

Chapter 6

Animation of plant development

The sequences of images used in Chapters 3 and 5 to illustrate the development of inflorescences and compound leaves suggest the possibility of using computer animation to visualize plant development. From a practical perspective, computer animation offers several advantages over traditional time-lapse photography.

Motivation

- Photography is sensitive to imperfections in the underlying experiment. A disease or even a temporary wilting of a plant may spoil months of filming.
- In nature, developmental processes are often masked by other phenomena. For example, the growth of leaves can be difficult to capture because of large changes in leaf positions during the day. Similarly, positions of tree branches may be affected by wind. Computer animation makes it possible to abstract from these distracting effects.
- Animation can be used when time-lapse photography is impractical because of the long development time of plants (e.g. years in the case of trees).
- In time-lapse photography, the initial position of the camera and the light conditions must be established a priori, without knowing the final shape of the plant. In computer animation all developmental stages of the modeled plant are known in advance, allowing for optimal selection of the model view.
- Animation can be applied to visualize developmental mechanisms that cannot be observed directly in real plants, such as the propagation of hormones and nutrients.

*Discrete
character of
L-systems*

- Animation offers an unprecedented means for visualizing the development of extinct plants on the basis of paleobotanical data.

The original formalism of L-systems provides a model of development that is discrete both in time and space. Discretization in time implies that the model states are known only at specific time intervals. Discretization in space means that the range of model states is limited to a finite number. Parametric L-systems remove the latter effect by assigning continuous attributes to model components. However, the model states are still known only in discrete time intervals. This presents a problem in animation, where a smooth progression of the developing forms is desirable.

This last statement requires further clarification. The very nature of animation is to produce the impression of continuous motion by displaying a sequence of still frames, captured at fixed time intervals. Why is a continuous model of plant development needed if it will be used to generate a fixed sequence of images in the final account? Wouldn't it be enough to retain the standard definition of L-systems and assume time slices fine enough to produce the desired progression of forms? This approach, while feasible and useful, has three major drawbacks.

- A model can be constructed assuming longer or shorter time intervals, but once the choice has been made, the time step is a part of the model and cannot be changed easily. From the viewpoint of computer animation it is preferable to control the time step by a single parameter, decoupled from the underlying L-system.
- The continuity criteria responsible for the smooth progression of shapes during animation can be specified more easily in the continuous time domain.
- It would be conceptually elegant to separate model development, defined in continuous time, from model observation, taking place in discrete intervals.

A developmental process is viewed as consisting of periods of continuous module expansion delimited by instantaneous module divisions. Special conditions are imposed to preserve the shape and growth rates of the organism during these qualitative changes. An analogy can be drawn to the theory of morphogenesis advanced by Thom [142], who viewed shape formation as a piecewise continuous process with singularities called *catastrophes*.

Formally, development taking place in continuous time is captured using the formalism of *timed DOL-systems*. The key difference between these L-systems and the types of L-systems considered so far lies in the definition of the derivation function. In “ordinary” L-systems, the derivation length is expressed as the number of derivation steps. In timed DOL-systems, the derivation length is associated with the total elapsed time since the beginning of the observation.

6.1 Timed DOL-systems

Let V be an alphabet and R the set of positive real numbers (including 0). The pair $(a, \tau) \in V \times R$ is referred to as the *timed letter* a , and the number τ is called the *age* of a . A sequence of timed letters, $x = (a_1, \tau_1) \dots (a_n, \tau_n) \in (V \times R)^*$, is called a *timed word* over alphabet V .

A *timed DOL-system* (*tDOL-system*) is a triplet $G = \langle V, \omega, P \rangle$, where

Definition

- V is the alphabet of the L-system,
- $\omega \in (V \times R)^+$ is a nonempty timed word over V , called the initial word, and
- $P \subset (V \times R) \times (V \times R)^*$ is a finite set of productions.

