BASES AND PROPOSALS FOR A MODEL IN CONNECTION WITH THE EARLY PHYLLOMORPHOGENESIS OF PISUM SATIVUM

Lenz, J. Institute of Botany, University of Bonn
and H. W. Ingensiep Federal Republic of Germany

The advantages that leaves of various genotypes of P. sativum show with regard to the application of morphogenetic models were discussed previously (1). This article considers some concrete proposals for a model of phyllomorphogenesis.

A general proposal for a morphogenetic model:

This model combines models for a biochemical pattern formation in reaction/diffusion systems with others, including the theory of growing polyautomata. The cormus or one of its organs is represented by the polyautomaton, and every one of the cells or group of cells by a corresponding single automaton. Each single automaton should be able to hold a discrete number of states. For these and the transitions between them, the following entities are supposed to be relevant: a) The state of activity of the genome (given by the pattern of all active genes of the genome), b) The positions of molecular switches (characterized by two or more steady states). Irreversible transitions among them are normal. They elicit a small apparent diffusion constant, which on the one hand serve as effectors of regulator proteins within gene regulation or on the other hand of allosteric enzymes within synthesis of signal substances, c) The concentrations of the above-mentioned signal substances — they are synthesized via specific pathways. Generally they produce a high apparent diffusion constant and can belong to complex reaction/diffusion systems. They influence essentially the positions of the molecular switches.

Transitions between the states of an automaton ought to be understood as changes in the state of differentiation of the corresponding cell.

The main points during the development of the shape of the plant, and above all that of the leaf, are to be found in the formation of the apical tip meristems of the respective organs. The temporal/spatial coordinated induction of these meristems ought to be guaranteed by an hierarchic control, in connection with a mutual communication of the meristems via signal substances. Descendents of the particular meristems form subcompartments in which certain processes of pattern formation can take place, which then lead to the formation of new tip meristems.

The initiation of one of more meristems of the same kind may take the following course. The concentration gradients of signal substances of hierarchic superior meristems cross certain thresholds in a group of cells. Thereupon a molecular switch is turned on in the cells concerned. This produces the synthesis of an activator/inhibitor pair, by means of the activation of a gene set. Hereafter, the activator forms a stable pattern of concentration. In all cells in which the corresponding concentration is above a threshold, the differentiation towards the tip meristem of a new organ identity will be started. At the same time a signal is synthesized there which, in certain surroundings, suppresses the synthesis of the activator/inhibitor pair. In that way the newly arisen meristems isolate themselves.

The position of such a meristem depends also on the geometry of the organ primordium, because it co-determines the patterns of concentration of the activators. By means of this mutual dependence the space determines the pattern, and the latter, once arisen, alters the space and the form emerges.

An application of the early phyllomorphogenesis of the wild-type:

During the development of a wildtype pea leaf the following hierarchy of participating meristems can be observed (Fig. 1):

1) meristem of the shoot apex (shoot-tip-meristem=SM);
2) tip meristem of the leaf axis (leaf-tip-meristem=LM);
3) tip-meristem of the primordium of the stipule (stipule-meristem=StM);
A) tip meristem of the leaflet/tendril primordium (leaflet/tendril-meristem=LTM).

As to the model, the development of a leaf can be summarized as follows:

The newly developed leaf primordium is first polarized in a way that future meristems can only develop on its upper side. The SM cooperates in this polarization. During the outgrowth of the leaf primodium, produced by the activity of the LM, two StM's are initiated. The StM's together with the LM determine the location within the leaf primordium where the first two LTM's are initiated. Generally the location at which a pair of LTM's is initiated is fixed by the next older pair and the LM.

Pisum shows marked anisophylly. Successive leaves formed during ontogeny become more ramified. _The following mechanism is supposed to be the molecular basis for the phenomenon_:

At various nodes the initiation of new ramifications at a leaf primordium is to be stopped at different points of time after the formation of the leaf primordium. If the concentration of a signal produced in the SM, the rate of production of which depends on the number of already existing nodes, falls short of a certain threshold in the LM, the furtherance of LTM's is interrupted there. This occurs at each node at a later point of the development of the leaf primordium.

