

An Automata-Theoretical Model of the Vegetative and Flowering Development of *Hieracium murorum* L.*

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Abstract. By means of a computer model certain essential aspects of the vegetative and flowering development of *Hieracium murorum* have been successfully simulated. The model is based on local control mechanisms operating over a large number of units and is stated in terms of the theory of developmental systems and languages. The model is constructed as a table deterministic $\langle 1,1 \rangle$ *L*-system. The model is especially concerned with the correlation mechanisms between the various differentiating parts of the plant.

To try to simulate the development of an entire flowering plant may generally be considered impossible. A complete description of such a developmental process would have to include all the biochemical, cytological and anatomical details of the plant. To achieve such a description would be completely out of the question. Only by drastic abstraction from all these details one can hope to obtain a biologically relevant simulation. Even with this abstraction, the simulation will require very extensive computations, which can be carried out only with the help of a large computer.

We approach the plant as a whole, not in terms of individual cells and tissues. We study the correlation mechanisms and the influences that certain parts of the plant exert on other parts of the plant in the course of development. Recently, developmental models have been introduced which are called *L*-systems (Lindenmayer, 1968, 1971, 1975; Herman and Rozenberg, 1975). Our simulation model is stated in terms of such *L*-systems and processed by a computer in the simulation language CELIA, a language intended to process models based on *L*-systems (Baker and Herman, 1970, 1972; Herman and Liu, 1973).

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In the present paper concepts are used which are similar to the ones which were used in the simulation of the development and flowering of *Aster novae-angliae* L. (Frijters and Lindenmayer, 1974). The structures of the branching patterns are stated in terms of uniform paracladial relationships. Such relationships apply to branching patterns where uniform relations are obtained during development between all pairs of daughter- and mother branches (Frijters and Lindenmayer, to appear).

We have concentrated in this work on the following features of the plant *Hieracium murorum* L.:

- (1) The lengths and positions of internodes, and their formation and elongation in the course of time.
- (2) The sequential order of appearance and development of floral buds, and their positions in the pattern.

In short, we have studied the mechanisms of development which regulate the formation and development of internodes and floral buds in time and space.

Biological Data:

Characteristics of *Hieracium murorum*

We collected shoot systems of *Hieracium murorum*. On a series of shoots we measured the lengths of the internodes and observed the flowering stages of the flowering heads (capitula). We made notes on the presence or absence of leaves and on the physical condition of (some parts of) the plant. Figures 1 and 2 are two examples of the representation of the data in two-dimensional diagrams, where the lengths of the internodes, the branching structure, and the position and relative sizes of the flowering heads are given. The plants represented in these figures have lengths of about 60 and 40 cm respectively. These diagrammatic representations of actual shoot systems were drawn by a CALCOMP plotter attached to the CDC 6400 computer of the University of Utrecht. The drawing

program has been described in a previous paper (Frijters and Lindenmayer, 1974).

The biochemical processes in the diverse tissues of this plant which are responsible for the developmental mechanisms of the plant as a whole are mostly unknown. Nevertheless, on the basis of mechanisms in other species and of general physiological considerations some plausible mechanisms may be assumed. We are primarily interested in the connection between these hypothetical processes at the local level and the overall development of the whole pattern. On the basis of our data, of which Figures 1 and 2 are two examples, we propose to introduce the following mechanisms.

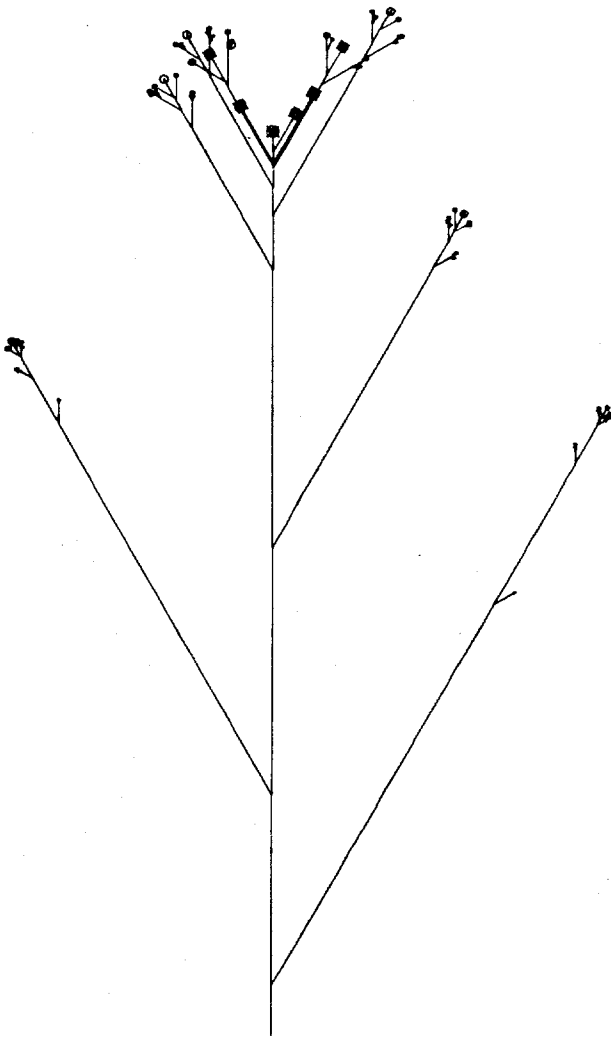


Fig. 1. Diagram of a flowering shoot system of *Hieracium murorum* showing the internodes and capitula. The symbols \uparrow \uparrow \uparrow denote the capitula, the size of the symbols correlates with the state of their development. The symbols \square designate fruit bearing capitula. In this shoot system the main axis bears 11 side branches. The main axis and the top 6 primary branches have reached their final length, the others are still elongating. All branches are formed at this stage. At the end of each branch a capitulum is present. The length of the main axis is about 60 cm

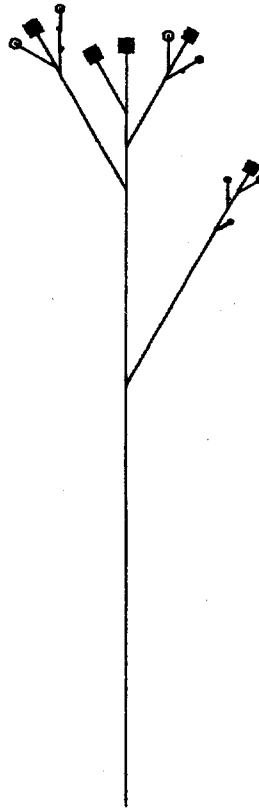


Fig. 2. Diagram of a flowering shoot system of *Hieracium murorum*. Symbols as in Figure 1. The main axis has only four side branches. The capitula of the main axis and of the first order branches all bear fruits. This shoot system is at a somewhat later developmental stage as in Figure 1. The length of the main axis is about 40 cm

At some stage in the development of the shoot the until then vegetatively developing apical buds are converted into floral buds. In some plant species this happens very abruptly and occurs simultaneously for all buds. In others this conversion of buds occurs gradually. In the case of *Hieracium murorum* we know that the plants are perennials with the root stock surviving from year to year. In the winter condition one finds on the root stocks some large old rosette leaves and a few small dormant buds. In the buds there are leafy apices of about two millimeters length. In the spring, new large rosette leaves develop and a month later new flowering shoot systems (inflorescences) begin to appear. The flower-heads are in a loose terminal corymb. We have reasons to assume that the development of the flowering shoot systems takes place as follows: Up to a certain moment vegetative growth takes place. In that period branches with scale-like leaves are formed. Then suddenly all the apices of such branched structures are converted into primordia of floral structures. Beginning with this conversion gradually the internodes and flowering stalks elongate. This process takes place within a few

weeks from the conversion. The plants continue to produce new flowering shoot systems from buds in the rosette throughout the summer. Flower-stems elongate to 30 to 70 cm high.

