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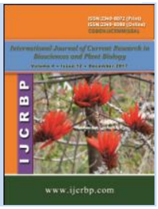

Review Article

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Effects and Mechanism of Nutrients on Root Hair Growth

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Abstract

Root hair is tubular projections from the root epidermal cell. In general, root-hair formation results in a significant increase in root surface area, which plays the important roles in nutrients and water uptake, plant anchorage, and interaction with soil microorganisms. In this paper, we discussed the effects of nitrogen, phosphorus, potassium, calcium, iron, and magnesium on root hair growth and their relevant mechanisms. Interaction exists between nutrients and phytohormones on root hair growth has also been discussion. As a result, more works are 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 the current knowledge of the signaling networks, which are involved in root hair cell fate specification, initiation, tip growth and maturation regulated by nutrients.

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Introduction

Root hair is tip-growing extensions from root epidermal cell (Grierson and Schiefelbein, 2002).

As extensions from root epidermis, root hairs can highly increase root surface area and play important roles in nutrient and water absorption, the adhesion of the growing root to the rhizosphere and to interact with soil microflora, such as arbuscular mycorrhizal (AM) fungi, nitrogen-fixing bacteria, etc (Grierson and Schiefelbein, 2002; Libault et al., 2010; Tanaka et al., 2014; Li et al., 2017; Vincent et al., 2017; Zou et al., 2017; Dolan, 2017). Especially, it is very important for plant to absorb scarcely mobile soil minerals, such as phosphorus (P) and potassium (K) from soil (Gahoonia et al., 1997; Gahoonia and Nielsen, 1998; Zuchi et al., 2011; Brown et al., 2012; Cao et al., 2013; Jungk, 2015).

Furthermore, water channels, as well as calcium, phosphate, potassium, etc are localized in root hair, and it has been suggested that root hair takes part in the absorption of most macro- and micro-nutrients in a number of crop plants (Gilroy and Jones, 2000; 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 both macro- and micro-nutrients in the early establishment of crops in nutrients-limited soil and low nutrients input environment cropping systems.

Root hair growth

Root hair growth consists of four stages, viz., cell fate specification, initiation, tip growth and maturation (Gilroy and Jones, 2000; Parker et al., 2000).

Cell fate specification

Many genes are participated in the regulation of root hair growth. The genes of *TRANSPARENT TESTA GLABRA* (*TTG*), *WEREWOLF* (*WER*) and *GLABRA2* (*GL2*), are specific expression in the non-hair epidermis cell, and are negative transcriptional regulators of root hair formation (Galway et al., 1994; Di et al., 1996; Masucci et al., 1996; Zhu et al., 2017). Conversely the MYB-like transcription factor encoded by the *CAPRICE* (*CPC*) and *TRYPTICHON* (*TRY*) genes are thought to be specific expression in the hair epidermis cell, and are positive regulate root hair development (Wada et al., 1997; Schellmann et al., 2002; Schiefelbein, 2003; Savage et al., 2008; Libault et al., 2010).

Root hair initiation

Root hair initiates from root epidermal cell. The initiation patterns of root hair have been divided into 3 types (Clowes, 2000; Kim et al., 2006). In type 1, root hair cell can differentiate from any epidermal cell (random type). The random type pattern occurs throughout *Soleirolia soleirolii* and *Poncirus trifoliata* (Clowes, 2000; Zhang et al., 2013). In type 2, the root epidermis consists of two sizes of cells (long and short), but only the short cell could differentiates into root hair cell (asymmetrical cell division type). The asymmetrical cell division type occurs in *Oryza sativa* (Kim and Dolan, 2011). Type 3 is position-dependent hair cell differentiation: root hair is located over epidermal cell overlying the junction of two cortical cells, whereas non-hair cell is located over a single cortical cell (positionally cued type). This positionally cued type has been found in *Arabidopsis* (Cormack, 1947; Dolan et al., 1993; Galway et al., 1994; Clowes, 2000; Dolan and Costa, 2001).

Root hair tip growth

During root hair tip growth, the deposition of new plasma membrane and cell wall material are confined to the expanding tip and the cytoplasm and pectic substance of the hair are highly polarized, with secretory vesicles concentrated located behind the hair tip, followed by the organelles required for the production and secretion of new cell wall and plasma membrane materials (Galway et al., 1997; Carol and Dolan, 2006). Ca^{2+} as well as cytoskeleton, annexins, calmodulin, GTPases and protein kinases are the candidate for the regulatory elements of the root hair tip-forced growth machinery (Gilroy and Jones, 2000).

Root hair maturation

In root hair maturation stage, ribosomes, mitochondria, and endoplasmic reticulum concentrate at the root hair tip (Cormack, 1947; Nestler et al., 2014).