Every leaf, independent of the number of ramifications, usually shows the same number of leaflets and tendrils on eithei side of the rachis (i.e. bilateral configuration). It can be supposed that a signal from the LM decides if a leaflet or a tendril will be developed. Wherever concentration of the signal falls short of a specific threshold, leaflets will be developed, otherwise tendrils. The production rate of the signal ought to depend on the number of the ramifications in a way that the position of the threshold will not be displaced in relation to the length of the leaf primordium.

It is also imaginable that the development of leaflets is predetermined, and once the concentration of the signal exceeds a certain threshold, tendrils will be developed. The threshold concentration of the signal will usually be situated in an internodal area of the leaf primordium. However, in case it is situated in the area of a ramification pair, it might happen that on account of differences in the state of development of the two ramifications or through fluctuations in the concentration gradient of the signal; one of the two LTM's gets into the area of concentration above the threshold and the other into the one beneath it. In this way, a tendril/leaflet pair might develop at once and at the same leaf nodium (Fig. 2).

Whether or not the series of molecular processes, as described in the preceding paragraph, will lead to a certain form has to be shown in a simulation of a diffentiated elaborated model. An imaginable general starting point for such a model has been introduced in the first paragraph. However, the translation of such a starting point into a concrete model and its simulation involves numerous theoretical and practical problems. In addition, quite a number of empiric studies, as well as a statistical recording of the forms of leaves and their deviations (not produced by mutations), are necessary.

1. Ingensiep, H. W. 1986. PNL 18:67-68.

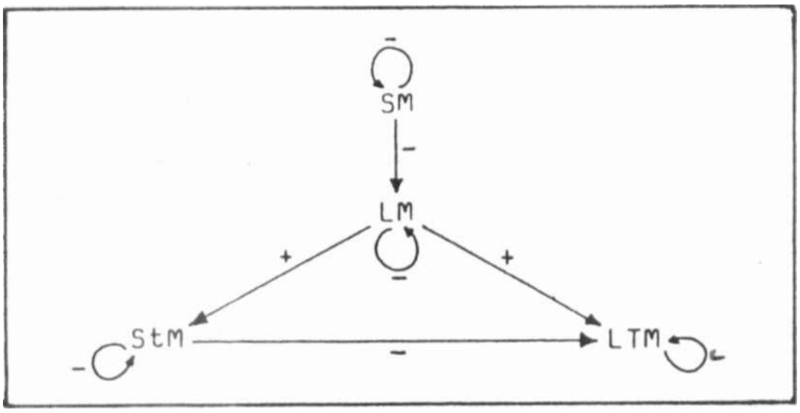

Fig. 1 Interactions among the meristems during the development of a leaf of _Pisum sativum_. + : Inhibition up to a certain distance, furtherance from this distance on. - : Inhibition up to a certain distance, no furtherance from this distance on. (Further explanations in the text.)

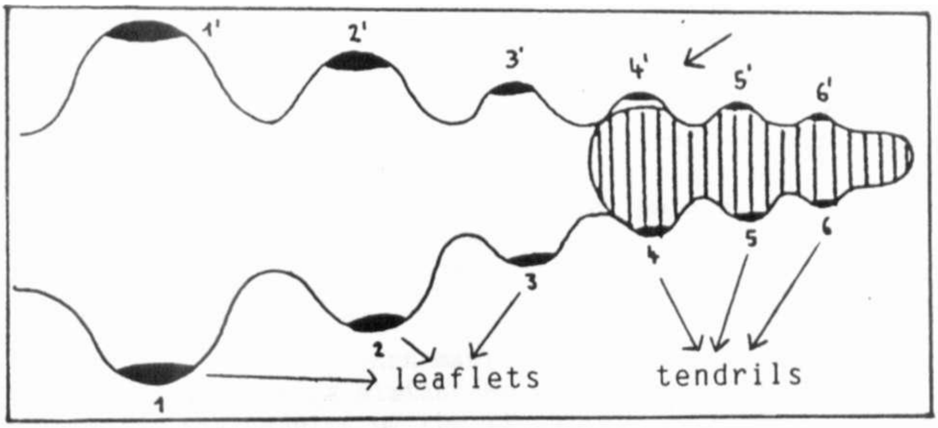

Fig. 2. Explanation of the induction of leaflet-tendril pairs because of an asymmetric gradient: 4" is induced to become a leaflet instead of a tendril.

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