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A Simple Model for the Growth of Ramified Leaf Structures

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Abstract—The detailed mechanism of the formation of net and branching leaf structures is not known yet. Several mathematical modelling attempts to generate those structures have been made previously, based on biochemical or purely mathematical assumptions. Here, we present a simple model, based on plausible biophysical suppositions, which is able to reproduce the formation of a ramified structure grown out of a single activated cell.

1. INTRODUCTION

The investigation of the formation and function of leaf venation is of current interest in plant biology. However, the detailed mechanisms are not known yet. The pattern of ramification is not only genetically but also physically fixed. It has been recognized that ramified structures are energetically more advantageous than non-ramified ones [1, 2]. Their growth is constrained by optimizing boundary conditions. The latter can be energy expense, load transmission, mass, occupation of space and speed. Leaf venation is both a transport and a construction system. Its function as supply system is the most important one.

Several attempts to model the formation of ramified structures are known. Based on the famous notion by Turing [3] of the chemical basis of biomorphogenesis, Gierer and Meinhardt [4] formulated a general theory of biological pattern formation and, furthermore, Meinhardt [5, 6] proposed a biochemical activator–inhibitor mechanism with memory and growth, forming net and branching structures similar to leaf venation. These patterns appear as spatially non-uniform stationary solutions of coupled reaction–diffusion equations for two morphogens, activating and inhibiting cell differentiation, respectively, as well as for a cell substrate and the memory component. The latter does not diffuse but memorizes the trail of the moving activator peaks, finally forming the net and branches of differentiated venation cells. The motion of the activator peaks is directed by a random distribution of the activator's growth rate. However, the experimental verification of such a mechanism is still pending.

Bell et al. [7] designed their models to simulate the essentials of botanical branching

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systems. They consider a plant to be built up of a series of shoot-units. Based on a botanical background, rules of growth governing different shoot-unit types and their capacity to bear daughter units, are formulated in numerical file form. Very artificial regular branching patterns of rhizomatous plants have been obtained. Horn [8] developed a theory of the adaptive geometry of trees which optimize their shape in order to gain a maximum of photosynthetically active radiation. This is a problem in plant succession, less related to mechanisms of ramification.

The generation of ramified structures is also of purely mathematical and computational interest. Hogeweg [9] designed computer programs to simulate growing and branching cell arrays in a cellular space. Yeh [10] described methods to characterize generations of monopodial, dichotomous and higher order branching. Lindenmayer [11, 12] proposed the mathematical formalism of L-systems as the foundation for an axiomatic theory of development. He explored a theory for the growth and branching of filaments, using discrete mathematics, i.e. the theory of sequential machines, with numerous fascinating numerical results of ramification patterns, of Prusinkiewicz and Hanan [13], and Prusinkiewicz and Lindenmayer [14]. Jean [15] made use of L-systems to develop a systemic theory of phyllotaxis. The L-systems are related to fractal geometry [16, 17]. The latter provides many examples of how a few simple mathematical mapping rules can generate patterns with a striking similarity to biological forms, but without any obvious biological background.

As opposed to these approaches, a semi-probabilistic minimal model with some biophysically based plausible assumptions for the growth of a ramified leaf-like structure is proposed and tested here. The aim of this paper is to demonstrate that phenotypic properties of a full-grown plant can be derived from a few, eventually genetically coded, growth rules in combination with a dynamical process. This is the usual procedure in the field of self-organization of pattern formation [18, 19].

2. THE MODEL ALGORITHM

The proposed model in rectangular co-ordinates (x, y) is now given in algorithmic form.

(a) The starting-point is a first unit of a leaf-stalk of supposed initial direction $\alpha = 0$ and length L with an active end at $\mathbf{r}_0 = (x_0, y_0) = (0, 0)$ which is the first node of further development.

(b) Growth can proceed with a certain probability $P(i)$ by adding a unit at an active node i in one of the three directions $\alpha \in \{-\beta, 0, \beta\}$. The probability $P(i)$ is the product of 4 independent probabilities $p_k(i)$, $k = 1, 2, 3, 4$;

$$P(i) = \prod_{k=1}^{4} p_k(i). \tag{1}$$

The first factor considers that early originated units generally develop most strongly:

$$p_1(i) = \exp\{-C_1 R(i)\}, \tag{2}$$

where $R(i)$ is the number of direction changes, counted from the initial node at $(0, 0)$. A sequence of grown units of the same direction belongs to the same number of direction changes.

