

## Review

# A review on the molecular mechanism of plants rooting modulated by auxin

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**Adventitious root formation is a key step in vegetative propagation of woody or horticultural species, and it is a complex process known to be affected by multiple factors. The process of roots development could be divided into three stages: root induction, root initiation, and root protrusion. Phytohormones, especially auxin, played an essential role in regulating roots developments. This review focused on recent advances in the research of plants rooting genomics and proteomics, including auxin biosynthesis, metabolism, transport, and signaling pathway which are involved in modulating plants rooting and the significances of proteomics on research the differences of rooting ability.**

**Key words:** Auxin, molecular mechanism, genomics, proteomics, rooting.

## INTRODUCTION

A lack of competence to form adventitious roots by cuttings occurs routinely and is an obstacle for the vegetative propagation and rapid fixation of elite genotypes (Céline et al., 2006). In dicotyledonous plants, adventitious roots can be defined as roots that develop from organs such as leaves and stems under unusual circumstances. Adventitious root formation is a key step in vegetative propagation of woody or horticultural species, and problems associated with rooting of cuttings frequently result in significant economic losses (De Klerk et al., 1999).

It is a complex process known to be affected by many factors. A moving signal, mediating plant phototropism,

had been first demonstrated when Charles Darwin studied the response of canary grass coleoptiles to unilateral light, and later known as auxin (Darwin, 1880; Tomasz et al., 2006). Auxin involves in many developmental processes including embryo and fruit development, organogenesis, vascular tissue differentiation, root patterning, elongation and tropistic growth, apical hook formation and apical dominance (Kepinski and Leyser, 2005a). Auxin is one of the major endogenous hormones known to play a role in the formation of adventitious roots; it has been shown to be effective inducers of adventitious roots in many woody species (Selby et al., 1992; Di'az-Sala et al., 1996; Goldfarb et al., 1998; De Klerk et al., 1999).

Auxins are usually synthesized in the stem tip and tender leaves of aerial parts of plants, and then transported to the action site (Ljung et al., 2001). Genetic and environmental factors, which have effects on auxin biosynthesis, metabolism, transport, and signaling pathway, could modulate plants development. Recent advances in studying mutations of *Arabidopsis* and rice increase the understanding of rooting mechanisms by auxin. More recently, proteome analysis has become a major approach for functional characterization of plants (Canovas et al., 2004). It has proven useful for the identification of proteins associated with a range of developmental or physiological processes (Plomion et al., 2000; Bae et al., 2003; Gallardo et al., 2003; Mang et al.,

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**Abbreviations:** IAA, indole-3-acetic acid; IBA, indole-butyric acid; NAA, 1-naphthalene acetic acid; DAG, days after germination; AUX1, auxin resistant 1; TIR1, transport inhibitor response 1; SCF<sup>TIR1</sup>, Skp1-Cullin-F-box complex; InsP<sub>6</sub>, inositol hexakisphosphate; NPA, N-1-naphthylphthalamic acid; PID, serine/threonine kinase; PINOID; ARFs, auxin-response factors; MAPK, mitogen-activated protein kinase; 2-DE, Two-dimensional electrophoresis; MALDI-TOF-MS, matrix-assisted laser desorption/ionization time of flying mass spectrometry.

2004; Schiltz et al., 2004; Vincent et al., 2005).

## ADVENTITIOUS ROOT FORMATION

Adventitious root formation is a key step for vegetative propagation. The process of adventitious root formation can be divided into three stages: root induction in which molecular and biochemical changes occur before any cytological event; root initiation when the first anatomical modifications take place; and protrusion, corresponding to the emergence of root primordia (Berthon, 1990; Heloir, 1996).

Lateral roots development in *Arabidopsis* provided a model for the study of hormonal signals that regulated postembryonic organogenesis in higher plants (Reed et al., 1998; Zhang and Forde, 2000; Casimiro et al., 2001). Lateral roots originated from pairs of pericycle cells, in several cell files positioned opposite the xylem pole, that initiated a series of asymmetric, transverse divisions to create 3 to 10 "short" daughter cells (Casimiro et al., 2001). These short daughter cells have undergone radial enlargement and subsequently divided periclinally to give rise to inner and outer cell layers. Further periclinal divisions resulted in the formation of lateral root primordia (Bhalerao et al., 2002).