On the shoot apices new organs (leaves, branches, flowers) are formed. The frequency at which new organs are formed may depend on a large number of influences, internal as well as external ones, such as the distribution of assimilates, growth hormones, senescence, temperature, exposure to light, and so on.

The flowering structure of *Hieracium*, a member of the family of the Compositae, is a capitulum. It is composed of numerous individual flowers, implanted on one central disk. A shoot system bearing such capitula is called an inflorescence.

The developmental rates of the floral buds quite often are different on the same plant. In this species every branch eventually bears a terminal capitulum. The development of the inflorescence is strictly basipetal, meaning that the capitulum at the end of the main axis flowers first, followed by the capitulum at the tip of the highest positioned branch of first order, and so on. The proportions among the floral rates are maintained during development while their absolute values change.

The capitula begin their development as a floral bud. The speed at which the flowering stages follow each other may depend not only on the initial differences in floral rates but also on factors which interfere with its development, such as senescence.

The peduncles (stalks) of the capitula all elongate to some extent. The differences in final lengths may depend on factors like the developmental rate of the capitula and the lengths of the branches on which they are born.

The internodes must elongate to some extent. In some species of the Compositae consecutive internodes on a shoot show a definite increasing or decreasing series in final length. In other species, as in this case, the sequence is much less regular. The possible control mechanisms of the elongation process of the internodes may be manifold.

At the point where a side branch is borne by its mother branch special mechanisms can be operating such as the mechanisms establishing the distribution of nutrients.

Senescence is a process which in many plants is directly connected with the process of flowering. Flowering often hastens the end of life of the plant. In this case, since we are dealing with a perennial plant, it only limits the life of the shoot systems, while the roots and the rosette buds survive during the winter season. Senescence sometimes proceeds so rapidly that it prevents the development of flowering of large parts of the plant.

Computing Techniques and Theoretical Framework

In L -systems (Lindenmayer, 1968, 1971) an organism is represented as a linear sequence of units where each unit is characterized by some number of parameters. All units of the organism are replaced simultaneously at discrete time steps by other units according to a finite set of transition rules. These transition rules can use several sources of information. If they use only the information which is present in the unit itself, the rules are called "interactionless". If the transition rules for all units in a certain developing organism are interactionless, the corresponding L -system is called an interactionless L -system or a $\langle 0,0 \rangle$ L -system. The transition rules can also use information concerning neighbouring units. They are then called transition rules with interactions and the corresponding L -system is called an L -system with interactions or a $\langle k,l \rangle$ L -system, where k and l are non-negative integers, and k denotes the number of units to the left and l denotes the number of units to the right from which information is to be obtained. The theory applies to branching as well as to non-branching filamentous organisms. A branch is usually placed between an opening parenthesis and a colon and a colon and closing parenthesis, "(:" and ":)". The branch is assumed to be attached to the node above the internode unit preceding the left parenthesis. For example, in case of a string of symbols $a (: b:) c$, the branch which contains b is attached to symbol a .

In the present version of CELIA no influence can be exerted by a branch on its mother branch. On the other hand, a branch can obtain information from its mother branch. These restrictions do not interfere with our present simulation. Should they be considered undesirable, one could change CELIA accordingly.

The present model of *Hieracium murorum* is based on a branching L -system with interactions. Although some transition rules use information which is transferred in one time through a large number of units, we will argue that this information, if necessary, can also be obtained directly from neighbouring units, and that our generating system can be described as a $\langle 1,1 \rangle$ L -system. To let every bit of information advance unit by unit would increase the cost in computing time.

The theory of L -systems has provided several ways of extending or restricting their computing power (Herman and Rozenberg, 1975). One way of restricting the systems is by requiring that there can only be one rule for every situation, that is, every situation is uniquely determined. This gives rise to deterministic L -systems or D L -systems. The systems can also be extended by using different tables of rules such that one table of rules is used at a particular time step, and

is replaced by another at another time step. If this applies to the whole organism, it gives rise to table *L*-systems or *T L*-systems. The model of *Hieracium murorum* uses deterministic rules and has two different tables of rules. It is, therefore, a *TD* $\langle 1,1 \rangle$ *L*-system. The sequence in which the two tables are applied in the model is very simple, namely the first table is applied for a limited number of steps (between 2 and 12 iteration steps) and then the second table is applied for another 20 to 40 time steps. Thus the control language for the tables is a finite and, therefore, regular language. The properties of table interactionless *L*-systems with regular control languages have been investigated by Ginsburg and Rozenberg (1975), the main result having been that the effect of regular table control is exactly equivalent to the addition of a non-terminal alphabet to such systems. It is conjectured (Rozenberg, pers. comm.) that the same equivalence relationship holds for table *L*-systems with interactions as well.

Baker and Herman (1970) designed the program CELIA to process strings of symbols in the way *L*-systems do. Liu (1972) and Herman and Liu (1973) developed later a more extensive version of this program.

The name is an acronym for Cellular Linear Iterative Array simulator. What we call "units" were originally called "cells". The program is written in FORTRAN. The states of the units are specified by a number of attributes. The attributes can be either expressed as integer or as real numbers. The user has to provide transition rules for each possible combination of attributes and CELIA applies these rules in a parallel way to all units in the string. Changes in the states of the units occur synchronously at discrete time steps. The state of a unit at the next time step is determined through its present state and the state of *k* neighbours to the left and *l* neighbours to the right. Increase of the number of units and new branches are possible by inserting new units and placing necessary branching markers at the proper places in the string. The input/output formats are specified by the user. The user can let print the string at any time step he wishes. The main program of CELIA keeps a double administration: The administration of the old string and the administration of the string which is processed. There are subprograms, which are either involved in the administration and in the processing of the strings or in surveying or intervening with the processing of the current string. There are subprograms for statistical survey of the strings, storage of the strings, changes in the environment, and so on. In fact, CELIA, is an elaborate program for simulation of growing branched organisms. It is a special purpose simulation computer language.

The units of the model plant are meant to designate internodes, apices, branch bases, capitula and peduncles. A branching organism consists of branches of different *branching orders*. A *branch* of order *i* bears branches of order *i*+1 at its nodes. Between the nodes are *internodes*. In our symbolism only internodes are named, and nodes are assumed to be incorporated in their basal internodal neighbour. A branch of order *i* can be written as a concatenation of symbols, as follows:

$$b^i = p^i j_1^i (: b_1^{i+1} :) \dots j_n^i (: b_n^{i+1} :) a^i, \quad (1)$$

where for all *k*, $0 \leq k \leq n$, j_k^i and b_k^i are internodes and branches of serial number *k* and of branching order *i*, and where p^i and a^i are a basal part and an apical part of the branch. The apical part of a branch consists either of a vegetative apex or of a peduncle and a capitulum.

