Root hair specification and its growth in response to nutrients

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Abstract

Plant root hairs are cylindrical tubular projections from root epidermal cells. They increase the root surface area, which is important for the acquisition of water and nutrients, microbe interactions, and plant anchorage. The root hair specification, the effect of root hairs on nutrient acquisition and the mechanisms of nutrients (calcium, iron, magnesium, nitrogen, phosphorus, and potassium) that affect root hair development and growth were reviewed. The gene regulatory network on root hair specification in the plant kingdom was highlighted. More work is needed to clone the genes of additional root hair mutants and elucidate their roles, as well as undertaking reverse genetics and mutant complementation studies to add to the current knowledge of the signaling networks, which are involved in root hair development and growth regulated by nutrients.

Keywords: calcium; iron; magnesium; nitrogen; phosphorus; potassium; root hair; ROS

Introduction of root hairs

The absorption of nutrients from soil is considered to be the main function of plant root hairs, which are long tubular-shaped outgrowths from root epidermal cells (Salazar-Henao et al., 2016; Huang et al., 2019; Liu et al., 2020). In citrus (trifoliate orange), root hairs rapidly grow, at a rate of 0.5 μm/min. They are approximately 14 μm in diameter and can grow to be 110 μm or more in length (Figure 1).

Root hairs have attracted a great deal of attention from plant scientists because their growth is a good subject for basic studies of plant cell biologists and physiologists (Grierson et al., 2015). As shown in Figure 2, citrus (trifoliate orange) roots grew along the surface of agarose-solidified nutrient medium in vertically-oriented petri plates, and root hairs are easily visualized using a stereomicroscope. Furthermore, the development and growth of root hairs occurs in a predictable and progressive manner in cells organized in files emanating from the root tip (Figure 3). This provides the opportunity for analysis of the cellular changes that occur during the process of root hair initiation and elongation.
Root hair specification

The specification patterns of root hairs have been divided into 3 types (Kim et al., 2006; Kim and Dolan, 2011). In type 1, root hair cells can be differentiating from other epidermal cells, such as in *Soleirolia soleirolii* and *Poncirus trifoliata* (Clowes 2000; Zhang et al., 2013). In type 2, the root epidermis consists of long and short cells, but only the short cells can initiate root hairs, such as in *Oryza sativa* (Kim and Dolan, 2011). Type 3 root hairs are located over epidermal cells (trichoblasts) which overly the junction of two cortical cells, whereas epidermal cells (atrichoblasts) which are located outside periclinal cortical cell walls cannot initiate root hairs, such as in *Arabidopsis* (Dolan and Costa, 2001; Grierson, 2014). Specifically, trichoblasts display a
greater cytoplasmic density, unique cell surface ornamentation, greater rate of cell division, distinct cell wall epitopes, and a lower rate of vacuolation (Grierson, 2014).

More precisely type 3 patterning information is governed by a network of transcriptional regulators. The GL2 (GLABRA2), which is the basic helix-loop-helix (bHLH) transcriptional activator, encodes a homeodomain transcription factor protein (Chen and Wang, 2019; Han et al., 2020). The GL2 gene is preferentially expressed in atrichoblasts within the meristematic and elongation regions of the root (Grierson, 2014; Chen and Wang, 2019). Careful examination using the GL2 reveals position-dependent gene expression within, or just one cell beyond, which implies that patterning information may be provided within these initial cells (Berger et al., 1998).

The WER (WEREWOLF) gene encodes a MYB transcription factor of the R2-R3 class (Lee and Schiefelbein, 1999; Wang et al., 2019). It is preferentially expressed in developing epidermal cells in atrichoblasts, which are the cells whose fate is mis-specified in the wer mutant (Grierson, 2014). In addition to the MYB DNA-binding domains, the WER protein possesses a phosphatidic acid (PA)-interacting region involved in nuclear localization (Yao et al., 2013). The Arabidopsis wer mutant forms root hairs on essentially every root epidermal cell, which implies that the normal role of WER is to promote atrichoblast cell differentiation and repress trichoblast cell differentiation (Yao et al., 2013; Grierson, 2014).

The TTG (TRANSPARENT TESTA GLABRA) gene encodes a small protein with WD40 repeats (Long and Schiefelbein, 2020). Long and Schiefelbein (2020) demonstrated the crucial role of TTG for the appropriate balance of target gene activation to achieve the proper pattern of root hair cell types during root development. TTG is able to physically interact with the basic helix-loop-helix (bHLH) transcriptional activator GL2 and MYB transcription factor WER which implies that a tripartite transcription factor complex is responsible for directing the non-hair cell fate (Song et al., 2011; Grierson, 2014).