The indole-3-acetic acid (IAA) exhibited a positive effect for lateral roots development (Bhalerao et al., 2002; Casimiro et al., 2001). IAA in the roots was derived predominantly from shoot tissues before 10 days after germination (DAG) in *Arabidopsis* seedlings and an accumulation of IAA at the root tip between 1 and 3 DAG was detected. At 5 to 7 DAG, the primary root experienced a short pulse of IAA that was derived from leaves 1 and 2. It had been proposed that lateral roots formation could be divided into two phases: an initiation phase that was dependent on a root tip-localized source of auxin, and an emergence phase that was dependent on a leaf-derived source.

## PHYSIOLOGICAL EFFECTS OF GROWTH HORMONES ON PLANTS ROOTING

The success of artificial growth hormones, as well as the equipment controlling temperature and humidity, made the cutting propagation simple and convenient. Now, the main sources of growth hormones widely used in the promotion of rooting cuttings are the indolic-3-butyric acid (IBA), 1-naphthalene acetic acid (NAA), indole-3-acetic acid (IAA), and commercialization of the root promoter such as ABT root powder. The successful formation of adventitious roots is an obligatory phase of vegetative propagation in many woody plants; this is related to the presence of auxin (McClelland et al., 1990; Kim et al., 1998). Rooting of gardenia microcuttings has achieved high percentages *in vitro* with the use of IBA (Pontikis, 1983).

Sunita Kochhar (2008) studied rooting and sprouting behaviour of stem cuttings of biofuel plant *Jatropha curcas* and their performance under field conditions in relation to auxin application; pretreatment with IBA and NAA increased both the rooting and sprouting. Although many researchers generally thought suitable growth hormones treatment have promotion on cuttings rooting, in particular to improve rooting number and lower the rate of partial root (Farmer, 1992), the rooting ratio declined with the hormone concentration increasing and high hormone concentration have side effects on the root development (Edson, 1991; Mason, 1989; Hare, 1974).

## PLANTS ROOTING GENOMICS

Auxin is a critical hormone regulating plants growth and development (Woodward et al., 2005; Teale et al., 2006), and plays an important role in modulating lateral roots formation (Ruegger et al., 1998; Rogg et al., 2001).

The effects of auxin biosynthesis and metabolism on plants rooting IAA is the main active form of auxin, and can be synthesized by two ways: one is tryptophan-dependent pathway; the other is tryptophan-independent pathway (Cohen et al., 2003). Lots of regulative genes had been found in auxin biosynthesis pathway, such as *SUR1* (Boerjan et al., 1995), *YUCCA* (Cheng et al., 2006), *FLOOZY* (Tobena-Santamaria et al., 2002), and so on. In *Arabidopsis* seedlings, overexpression of the bacterial auxin synthesis gene – *iaaM*, *IAM* changed into IAA under the effect of hydrolase (Romano et al., 1995). *YUCCA* gene encoded a flavin monooxygenase-like enzyme, and have a function in catalyzing tryptamine into hydroxyl-tryptamine (Zhao et al., 2001). Functional changes of these genes would influence auxin biosynthesis, and then changed the rooting process.

Auxin metabolism includes formation of binding-auxin and oxidative decomposition. Plants have two different types of binding-auxin. One is ester-bonds, which consists of carboxyl in auxin and sugar or myoinositol by oxygen bridge; the other is amino-bonds, which is formed by peptide bond between carboxyl in auxin and amino acid or polypeptide (Woodward et al., 2005).

IBA is more effective in inducing plants rooting than IAA, because the former is more stable than the latter, and more important, IBA can be changed into IAA by the mechanism of parallel to fatty acid  $\beta$ -oxidation (Bartel et al., 2001). Auxin usually combines with sugars, sugar alcohols, amino acids, and proteins (Bandurski et al., 1995; Slovina et al., 1999). Binding-auxin was known as a form of active auxin storage and long-distance transportation, but binding-auxin itself has special auxin activities (Szmids-Jaworska et al., 1997; Tam et al., 2002), and could regulate plants growth and development.

