A MODEL FOR THE GROWTH AND FLOWERING OF ASTER NOVAE-ANGLIAE

ON THE BASIS OF TABLE < 1,0 > L-SYSTEMS

D. FRIJTERS and A. LINDENMAYER

Theoretical Biology Group

University of Utrecht

Heidelberglaan 2

Utrecht, The Netherlands

Summary

L-systems (1, 2, 3)[*] were introduced by one of us in order to model morphogenetic
processes in growing multicellular filamentous organisms. We will show here, how a
computer model of the growth and flowering of Aster novae-angliae could be built
using a particular L-system.

Introduction

Champagnat (4) and Nozeran, Bancilhon and Neville (5) classified various internal
correlations in the morphogenesis in higher plants: They argue that often there is
evidence of internal correlations which involve the whole plant and of correlations
which involve parts of the plant such as organs, regions or even one tissue. Inter-
nal correlations with respect to pattern formation in growth and flowering of higher
plants are interesting, because of the relationships between position and time of
flowering and flower development.

---

[*]Since our references are mostly to biological papers, we deviate from the format
used in this book and we list our references at the end of this article.

There seems to be enormous diversity in the inflorescences and inflorescence forma-
tion in higher plants. Within a plant species, however, the pattern of the inflo-
rescence and its development are quite constant and show great similarity to the
patterns of related species as has been shown by Troll (6) and Weberling (7). Seve-
ral theories and models have been put forward to explain the evolution of inflo-
rescences, cf. Maresquelle (8, 9, 10, 11), Stauffer (12) and Sell (13). Champagnat (4)
and Nozeran, Bancilhon and Neville (5) held gradients responsible for the pattern-
formation in their plants. Maresquelle and Sell (14) also assumed gradients which in
their opinion controlled the descending inflorescences in higher plants (these are
inflorescences where flowering proceeds from the top down). Sell (15, 16) and
Jauffret (17) also gathered experimental data about correlations between growth and
flowering. However, the question how growth and flowering in plants are correlated
is still open. This is mainly due to the fact, that no suitable representation and
calculation devices are available to work out the consequences of different theore-
tical correlation mechanisms. Most correlations were supposed to depend on gradients.
These gradients are supposedly formed by diffusion and / or active transport. For the
calculation of their effects differential equations must be solved. Because the
plant is also growing, the equations cannot be solved analytically, but by step-by-
step approximations. L-systems can be used to obtain approximate solutions. In this
case, all states of a growing filament are simultaneously replaced by new states at
discrete time steps, according to certain transition rules (as for example growth
and division rules). Furthermore, L-systems have been defined so that computer pro-
grams can be based on them, cf. Baker and Herman (18, 19, 20). They are suitable for
representing and quantifying correlations in growing systems as long as these sys-
tems can be treated as simple or branching filaments.

In personal communication Sell advised us on the suitability of _Aster_ as a subject
for an inflorescence development model. This genus belongs to a large family
(Compositae) that makes it convenient to compare it with other plants. _Aster novae-
angliae_, a species of _Aster_, reaches a height of about one meter. Its pattern of
growth and flowering is quite complex. It can form up to 30 side-branches on any

one branch. It shows apices which turn into flowers and apices which stay vegeta-
tive. It produces hundreds of easily countable and classifyable flowers. Branches
in various parts of the plant exhibit easily recognizable patterns of growth.
Flowering is presumably triggered by an environmental signal (short days). Fully
developed flowers appear first midway along the plant and susequently appear above
and below this point (ascending and descending flowering sequence). Aster forms its
organs at the apices of its shoots. Growth in length only takes place in a zone just
under the apex, growth in girth might take place anywhere.

We had to formulate first the minimum requirements for a meaningful model. A number
of characteristics of Aster are not relevant to our purpose. Therefore, we decided
to disregard phyllotaxis and shape and size of leaves. We regarded as essential to
the model: (1) the number and order of branches, and their positions, (2) the posi-
tions and time order of the appearance of floral buds, and their development, and
(3) the lengths of all internodes. We insisted that the computer model should show
the same features in these respects as the actual plant.

Characteristics of Aster novae-angliae

The features of Aster novae-angliae, limited to those which were under consideration
in the computer model, were as follows.

Figures 1 and 2 (all figures which are shown have been drawn by computer, as will be
described later) show a diagrammatic representation of a plant of Aster novae-angliae
growing in a garden in Huis ter Heide, The Netherlands, on 7 Sept. 1973. The inter-
nodes on the main branch (the 0-order branch), and the branches of the main axis and
their "flowers" have been indicated (Aster plants have compound inflorescences typi-
cal of Compositae, where the smallest inflorescence units are the so called "heads".
These we shall refer to as individual "flowers"). The internodes seem to decrease
gradually in length from base to apex. The 15 lower internodes bear no branches
(leaves are not shown in these figures). The first order branches increase suddenly
in length as function of their position on the main axis (from base up) and decrease
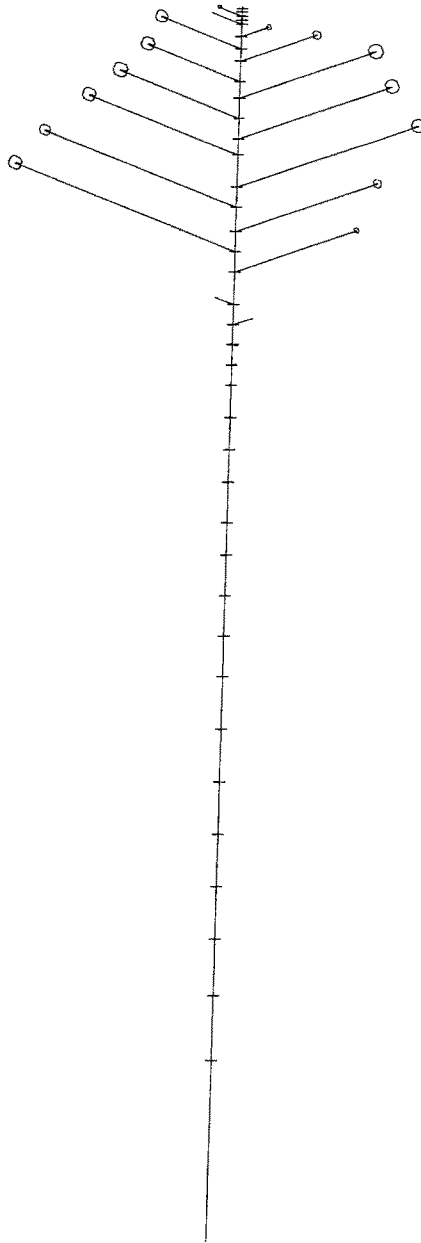gradually after that. The plant does not seem to posess either purely descending or