Another the basic helix-loop-helix (bHLH) transcriptional gene, CPC (CAPRICE), causes root epidermis cells to differentiate to root hair cells (Kirik et al., 2004; Savage et al., 2013). Rather than causing ectopic root hair cells, the cpc mutant produces a reduced number of root hair cells (Wada et al., 1997; Savage et al., 2013). This implies that CPC is a positive regulator of the root hair cell fate. The gl2 mutation is epistatic to cpc, which suggests that CPC acts in the WER/TTG/GL2 pathway as a negative regulator of GL2 (Grierson, 2014). CPC can inhibit the function of the WER-GL3/EGL3-TTG complex by interfering with WER binding to GL3/EGL3 in a competitive manner (Song et al., 2011; Kang et al., 2013).

The SCRAMBLED (SCM) gene differs from the preceding genes because its mutant phenotype does not eliminate one of the epidermal cell types but merely alters the distribution of root hair cells and non-hair cells (Kwak et al., 2005; Kwak and Schiefelbein, 2014). SCM, an atypical leucine-rich repeat receptor-like kinase (LRR RLK) mediates the positional information to the epidermal cells and preferentially accumulates in cells adopting the root hair cell fate (Kwak et al., 2005; Kwak and Schiefelbein, 2014). Interestingly, the SCM gene is itself under the transcriptional feedback regulation of the WER-GL3/EGL3-TTG complex, because atrichoblast cells exhibit a complex-dependent reduction in SCM accumulation, relative to trichoblast cells (Kwak and Schiefelbein, 2008). This negative regulatory loop may serve to amplify SCM signaling in trichoblast cells.

Figure 4 shows a model for the specification of trichoblast (root hair cell) and atrichoblast (non-hair cell) types in the Arabidopsis root epidermis (modified from Bruex et al., 2012; Grierson, 2014). The proposed accumulation and interaction of cell fate regulators is shown within root epidermal cells destined to be trichoblast cells (in root hair cells) or atrichoblast cells (in the non-root hair cells). In this model, the pattern of hair and non-hair cell types relies on the relative activity of two competing sets of transcription factors, the R2R3 WER and MYB23 proteins vs. the one-repeat Mybs CPC, TRY, and ETC1 (Grierson, 2014).
Figure 3. Photograph of the root tip showing the progressive development of root hairs of citrus (trifoliate orange)

Figure 4. Model for the specification of trichoblasts and atrichoblasts in the *Arabidopsis* root epidermis (modified from Bruex *et al.*, 2012; Claire, 2014)

Note: The default fate for an epidermal cell is a root hair cell. Arrows indicate positive control, blunt lines indicate negative regulation, and broken lines indicate intercellular or intracellular protein movement.

These are able to form an active or inactive complex, respectively, with the TTG and GL3/EGL3 proteins. In immature epidermal cells in the atrichoblast cell position, it is proposed that a relatively high level
of WER is present and this predominately leads to the formation of the active complex, expression of GL2 (and probably other genes), and non-hair cell differentiation (Grierson, 2014). On the other hand, immature epidermal cells located in the trichoblast cell position are proposed to accumulate a relatively high level of CPC, which leads to inactive complexes, repression of GL2, and root hair cell differentiation (Grierson, 2014). SCM is proposed to mediate the effects of a position cue and initiate differential accumulation of the WER and CPC regulators (Grierson, 2014). The downstream feedback loops, including the negative effect of CPC and positive regulation by MYB23, are thought to stabilize and amplify the initial asymmetry in gene expression patterns (Grierson, 2014).

After specification, root hairs enter the phase of tip growth. Plants’ root hair tip growth can be influenced by soil permeability and edaphon, plant growth regulators, and mineral nutrients. Many researchers focused on the effects of phytohormones (such as auxins, ethylene, jasmonic acid, methyl jasmonate, strigolactone, and brassinosteroids) on root hair growth. However, research on nutrients affecting root hair development and growth is of great significance because the soil is often deficient in nutrients.