In our model an internode or apical unit is characterized by four attributes. A unit is written between sharp brackets and the attributes are separated by commas. The four attributes are symbolized by *T*, *C*, *P*, and *D*, and a unit is written as $\langle T, C, P, D \rangle$.

The *attribute T* denotes the type of the unit. We let 1 stand for an apex, floral bud, or flowering capitulum; 2 stand for a peduncle (= stalk, bearing the capitulum); 3 stand for an internode; and 6 for the basal unit of a branch, also called a "branch-base".

The *attribute C* has always an integer value. A value of -1 means for all types of units that the development of the unit is irreversible halted. For units of type 1 the attribute *C* indicates their progress in floral development. For units of types 2, 3, and 6 the attribute *C* serves to keep track of time in the elongation process.

The *attribute P* denotes the rate of development either in vegetative or in flowering conditions. It is only used for units of type 1. In case of the vegetative rate, it always has positive real values. In case of the floral rate, it always has values between zero and one.

The *attribute D*, finally, denotes the length or the developmental stage of a unit. For units of types 2, 3, and 6, it gives the length. This length can vary from 0.3 to approx. 250. The length variable is in arbitrary units, which can be expressed in actual length units. For units of type 1, *D* denotes the developmental stage. If a unit is in vegetative condition, its developmental stage has always a value smaller than one. In flowering condition, the variable has a value greater than or equal to zero.

The transition rules are always of the following form:

If conditions R_1, \dots, R_n are applicable then either $\langle T, C, P, D \rangle \rightarrow \langle T^1, C^1, P^1, D^1 \rangle$

or

$$\langle T, C, P, D \rangle \rightarrow \langle T^1, C^1, P^1, D^1 \rangle \langle T^2, C^2, P^2, D^2 \rangle$$

or

$$\langle T, C, P, D \rangle \rightarrow \langle T^1, C^1, P^1, D^1 \rangle$$

$$\cdot (: \langle T^2, C^2, P^2, D^2 \rangle \langle T^3, C^3, P^3, D^3 \rangle :) \langle T^4, C^4, P^4, D^4 \rangle$$

or

$$\langle T, C, P, D \rangle \rightarrow \text{Sbt} \langle T^n, C^n, P^n, D^n \rangle,$$

where Sbt consists of $(n-1)/3$ substrings of the form

$$\langle T^1, C^1, P^1, D^1 \rangle (: \langle T^2, C^2, P^2, D^2 \rangle \langle T^3, C^3, P^3, D^3 \rangle :).$$

The new value of each of the attributes T, C, P, D is calculated (1) from the attribute values of the unit itself, (2) from the value of the attributes in the left and right neighbour units, (3) from the values of the apex or of the subtending internode of the particular branch on which the unit is located, and (4) from the four extra information parameters E, H, Q , and IT .

The conditions R_1, \dots, R_n use the same information as that from which the new state of each of the attributes T, C, P, D is calculated, and no other information.

The extra information consists of the parameters E, H, Q and IT , and of the states of the attributes of the apex and of the subtending internode of the branch on which the unit is present.

The parameter IT denotes the number of time steps at which the development of the organism is at the present time. Instead of IT one could have an extra unit which would keep track of the time steps. That would be within the limits of a $TD \langle 1, 1 \rangle$ L -system. However, as it is, CELIA keep track of the number of time steps anyway. Therefore, we do not need to increase the costs of the computation by adding an extra attribute.

The parameter H denotes the "height" of a unit in the organism. H is equal to the sum of the values of the attribute D (lengths of internodes) in all the internodes to the left of the unit. In the model, H is calculated globally. This could be brought back to a unit to unit calculation so that the calculation would fit into the framework of a $TD \langle 1, 1 \rangle$ L -system. However, in that case, all the other processes would have to be scaled down because of this very slow procedure. This would require an increase in the number of attributes, in computing time and in the complexity of the transition rules.

The parameter Q and the states of the attributes of the apex of the branch, on which the unit is present, can be calculated as follows. Let $X(A)$ be attribute X of apex A . Then the CELIA program is instructed to look at the values of the attributes of 13 right neighbours of a certain unit. It so happens that in our

simulation a branch never consists of more than 13 units; therefore, one of the 13 right neighbours will be the apex of the branch. It can be recognized as such because of the particular value of its T attribute, $T(A)=1$. The values of $C(A)$, $P(A)$, and $D(A)$, then, can also be obtained for the same unit. The apical unit is preceded by a number of internodal units. Q , now, is the sum of the values of the attribute D of the internodal units between the unit under consideration and the apical unit. In fact, $X(A)$ and Q would be computable within a $\langle 1, 13 \rangle$ L -system. By adopting a unit to unit procedure, in this case also, the system could be reduced to a $TD \langle 1, 1 \rangle$ L -system.

Parameter E can be calculated at every internode by the following formula:

$$E = P(A) \times 0.85^{Q/0.3}. \quad (2)$$

Parameter E is, therefore, defined in terms of two other extra information parameters.

The value of E is used in another way as well. Let us call the internode subtending a branch I . $E(I)$ then designates the value of E calculated for the internode subtending the branch which we are interested in. At every time step the apex of a branch is given access to its $E(I)$ value. But the $E(I)$ of the main axis cannot be established in this way (there is no internode subtending it) and, therefore, it is given an arbitrarily fixed value of 1. Instead of the calculation by the above formula and instead of the immediate transmission of the value of E from the internode to its laterally attached side branch, the value of E could also be calculated in a unit to unit procedure and transmitted in the same way so that it would still fit into a $TD \langle 1, 1 \rangle$ L -system.

Glossary

The following symbols are used in our rules.

$\text{ent}(x)$ the lower entier of the number x .

$$\times_{j=1}^m \{St_{(j)}\} = St_{(1)} * St_{(2)} * \dots * St_{(m)}$$

(where \times means the concatenation of strings of symbols)

$X(M)$ the value of the attribute X of the unit under consideration.

$X(L)$ the value of the attribute X of the left neighbour unit.

$X(R)$ the value of the attribute X of the right neighbour unit.

$X(A)$ the value of the attribute X of the apex of the branch on which the unit under consideration is located.

$E(I)$ the value of parameter E for the internode subtending the branch on which the unit under consideration is located.

T the attribute denoting the "type" of the unit.

C the attribute denoting the "condition" of the unit.

P the attribute denoting the "progress in development" of a unit.

D the attribute denoting the "developmental stage" of a unit.

IT the number of time steps at which the development of the organism is at the present time.

S the time step at which the tables of transition rules are switched.

H the "height" of a unit: the sum of the values of the length parameters of all internodes to the left of the unit under consideration.

Q the sum of the lengths of the internodal units between the unit under consideration and the apical unit on the same branch.

$$E = P(A) \times 0.85^{Q/0.3}.$$

$$\text{Senescence factor} = (S + 25 - IT)/25.$$

$$\text{Floral rate factor} = P(R).$$

Elongation factor = $F[i]$, where $0 \leq i \leq 8$ and $i = C(M)$ and the values for $F[0] - F[8]$ are given under rule 15 in the next section.