Instead of writing $((a, \beta), (b_1, \alpha_1) \dots (b_n, \alpha_n)) \in P$, the notation $(a, \beta) \rightarrow (b_1, \alpha_1) \dots (b_n, \alpha_n)$ is used. The parameter β is referred to as the *terminal age* of the letter a , and each parameter α_i is the *initial age* assigned to the letter b_i by production P . The following assumptions are made:

- C1. For each letter $a \in V$ there exists exactly one value $\beta \in R$ such that (a, β) is the predecessor of a production in P .
- C2. If (a, β) is a production predecessor and (a, α) is a timed letter that occurs in the successor of some production in P , then $\beta > \alpha$.

According to these conditions, each letter has a uniquely defined terminal age. Furthermore, an initial age assigned to a letter by a production must be smaller than its terminal age, *i.e.*, its *lifetime* ($\beta - \alpha$) must be positive.

Let $(a, \beta) \rightarrow (b_1, \alpha_1) \dots (b_n, \alpha_n)$ be a production in P . A function $\mathcal{D} : ((V \times R)^+ \times R) \rightarrow (V \times R)^*$ is called a *derivation function* if it has the following properties:

Derivation

- A1.** $\mathcal{D}((a_1, \tau_1) \dots (a_n, \tau_n), t) = \mathcal{D}((a_1, \tau_1), t) \dots \mathcal{D}((a_n, \tau_n), t)$
- A2.** $\mathcal{D}((a, \tau), t) = (a, \tau + t)$, if $\tau + t \leq \beta$
- A3.** $\mathcal{D}((a, \tau), t) = \mathcal{D}((b_1, \alpha_1) \dots (b_n, \alpha_n), t - (\beta - \tau))$, if $\tau + t > \beta$

A derivation in a timed DOL-system is defined in terms of two types of time variables. Global time t is common to the entire word under consideration, while local age values τ_i are specific to each letter a_i .

Axiom **A1** identifies t as the variable that synchronizes the entire development, and specifies that the lineages of all letters can be considered independently from each other (thus, no interaction between letters is assumed). With the progress of time t , each letter “grows older” until its terminal age is reached (axiom **A2**). At this moment subdivision occurs and new letters are produced with initial age values specified by the corresponding production (axiom **A3**). Condition **C1** guarantees that the subdivision time is defined unambiguously, hence the development proceeds in a deterministic fashion. Condition **C2** guarantees that, for any value of time t , the recursive references specified by axiom **A3** will eventually end.

Anabaena

The above concepts are examined by formulating a timed DOL-system that simulates the development of a vegetative part of the *Anabaena catenula* filament. Given the discrete model expressed by equation (1.1) on page 5, the corresponding tDOL-system is as follows:

$$\begin{aligned}
 \omega &: (a_r, 0) \\
 p_1 &: (a_r, 1) \rightarrow (a_l, 0)(b_r, 0) \\
 p_2 &: (a_l, 1) \rightarrow (b_l, 0)(a_r, 0) \\
 p_3 &: (b_r, 1) \rightarrow (a_r, 0) \\
 p_4 &: (b_l, 1) \rightarrow (a_l, 0)
 \end{aligned} \tag{6.1}$$

In accordance with the discrete model, it is assumed that all cells have the same lifetime, equal to one time unit. The derivation tree is shown in Figure 6.1. The nodes of the tree indicate production applications specified by axiom **A3**, and the triangular “arcs” represent the continuous aging processes described by axiom **A2**. The vertical scale indicates global time. For example, at time $t = 2.75$ the filament consists of three cells, b_l , a_r and a_r , whose current age is equal to 0.75.

According to the definition of time intervals corresponding to axioms **A2** and **A3**, a production is applied *after* the age $\tau + t$ exceeds the terminal age. Consequently, at division time the “old” cells still exist. For example, at time $t = 2.0$ the filament consists of two cells, a_l and b_r , both of age $\tau = 1$.

The above L-system can be simplified by considering cells of type b as young forms of the cells of type a . This is suggested by Figure 6.1 where cells b simply precede cells a in time. The simplified L-system has two productions:

$$\begin{aligned}
 p_1 &: (a_r, 2) \rightarrow (a_l, 1)(a_r, 0) \\
 p_2 &: (a_l, 2) \rightarrow (a_l, 0)(a_r, 1)
 \end{aligned} \tag{6.2}$$

The corresponding derivation tree starting from cell $(a_r, 1)$ is shown in Figure 6.2. Note the similarity to the tree from the previous example.

