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The Role of Auxin in Plastic Development of Plant Root System Architecture in Response to Abiotic Stimuli

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ABSTRACT

Plants have evolved abilities to cope with changes in their external environment because of their sessile nature. This regulatory plasticity leads to modifications in physiology, morphology and/or development, which improve the chances of survival and reproductive success under adverse environmental conditions. Hormones are involved in the link between the genome and the environment, and directly affect phenotypic characteristics. The growth hormone auxin has been considered as a master regulator controlling almost every aspect of plant growth; however, the role of auxin in plant developmental plasticity in response to biotic and abiotic stimuli has not drawn much attention. Recently, genetic and biochemical analyses have revealed that changes in auxin biosynthesis, polar transport and auxin sensitivity in response to various abiotic stresses can produce changes in gene transcription and modification of metabolic rates in stressed plants. Dynamic localization of auxin and inhibitory, stimulatory and/or synergistic interaction with other hormones both influence phenotypic plasticity. These results have provided novel insights into a molecular basis for auxin regulation of developmental plasticity in coupling extrinsic and intrinsic cues. In this review, we summarize recent advances in plant root morphological adaptation with a particular focus on understanding the interaction between the auxin and environmental cues in plant root plastic morphogenesis.

Keywords: adaptive response, auxin, environmental stimuli, developmental plasticity, abiotic stress

Abbreviations: ABA, absisic acid; **ARF**, auxin-response factor; **AUX/IAA**, auxin/indole-3-acetic acid; **IAA**, indole-3-acetic acid; **LRs**, lateral roots; **N**, nitrogen; **NPA**, naphthylphthalamic acid; **P**, phosphorus; **PIN**, pin-formed; **QC**, quiescent center; **RSA**, root system architecture; **SOS**, salt overly sensitive; **TIR1**, transport inhibitor response 1

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INTRODUCTION

Recent global environmental changes have raised many new problems for ecology and human beings that how the global environment will change and the physiological, ecological and evolutionary responses to the environment of individual organisms, communities and ecosystems have drawn extensive attention in recent years. Because many

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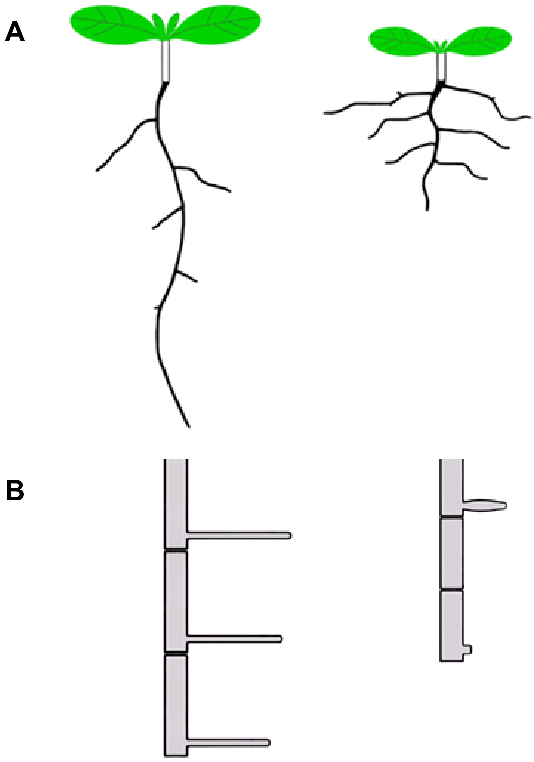

Fig. 1 Schematic diagram of the morphological changes associated with plant adaptation to salt stress. When the plants are exposed to high salinity, growth of primary root is inhibited and lateral roots are stimulated (**A**). Initiation and elongation of root hairs are also negatively affected by salt stress (**B**).

plants and animals are capable of developing specific characteristics that are well adapted to particular environments, research into evolutionary ecology, molecular biology and behavioral development has focused on the interplay between the developing organism and the environment in which it lives. The key finding is that a given genotype can give rise to different phenotypes depending on environmental conditions.

As sessile organisms, plants have evolved a great capacity to adapt to adverse environmental conditions. The process of adaptation is complex, and there can be immediate and short-term changes in physiology, behavior and morphology. Long-term adaptation to the environment can also be expressed in various aspects of development of the next generation. Such adaptive responses allow plants to cope with environmental stresses and pressures. For example, under salt stress, plants activate ion transporters/antiporters to exclude excessive Na^+ or get the Na^+ into the vacuoles to maintain ion homeostasis (physiological adaptation) (Serrano and Rodriguez-Navarro 2001; Zhu 2003) and *Arabidopsis* seedlings change their root growth direction to avoid damage from excessive ions (behavior adaptation) (Sun *et al*. 2008). Plants also show reduced root growth and enhanced formation of lateral and adventitious roots (morphological adaptation) (West *et al*. 2004; He *et al*. 2005; Saqib *et al*. 2005; Sun *et al*. 2008) because the ultimate size, shape, and structure of a plant mainly depends on postembryonic development, morphological adaptation, also known as phenotypic plasticity, in response to external stimuli is essential for reproductive success and survival. As shown in **Fig. 1**, different plant species showed similar characteristics in morphological adaptation in response to mild and chronic stress, including inhibition of root elongation, stimulation of lateral root (LR) development and ultimate coordinate morphological changes (Potters *et al*. 2007, 2009).