**Effect of root hairs on nutrients acquisition**

Root hairs can greatly increase the root surface area and hence vastly facilitate the absorption of nutrients from the soil. Water channels, as well as calcium, phosphate, and potassium, are located in the root hair surface area, and it has been suggested that root hairs take part in the absorption of most nutrients in plants (Libault et al., 2010). Even more, Wang et al. (2016) considered that long and dense root hairs are important traits in ensuring efficient absorption of nutrients in the early establishment of plants in nutrient-limited soil and low nutrients input environment cropping systems. As an adaptive response to nutrient deficiency, an increase in root hair length and density enhances root-soil contact and the absorptive area for nutrient absorption (Kohli et al., 2020). For example, the Arabidopsis mutant has more and longer root hairs which are more efficient in acquiring phosphate from infertile soil environments (Huang et al., 2018; Narang et al., 2000). Root hairs play a crucial role in nutrients acquisition by contributing 20-80% to the total nutrient uptake (Jungk, 2001; Kohli et al., 2020).

**Root hair growth in response to nutrients**

**Calcium**

The calcium ion (Ca^{2+}) is involved in most biological processes in the plant kingdom (Tortosa et al., 2019). As a second messenger, Ca^{2+} regulates a multitude of adaptational and physiological processes in plants, including cell expansion, cell division, responses to abiotic stress, cytoplasmic streaming, and pathogen defense (Westphal et al., 2019). Cytoplasmic Ca^{2+} regulates cytoskeletal rearrangements and vesicular trafficking in tip-growing systems such as root hair growth and development (Hepler et al., 2001). Wymer et al. (1997) reported that the Ca^{2+} gradient exists in growing root hairs, which is most pronounced in rapidly elongating root hairs. Studies have shown that a growing root hair has a localized gradient of Ca^{2+} concentration toward the growing apex, and the intensity of this gradient correlates with the growth rate of the root hairs (Takeda et al., 2008; Li et al., 2012). Confocal ratio imaging demonstrated that a tip-focused Ca^{2+} gradient is centered at the site of active growth of root hairs (Bibikova et al., 1997). Imposing an artificial tip-focused Ca^{2+} gradient reorients root hair growth toward the new gradient (Bibikova et al., 1997; Gilroy and Jones, 2000). Further evidence for the role of Ca^{2+}, using Ca^{2+} ionophores and channel blockers, suggests that disruption the Ca^{2+} concentration gradient results in inhibiting root hair tip growth (Wymer et al., 1997).

Foreman et al. (2003) and Takeda et al. (2008) showed that ROS produced by NADPH oxidase activates Ca^{2+} channels in the apical plasma membrane, leading to the tip-focused Ca^{2+} concentration gradient required for root hairs tip growth. Additional evidence from the Arabidopsis rhd2 mutant indicates that
application of exogenous ROS to *in vivo* root apices stimulates cell growth and Ca\(^{2+}\) influxes in root hairs, which induce root hair elongation (Foreman *et al*., 2003). The positive effect of exogenous ROS on root hair growth and development can be blocked by pharmacological inhibitors of calcium channels (Foreman *et al*., 2003). Artificially increasing cytosolic Ca\(^{2+}\) by treatment with calcium ionophore A23187 (mixed calcium-magnesium salt) induces production of elevated level of ROS around the root hair tip and inhibits tip growth because these large amounts of ROS disrupt the Ca\(^{2+}\) concentration gradient (Foreman *et al*., 2003).

As a consequence, the Ca\(^{2+}\) concentration gradient is a requirement in sustaining root hair growth and ROS can activate the calcium channel-mediated influx of Ca\(^{2+}\), which creates a Ca\(^{2+}\) concentration gradient and subsequently regulates root hair growth.

**Iron**

Iron (Fe) is an essential nutrient for plants because it catalyzes crucial cellular functions such as antioxidative cell protection, photosynthesis, chloroplast development, and chlorophyll synthesis. (Curie and Mari, 2017; Tsai and Schmidt, 2017). Although Fe is one of the most abundant elements in soils, it is mainly insoluble and non-available to plants (Tsai and Schmidt, 2017). So, plants have evolved efficient strategies to increase iron solubility and absorption efficiency, such as increasing root hairs (Cao *et al*., 2013). The number of root hairs was increased in response to Fe deficiency in *Arabidopsis* and citrus (Muller and Schmidt, 2004; Cao *et al*., 2013). Fe regulates root hair growth and development through the plant ferredoxin-like protein (PFLP), which affects ROS content by NADPH oxidase (NOX) (Sundaravelpandian *et al*., 2013; Nestler *et al*., 2014; Lin *et al*., 2015). Further evidence suggests that Fe has an interactive effect with ethylene on root hair initiation and elongation. Fe deficiency can lead to the formation of extra root hairs located in positions normally occupied by non-hair cells, which is dependent on ethylene signaling and requires functional EIN2 and ETR1 genes (Schmidt and Schikora, 2001).

