Plant Root Hair Growth in Response to Hormones

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Abstract

Plant root hair is tubular projections from the root epidermis. Its can increase root surface area, which is very important for nutrients and water uptake as well as interaction with soil microorganisms. In this short review, we discussed the effects of hormones (auxin, ethylene, jasmonic acid, methyl jasmonate, strigolactones, and brassinosteroids) on root hair growth. It was highlight the interaction between auxin and ethylene on root hair growth. Furthermore, the mechanisms of jasmonic acid, methyl jasmonate, strigolactone and brassinosteroids on root hair growth may through auxin or ethylene signaling pathway partly. In future, more genes relating to root hair growth needed clone 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 growth that regulated by hormones.

Keywords: auxin; brassinosteroids; ethylene; jasmonic acid; methyl jasmonate; root hair; strigolactones

Introduction of root hair

Root hairs can increase root surface area greatly and enhance the absorption of nutrients and water (Cao et al., 2013; Vincent et al., 2017; Dolan, 2017; Liu et al., 2018). Its growth always consists of four stages, viz., cell fate specification, initiation, tip growth and maturation (Fig. 1).

In the stage of cell fate specification, TRYPHTICHON (TRY) and CAPRICE (CPC) genes were been confirmed specific expression in the trichoblasts (epidermis which bulge to root hair), that positively regulated root hair formation (Wada et al., 1997; Schellmann et al., 2002; Savage et al., 2008; Libault et al., 2010). In contrast, GLABRA2 (GL2), TRANSPARENT TESTA GLABRA (TTG), and WEREWOLF (WER) were specific expression in the atrichoblasts (epidermis which cannot initiate to root hair), that negatively regulated root hair initiation (Cristina et al., 1996; Masucci et al., 1996; Walker et al., 1999; Zhu et al., 2017). The initiation patterns of root hair have been divided into 3 types: asymmetrical cell division type, random type and positionally cued type (Clowes, 2000; Kim et al., 2006a). In asymmetrical cell division type, the root epidermis (such as Oryza sativa) consists of two sizes of cells, long and short, but only the short cell can differentiates into root hair cell (Kim and Dolan, 2011). In random type, root hair cell can differentiate from any root epidermis of plants, such as citrus (Zhang et al., 2013) and Soleirolia soleirolii (Clowes, 2000). The positional cued type has been found in Arabidopsis: a trichoblast is located over a single cortical cell, whereas trichoblast overlying the junction of two cortical cells (Clowes, 2000; Dolan and Costa, 2001).

In root hair tip growth, the deposition of new plasma membrane and cell wall material are confined to the expanding tip and the cytoplasm 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, 2002, 2006; Nielsen, 2009). During root hair maturation, ribosomes, mitochondria, and endoplasmic reticulum concentrate at the root hair tip (Nestler et al., 2014).

Root hair growth could be influenced by various factors such as soil edaphon, culture substrates, plant growth regulators, mineral nutrients and so on. However, many researchers focused on the effects of auxin, ethylene, jasmonic acid, methyl jasmonate, strigolactone, brassinosteroids on plant root hair development and growth.
Root hair growth in response to hormones

**Auxin**

Auxin is considered as the important signaling molecule involved in regulating root hair growth (Liu et al., 2018a, b). Exogenous auxins (1-naphthylacetic acid and Indole butyric) can promote root hair growth significantly (Rahman et al., 2002; Liu et al., 2016; Zhang et al., 2018). In Arabidopsis, the auxin response mutant axr1 and aux1 have shorter and fewer root hairs for missing auxin signal (Rahman et al., 2001, 2002). Based on transcriptome sequencing data, 90% of genes related to root hair growth were positively regulated by auxin (Bruex et al., 2012).

It has been demonstrated that PIN, ATP-BINDING CASSETTE B (ABCB), AUXIN RESISTANT 1 (AUX1) and LIKE AUX1 (LAX) genes which regulating auxin transport in root has positive correlation with root hair growth (Rahman et al., 2002; Ganguly et al., 2010; Zhang et al., 2018). 1-naphthoxyacetic acid and 2-naphthoxyacetic acid, as auxin transport inhibitors, blocked root hair growth for missing auxin signal (Rahman et al., 2002; Zhang et al., 2018). The auxin transportation channel from root tip to root hair zone was been blocked in Arabidopsis mutant ein2, which blocked root hair growth (Rahman et al., 2002). Auxin synthesis which controlled by tryptophan aminotransferase related (TAR), flavin-containing monoxygenase (YUC3), etc, also affects root hair growth (Zhang et al., 2016, 2018). Understanding auxin biosynthesis is another factor in understanding root hair growth.