*Model
observation*

Whether a natural developmental process or its mathematical model is considered, the choice of observation times and the act of observation should not affect the process itself. In other terms, each derived word should depend only on the *total elapsed time* t , and not on the partition

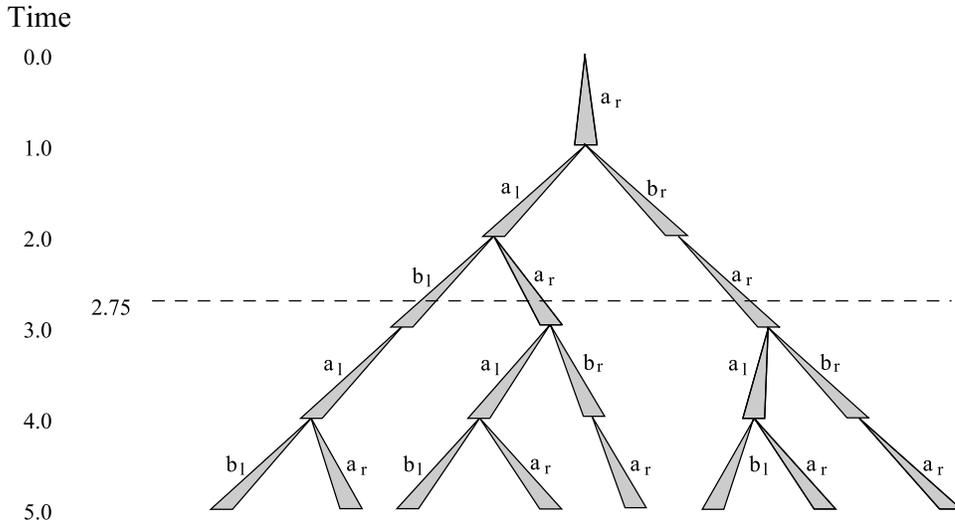


Figure 6.1: Derivation tree representing the continuous development of *Anabaena catenula* described by the L-system in equation (6.1). Sections of the triangles represent cell ages.

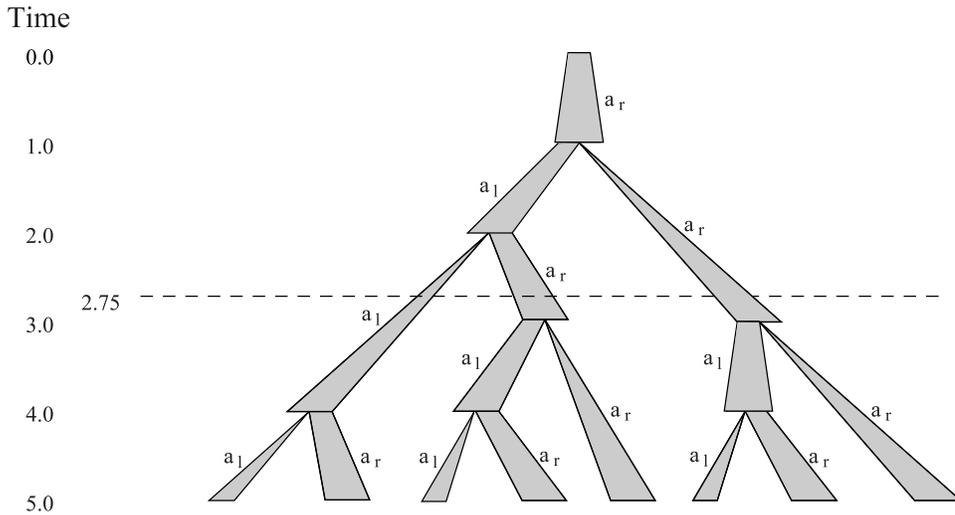


Figure 6.2: Derivation tree representing the continuous development of *Anabaena catenula* corresponding to the rules specified in equation (6.2)

of t into intervals. The following theorem shows that timed DOL-systems satisfy this postulate.