The Model

We use two tables of transition rules, designated as Table I and Table II. We instruct CELIA to let the plant develop for a number of time steps under Table I, after which development is continued under Table II. Table I gives the rules under which the branching structure develops, and Table II gives the rules which apply after the apices are converted into flowering primordia.

The transition rules form the core of the model. The most important differences in the rules are based on the attribute "Type". We list the rules accordingly.

Table I—Rules which Apply under Vegetative Conditions

1. If $T=1$ and $D+P \geq 1$ then

$$\langle T, C, P, D \rangle \rightarrow \begin{matrix} \text{ent}(D+P) \\ \times \\ \{ \langle 3, 0, 0, 0.3 \rangle \} \\ \times \\ \{ \langle 6, 0, 0, 0.3 \rangle \} \\ \times \\ \{ \langle 1, 0, 1.4P, 1.4(D+P-j) - P \rangle \} \end{matrix} \langle T, C, P, D+P - \text{ent}(D+P) \rangle.$$

Rule 1 allows the production of a number of new internodes and side branches under a developing apex. Let an internode set be an internode bearing a branch consisting of a branch-base and branch apex. Then with the help of the concatenation operator \times we express the production of more than one internode set in one time step according to the value of $\text{ent}(D+P)$.

Each new internode, units of type 3, gets assigned to it an initial length of 0.3. Each new side branch begins with a branch-base of type 6, which gets an initial and at the same time final length of 0.3. The branch-base is followed by an apical unit of type 1, which has a C attribute value of zero, a new vegetative rate P' , which is 1.4 times the developmental rate of the apical unit of its mother branch, and a new developmental stage D' , which is $1.4(D+P-j) - P$. This rule is similar to rules given for the production of organisms with uniform paracladial relationships (Frijters and Lindenmayer, to appear). Accordingly, a newly formed side branch repeats (or anticipates) the development of its mother branch with vegetative rate 1.4-fold as fast as the rate of its mother branch, while a delay period of one time the vegetative rate of its mother branch is observed before the repetitive development begins.

2. If $T=1$ and $D+P < 1$ then

$$\langle T, C, P, D \rangle \rightarrow \langle T, C, P, D+P \rangle.$$

As long as the new vegetative developmental stage $D' = D+P$ is less than 1, no new internodes and side branches are formed. The developmental stage at each time step is increased with the value of variable P , the vegetative rate.

3. If $T=2$ or 3 or 6 then

$$\langle T, C, P, D \rangle \rightarrow \langle T, C, P, D \rangle.$$

Units of types 2, 3, and 6 do not change under vegetative conditions.

Table II—Rules which Apply under Flowering Conditions

4. If $C = -1$ then

$$\langle T, C, P, D \rangle \rightarrow \langle T, C, P, D \rangle.$$

Units do not alter when their C attribute has a value of -1 .

5. If $T=1$ and $C=0$ and $E=0$ then

$$\langle T, C, P, D \rangle \rightarrow \langle T, C, P, 0 \rangle.$$

When an apex develops under Table II it begins with a C value of zero. Its future floral rate P will be determined by the value of the variable E according to rule 6. But when the value of E is still zero the floral rate cannot yet be assigned. The information carried by variable E can advance one order of branching per time step only. Consequently, it always takes a number of time steps after the switch before an apex can calculate its floral developmental rate. In the meantime this rule applies.

6. If $T=1$ and $C=0$ and $E > 0$ then

$$\langle T, C, P, D \rangle \rightarrow \langle 2, 0, 0, 0.3 \rangle \langle T, 1, E, E \times (S+25-IT)/25 \rangle.$$

In contrast to the situation encountered in rule 5, here we can assign a floral rate P to the apex. This apex gives rise to a peduncle of type 2 and a floral bud of type 1. The peduncle starts with an initial length of 0.3. The floral bud starts with a C value of 1, a P value equal to E , and a D value of E times the senescence factor. The senescence factor, $(S+25-IT)/25$, is constructed as follows: S is the time step at which the table switch takes place; 25 is the number of time steps in which senescence is going to be completed; and IT is the current time step.

7. If $T=1$ and $C=0$ and there is no value for E then

$$\langle T, C, P, D \rangle \rightarrow \langle 2, 0, 0, 0.3 \rangle \langle T, 1, 1, D \rangle.$$

This rule is only used at the moment of the table switch for the apex of the main axis. Since flowering development has to start somewhere, after the table switch we give the apex of the main axis an initial floral rate of 1. From this rate in the following time steps the floral rates for the other apices will be calculated according to rule 6. The P value of the floral bud of the main axis from the time of the table switch on is fixed with the value of 1. Its peduncle is formed at the same time as well.

8. If $T=1$ and $C=1$ then

$$\langle T, C, P, D \rangle \rightarrow \langle T, 2, P, D+P \times (S+25-IT)/25 \rangle.$$

When a floral bud has a C value of 1 it gets at the next time step always a C value of 2. During the one time step the bud has a C value of 1 the floral rates of the side branches of that axis can be calculated according to rule 6. The D value of the floral bud is regularly increased by the P value times the senescence factor, as in rule 6.

9. If $T=1$ and $C=2$ and $D+P \times (S+25-IT)/25 < 2$ then

$$\langle T, C, P, D \rangle \rightarrow \langle T, C, P, D+P \times (S+25-IT)/25 \rangle.$$

As long as the D value of the floral bud plus its increase is less than 2 the floral bud keeps a C value of 2.

10. If $T=1$ and $C=2$ and $D+P \times (S+25-IT)/25 \geq 2$ then

$$\langle T, C, P, D \rangle \rightarrow \langle T, 4, P, D+P \times (S+25-IT)/25 \rangle.$$

Under the given conditions the floral bud becomes a flowering capitulum, characterized by C values of 3 or 4.

11. If $T=1$ and $C=4$ and $D+0.8 < 6.5$ then

$$\langle T, C, P, D \rangle \rightarrow \langle T, C, P, D+0.8 \rangle.$$

The D value of a flowering capitulum is increased at every time step with a constant value of 0.8. As long as D plus its increase is less than 6.5 the flowering capitulum keeps a C value of 4.

12. If $T=1$ and $C=3$ or 4 and $6.5 \leq D+0.8 < 10$ and $H < 150$ then

$$\langle T, C, P, D \rangle \rightarrow \langle T, 3, P, D+0.8 \rangle.$$

If the value of D plus its increase is between 6.5 and 10, and the height H of the flowering capitulum is less than 150 then the unit gets a C value of 3. If the H parameter has a value greater than or equal to 150 then the flowering capitulum gets a C value of 4 according to rule 13.

13. If $T=1$ and $C=3$ or 4 and $6.5 \leq D+0.8 < 10$ and $H \geq 150$ then

$$\langle T, C, P, D \rangle \rightarrow \langle T, 4, P, D+0.8 \rangle.$$

See rule 12.

14. If $T=1$ and $C=3$ or 4 and $D+0.8 \geq 10$ then

$$\langle T, C, P, D \rangle \rightarrow \langle T, -1, P, D+0.8 \rangle.$$

A flowering capitulum finishes its flowering development, i.e., it has a C value assigned to it of -1 , when its D value has reached a value of 10.

