



Review

A gateway with a guard: How the endodermis regulates growth through hormone signaling



José R. Dinneny*

Carnegie Institution for Science, Department of Plant Biology, Stanford, CA 94305, USA

ARTICLE INFO

Article history:

Received 18 July 2013

Received in revised form

18 September 2013

Accepted 19 September 2013

Available online 26 September 2013

Keywords:

Endodermis

Abscisic acid

Gibberlic acid

Root

Development

Salt stress

Auxin

ABSTRACT

The endodermis is a defining feature of plant roots and is most widely studied as a differentially permeable barrier limiting solute uptake from the soil into the vascular stream. Recent work has revealed that this inner cell layer is also an important signaling center for hormone-mediated control of growth. Auxin, gibberellin, abscisic acid and strigalactones all appear to depend on the endodermis to regulate root biology and point to this cell type as having important inter-cell layer regulatory activity, as well. In this review I discuss recent work detailing the importance of the endodermis in growth control and how this function is affected during responses to the environment.

© 2013 Elsevier Ireland Ltd. All rights reserved.

Contents

1. Introduction	14
2. The defining feature of the endodermis: the Casparian strip	15
3. Gibberellin-mediated growth control from the endodermis	15
4. Salinity-mediated growth regulation through ABA signaling in the endodermis	17
5. PIN-mediated auxin flux through the endodermis	18
6. Conclusions	19
Acknowledgment	19
References	19

1. Introduction

The root system of plants is intimately associated with the environment. As the root navigates through the heterogeneous soil matrix, a constantly changing set of environmental stimuli is perceived at the tip. Contact with organic and inorganic particles, pockets of air, non-uniform distributions of water and nutrients are encountered by the root tip as it grows. Add to this, interactions with other roots, fungi, microbes and animals and you have a network of interactions one could easily characterize as complex. Like our own modern world where we are bombarded by a

flush of advertisements seeking our attention, the root must integrate environmental stimuli and respond appropriately in order to successfully support plant growth.

Environmental stimuli could theoretically be sensed independently in each cell of the root and this response determined without regard to the activity of other cells. Alternatively, the root may sense and respond to stimuli in ways much more similar to animal systems, where sensory cells and a central nervous system collects and integrates information on the environment and where a coherent response is generated. While plants clearly lack structures that could operate like a brain, the problem of how to generate coherent responses based on information perceived from a complex environment in a multicellular context is very much common to both animals and plants. Indeed studying plant environmental responses is interesting from a basic biology standpoint, as plants

* Tel.: +1 650 739 4257.

E-mail addresses: dinneny@stanford.edu, jdinneny@carnegiescience.edu

probably have evolved independent mechanisms for generating such responses.

How do plants sense changes in their external environment? Do plants have sensory cells? Where are responses determined? These are important questions in plant biology and the answers to each one could be considered a significant discovery. Responses to light are arguably the most understood, but even for these stimuli, an exact understanding of which parts of the plant and which cell types are critical in regulating light-mediated responses are not clear.

To understand, at the mechanistic level, how plants respond to their environment, I think it is useful to make a comparison to other model systems to see what advances have been made and where we need to bridge gaps in our understanding of plants. In this regard, the study of the taste sensory system in mammals is one of the most advanced. The mouse taste receptors that directly perceive chemical stimuli for sweet, salty, sour, bitter and umami have been discovered [1]. The exact cells that express these receptors are known. The communication pathways from sensory neuron to brain are known. Finally, the cells within the brain where this information is communicated are known, and a gustotopic map of taste perception has been determined [2]. This work represents a truly phenomenal collection of knowledge and is at a level of detail absolutely essential to understand how a mouse interprets just five environmental variables. Clearly in plant biology, we must place a greater emphasis on understanding the mechanisms of perception, the cell types where perception occurs, the spatial scale for perception, and how information from different cell types and different parts of the plant is integrated to generate a coherent response.

If the plant root were a tongue, it would need more than five taste receptors. Just considering the micro- and macro-nutrients contained in Murashige and Skoog media [3], the root would need to interpret 17 different chemicals. This does not include the need to perceive proton concentration (pH), salinity, or heavy metals, nor organic compounds exuded by roots, microbes, and their secretions, or other organisms. How does the root sense all of these environmental variables and integrate this information into a coherent response? While the receptors for few of these substances have been discovered, many of the transporters that enable the influx or efflux of nutrients have been identified [4,5]. In particular, the spatial distribution and localization of some of these transporters have shown that specific tissue layers within the root may act as gateways for chemical transport.