## The effects of auxin transport on plants rooting

Auxins are usually synthesized in the stem tip and tender

leaves of plants, and transported to the basal part of stem by transport carrier along the main stem (Friml, 2003). The gradient of auxin associated with the transportation is important in organs formation, apical dominance, latent roots production, and tropic movement. Auxin transporters include auxin-effluxes and auxin-influxes; the direction of auxin flow has been determined by the localization of these carriers at the plasma membrane.

Plants hormones researches had been coming on apace in the past few years. The receptors for these hormones had been identified, especially auxin-receptors, and had turned out to be surprisingly different from those in the animal (Bishopp et al., 2006). AUX1 (auxin resistant 1) is a kind of acknowledged auxin-influx in *Arabidopsis*. *aux1* mutant has defects in lateral root development, that resulted from the disruption of AUX1-mediated transport between IAA source and sink tissues (Alan, 2002). In 2005, a receptor for auxin was identified as the F-box protein TIR1 (transport inhibitor response 1), which is a component of a cellular protein complex known as SCF<sup>TIR1</sup> (Skp1-Cullin-F-box complex). This complex, consisting of AtCUL1, RBX1, and ASK1/ASK2-similar to SKP of *Arabidopsis* (Gray et al., 2001; Cardozo and Pagano, 2004), was recruited to the receptor in an auxin-dependent manner and, after binding to TIR1 and repressors Aux/IAA, was degraded. The *Arabidopsis tir3* mutation caused a reduction in polar auxin transport, leading to fewer lateral roots (Ruegger et al., 1997). The research showed that the TIR1-ASK1 complex had a mushroom shape, with the leucine-rich-repeat domain of TIR1 forming the cap, and the F-box of TIR1 along with ASK1 forming the stem. The research of TIR1 as a receptor increased the understanding of the auxin signal pathway, but further questions were the inevitable. An inositol hexakisphosphate (InsP<sub>6</sub>) is at the bottom of auxin binding site; its association with TIR1 could be essential for auxin binding and function of the receptor, but the mechanism are unknown.

PIN proteins are the main auxin efflux facilitators and associates with auxin maxima in distal regions of both shoots and roots (Berleth et al., 2007; Leyser, 2005; Jones, 1998). PIN proteins might participate directly in auxin transport or help in the assembly of other proteins with efflux activity such as the AtMDR/PGP proteins (Noh et al., 2001, 2003). The PIN genes were thought to encode components of the auxin efflux machinery (Gälweiler et al., 1998; Utsuno et al., 1998; Friml et al., 2002). Mutations in the every member of PIN gene family led to developmental defects (Friml et al., 2002, 2003). Aida et al. (2004) and Ikram et al. (2005) investigated the collective contribution of five PIN genes in the control of cell division and cell expansion during root outgrowth; furthermore, they assessed how the PLETHORA (PLT) genes regulate PIN gene activity during pattern formation.

The auxin transport inhibitor N-1-naphthylphthalamic acid (NPA) arrests lateral roots development by blocking the first transverse division and causes indoleacetic acid to accumulate in the root apex while reducing concentra-

tion in basal tissues. In *Arabidopsis* roots development, a distal auxin maximum correlated with pattern formation and the orientation and extent of cell division, inhibition of polar auxin transport strongly affected these processes (Sabatini et al., 1999). The initiation of lateral roots and leaf primordia were also associated with changes in auxin transport (Benkova et al., 2003; Friml et al., 2003). These conclusions revealed that auxin transportation strongly affected plants rooting.