Fig. 1. Diagram of a plant of _Aster novae-angliae_ on 7 Sept. 1973. The main axis with its internodes, its side branches, and the apically born flowers (heads). The symbols ⬤ denote the flowers, the size of the symbols show the state of their development.
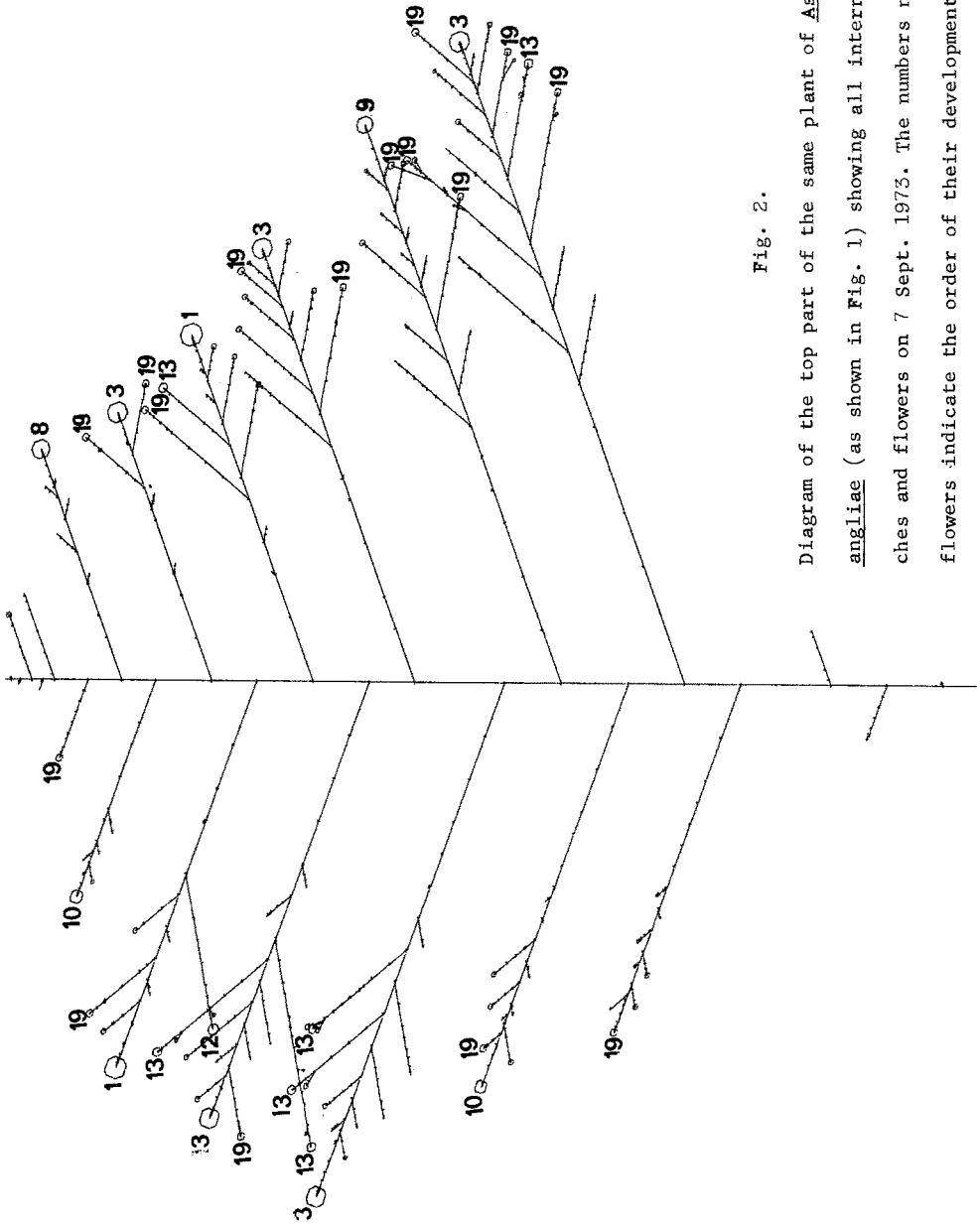
Fig. 2.

Diagram of the top part of the same plant of _Aster novae-angliae_ (as shown in Fig. 1) showing all internodes, branches and flowers on 7 Sept. 1973. The numbers next to the flowers indicate the order of their development.

purely ascending order of flowering, the most developed flowers are found on the branches positioned midway along the main axis.

Figure 2 is an enlarged detail of the top part of Fig. 1. Here, all internodes and flowers, and to some extent the order of development of the flowers, have been indicated. As **on** the 0-order branch, it can be seen that the internodes of the higher order branches decrease in length gradually from base to apex. The lower placed branches on any branch, have shorter internodes than their mother branch above the branching point, the higher placed branches have internode lengths equal to their mother branch above the branching point.

The first order branches seem to be able to grow faster than the 0-order branch: starting with the longest first order branch, they show about twice as many internodes as the corresponding parts of the 0-order branch above the branching points. This phenomenon appeared to be repeated in the higher order branches. The 0-order branch had 15 branchless internodes, the higher order branches showed always less branchless internodes, frequently exactly 3, while the branches nearest to the base often had the highest number of branchless internodes and the ones nearest to the top the lowest. In total numbers this plant had on that date: 25 first order branches, 125 second order branches, 200 third order branches, 10 fourth order branches and no fifth order branches. Other plants frequently show more branches, as well as fifth and even sixth order branches.

The flowering order which consists of flower development starting midway along the first order branches, was also encountered in the higher order branches. However, the topmost flower of a certain branch was nearly always further developed than the flowers of the side branches of that branch. We noticed that the larger a plant had grown or the longer a particular branch had become, the less developed was the apex of that plant or branch as compared to some of the flowers on its side-branches. In our plant this was visible in the complete absence of a flower at the top of the main axis.

On 26 Sept. 1973, we observed again the same plant represented in Figs. 1 and 2. We
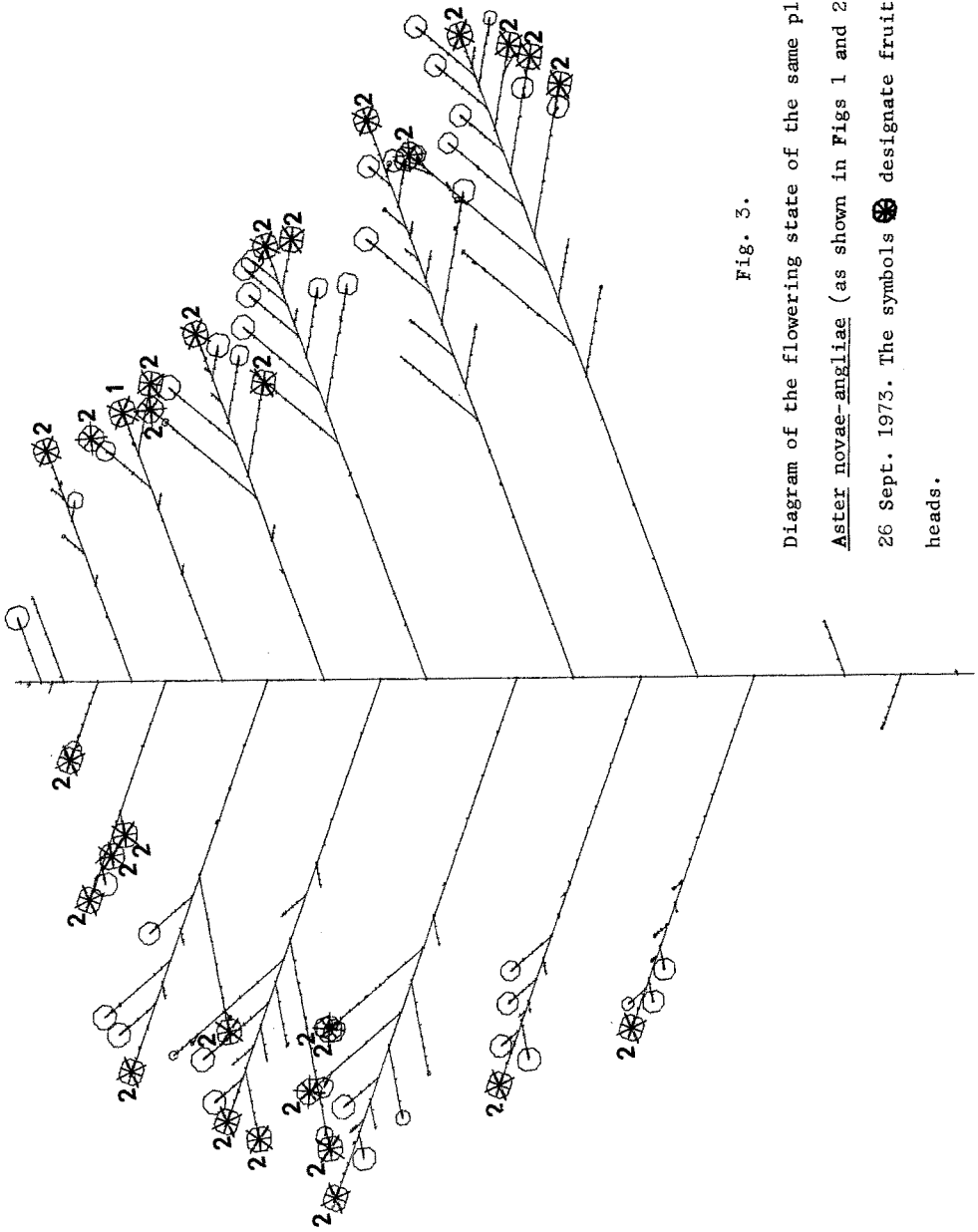
Fig. 3.

