Computer Simulation of Branching Pattern in *Magnolia denudata* Desr.

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백목련의 分枝型에 관한 Computer Simulation

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ABSTRACT

The observation of branching pattern on *Magnolia denudata* Desr. was performed from July 1982 to September 1983 and then computer simulation was carried out.

Tree crown pattern depends on not only genetic factors but also environmental factors and the determination of branching pattern which characterized it appears to properly explain the relationships such as branching pattern and allocation of materials through the analysis of influence between branches under several assumptions.

Now that computer simulated pattern was considered as the accumulation of two factors which controled the growth, it was represented as the stimulated tree which differs in branching rate that described allocation of material necessary for the growth of each branch. There was a tendency of allocation ratio of nutrients, i.e. subbranch to main branch to decrease by the passage of year. Under assumption that branch was branched when accumulated material reached 1, it was possible to represent the allocation of nutrients as residual nutrient $\times \dfrac{1}{1+F}$ in main branch, residual nutrient $\times \dfrac{F}{1+F}$ in subbranch, $A(iA,iC)+F^{(iA-1)}$ in current twig.

Like this, the basic minute difference of the allocation of nutrients according to the branch resulted in complicated patterns in the tree crown.

INTRODUCTION

The growth of plant depends on environmental and genetic factors in a very complicated way. Hallé and Tomlinson(1978) suggested a "tree" that a system in which any two points are connected via only one possible path way(i.e., the system, is not a reticulum and lacks loops). In this very general sense one may find trees in many discipline-in heraldry as a genealogical chart(a family tree), in geomorphology as the tributaries of a stream sys-tem, in cybernetics as a decision-making process, each providing as example of simulated mathematical tree. The mathematical concept of tree may have useful analytical and predictive purposes and is helpful in constructing computer programs by which real botanical trees may be mimicked(Cohen. 1967; Legay, 1971; McMahon and Kronauer, 1976; Fisher and Honda, 1977, 1979a, b; Fisher and Hibbs, 1982). Paltridge(1973) considered a tree to be an assembly of leaves attached to the ground by the number of limbs whose function is to provide support for the leaves and to provide access to the

moisture in soil. Oohata and Shinozaki(1979) considered a tree the assemblage of unit pipe systems as composed simply of a set of a unit amount of leaves and pipe of unit thickness of nonphotosynthetic tissue. And Honda *et al.*(1982), suggested that a botanical tree can be regarded conceptually as a system of axes which develops by a process of repeated branching or bifurcation. A complicated tree can be described by a few parameters of bifurcation which determine the geometry of the bifurcation process. According to Fisher and Honda(1979a, b) and Honda *et al.*(1981), in botanical trees the frequency of branching is never the same at every terminal branch. Thus the number of terminal branches does not increase by a regular exponent, since the rate of increment normally decreases. This decrease can be attributed to two theoretical constraints on growth; the one is an environmental or exogenous factor, resulting in interbranch competition or interaction. The use of inhibition can be justified as a result of shading effects together with phisical damage where leaves and particularly buds make mechanical contact. The other is an intrinsic or endogenous factor.

In this study, we investigated both exogenous and endogenous constraints by using a tree model programmed by authers for computer simulation. Examples of computer simulated patterns are illustrated by different allocation of material are compared with branch tiers in *Magnolia denudata* Desr.

MATERIALS AND METHODS

The observation on *Magnolia denudata* trees at Ewha womans Univ. campus were performed from July 1982 to September 1983. Branching angle of small trees and lower branches of large trees were measured directly by protractor and goniometer and the number of terminal branches were counted for discrete time N.

The computer programming and simulation were done by the FORTRAN language and MV 8000 computer. Total number of terminated branches after N discrete step of time is calculated. First, the branches grown with the critical value of nutrient allocation($F=1$) is calculated for N, and the status of bifurcated branches from the terminal with $F=1$ is stored in $A(1,i)$. Second, the terminated branches with the nutrient F is calculated for N discrete years, the bifurcated branches will grow with of $F \times F$. For the calculated of this branches, the growing status is stored in $A(2,i)$ which is originated from the branches with F. In the calculation of branches with the rate of $F \times F \times F$, the status variable $A(3,i)$ will be used, $A(K,i)$ corresponds with the rate of F^k originated from $F^{(k-1)}$ branches. The total number of term inated branches NC is counted by the collection of $A(i,j)$ which has a value of less than one.