Auxin is an endogenous signal regulating plants development. Friml et al. (2004) proved auxin efflux was controlled by the PIN-FORMED (PIN) family of proteins, whose localization was regulated through the action of the serine/threonine kinase, PINOID (PID). PIN proteins are asymmetrically localized at the plasma membrane that directs the auxin flow. The research on *pin*-mutant found that root collapse was significantly delayed, with the accumulation of auxin in the roots. This revealed that function-loss in PID had influence on auxin transport, as well as roots development. More importantly, over expression of PID shifted the polarity of PIN from basal to apical, which reversed the auxin flow and resulted in agravitropy and mis-specification of the root pole. But it needs to be researched thoroughly whether PIN is a direct target of PID, and how PID is regulated.

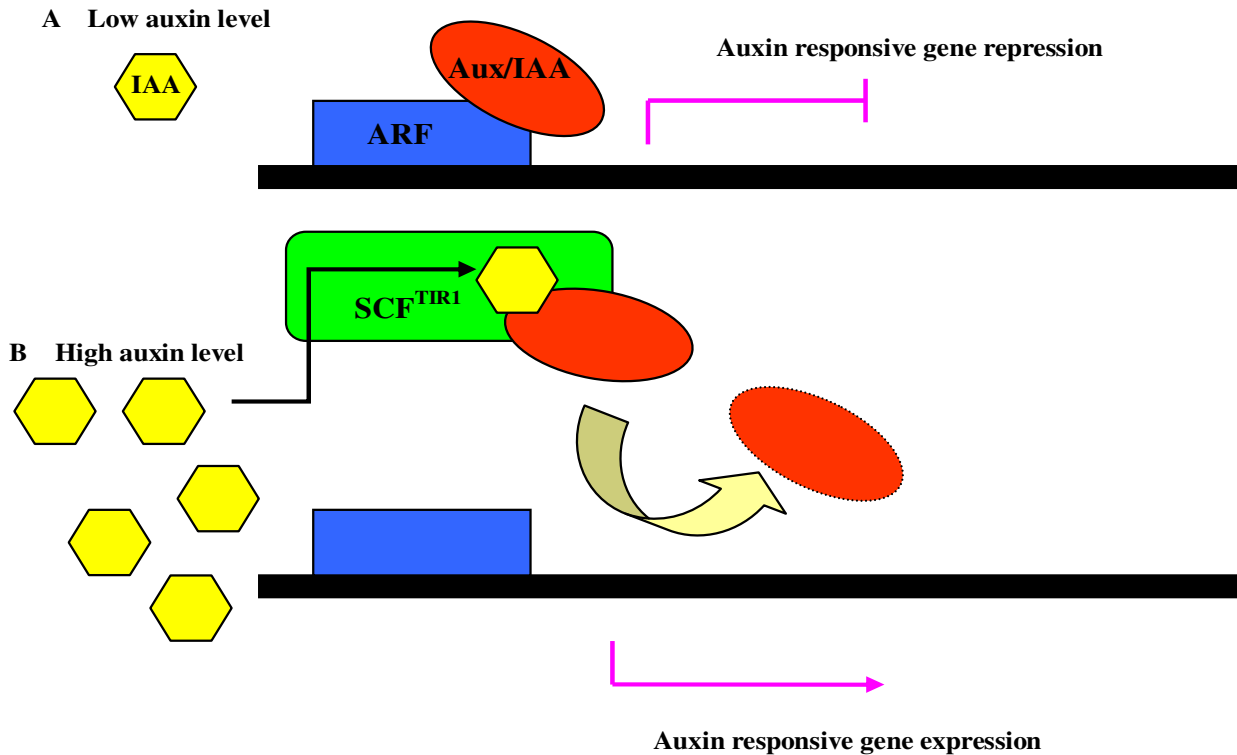
### The effects of auxin signal pathway on plants rooting

Auxin signal pathway has been mediated by ubiquitin-dependent proteolysis. Many auxin-induced genes are regulated by the interplay of two classes of gene transcription factors, auxin-response factors (ARFs) and the Aux/IAA repressors. Figure 1 is a schematic of IAA signaling pathway.

ARFs bind to auxin-response promoter elements in auxin-response genes. (A) When auxin concentration is below a threshold level, Aux/IAA repressors associate with ARF activators and repress the expression of these genes. (B) Conversely, higher concentration of auxin leads to destruction of the Aux/IAA repressors, and to activation of the genes.

