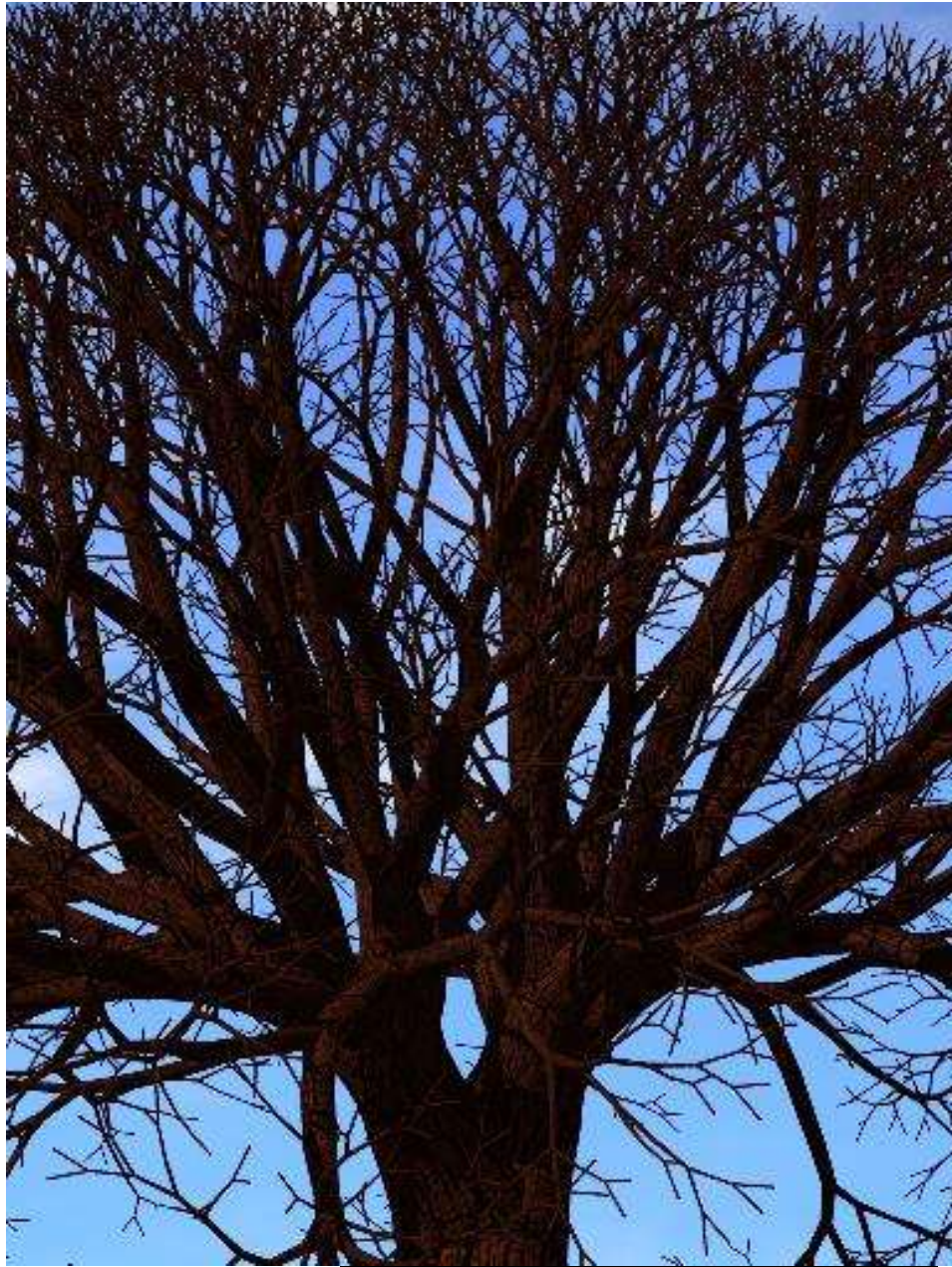
- The image below shows a three-dimensional extension of the previous model, based on the work of Clausnitzer and Hopmans [Cla1994]. Water concentration is visualized by a semi-transparent iso-surface surrounding the roots. As a result of competition for water, the main roots grow away from each other. If the rootlets grow more slowly, the area of influence of each root system is smaller, and the main roots grow closer to each other [\[anim29\]](#).



Interaction Between Plants and their Environment

- The image below shows a model of a horse chestnut tree inspired by the work of Chiba [Chi1994] and Takenaka [Tak1994].

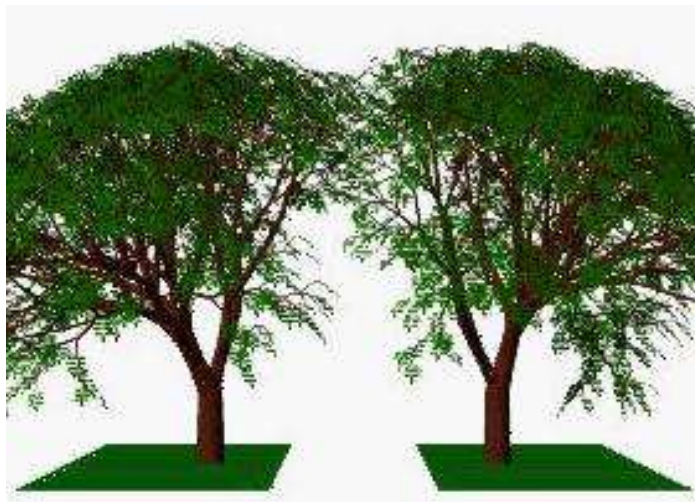




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Interaction Between Plants and their Environment

- Here branches compete for light from the sky hemisphere. Clusters of leaves cast shadows on branches further down. An apex in shade does not produce new branches. An existing branch whose leaves do not receive enough light dies and is shed from the tree. In such a manner, the competition for light controls the density of branches in the tree crowns [\[anim30\]](#).



