Chapter 3

Developmental models of herbaceous plants

The examples of trees presented in the previous chapter introduce L-systems as a plant modeling tool. They also illustrate one of the most striking features of the generative approach to modeling, called *data base amplification* [136]. This term refers to the generation of complex-looking objects from very concise descriptions – in our case, L-systems comprised of small numbers of productions. Yet in spite of the small size, the specification of L-systems is not a trivial task.

In the case of highly self-similar structures, the synthesis methods based on edge rewriting and node rewriting are of assistance, as illustrated by the examples considered in Section 1.10.3. However, a more general approach is needed to model the large variety of developmental patterns and structures found in nature.

Developmental models

The methodology presented in this chapter is based on the simulation of the development of real plants. Thus, a particular form is modeled by capturing the essence of the *developmental process* that leads to this form. This approach has two distinctive features.

- **Emphasis on the space-time relation between plant parts.** In many plants, organs in various stages of development can be observed at the same time. For example, some flowers may still be in the bud stage, others may be fully developed, and still others may have been transformed into fruits. If development is simulated down to the level of individual organs, such *phase effects* are reproduced in a natural way.

- **Inherent capability of growth simulation.** The mathematical model can be used to generate biologically correct images of plants at different ages and to create sequences of images illustrating plant development in time.

The models are constructed under the assumption that organisms control the important aspects of their own development. According to Apter [3, page 44], this simplification must be accepted as a necessary evil, as long as the scope of the mathematical model is limited to an isolated plant. Consequently, this chapter focuses on the modeling and generation of growth sequences of *herbaceous* or non-woody plants, since internal control mechanisms play a predominant role in their development. In contrast, the form of woody plants is determined to a large extent by the environment, competition among branches and trees, and accidents [164].

Herbaceous plants

3.1 Levels of model specification

L-systems can be constructed with a variety of objectives in mind, ranging from a general classification of branching structures to detailed models suitable for image synthesis purposes. Accordingly, the L-systems presented in this chapter are specified at three levels of detail. The most abstract level, called *partial L-systems*, employs the notation of nondeterministic OL-systems to define the realm of possibilities within which structures of a given type may develop. Partial L-systems capture the main traits characterizing structural types, and provide a formal basis for their classification. Control mechanisms that resolve nondeterminism are introduced in the next level, termed *L-system schemata.*[1] The topology of individual plants and temporal aspects of their development are described at this level. Schemata are of particular interest from a biological point of view, as they provide an insight into the mechanisms that control plant development in nature. The geometric aspects are added in *complete L-systems* that include information concerning growth rates of internodes, the values of branching angles, and the appearance of organs. The difference between all three levels is illustrated using models of a single-flower shoot as a running example.

Partial L-systems

L-system schemata

Complete L-systems

3.1.1 Partial L-systems

Single-flower shoot

Consider the development of a shoot which, after a period of vegetative growth, produces a single flower. The partial L-system is given below.

$$\begin{array}{rl} \omega : & a \\ p_1 : & a \rightarrow I[L]a \\ p_2 : & a \rightarrow I[L]A \\ p_3 : & A \rightarrow K \end{array} \qquad (3.1)$$

The lower-case symbol a represents the *vegetative apex*, while the upper-case A is the *flowering apex*, capable of forming reproductive organs.

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[1] In the literature, the term “scheme” is also used to denote the class of L-systems with the same alphabet and productions, but with different axioms [62, page 54].

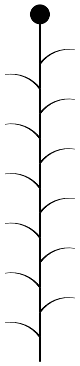

Figure 3.1: Single-flower shoot

A derivation step corresponds to a *plastochron*, defined as the time interval between the production of successive internodes by the apex. At each step apex a has a choice of forming either leaf L, internode I and new apex a (production p_1), or forming the same structures and transforming itself into a flowering apex A (p_2), which subsequently creates flower K (p_3). Once this transformation or *developmental switch* has taken place it cannot be reversed, since there is no rule allowing the transformation of A to a. Examples of strings generated by the L-system specified in equation (3.1) are given below.

a	a	a
$I[L]A$	$I[L]a$	$I[L]a$
$I[L]K$	$I[L]I[L]A$	$I[L]I[L]a$
$I[L]K$	$I[L]I[L]K$	$I[L]I[L]I[L]A$
	$I[L]I[L]K$	$I[L]I[L]I[L]K$
		$I[L]I[L]I[L]K$

A diagrammatic representation of a single-flower inflorescence is shown in Figure 3.1.

3.1.2 Control mechanisms in plants

L-system schemata

Lineage vs. interaction

A partial L-system does not specify the moments in which developmental switches occur. The timing of these switches is specified at the level of L-system schemata, which incorporate mechanisms that control plant development. In biology, these mechanisms are divided into two classes depending on the way information is transferred between modules. The term *lineage* (or *cellular descent*) refers to the transfer of information from an ancestor cell or module to its descendants. In contrast, *interaction* is the mechanism of information exchange between neighboring cells (for example, in the form of nutrients or hormones). Within the formalism of L-systems, lineage mechanisms are represented by context-free productions found in OL-systems, while the simulation of interaction requires the use of context-sensitive 1L-systems and 2L-systems.[2] Several specific mechanisms are listed below. Although they are described from the modeling perspective, a relation to physiological processes observed in nature can often be found.

Stochastic mechanism

The simplest method for implementing a developmental switch is to use a stochastic L-system. In this case the vegetative apex a has a probability π_1 of staying in the vegetative state, and π_2 of transforming itself into a flowering apex A.

$$\begin{aligned} \omega &: \ a \\ p_1 &: \ a \xrightarrow{\pi_1} I[L]a \\ p_2 &: \ a \xrightarrow{\pi_2} I[L]A \\ p_3 &: \ A \xrightarrow{1} K \end{aligned}$$

The probability distribution (π_1, π_2) is found experimentally, with $\pi_1 + \pi_2 = 1$.

The effect of environment

Many plants change from a vegetative to a flowering state in response to environmental factors such as temperature or the number of daylight hours. Such effects can be modeled using one set of productions (called a *table*) for some number of derivation steps, then replacing it by another set:

Table L-systems

Table 1	Table 2
$\omega : \ a$	$p_1 : \ a \rightarrow I[L]A$
$p_1 : \ a \rightarrow I[L]a$	$p_2 : \ A \rightarrow K$

The concept of table L-systems (*TOL-systems*) was introduced and formalized by Rozenberg [62, 127]. Note that the use of tables provides only a partial solution to the problem of specifying the switching time, since a control mechanism external to the L-system is needed to select the appropriate table.

Delay mechanism

The delay mechanism operates under the assumption that the apex undergoes a series of state changes that postpone the switch until a particular state is reached.

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[2] The clarity of this dichotomy is somewhat obscured by parametric OL-systems, which can simulate the operation of context-sensitive L-systems using an infinite set of parameter values.

This is captured by the following L-system in the case of a single-flower shoot.

$$\begin{array}{lll} \omega & : & a_0 \\ p_i & : & a_i \rightarrow I[L]a_{i+1} \quad 0 \leq i \leq n-1 \\ p_n & : & a_n \rightarrow I[L]A \\ p_{n+1} & : & A \rightarrow K \end{array}$$

According to this model, the apex *counts* the leaves it produces. While it may seem strange that a plant would count, it is known that some plant species produce a fixed number of leaves before they start flowering.

Accumulation of components

A developmental mechanism based on the accumulation of components is similar to that of delay, but emphasizes the physiological nature of the counting process. According to this approach, counting is achieved by a monotonic increase or decrease in the concentration of certain cell components. This process can be captured by the following parametric L-system:

$$\begin{array}{lllll} \omega : & a(0) & & & \\ p_1 : & a(c) & : & c < C & \rightarrow I[L]a(c+\Delta c) \\ p_2 : & a(c) & : & c \geq C & \rightarrow I[L]A \\ p_3 : & A & : & * & \rightarrow K \end{array} \tag{3.2}$$

The parameter c indicates current concentration of the controlling components in the apex a. In each derivation step, this concentration is increased by a constant Δc. The developmental switch occurs when the concentration reaches the threshold value C.

Development controlled by a signal

In many plants, the switch from a vegetative to a flowering state is caused by a flower-inducing signal transported from the basal leaves towards the apex. The time of signal initiation is determined using one of the previously described methods, for example by counting. A sample L-system is given below.

$$\begin{array}{lrcll} \omega : & D(1)a(1) & & & \\ p_1 : & a(i) & : & i < m & \rightarrow a(i+1) \\ p_2 : & a(i) & : & i = m & \rightarrow I[L]a(1) \\ p_3 : & D(i) & : & i < d & \rightarrow D(i+1) \\ p_4 : & D(i) & : & i = d & \rightarrow S(1) \\ p_5 : & S(i) & : & i < u & \rightarrow S(i+1) \\ p_6 : & S(i) & : & i = u & \rightarrow \varepsilon \\ p_7 : & S(i) < I & : & i = u & \rightarrow IS(1) \\ p_8 : & S(i) < a(j) & : & * & \rightarrow I[L]A \\ p_9 : & A & : & * & \rightarrow K \end{array}$$

The apex a produces internodes I and leaves L on the main axis (p_2). The time between the production of two consecutive segments, or the plastochron of the main axis, is equal to m derivation steps (p_1). After a delay of d steps (p_3), a signal S is sent from the plant base towards the apices (p_4). This signal is transported along the main axis with a delay of u steps per internode I (p_5,p_7). Production p_6 removes the signal from a node after it has been transported along the structure (ε stands for the empty string). When the signal reaches the apex, a is transformed into flowering state A (p_8) which yields flower K (p_9). Note that the signal has to propagate faster than one node per plastochron ($u < m$), otherwise it would not be able to catch up with the apex. The above processes are illustrated by the following developmental sequence, for $d = 4$, $m = 2$ and $u = 1$.

$$\begin{array}{l}
D(1)a(1)\\
D(2)a(2)\\
D(3)I[L]a(1)\\
D(4)I[L]a(2)\\
S(1)I[L]I[L]a(1)\\
IS(1)[L]I[L]a(2)\\
I[L]IS(1)[L]I[L]a(1)\\
I[L]I[L]IS(1)[L]a(2)\\
I[L]I[L]I[L]A\\
I[L]I[L]I[L]K
\end{array}$$

Although the above model may appear unnecessarily complicated, signals are indispensable in the simulation of complex flowering sequences discussed later.