15. If $T=2$ and $C(R) \geq 3$ and $C(M) < 9$ and [if $T(L)=3$ then $C(L) > 0$] then

$$\langle T, C, P, D \rangle \rightarrow \langle T, C+1, P, D+0.75D \times F[C(M)] \times ((S+25-IT)/25) \times P(R)^{-1/2} \rangle.$$

else if $T=2$ but one of the other conditions does not hold then

$$\langle T, C, P, D \rangle \rightarrow \langle T, C, P, D \rangle.$$

This rule states that a peduncle elongates only when the three following conditions are applicable:

(1) The C value of the right neighbour unit must be greater than or equal to 3. The right neighbour unit in this case is always the capitulum of the branch. A C value greater than or equal to 3 means that the capitulum must be flowering, see rule 10.

(2) The C value of the unit under consideration must be smaller than 9. A peduncle elongates in the course of 9 time steps at the most, see below. The C attribute of this unit counts these time steps.

(3) If the left neighbour happens to be an internode, $T(L)=3$, then this internode must have a C value greater than zero. This is the case when the internode has started to elongate, see rule 18.

If the three given conditions are all applicable, the peduncle will elongate. The elongation itself is also complicated. First, the C value increases by 1, for it serves as a counter of the time steps of the elongation. Further, its existing length D is increased by 0.75 times D times an elongation factor times the senescence factor times a floral rate factor. The elongation factor $F[i]$ denotes the i -th item of the array $F[0]$ to $F[8]$, the value of which is obtainable from the following series: $F[0]=0$, $F[1]=1$, $F[2]=1$, $F[3]=1.5$, $F[4]=1.6$, $F[5]=0.9$, $F[6]=0.6$, $F[7]=0.5$, and $F[8]=0.5$. The senescence factor is the same one as we used in rules 6 to 10. The floral rate factor $P(R)^{-1/2}$ is the inverse of the square root of the P value of the right neighbour unit, the capitulum. Taking the inverse of the square root of the P value of the capitulum has the effect that the elongation of a peduncle, which neighbours a capitulum with a low P value, is stimulated. In practice, however, this stimulation can be counteracted by the senescence factor, because it takes capitula with a low P value a relatively long time before they are flowering.

16. If $T=3$ and $C(A)=-1$ then

$$\langle T, C, P, D \rangle \rightarrow \langle T, -1, P, D \rangle.$$

An internode halts its development, i.e. C becomes -1 , when the C value of the apex on the same branch has a value of -1 .

17. If $T=3$; and either $C(M)=9$, or $C(L)=0$, or $D(A) < 1$ then

$$\langle T, C, P, D \rangle \rightarrow \langle T, C, P, D \rangle.$$

This rule is similar to rule 15 for the elongation of a peduncle. But here alternative conditions are given under which no elongation takes place. These conditions are:

(1) The C value of the unit under consideration is equal to 9. This happens when the internode is fully elongated, compare to condition 2 of rule 15.

(2) The C value of the left neighbour unit is equal to zero. This happens when the neighbour has not begun to elongate.

(3) The D value of the apex on the same branch is smaller than one. In fact, the elongation of the internodes on a branch cannot begin before the floral bud on their branch has reached a D value of 1.

18. If $T=3$ and none of the other conditions stated in rule 17 applies and $C(A) \neq 3$ then

$$\langle T, C, P, D \rangle \rightarrow \langle T, C+1, P, D+D \times F[C(M)] \times (S+25-IT)/25 \rangle.$$

This rule specifies when and how an internode elongates. Its length D is increased by D times an elongation factor times the senescence factor. The elongation factor and the senescence factor are the same as used in rule 15.

19. If $T=3$ and none of the other conditions stated in rule 17 applies and $C(A)=3$ and $C(M) < 8$ then

$$\langle T, C, P, D \rangle \rightarrow \langle T, C+1, P, D+1.5D \times F[C(M)] \times (S+25-IT)/25 \rangle.$$

When the C value of the apex on the same branch is equal to 3 the internode does not elongate in the normal way as in rule 18. Its length increases 1.5-fold as much as under the conditions stated there.

20. If $T=3$ and none of the other conditions stated in rule 17 applies and $C(A)=3$ and $C(M)=8$ then

$$\langle T, C, P, D \rangle \rightarrow \langle T, C, P, D+1.5D \times F[C(M)] \times (S+25-IT)/25 \rangle.$$

This rule is an extension of rule 19. It covers the situation in which the internode has already elongated during 8 time steps, $C=8$, and now should finish its elongation, but, because of the circumstance that the C value of the apex is equal to 3, it is granted an extra elongation time step. Its C value for that purpose is not increased.

21. If $T=6$ and $C(L) > 0$ then

$$\langle T, C, P, D \rangle \rightarrow \langle T, 1, P, D \rangle.$$

Else, if $T=6$ and $C(L) \leq 0$ then

$$\langle T, C, P, D \rangle \rightarrow \langle T, C, P, D \rangle.$$

A branch-base never elongates. Under certain conditions, its C value changes. This is in order to enable its right neighbour internode to start elongating, see condition 2 of rule 17. The C value of the branch-base changes when the internode on the mother branch at which the branch-base is attached, has begun to elongate, this is when $C(L) > 0$.

Extra Information

The calculations of E , H , Q , IT and $X(A)$ were treated in the preceding section. It suffices to add one additional remark.

Parameter E is equal to $P(A) \times 0.85^{Q/0.3}$ by formula (2). The initial length of an internode is according to rule 1 equal to 0.3. Therefore, as long as the internodes preceding the apex have not elongated, E will have values $P(A) \times 0.85^1$, $P(A) \times 0.85^2$, ..., $P(A) \times 0.85^n$, dependent on the number of internodes on the right of the internode where E is calculated.

Results

Having specified some initial units, a time step at which the table switch must take place, and the number of time steps the string of units must be