**Ethylene**

Ethylene is considered as another vital signal molecule involved in regulating root hair growth (Pitts et al., 1998). Zhang et al. (2016) confirmed that ethylene stimulates the growth of root hair of citrus. EIN2 as a positive regulator of ethylene responses, has been demonstrated that inducing root hair growth (Rahman et al., 2002; Zheng and Zhu 2016). In Arabidopsis, the ethylene response mutations ein2 and etr1 have fewer root hairs, while the ethylene overproducing mutant eto1 has longer root hairs (Masucci and Schiefelbein, 1996; Pitts et al., 1998; Rahman et al., 2002). Furthermore, the ethylene precursor (1-aminocyclopropane-1-carboxylic acid) can induce root hair growth, whereas ethylene biosynthesis inhibitors (aminooxvylnlyglycine and AgN03) can block it (Leblanc et al., 2008; Zhang et al., 2016).

What’s fascinating is that the interaction between ethylene and auxin on root hair growth. The ethylene precursor (1-aminocyclopropane-1-carboxylic acid) could restore root hair growth in Arabidopsis auxin response mutant axr1, while exogenous auxin (naphthylacetic acid) can relieve the inhibitory effect on root hair growth in ethylene signal transduction mutant ein2 (Pitts et al., 1998; Rahman et al., 2002; Muday et al., 2012). On one side, endogenous auxin plays a major role in root hair growth, and its concentration in trichoblast determines the initiation and growth of root hair (Jones et al., 2009; Ganguly et al., 2010). On the other side, ethylene is a key signal of root hair growth for that of growth regulators or mineral nutrients regulate root hair growth by control the concentration of endogenous ethylene in root hair cells (Michael et al., 2001). Ethylene could affect endogenous auxin level by regulating its biosynthesis and transport way, which is important for root and root hair initiation (Rahman et al., 2002; Rüžička et al., 2007; Zhang et al., 2016). Furthermore, Auxin can stimulate ethylene biosynthesis, which regulating root hair growth positively (Pitts et al., 1998; Muday et al., 2012).

**Jasmonic acid and Methyl jasmonate (JA and MeJA)**

JA and MeJA can also regulate root hair growth positively (Zhu et al., 2006; Liu et al., 2016). However, there is interaction between JA/MeJA and ethylene on regulating root hair growth. On the one side, the positive effects of JA and MeJA on root hair growth can diminish in ethylene inhibitor (aminooxvylnlyglycine or AgN03) treatment and in Arabidopsis ethylene-insensitive mutant etr1 (Zhu et al., 2006). On the other side, the JA biosynthesis inhibitor (ibuprofen or salicylhydroxamic acid) not only diminished the facilitating effect of ethylene precursor (1-aminocyclopropane-1-carboxylic acid) on root hair growth, but also decreased the growth of root hair in ethylene over-producing mutant eto1 (Zhu et al., 2006).

**Strigolactone (SLs)**

Recently studies shown that SLs are a novel class of plant hormones that regulate plant’s shoot and root growth (Xie et al., 2010; Waters et al., 2017). GR24 (a synthetic bioactive SL) positively regulated root hair growth in Arabidopsis (Kapulnik et al., 2011). However, excess GR24 could lead to disrupting auxin transport and high level of auxin in root hair, which has a negative effect on root hair growth (Kapulnik et al., 2011). Studies have presented that SLs affect root hair growth by the genes of PINs and TIR1 which regulating auxin transport in root (Koltai et al., 2010; Kapulnik et al., 2011; Mayzlish-Gati et al., 2012). Hence, there is interaction between SLs and auxin on regulating root hair growth.
Fig. 2. The model of the interactions among hormones in regulating root hair growth

**Brassinosteroids (BRs)**

BRs have different effects on root hair growth, that it reduced the growth of root hairs in Arabidopsis but induced its growth in Oryza sativa (Kim et al., 2006b; Hardtke et al., 2007). Studies showed that AXR3/IAA17 involving in BR signaling pathway (Mouchel et al., 2004, 2006; Kim et al., 2006b). In addition, the gain-of-function mutations axr3/iaa17 inhibited root hair growth by affecting BR signal (Knox et al., 2003). Thus, there has a cross-talk of BR and auxin in regulating root hair growth.

**Brassinosteroids (BRs)**

**Future perspectives and Conclusions**

There have complicated interactions among hormones in regulating root hair growth (Fig. 2). However, auxin and ethylene might play leading roles in root hair growth. Improving plants to make root hair high efficiency of water and nutrients uptake should increase crop production. Even abundant research papers carry on deeper studying on root hair growth, but root hair morphogenesis is driven by an amalgam of interacting processes controlled by complex signaling events, such as auxin, ethylene, etc. It is not clear how these signaling components interaction regulating root hair at the molecular and cellular level. More works are need to clone the genes of additional root hair mutants and undertake reverse genetics and mutant complementation studies to add to our current knowledge of the signaling networks involving hormones regulating root hair growth.

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**References**