3.1.3 Complete models

The L-systems considered so far are not directly suitable for image synthesis purposes. To this end, they must be completed with geometric information. The relation between an L-system scheme and a corresponding complete L-system is discussed using the model of crocuses shown in Figure 3.2 as an example.

Crocus

The development is controlled using a delay expressed as an accumulation mechanism (equation (3.2)). In contrast to L-system schemes in which symbols represent module types, the L-system in Figure 3.2 is specified in terms of turtle symbols. Production p_1 describes the creation of successive internodes F and leaves L by the vegetative apex a. The leaves branch from the stem at an angle of 30° and spiral around the main axis with a divergence angle equal to 137.5° (see Chapter 4). Productions p_2 and p_3 describe the developmental switch and the creation of flower K taking place respectively in steps T_a and T_{a+1}. Productions p_4 and p_5 capture the development of leaves and flowers until they reach their final shapes T_L and T_K steps after creation. For each

```
#define T_a 7              /* developmental switch time */
#define T_L 9              /* leaf growth limit */
#define T_K 5              /* flower growth limit */
#include L(0),L(1),...,L(T_L)  /* leaf shapes */
#include K(0),K(1),...,K(T_K)  /* flower shapes */

ω   :  a(1)
p_1 :  a(t)  :  t<T_a  →  F(1)[&(30)~L(0)]/(137.5)a(t+1)
p_2 :  a(t)  :  t=T_a  →  F(20)A
p_3 :  A     :  *      →  ~K(0)
p_4 :  L(t)  :  t<T_L  →  L(t+1)
p_5 :  K(t)  :  t<T_K  →  K(t+1)
p_6 :  F(l)  :  l<2    →  F(l+0.2)
```

Figure 3.2: Crocuses

branch			
main apex terminates		main apex continues	
all lateral apices terminate	some lateral apices continue	all lateral apices terminate	some lateral apices continue
terminal	sympodial	monopodial	polypodial

Table 3.1: Basic growth patterns of branching structures

value of parameter t, the corresponding organ shapes $L(t)$ and $K(t)$ are modeled using bicubic patches incorporated into the plant structure as described in Section 5.1. Production p_6 specifies the gradual elongation of internodes.

3.2 Branching patterns

Subapical growth

The partial L-system in equation (3.1) and the related schemata employ *subapical growth* mechanisms in which new branches are created exclusively by apices. All herbaceous plants develop this way. The architecture of a branching structure is to a large extent determined by the relationships between *terminal* and *continuing* apices. While a continuing apex produces branches again and again, a terminal one either gives rise to an appendage such as a flower or dies. The possible combinations are listed in Table 3.1. Of the four terms assigned to these possibilities, two are commonly used in biology, namely, *sympodial* and *monopodial*, while the other two terms are introduced here to denote the remaining cases, usually not characterized in the literature.

Expression using L-systems

The above branching patterns can be represented conveniently using partial bracketed L-systems. Let A, B, C denote continuing apices, X a terminal apex, and I an internode. The terminal and sympodial patterns are characterized by rules of the form

$$A \rightarrow I[B]^n[X]^m X,$$

with $n = 0$, $m > 0$ in the case of terminal patterns and $n > 0$, $m \geq 0$ in the case of sympodial patterns. The important property is that the main apex terminates its development in all these cases.

Monopodial and polypodial patterns have rules of the form

$$A \rightarrow I[B]^n[X]^m C,$$

with $n = 0$, $m > 0$ in the case of monopodial patterns and $n > 0$, $m \geq 0$ in the case of polypodial ones. In these cases, it is important that the apex remains active.

The terms defined here apply to branching structures in general, whether they only produce vegetative organs (branches and leaves) or reproductive organs as well. In the latter case, the terminal organs develop from flower buds to flowers to fruits but do not give rise to vegetative structures (there are exceptions to this statement but they can be neglected here).

3.3 Models of inflorescences

The following discussion focuses on the modeling of compound flowering structures or *inflorescences*. In some cases an entire shoot system can be considered an inflorescence, in others only some of the branches bear flowers and are inflorescences. Inflorescence architecture is an elaboration of branching structures in general.

Classification

In the domain of botanical applications of L-systems, the study of inflorescences has played a particularly visible role [44, 45, 46, 47, 77, 86]. Unfortunately, the terms used for the various inflorescence types are not uniform in the literature. Besides a purely morphological terminology, attempts have been made to construct a "typological" terminology, expressing the "essential" features of flowering structures [144, 145, 157, 158]. However, these terms are not generally accepted [12]. A compromise has been proposed by D. and U. Müller-Doblies [100], which serves as a basis for the classification that guides this presentation.

3.3.1 Monopodial inflorescences

Simple racemes (open)

Racemes are characteristically monopodial inflorescences; a shoot has lateral apices with terminal structures and a main apex that continues to development. A raceme is *open* if the main apex does not form a flower. The partial L-system for this widely occurring type of inflorescence is:

$$\begin{array}{rcl} \omega : & a & \\ p_1 : & a & \rightarrow & I[L]a \\ p_2 : & a & \rightarrow & I[L]A \\ p_3 : & A & \rightarrow & I[K]A \end{array} \tag{3.3}$$

This system differs from that modeling a shoot with a single flower (equation (3.1)) only in production p_3. Here it is designed to repeatedly produce lateral flowers (Figure 3.3), while in the previous system A produces a single flower.

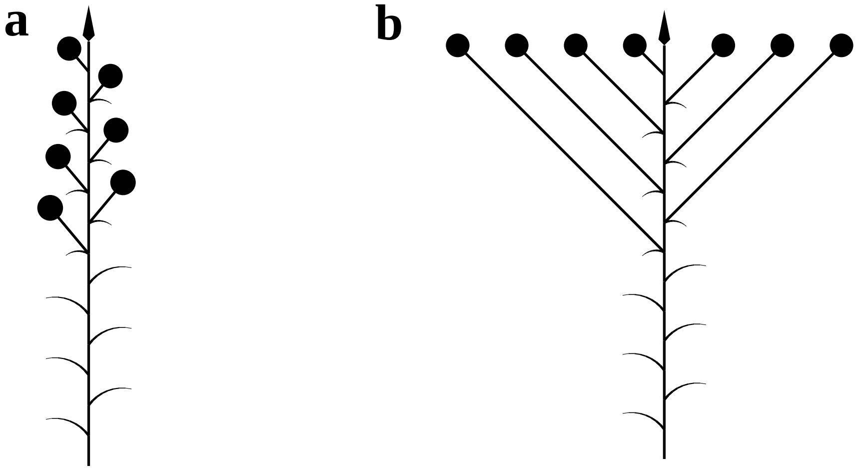


Figure 3.3: Open racemes: (a) elongated form, (b) planar form

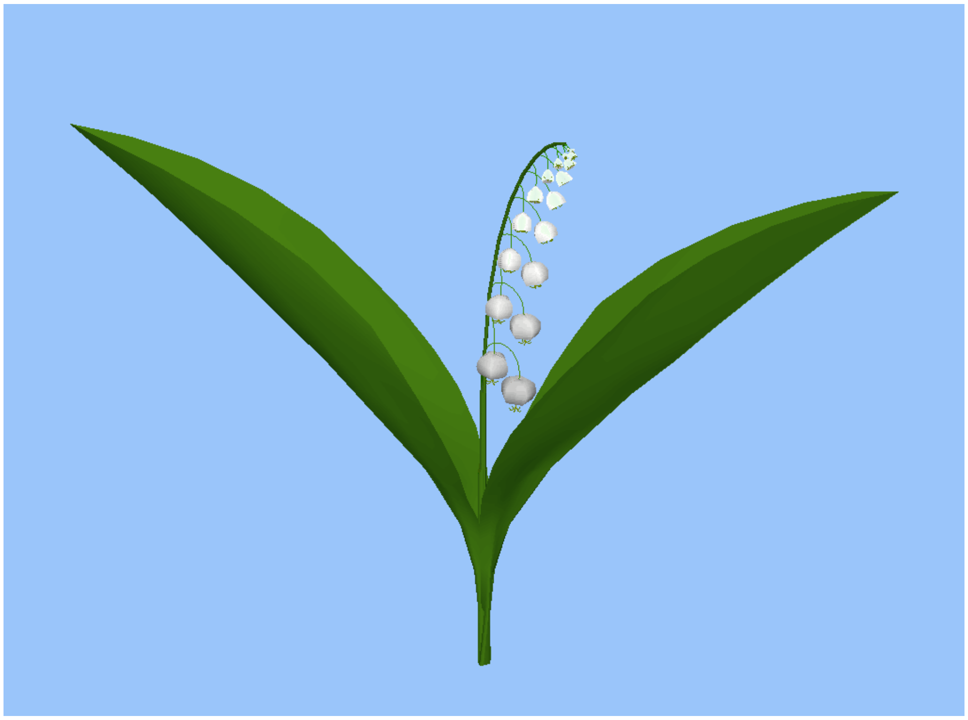


Figure 3.4: Lily-of-the-valley

Acropetal sequence

The flowering sequence in open racemes is always *acropetal* (from base to top). This can be observed after substituting production p_3 in the L-system in equation (3.3) with productions $p_3^{'}$ and p_4, which use indexed symbols K_i to denote subsequent stages of flower development.

