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Short Review

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 a,b). 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, *TRYPTICHON* (*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.

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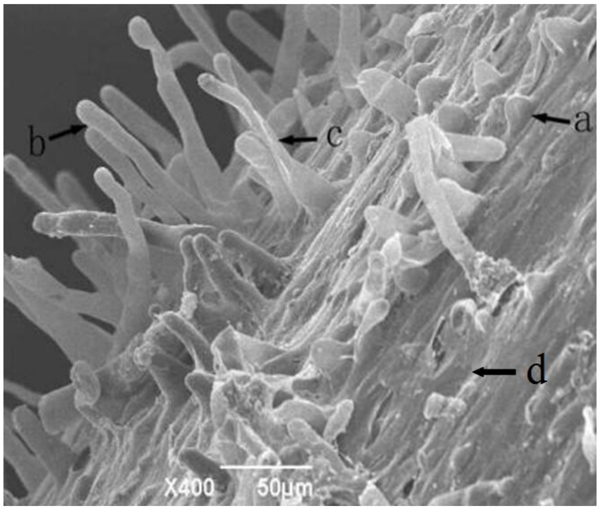

Fig. 1. The growth stages of root hair of citrus. Note: a-initiation, b-tip growth, c-maturation, d-cell fate specification

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-BINGING 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 (*TARs*), flavin-containing monooxygenase (*YUCs*), 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 stimulate 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) could induce root hair growth, whereas ethylene biosynthesis inhibitors (aminoethoxyvinylglycine and $AgNO_3$) 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; Růžička *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 has 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 (aminoethoxyvinylglycine or $AgNO_3$) 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 has interaction between SLs and auxin on regulating root hair growth.

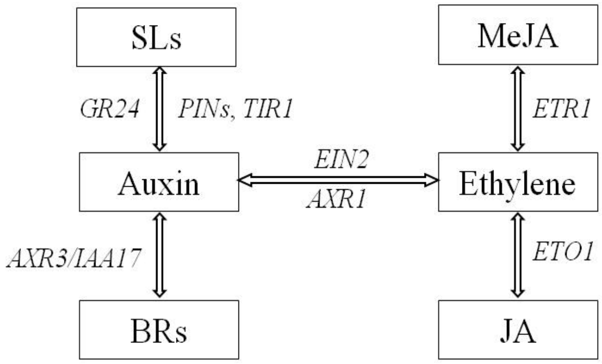

Fig. 2. The model of the interactions among hormones in regulating root hair growth

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.

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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