One of the most important gateway cell types is the endodermis, whose Casparian strip is a defining feature of plant roots and is thought to endow this organ with many of the selectively absorptive properties necessary for nutrient and water uptake [6] (Fig. 1). In a quite fascinating way, work over the past five years has revealed that the endodermis does not just affect the transport of solutes between the outer and inner tissue layers, but may also be an important signaling center where responses controlling growth and morphogenesis are determined. Thus, like many of the gateways and borders that limit human traffic, which are often equipped with surveillance cameras and guards to detect an unlawful entry, the endodermis may also regulate the growth of the root if toxic chemicals pass into this cell layer.

The emphasis of this review will be on the hormonal signaling pathways acting in, or through, the endodermis that regulate growth. While a brief section is devoted to summarizing excellent work on the formation of the Casparian strip, I would recommend a recent review on this topic for those interested in delving deeper [6].

2. The defining feature of the endodermis: the Casparian strip

The endodermis with its Casparian strip is one of the central distinguishing features of roots and is familiar to anyone who has taken a course in basic plant anatomy (Fig. 1). While the number of layers for other cell types can vary to a great degree in roots of different species, there is nearly always a single layer of cells that have Casparian strips and surround the central vascular cylinder. In *Arabidopsis thaliana*, the mechanism specifying only one endodermal layer has been elucidated and involves the regulated diffusion of the SHORTROOT (SHR) transcription factor out of the stele by a related transcription factor SCARECROW (SCR) [7]. When the SHR protein enters into the cortex/endodermal initial cell, it interacts with low levels of the SCR protein, forming a heterodimer, which enters the nucleus. SHR and SCR induce SCR transcription, which further recruits SHR into the nucleus and it is thought that this restricts SHR from moving further into the outer tissues. SHR and SCR together activate the reorientation of the cell division plane and generate a periclinal division that leads to two cell layers. SHR acts in the innermost daughter cell and promotes endodermal identity, though the direct downstream targets responsible for such differentiation are not known.

Despite the clear function that is often ascribed to the endodermis, the actual physiological role of the endodermis and Casparian strip in plant–environment interactions is less clear [6]. Indeed the composition of the Casparian strip has only recently been dissected at the molecular-genetic level with any rigor [8–10]. The Casparian strip is a structure formed in the extra-cellular matrix of cells at the cross-wall between adjacent endodermal cells. This lattice-like network limits the ability of chemicals to diffuse through the extracellular space (apoplast) and presumably ensures that uptake of these compounds into the symplast must occur in the outer tissue layers or endodermis itself [9,11] (Fig. 1B). Based on this proposed pathway it logically follows that all compounds delivered to the vascular stream must at some point pass through the cytoplasm of the endodermis.

The endodermis undergoes several stages of maturation and not all cells within this layer are identical [6]. Indeed passage cells, which tend to accumulate less lignin and suberin in their extra-cellular matrix, are thought to provide routes for absorption of nutrients in more mature regions of the root [6]. How the Casparian strip affects absorption of nutrients at the root tip is less clear. The elongation zone, and early maturation zone are important sites for nutrient uptake, yet the Casparian strip is not fully formed in these regions. These data suggest that the function of the Casparian strip as barrier to solute uptake may differ depending on where along the longitudinal axis these solutes are taken up. It is also important to note that differences in the localization of transporters between the outer (cortex proximal) and inner (pericycle proximal) sides of the endodermis can occur before the deposition of lignin in the casparian strip and the formation of a diffusion barrier. Casparian strips may be more important in preventing back-flow of nutrients out of the stele during the transport of these molecules to the shoot, than in facilitating selective uptake. Indeed, apoplastic movement may be slow for some molecules and the symplastic route may be more rapid. A bucket-brigade model was proposed whereby transport of nutrients into and out of cells, as is done with auxin, would move nutrients up the concentration gradient into the stele [6].

3. Gibberellin-mediated growth control from the endodermis

Plant hormones are essential intermediary signals that communicate the developmental and physiological status of the plant,

Download English Version:

<https://daneshyari.com/en/article/2017116>

Download Persian Version:

<https://daneshyari.com/article/2017116>

[Daneshyari.com](https://daneshyari.com)