$$\begin{array}{llll} p_3^{'}: & A & \rightarrow & I[IK_0]A \\ p_4: & K_i & \rightarrow & K_{i+1}, \qquad i \geq 0 \end{array}$$

The indexed notation $K_i \rightarrow K_{i+1}$ stands for a (potentially infinite) set of productions $K_0 \rightarrow K_1, K_1 \rightarrow K_2, K_2 \rightarrow K_3$,.... The developmental sequence begins as follows:

$$\begin{array}{l} A \\ I[IK_0]A \\ I[IK_1]I[IK_0]A \\ I[IK_2]I[IK_1]I[IK_0]A \\ I[IK_3]I[IK_2]I[IK_1]I[IK_0]A \\ \cdots \end{array}$$

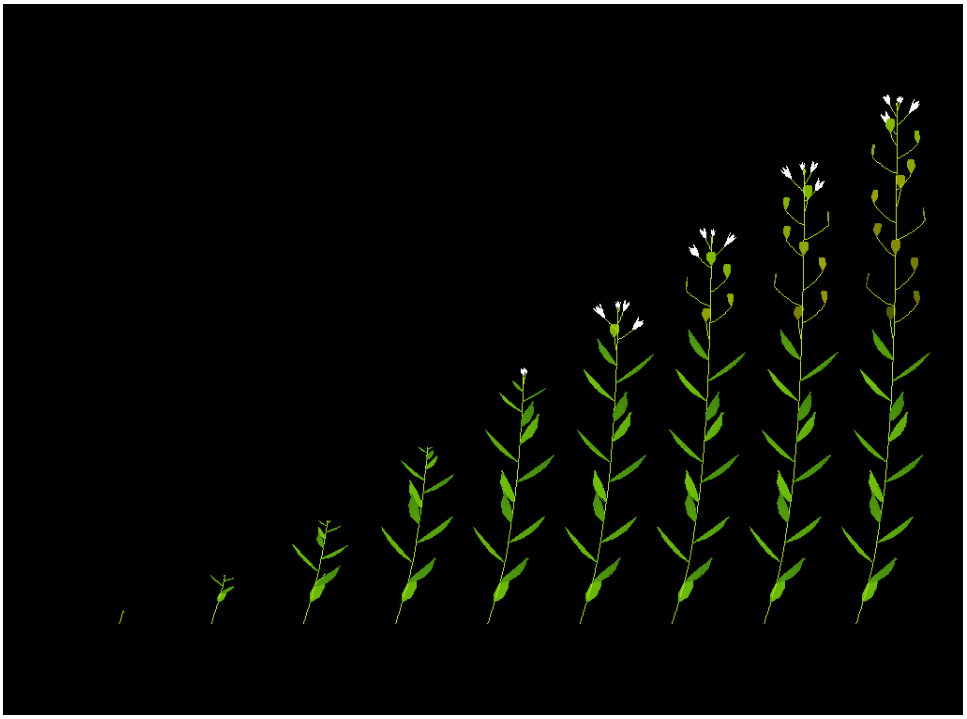
Lily-of-the-valley

At each developmental stage the inflorescence contains a sequence of flowers of different ages. The flowers newly created by the apex are delayed in their development with respect to the older ones situated at the stem base. Graphically, this effect is illustrated by the model of a lily-of-the-valley shown in Figure 3.4. The following quotation from d'Arcy Thompson [143] applies:

> A flowering spray of lily-of-the-valley exemplifies a growth-gradient, after a simple fashion of its own. Along the stalk the growth-rate falls away; the florets are of descending age, from flower to bud; their graded differences of age lead to an exquisite gradation of size and form; the time-interval between one and another, or the "space-time relation" between them all, gives a peculiar quality – we may call it phase-beauty – to the whole.

Capsella

Another example of "phase beauty" can be seen in the shoot of shepherd's purse (*Capsella bursa-pastoris*) shown in Figure 3.5. Productions p_1, p_2 and p_3 describe the activities of the apex in the vegetative and flowering states, in accordance with the L-system in equation (3.3). The developmental switch is implemented using a delay mechanism. Productions p_4 and p_5 capture the linear elongation of internodes in time, while p_6 and p_7 describe the gradual increase of the angle at which the flower stalks branch from the main stem. Productions p_8, p_9 and p_{11} specify the shapes of leaves L, flower petals K and fruits X using developmental surface models discussed in Section 5.2. Production p_{10} controls the flowering time. Symbol % in the successor of production p_{11} simulates the fall of petals by cutting them off the structure at the time of fruit formation. The default value of the angle increment corresponding to the symbol + with no parameter is 18°.



ω : `I(9)a(13)`

p_{1} : `a(t)` : `t>0` $\rightarrow$ `[&(70)L]/(137.5)I(10)a(t-1)`

p_{2} : `a(t)` : `t=0` $\rightarrow$ `[&(70)L]/(137.5)I(10)A`

p_{3} : `A` : `*` $\rightarrow$ `[&(18)u(4)FFI(10)I(5)X(5)KKKK]`
`/(137.5)I(8)A`

p_{4} : `I(t)` : `t>0` $\rightarrow$ `FI(t-1)`

p_{5} : `I(t)` : `t=0` $\rightarrow$ `F`

p_{6} : `u(t)` : `t>0` $\rightarrow$ `&(9)u(t-1)`

p_{7} : `u(t)` : `t=0` $\rightarrow$ `&(9)`

p_{8} : `L` : `*` $\rightarrow$ `[{.-FI(7)+FI(7)+FI(7)}]`
`[{.+FI(7)-FI(7)-FI(7)}]`

p_{9} : `K` : `*` $\rightarrow$ `[&{.+FI(2)--FI(2)}]`
`[&{.-FI(2)++FI(2)}]/(90)`

p_{10} : `X(t)` : `t>0` $\rightarrow$ `X(t-1)`

p_{11} : `X(t)` : `t=0` $\rightarrow$ `∧(50)[[-GGGG++[GGG[++G{.].].].`
`++GGGG.--GGG.--G.}]%`

Figure 3.5: Development of *Capsella bursa-pastoris*. Every fourth derivation step is shown.

Figure 3.6: Apple twig

Simple raceme (closed)

The inflorescence of an apple tree (Figure 3.6) provides an example of a closed raceme. In this case, the main apex eventually terminates its development and produces a terminal flower (Figure 3.7). The corresponding partial L-system is given below.

$$\begin{array}{ll} \omega : & a \\ p_1 : & a \rightarrow I[L]a \\ p_2 : & a \rightarrow I[L]A \\ p_3 : & A \rightarrow I[K]A \\ p_4 : & A \rightarrow K \end{array}$$

Developmental switches are associated with two symbols, a and A. Thus, in order to obtain an L-system scheme it is necessary to specify how both of these switches will be controlled.

The flowering sequence is usually acropetal but could also be basipetal, *i.e.*, progressing downward after the formation of the terminal flower on the main axis. In the latter case a basipetal signal, as discussed in Section 1.8, can be applied to induce the transformation of dormant flower buds into flowers.

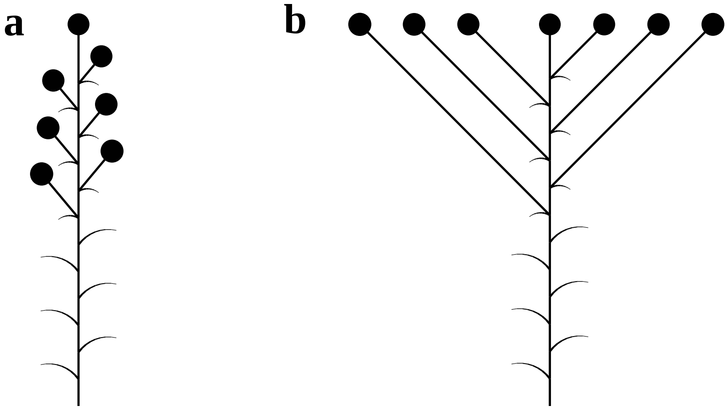


Figure 3.7: Closed racemes: (a) elongated form, (b) planar form

Compound raceme (open dibotryoid)

Racemes can also occur on complex branching structures. The simplest of these inflorescences is one with open racemes on the first order branches as well as on the main axis (Figure 3.8a). This two-level compound structure (thus *dibotryoid*) is described by the following partial L-system.

$$
\begin{array}{rll}
\omega: & a & \\
p_1: & a & \to I[L]a \\
p_2: & a & \to I[L]A \\
p_3: & A & \to I[L][b]A \\
p_4: & A & \to I[L][b]B \\
p_5: & b & \to I[L]b \\
p_6: & b & \to I[L]B \\
p_7: & B & \to I[K]B
\end{array}
\qquad (3.4)
$$

Three developmental transformations are necessary: the first for the change from leaf to branch creation along the main axis (production p_2), the second for the switch from branching to lateral flower creation on the main axis (p_4), and the third for the transition from leaf to lateral flower formation along the first-order branches (p_6). Each branch is subtended by a leaf, which is why productions p_3 and p_4 specify two appendages L and b. Branches with flowers K need not have subtending leaves, which is reflected in production p_7.