Theorem. Let $G = \langle V, \omega, P \rangle$ be a tDOL-system, and $x \in (V \times R)^+$ be a timed word over V . For any values of $t_a, t_b \geq 0$, the following holds:

$$\mathcal{D}(\mathcal{D}(x, t_a), t_b) = \mathcal{D}(x, t_a + t_b)$$

Proof. Let us first consider the special case where the word x consists of a single timed letter, (a_0, τ_0) , and all productions in the set P take single letters into single letters. According to condition **C1**, there exists a unique sequence of productions from P such that:

$$(a_i, \beta_i) \rightarrow (a_{i+1}, \alpha_{i+1}), \quad i = 0, 1, 2, \dots$$

Let (a_k, τ_k) be the result of the derivation of duration t_a that starts from (a_0, τ_0) . According to axioms **A2** and **A3**, and assuming that $t_a > \beta_0 - \tau_0$, this derivation can be represented in the form

$$\begin{aligned} & \mathcal{D}((a_0, \tau_0), t_a) \\ &= \mathcal{D}((a_1, \alpha_1), t_a - (\beta_0 - \tau_0)) \\ &= \mathcal{D}((a_2, \alpha_2), t_a - (\beta_0 - \tau_0) - (\beta_1 - \alpha_1)) \\ &= \dots \\ &= \mathcal{D}((a_k, \alpha_k), t_a - (\beta_0 - \tau_0) - (\beta_1 - \alpha_1) - \dots - (\beta_{k-1} - \alpha_{k-1})) \\ &= (a_k, \tau_k), \end{aligned}$$

where

$$\tau_k = \alpha_k + [t_a - (\beta_0 - \tau_0) - \sum_{i=1}^{k-1} (\beta_i - \alpha_i)].$$

Since the sequence of recursive calls can be terminated only by an application of axiom **A2**, the index k and the age τ_k satisfy the inequality

$$\alpha_k < \tau_k \leq \beta_k.$$

Due to condition **C2**, such an index k always exists and is unique.

Let us now consider a derivation of duration $t_b > \beta_k - \tau_k$ that starts from (a_k, τ_k) . Following the same reasoning, the result can be represented as (a_m, τ_m) , where

$$\tau_m = \alpha_m + [t_b - (\beta_k - \tau_k) - \sum_{i=k+1}^{m-1} (\beta_i - \alpha_i)]$$

and

$$\alpha_m < \tau_m \leq \beta_m.$$

By substituting the value of τ_k into the formula for τ_m , we obtain after simple transformations

$$\tau_m = \alpha_m + [(t_a + t_b) - (\beta_0 - \tau_0) - \sum_{i=1}^{m-1} (\beta_i - \alpha_i)].$$

Thus, the timed letter (a_m, τ_m) also results from the derivation of duration $t_a + t_b$ starting with (a_0, τ_0) :

$$(a_m, \tau_m) = \mathcal{D}(\mathcal{D}((a_0, \tau_0), t_a), t_b) = \mathcal{D}((a_0, \tau_0)x, t_a + t_b).$$

So far, we have considered only the case

$$t_a > \beta_0 - \tau_0, \quad t_b > \beta_k - \tau_k.$$

Two other cases, namely,

$$0 \leq t_a \leq \beta_0 - \tau_0, \quad t_b > \beta_k - \tau_k$$

and

$$t_a > \beta_0 - \tau_0, \quad 0 \leq t_b \leq \beta_k - \tau_k$$

can be considered in a similar way. The remaining case,

$$0 \leq t_a \leq \beta_0 - \tau_0, \quad 0 \leq t_b \leq \beta_k - \tau_k,$$

is a straightforward consequence of condition **C2**. This completes the proof of the special case. In general, a derivation that starts from a word $(a_1, \tau_1) \dots (a_n, \tau_n)$ can be considered as n separate derivations, each starting from a single letter. This observation applies not only to the initial word specified at time $t = 0$, but also to any intermediate word generated during the derivation. Consequently, any *path* in the derivation tree can be considered as a sequence of mappings that takes single letters into single letters. Application of the previous reasoning separately to every path concludes the proof. \square

