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Trajectories of genetics, 150 years after Mendel/Trajectoires de la génétique, 150 ans après Mendel

Genetics and plant development

Génétique et développement des plantes

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ABSTRACT

There are only three grand theories in biology: the theory of the cell, the theory of the gene, and the theory of evolution. Two of these, the cell and gene theories, originated in the study of plants, with the third resulting in part from botanical considerations as well. Mendel's elucidation of the rules of inheritance was a result of his experiments on peas. The rediscovery of Mendel's work in 1900 was by the botanists de Vries, Correns, and Tschermak. It was only in subsequent years that animals were also shown to have segregation of genetic elements in the exact same manner as had been shown in plants. The story of developmental biology is different – while the development of plants has long been studied, the experimental and genetic approaches to developmental mechanism were developed via experiments on animals, and the importance of genes in development (e.g., Waddington, 1940) and their use for understanding developmental mechanisms came to botanical science much later – as late as the 1980s.

RÉSUMÉ

Il y a seulement trois grandes théories en biologie : la théorie de la cellule, la théorie du gène et la théorie de l'évolution. Deux d'entre elles, les théories cellulaires et géniques, trouvent leur origine dans l'étude des plantes, et la troisième résulte aussi, en partie, de considérations botaniques. L'élucidation par Mendel des lois de l'hérédité a été le résultat de ses expériences sur les pois. La redécouverte de l'œuvre de Mendel en 1900 fut le fait de botanistes : de Vries, Correns et Tschermak. Ce n'est que dans les années ultérieures qu'on démontrera que les éléments génétiques ségrègent chez les animaux de la même manière que chez les plantes. L'histoire de la biologie du développement est toute différente – alors que le développement des plantes était étudié depuis longtemps, les approches expérimentales et génétiques des mécanismes du développement ont été élaborées par des expériences sur les animaux, et l'importance des gènes dans le développement (par exemple, Waddington, 1940) et leur utilisation pour la compréhension des mécanismes de développement ne sont entrées dans la science botanique que beaucoup plus tard – après les années 1980.

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1. Introduction

While it could be said that genetical study of plant development started, in a way, 150 years ago with the publication of Gregor Mendel's paper on ratios in pea genetics, as certain of the phenotypes studied would now be considered developmental alterations, such as fasciation, constricted seed pods, or axial versus terminal pods, the fusion of plant genetics and developmental biology was only to happen long after the rediscovery of Mendel's paper [1–5].

2. Plant genetics and development as separate endeavors

There is no indication that Mendel thought of his characters as developmental alterations, or that he considered his work related to developmental biology as it existed in his day (for example in the work of Payer [6], Fig. 1A, on flower development). The detailed study of plant development began even earlier, not long after the foundation of the Académie des Sciences, with Caspar Friedrich Wolff's 1759 thesis (see Wolff, 1774 [7]), where meristems first were described, with Nehemiah Grew's The Anatomy of Vegetables Begun in 1672 [8] that treated buds as growing shoots (p. 9), or perhaps with Marcello Malpighi's description of a plant embryo in 1679 [9]. The subjects of genetics and development appear to have been separated in the thinking of plant scientists for a very long time afterward, as Bateson points out in his 1894 Materials for the Study of Variation [10], "*It has been the custom ... to speak of 'Heredity' and 'Variation' as two antagonistic principles; sometimes they are even spoken of as opposing 'forces*'" [p. 75]. Bateson agrees with this custom: "*In the first examination of the facts of Variation, I believe it is best to attempt no particular consideration of the working of Heredity*" [p. 76].

That this principle was followed by his successors is indicated by the contents of widely used textbooks, such as Steeves and Sussex's Patterns in Plant Development (1972) [11], where genes and mutants do not seem to be mentioned. Mutants are mentioned in the 1989 update of the book [12], and represent the source of much of the developmental information by the 2003 text Mechanisms of Plant Development by Leyser and Day [13]. Thus, there was a transition from considering plant genetics and plant development as unrelated subjects, to considering genetic approaches to be the key to understanding the mechanisms of development that occurred over the past 50 years (see [14]). The use of genetics to understand plant development took far longer, then, than the rediscovery of Mendel's work in the early years of the past century.

To review the history of genetical analysis of plant development, we will take examples from the study of the development of shoots and flowers, a persistent and active subject throughout the history of botanical science. There are earlier examples of the use of developmental phenotypes of plants, such as fasciated plants or double flowers, to study modes of inheritance (for example, White [15,16]; Miyake and Imai [17]; for additional examples in flower development see [18]), and a literature in which developmental mutants are considered as evidence for evolutionary scenarios (e.g., Saunders [19]) – that is, as atavisms. That this is an illogical way to infer evolutionary pathways has been pointed out, in detail, since at least 1900 (Goebel [20]; Leavitt [21]; Arber [22]). In the many works on what we now would call developmental mutants in plants that were published in the 19th and early 20th centuries, and summarized in the compilations of Moquin-Tandon [23], Masters [24], Penzig [25] and Worsdell [26], there was no consideration of whether the phenotypes were inherited (see [18]). The same can be said for Goethe's model for flower development based on abnormal flowers [27] – while this may be the first mechanistic consideration of development, heredity (as expected from the date) plays no role.

3. Early connections

There are nonetheless a few publications in which the potential importance of inherited abnormalities for an understanding of development is highlighted, though without achieving such understanding. For example Leavitt [21] wrote in a review of homeotic variants in plants "*The idea of homoeosis unites for descriptive purposes a great number of facts of ontogenesis which, even though they may not at the present juncture point a way to the correct mechanical explanation of development, possess in this connection a considerable prospective value*".

One early, even prescient, use of floral homeotic mutants to propose a model for development of flowers [28] led to the proposal that special hormones were directed to different regions of the developing flower, with the mutations studied leading floral organs to be formed in abnormal locations, thereby missing the hormonal influence. While the direct role of genes in the process is not commented upon, this does introduce a regulatory role for the hormones, if not the genes, whose role is in positioning of organ primordia – the paper is an early example of the use of mutations to develop a mechanistic developmental model.

Another, later example of the use of genetics to understand the mechanism of development in a plant is Stebbins' work on hooded and awned barley. The mutant form, hooded, has an extra inverted flower that develops on the lemma (one of the bract-like structures that encases a grass floral bud). As Stebbins and Yagil stated [29], "*Until recently, the use of genes having pronounced effects on morphology as an aid to the solution of problems of morphogenesis has not been given the attention which it deserves*". They attribute this to the recency of the recognition that genes provide information for the structure of a peptide chain, and on this basis conclude that the goal of plant developmental genetics is to establish the "complete chain of events from primary gene activity to ... morphological differences". To begin this, Stebbins and Yagil made a careful histological analysis of the development of hooded (mutant) and awned (wild type) to find the earliest differences, and found them in more rapid cell divisions in the lemma primordium. The connection between this and the development of a lemma of different structure in the two genotypes was not resolved; in

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