Single-signal model

Within each component raceme, the flowering sequence is always acropetal, but the timing of switches has a crucial impact on the overall flowering sequence and appearance of the plant. For example, let us assume that the switch from leaf to branch production is controlled by a delay, while the remaining two switches are caused by an acropetal flower-inducing signal (representing the hormone *florigen*). Such a development is captured by L-system 3.1 (see below). Initially, the veg-

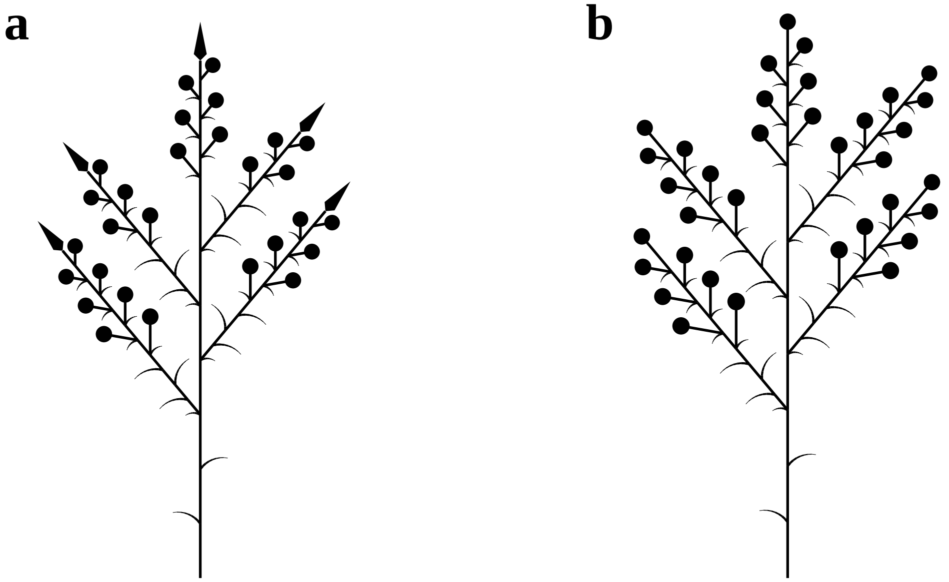


Figure 3.8: Dibotryoids: (a) open, (b) closed

```
#define d 13        /* delay for sending florigen */
#define e 3         /* delay for creating branches */
#define m 2         /* plastochron - main axis */
#define n 3         /* plastochron - lateral axis */
#define u 1         /* signal delay - main axis */
#define v 1         /* signal delay - lateral axis */

ω   : S(0)a(1,0)
p1  :           a(t,c) : t<m          → a(t+1,c)
p2  :           a(t,c) : (t=m)&(c<e)  → I(0,u)[L]a(1,c+1)
p3  :           a(t,c) : (t=m)&(c=e)  → I(0,u)[L][b(1)]a(1,c)
p4  :           b(t)   : t<n          → b(t+1)
p5  :           b(t)   : t=n          → I(0,v)[L]b(1)
p6  :           S(t)   : *            → S(t+1)
p7  :    S(t) < I(i,j) : t=d          → I(1,j)
p8  :           I(i,j) : (0<i)&(i<j)  → I(i+1,j)
p9  : I(i,j) <  I(k,l) : (i=j)&(k=0)  → I(1,l)
p10 : I(i,j) <  a(k,l) : i>0          → I[L][b(1)]B
p11 : I(i,j) <  b(k)   : i>0          → I[L]B
p12 :           B      : *            → I[K]B
```

L-system 3.1: A model of dibotryoids

etative apex a creates internodes I and leaves L with plastochron m (productions p_1 and p_2). After the creation of e leaves a developmental switch occurs, and apex a starts creating branches with the same plastochron (p_3). The change of state is indicated by the value of the second parameter in the module $a(t, c)$, which is now equal to e. The lateral apices b create internodes and leaves with plastochron n (p_4 and p_5). After a delay of d steps from the beginning of the simulation (p_6), the flowering signal is introduced to the basal internode (p_7), as indicated by a non-zero value of the first parameter in the module $I(i, j)$. The signal is passed along an axis at the rate of j steps per internode (p_8 and p_9), where $j = u$ for the main axis and $j = v$ for the lateral axes. These rates are assigned to internodes by productions p_2, p_3 and p_5. When the signal reaches an apex (either a or b), the apex is transformed into flowering state B (p_{10} and p_{11}). From then on, new flowers K are produced in each derivation step (p_{12}).

Model analysis

In order to analyze the plant structure and flowering sequence resulting from the above development, let T_k denote the time at which apex b of the k-th lateral axis is transformed into the flowering state, and l_k denote the length of this axis (expressed as the number of internodes) at the transformation time. It is assumed here that the first e leaves count as lateral axes, thus $k > e$. Since it takes km time units to produce k internodes along the main axis and $l_k n$ time units to produce l_k internodes on the lateral axis, we obtain:

$$T_k = km + l_k n$$

On the other hand, the transformation occurs when the signal reaches the apex. The signal is sent d time units after the development starts. It uses ku time units to travel through k zero-order internodes and $l_k v$ time units to travel through l_k first-order internodes:

$$T_k = d + ku + l_k v$$

Solving the above system of equations for l_k and T_k (and ignoring for simplicity some inaccuracy due to the fact that this system does not guarantee integer solutions), we obtain:

$$T_k = k\frac{un - vm}{n - v} + d\frac{n}{n - v}$$

$$l_k = -k\frac{m - u}{n - v} + \frac{d}{n - v}$$

In order to analyze the above solutions, let us first notice that the signal transportation delay v must be less than the plastochron of the lateral axes n, otherwise the signal would never reach the lateral apices. Under this assumption, the sign of the expression $\Delta = un - vm$ determines the overall flowering sequence, which is acropetal for $\Delta > 0$ (Figure 3.9) and basipetal for $\Delta < 0$ (Figure 3.10). If $\Delta = 0$, all flowering switches

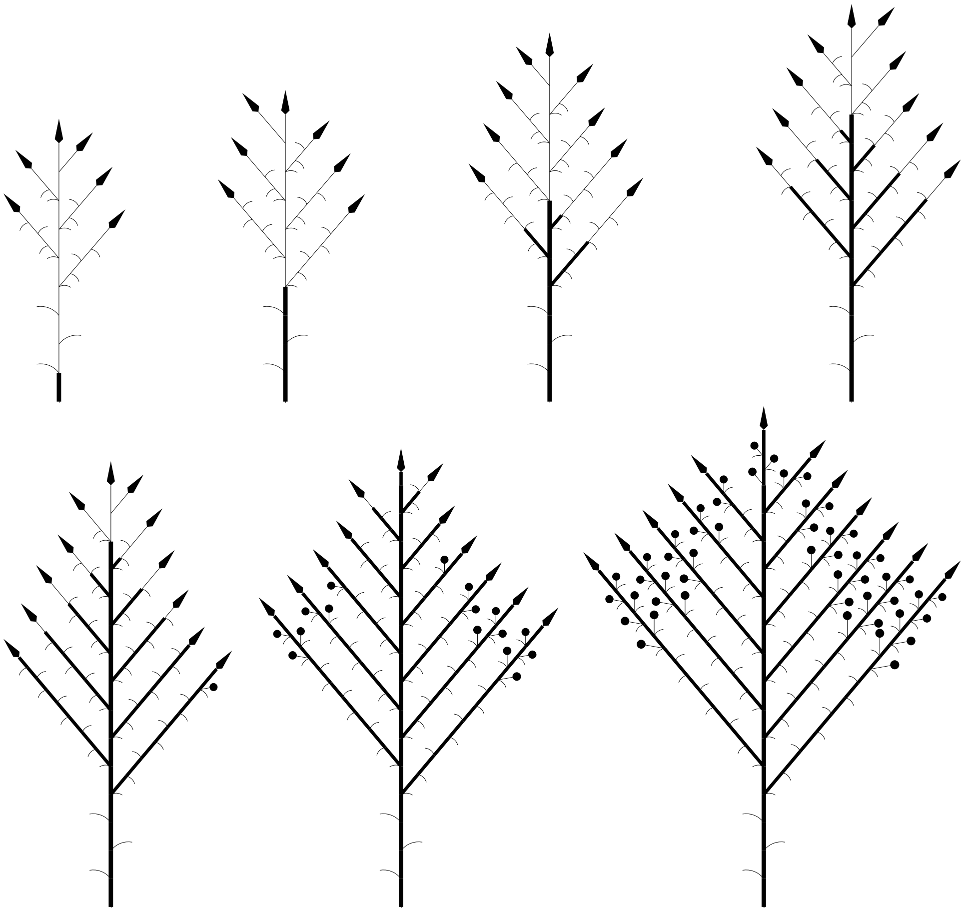


Figure 3.9: An acropetal flowering sequence in an open dibotryoid: $m = 2$, $n = 3$, $u = v = 1$, $\Delta = 0.5$; derivation lengths: $15-18-21-24-27-30-33$

occur simultaneously. The sign of the expression $m - u$ determines whether the vegetative part of the shoot is more developed at the base ($m - u < 0$) or near the top of the structure ($m - u > 0$). Figure 3.11 shows a model of a member of the mint family that exhibits a basipetal flowering sequence.