Diagram of the flowering state of the same plant of
Aster novae-angliae (as shown in Figs 1 and 2), on
26 Sept. 1973. The symbols ✸ designate fruit bearing
heads.

took new measurements of some branches and noticed that several branches had conti-

nued to grow, while others had not. It appeared that the branches nearest to the

top of their mother branch had grown more than the branches nearest to the base.

This phenomenon was strongest   near the top of the plant. The flower de-

velopment had also most strongly proceeded at the top of the plant and on the

branches positioned nearest to the top of their mother branches. The data we had

gathered about the lengths of the internodes were not complete enough to elaborate

them in a new figure. We had gathered, however, all the necessary data of the flo-

wers of the plant. Figure 3, therefore, which is identical to Fig. 2 except for the

flower development, shows all floral buds and flowers of the plant at the later

stage. A number of flowers had already formed plumed fruits (🌸) and it was diffi-

cult to assign flowering stages to them. One flower, however, had lost its fruits

and therefore could definitely be classified as being the most developed flower. All

the other plumed fruits were classified equally as second in the flowering order.

The computer model

As mentioned before, Baker and Herman (18, 19, 20) and Liu (21) designed a computer

program, called CELIA, to process strings in the way L-systems do. The first version

of CELIA was followed by a second, more extensive, version (22), which we used in

our model. CELIA consists of a main program which can be instructed by a total num-

ber of 16 fixed control and data cards and by several user-written subroutines. We

wrote the developmental rules for the model in the (user-written) DELTA subroutine.

We found inspiration for the formulation of the rules for our model in the work of

Cohen (23). As "cells" or "units" in the sense of L-systems we took already mentio-

ned segments of the plant: internodes, apices, lateral buds, and first internodes on

a branch. We instructed CELIA by the control card MODEL to process out organism as a

branching < 1,0 > L-system. This latter system is a branching system in which the

information for a cell only comes from its own state and that of its first neighbour

on the left. The first internode of a branch receives its left neighbour information

from the internode on the mother branch which bears the branch in question. The

strings were written out in the conventional way, that is, the shoot apex at the

right and the base at the left. We introduced four attributes per unit. For the sake of convenience, a unit with its attributes was placed between sharp brackets. The four attributes were, in order of appearance: TYPE, FORS, LONG,and BULK (the whole unit abbreviated as < T, F, L, B >).

The variable TYPE can have only three values: 1, standing for an apex or flower; 3, standing for an internode; and 6, standing for a lateral bud or for a first internode on a branch.

FORS is a variable applicable to apices or internodes (it can have values greater than or equal to -2). The FORS value of an apex is simply equal to the number of internodes which were produced by that apex (from the stage of a lateral bud on). The FORS value of an internode is equal to twice the number of internodes produced above it on that branch. The fact that an internode keeps account of the number of internodes produced above it does not necessarily mean that we have here to do with long range communication between parts of a branch. An internode can simply measure the time since its production and the degree of inhibition applicable to that branch and compute from that at any time the number of internodes which have arisen above it. Using twice the number of internodes in FORS is due to our wish to let the growth function of internodes look more realistic, as we shall show later. The negative values for the number of plastochrones were introduced for practical programming reasons, they had no further significance.

The variable LONG can only have values greater than or equal to zero. It stands for the initially determined length of the mother branch of the particular bud or internode. Its value has to do with the degree of inhibition.

We let our plant grow (expand) until a certain stage, at which stage we switch the set of rules. This switch,called "table-switch", is meant to represent the change from vegetative to flowering conditions in the whole plant.

Outside the scope of the table < 1,0 > L-system we make information available concerning the length and inhibition of the branch and of its mother branch. We

will argue that this extra information can be deduced to one-step-at-a-time left-sided information transmission, so that it could be fitted into a table $< 1,0 >$

L-system, if we so desired. We will explain later why we thought it was/convenient
to do that.

The core of the model: production rules

The most important differences in the rules for the units are based on their first attribute, their TYPE. Therefore we classify the rules according to their TYPE.

A unit (internode or apex) is represented by a quadruple of attributes,
$< T, F, L, B >$. L(L1) designates the value of the attribute LONG of the left neighbour of a unit. The rules which specify how certain quadruples change to other quadruples are shown below. For certain combinations of attributes the same rule is used under both vegetative and floral environmental conditions. For other combinations, the rule which is applicable depends on the environment (vegetative or floral condition). The term "int (F)" indicates the integer portion of the value of the variable F (the lower entire of F).

Rules_which_apply_under_both_vegetative_and_floral_conditions.

TYPE 3

1. If F is greater than or equal to 6 then
$< 3, F, L, B > \longrightarrow < 3, F, L, B >$.
This rule states that an internode unit is fully grown when the value of its variable FORS (the number of plastochrones) is greater than or equal to 6.

2. If F is smaller than 6 and int (F) is equal to int (F + 2K) then
$< 3, F, L, B > \longrightarrow < 3, F + 2K, L, B >$.
This states that an internode unit does not grow (does not increase the value of its variable LONG), but just increases the value of its plastochrone number (the value of the variable FORS) with twice the value of the variable K (the degree of inhibition - the behaviour of which will be explained later -), whenever the value of its variable FORS is smaller than 6 and the value of the lower entire of its variable

F is equal to the value of F + 2K.