Root hair and nitrogen (N)

The NH_4^+ and NO_3^- are main N-compounds in soil for plants utilization (Forde, 2002). With respect to NH_4^+ and NO_3^-, there is now clear molecular and electrophysiological evidence that root hair could transport N-compounds. The expression of two putative NH_4^+ and NO_3^- transporters genes (*LeNRT1-2* and *LeAMT1*) is root-hair-specific in tomato, which regulated by an external N supply (Lauter et al., 1996; Becker et al., 2002). In addition, Meharg and Blatt (1995) have revealed that the high-affinity NO_3^- transporter in *Arabidopsis* root hair is greatly up-regulated under NO_3^- deficiency, indicating that root hair providing adequate nutrients to the root. Direct evidence using SEM (scanning electron microscope) has suggested that split root hair were found in *Arabidopsis thaliana* after the addition of NH_4NO_3 (Yang et al., 2011). Furthermore, the effects of NH_4^+ and NO_3^- on split root hair may through Methyl jasmonate and ethylene signaling pathway that Methyl jasmonate can enhance the effect on split root hair while ethylene decrease it (Yang et al., 2011). NH_4^+ and NO_3^- may regulate calcium ion (Ca^{2+}) in root hair cell though Rho-related GTPase from plants (ROPs) and reactive oxygen (ROS), however, Ca^{2+} gradient is indispensability for root hair tip growth (Shin et al., 2005; Bloch et al., 2011; Bai et al., 2014). Thus, N may has interactions with phytohormones, ROS and calcium ion in regulating root hair growth.

Root hair and phosphorus (P)

Phosphorus (P) is extremely immobile in soil is an important macronutrient in plants, not only as a constituent of key cellular molecules such as ATP, phospholipids, and nucleic acids, but also playing a pivotal role in energy conservation and metabolic regulation (Marschner, 1995; Raghothama and Karthikeyan, 2005; Shin et al., 2005). Many studies focused on understanding the mechanistic basis of P efficiency, to develop crops that require less input. Gahoonia et al., (1997) confirmed that root hairs can satisfy 60% of the plant's P demand in soil (Gahoonia and Nielsen 1998). 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 increase significantly, 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 the 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 was accompanied by an increase in ROS, which necessary for root hair initiation and elongation through Ca^{2+} gradient (Foreman et al., 2003; Shin et al., 2005; Carol and Dolan, 2006). In short, there has an interaction between ROS and P on root hair growth.

Root hair and potassium (K)

Potassium (K) plays a crucial role in plant growth and development, such as photosynthesis, assimilate transport, enzyme homeostasis and activation, etc (Gassmann and Schroeder, 1994; Miao et al., 2010). K deficiency not only reduces crop resistance to pathogens, nutritional quality and mechanical stability, but also decreases root hair growth, such as citrus root hair (Pettigrew, 2008; Cao et al., 2013). Gassmann and Schroeder (1994) considered that inward-rectifying K^+ channel in root hairs can function as both a physiologically important mechanism for low-affinity K^+ uptake and as regulator of membrane potential. It was demonstrated that the mutant *trh1* (AtKT/AtKUP/HAK K^+ transporter family) has partially impaired in K^+ transport, which also blocked root hair growth in *Arabidopsis* (Rigas et al., 2001). However, the defected root hair phenotype in *trh1* could not restore when mutant seedlings were grown at high external K concentrations (Rigas et al., 2001). Rigas et al., (2001) considered that *TRH1* mediated K^+ transport in *Arabidopsis* roots and was responsible for specific K^+ translocation, which was essential for root hair elongation. Interestingly, researchers also found that K interacted with phytohormones on root hair growth, such as ethylene and auxin. When treated with K starvation, both endogenous ethylene level and the ethylene biosynthesis genes expression levels were increased (Shin and Schachtman, 2004; Jung et al., 2009). Ethylene signaling is a component of the plant's response to low K that stimulates the production of reactive oxygen species (ROS) and is important for changes in root hair morphology and whole plant tolerance to low K conditions (Jung et al., 2009). With regards to auxin, Rigas et al., (2013) consider that auxin modulates root hair morphogenesis at the differentiation zone. *TRH1* (the K transporter) was cell-specific subcellular localized in stele and epidermis, which engagement in auxin transport (Rigas et al., 2013). In *Arabidopsis* mutant *trh1*, auxin imbalance caused poor root hairs (Vicente-Agullo et al., 2004; Rigas et al., 2013). Hence, K may regulate root hair growth though the ethylene and auxin signalings.

Root hair and calcium (Ca)

Calcium (Ca) is involved in most biological processes in the plant kingdom (Weinl and Kudla, 2009). It serves as a second messenger and regulates a multitude of adaptation, developmental, and physiological processes in plants, including cell division, cytoplasmic streaming, responses to abiotic stress, adjustment of ion homeostasis, and pathogen defense (Bush, 1995; Sanders et al., 2002; White and Broadley, 2003; Kim et al., 2009). Cytoplasmic Ca^{2+} is known to regulate cytoskeletal rearrangements and vesicular trafficking in tip-growing systems such as root hair growth system (Hepler et al., 2001). Early research has discovered that the Ca^{2+} gradient was existed in the growing root hairs, which being most pronounced in the rapidly elongating root hairs (Wymer et al., 1997). Studies also 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 hair (Schiefelbein et al., 1992; Pierson et al., 1996; Felle and Hepler, 1997; Wymer et al., 1997; Takeda et al., 2008; Li et al., 2012). Furthermore, electrophysiological studies which using the vibrating probe, showed that Ca^{2+} influx was higher at root hair tip than at the base or sides of growing root hair (Schiefelbein et al., 1992; Herrmann and Felle, 1995; Jones et al., 1995).