Compound racemes (closed dibotryoids)

This inflorescence type differs from the previous one only in that each branch, including the main axis, bears a terminal flower (Figure 3.8b). A partial L-system can be obtained from that of equation (3.4) by adding one more production:

$$p_8 : B \to K$$

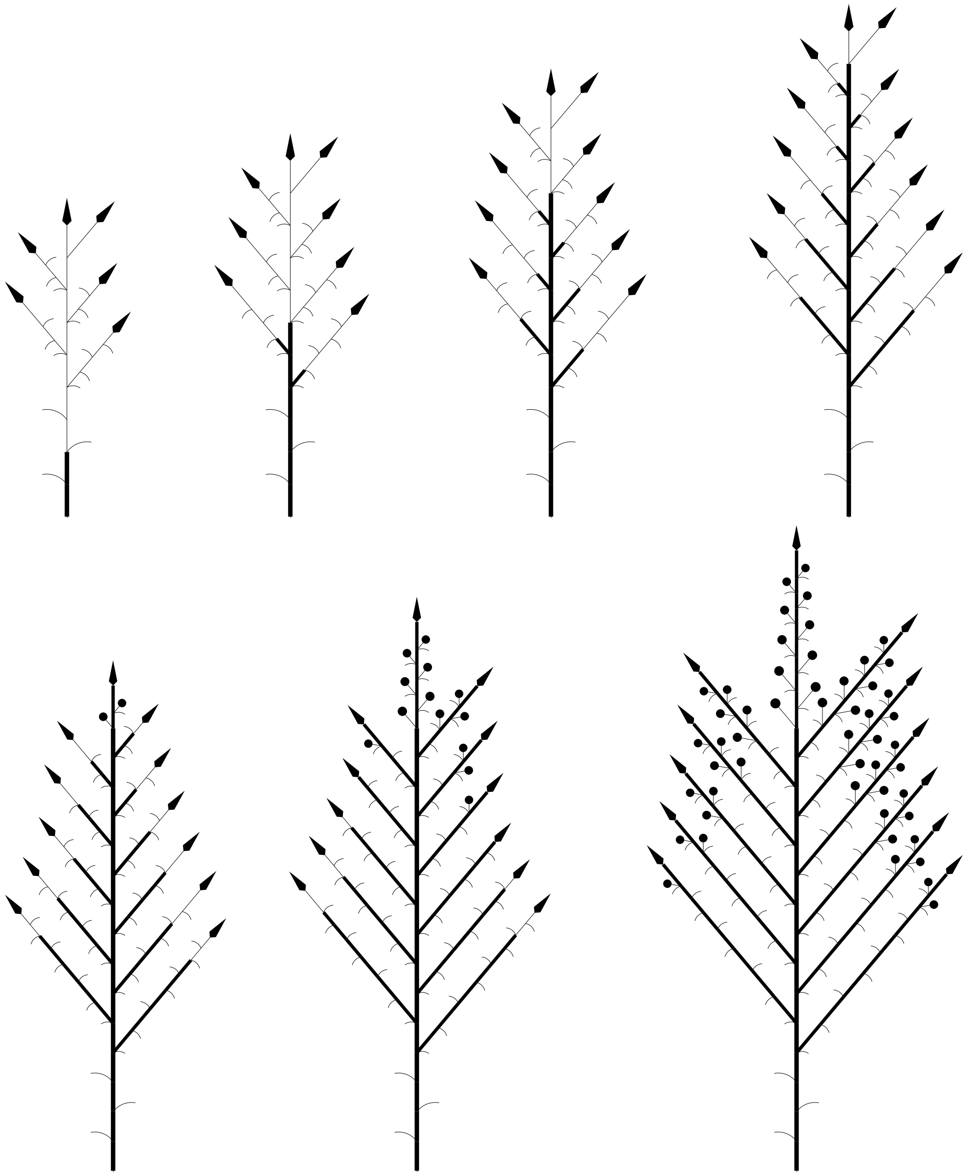


Figure 3.10: A basipetal flowering sequence in an open dibotryoid: $m = 2$, $n = 5$, $u = 1$, $v = 3$, $\Delta = -0.5$; derivation lengths: $16 - 20 - 24 - 28 - 32 - 36 - 40$

Figure 3.11: A mint

Compound raceme (closed tribotryoid)

Racemic inflorescences can be compounded to a higher number of levels. The following is a partial L-system for a closed tribotryoid inflorescence, where closed racemes occur on second-order branches as well as on the terminal portions of first-order branches and of the main axis (Figure 3.12). The developmental process involves six developmental transformations.

ω : a
p_1 : $a \rightarrow I[L]a$
p_2 : $a \rightarrow I[L]A$
p_3 : $A \rightarrow I[L][b]A$
p_4 : $A \rightarrow I[L][b]B$
p_5 : $b \rightarrow I[L]b$
p_6 : $b \rightarrow I[L]B$

p_7 : $B \rightarrow I[L][c]B$
p_8 : $B \rightarrow I[L][c]C$
p_9 : $c \rightarrow I[L]c$
p_{10} : $c \rightarrow I[L]C$
p_{11} : $C \rightarrow I[K]C$
p_{12} : $C \rightarrow K$

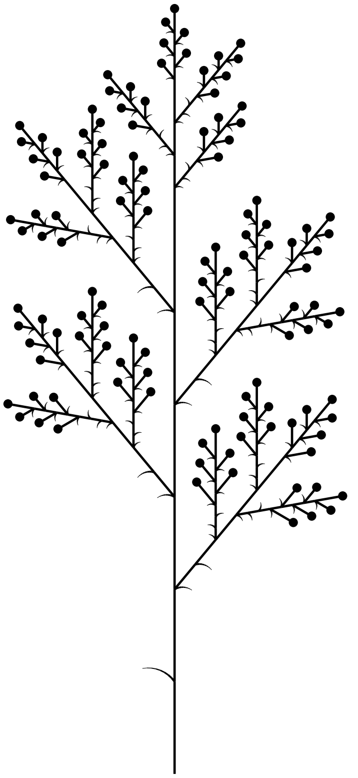


Figure 3.12: Closed tribotryoid

3.3.2 Sympodial inflorescences

Simple cymes (open)

In racemes, the apex of the main axis produces lateral branches and continues to grow. In contrast, the apex of the main axis in *cymes* turns into a flower shortly after a few lateral branches have been initiated. Their apices turn into flowers as well, and second-order branches take over. In time, branches of higher and higher order are produced. Thus, the basic structure of a cymose inflorescence is captured by the partial L-system:

$$\begin{array}{rl} \omega : & a \\ p_1 : & a \rightarrow I[L]a \\ p_2 : & a \rightarrow I[L]A \\ p_3 : & A \rightarrow I[A]K \end{array} \tag{3.5}$$

As in the open raceme, there is a single symbol with alternative rules which specify that the vegetative apex a may change into a flower-producing apex A. Any one of the previously discussed mechanisms is available for timing this decision. Figure 3.13a shows an open cyme with branches curving in a spiral fashion, while Figure 3.13b shows one

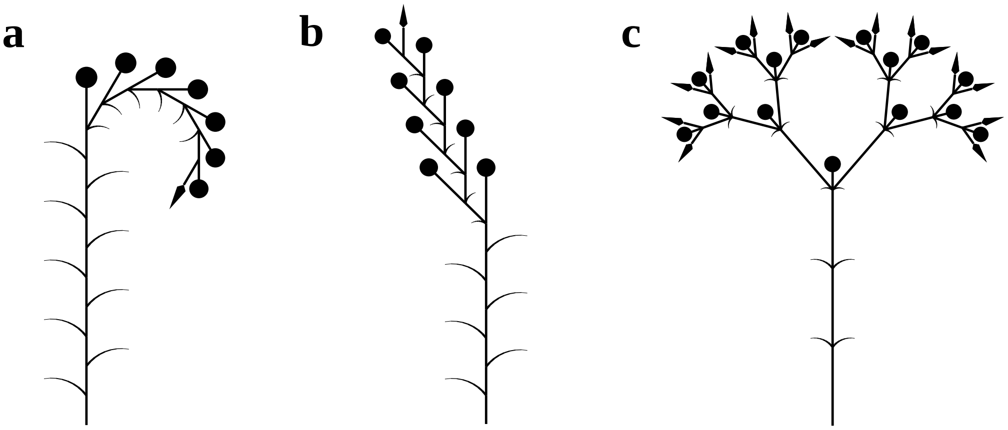


Figure 3.13: Open cymes: (a) spiral form, (b) zig-zag form, (c) double with a zig-zag branching form.