3. If F is smaller than 6 and int (F) is smaller than int (F + 2K) then

$< 3, F, L, B > \rightarrow < 3, \text{int}(F) + 1, L + L \times (\text{int}(F) + 1 - 0.15(\text{int}(F) + 1)^2), B >.$

This states that an internode unit grows and at the same time increases its plasto-chrone number whenever the value of its variable FORS is smaller than 6 and the value of the lower entire of its variable FORS is smaller than the value of FORS + 2K. The new length of the internode becomes LONG + LONG x $(\text{int}(\text{FORS}) + 1 -$

$- 0.15 \ (\text{int}(\text{FORS}) + 1)^2)$, which can also be written as $x_t = x_{t-1} + x_{t-1} (t - 0.15t^2)$,

where x_t is the length of the internode at time t and t is the plastochrone number $(0 \leq t \leq 6)$. This formula provides an S-shaped growth curve for the internodes, the derivation of which shall be given later. The new plastochrone number of the internode unit becomes $\text{int}(\text{FORS}) + 1$ and not   (FORS + 2K) as in the preceding rule. This is in order to make it impossible to let the increase of the plastochrone number amount to more than one integer unit, for this would mean that the growth formula for an internode possibly would not be applied at every integer unit, lea-ding to false results.

TYPE 6

4. If F is greater than or equal to 6 then

$< 6, F, L, B > \rightarrow < 6, F, L, B >,$

Similar to Rule 1.

5. If F is smaller than 6 and int(F) is equal to int(F + 2K) then

$< 6, F, L, B > \rightarrow < 6, F + 2K, L, B >.$

Similar to Rule 2.

6. If F is smaller than 6 and int(F) is smaller than int(F + 2K) then

$< 6, F, L, B > \rightarrow < 6, \text{int}(F) + 1, L + L \times (\text{int}(F) + 1 - 0.15 \ (\text{int}(F) + 1)^2), B >.$

Similar to Rule 3.

Rules,_which_apply_only_under_vegetative_conditions

TYPE 1

7. If int(F) is equal to int(F + K) then

< 1, F, L, B > → < 1, F + K, L, B >.

This rule states that an apical unit does not give rise to new organs, but just

increases the value of its plastochrone variable by the value of K (the degree of

inhibition), whenever the value of the lower entire of its variable FORS is equal

to the value of the lower entire of FORS plus K.

8. If int(F) is smaller than int(F + K) then

< 1, F, L, B >→< 3,-1, L(L1)x 0.9, B > (: < 6,-2, L(L1), A > :) < 1, F + K, L, B >.

We state here that an apical unit gives rise to a lateral bud and to an internode,

whenever the value of the lower entire of its variable F is smaller than the value

of the lower enire of F + K. The unit standing for the lateral bud is placed be-

tween parentheses and colons as follows: (: < 6, F, L, B > :). The apex in-

creases the value of its plastochrone number (FORS) by K (the degree of inhibition),

as in Rule 7. The newly formed lateral bud gets a FORS value of -2. The value for

the length (LONG) of the newly formed lateral bud is equal to the length of the

first internode on the left. The lateral bud, therefore, will have the length of

the internode, which is going to bear the new branch (Rule 9). The value for the

variable BULK of the newly formed lateral bud is equal to the value of A, which is

the length of the mother branch of the lateral bud. The behaviour of the variables

BULK and A will be explained later. The newly formed internode gets a FORS value

of -1. This negative value for the plastochrone number ensures that it will take at

least two iterations before the newly formed internode will grow (see the formula

given in Rule 3). In the meantime it is very easy to determine the initial length

of the next internode which will be formed on the same branch, because the initial

length of the previously formed internode on the branch is still available. The

LONG value of the newly formed internode is equal to the length of the first inter-

node on the left, multiplied by 0.9. This ensures that the length of the newly

formed internode will be somewhat smaller than the length of the previously formed

internode on that branch.

TYPE 6

9. If F is equal to -2 then

$< 6, F, L, B > \rightarrow <6, -1, \underset{A}{\underline{LxB}}, B > < 1, 0, 0, B >.$

This rule states that a lateral bud unit (with FORS equal to -2) develops into a first internode on a branch and into an apex. The FORS value of the newly formed first internode on this branch is equal to -1 (see Rule 8). The value for the length (LONG) of the newly formed first internode is equal to LONG x BULK, divided by A (the length of the mother branch from base to branching point). Since the variable BULK is equal to the length of the mother branch of the time when the lateral bud is formed (see Rule 8), BULK divided by A implies that the initial length for the newly formed internode depends on the increase in the degree of inhibition (an explanation of this will be given later) which has taken place since the formation of the lateral bud. The FORS and LONG values of the newly formed apex are set equal to zero.

Rules_which_apply_only_under_flowering_conditions

TYPE 1

10. If $L + \dfrac{F \times K}{10}$ is greater than or equal to 4, then

$< 1, F, L, B > \rightarrow <1, F, L + \dfrac{F \times K}{10}, B >.$

An apical unit is considered to be a flower whenever its LONG value is greater than or equal to
/4. The value for the plastochrone number of a flower does not increase anymore. The LONG value of this unit now indicates its flowering state. According to the rule, LONG increases by FORS x K divided by 10. The derivation of this formula shall be given later. Under floral induction, the apices also loose gradually their ability to give rise to internodes and to lateral buds, as a consequence of this rule.

11. If $L + \dfrac{F \times K}{10}$ is smaller than 4 and int(F) is equal to int(F + K) then

$< 1, F, L, B > \rightarrow < 1, F + K, L + \dfrac{F \times K}{10}, B >.$

As Rule 7, this rule also states that an apical unit does not give rise to new organs whenever the value of F x K divided by 10 is smaller than 4 and the value of the lower entire of the variable F is equal to the value of the lower entire of F + K. The FORS value of the apex is increased by K (see Rule 7).

12. If $L + \dfrac{F \times K}{10}$ is smaller than 4 and int(F) is smaller than int(F + K) then

$< 1,\ F,\ L,\ B > \rightarrow < \$,-1,\ L(L1) \times 0.9,\ B > (:\ < 6,-2,\ L(L1),\ A > :)\ < 1, F+K, L+\dfrac{F \times K}{10}, B >.$

Here we state that an apical unit gives rise to a lateral bud and to a new internode (see Rule 8), whenever the condition of the rule holds. The value for all variables of the apex, the newly formed lateral bud and the internode are equal to the values given for these variables in Rules 8 and 11.

TYPE 6

13. If F is equal to -2 then

$< 6,\ F,\ L,\ B > \rightarrow < 6,\ F,\ L,\ B >.$

This states that a lateral bud unit does not develop any further if the plant is under flowering condition. This rule prevents the formation of new branches (Rule 9) when the plant has come under flowering conditions. This restriction is not necessary for the construction of the model. It ensures that the model plant does not become too extensive, which is convenient from the viewpoint of computer processing.

Extra information

Variable A is the sum of the lengths of the internodes of a certain branch and variable K is the degree of inhibition of that branch. We have built a common block of information into the CELIA main program and into the DELTA subroutine. This common block makes it possible to assign to each unit $< T, F, L, B >$ a value for A and a value for K. The computation of A and K at every computing step proceeds from left to right along the filament.

14. If a unit is encountered which is of TYPE 6 and its F value is equal to -2, then the variables A and K assigned to it have the same value which they have in the pre-

vious unit lying on the mother branch. In other words, the values for A and K are not affected by the encounter of a lateral bud as the computation proceeds along the filament.