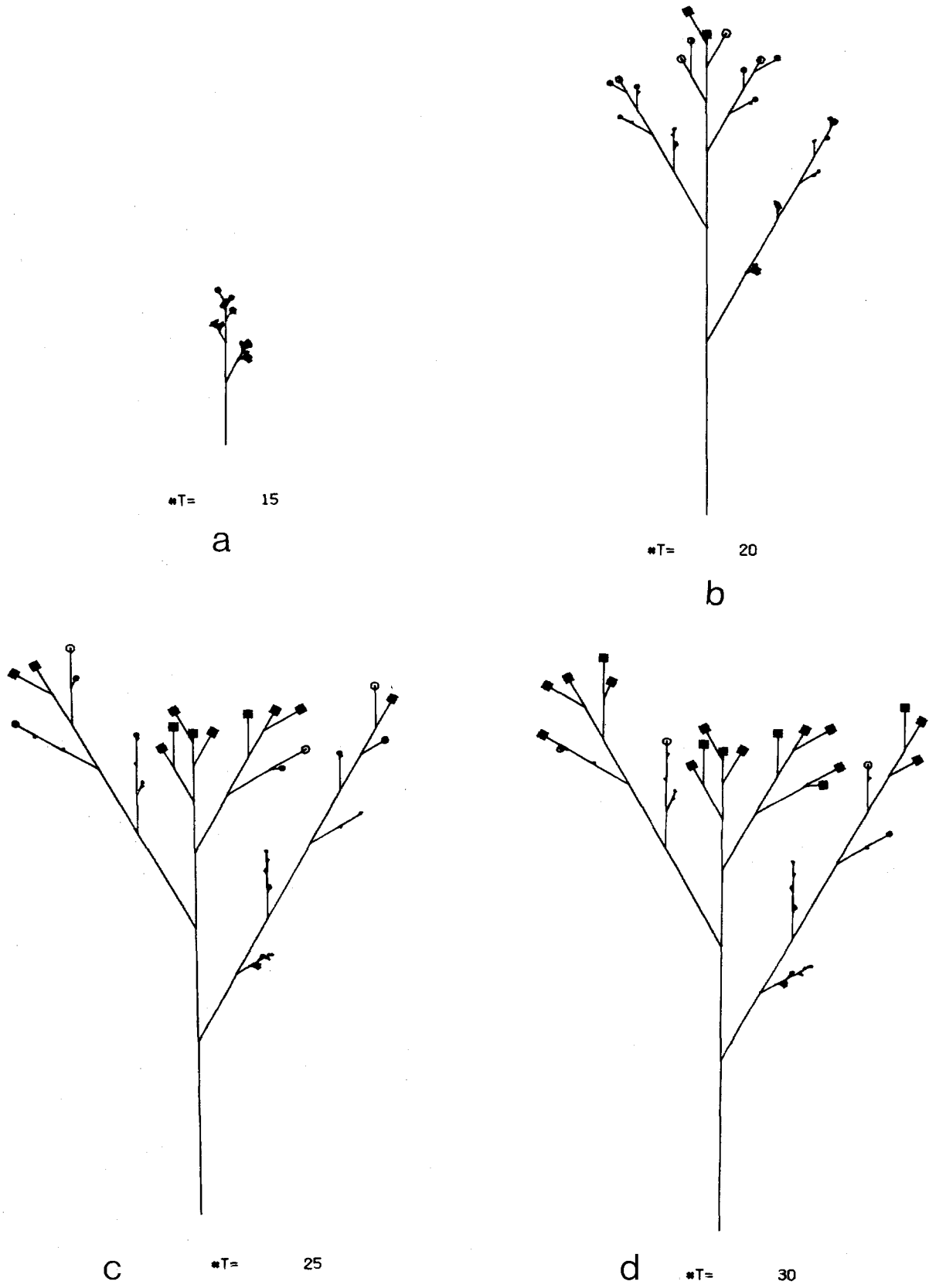


Fig. 3. Four diagrams (a—d) of the developmental stages of a model plant at time steps 15, 20, 25, and 30. Symbols as in Figure 1. Table switch at time step 7

iterated, the CELIA program is able to perform the simulation. The output data, see below can be used for a plotter program to draw the model plant at several time intervals (see Frijters and Lindenmayer, 1974).

The first 3 time steps of the computer simulation of the model plant of *Hieracium murorum* are as follows:

1. $\langle 6, 1, 0, 0.1 \rangle \langle 3, 0, 0, 0.3 \rangle (: \langle 6, 0, 0, 0.3 \rangle \langle 1, 0, 1.4, -0.86 \rangle :)$
 $\langle 1, 0, 1.0, 0.1 \rangle$
 2. $\langle 6, 1, 0, 0.1 \rangle \langle 3, 0, 0, 0.3 \rangle (: \langle 6, 0, 0, 0.3 \rangle \langle 1, 0, 1.4, 0.54 \rangle :)$
 $\langle 3, 0, 0, 0.3 \rangle (: \langle 6, 0, 0, 0.3 \rangle \langle 1, 0, 1.4, -0.86 \rangle :)$
 $\langle 1, 0, 1.0, 0.1 \rangle$
 3. $\langle 6, 1, 0, 0.1 \rangle \langle 3, 0, 0, 0.3 \rangle (: \langle 6, 0, 0, 0.3 \rangle (: \langle 6, 0, 0, 0.3 \rangle$
 $\langle 1, 0, 1.96, 0.44 \rangle :)$
 $\langle 1, 0, 1.4, 0.94 \rangle :)$
 $\langle 3, 0, 0, 0.3 \rangle (: \langle 6, 0, 0, 0.3 \rangle$
 $\langle 1, 0, 1.4, 0.54 \rangle :)$
 $\langle 3, 0, 0, 0.3 \rangle (: \langle 6, 0, 0, 0.3 \rangle$
 $\langle 1, 0, 1.4, -0.86 \rangle :)$
 $\langle 1, 0, 1.0, 0.1 \rangle$
-

We start the simulation with two initial units

$\langle 6, 1, 0, 0.1 \rangle \langle 1, 0, 1, 0.1 \rangle$.

We command a table switch after 7 time steps, and we stop the simulation after 30 iteration steps. Figure 3 shows the results.

Diagram a of Figure 3 shows the model plant at the 15-th time step, 8 time steps after the table switch. The timesteps of the simulation occur as follows. Under Table I, vegetative condition, per time step one new internode and side branch is formed by the apex of the main axis. In other words, then one time step corresponds to one plastochron of the main axis. The length of the plastochron interval varies in this plant according to environmental conditions between 1 day and 1 week. Under Table II, flowering condition, the flowering capitulum of the main axis takes 10 to 15 time steps to reach the fruiting stage, which corresponds to 2 to 3 weeks. The final length of the main axis reaches 30 to 60 cm, and the side branches are scaled accordingly. Some internodia have begun to elongate. The capitula are all present, but they are in clusters and difficult to distinguish on this plot. Diagram b, five time steps later, shows the plant at a stage at which the capitulum of the main axis has reached the fruit stage. The internodes of the main axis have reached their final lengths, those of the side branches still continue to elongate. Diagram c shows the plant at the 25-th time step. The capitula of the first order branches all have reached the fruit stage. Some of the capitula of the second order branches as well. The internodes on the branches which bear a fruiting capitulum have reached their final lengths, the others have not. The stage of diagram c is somewhat later than that of the flowering shoot systems of the observed plants shown in Figures 1 and 2. The developmental

stage of the shoot system of Figure 2, however, is very close to the stage of the model plant shown in Figure 3c. Diagram d, finally, shows the model plant at a moment where many of the second order branches have reached the fruit stage, as well as some of the third order branches. Senescence has an influence at this stage, so that virtually all elongation is halted as compared to diagram c. Some capitula will still be able to reach the fruit stage, but most will be impeded to do so because of senescence.

Another simulation has been done with the table switch at an earlier step. The results are shown in Figure 4. This model has approximately the same branching structure as the observed plant in Figure 2.

Discussion: Developmental Mechanisms in the Model and in the Real Plant

The features of the model plant are achieved by applying repeatedly the rules stated in the previous section. These rules are based on certain ideas about the most suitable and efficient control mechanisms which are also biologically acceptable. We are dealing with the following set of mechanisms.

1. The Floral Switch

At a certain time the plant is suddenly converted from a vegetative state into a flowering state. Before this abrupt change of states the apices form internodes and side branches. After it, the apices give rise to peduncles and floral buds, and the internodes begin to elongate.

Floral induction is a well known developmental process. It occurs in many flowering plants (Salisbury, 1963; Evans, 1969). It is known that a shoot system sometimes waits with its elongation until its apical meristems have reached the flowering stage.