Double cymes (open)

Frequently, not one but two lateral apices are produced under each terminal apex as in Figure 3.13c. In this case the partial L-system is:

$$\begin{array}{rl} \omega : & a \\ p_1 : & a \rightarrow I[L]a \\ p_2 : & a \rightarrow I[L]A \\ p_3 : & A \rightarrow I[A][A]K \end{array} \tag{3.6}$$

The two continuing lateral apices may develop at approximately equal rates (with the same plastochron) or with different rates, giving rise to asymmetric inflorescences. For example, the following L-system scheme describes the development of rose campion (*Lychnis coronaria*) as analyzed by Robinson [126]:

Lychnis

$$\begin{array}{rlr} \omega : & A_7 & \\ p_1 : & A_7 \rightarrow I[A_0][A_4]IK_0 & \\ p_2 : & A_i \rightarrow A_{i+1}, & 0 \leq i < 7 \\ p_3 : & K_i \rightarrow K_{i+1}, & i \geq 0 \end{array}$$

Production p_1 shows that at their creation time, the lateral apices have different states A_0 and A_4. Consequently, the first apex requires eight derivation steps to produce a flower and new branches, while the second requires only four steps. Each flower undergoes a sequence of changes, progressing from the bud stage to an open flower to a fruit. This developmental sequence is illustrated in Figure 3.14. According to production p_1, the lateral apices branch at an angle of 45° and lie in a plane perpendicular to that defined by the mother axis and its sibling. Production p_3 describes the linear elongation of internodes, while p_4

```
#include L(0),L(1),...   /* leaf shapes */
#include K(0),K(1),...   /* flower shapes */

ω  : A(7)
p1 : A(t) : t=7 → FI(20)[&(60)~L(0)]/(90)[&(45)A(0)]/(90)
                  [&(60)~L(0)]/(90)[&(45)A(4)]FI(10)~K(0)
p2 : A(t) : t<7 → A(t+1)
p3 : I(t) : t>0 → FFI(t-1)
p4 : L(t) : *   → L(t+1)
p5 : K(t) : *   → K(t+1)
```

Figure 3.14: Development of *Lychnis coronaria*

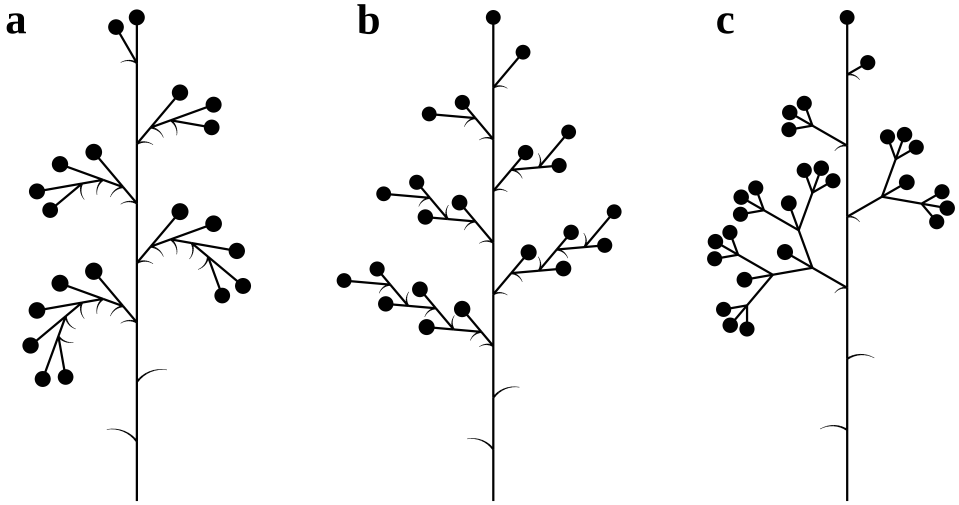


Figure 3.15: Thyrsus: (a) spiral form, (b) zig-zag form, (c) double

and p_5 capture the development of leaves and flowers over time. It is interesting to note that at different developmental stages there are some open flowers that have a relatively uniform distribution over the entire plant structure. This is advantageous to the plant since it increases the time span over which seeds will be produced.

Cymes (closed)

Sympodial inflorescences that produce a terminal flower at some point during their development are called *closed cymes*. They result from the addition of production

$$p_4 : A \rightarrow K$$

to the L-systems specified in (3.5) and (3.6), which define open single and open double cymes.

Thyrsus (closed)

A *thyrsus* is an inflorescence with branches of cymes borne on a monopodially branching axis. Thus, it represents a mixed sympodial and monopodial organization. Depending on the orientation of the flowers, a distinction between a thyrsus with cymes in a spiral form and in a zig-zag form can be made (Figure 3.15, a and b). Both of these types are described by the following partial L-system:

$$
\begin{array}{rl}
\omega: & a \\
p_1: & a \rightarrow I[L]a \\
p_2: & a \rightarrow I[L]A \\
p_3: & A \rightarrow I[L][B]A \\
p_4: & A \rightarrow K \\
p_5: & B \rightarrow I[B]K \\
p_6: & B \rightarrow K
\end{array}
$$

In addition, a thyrsus may have double cymes (Figure 3.15c). In the closed structure there are three developmental transformations. The first represents the change from vegetative to flowering development on the main axis (production p_2). The second is necessary for the closure of the main axis with a terminal flower (p_4). Both switches are related to the monopodial development of the main axis. The third transformation is responsible for the formation of the flowers that terminate the development of the sympodial structures (p_6).

3.3.3 Polypodial inflorescences

Panicle

The term *polypodial* is not used in the botanical literature but is coined here to draw attention to the type of branching that represents continuing development of the main axis as well as of the lateral apices of a branch. The corresponding inflorescence type is usually called a *panicle*. The presence of two continuing apices at each new node is expressed by the following production:

$$A \rightarrow I[L][A]A$$

Since there can be nodes near the base of the plant that do not bear branches, the usual initial rules are included to model the transition from a purely vegetative to a flowering state. The resulting partial L-system is:

$$
\begin{array}{rl}
\omega: & a \\
p_1: & a \rightarrow I[L]a \\
p_2: & a \rightarrow I[L]A \\
p_3: & A \rightarrow I[L][A]A \\
p_4: & A \rightarrow K
\end{array}
$$

An example of a paniculate structure is shown in Figure 3.16. Note the presence of higher order branching and the lack of terminal racemes. Due to the repetitive application of production p_3 at various levels of branching, the resulting structure is highly self-similar. The model includes only two types of developmental transformations: the switch

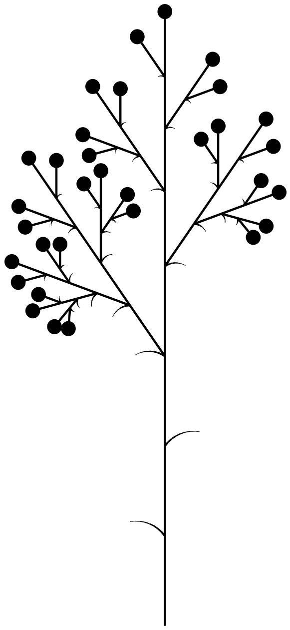


Figure 3.16: Panicle (elongated form)

from purely vegetative growth to the formation of the branching structure (production p_2), and the creation of terminal flowers (p_4). The timing of the last production determines the flowering sequence of the plant. Two possible control mechanisms will be examined in detail, using developmental models of the branching part of wall lettuce (*Mycelis muralis*) as examples.

Mycelis

The development of *Mycelis* is difficult to model for two reasons. First, the plant exhibits a basipetal flowering sequence, which means that flowering starts at the top of the plant and proceeds downwards. Secondly, at some developmental stages the plant has an *acrotonic* structure, where the upper branches are more developed than the lower ones. Both phenomena are in a sense counter-intuitive, since it would seem that the older branches situated near the plant base should start growing and producing flowers before the younger ones at the plant top. To explain these effects, several models were proposed and formally analyzed by Janssen and Lindenmayer [77]. Their *model II* is restated here as parametric L-system 3.2.

Model II

The axiom consists of three components. Modules F and $A(0)$ represent the initial segment and the apex of the main axis. Module $I(20)$ is the source of a signal representing florigen. In nature, florigen is sent towards the apex by leaves located at the plant base, which is not included in this model.

The developmental process consists of two phases that take place along the main axis and are repeated recursively in branches of higher orders. First, the main axis is formed in a process of subapical growth

```
#include O             /* flower shape specification */
#ignore / + ~ O

ω   :  I(20)FA(0)
p1  :     S < A(t)       : *   → T(0)~O
p2  :         A(t)       : t>0 → A(t-1)
p3  :         A(t)       : t=0 → [+(30)G]F/(180)A(2)
p4  :     S < F          : *   → FS
p5  :         F > T(c)   : *   → T(c+1)FU(c-1)
p6  :  U(c) < G          : *   → I(c)FA(2)
p7  :         I(c)       : c>0 → I(c-1)
p8  :         I(c)       : c=0 → S
p9  :         S          : *   → ϵ
p10 :         T(c)       : *   → ϵ
```

L-system 3.2: *Mycelis muralis* – Model II

specified by production p_3. The apex produces consecutive segments F at the rate of one segment every three derivation steps (the delay is controlled by production p_2), and initiates branches G positioned at an angle of 30° with respect to the main axis. The symbol G is interpreted here in the same way as F. At this stage, the branches do not develop further, which simulates the effect of *apical dominance* or the inhibition of branch development during the active production of new branches by the apex.