RESULTS AND DISCUSSION

Branch interactions

As showed in Fig. 1, a mother branch of *Magnolia denudata* produces two daughter ones by branching process. The respective bifurcation period was defined discrete time(N). Branch tier of young tree was presented in Fig. 2. A. Thick line of the figure shows the main branch and thin line of that shows the subbranch. Small figure in the right side is an schematic diagram of mean angles. The branching angles formed by the new units(M and S, respectively) are usually unequal, and represented divergence angles are 34 between main branch and mother branch and 39 between subbranch and mother at average. The simulated tree in Fig. 2. B is a schematic diagram of Fig. 2. A., which angle, that is 73, represents between main branch and subbranch. Fig. 2. A and Fig. 2. B suggest that some bifurcations may be limited due to an interaction between the branches. At each bifurcation two kinds of branches are produced, a more vigorous one (Unit M) and a less or equally vigorous one (Unit S). When a particular terminal point of a branch unit is close to end points of other branches, its

Fig. 1. Branching pattern in the tree crown of *Magnolia denudata*

growth and bifurcation may be interfered with.

Different flow rate

In an actual tree every terminal branch does not bifurcate, because the frequency of bifurcation is different at each terminal branch unit. The mechanism that determines these frequency, presumably, is determined by the morphogenetic status of the meristem and its position in the complex. In our model. the difference of bifurcation frequency is attributed to a difference of nutrient allocation of some hypothetical material. The material could be an unidentified substance a determiner for the growth and branching of units. The amount of the material transported through a less vigorous branch unit S in a certain time is represented f, the relative allocation ratio. This is some fraction of the amount (set at 1.0) transported through the branch unit M, the more vigorous partner of the unit S. Usually f is less than 1.0 because branch unit M is generally more vigorous than a unit S. Initially, f is assumed
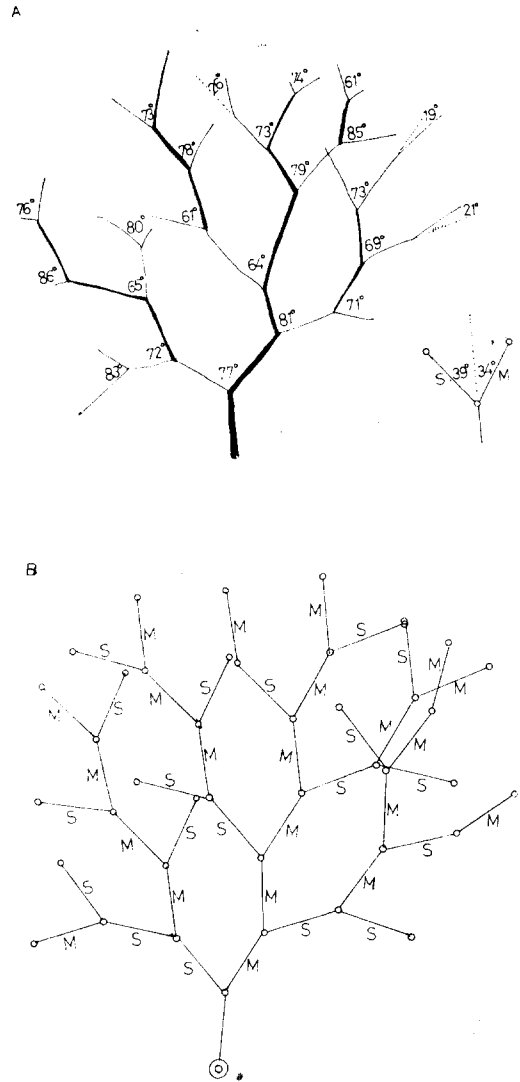

Fig. 2. Actual and model terminal branches. Fork angle and sympodial unit sequence indicated. A; actual branch with various fork angles. B; Model of upperside of same branch (A) using unequal fork angles as indicated in diagrams.