15. If a unit is encountered with TYPE 6 and an F value which is not equal to -2, then an A value is assigned to this unit equal to the length (LONG) of the first internode on this branch. Further, we assign a value for K equal to the K value of the mother branch times twice the value of BULK, divided by the length of the mother branch from its base to the branching point. (The values for K are always greater than or equal to zero. A value for K of zero stands for complete inhibition, values for K greater than 1 stand for negative inhibition. The main axis always has a K value of 1). In other words, A takes as its value the value of the length of the first internode of that branch, and K determines the degree of inhibition for the branch according to the given formula. The derivation of this formula shall be given later.

16. If a unit is encountered of TYPE 3 or of TYPE 1, then the value of the variable K stays the same as in the previous unit, and the value for the variable A is increased by the length of this unit. In other words, the degree of inhibition (K) for the branch is not affected while the sum of the lengths of the internodes of the branch (A) is increased by the value of the length of the internode we are looking at. When the end of a branch is reached (when a unit of TYPE 1 has been processed), the degree of inhibition (K) and the length of the branch (A) are not carried on any further.

The drawing program

A computer program was also written in order to draw diagrams based on the CELIA output. We used this program to make diagrams of the actual plant as well, where we indicated the lengths of all internodes and the floral states of the apices. The computer program drew the first side branch of a certain branch always at the left hand side and all following side branches alternately to the right and to the left. We had an option in the program for the angles of the branches. In the pictures we

allowed the first order branches to make angles of 70 degrees with the main axis, the second order branches to make angles of 30 degrees with the first order branches, and the third and higher order branches to make angles of 20 degrees with their mother branches. The value of the variable LONG of the apices in the model determined the size of the flower (⊙). If the value of the variable LONG was greater than 10, we considered the flower to have formed fruits (❀). The numbers next to the flowers were handdrawn and give the time order of development of the flowers (according to the value of the variable LONG).

The computations and drawings were carried out by a CDC 6400 (CYBER 73) computer at the University of Utrecht.

Results

Starting with an initial filament of two units < 6, -1, 0.9, 0.5 > < 1, 1.0, 0, 0 > we expanded the filament for 45 iterations. We let the table-switch from vegetative to floral condition occur at iteration 35. The computer drawing program supplied us with the drawings of the filaments at iterations 5, 15, 25, 35, 40 and 45. The drawings are collected in Figs. 4, 5, 6, and 7. The drawings of the filament at iteration 40 and 45 (Figs. 6 and 7) may be compared with the drawings of the actual plant (Figs. 1, 2 and 3). Comparison with Fig. 1 shows that the computer output does not have the same general appearance as the actual plant. This was mainly due to the absence in the computer model of the long stretch of branchless internodes at the base of the main axis. As we pointed out before, the main axis of the real plant has at its base a part which is quite different in appearance from any higher order branch. When we were building our model we discovered that we could only include this characteristics of the main axis if we adopted a special set of rules for the first part of the development of the plant. This seemed to us unnecessary for our model, so we confined ourselves to building a model of the actual plant without the basal part of the main axis. Our output, therefore, can only be compared with Figs. 2 and 3. Figure 6 is a drawing of the model plant at about the same stage of development as the actual plant in Fig. 2. The two figures can be matched to a
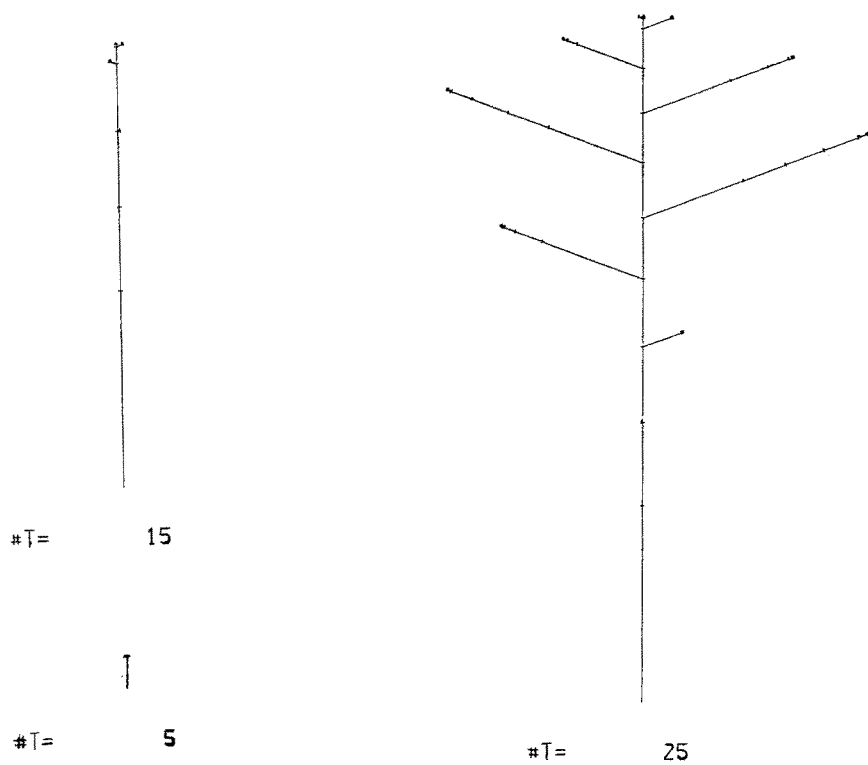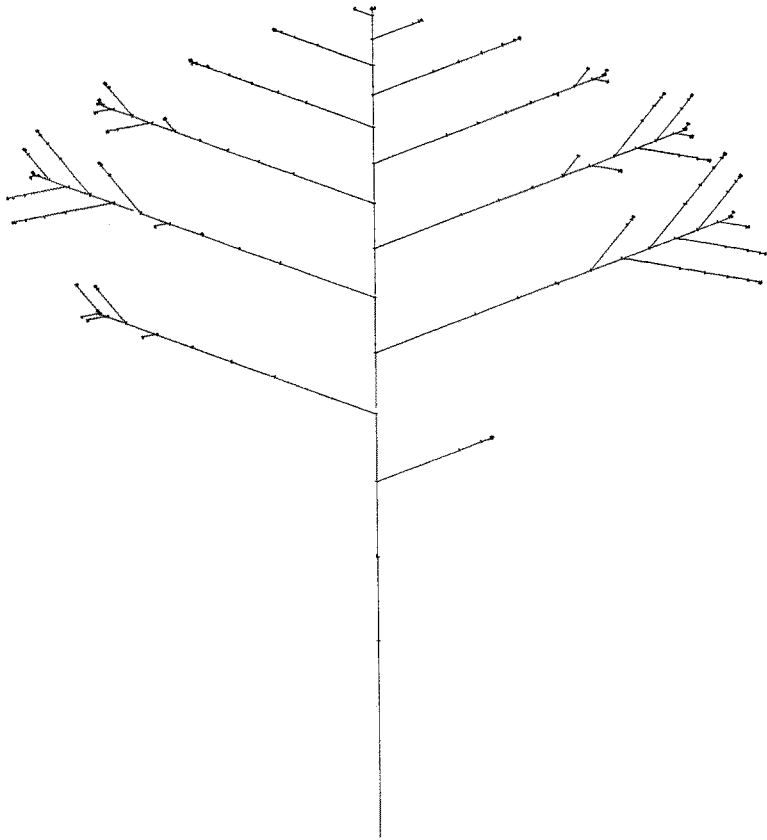
#T= 15

#T= 5

#T= 25

Fig. 4. Diagrams of the early stages of the model plant at iterations 5, 15 and 25.