2. The Formation of Internodes and Side Branches

Apices form the new plant organs. The frequency at which new organs are formed is dependent on the position of the apex. The resulting branching pattern can be completely described in terms of a uniform paracladial relationship, as defined in a previous paper by Frijters and Lindenmayer (to appear). In short, a paracladial relationship means that on a branch x the number of internodes—and consequently also the number of side branches—is linearly correlated to the number of internodes present on its mother branch y counted above the point where x is attached to y . The relationship can be written in a formula, (3), as follows:

$$\text{In}(x) = a \times (\text{In}(y) - b) \quad (3)$$

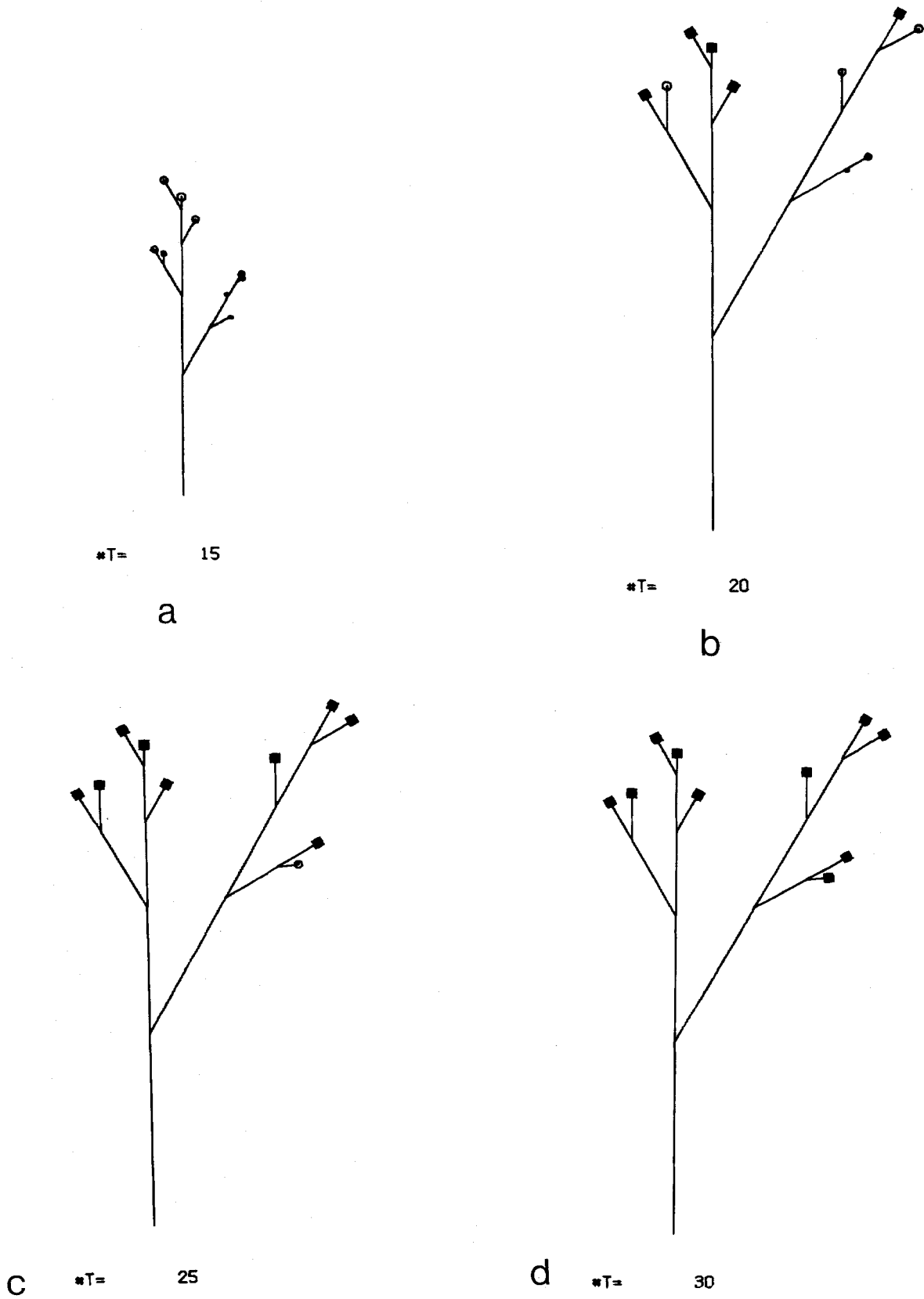


Fig. 4. Four diagrams (a—d) of the developmental stages of a model plant at time steps 15, 20, 25, and 30. Symbols as in Figure 1. Table switch at time step 5

where $\text{In}(x)$ means the number of internodes on x , $\text{In}(y)$ the number of internodes on y , a is the rate at which branch x is repeating (or anticipating) its mother branch y , and $a \times b$ is the period of delay before branch x starts to repeat branch y . A paracladial relationship is called uniform when for all branches in the pattern the same paracladial relationship applies. Frijters and Lindenmayer (to appear) have shown how every pattern which displays uniform paracladial relationships can be generated by a $\langle 0, 0 \rangle$ L -system. In rules 1 to 3 the preceding section we have used the same developmental rules as described in that paper. The variable a in formula (3) has been given a value of 1.4 and the variable b a value of 1. In our model, variable a is greater than 1, meaning that a side branch ultimately develops faster than its mother branch. We let the time steps of the model take place so that per time step one new internode and side branch is formed by the apex of the main axis. In other words one time step corresponds to one plas-tochron of the main axis. The conditions and calculations in rules 1 and 2 of the preceding section take care of the fact that the behaviour of all other apices must be scaled down to the behaviour of the apex of the main axis.

Plant morphologists talk frequently about repetitions of development of constituent parts of the plant. Troll (1964) uses the term "paracladium" to denote a flowering system which repeats the flowering system of the main axis. Maresquelle (1964), Maresquelle and Sell (1965) and Sell (1969) speak in that connection about «fleurs de renfort et inflorescences de renfort» and about «repetitions morphogenetiques». Sell (1970), Jauffret (1970) and many others have looked at the physiological connections between systems where one repeats the other. Our paracladial relationships define some special cases of such connections.

3. The Formation of the Peduncles and Floral Buds

After the floral switch, the apical units divide into floral stems (peduncles) and floral buds. But this does not happen simultaneously everywhere in the plant. Each apex waits until it has acquired from the apex of its mother branch the necessary information to determine the floral rate of its newly formed floral bud.

4. The Assignment of the Floral Rate of Development

After the switch, first of all the floral rate of development is fixed at a value of 1 for the newly formed floral bud of the main axis. The floral rates of the other floral buds are derived from and scaled down to the rate of the main axis. These floral rates are determined as follows. Each successive floral bud of the same order

of branching along a communal mother branch in basal direction gets a floral rate $P^1 = E$ of respectively $0.85^1, 0.85^2, 0.85^3, \dots$ times the floral rate of its mother branch. The successive values of

$$E = P(A) \times 0.85^{Q/0.3}$$

are equal to the number of internodes from the attachment points of the branches to the floral bud of their mother branch. If any of the internodes has elongated before E is determined for the apex of one of the side branches, then $Q/0.3$ increases with bigger steps than 1 unit per internode, and this means that a side branch of which the floral rate is being determined receives a low floral rate value.