to be constant throughout the branch complex; its variation with the complex will be considered later in the present report. The material accumualtes at the end point of f terminal branch. The critical amount 1.0 of the material is assumed to be nece-
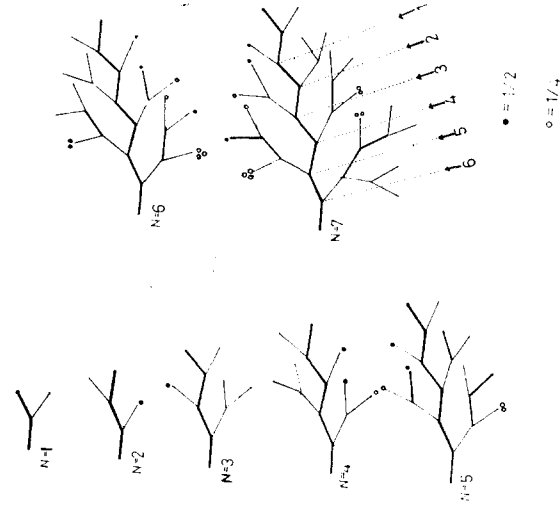
Fig. 3. Diagrams of the branching model with different allocation ratios In example, $f=1/2$. During the discrete time $N=1$, the amount 1.0 and 1/2 of material required for branching accumulates at the end points of terminal branch unit M(thick line) and S(thin line), respectively.
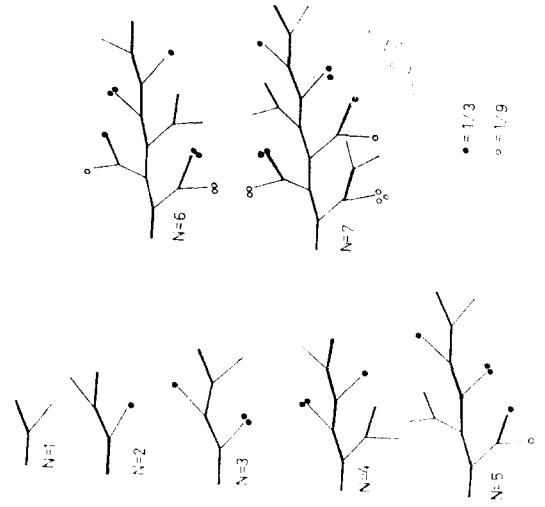

Fig. 4. Diagrams of the branching model with different allocation ratios In example, $f=1/3$. During the discrete time $N=1$, the amount 1.0 and 1/3 of material required for branching accumulates at the end points of terminal branch unit M(thick line) and S(thin line), respectively.(Honda, *et al.*, 1981).

ssary to permit subsequent bifurcation.

An example when $f=1/2$ is shown in Fig. 3. There is a pair of branch units at $N=1$. The material accumulates at both end points until $N=2$. At $N=2$, unit M has accumulated the amount 1.0 and bifurcates, whereas unit S has only the amount 1/2 and remains as a single unit. Unit S does not bifurcate during two discrete steps or units of time. At $N=3$, unit S has accumulated the amount 1.0 (1/2+1/2) and bifurcates.

Fig. 4, is an example of $f=1/3$, At $N=2$, unit M has accumulated the amount 1.0 and bifurcate, whereas unit S has only the amount 1/3 and remains as a single unit. Unit S does not bifurcate during three discrete steps or units of time.

Fig. 5. is an example of $f=2/3$. At $N=2$, unit S has the amount 2/3 and remains as a single unit. At $N=3$, unit S has accumulated the amount 4/3 (2/3+2/3) and bifurcates 3/3 and reserves 1/3. Reserved 1/3 of the amount is allocated in the ratio, 1/1+2/3 to 2/3/1+2/3. In this manner we can devide the reserves at every terminal buds.