6.2 Selection of growth functions

Timed L-systems capture qualitative changes in model topology corresponding to cell (or, in general, module) divisions, and return the age of each module as a function of the global time t . In order to complete model definition, it is also necessary to specify the shape of each module as a function of its age. Potentially, such growth functions can be estimated experimentally by observing real organisms [72, 73]. However, if detailed data is not available, growth functions can be selected from an appropriate class by choosing parameters so that the animation is smooth. This approach can be viewed as more than an *ad hoc* technique for constructing acceptable animated sequences. In fact, Thom presents it as a general methodology for studying morphogenesis [142, page 4]:

The essence of the method to be described here consists in supposing a priori the existence of a differential model underlying the process to be studied and, without knowing explicitly what the model is, deducing from the single assumption of its existence conclusions relating to the nature of the singularities of the process.

A technique for computing parameters of growth functions in the case of nonbranching filaments and simple branching structures is given below.

6.2.1 Development of nonbranching filaments

In a simple case of geometric interpretation of timed L-systems, symbols represent cells that elongate during their lifetime and divide upon reaching terminal age. Model geometry does not change suddenly, which means that

- the length of each cell is a continuous function of time, and
- the length of a cell before subdivision is equal to the sum of the lengths of the daughter cells.

Continuity requirements

The above *continuity requirements* are formalized in the context of a tDOL-system $G = \langle V, \omega, P \rangle$ as follows:

- R1. Let $[\alpha_{min}, \beta]$ describe the life span of a timed letter $a \in V$. The age α_{min} is the minimum of the initial age values assigned to a by the axiom ω or by some production in P . The terminal age β is determined by the predecessor of the production acting on symbol a . The *growth function* $g(a, \tau)$, which specifies the length of cell a as a function of age τ , must be a continuous function of parameter τ in the domain $[\alpha_{min}, \beta]$.
- R2. For each production $(a, \beta) \rightarrow (b_1, \alpha_1) \dots (b_n, \alpha_n)$ in P the following equality holds:

$$g(a, \beta) = \sum_{i=1}^n g(b_i, \alpha_i) \quad (6.3)$$

In practice, requirement **R1** is used to select the class of growth functions under consideration, and the equations resulting from requirement **R2** are used to determine the parameters in function definitions.

Linear growth

For example, in the case of the timed L-system specified in equation (6.2), requirement **R2** takes the form

$$\begin{aligned} g(a_r, 2) &= g(a_l, 1) + g(a_r, 0) \\ g(a_l, 2) &= g(a_l, 0) + g(a_r, 1). \end{aligned} \quad (6.4)$$

Let us assume that the growth functions are linear functions of time:

$$\begin{aligned} g(a_l, \tau) &= A_l \tau + B_l \\ g(a_r, \tau) &= A_r \tau + B_r \end{aligned} \quad (6.5)$$

