GENERAL CONSIDERATIONS FOR THE USE OF PEA GENOTYPES FOR MODELS OF PLANT MORPHOGENESIS

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Genotypes of *Pisum* with clear morphological deviations from the normal form are well known and described, especially those concerning the morphology of the whole shoot, leaves, and flowers (e.g. by Gottschalk, Lamprecht, Marx). These pea genotypes have been considered primarily from an evolutionary point of view (1), but their significance for ontogenetic theories and models has less frequently been discussed - this mainly because of a lack of molecular genetic information and precise models for the underlying mechanisms. However, in recent years useful models for developmental processes have been elaborated (e.g. by Meinhardt and Gierer), which allow computer simulations and an application of their basic principles to plant developmental processes (2). The time has now come to attempt to interpret different morphological genotypes in terms of these theories. In the following questions I offer a rough guide and some suggestions for the use of pea genotypes in such models.

1. Which organs of pea plants seem to be best suited for an interpretation in terms of these models? I think that the leaf is very appropriate, because it is not as complex as the whole shoot or flower and differences in leaf morphology are easily observed, which is not the case with roots. An advantage is that the leaves of *Pisum* are arranged in a relatively simple manner along the shoot axis (distichous with a divergence of 180) and show distinct morphological differences depending on their position (trifid bracts, first true leaf, and adult leaves). Moreover, the main parts of the normal leaf are easy to distinguish (stipules, leaflets, tendrils) and show pair configuration in a polar, orderly manner along the leaf axis.

2. Which principles are useful for the interpretation of the normal morphogenesis of pea leaves? A specific model already has been proposed for distichous phyllotaxis (2). It is more difficult to find the framework for phyllomorphogenesis itself. A first approach for the differentiation along the leaf axis during the embryonic and vegetative phase seems to be the model for mutual activation of different determined cell types and of positional information using a graded "morphogen" gradient within the leaf primordia.

3. Which leaf mutants of Pisum might be interesting candidates to test these models? Mutants with striking differences in the foliar configuration are clear choices. Among these are the mutants afila (af) (transformation of leaflets into tendrils), acacia (tl) (transformation of tendrils in leaflets), *tendrilled acacia* (*tac*) as an intermediate form between tl and the normal form, and the mutant *unifoliata* (*uni*) having a single leaflet at each node instead of paired leaflets on normal plants. Another, more complex, case is presented by the mutant *cochleata* (*coch*) with modified stipules which sometimes may resemble whole leaves (Lit. in [1]).

4. Which principles could be used to explain such leaf mutants of Pisum? There is no satisfactory answer at the moment, but it can be assumed that a change in the regulative part of the genetic program is responsible for some of these morphological phenomena. If a model of gene regulation like that of Britten and Davidson is applicable to plants, we could expect sequence changes in regulatory elements like "integrator" genes or at the site of "receptor" genes, or possibly at the top of the hierarchy at the site of "sensor" genes or on the lowest level of "producer" genes. This could lead to an increase or decrease of special regulatory gene products ("morphogens"), which allow the establishment of positional information for cells. The increase or decrease of such gene products may lead to an abnormal interpretation of the positional Information and consequently to the initiation of abnormal morphogenesis. For instance, in the case of afila a defect in the regulatory element for the initiation of leaflets on chromosome 1 could lead to an activation of the genes for tendril formation on chromosome 7. A cause could be a higher amount of "inhibitor" or a lower amount of "activator" for leaflet formation. Similar considerations are possible for the acacia phenotype as a consequence of an alteration in regulating elements in genes for normal tendril formation on chromosome 7.

5. What role do recombinants of leaf mutants play for models of morphogenesis? If the parental mutants, e.g. afila and acacia, are interpreted in terms of a model, it should be possible to predict the morphological behavior of the foliar configuration of their recombinant afila/acacia. This is at the moment impossible - the morphological configuration is too complex - but this would be a very good test for the underlying models developed for the single mutants and the normal form. Another interesting point Is the use of recessive homozygotes (--), dominant homozygotes (++), and heterozygotes (+-) of presumed regulatory mutations. Their morphological state might be correlated with normal (++) or reduced (+—) amounts, or an absence (—) of a specific morphogen. If a certain threshold in the amount of such a regulating substance is crossed, we might expect a change in the morphogenetic process.

All these considerations give only a first hint for the use of pea genotypes in ontogenetic models. Perhaps these models also afford an Insight into evolutionary mechanisms of the leaf formation in legumes, for instance into the theory of a reduction line of leaflets observable within the legume family. However, many ideas, observations, and experiments are still necessary before the current models i an be used to understand such morphological phenomena.

1. Gottschalk, W. Die Bedeutung der Genmutationen fur die Evolution de Pflanzen. Fischer, Stuttgart, 1971.
2. Meinhardt, H. Models of biological pattern formation. Academic Press, London/New York, 1982.