Interaction Between Plants and their Environment

- In the image below two genetically identical trees compete for light. Moving the trees apart after they have grown reveals the adaptation of each crown to the presence of the neighbour tree.



Interaction Between Plants and their Environment



Interaction Between Plants and their Environment



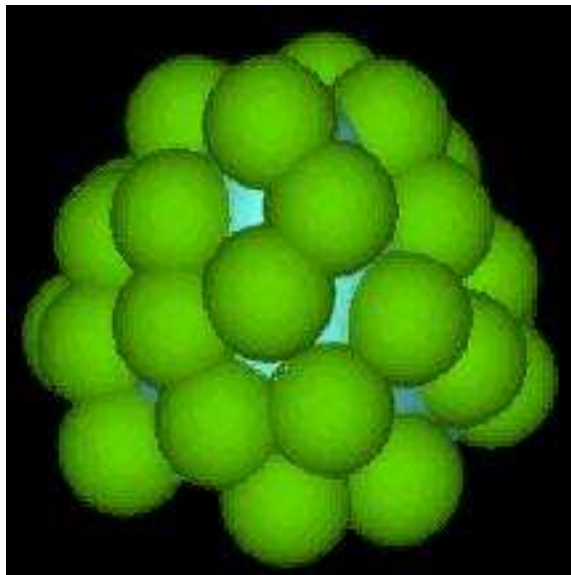
Spiral Phyllotaxis

- Exogenous control mechanisms may occur not only between a plant and its environment, but also between components of the same plant. We will illustrate this phenomenon using a model of *spiral phyllotaxis*, or spiral arrangement of organs such as leaves, florets, or seeds. An example of spiral phyllotaxis is shown below.



Spiral Phyllotaxis

- Many models were proposed to explain the emergence of phyllotactic patterns in nature. One of them is the *collision-based model*, introduced as a biological theory by Battjes [Bat1992], and subsequently applied to image synthesis by Fowler *et al.* [Fow1992]. The model describes distribution of flower initials, or *primordia*, on a supporting surface, the *receptacle*, which determines the shape of the entire structure [\[anim31\]](#).



Spiral Phyllotaxis

- The green coneflower (*Rudbeckia laciniata*) shown in the first image below and the cacti shown in the second image present sample structures generated using this model. In both cases, the primordia have been replaced by models of mature organs.



Introduction to Morphogenesis

- This document presented a review of selected models of morphogenesis that use computer graphics techniques to visualize the results of simulations.
- These models can be used for image synthesis purposes and provide a research tool for studying morphogenesis in nature.
- In the absence of formal measures of what makes two patterns look alike, visual inspection is a valuable method for comparing the models with reality.
- Photorealistic presentation adds credibility to this inspection by removing artefacts that might affect the comparisons.

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- The source for the information in this document is:

Visual Models of Morphogenesis

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- Gareth Edwards has made those changes appropriate for the usage of the primary source as a PowerPoint presentation.

Required For Next Week

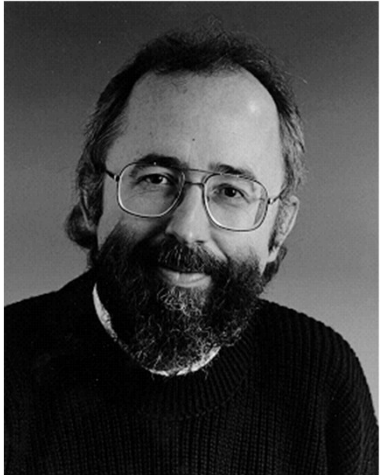
Required - reading for next week....

So:

- Read the course book “The Algorithmic Beauty of Plants”
- Przemyslaw Prusinkiewicz & Aristid Lindenmayer



PRZEMYSŁAW PRUSINKIEWICZ (pronounced: pru-ciŋ-k-jev-its)



“One of the main goals of science is to find principles that unify apparently diverse phenomena. With this broad objective in mind, I apply notions and methods of computer science to gain a better understanding of the emergence of forms and patterns in nature. The focal point of my work is the modelling, simulation and visualization of the development of plants. I find this area very interesting because of its interdisciplinary character. Ideas pertinent to plant modelling are related to computer science (computer graphics, formal language theory, programming language design, and simulation), as well as biology, artificial life, mathematics, and physics. The modelling of plants has also an artistic flavour, since the beauty of plants presents a constant challenge for creating visually appealing models”.

Required - reading for next week....

And:

- Read the various papers.....

Required - Fundamentals....

Fundamentals - last warning – you must have a working understanding of:

- How to edit, debug, compiling and run the RTVS_Lite demos
- The real-time framework
- What the 3D pipeline is and how the framework relates to it
- Vertex, index and attribute buffers
- Loading an .X format object
- Loading, creating and using a texture
- Materials
- Creating lights
- Object, world, view and projections transforms
- Drawing an object
- Drawing a vertex

Required - Assignment....

Assignment 1:

- Read, and make notes
- Ask Questions
- Focus your reading

End