#T= 35

Fig. 5. Diagram of the model plant at the moment of the table-switch from vege-
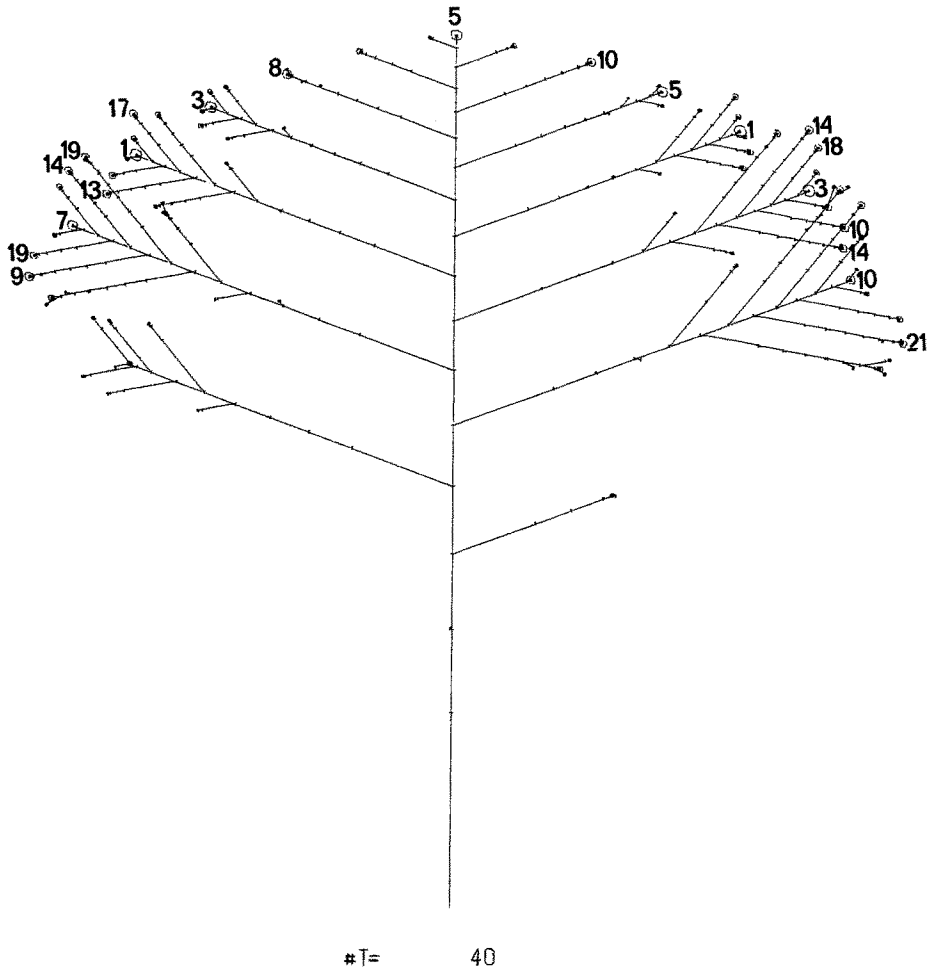tative to flowering condition at iteration 35.

Fig. 6. Diagram of the model plant at iteration 40. (This Figure may be compared with Fig. 2)

considerable extent.The model plant is somewhat smaller than the real plant, but keeping it smaller was more practical for the computer simulation. If we had postponed the table-switch by another 10 iterations, the model plant would have been just as extensive as the actual plant (as we have tested it in some additional simulations). The strictly regular appearance of our model plant is not entirely realistic, namely with respect to the lengths of the internodes, where the higher positioned internodes were always smaller than their preceding ones, and with respect to the lengths of the branches which increased after a certain point to a maximum and decreased very regularly afterwards. These aspects of the model plant are the results of exclusively deterministic values for the constants in the rules; with stochastic values we could introduce more variation into the model. Figs. 4 and 5 could not be compared with the figures of the actual plant, because we did not observe its comparative stages. The figures show how the computer model developed from the initial filament to the stage where it can be compared. Fig. 7 on the other hand, was produced in order to show the progress in the development of the model plant and should be compared with Fig. 3 (except that Fig. 3 is only accurate for floral stages and not for internode lengths at that date of observation).

Discussion: The computer model vs. the actual plant

The rules and notions in our model had to satisfy the following demands: they had to be able to produce the desired pattern, they had to be physiologically reasonable they had to produce stable, but adaptable patterns, which were flexible enough to account for variations in the plants of Aster novae-angliae (and even in related species).

The first attribute in our model, TYPE, is assumed to represent the more or less permanently differentiated character of the units which constitute the plant. Clearly, meristematic apices, internodes and flowers (or inflorescences) are both morphologically and developmentally distinct plant organs. We have distinguished between the apices which are born at the tips of branches, and those which are in a lateral position. This distinction was necessary in order to be able to control the further
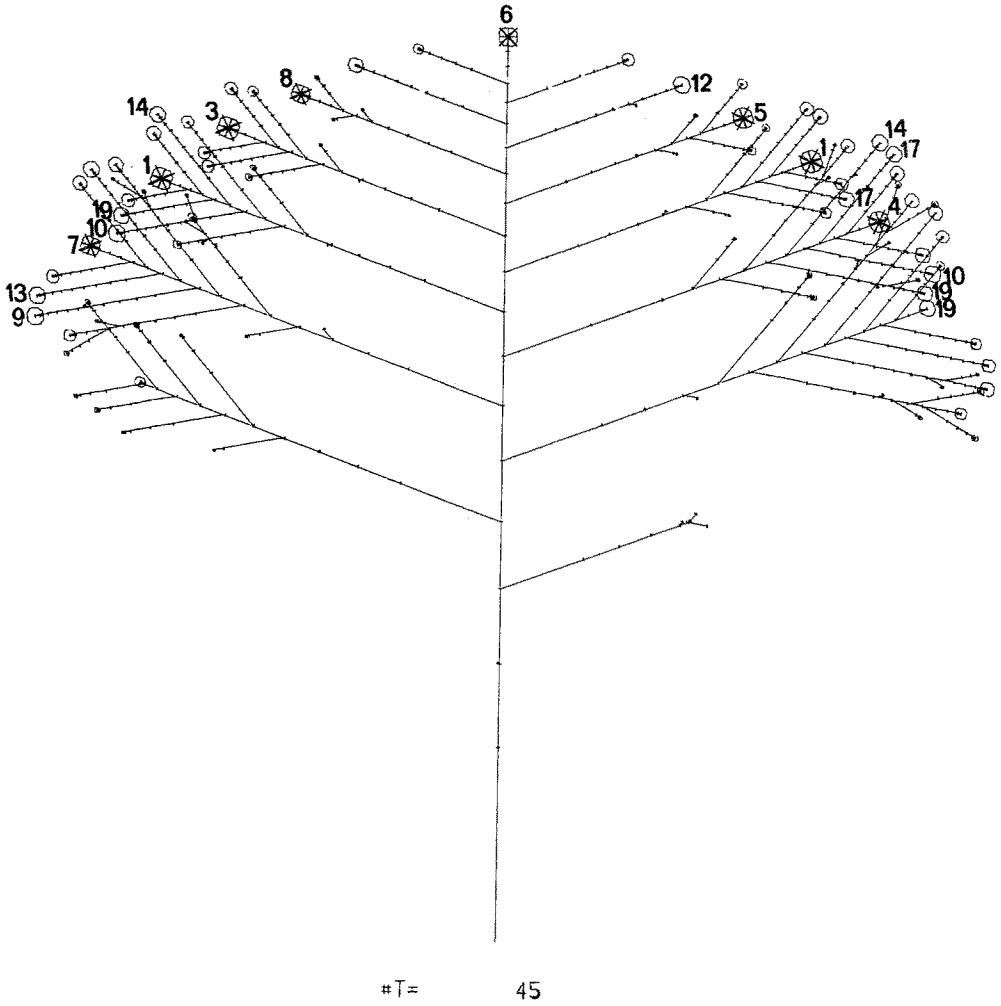
#T=   45