**Magnesium**

Magnesium (Mg) is one of the essential nutrients for plants, playing a key role in plant metabolic processes and reactions, such as in photosynthesis as the central atom in chlorophyll, protein synthesis, phloem loading, photosynthetic CO\(_2\) fixation, and generation of ROS (Wang *et al*., 2020). Mg is also involved in a series of enzyme activities and protein synthesis, functioning as a bridge element between enzymes and substrates (Shaul, 2002; Gransee and Führs, 2013).

Recently, the effect of interactions among Mg, ROS, and Ca\(^{2+}\) on root hairs was reported. Low Mg availability results in longer and denser root hairs in *Arabidopsis* with higher concentrations of ROS and Ca\(^{2+}\) in the root tip and the root hair tip (Niu *et al*., 2014). However, when treated with diphenylene iodonium (an NADPH-oxidase inhibitor) or 1,2-bis (*o*-aminophenoxy) ethane-N,N,N',N'-tetraacetic acid (a Ca\(^{2+}\) chelator), the Ca\(^{2+}\) concentration gradient was eliminated for the enhanced growth of root hairs in low-Mg treatment (Yoshioka *et al*., 2001; Kadota *et al*., 2004). However, root hair development was blocked in high-Mg treatment and its inhibiting effect was restored when supplied with CaCl\(_2\) or phenazine methosulfate (a ROS generator) in *Arabidopsis* (Zhang *et al*., 2009; Niu *et al*., 2014). Niu *et al*. (2014) found that NADPH oxidase in roots is positively regulated by low Mg and is inhibited by high Mg levels, which is further evidence that Mg can control ROS in regulating root hair development. Therefore, the growth of root hairs is closely related to Mg availability by ROS and Ca\(^{2+}\) signaling.

**Nitrogen**

Ammonium (NH\(_4^+\)) and nitrate (NO\(_3^-\)) are the major forms of inorganic nitrogen absorbed in plants, which can increase the nutrient uptake to the optimal uptake of essential elements (Tavakoli Hasanaklou, 2020). There is clear molecular and electrophysiological evidence that root hair growth is regulated by NH\(_4^+\) and NO\(_3^-\). Expression of two putative NH\(_4^+\) and NO\(_3^-\) transporters genes (**LeNRT1-2** and **LeAMT1**) is root hair specific in tomato, which is regulated by an external N supply (Becker *et al*., 2002). Direct evidence using
scanning electron microscopy suggested that split root hairs are initiated in *Arabidopsis thaliana* after the addition of NH$_4$NO$_3$ to its roots (Yang et al., 2011). Yang et al. (2011) considers that the effects of NH$_4^+$ and NO$_3^-$ on split root hairs may be through the methyl jasmonate or ethylene signaling pathways, and that methyl jasmonate enhances the effect on split root hairs while ethylene decreases it. Furthermore, NH$_4^+$ and NO$_3^-$ may regulate calcium ions (Ca$^{2+}$) in root hair cells through Rho-related GTPase from plants and reactive oxygen species (Bloch et al., 2011; Bai et al., 2014). Thus, N may have interactions with hormones, ROS, and calcium in regulating root hair growth.

**Phosphorus**

Phosphorus (P) is extremely immobile in the soil and plays a variety of essential roles in plants (Kohli et al., 2020). It is an important mineral nutrient in plants, not only as a constituent of key cellular molecules such as ATP, phospholipids, and nucleic acids, but also has a pivotal role in cellular signaling, energy conservation and metabolic regulation (Shin et al., 2005; Macdonald et al., 2011; Kohli et al., 2020).

Many studies focused on understanding the mechanistic basis of P efficiency in order to develop crops that require less P input. Root hairs play a crucial role in P acquisition by contributing 50-80% to the total P uptake (Gahoonia and Nielsen, 1998; Jungk, 2001). P deficiency in the soil often induces dense root hairs in plants such as *Arabidopsis* and citrus (Zhu et al., 2005; Cao et al., 2013). In P deficient soil, the length and density of *Arabidopsis* root hairs significantly increases, expanding the root’s surface area from 0.21 mm$^2$ mm$^{-1}$ root under P sufficient conditions to 1.44 mm$^2$ mm$^{-1}$ roots under P starvation conditions, with root hairs constituting 91% of the total root’s surface area (Bates and Lynch, 1996). In addition, the response to P deprivation in root hairs is accompanied by an increase in ROS, which is necessary for root hair initiation and elongation through the Ca$^{2+}$ gradient (Carol and Dolan, 2006). In addition to ROS, auxins also participate in the interaction between root hair growth and P. Activation of the AUXIN RESPONSE FACTOR19 (ARF19) in low P conditions activates an important key basic helix-loop-helix (bHLH) transcription factor, ROOT HAIR DEFECTIVE6-LIKE 4 (RSL4), facilitating root hair growth and development (Bhosale et al., 2018; Giri et al., 2018). Thus, there is an interactive between ROS, auxins, and P on root hair growth and development.