The second factor is due to weaker growth of shoot-units with higher generation number $G(i)$, i.e. growth declines with increasing distance from the origin:

$$p_2(i) = \exp\{-C_2 G(i)\}. \tag{3}$$

The third factor considers the direction of growth, i.e.

$$
p_3(i) = \begin{cases} 0 & \text{if chosen direction is already occupied,} \\ C_3 & \text{for } \alpha = 0, \\ \frac{1}{2}(1 - C_3) & \text{for } \alpha = \pm\beta, \end{cases} \tag{4}
$$

with $\frac{1}{3} \leq C_3 \leq 1$. Hence, growth proceeds

(i) straight with highest probability, i.e. a certain moment of inertia is assumed for the growth in the preceding direction $\alpha = 0$;

(ii) with lower probability to the right or to the left side under fixed equal angles β.

The fourth factor considers the decreasing growth capacity of shoot-units with low generation number $G(i)$, i.e. the effect of ageing:

$$
p_4(i) = \exp\{-C_4[G(\max) - G(i)]\}, \tag{5}
$$

where $G(\max)$ is the actual maximum generation number of the whole generated structure. Hence, the growth is limited by exponential decline of growth probability for increasing number of direction changes, increasing distance from the leaf-stalk (generation number) and increasing age. This natural saturation-like property of the model is typical for a number of known macroscopic growth laws, e.g. logistic and hyperlogistic growth [20]. It is an important advantage, compared with L-systems with unlimited growth.

(c) The position $\mathbf{r}_{i+1}$ of the new active node $(i + 1)$ can be obtained from the position $\mathbf{r}_i$ of the actual node i by

$$
\mathbf{r}_{i+1} = \begin{pmatrix} x_{i+1} \\ y_{i+1} \end{pmatrix} = \begin{pmatrix} x_i \\ y_i \end{pmatrix} + L C_5^{R(i)} \begin{pmatrix} \cos(\beta + \varepsilon_x) \\ \sin(\beta + \varepsilon_y) \end{pmatrix}, \tag{6}
$$

where the factor $C_5^{R(i)} \leq 1$ describes the continuous shortening of shoot-units with increasing number of direction changes $R(i)$. All three ongoing directions are subject to weak environmental noise, modelled through Gaussian random numbers $\varepsilon_{x,y} \in [0, 1]$, generated with the Box–Muller algorithm [21].

(d) If a growing unit intersects an already existing one, growth is stopped at the intersection point. The latter forms an inactive node which is incapable of further development.

(e) The new number of direction changes and the new generation number simply follow from

$$
\begin{aligned} R(i + 1) &= R(i) & \text{for } \beta = 0, \\ R(i + 1) &= R(i) + 1 & \text{for } \beta \neq 0, \\ G(i + 1) &= G(i) + 1. \end{aligned} \tag{7}
$$

(f) The thickness of each unit depends on its necessary transport capacity, i.e. it should be sufficient to supply the following units.

The model assumptions are sketched and summarized in Fig. 1.

3. RESULTS AND CONCLUSIONS

Three resulting simulation patterns for different sets of control parameters $C_1, \ldots, C_5$ are presented in Fig. 2(a)–(c). The drawing of a boundary, connecting the end-points of the outer units, has been omitted. The striking similarity to leaf-venation patterns is readily

$$\alpha = 0 + \varepsilon_0$$

$$\alpha = -\beta + \varepsilon_1 \qquad \alpha = \beta + \varepsilon_2$$

Model assumptions:

(1) Angle β + Gaussian random numbers $\varepsilon_0, \varepsilon_1, \varepsilon_2$

(2) Probability of the direction of growth (Preference of preceding direction)

(3) Only 3 branchings per node

(4) Points of intersection do not ramify and grow

(5) Probability to ramify and to grow declines with increasing generation (distance from the root) and with increasing number of direction changes

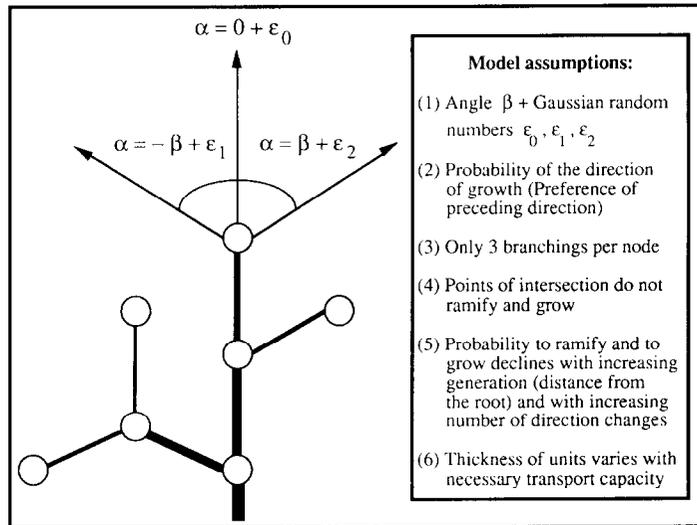(6) Thickness of units varies with necessary transport capacity