Fig. 7. Diagram of the model plant at iteration 45. (This Figure may be compared with Fig. 3).

growth of the branch which originates from a lateral bud, by assigning it a certain

BULK value. We also distinguished between first internodes of branches and later

internodes, for the reason that the degree of inhibition for a branch (K) can be

determined for the whole branch by using a special formula for the first internode

of the branch. This procedure was adopted here for our convenience, another model

could easily be constructed without distinction between first and lateral internodes.

Formally, we used only three symbols for designating the TYPE of a unit, namely 1,

3, and 6. The symbol 1 was used to designate apices in terminal positions as well as

flowers (no confusion arises from having the same symbols used in these two sense).

The symbol 3 was used for internodes, other than first internodes of a branch. The

symbol 6 was used to designate lateral buds or first internodes of branches.

The following state transition diagram shows the possible transitions among the dif-

ferentiated states of organs.
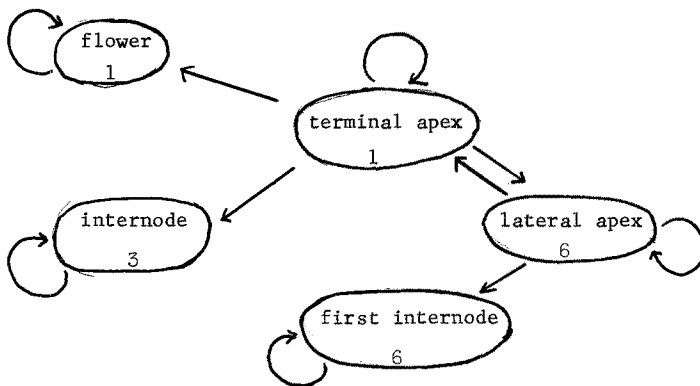
Often other differentiated units may also be recognized. Nozeran, Bancilhon and

Neville (5) for example show that at the beginning of the development of the main

axis of Phyllanthus amarus another kind of differentiation may take place. The

organs formed during this differentiation, when isolated, kept different potentia-

lities. We remarked already, that the basal part of Aster novae-angliae behaved dif-

ferently from the rest of the plant. This could in our model only be reflected if we would have applied a separate set of rules for the formation of this part of the plant. Apart from the basal part, the main axis was in one more aspect different from the rest of the plant (which is often observed in higher plants) : Its apex sometimes did not form a flower (Figs. 2 and 3). According to our set of rules it would always form a flower, although not necessarily the most vigo rous one (Figs. 5 and 6).

The question arises whether this plant could be simulated by a developmental system in which no interactions take place among the constituent parts (as in a < 0,0 > L-system). But then for every lateral bud and its resulting branch there would have to be a different sequence of states, because for every branch the slowing down of its growth seemed to be different and dependent on its position in the plant. There-fore, only interacting systems seemed to be suitable for the simulation of Aster. In addition, we decided to use a table-switch, because we have seen plants of many dif-ferent sizes in flowering condition which indicates that the production of the flo-wering stimulus is not internally regulated. Furthermore, a table-switch is physio-logically well defendable because of the well-known "short-day" induction mechanism.

We first thought of using a table < 1,1 > L-system. This is an interacting system with tables in which the next state of a unit is determined by its own state, by the state of its first neighbour on the left, and by the state of its first neighbour on the right. This kind of developmental control could be natural from a physiological point of view, namely involving both apical dominance and basal information about the extent of growth. But we decided to try first the simpler system with basal information only. It proved possible to build a model exclusively using basal infor-mation, represented by our table < 1,0 > L-system. Further work might prove inter-esting on the construction of a model with both basal and apical information.

Development with interaction can be modelled not only by < 1,1 > L-systems but also by < k,ℓ > L-sysjems, where each cell is influenced by k left and ℓ right neighbours. Since < k,ℓ > L-systems can be programmed in CELIA (22), they could provide an

opportunity to speed up the flow of information through a filament. The advantages, however, are limited. The rules become much more complicated. We found it easier to introduce common blocks of information in the CELIA program and in the DELTA sub-routine rather than to make use of information arriving faster from more distant neighbours.

The slowing down of growth (or inhibition) of branches as function of their position, had to be provided by interaction rules. It was not easy to formulate these rules. We cannot claim that the rules we adopted are the rules which the plant uses. The interaction rules must be of the following kind: First, inhibition must become stronger the further the branching points are left behind the apical meristem which split them off; this relationship is, however, not linear with distance, but is dependent on the size of the whole branch. Secondly, the existing inhibition in a certain branch has to govern the inhibition of its side branches. And thirdly, the side branches near the top of a long branch have to be negatively inhibited, in other words, they had to grow faster than their mother branch, with a factor up to twice.

The first property could only be built into our rules by a rather complicated pro-cess. This process involves in the first internode an imprinting (Rules 8 and 12) of the length of its mother branch at the time that the lateral bud is formed (this is stored in the value of the variable BULK). In addition, the rules specify (Rule 15) that the first internode of a branch must keep a measure at all times of the length of its mother branch (from its base to the branching point). And finally, the rules state (Rule 15) that the first internode of a branch must compute the degree of its inhibition from the two previous pieces of information, by dividing the imprinted original length by the new length of the mother branch. This process may be hard to envisage, but it produces the required property and all other methods that we could think of involve far more complicated rules. We got the idea of having an imprinted original length of the mother branch from Sell (15, 16). He demonstrated that buds after isolation showed a different rate of development, depending on their

previous position on their mother branch. This implied the imprint of some kind of message.

The second property, that the inhibition of a side branch is controlled by the inhibition of the mother branch, could very easily be built into our rules. This was done by multiplying the inhibition of a particular branch by the inhibition of its mother branch (Rule 15).

The third property, of negative inhibition, could also be easily built into the rules, namely by multiplying the inhibition of any side branch by the factor of two (Rule 15).

