Plasticity in Plant Development:
The Changing Mind of Root Epidermal Cells

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Form follows function

Roots provide the plant with water and nutrients and play a pivotal role in the interaction with beneficial soil microbes. The tissue that is in direct contact with the soil solution, the root epidermis, is composed of two cell types: root hair cells with a long tubular-shaped outgrowth, and non-hair cells. Root hairs are of particular importance for the uptake for mineral nutrients with a limited mobility such as phosphate (P) or iron (Fe). These nutrients are essential for the plant to function and reproduce, but are tightly bound to soil particles and cannot be transported to the plant by mass flow or diffusion. Thus, plants have to explore a greater soil volume to avoid depletion of these ions around the roots. Root hairs substantially increase the surface area of the root and allows for a more efficient uptake of these nutrients. It is, therefore, not surprising that a high number of root hairs provides a competitive advantage when iron or phosphate are limited: indeed, it has been found that species with more root hairs grow better on soils low in bio-available iron or phosphate than species or cultivars that have the genetic setup for a low frequency of root hairs.

Positional information is encrypted in the DNA

In roots of the model plant Arabidopsis root hairs and non hair cells are arranged in a so-called position-biased pattern: those cells that have contact to two cells of the underlying tissue develop into a hair cell, those cells that are in contact to only one cell will enter the non-hair cell fate. The decision is made by a complex interaction of transcription factors, small proteins that precisely regulate the activity of genes coding for proteins that participate in this process. Some of the proteins can move from the site of their production to neighboring cells. Cells that are receiving these proteins in turn, export other transcription factors back to their neighbors. In this way cells can communicate with each other and the pattern of alternating root hair and non-hair cell files is established. How come then that despite the fact that all cells contain identical genetic information, neighboring cells can have different structures? The different cell fate decisions are due to positional signaling, a layer of information that is delivered with, but is not encoded by the sequences of the DNA. In the Arabidopsis root, a positional signal is conveyed from the cell layer underneath the epidermis via the spaces in the cell wall. Those epidermal cells that lie over the cell wall joining two underlying cells are receiving a slightly higher amount of this signal than the cells that are more remote from the source of the signal. This causes a bias in the production of one of the transcription factors and the pattern can be established without any differences in genetic information between the cells.

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From priming to plasticity

This pattern is not irreversibly fixed and can be changed according to the prevailing conditions. Plants have limited possibilities to escape from their origin, and their developmental plasticity is in general much greater than that of animals. The availability of nutrients can affect the overall architecture of the roots. Being directly exposed to the exterior, the cells in the epidermis are particularly responsive to environmental changes. The absence of both iron and phosphate causes an increase in the number of root hairs, in a manner which is typical of the respective situation. When the supply with phosphate is low, root hairs are significantly longer than those of plants that grow with sufficient amounts of P. In addition of extra hairs in the correct position, hairs are also formed in positions that are normally occupied by non-hair cells. In contrast, the lack of iron causes only a slight increase in the frequency of hairs. However, root hairs formed in response to iron deficiency develop two tips, which almost double the surface of the root hair cells. Although both situations ultimately lead to an increase in the root's surface area, different pathways are engaged to perceive, convey, and execute the respective signal.

Biology meets Math: modeling the dynamic of biological systems

How are these alterations in cell fate regulated? We assume that two different mechanisms account for the root epidermal patterning of adult plants. The initial position-biased patterning, which is already active in the embryo, is dominating in seedling roots. However, the genes causing this pattern are only active in a very narrow zone in the root. In roots of adult plants, this zone accounts only for a very low percentage of the total of epidermal cells. A second mechanism consistsing of an activator that triggers its own synthesis, and an inhibitor, which is also produced by the activator is important at later stages. Both the activator and the inhibitor diffuse away from their origin, but the inhibitor diffuses faster then the activator. At a certain distance from an activator peak the concentration of the inhibitor is very low and allows a second peak of activator to be established. The result is periodic peaks of activator that is translated into the formation of root hairs. This mechanism is dominating in the adult root and causes equal spacing of hairs along the root. An almost equal spacing of root hairs is important to avoid depletion zones of immobile nutrients around the root. A multitude of biological patterns has been explained by the inhibitor/activator mechanism which was first proposed during the 1950s by the English mathematician Alan Turing. Turing is also known for his participation in decoding the German Enigma code during WWII and his fundamental work on computer theory. Using mathematics, he proved that such a simple system could produce a variety of patterns. The patterning of epidermal cells represents a molecular expression of these theoretical considerations.

Epidermal epigenetics: more encrypted information

Genetic information is encoded by the sequence of the bases in the DNA. However, the example of positional information shows that the form of an organism cannot simply be deduced from the sequence of the genes. Another level of encrypted information is caused by the packaging of the long DNA molecules. In plant and animal cells the DNA is wrapped around proteins, so-called histones, like beads on a string. In this conformation the DNA is not assessable to the machinery that causes the genes to function. Before this can happen the histones have to be chemically modified, which causes a re-modelling of the whole complex. Such changes can occur during development or in response to environmental signals, and is referred to as epigenetic. The phenomenon of epigenetics is defined as all heritable changes in gene function that is not reflected in the sequence of the DNA. We have observed that mutants defective in the organization of chromatin (the complex made of DNA, histones and some other proteins), form either more or less root hairs when compared to the wild-type. In addition, the hairs are at random position and do not show the almost equal spacing that allows optimal acquisition of nutrients. We conclude that the disruption of "special awareness" is caused by an impaired communication among epidermal cells. Evidently, a correct packaging of the DNA is crucial for the patterning of epidermal cells. Interestingly, growth of the plants in low P medium affects chromatin structure, which can be interpreted as a potential regulatory mechanism to adapt the plant to its environment.