Fig. 1. Summary and sketch of model assumptions.

seen, i.e. the model has demonstrated its capacity to generate ramified structures by application of only a few biophysically plausible local growth rules. For the generation of more realistic symmetric structures, one has to include at least one non-local rule. For further improvement of the model, the already mentioned functional optimization parameters for the ramified transport and construction system as energy expense, load transmission, mass, occupation of space and speed have to be considered. Another optimization control could come from a fixed shape of the leaf's boundary.
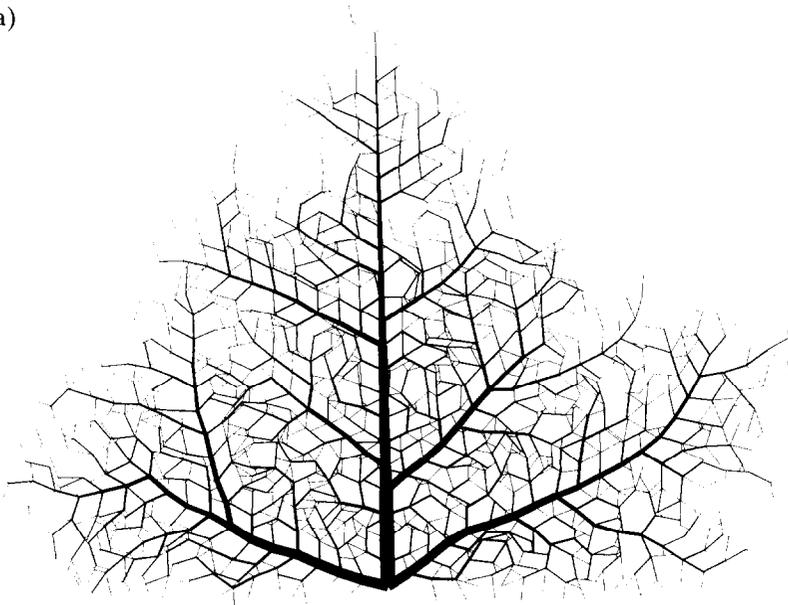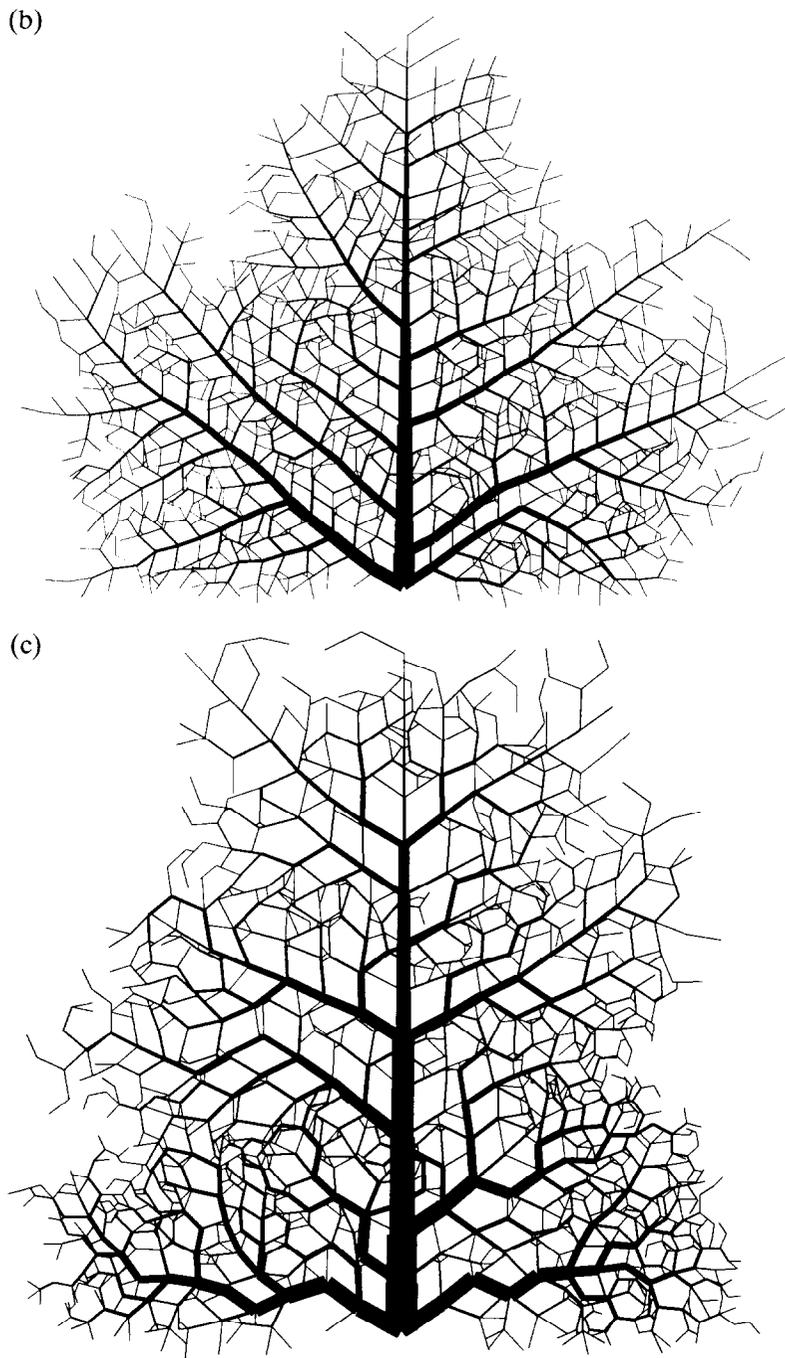
(a)

