

Organisms as Activities - Cytoskeleton, Cellular Integrity, And Self Organisation in Plants

Plant cells are endowed with totipotency – each individual cell can (in principle) give rise to the entire organism. In multicellular animals only the fertilised egg is able to do so. Obviously, plant cells are highly autonomous cells and, obviously, there is no strong hierarchy guiding the behaviour of the individual cell. How is the pattern organised in space (and time)? Moreover, pattern formation in plants, with a few exceptions (such as identity of flower organs) is open patterning, i.e. the outcome is not predetermined, but depends on the environment (which is a need from organisms that cannot run away, when they do not like their environment).

Setting off two decades ago to understand, for what purpose plant cells have muscle proteins (the usual functions assigned to actin, tip growth and cytoplasm streaming, are not relevant in the majority of cells), we discovered that actin is remodelled in response to the plant hormone auxin. On the other side, actin organisation controls the directional transport of auxin through the plant establishing a self-referring circuit that is oscillating with a period of around 20 min. What is the function of this actin-auxin oscillator?

To understand this, we have to consider an important principle of plant evolution: all land plants (except the mosses) are composed of modular building blocks, the so called telomes that consist of a vascular bundle, surrounded by parenchymatic tissue (able to form new vascular tissues in case of need), and an epidermal layer with stomata which allow controlled exchange of gas and water. These telomes have later fused, branched, overtopped, or webbed to give rise to all the known plant organs. The secret of plant morphogenesis is in the flexible and robust formation and adjustment of these telomes. Tsvi Sachs has shown by elegant and simple experiments that new telomes are laid down along auxin fluxes through parenchymatic cells in a self-amplifying canalisation. To understand, how auxin flow interferes with cellular directionality, we established a system, where we strip plant cells from their direction by digesting the cell wall. The resulting round protoplasts can be induced to develop a new direction. We integrated this system into a microchip, where artificial rectangular “cells” could be either arranged in parallel or perpendicular to a gradient of auxin. We noted that the regenerating direction followed the geometry of the microvessel in the absence of an auxin cue, but followed the auxin gradient, if it was strong enough. We also saw that the geometry sensing was suppressed, when auxin efflux was blocked – so, direction results from a kind of “auxin echolot” like in the orientation system of bats. The actin-auxin oscillator system allows the cell to sense gradients in the tissue and to adjust with these gradients, which is crucial for the channelling of auxin flow and thus of vascular genesis (adjustment of the telomic building blocks).

Actin remodelling is not confined to auxin-dependent development, but is also observed in response to perturbations of membrane integrity as early hallmark of programmed cell death (a plant version of apoptosis). Programmed cell death plays a pivotal role for plant adaptation, for instance in response to biotrophic pathogens, but also to survive under salinity or drought stress. This actin response involves a self-referring circuit linked with a membrane located NADPH oxidase (Respiratory burst oxidase Homologue, RboH) and can be mitigated by auxin, indicating that both circuits are competing for a common limited factor. This common limited factor is superoxide, which is also needed to transduce the auxin signal

across the membrane. The “oscillator of life” and the “oscillator of death”, thus are linked in a dynamic manner. “Integrity” of “organisms” is therefore not a state, but a dynamic process organised by oscillators that can be synchronised by weak coupling of signals exchanged between cells. A few (bold) hypotheses on the consequences from this dynamic view on self organisation are proposed.

As epilogue, some technical applications of this self-organisation model are briefly demonstrated: plant cell fermentation of pharmacologically interesting plant compounds has remained limited to very few cases. The situation in a real plant tissue is complex, because these compounds are produced in a cooperative effort of different cell types that exchange not only metabolites, but signals that regulate metabolic potencies. By mimicking plant evolution and playing “metabolic LEGO”, we have succeeded to obtain the anti-Alzheimer compound nornicotine from modular interaction of two tobacco cell strains, and the anti-tumour compound vincristine from two metabolically complementary strains of *Catharanthus* cells. We have developed, together with microsystems engineers, a modular biochip for plant cells, which allows to mimick (and hopefully to identify) the regulatory signals that are exchanged between cells to establish a metabolic “organism”.

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