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Editorial

Decipher Plant Gene Regulatory Networks Using Single Plant Cell Types

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Gene expression is under the control of transcription factors and various epigenomic modifications of the chromatin such as the methylation patterns of the genomic DNA (gDNA) and various chemical changes of histone proteins. Small RNAs are another important regulator of plant chromatin structure and gene expression [1,2]. The integration of different epigenomic marks (i.e. gDNA methylome, histone modifications) with nucleosome occupancy, pool of small RNA, cis-elements recognized by transcription factors and transcriptome profiling is essential to fully understand how the epigenome and transcription factors controls chromatin structure and gene expression. In plants, histone post-translational modifications and gDNA methylation are reliable marks of euchromatin (transcriptionally active genes) or heterochromatin (transcriptionally inactive genes; for review, [3]). For instance, in *Arabidopsis thaliana*, 5-methyl cytosine (5-mC) is present predominantly over repetitive DNA sequences (e.g. silent transposable elements) but is also detected in the body of expressed genes [1,3-11]. H3K4me3 and H3K27me3 are mainly associated with actively expressed and repressed/lowly expressed genes, respectively, and not with intergenic or heterochromatic sequences [7,12,13].

To date, plant biologists integrate the transcriptome with the chromosomal position of epigenomic marks on the chromatin fiber and the pool of small RNAs collected from entire plant or plant organs to understand the impact of the epigenome and small RNAs on gene expression. The multicellular complexity of the plant samples used in these studies is a difficulty when accessing in details the molecular mechanisms controlling gene expression because the data collected reflect the average contribution of each cell composing the plant and organ. As a consequence, working at the level of complex organs is diluting the datasets, are not revealing cell type specific transcripts, small RNA and epigenomes, and is challenging researchers when correlating epigenomic changes and role of transcription factors with the transcriptional regulation of genes.

Ideally, what is needed is a system biology approach at the level of a single cell to deeply investigate and integrate the transcriptome, the epigenome, the molecular function of DNA-binding proteins (i.e. protein-protein interactions of transcription factors and chromatin remodeling complexes, protein-DNA interactions) and the role of non-coding small RNAs. Of course, these regulations and interactions will change over time increasing the complexity of the model. Technological limitations are restraining the capture of these molecular changes at the level of one single cell. However, upon isolation, current technologies can be used to unravel the mechanisms controlling gene expression focusing on one single cell type.

The root hair cell (Figure 1) has recently emerged as an attractive single cell type model complementing already existing single plant cell type models such as pollen and cotton fiber. The advantage of the root hair cell compared to these two other models is related to the basic functions of the root hair cell: uptake of water and nutrients for the plant. Such essential function makes the root hair cell an attractive model to study the adaptation of plant cell to various environmental stresses including drought, salinity, nutrient deprivation, extreme pH, etc. Based on their characteristic lateral expansion, the root hair cell is also a model for studying plant cell determination, differentiation and elongation. Finally, when working on legume root hair cells, this single cell type is also a valuable system to investigate plant cell response to biotic stress (i.e. numerous –omic studies focused on the response of the soybean root hair cells to its inoculation by *Bradyrhizobium japonicum*, the soybean nitrogen-fixing symbiotic bacteria involved in nodulation [14-16]).

The root hair cell has received for years the interest of the plant science community. Many genes, mostly characterized in the model plant *Arabidopsis thaliana*, have been characterized for their role in controlling root hair biology. Recently, iRootHair [17], a comprehensive database of root hair genomics, lists these

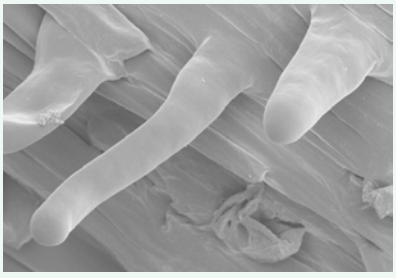

Figure 1 Surface electron microcopy picture of soybean root hair cells.

genes as well as genes from other plant species controlling root hair determination, initiation and elongation. Among these genes, transcription factor genes are characterized as master regulators of root hair cell development. These include the *A. thaliana WEREWOLF* and *CAPRICE* genes encoding MYB-related proteins and *GLABRA2* encoding a homeobox transcription factor [18-20]. In legume, root hair development is under the control of the *Lotus japonicus ROOTHAIRLESS1* (*RHL1*) gene which encodes a basic helix-loop-helix (bHLH) protein [21]. *A. thaliana RHL1* orthologs (At2g24260, At4g30980 and At5g58010) share the same function [21]). In rice, another bHLH protein, Os*RHL1* (*ROOTHAIRLESS1*), regulates root hair growth (i.e. the *Osrhl1* mutant shows a defect in root hair cell elongation compared to wild-type plants [22]). A similar phenotype was observed consecutively to the mutagenesis of the *Arabidopsis thaliana* R2R3-MYB transcription factor At5g45420 [23] and the bHLHs At*RSL2* and At*RSL4* gene (*ROOT HAIR DEFECTIVE 6-LIKE 2 and 4*, At4g33880 and At1g27740, respectively; [24]). Interestingly, *RSL4* gene is expressed just before the outgrowth of root hair cell and exclusively during root hair cell elongation (i.e. the expression of At*RSL4* in not detected in fully elongated root hair cells). Its overexpression leads to an unprecedented elongation of root hair cell supporting At*RSL4* to be a master regulator of root hair cell development [24].

To provide a more global understanding of the root hair cell biology and more specifically focus on the gene regulatory networks controlling gene expression and root hair cell adaptation to stresses, a system biology approach is needed. This approach will require the use of high-throughput sequencing technologies to generate transcriptomic, and epigenomic data sets as well as identify the pool of root hair small RNAs. Strong bioinformatic support will allow the integration of the various datasets. Ultimately, visualization tools might be developed enhancing the analysis of the datasets. Preliminary to any analysis, plant root hair cells will need to be evenly treated to insure consistency and repeatability of the experiments then isolated from the rest of the root system.

Having access to isolated root hair cell will have several major impacts on plant biology. Working at the level of one single cell type will help to clarify the regulation of gene expression and their perturbation to environmental stresses and will enhance the mapping of gene regulatory networks. Ultimately, controlling the activation and repression of these networks will lead to enhance plant root hair resistance to stresses.

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