Because the growth of the internodes exert an effect on the inhibition of their branches it appears to be important to have a realistic time course for internode growth. From data in the literature (16) we found that full growth of internodes in Coleus takes about 5-7 plastochrone units. Aster novae-angliae may not be much different. More exact data on internode growth, however, were unobtainable. Therefore we compared the 5-7 plastochrone time-units of Coleus with the data of root growth of Zea mays (24). This comparison gives us an indication of the order of length increase which takes place in internodes per time-unit. We obtained a formula which in the case of Zea mays root would push a newly formed internode in 6 plastochrone time-units out of the growth zone : $x_t = x_{t-1} + x_{t-1} (t - 0.15 t^2)$, where x_t the length of the internode at time t and t is expressed in plastochrone time-units ($0 \leq t \leq 6$). We are fully aware that this formula is rather arbitrary for the internode growth of shoots of Aster, but it proved to be adequate (Rules 3 and 6).

Apart from considering the growth rates of internodes we must also deal with different final sizes of internodes throughout the plant. It appeared that the rules must satisfy the following requirements:
First, a certain apex, which gives rise to internodes, must gradually give rise to smaller internodes. Secondly, internodes on a strongly inhibited branch must be smaller than the internodes on the mother branch above the branching point, while

not heavily inhibited branches must have internodes of the same size as the mother branch.

The first requirement could be satisfied by letting a newly formed internode be 0.9 times the length of the preceding internode on that branch (Rule 8). The second requirement is satisfied by letting the size of the first internode and consequently all following internodes on a new branch depend upon the inhibition exerted at the time of formation (Rule 9). These rules were simple enough and possibly physiologically defendable.

The last phenomenon, which has to be regulated by the rules, is the process of flowering. The rules for this process must satisfy the following requirements. First, the apices must develop in a particular time sequence dependent on their position in the plant. Secondly, after some time the process has to proceed faster in the higher positioned apices than in the lower positioned ones. Thirdly, the plant must continue to grow after floral induction.

It proved to be possible to satisfy all three requirements based on a principle we call "vigour" (Rules 10, 11, 12). We define "vigour" of a certain apex as the number of plastochrone-units that apex has gone through, multiplied by its inhibition. In the real plant there is an observable connection between branch growth and flower development. Therefore, the parameter "vigour" connects these two in the model. Thanks to repeated observations of a plant of Aster novae-angliae (Figs. 2 and 3, and explanatory text) it was possible to estimate the developmental speed of the flowers against the continuing vegetative growth of the plant. This resulted in the formula for the attribute LONG (as in Rule 10).

As growth continues, "vigour" changes, and it changes in such a way that higher positioned apices in the plant benefit more from it than lower positioned ones. The principle of "vigour", therefore, works so well in our model, that it would not be surprising if the real plants control the development of their flowers in this way. Side branches near to the top of a large branch often bear more developed flowers than the mother branch. This is possible in our model, because the increase in

"vigour" is related to the rate of growth of the branch, and branches near to the apex of a large branch can be negatively inhibited up to a factor of two. This means that the "vigour" of those branches can become larger than the "vigour" of their mother branch and consequently that the developmental rate of their flowers is higher than the developmental rate of the flower of the mother branch.

Finally we should require that the model be stable and flexible. In the course of our computer work we tried a variety of values for the constants in the formulas. These provided us with some insight in the stability of the model. Future work with stochastic variables might yield more stable models. The flexibility of tne model could be tested by investigating the rules for their creative power, i.e., their power to simulate patterns of growth and flowering in related species.

References

1 Lindenmayer, A., 1968, Mathematical models for cellular interactions in develop-ment, Part I, Filaments with one-sided inputs, J. Theor. Biol., 18: 280-299.

2 Lindenmayer, A., 1968, Mathematical models for cellular interactions in develop-ment, Part II, Simple and branching filaments with two-sided inputs. J. Theor. Biol., 18: 300-315.

3 Lindenmayer, A., 1971, Developmental systems without cellular interactions, their language and grammars, J. Theor. Biol., 30: 455-484.

4 Champagnat, P., 1973, Introduction a l'étude des correlations complexes, manus-cript.

5 Nozeran, R., Bancilhon, L., Neville, P., 1971, Intervention of internal correla-tions in the morphogenesis of higher plants, Advances in Morphogenesis, 9: 1-66.

6 Troll, W., 1964/1969, Die Infloreszenzen. Typologie und Stellung im Aufbau des Vegetationskörpers. Bd I (1964). Bd II (1969), Gustav Fischer Verlag, Jena.

7 Weberling, F., 1965, Typology of inflorescences, J. Linn. Soc. (Bot.), 59: 215-221.

8 Maresquelle, H.J., 1961, Sur la filiation des inflorescences. Bull. Soc. Bot. Fr., 108: 117-119.

9 Maresquelle, H.J., 1965, Sur la filiation des inflorescences, 2e apport, Ann. Sc. Nat. Bot., 437-446.

10 Maresquelle, H.J., 1964, Sur la filiation des inflorescences, 3e apport, Fleurs de renfort et inflorescences de renfort, Mem. Soc. Bot. Fr., 1964, 96-100.

11 Maresquelle, H.J., 1964, Sur la filiation des inflorescences, 4e apport, La notion de racémisation en morphologie végétale, Mem. Soc. Bot. Fr., 1964, 96-100.

12 Stauffer, H.U., 1963, Gestaltwandel bei Blütenständen von Dicotycedonen, Bot. Jahrbucher, 82: 216-251.

13 Sell, Y., 1969, Les complexes inflorescentiels de quelques Acanthacées. Etude particulière des phénomènes de condensation, de racémisation, d'homogénéisation et de troncature, Ann. Sci. Nat. Bot., 10: 225-300.

14 Maresquelle, H.J., Sell, Y., 1965, Les problèmes physiologiques de la floraison descendante, Bull. Soc. Fr. Physiol. Végét., 11: 94-98.

15 Sell, Y., 1970, Etude préliminaire des rapports entre la floraison descendante et le dévelopement végétatif, Bull. Soc. Bot. Fr., 117: 25-36.

16 Sell, Y., 1970, Rapports entre morphogénèse végétative et morphogénèse florale chez Ruellia lorentziana Griseb. et Justicia simplex D. Don (Acanthacées), Bull. Soc. Bot. Fr., 117: 270-284.

17 Jauffret, F., 1970, Etude de corrélations en régime de floraison descendante, Bull. Soc. Bot. Fr., 117: 21-24.

18 Baker, R., Herman, G.I., 1970, CELIA - a cellular linear iterative array simulator, Proceedings of the Fourth Conference on Applications of Simulations, pp. 64-73.

19 Baker, R., Herman, G.T., 1972, Simulation of organisms using a developmental model, Part I. Basic description, Internat. J. Bio-Med. Computing, 3: 201-215.

20 Baker, R., Herman, G.T., 1972, Simulation of organisms using a developmental model, Part II. The heterocyst formation problem in blue-green algae, Internat. J. Bio-Med. Computing, 3: 251-267.

21 Liu, W.H., 1972, CELIA user's manual, Department of Computer Science, State University of New York at Buffalo.

22 Herman, G.T., Liu, W.H., 1973, The daughter of CELIA, the French flag and the firing squad, Simulation, $\underline{21}$: 33-41.

23 Cohen, D., 1967, Computer simulation of biological pattern generation processes, Nature, $\underline{216}$: 246-248.

24 Erickson, R.O., Sax, K.B., 1956, Elemental growth rate of the primary root of Zea mays, Proc. Amer. Philos. Soc., $\underline{100}$: 487-498.