**Potassium**

Potassium ion (K$^+$) is the most abundant cation in cells of plants, and plays a crucial role in plant development, such as enzyme homeostasis, leaf movements, assimilating transport, photosynthesis, and enzyme activation (Miao et al., 2010). K deficiency not only reduces mechanical stability, nutritional quality, and crop resistance to pathogens but also decreases root hair growth, such as in citrus root hairs (Cao et al., 2013). Gassmann and Schroeder (1994) considered that inward-rectifying K$^+$ channels in root hairs can function as both a physiologically important mechanism for low-affinity K$^+$ uptake and as regulators of membrane potential. *TRH1* (AtKt/AtKUP/HAK K$^+$ transporter family) was demonstrated in *Arabidopsis* that its mutant *trh1* partially impairs K$^+$ transport, which also blocks root hair development (Rigas et al., 2001). However, *trh1* cannot restore its defected root hair phenotype when it is grown at high external K concentrations (Rigas et al., 2001). This demonstrates that *TRH1* mediates K$^+$ transport in *Arabidopsis* roots and is responsible for specifics K$^+$ translocation, which is essential for root hair growth (Rigas et al., 2001).

Interestingly, studies found that K interacts with ethylene and auxins on root hair growth and development. When under K stress, both ethylene production and its biosynthesis gene expressions were increased (Jung et al., 2009). Ethylene signaling is a component of the plant’s response to low K that stimulates reactive oxygen species (ROS) production which is important for changes in root hair morphology (Jung et al., 2009). Rigas et al. (2013) consider that auxins modulate root hair specification at the differentiation zone. *TRH1* (the potassium transporter) is cell-specifications subcellular localized in the stele and epidermis, which engages in auxin transport and redistribution (Rigas et al., 2013). *TRH1* has a role in the sensing of external K$^+$ and the regulation of K dependent root hair growth (Rigas et al., 2013). In the *Arabidopsis* mutant *trh1*, auxin
imbalance causes poor root hairs (Vicente-Agullo et al., 2004; Rigas et al., 2013). Hence, K may regulate root hair growth and development though ethylene and auxin signaling.

Conclusions

To understand the development and function of a type of cell, the studies of root hairs have provided a useful and visual model to clarify new insights into general principles for plant cell biologists and physiologists, such as the inherent flexibility and plasticity in the growth and development of plant cells, in that the flexibility and plasticity are important for plants to adequately respond to their changing environment.

Improving plants to give root hairs high efficiency for nutrient absorption could reduce the adverse impact from stressful environments as well as enhancing agricultural sustainable development. More study is needed on the effects of nutrients on root hair development and growth, while root hair morphogenesis is driven by an amalgam of interacting processes controlled by complex signaling events. Some of the major factors involved in the signaling process during root hair growth and development have been identified, such as N, Ca^{2+}, Mg^{2+}, and P. It is not clear how these signaling component interactions regulate root hairs at the molecular and cellular level or how these signals interact with phytohormones to regulate its development and growth, such as auxins, ethylene, and JAs. Furthermore, the role and regulatory mechanism of the Ca^{2+} gradient in root hair initiation and tip growth still needs further study.

More works are needed to clone the genes of additional root hair mutants and elucidate their roles, as well as add to our current knowledge of the signaling networks involving nutrients, ROS, and phytohormones regulation on root hair specification, initiation, and tip growth by reverse genetics and mutant complementation studies.

Authors' Contributions

Conceptualization: MFS and DJZ; Data curation: XH, ML, and CHH; Formal analysis: TZG; Funding acquisition: MFS and DJZ; Investigation: XH and TZG; Project administration: DJZ; Supervision: MFS; Writing - original draft: XH and TZG; Writing -review and editing: MFS and DJZ. All authors read and approved the final manuscript.

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Conflict of Interests

The authors declare that there are no conflicts of interest related to this article.
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