After a delay of 20 derivation steps, counted using production p_7, an acropetal flower-inducing signal S is sent by production p_8. Production p_4 transports S across the segments at the rate of one internode per step. Since new internodes are produced by the apex at a three times slower rate, the signal eventually reaches the apex. At this point, the second developmental phase begins. Production p_1 transforms apex $A(t)$ into a bud O. Further branch production is stopped and a signal $T(c)$ is sent towards the base in order to enable the development of lateral branches. Parameter c is incremented by production p_5 each time signal $T(c)$ traverses an internode. Subsequently, production p_6 introduces the value of parameter c into the corresponding branches, using module $U(c)$ as a carrier. The successor of production p_6 has the same format as the axiom, thus module $I(c)$ determines the delay between the initiation of branch development and time signal S, sent to terminate further internode creation. This delay c is smallest for the top branches and increases towards the plant base. Consequently, parameter c can be interpreted as the *growth potential* of the branches, allowing lower branches to grow longer than the higher ones. On the other hand, the development of the upper branches starts sooner, thus in some stages they will be more developed than the lower ones, and the flowering sequence will progress downwards, corresponding to ob-

```
#include K            /* flower shape specification */
#consider M S T V

ω   :  I(20)FA(0)
p1  :  S < A(t)  : *    → TV K
p2  :  V < A(t)  : *    → TV K
p3  :      A(t)  : t>0  → A(t-1)
p4  :      A(t)  : t=0  → M[+(30)G]F/(180)A(2)
p5  :  S < M     : *    → S
p6  :      S > T : *    → T
p7  :  T < G     : *    → FA(2)
p8  :  V < M     : *    → S
p9  :      T > V : *    → W
p10 :      W     : *    → V
p11 :      I(t)  : t>0  → I(t-1)
p12 :      I(t)  : t=0  → S
```

L-system 3.3: *Mycelis muralis* – Model III

servations of the real plant [77].

A diagrammatic developmental sequence of *Mycelis muralis* simulated using L-system 3.2 is shown in Figure 3.17. Initially, the segments are shown as bright green. The passage of florigen S turns them purple, and the lifting of apical dominance changes their color to dark green. Figure 3.18 represents a three-dimensional rendering of the same model. The three-dimensional structure differs from the two-dimensional diagram only in details. The angle value associated with the module "/" in production p_3 has been changed to 137.5°, resulting in a spiral arrangement of lateral branches around the mother axis. The leaves subtending branches have been included in the model, and flowers have been assumed to undergo a series of changes from bud to open flower to fruit.

Model III

Another developmental model of *Mycelis*, referred to here as *model III*, is given by L-system 3.3. The initial phases of development are the same as in model II. First, apex A creates the main axis and initiates lateral branches (productions p_3 and p_4). Symbol M in the successor of production p_4 marks consecutive branching points. After a delay of 20 steps (ω) counted by production p_{11}, flowering signal S is generated at the inflorescence base (p_{12}) and sent up along the main axis (p_5). Upon reaching the apex, S induces its transformation into a terminal flower K, and initiates two basipetal signals T and V (p_1). The basipetal signals also can be initiated by production p_2, which is needed for the proper timing of signals in the topmost lateral branch. Signal T propagates basipetally at the rate of one internode per derivation step (p_6) and lifts apical dominance, thus allowing the lateral branches to grow (p_7). The presence of the second basipetal signal V is the distinctive

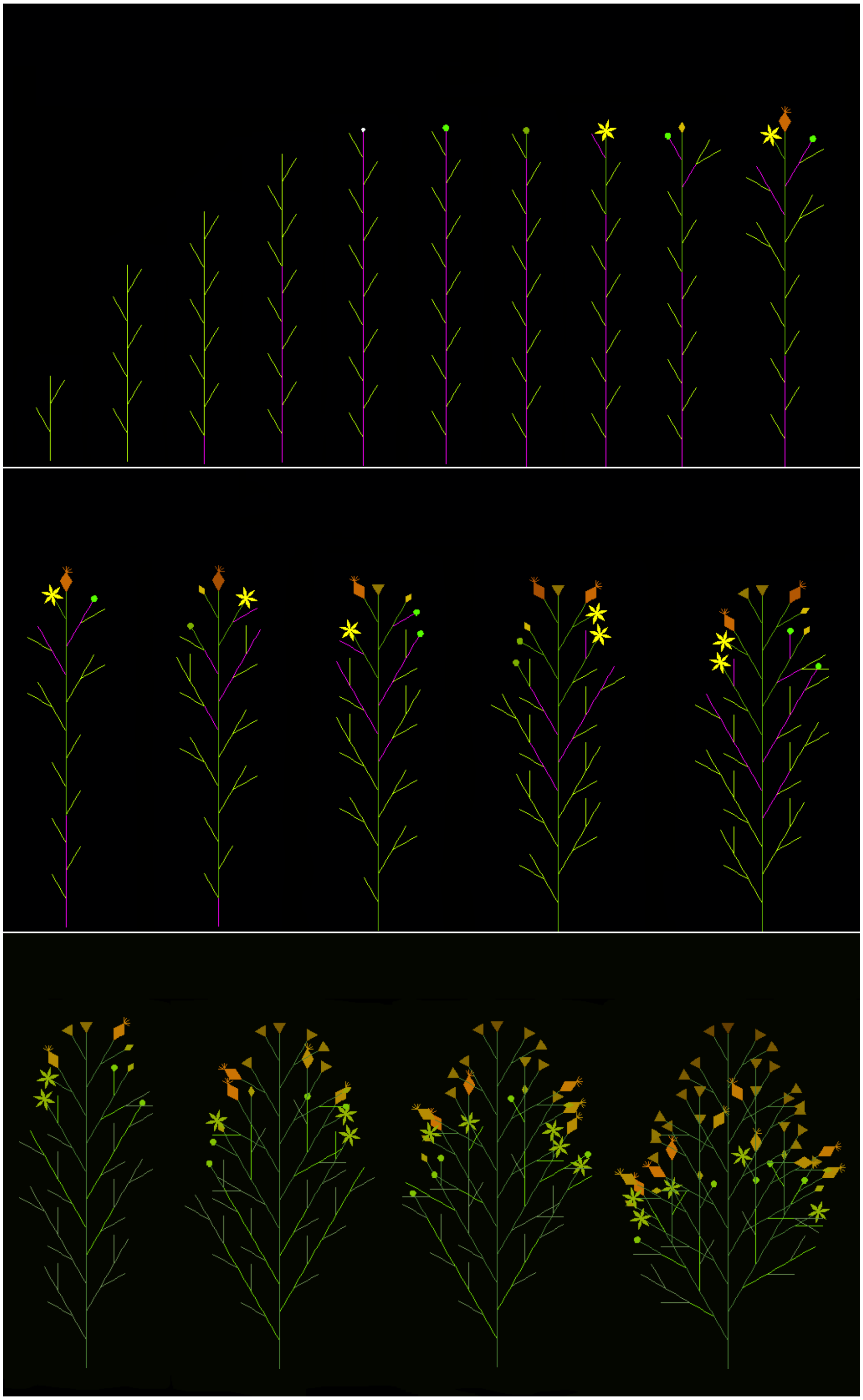


Figure 3.17: Development of *Mycelis muralis*

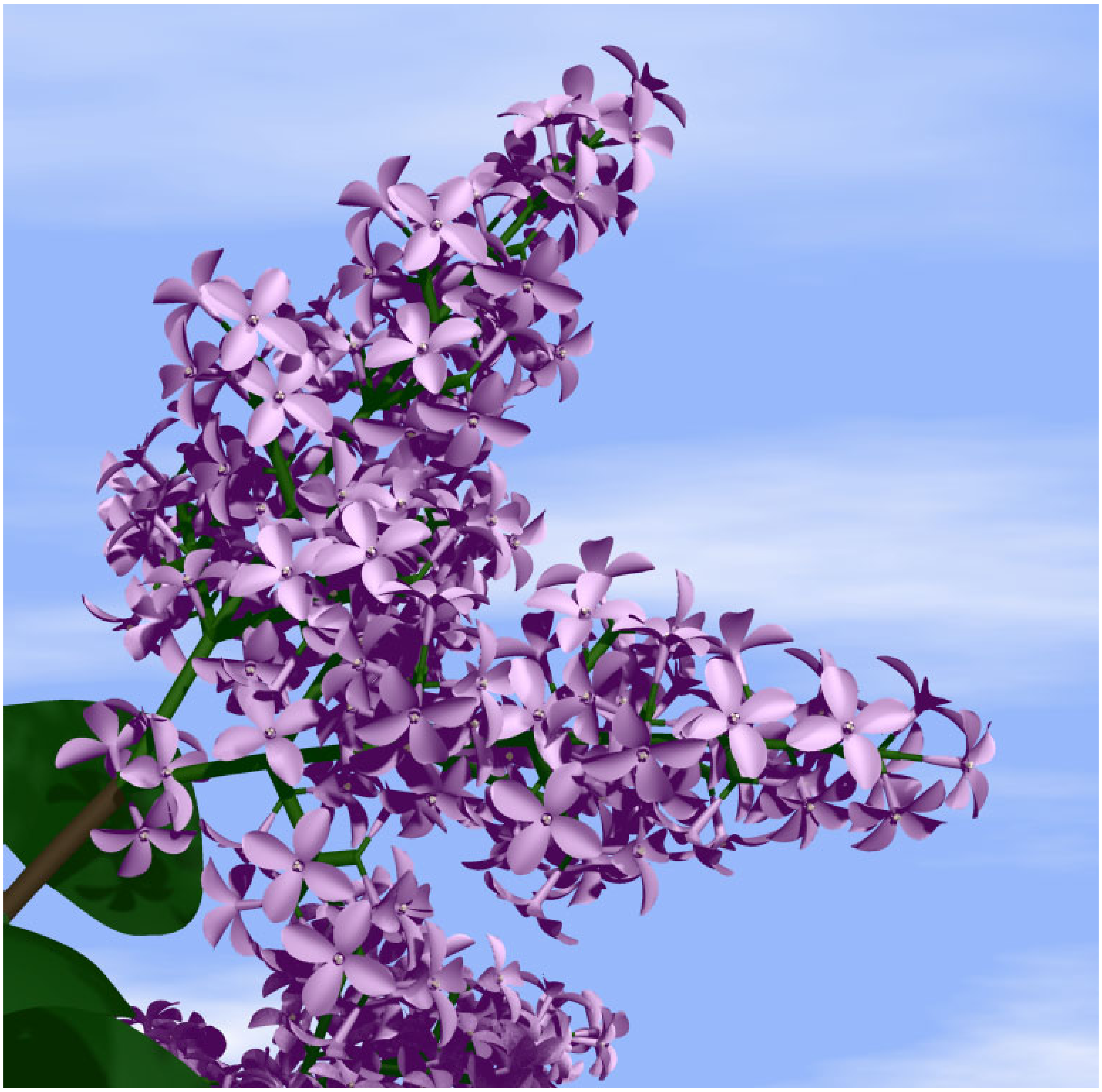
Figure 3.18: A three-dimensional rendering of the *Mycelis* model