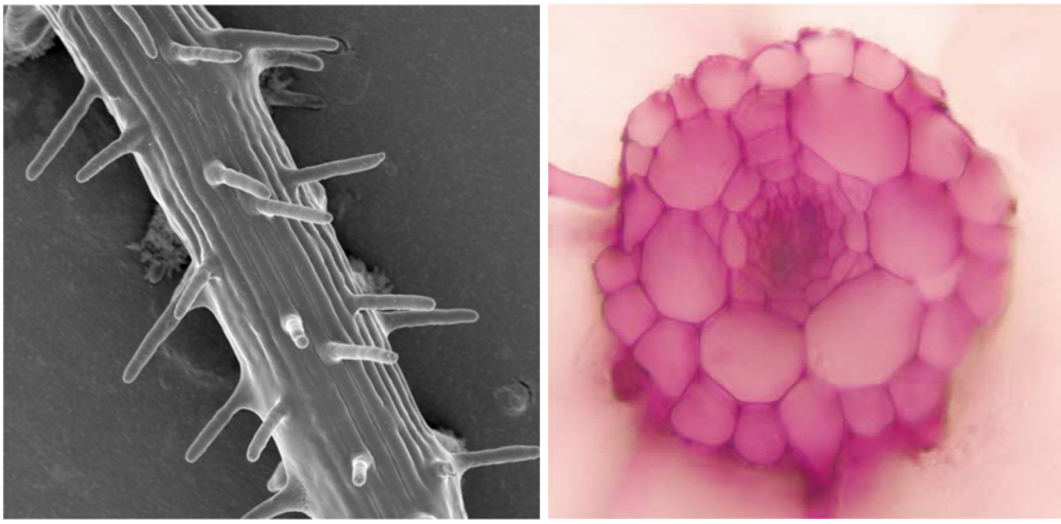
Democratic decisions: long distance signaling

The amount of bio-available nutrients changes both in time and space. Thus, not all roots are exposed to the same concentrations of minerals. In addition, the demand of nutrients depends on the developmental stage of the plant and varies with time. It is therefore necessary to integrate the signals and to control the uptake at the whole plant level.

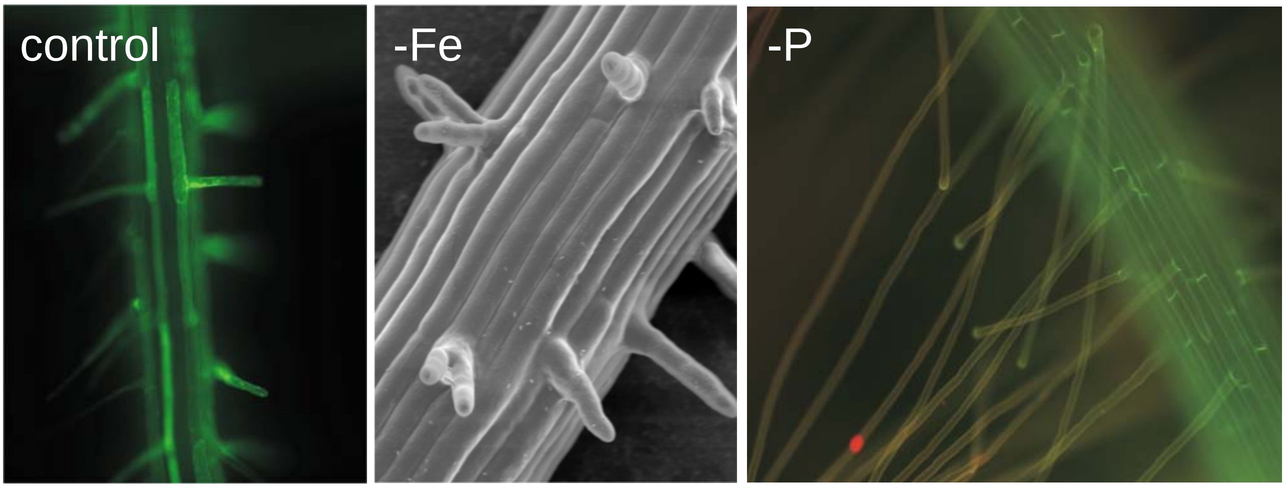
Our experiments have shown that both local and long-distance signals are involved in cell fate decisions. Mutants that cannot "feel" the amount of phosphate in their cells, and that are, therefore, constitutively issuing a deficiency mayday call from the shoots to the roots, form more root hairs even though the roots are supplied with sufficient amounts of the nutrient. When we grow these mutant plants without a shoot (to cut off the signal from the leaves), the increase in the number hairs was only evident when the plants were grown in P-free medium. This shows that either a local or a long-range signal is necessary and sufficient to induce the phenotype that is typical of P-deficient plants.

Plasticity: prerequisite for survival

Developmental plasticity is crucial for plants to survive, reproduce, and compete in their natural environment. Root hairs provide a simple model to study the effects of environmental signals on changes in developmental programs. Plant cells are totipotent, i.e. they have the ability to regenerate whole individuals from single differentiated somatic cells. This ability is reflected in the plasticity in cell fate acquisition in root epidermal cells in response to external signals that adapt the plant to the prevailing environmental conditions. Root epidermal cells provide a tool to gain insights into the mechanisms underlying the re-programming of cells. This knowledge, in turn, can be used to generate plants that are better adapted to limited resources and avoid the requirement of expensive and potentially damaging inorganic P fertilizers.



Organization of the Arabidopsis root



Differences in root hair patterning under control conditions and under Fe- or P- Deficient conditions