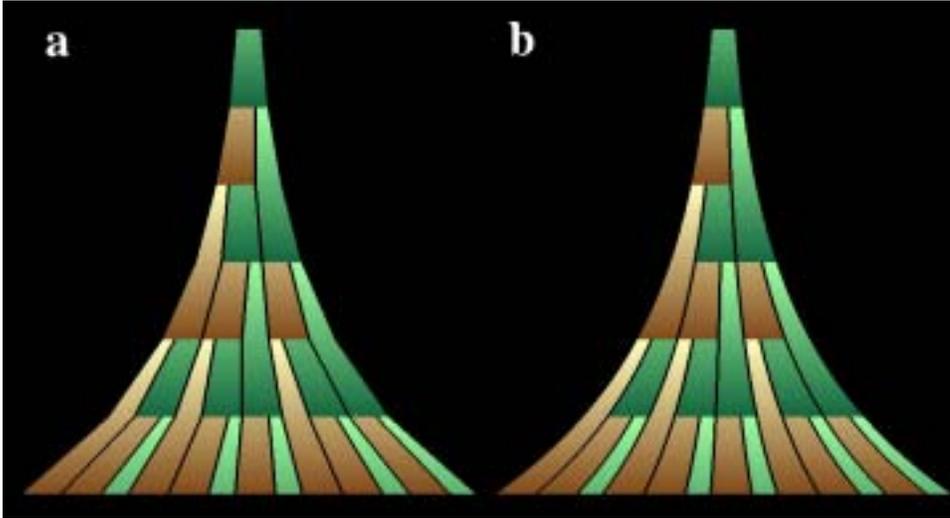


Figure 6.3: Diagrammatic representation of the development of *Anabaena catenula*, with (a) linear and (b) exponential growth of cells

By substituting equations (6.5) into (6.4), we obtain

$$\begin{aligned} 2A_r + B_r &= (1A_l + B_l) + (0A_r + B_r) & \text{or} & \quad 2A_r = A_l + B_l \\ 2A_l + B_l &= (0A_l + B_l) + (1A_r + B_r) & \text{or} & \quad 2A_l = A_r + B_r. \end{aligned}$$

The desired continuity of development is provided by all solutions of this system. They can be expressed in terms of coefficient c , which relates the growth rate of cells a_l to that of cells a_r :

$$\begin{aligned} A_l &= cA_r \\ B_l &= A_r(2 - c) \\ B_r &= A_r(2c - 1) \end{aligned}$$

Figure 6.3a illustrates the developmental process considered for $c = 1$. The diagram is obtained by plotting the cells in the filament as horizontal line segments on the screen. Colors indicate cell type and age. The observation time t ranges from 1 (at the top) to 7 (at the bottom), with increment $\Delta t = 0.009$.

The slopes of the side edges of the diagram represent growth rates of the entire structure. Notice that they remain constant in the periods between cell divisions, then change. This effect is disconcerting in animation, since the rate of organism growth suddenly increases with each cell division. In order to prevent this, it is necessary to extend requirements **R1** and **R2** to a higher order of continuity N . Specifically, equation (6.3) takes the form

$$g^{(k)}(a, \beta) = \sum_{i=1}^n g^{(k)}(b_i, \alpha_i) \quad \text{for } k = 0, 1, \dots, N, \quad (6.6)$$

where $g^{(k)}(a, \tau)$ is the k^{th} derivative of the growth function $g(a, \tau)$ with respect to age τ .

*Exponential
growth*

In the case of *Anabaena*, an attempt to achieve first-order continuity assuming linear growth functions yields an uninteresting solution, $g(a_l, \tau) = g(a_r, \tau) \equiv 0$. Thus, more complex growth functions must be considered, such as an exponential function that can be used to approximate the initial phase of sigmoidal growth. Assume that the growth function has the form

$$g(a_l, \tau) = g(a_r, \tau) = Ae^{B\tau}. \quad (6.7)$$

The objective is to find values of parameters A and B that satisfy equation (6.6) for $k = 0, 1$. By substituting equation (6.7) into (6.6), we obtain

$$AB^k e^{2B} = AB^k e^B + AB^k, \quad (6.8)$$

which implies that zero-order continuity yields continuity of infinite order in this case. Solution of equation (6.8) for any value of k yields

$$B = \ln \frac{1 + \sqrt{5}}{2} \approx 0.4812. \quad (6.9)$$

Parameter A is a scaling factor and can be chosen arbitrarily. The corresponding diagrammatic representation of development is shown in Figure 6.3b. The side edges of the diagram, representing the growth rates of the whole structure, are smooth exponential curves.

6.2.2 Development of branching structures

The notions of tDOL-system and growth function extend in a straightforward way to L-systems with brackets. For example, the following tDOL-system describes the recursive structure of the compound leaves analyzed in Section 5.3.

$$\begin{aligned} \omega &: (a, 0) \\ p_1 &: (a, 1) \rightarrow (s, 0)[(b, 0)][(b, 0)](a, 0) \\ p_2 &: (b, \beta) \rightarrow (a, 0) \end{aligned}$$

According to production p_1 , apex a produces an internode s , two lateral apices b and a younger apex a . Production p_2 transforms the lateral apices b into a after a delay β . The daughter branches recursively repeat the development of the mother branch.