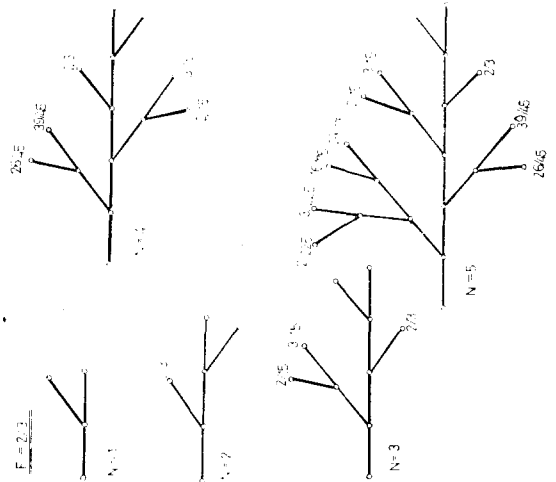**Fig. 5.** Diagrams of the branching model with different allocating ratios when $f=2/3$.
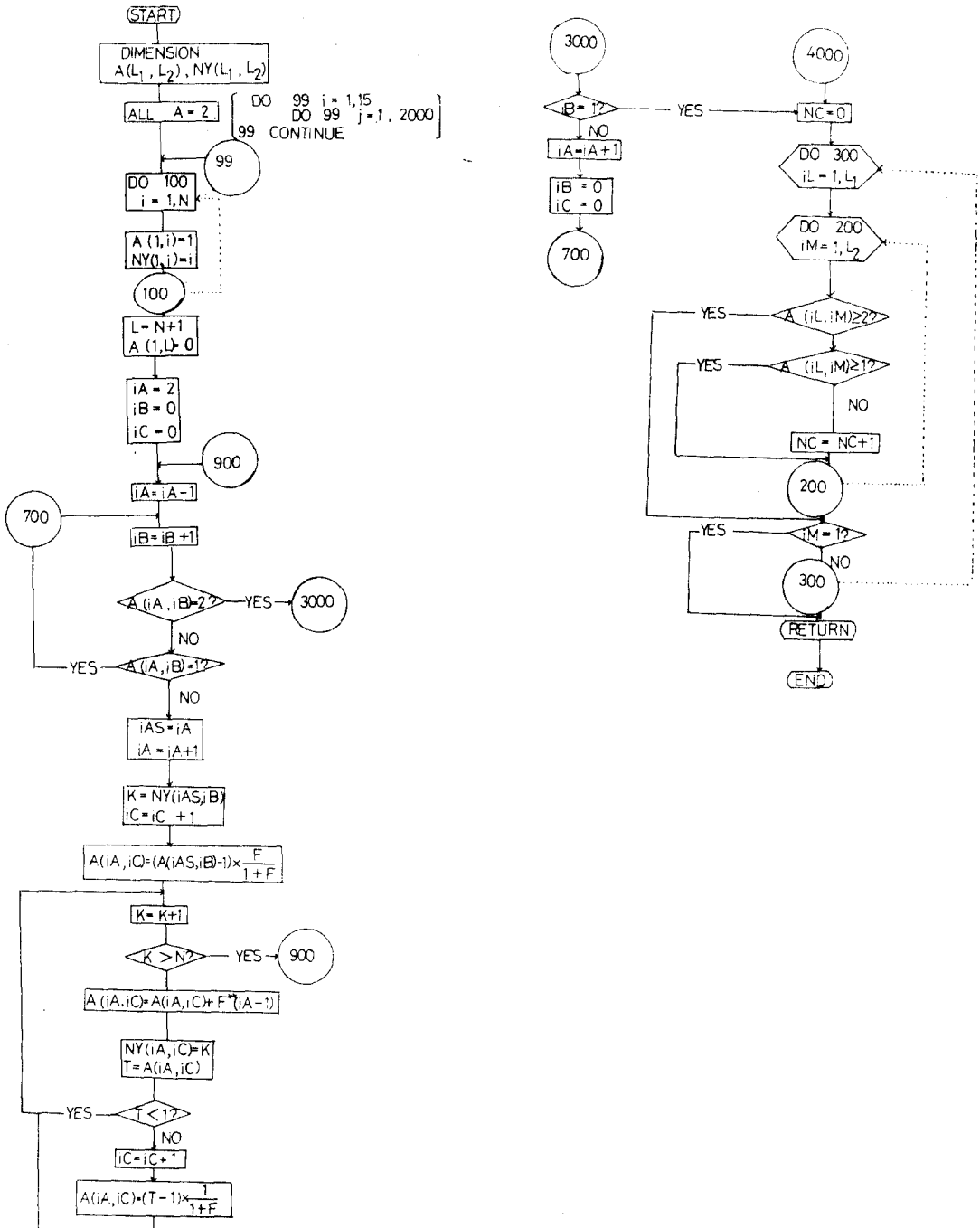
SUBROUTINE TREE(N, F, NC)

Fig. 6. Flow chart of the model.

Programming for computer simulation

The flow rate of some substances from main branch to subbranch is denoted by Fig. 3, 4, 5. The growing energy A will be distributed to main branch by $(1/1+F) \times A$ and to its subbranch by $(F/1+F)A$. N denoted the discrete time and F is the allocating ratio of a subbranch to its main branch. It is assumed that stored energy to each branch is represented by $A(i, j)$. Terminated branch which is under growing have the A's value such that $0 \leq A < 1$. When the value of A exceeds 1, this branch will bifurcate a subbranch. The computer program with FORTRAN language is attached to Appendix A. The allocating ratio $F/1$, 0.998, 0.98, 0.9, 0.75, 0. 667, 0.5, 0.4, 0.333, 0.25 and 0 is selected. The total number of terminated branches NC are calculated and printed for the discrete time $N=1 \sim N= 12$.

