

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 $\mu\text{m}/\text{min}$. 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.

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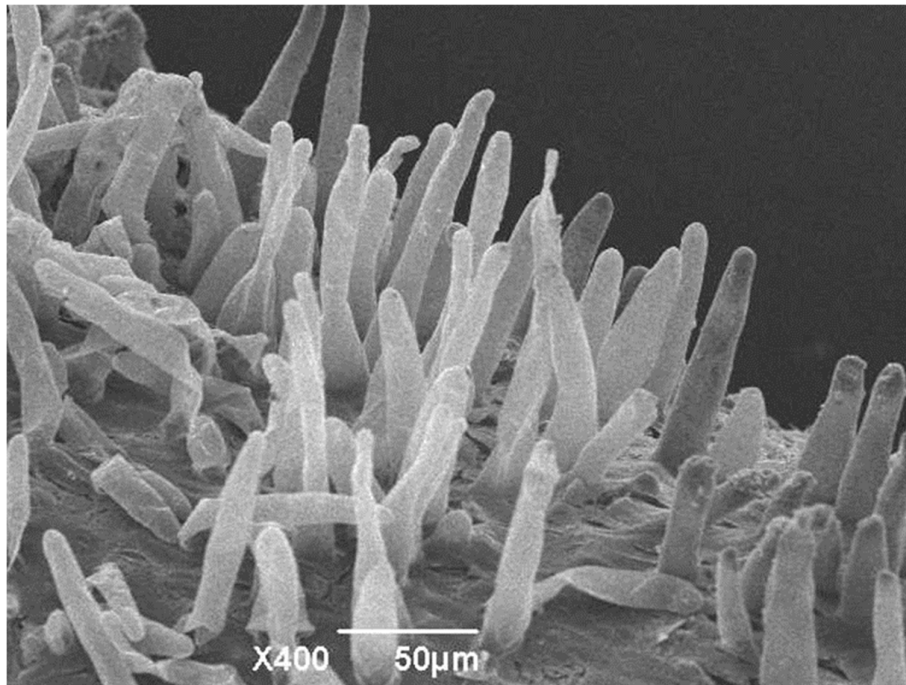


Figure 1. Scanning electron micrograph of root hairs of citrus (trifoliolate orange)

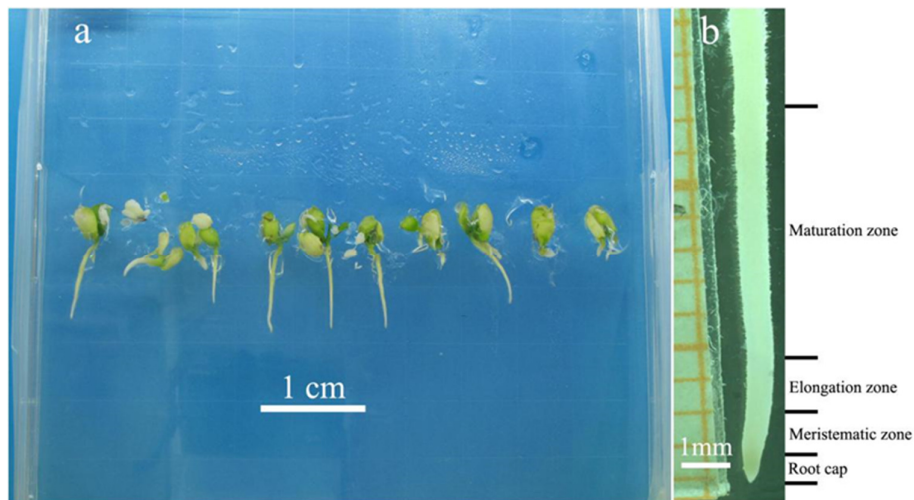


Figure 2. Development of citrus (trifoliolate orange) seedlings growing on agarose-solidified nutrient medium in vertically-oriented Petri plates (a). The roots grew along the surface of the medium, and root hairs are easily visualized by using a stereomicroscope (b)

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 (atrachoblasts) 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).

