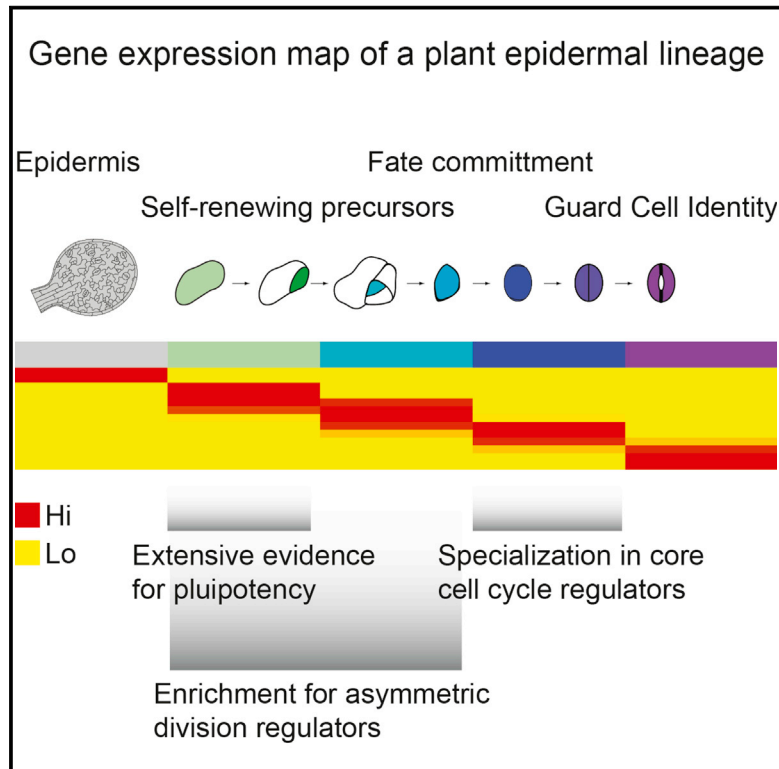


Developmental Cell

Transcriptome Dynamics of the Stomatal Lineage: Birth, Amplification, and Termination of a Self-Renewing Population

Graphical Abstract



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In Brief

Stomata facilitate plant gas exchange with the atmosphere. Adrian et al. profile the developing stomatal lineage, revealing increasing canalization of gene expression as cells become committed to specific fates and linking cell types previously thought to be independent. The data serve as a resource for further investigation of lineage specification in plants.

Highlights

- A gene expression atlas has been created for the *Arabidopsis* stomatal lineage
- Individual cell-type profiles complement profiles from shoot meristems and roots
- Profiling of meristemoids reveals unexpected pluripotency in the early lineage
- ENODLs and CYCD7 are regulators of cell division in stem cell contexts

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Transcriptome Dynamics of the Stomatal Lineage: Birth, Amplification, and Termination of a Self-Renewing Population

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SUMMARY

Developmental transitions can be described in terms of morphology and the roles of individual genes, but also in terms of global transcriptional and epigenetic changes. Temporal dissections of transcriptome changes, however, are rare for intact, developing tissues. We used RNA sequencing and microarray platforms to quantify gene expression from labeled cells isolated by fluorescence-activated cell sorting to generate cell-type-specific transcriptomes during development of an adult stem-cell lineage in the *Arabidopsis* leaf. We show that regulatory modules in this early lineage link cell types that had previously been considered to be under separate control and provide evidence for recruitment of individual members of gene families for different developmental decisions. Because stomata are physiologically important and because stomatal lineage cells exhibit exemplary division, cell fate, and cell signaling behaviors, this dataset serves as a valuable resource for further investigations of fundamental developmental processes.

INTRODUCTION

Multicellular organisms are comprised of diverse cell types that exhibit unique transcriptional profiles appropriate to their identity and function. The development of these cell types from a common precursor requires a profound set of changes in gene expression. Recent studies following the programming and reprogramming of embryonic stem cells or induced pluripotent cells have revealed a complex, yet fairly ordered set of changes (Xie et al., 2013; Young, 2011). Similar dynamic transcriptional profiles in intact developing organisms, however, have been more

challenging to obtain. Profiles of individual cell types from intact plants have revolutionized the way cell fates and responses can be understood, but these profiles largely feature terminally differentiated cell types (e.g., Birnbaum et al., 2003; Deal and Henikoff, 2010; Yang et al., 2008). Computational approaches have been used to infer the developmental states of specific cells (Brady et al., 2007), but we lack profiles isolated directly from true intermediate cell types along a developmental trajectory.

The production and pattern of stomata in the *Arabidopsis* epidermis have received considerable recent attention as a model for cell fate determination, cell-cell communication, and cell polarity and provide a clear and accessible model for adult stem cell lineages (Pillitteri and Torii, 2012). The stomatal lineage can be parsed into discrete intermediate steps, and cells representing those intermediate steps can be identified by gene expression markers, making this an ideal system from which to generate transcriptional profiles tracing the intermediate identities and fate transitions during development. The stomatal lineage begins with asynchronous and indeterminate early divisions and lacks a strict prepattern, allowing for flexible development. Flexibility is key because the stomatal lineage generates the majority of cells in the leaf epidermis and has the potential to modify both numbers and cell types in response to environmental cues (Hetherington and Woodward, 2003).

Beyond its utility as a developmental model, the lineage produces, as its ultimate products, stomatal guard cells (GCs), that act as valves facilitating plant/atmosphere gas exchange. Because they are essential for plant physiology and are present on all large land plants, stomata have been the subject of studies ranging from probes of single molecules to global scale eco-physiology. As a consequence of the wide-scale interest in stomatal properties, mature GC transcriptomes, proteomes, and metabolomes have been generated and stomatal activities modeled (Misra et al., 2014; Yang et al., 2008; Zhao et al., 2008). Because of increasing interest and progress elucidating the integration of environmental cues (such as light and carbon dioxide) with endogenous circuits to control stomatal production and activity (e.g., Casson and Hetherington, 2014; Engineer

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