feature of model III. Its role is to enable the formation of flowers on the lateral branches by generating the flowering signal S at their bases (p_8). Since signal V propagates down the main axis at the rate of one internode per two derivation steps (p_9, p_{10}), the interval between the lifting of apical dominance by signal T and induction of flowering signal S by signal V increases linearly towards the inflorescence base. This allows the lower branches to grow longer than the upper ones, resulting in a structure that is more developed near the base than near the apex in later developmental stages.

This entire control process repeats recursively for each axis: its apex is transformed into a flower by signal S, the growth of lateral axes is successively enabled by signal T, and the second basipetal signal V is sent to induce the flowering signal S in the next-order axes. Consequently, a basipetal flowering sequence is observed along all axes of the panicle.

Biological relevance

Model II controls the flowering on lateral branches using growth potential c accumulated by signal T on its way down, while model III employs the time interval between signals T and V for the same purpose. Since both models produce identical developmental sequences, it is not possible to decide which one is more faithful to nature without gathering additional data related to plant physiology. Nevertheless, the models clearly indicate that the flowering sequence of *Mycelis* cannot be explained simply in terms of two commonly recognized mechanisms,



n=10, $\delta = 60^\circ$

`#include K /* flower shape specification */`

ω : `A~K`
p_1 : `A : * → [-/~K][+/~K]I(0)/(90)A`
p_2 : `I(t) : !(t=2) → FI(t+1)`
p_3 : `I(t) : t=2 → I(t+1)[-FFA][+FFA]`

Figure 3.19: Lilac inflorescences

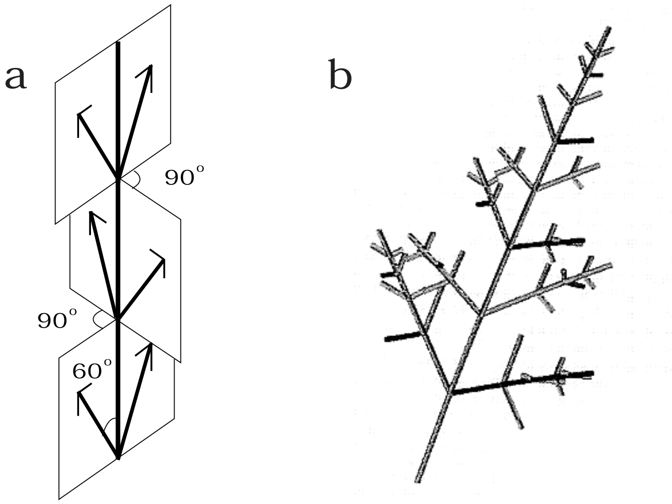


Figure 3.20: Geometry of a lilac inflorescence: (a) the decussate branching pattern, (b) the inflorescence skeleton without flowers

the flowering signal and the lifting of apical dominance. Another factor, whether it is an accumulated delay or a third signal, is needed. The mathematical models bring forward evidence and assist in formulating plausible hypotheses related to the control mechanisms that may be employed by nature. The final answer will require further study of the real plant.

Lilac

The models of *Mycelis* employ relatively complicated control processes to explain the developmental sequence of a plant. On the other hand, if only a static image of a panicle in a particular developmental stage is needed, much simpler L-systems can be used. The L-system that generates the lilac inflorescences shown in Figure 3.19 is an example. Production p_1 describes the subapical development of an axis. Production p_2 models linear elongation of internodes in time and introduces a delay before p_3 creates the lateral axes. The rotation of the apex by 90° (p_1) results in a *decussate* branching pattern with consecutive pairs of $(n+1)$-order axes lying in the planes that pass through the n-order axis and are perpendicular to each other (Figure 3.20). A scene including lilac inflorescences is shown in Figure 3.21.

3.3.4 Modified racemes

There are four frequently encountered types of inflorescences that are morphological modifications of racemes. Their mature forms are of a special kind and need to be specified separately.

Figure 3.21: The garden of L

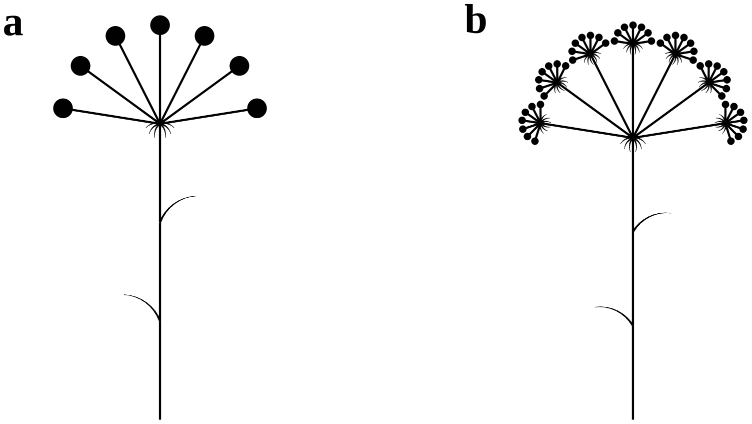


Figure 3.22: Umbels: (a) simple, (b) compound

Umbel

An *umbel* is characterized by more than two internodes attached to a single node, resulting in a typical umbrella-like shape. In a simple umbel there are flowers at the ends of the lateral internodes (Figure 3.22a), while in compound umbels the branching pattern is repeated recursively a certain number of times (Figure 3.22b). The partial L-system for a simple umbel is

$$\begin{aligned} \omega &: \ A \\ p_1 &: \ A \rightarrow I[IK]^n \end{aligned}$$

and for a compound umbel of recursion depth two is

$$\begin{aligned} \omega &: \ A \\ p_1 &: \ A \rightarrow I[IB]^k B \\ p_2 &: \ B \rightarrow I[IC]^l C \\ p_3 &: \ C \rightarrow I[IK]^m \end{aligned}$$

This type of inflorescence is commonly found in the family Umbelliferae. For example, Figure 3.23 presents a model of a wild carrot. Note that the size of leaves decreases towards the top of the plant, producing a phase effect similar to that observed in simple racemes. In contrast, the most developed inflorescence is placed at the top of the plant, indicating developmental control by a hormone similar to that observed in mints (Figure 3.11). *Wild carrot*

Spike

An elongated raceme with closely packed flowers is called a *spike.* Many grasses and sedges have this kind of inflorescence (Figure 3.24a). See Figure 4.17 (page 117) for a realistic model.

Figure 3.23: Wild carrot

Spadix

A fleshy elongated raceme is called a *spadix*, and is frequently found in the family Araceae (Figure 3.24b).

Capitulum

A fleshy spherical or disk-shaped raceme is called a *capitulum* or "head." The sunflower head is an inflorescence of this kind, the oldest flowers being at the margin and the youngest at the center (Figure 3.24c). Members of the family Compositae commonly have this type of structure. One characteristic feature is the spatial arrangement of components, such as flowers or seeds, which form early discernible spiral patterns. A detailed description of these patterns is presented in the next chapter.

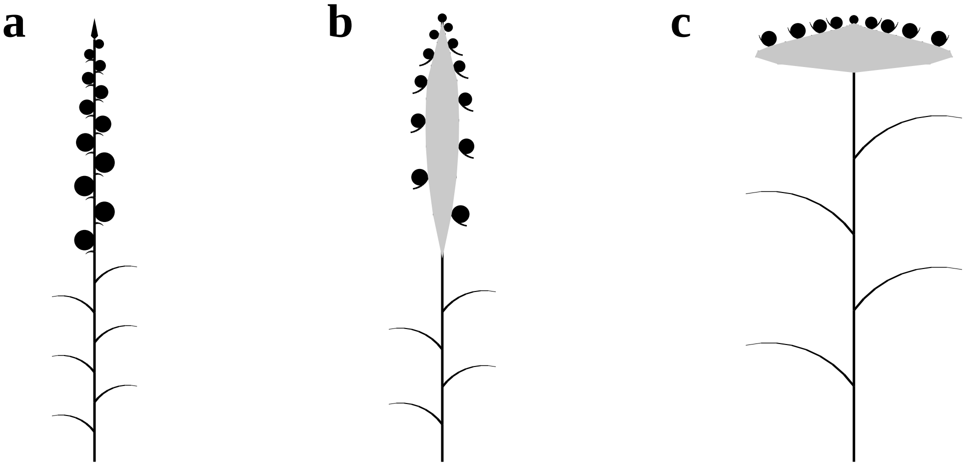


Figure 3.24: Modified racemes: (a) spike, (b) spadix, (c) capitulum