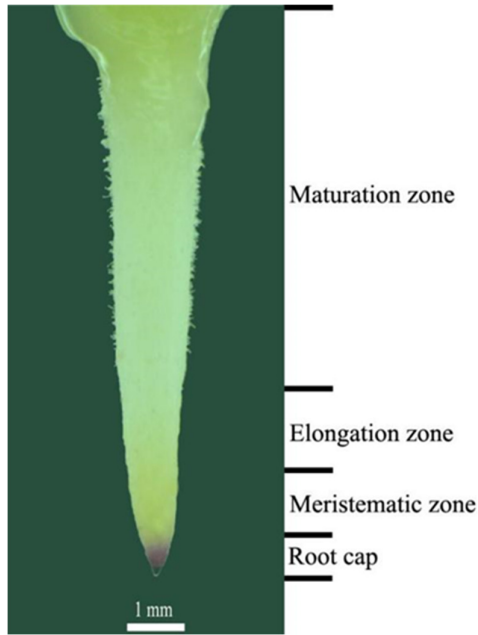


Figure 3. Photograph of the root tip showing the progressive development of root hairs of citrus (trifoliolate orange)

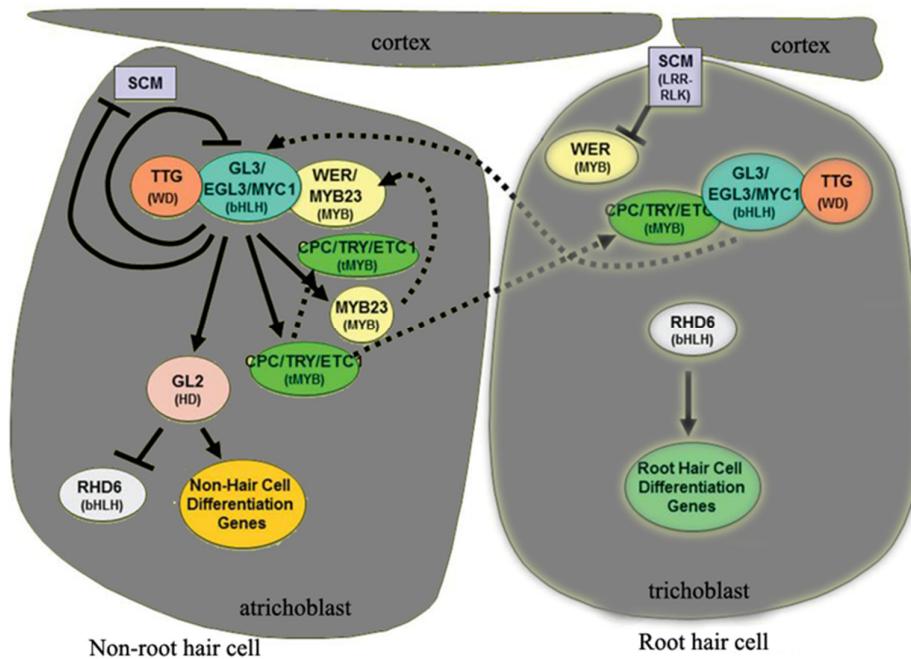


Figure 4. Model for the specification of trichoblasts and atrichoblasts in the *Arabidopsis* root epidermis (modified from Bruex *et al.*, 2012; Claire, 2014)

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 Führes, 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_4NO_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 $0.21 \text{ mm}^2 \text{ mm}^{-1}$ root under P sufficient conditions to $1.44 \text{ mm}^2 \text{ mm}^{-1}$ 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. *TRHI* (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 *TRHI* mediates K^+ transport in *Arabidopsis* roots and is responsible for specific 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. *TRHI* (the potassium transporter) is cell-specific subcellular localized in the stele and epidermis, which engages in auxin transport and redistribution (Rigas *et al.*, 2013). *TRHI* 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 through 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, Ca²⁺, Mg²⁺, 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 Ca²⁺ 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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