Fig. 2(a).

(b)

(c)

Fig. 2. Final stationary simulation patterns for parameters. (a) $C_1 = 0.6$, $C_2 = 0.2$, $C_3 = 0.4$, $C_4 = 0.0$, $C_5 = 1.00$; (b) $C_1 = 0.7$, $C_2 = 0.5$, $C_3 = 0.4$, $C_4 = 0.1$, $C_5 = 0.85$; (c) $C_1 = 0.2$, $C_2 = 0.4$, $C_3 = 0.3$, $C_4 = 0.1$, $C_5 = 0.85$.

REFERENCES

1. A. Herbig, Trees and leaves – basic considerations, in *Verzweigungen, Mitteilungen des Sonderforschungsbereiches* 230, vol. 4, pp. 21–31. Stuttgart Tübingen (1992) (in German).

2. U. Kull, Architecture and ramification in botany, in *Verzweigungen, Mitteilungen des Sonderforschungs-bereiches* 230, vol. 4, pp. 9–19. Stuttgart and Tübingen (1992) (in German).
3. A. M. Turing, On the chemical basis of morphogenesis, *Phil. Trans. R. Soc. Lond.* **B237**, 37–72 (1952).
4. A. Gierer and H. Meinhardt, A theory of biological pattern formation, *Kybernetik* **12**, 30–39 (1972).
5. H. Meinhardt, Morphogenesis of lines and nets, *Differentiation* **6**, 117–123 (1976).
6. H. Meinhardt, *Model of Biological Pattern Formation*. Academic Press, London (1982).
7. A. D. Bell, D. Roberts and A. Smith, Branching patterns: the simulation of plant architecture. *J. Theor. Biol.* **81**, 351–375 (1979).
8. H. S. Horn, The Adaptive Geometry of Trees, *Monographs in Population Biology*, Vol. 3. Princeton University Press, Princeton, NJ (1971).
9. P. Hogeweg, Simulating the growth of cellular forms. *Simulation*, September, 90–96 (1978).
10. H. C. Yeh, Modeling of biological tree structures, *Bull. Math. Biol.* **41**, 893–898 (1979).
11. A. Lindenmayer, Mathematical models for cellular interactions in development, parts I & II. *J. Theor. Biol.* **18**, 280–299 & 300–315 (1968).
12. A. Lindenmayer, Developmental systems without cellular interactions, their languages and grammars, *J. Theor. Biol.* **30**, 455–484 (1971).
13. P. Prusinkiewicz and J. Hanan, *Lindenmayer Systems, Fractals, and Plants. Lecture Notes in Biomathematics*, vol. 79. Springer, Berlin (1989).
14. P. Prusinkiewicz and A. Lindenmayer, *The Algorithmic Beauty of Plants*. Springer, Berlin (1990).
15. R. V. Jean, A theory and a model for pattern generation in plants, *J. Biol. Systems* **1**, 159–186 (1993).
16. B. B. Mandelbrot, *The Fractal Geometry of Nature*. Freeman, San Francisco (1982).
17. M. Barnsley, *Fractals Everywhere*. Academic Press, London (1988).
18. W. Ebeling and R. Feistel, *Physik der Selbstorganisation und Evolution*. Akademie-Verlag, Berlin (1982).
19. J. D. Murray, *Mathematical Biology, Biomathematics Texts*, vol. 19. Springer, Berlin (1989).
20. M. Peschel and W. Mende. *The Predator–Prey model*. Akademie-Verlag, Berlin (1986).
21. W. H. Press, S. A. Teukolsky, W. T. Vetterling and B. P. Flannery, *Numerical Recipes in FORTRAN*. Cambridge University Press, Cambridge (1992).