Let us assume that the leaf development is first-order continuous, yielding the following equations for $k = 0, 1$:

$$g^{(k)}(a, 1) = g^{(k)}(s, 0) + g^{(k)}(a, 0) \quad (6.10)$$

$$g^{(k)}(b, 0) = 0 \quad (6.11)$$

$$g^{(k)}(b, \beta) = g^{(k)}(a, 0) \quad (6.12)$$

Equation (6.10) provides continuity along an existing axis upon the formation of a new internode s . Equation (6.11) specifies that a newly formed lateral apex b has zero length and zero growth rate. Equation (6.12) guarantees smooth transformation of apices b into apices a .

Let us further assume that apices a and internodes s expand exponentially,

$$g(a, \tau) = A_a e^{B_a \tau} \quad (6.13)$$

$$g(s, \tau) = A_s e^{B_s \tau}, \quad (6.14)$$

for $\tau \in [0, 1]$. The expansion of the lateral apices cannot be described by an exponential function, since it would not satisfy equations (6.11). Consequently, a polynomial growth function $g(b, \tau)$ is chosen. Equations (6.11) and (6.12) fix the function's endpoints and the tangents at the endpoints. Thus, in general, $g(b, \tau)$ must be a polynomial of degree three or more, such as

$$g(b, \tau) = A_b \tau^3 + B_b \tau^2 + C_b \tau + D_b. \quad (6.15)$$

The system of equations (6.10) through (6.12) is solved using the initial size A_a and the growth rate coefficient B_a as independent variables. By substituting (6.13) and (6.14) into equations (6.10) for $k = 0, 1$, we obtain

$$\begin{aligned} A_s &= A_a (e^{B_a} - 1) \\ B_s &= B_a. \end{aligned}$$

Equations (6.11) and (6.15) yield

$$C_b = D_b = 0.$$

Finally, substitution of (6.13) and (6.15) into (6.12) results in

$$\begin{aligned} A_b &= \frac{A_a}{\beta^3} (\beta B_a - 2) \\ B_b &= \frac{A_a}{\beta^2} (3 - \beta B_a). \end{aligned}$$

Figure 6.4 shows a sequence of images produced by this model using values $\beta = A_a = 1$ and $B_a = 0.48$. The branching angles are equal to 45° . The observation time t ranges from 6.9 to 7.7, with an increment of 0.2. Note the gradual formation of lateral segments.

In the examples considered above, modules are represented as straight lines, with growth functions controlling line lengths. Other parameters, such as the branching angle, the diameter of segments and the size of predefined surfaces, can be controlled in an analogous way. Generally, any developmental model captured by an OL-system with turtle interpretation can be converted into a tDOL-system and animated.

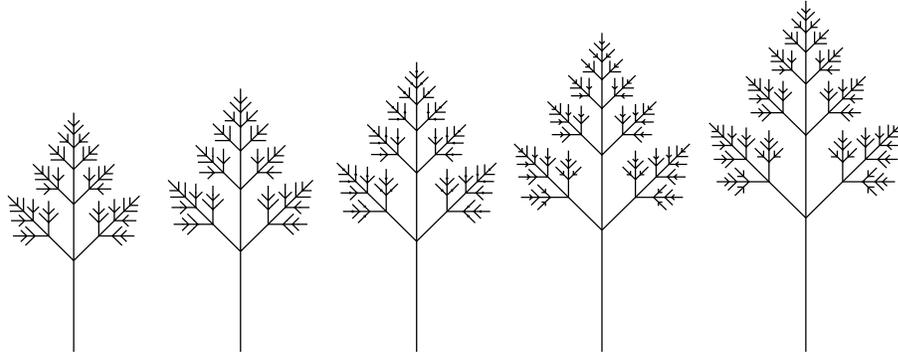


Figure 6.4: Developmental sequence of a branching structure modeled using a tDOL-system