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Plant development: A new old story

Le développement des plantes : renouveau d'une histoire ancienne

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The fundamental importance of the problem of development in plant biology was first recognized by the German botanist Matthias Schleiden [1]:"*The mode in which one cell forms many, and how these, dependent on the influence of the former, assume their proper figure and arrangement, is exactly the point upon which the whole knowledge of plants turns; and whosoever does not propose this question... or does not reply to it, can never connect a clear specific idea with plants and their life*".

The major vegetative phase of flowering plant development (the sporophyte) begins with a single cell, the zygote, resulting from egg cell and sperm cell fusion [2], within the so-called 'alternative of generations', or succession of gametophyte-sporophyte first described by Hofmeister (1862) [3]. The zygote initiates a special sequence of development: embryogenesis. Embryogenesis can be defined in flowering plants as the part of development that takes place in the embryo sac of the ovule or immature seed. This process occurs in well-defined stages, resulting from specific patterns [2].

The plant body typically consisting of an embryonic axis and two cotyledons (in the case of a dicot), is also characterized by a typical polarity with a shoot and a root. What is the determinant of this polarity? The answer is that polarity already exists within the unfertilized egg cell [4]; the growth of the plant zygote is polar, and its division asymmetric. The first fundamental decision that promotes elongation of the Arabidopsis zygote and development of its basal daughter cell into the extra-embryonic suspensor is regulated by *YODA (YDA)*-dependent signalling. Loss of this mitogen-activated protein kinase, kinase (MAPKK) kinase YDA, suppresses elongation of the zygote [4]. It was recently reported that the interleukin-1 receptor-associated kinase (IRAK)/Pelle-like kinase gene *SHORT SUSPENSOR (SSP)* links activation of the *YDA*-MAP kinase cascade for fertilization through a previously unknown parent-of-origin effect [5]. *SSP* transcripts are produced in mature pollen, but do not appear to be translated. They are delivered via the sperm cells to the zygote and the endosperm, where SSP protein transiently accumulates. Direct delivery of transcripts to seed would provide a general mechanism for subverting such epigenic regulation [5].

There exists a large diversity of plant development and a current question is related to the choice of the appropriate model to investigate this highly complex question. *Arabidopsis thaliana* seems to be like *Escherichia coli* of the 1980s! Is this powerful model system soon to be abandoned because it has made more complex systems accessible? Probably not yet, but some alternative model species (tomato, pea, maize, rice, petunia, physcomitrella, poplar for tree species, etc.) and comparative analyses are beginning to regain popularity [6].

Accumulated genetic data are stimulating the use of mathematical and computational tools for studying the concerted action of genes (gene network) during both differentiation and morphogenetic mechanisms [7]. And, as the French Nobel prize François Jacob said: *"Biology cannot, either reduce it to physics, or solve it without physics*" [8].

The German scientist Caspar Wolff in his thesis entitled « *Theoria Generationis* » (1759) refuted the preformation theory when he observed the progressive apparition of leaves in a dissected kale vegetative bud as well as vessels and petiols. He made such observations with the aid of a microscope near a translucid zone that he named the *« punctum vegetationis »* or vegetative apex [9]. From this observation, he proposed that in plants undifferentiated regions are transformed (specialized) in tissues and organs then built up *de novo* into living organisms by epigenesis. He hypothesized the role of a vital force named « *vis*

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essentialis ». Later, the Swiss Karl Wilhelm von Nägeli observed in algae and mosses the continuous apical cell divisions, which seemed to be at the origin of tissues and organs. He termed them meristems (1858), from the Greek « *merizein* », to divide [8]. The origin of many plant developmental patterns can be tracked back to meristems that are located at the growing tips of roots and shoots, from which most postembryonic structures are derived. The shoot apical meristem, especially the region of undifferentiated cells at the very apex, is regulated through a negative feedback loop between the transcription factor WUSCHEL (WUS) and a small secreted peptide CLAVATA3 (CLV3). CLV3, in turn, acts together with the receptor kinase CLV1 to repress WUS expression, thus creating a negative feedback loop [10]. Some conserved factors regulate signalling in shoot and root stem cell organizers like WOX5 and WUS that maintain stem cells in either a root or a shoot context [11].

Auxin is one of the main agents that regulate plant growth and development [12] as well as the recent discovery of a brassinoid hormone, brassinolide, involved in photomorphogenesis [13].

Finally, plant development is also strictly dependent on the physiological stage of development and on environmental conditions. For example, it is interesting to focus on the so-called heterophylla characters observed in the leaves of some species. One kind of heterophylly is related to the age of the plant. In ivy (*Hedera helix*), age-dependent changes in leaf form are related to the reproductive maturity of plant. Juvenile ivy plants have three lobes whilst in the mature flowering plant, the leaves are entire without any lobes. Buttercup (*Ranunculus aquatilis*) leaves that form when the shoot is under water are thin and more deeply lobed; those that form in the air are thicker and less lobed.

According to Esau [14] : "*The intrinsic unity of the shoot has been recognized since the early days of the botany, but the morphologic value of the concepts of leaf and stem have been interpreted in a variety of ways (phytons, phyllomes, and others) each comprising a leaf and the subjacent part of stem, or the axis is a fundamental organ and the leaf*". Regardless of the merits of the various theories, their discussions have served to emphasize the intimate relation between the stem and the leaf is its modification differentiated in the course of the phylogeny. Goethe said: "*In my opinion, the chief concept underlying all observation of life – one from which we must not deviate – is that a creature is self-sufficient, that its parts are inevitably interrelated, and that nothing mechanical, as it were, is built up or produced from without, although it is true that the parts affect their environment and are in turn affected by it*". And also, "*I had the ability, ... to perceive the flower in such a way that it did not remain in its original form for a single moment, but spread out, and from within there unfolded again new flowers with coloured as well as green leaves... Perhaps these offered themselves so readily because they had their roots in many years of contemplation of the metamorphosis of plants*" [15]. He searched a deep unit through all organisms and assumed that in plants the leaf is the basic unit. '*All is leaf and by this simplicity the most great diversity becomes possible*' [16]. He considered that his scientific work was so far more important than all his other achievements. In the 20th century his ideas on the metamorphosis of plants were largely supported by data from developmental genetics [17]. In a certain way, we can consider that his idea was partly supported by the recent analysis of *sepallata* mutants of *Arabidopsis*, especially *sep4* [18].

Goethe thought that knowledge of phenomena, like plant metamorphosis or plant development, the subject of this special issue, can arise only from a contemplative relationship with nature, in which our feelings of awe and wonder are intrinsic [19]. He was obviously, at least partly correct, but today we also need a scientific multidisciplinary approach [20].

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