Subroutine tree(N, F, NC) is programmed to count all the terminated branches of a tree which represented in Fig. 6. N and F are inputs and NC is an output. The output NC represents all the terminated branches after N discrete steps of time. Initial starting value of $A(i, j)$ is given by 2; $A(i, j) = 2$. But this is only initiated state where no growing energy is stored and we know $A(i, j)$ never reach or exceed the value of 2. The total number of terminated branch NC is found from line number 4000, where all the terminated branch with $0 \leq A(i, j) < 1$ are counted.

Results of different allocation ratios

Number of terminal branches for the discrete time N are listed in Table 1. and plotted in Fig. 7. When $f = 1.0$, that is, a branch unit S has the same flow rate as a branch unit M, all end points of terminal branches bifurcate. The branching pattern is very complicated and the number of terminal branches increases exponentially. As the value of f decreases, that is, unit S transports material more slowly than unit M, the overlap of branches decreases. We have assumed that the f value is the same in every pair of branch units. We can now examine the case of different f values in certain locations of a branch complex. In some branch complexes a main axis, which is thick and zigzag, is very distinct and can easily be distinguished from other parts(side branches) of the branch complex. In the real tree, allocating ratios of unit on unit M were gradually decreased. It representes the differ-

Table 1. Number of terminal branches in simulations of branching patterns

F / N	1	2	3	4	5	6	7	8	9	10	11	12
1.000	2	4	8	16	32	64	128	256	512	1024*	2048*	4096*
.998	2	3	5	9	17	33	65	129	235	368	624*	1136*
.980	2	3	5	9	17	32	50	82	146	266	431	704*
.900	2	3	5	9	14	22	37	57	88	134*	204*	303*
.750	2	3	5	8	12	18	26	37	52	72*	99*	134*
.667	2	3	5	7	11	15	21	29	39	52	68*	89*
.500	2	3	5	7	10	13	18	23	30	37	47	57*
.400	2	3	4	6	8	10	13	16	20	25	30	36
.333	2	3	4	6	8	10	13	16	19	23	27	31
.250	2	3	4	5	7	9	11	13	16	19	22	25
.000	2	3	4	5	6	7	8	9	10	11	12	13

F : Various allocating ratio

N : Discrete time

* : Calculated by the authors (The other was cited from Honda *et al*.(1981))
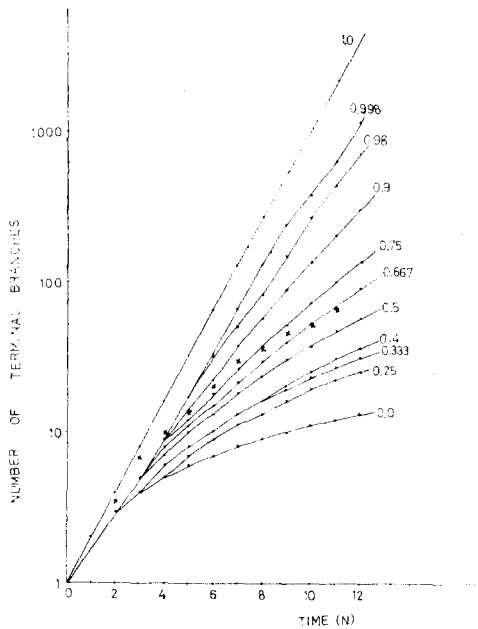
Fig. 7. The number of terminal branches plotted on a logarithmic scale against discrete time *N*. Respective *f* values are indicated. ✕ : actual number of terminal branches observed in *Magnolia denudata*

ence of allocation of stored reserves to shoot extention. In Fig. 7, observed value shows that the allocation ratio is gradually decreased approaching to the value of $F = 0.667$.

Feedback mechanisms in terms of nutrient and growth substance supply could be the actual regulatory mechanism. The model assumes that there is a hypothetical material which flows through branches and accumulates up to a critical threshold above which bifurcation takes place. Such material might be carbonates, a regulating substance like a mineral or hormone, water which could affect photosynthesis and meristem activity, or a combination of these.

Some supportive data is presented by Zimmermann(1978) who showed that difference in the flow rates of dilute KCL solution through the xylem exist within one tree he interprets this as the re-

sult of hydraulic constrictions between the trunk and lateral branches. These physiological constrictions are related to anatomical difference and result in differing, and presumably regulating, allocating ratios within the entire system. And intrinsic allocation ratio is related to the weight of leaves attached to the distal branches and has been described by the "Pipe model theory"(Shinozaki *et al.*, 1964).