Many researches showed that the AXR1 gene aided the assembly of an active SCF (Skp1/Cullin/F-box) complex that probably promoted degradation of the AUX/IAA transcriptional repressors in response to auxin (Ouellet et al., 2001; Gray et al., 2001; Ramos et al., 2001; Zenser et al., 2001). The transcription activator NAC1 is a member of the NAM/CUC family of transcription factors. SINAT5 has ubiquitin protein ligase activity and can ubiquitinate NAC1; over expressing SINAT5 produced fewer lateral roots in *Arabidopsis*. Low expression of NAC1 in roots can be increased by treating with a proteasome inhibitor, which indicated that SINAT5 targets NAC1 for ubiquitin-mediated proteolysis to down-regulation auxin signals in plant cells (Qi Xie et al., 2002).

*Crl1* encodes a member of the plant-specific AS2/LOB protein family and mediate the negative transcription fac-



**Figure 1.** A schematic of IAA signaling pathway

tors AUX/IAAs to the initiation of crown and lateral root development (Inukai et al., 2005). Therefore rice mutants, *crl1* and *crl2*, were defective in crown roots formation (Inukai et al., 2001, 2005; Liu et al., 2005).

Auxin activates many early-response genes that are thought to be responsible for diverse aspects of plants growth and development (Abel et al., 1996). It had been reported that the mitogen-activated protein kinase (MAPK) signal cascade involved in auxin signal pathway (Mizoguchi et al., 1994); NPK1 activated a MAPK cascade that led to the suppression of early auxin response gene transcription (Yelena et al., 1998). Although many plants MAPK signal cascade had been identified, their precise physiological functions in plants are barely unknown (Hirt, 1997).

## PLANTS ROOTING PROTEOMICS

### Research survey of plants rooting proteomics

At present, the research of functional genomics focus on the mRNA, but lots of experiments showed that the correlation between mRNA abundance and protein abundance was not good (Mackay et al., 2004; Tian et al., 2004). As opposed to the relatively constant genome sequence that defines the organism as a whole, the physiologic and developmental state of any particular cell

is best depicted by the array of proteins that it contains at any given time. The complete array of proteins that a cell produces (that is, its proteome) may be experimentally trickier to define than its genome, but the science of proteomics will surely be one of the greatest dividends to come from genome sequencing (Harry, 2000). Access to complete genomic data will mean that even very limited peptide sequence analyses can provide enough information to identify proteins and specify their complete primary structures from public databases. The power of proteomics is thus clear.

After the proteins are resolved into spots by two-dimensional electrophoresis, they can be digested into fragments (by an endoprotease such as trypsin) that are then sequenced. It is mass-spectrometric sequencing technology that brings proteomics efforts to fruition. Two-dimensional electrophoresis (2-DE) is the important technique in proteomics; the differential protein spots could be identified by matrix-assisted laser desorption/ionization time of flying mass spectrometry (MALDI-TOF-MS). Tsugita (1994) separated 4892 protein spots by 2-DE from rice in roots, stems, leaves, seeds, and identified 3% proteins. Konishi (2005) found several kinds of proteins from maize correlated with rooting by 2-DE. One of the proteins, fructose-bisphosphate aldolase, increases roots development. Céline (2006) discovered 11 proteins related to the contents of endogenous hormones and the number of adventitious roots primor-dial

by investigated *Arabidopsis* mutant. Therefore, proteomics is a useful tool not only in finding rooting related proteins, determining function in organ formation, but also as a means of molecular marker to identify rooting ability of plant.

### Proteomics database

Proteomics database stored lots of protein information expressed by the organisms, making it possible to identify the found protein. At present, all kinds of 2-D databases can be searched on the internet, for example, WORLD-2DPAGE of ExPASy server provides about 30 2-D databases; Make2dbb is a software package for constructing 2-D databases freely. But when we provide fundamental insights into organic development of genome sequence, there is a little information. So the advanced research of organ-proteomics should be done.

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