Foreman et al., (2003) and Takeda et al., (2008) both considered that ROS produced by NADPH oxidase which activated Ca^{2+} channels in the apical plasma membrane, leading to the tip-focused Ca^{2+} concentration gradient required for root hair polar growth. Additional evidence from *Arabidopsis rhd2* mutant indicated that application of exogenous ROS to in vivo root apices stimulated cell growth and Ca^{2+} influxes in root hair, which induced root hair elongation (Foreman et al., 2003). The positive effect of exogenous ROS on root hair growth could be blocked by pharmacological inhibitors of calcium channels (Foreman et al., 2003). Artificially increasing cytosolic Ca^{2+} by treating with calcium ionophore A23187 (mixed calcium-magnesium salt) induced production of elevated level of ROS around the root hair tip and inhibited its tip growth for that these large amounts of ROS disrupted the Ca^{2+} concentration gradient (Foreman et al., 2003). In short, Ca^{2+} concentration gradient is a requirement in sustaining root hair elongation and ROS can activate calcium channel-mediated influx of Ca^{2+}, which creates a Ca^{2+} concentration gradient and subsequently influences root hair tip growth.

Root hair and iron (Fe)

Iron (Fe) is an essential nutrient for plants, which catalyzes crucial cellular functions such as photosynthesis, chlorophyll synthesis, chloroplast development, antioxidative cell protection, etc (Siminis and Stavrakakis, 2008; Curie and Mari, 2017; Tsai and Schmidt, 2017). Although Fe is one of the most abundant elements in soils, but it mainly exists as the insoluble and nonavailable to plants (Tsai and Schmidt, 2017). So plants have evolved efficient strategies to increase iron solubility and absorption efficiency, such as increasing root hair (Muller and Schmidt, 2004; 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 may though plant ferredoxin-like protein (PFLP), which affects ROS content by NADPH oxidase (NOX) (Shin et al., 2011; Sundaravelpandian et al., 2013; Nestler et al., 2014; Lin et al., 2015). Further evidence suggests that Fe has interaction 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).

Root hair and magnesium (Mg)

Magnesium (Mg) is an essential mineral nutrient for plant metabolic processes and reactions, such as photophosphorylation, photo-oxidation in leaf tissues, chlorophyll formation, protein synthesis, photosynthetic CO_2 fixation, phloem loading, generation of ROS, and so forth (Cakmak and Yazici 2010). Mg is also involved in many critical biochemical and physiological processes in plants, thus, influencing plant growth and development (Cakmak and Yazici 2010; Gransee and Führs 2013).

Recently, the effect of interactions among Mg, ROS, and Ca^{2+} on root hair has been reported. Low Mg availability resulted in longer and denser root hair in *Arabidopsis* with greater concentrations of ROS and Ca^{2+} in the root tip and a stronger Ca^{2+} concentration gradient in the root hair tip (Niu et al., 2014). However, when treated with diphenylene iodonium (DPI, an NADPH-oxidase inhibitor) or 1,2-bis(*o*-aminophenoxy)ethane-N,N,N',N',-tetraacetic acid (BAPTA, a Ca^{2+} chelator), the Ca^{2+} concentration gradient was eliminated for the enhanced growth of root hair in low-Mg treatment (Frahry and Schopfer, 1998; Yoshioka et al., 2001; Kadota et al., 2004). Instead, root hair growth was blocked in high-Mg treatment and the inhibiting effect was restored when supplied with $CaCl_2$ or phenazine methosulfate (PMS, a ROS generator) in *Arabidopsis* (Zhang et al., 2009; Niu et al., 2014). The study outlined by Niu et al., (2014) showed that NADPH oxidase in root was positive regulated by low Mg and was inhibited by high Mg level, which is further evidence that Mg could control ROS to regulating root hair growth and development. Therefore, the growth and development of root hair is closely related to Mg availability, which though ROS and Ca^{2+} signaling.

Future Perspectives and Conclusions

Improving plants to make root hair high efficiency of nutrients and water uptake should reduce the environmental impact of agriculture as well as increase crop production and enhance agricultural sustainable development. Even abundant research papers carry on deeper studying to the effects of nutrients on root hair growth. But 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 have been identified, such as N, Ca^{2+}, Mg^{2+}, P, and so forth. It is not clear how these signaling components interaction regulate root hair at the molecular and cellular level, or how these signals interact with phytohormones to regulate root hair growth, such as auxin, ethylene, etc.

Furthermore, the mechanism of Ca^{2+} gradient on root hair tip growth is still scarce.

In brief, more works are 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 the current knowledge of the signaling networks, which are involved in root hair cell fate specification, initiation, tip growth and maturation regulated by nutrients.

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