Computer simulation of branching patterns above decribed is ideal for studies of several large branches or for entire trees less than 20 years old. But further study should be done in the older trees because of many variations of branching pattern according to the environmental differences.

Appendix A(Programed by Park and Choi)

```
    SUBROUTINE TREE(N, F, NC)
    DIMENSION A(15, 2000), NY(15, 2000)
    DO 99 I=1, 15
      DO 99 J=1, 2000
        A(I, J) =2
99  CONTINUE
    DO 100 I=1, N
      A(1, I) =1
      NY(1, I) =I
100 CONTINUE
    L=N+1
    A(1, L) =0
    IA =2
    IB =0
    IC =0
900 IA =IA-1
700 IB =IB+1
1000 IF(A(IA, IB).EQ.2.) GOTO 3000
    IF(A(IA, IB).LT.1.) GOTO 700
    IAS=IA
    IA =IA+I
    K =NY(IAS, IB)
    IC =IC+1
    A(IA, IC) =(A(IAS, IB) -1.)*F/(1. +F)
1100 K =K+1
    IF(K.GT.N) GOTO 900
    A(IA, IC) =A(IA, IC)+F**(IA-1)
    NY(IA, IC) =K
```

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```
      T=A(IA,IC)
      IF(T.LT.1.) GOTO 1100
      IC=IC+1
      A(IA,IC)=(T-1.)*1./(1.+F)
      GOTO 1100
 3000 IF(IB.EQ.1) GOTO 4000
      IA=IA+1
      IB=0
      IC=0
      GOTO 700
 4000 NC=0
      DO 300 IL=1,15
      DO 200 IM=1,2000
      IF(A(IL,IM),GE.2.) GOTO 10
      IF(A(IL,IM),GE.1.) GOTO 200
  200 CONTINUE
   10 IF(IM.EQ.1) GOTO 20
  300 CONTINUE
   20 RETURN
      END
      DIMENSION FL(11), M(12)
      DATA FL/1, .998, .9, .75, .667, .5, .4, .333,
     .25,0./
      PRINT 20
   20 FORMAT(///////50X, "N", //10X, 100("-"),
     //13X, "F", 7X, "1", 6X, "2", 6X, "3", 6X,
     "5", 6X, "6", 6X, "7", 6X, "8", 6X, "9",
     5X, "10", 5X,"11",5X,"12"//10X, 100("-")//)
      DO 1 L=1,11
      F=FL(L)
      DO 2 IL=1,12
      CALL TREE(IL,F,NC)
      M(IL)=NC
    2 CONTINUE
      PRINT 30,F,(M(I),I-1,12)
   30 FORMAT(7X, F7.4, 1X, 1217//)
    1 CONTINUE
      STOP
      END
```

摘　　要

1982년 7월부터 1983년 8월까지 사이에 백목련(*Mag-nolia denudata* Desr.)의 分技型을 관찰하고 이에 관한 Computer simulation을 시도하였다.

樹冠形은 유전적 조건에 의하여 결정될 뿐아니라 환경조건에 의하여 영향을 받는 것으로서 그것을 특징짓고 있는 分技型의 결정은 몇가지 假定下에 가지상호간의 영향을 분석함으로써 分技型과 물질의 분배와 같은 관계를 합리적으로 설명할 수 있다. Computer simulated pattern은 生長을 지배하는 두 요인이 집약하여 나타나는 것으로보아 각 分技들의 생장에 필요한 물질량의 분배률(Allocation ratio)로 묘사하여 分技率이 다른 Simulated tree로 표현할 수 있었다. 主技(Main branch)에 대한 副技(Subbranch)의 양분이동 비율은 年次가 거듭함에 따라 작아지는 현상을 나타냈고, 축적된 양분이 1에 달했을 때 分技된다는 가정아래 主技에서는 남는 양분$\times\frac{1}{1+F}$, 副技에서는 남는 양분$\times\frac{F}{1+F}$로 분배된다고 표현할 수 있었다. 또한 잔가지에서는 $A(iA,iC)+F^{(iA-1)}$의 양분이 축적됨을 표현하였다.

이와같이 가지내에서 일어나는 양분분배의 기초적인 작은 차이가 결국 樹冠內의 복잡한 形態로 나타난다는 것을 밝힐 수 있었다.

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