The floral rate is always derived from the floral rate of the mother branch. The assignment of floral rates in our model can, therefore, only proceed one order of branching per time step.

The mechanisms under point 3 and 4 are closely related to the concept of "apical dominance". This well known phenomenon can be observed in numerous ways. It is known that growth hormones like auxine often play an important role. Our mechanisms provide a way how a substance like auxin can be distributed throughout the plant in such a way that they influence floral development in the desired manner. The value of E , standing for the distribution of an auxine-like substance, is calculated from the activity of the apex, $P(A)$, of a branch, and is diminished by the distance, Q , from the apex.

5. The Development of the Capitula

The terminal flowering structures of this plant are the capitula. A floral bud develops into a flowering capitulum and later on into a fruit bearing capitulum. The development from a flowering capitulum into a fruit bearing capitulum takes place in a highly regular fashion with a speed of 0.8 flowering stage units per time step. The development stops when the fruit forming stage is reached. The duration of development of a newly formed floral bud into a flowering capitulum differs for each floral bud. It is based on the individual floral rates and on the particular senescence factor present at the successive time steps. As a consequence not all floral buds are able to reach a flowering stage before they are ultimately halted in their development because of the senescence of the entire shoot system.

Often capitula, which have reached a certain developmental stage, continue without any additional control. For commercial purposes, therefore, flowers can be sold which are not yet opened. They will, when cut, open soon, sometimes even faster than could be expected otherwise. The capitula of *Hieracium murorum* after some stage also continue to develop into fruits, despite of senescence.

6. The Elongation of the Peduncles

A peduncle begins to elongate when its apically neighbouring capitulum begins to flower and its basally neighbouring internode, if present, begins to elongate. The elongation formula for a peduncle is quite similar to the elongation formula for an internode. There are only two differences; one, the elongation rate of internodes is multiplied by 0.75; and two, the rate is additionally multiplied by a floral rate factor. The latter is equal to the inverse of the square root of the floral rate of the apically neighbouring capitulum.

7. The Elongation of the Internodes

An internode begins to elongate when the capitulum on its branch surpasses a certain developmental stage, and when at the same time its basally neighbouring internode begins to elongate. The elongation usually goes on during 9 time steps. It can be halted earlier when the capitulum of the branch on which the internode is situated has reached the fruit forming stage. Conversely, it can be continued for longer than 9 time steps when the capitulum of the branch on which the internode is situated has reached a flowering stage but has not yet reached a particular height. The elongation formula consists of an elongation factor multiplied by a senescence factor. The elongation factor has 9 discrete values, one for each time step of the elongation process, having a maximum value at the fifth step. This gives an S-shaped elongation curve, which is well established in plant physiology. The senescence factor causes a decrease in the elongation according to the number of time steps which have occurred since the table switch. At 25 time steps after the switch all elongation ceases. Under certain conditions when the height of the capitulum is not large enough, the elongation rate is multiplied by 1.5.

The mechanisms under point 6 and 7 are intended to produce the kind of corymb-shaped, flat-topped, inflorescence structures as actually occurs in *Hieracium* (Pugsley, 1948), see Figure 5. The rate at which the capitula develop decreases from center to periphery, while the lengths of the stems increase from center to periphery. Clearly, this can be achieved only by an inverse relationship between the flowering rate and the process of stem elongation. The assumptions incorporated in point 6 and 7 are expressions of this inverse relationship. More details will be given in a subsequent paper.

8. The Development of the Branch-Base

The branch-base plays a role in the transmission of information from the mother branch to its side branches. The type assigned to a branch-base unit serves as a branch begin-marker. The branch-base can

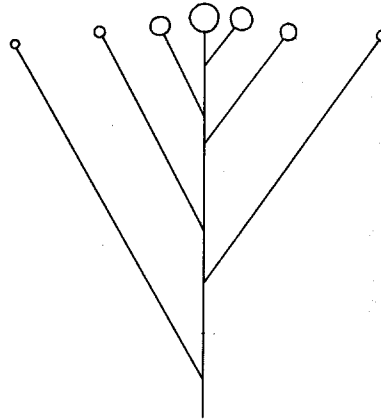


Fig. 5. Corymb of *Hieracium murorum*

also be considered as the node where the branch is attached. To facilitate calculations this node has been made part of the side branch. It is for this reason that a branch-base does not elongate. It only alters its C value once, when the internode on the mother branch to which it is attached, begins to elongate. By doing this, the branch-base makes it possible for the internodes on *its* own branch to begin to elongate. Further, the branch-base is also useful in the process of calculating the height parameter H .

9. Senescence

Senescence begins with the occurrence of the table switch. In 25 time steps it reaches a level at which all development is halted. The senescence factor begins with a value of 1, no senescence, and goes to a value of zero, complete senescence. Senescence effects the elongation of peduncles and internodes and also the rate of development of the floral buds into a flowering capitulum. It does not effect the development of flowering capitula into fruits.

The mechanisms of development described for the model in the preceding section are not necessarily the ones which are used by the real plants to regulate their development. However, we presume that some of the hypothetical mechanisms are closely related to the actual ones. The hypothetical mechanism of the table switch from vegetative to flowering condition of the shoot system of *Hieracium murorum* is presumably matched by the real plant in the following way:

It proves that in each flowering shoot system of this plant the branching pattern can be described in terms of some uniform paracladial relationship. It seems unlikely that such a relationship can occur when the formation of the branching pattern is not strictly bounded in time. For example, if in one branch of the organism the formation of new branches has stopped, but is continued in one of its side branches, a uniform paracladial relationship for the whole

organism can never be expected. Therefore, at least two switches seem necessary in the development of the flowering shoot systems. Because the first switch implies that an apex begins to form the branching pattern, and this corresponds to the start of our simulation, we actually need only one table switch. The uniformity of the paracladial relationships in this plant also puts severe restrictions on the frequency at which internodes and branches are formed. Therefore, also the hypothetical mechanism about this frequency seems justified.

By letting the switch occur earlier than in the model plant represented in Figure 3, one gets another model plant shown in Figure 4. This structure resembles a comparable real plant, in this case a plant as shown in Figure 2, more closely in respect to its branching structure and order of flowering, but less in the elongation of the diverse internodia and peduncles. The mechanisms which control the elongation of the peduncles and internodes are quite complicated. The variation in internode lengths is often enormous, but limited. Nevertheless, or perhaps because of that, it has proved difficult to develop suitable mechanisms to take care of all the observed lengths. The mechanisms which are employed, work at best when the table switch occurs at about 7 time steps, as in Figure 3. When the switch takes place at 5 time steps, as in Figure 4, the lengths we obtain fit more poorly. We think that also some external factor like exposure to light affects the elongation process. Such a factor is hard to account for in our model. However, our mechanism calculating the "height" of every unit and directing the elongation processes accordingly comes near to it.

Even if some of the hypothetical mechanisms which were assumed do not stand up to future physiological evidence, they still have the merit that on their own and in combination with each other they have proved to be sufficient to produce a pattern of development and flowering similar to that in real plants.

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