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Specificities of plant development

Spécificités du développement des plantes

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Unlike animals that move in the environment to find their food and shelter, plants are obliged to adapt to the specificities of their environment without moving from the place where they are rooted. For instance, plant species growing in mountain habitats must adapt to freezing temperatures at night and sometimes up to 50 °C during the day. Plant architecture is shaped by the environment and this involves different signalling processes unique to the plant kingdom. In the animal kingdom, embryogenesis organizes the body plan very precisely. Cell lineage plays a crucial role in the differentiation process generating organs and the environment has little effect on this process. In the nematode *C. elegans* an extreme situation is found where all cell types are generated by a precise lineage [1]. When a cell from the embryo is killed, neighbouring cells cannot generate a substitute by extra rounds of division. This is in agreement with the poor ability of *C. elegans* to regenerate organs. In the plant kingdom the regeneration process can operate easily. This is exploited for vegetative propagation of clones for many tree species. This plasticity is a consequence of a major characteristic of cell differentiation, which is determined by position, not by lineage. The reproducible pattern of cell division observed during *Arabidopsis* embryogenesis would suggest that a cell lineage process operates in which the apical-basal polarity is established. The two meristems, which subsequently generate plant organs also display regular structures compatible with a cell lineage process. For instance, the three cell layers found in the apical meristem, L1, L2 and L3, behave as three cellular pools that do not mix. For instance, the L2 layer, unlike the L1 layer, ultimately generates gametes. These observations would also suggest a cell lineage process operates. However, the surgical ablation of a L2 cell is compensated by an anticlinal division of a L1 cell to generate a new L2 cell [2]. Genetic proof of a position-dependant differentiation process comes from the characterization of *tonneau* mutants. These extremely dwarf mutants have lost the ability to form a preprophase band during mitotic divisions. As a consequence of this, the division plane is positioned randomly, leading to a complete disruption of cell lineages [3]. Nevertheless, the resulting plants still generate organs, including flower whorls. The shape of the organs is modified due to the fact that elongation processes are also disrupted in the mutant. Nevertheless, organs are generated at the right place during development. Such a mutation disrupting the positioning of cell division planes would be lethal in the animal kingdom.

The position-dependant differentiation of a plant cell in a specific tissue requires signals emitted by different cell types and perceived by neighbouring cells. These signals are still largely unknown and their discovery is a major challenge. Such a cross talk between adjacent cells has been illustrated by Laux et al. who showed that cells from the quiescent centre expressing the *Wushel* protein stimulate the proliferation of cells in the adjacent layer, which generates stem cells. These stem cells excrete a peptide, the product of the *Clavata3* gene, which migrates to the quiescent centre and counteracts the expression of *Wushel*. This makes a regulatory loop controlling the size of the stem cell pool [4]. As a consequence of their position-dependant function, plant cells rapidly loose their differentiation features when they are isolated from tissues, for instance by making protoplasts. In the right environment, requiring the presence of growth regulators (auxin and cytokinins are critical) such cells can be induced to regenerate plants. The epigenetic processes involved in plant cell function specification are, therefore, reversible, as opposed to most of the differentiation processes that occur in the animal kingdom (although progress has been made recently in the convertion of differentiated mammalian cells into stem cells by the transient expression of appropriate transcription factors).

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Plants derive from unicellular green algae through a long process of evolution. Green algae themselves are presumed to result from the symbiosis of a primitive eukaryote cell unable to perform photosynthesis with a photosynthetic cyanobacteria. In the process of symbiosis a large set of cyanobacterial genes have been introduced in the symbiote. The analysis of plant genome sequences shows that orthologs of cyanobacterial genes are found in the chloroplast genome, suggesting that chloroplasts derived from cyanobacteria. Many orthologs of cyanobacterial genes are also found in the nuclear genome [5]. These genes are derived from events of nuclear capture of chloroplast genes, a process still ongoing in higher plants. The transferred genes have the features of eukaryotic genes, (for example, presence of introns), but the proteins they encode still fulfil functions related to those in cyanobacteria (for example, photosynthetic apparatus) [6]. Some of these genes now play a role in developmental processes. A striking situation concerns the so-called two component systems, which are commonly found in bacteria and play regulatory functions in environment sensing (for example, chemotaxis). These two component systems are histidine kinase phospho-relays that induce cascades of phosphorylation upon binding of a specific molecule to the receptor domain of a kinase. In higher plants several phospho-relays have been identified that are clearly related to two component systems. They have been "recycled" through evolution and carry out functions as receptors for the plant hormones ethylene and cytokinin [7].

The analysis of plant hormone action is progressing rapidly as illustrated by the recent discovery of several plant hormone receptors. The proteasome plays an important role in the animal kingdom, as well as in the plant kingdom. Strikingly several plant hormone receptors are F box proteins involved in targeted degradation of negative regulators. The auxin receptor *TIR1*, [8] the gibberellin receptor *GID1* [9] and the receptor of jasmonic acid are F box proteins. That F box proteins play the role of hormone receptors is unique to plants. New plant hormones such as brassinosteroïds [10] and strigolactones [11] have been discovered recently. Apart from brassinosteroïds which have structural properties related to steroïd hormones, it is striking that most plant hormones are not related to the hormones identified in the animal kingdom, again illustrating the fact that plant and animal development involve processes which are strikingly different. It is expected that important growth regulators remain to be discovered, as illustrated by the recent identification of a hormone involved in the guidance of pollen tube growth [12]. As illustrated by the different speakers participating in this meeting on vegetative development, plant development is an exciting area of research in which major discoveries are still to be made.

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