Stress-induced physiological, behavioral and morphological adaptation is mainly influenced by plant hormones. Among these factors, abscisic acid (ABA) plays very important roles in many aspects of plant development and in initiation of adaptive responses to various abiotic stresses. Great progress has been achieved in understanding ABA-dependent signaling pathways that modulate the physiological, behavioral and morphological adaptation of plants in response to drought, cold and salinity (Xiong *et al.* 1999; Verslues and Zhu 2005). Ethylene is another so-called stress hormone having roles in plant adaptation. It has been documented that ethylene is involved in stress-induced growth retardation and promotion of root hair development (Tanimoto *et al.* 1995; Morgan and Drew 1997; Alonso *et al.* 1999; Dolan 2001). However, we still lack a clear understanding of the regulatory role of the major plant hormones auxin and cytokinin in plant adaptation to various abiotic stresses. Plant hormone auxin indole-3-acetic acid (IAA) is known to control almost every aspect of plant growth from putting down roots to determining where to start a new root or branches. Although growing evidence implicates a link between auxin and plant morphological adaptation, the exact role of auxin in shaping the response to environmental stresses and the underlying mechanisms for phenotypic plasticity are not well defined. Since there are some excellent reviews that summarize the recent advances in understanding the effects of ABA and ethylene on plant stress responses (Morgan and Drew 1997; Verslues and Zhu 2005), this review will focus on major recent advances in auxin-mediated plant growth and developmental responses to various abiotic stresses.

HOW AUXIN SHAPES PLANT MORPHOGENESIS

Just like its name implies, auxin plays a central role in plant growth. Plant growth refers to an irreversible increase in size consisting of an increase in both cell number and cell size. Since the first documentation by Charles and Francis Darwin in *The Power of Movement in Plants*, the isolation and function of auxins have drawn much attention over the past century. Recent systematic application of genetic and molecular techniques has led to the elucidation of molecular mechanisms of auxin-mediated growth regulation.

The most important advance was the discovery of a central regulatory role of auxin in root development and specification from the earliest stages of embryogenesis (Sabatini *et al.* 1999; Friml *et al.* 2003). Auxin was found to accumulate in the small apical derivatives after division of the zygote of *Arabidopsis* plant and maximum remains apically positioned throughout the development of the preglobular embryo (Friml *et al.* 2003). During late embryo development, auxin response maxima can be clearly detected at the root pole (Mravec *et al.* 2008). The pattern of auxin distribution and maximum are dynamically regulated, which subsequently specify the root meristem organization and determine the ability of roots to grow (Blilou *et al.* 2005).

The changes in the patterns of auxin accumulation and redistribution are correlated with the distribution of the specific members of the Pin-formed (PIN) protein family, the auxin efflux carriers (Aida *et al.* 2002; Friml *et al.* 2003). For example, during *Arabidopsis* embryogenesis, a location shift of PIN1, PIN4 and PIN7 was found to be responsible for auxin distribution and determination of auxin maximum. It is proposed that different auxin efflux carriers have varied transport rates of auxin which may also contribute to changes in auxin gradients and relocation (Vanneste and Friml 2009). In addition, local differences in auxin synthesis and/or metabolism may also influence the auxin gradient and maximum (Zazimalova and Napier 2003). Furthermore, several lines of evidence suggest that auxin regulates the cell cycle and proliferation of root meristem via changes in cellular redox status (Jiang and Feldman 2005). In the root tip, the redox status of the quiescent center (QC), a small population of cells that rarely divides, and the adjacent rapidly dividing cells are different, and the QC displays higher oxidation levels (Kerk and Feldman 1995; Takahama 1996; Kert *et al.* 2000; Jiang *et al.* 2003). High levels of auxin induce generation of reactive oxygen species (ROS)

(Joo *et al.* 2001; Schopfer *et al.* 2002; Kawano 2003; Jiang and Feldman 2005). Auxin-induced ROS generation may involve free radical generation via peroxidase-catalyzed oxidation of IAA (Kawano 2003), alteration in the activities of redox-associated systems (Jiang *et al.* 2003; Pignocchi and Foyer 2003) and/or induction of NADH oxidase that leads to the production of H_2O_2 (Liszkay *et al.* 2003; Morre *et al.* 2003). However, the mechanism of how auxin leads to generation of ROS is still unknown. In plants, there is convincing evidence that cellular redox status is directly linked to the cell proliferation (Kerk and Feldman 1995; Jiang *et al.* 2003; Liso *et al.* 2004). It is proposed that during embryogenesis, development modulation of auxin homeostasis and redox status is critical for establishment and maintenance of the QC and meristem integrity (Jiang and Feldman 2005).

The levels and the patterns of auxin distribution are crucial for cell expansion and enlargement. Addition of low levels of IAA stimulated rapid elongation of corn (*Zea mays* L.) coleoptiles (Rayle *et al.* 1970). Campanoni and Nick (2005) showed that 1-naphthaleneacetic acid (NAA) promoted tobacco cell elongation through an auxin binding protein 1 (ABP1) mediated pathway. Loss of function in *ABP1* or over-expression of *ABP1* resulted in altered cell elongation in *Arabidopsis* (Jones *et al.* 1998; Chen *et al.* 2001). Other evidence of auxin dependent regulation of cell elongation/expansion includes that mutants deficient in auxin and auxin response are dwarf (Ruegger *et al.* 1997; Takase *et al.* 2004). These results suggest a critical role of auxin and auxin sensitivity in plant cell elongation. Most recently, Grieneisen *et al.* (2007) demonstrated that PIN-mediated regulation of auxin gradients and maxima in the root tip guide root growth by modulating cell fate specification, cell division and elongation.

Auxin and auxin redistribution is also required for development of lateral roots (LRs), particular LR meristem initiation and primordium development (Laskowski *et al.* 1995; Casimiro *et al.* 2001; Benková *et al.* 2003; Fukaki *et al.* 2007; Fukaki and Tasaka 2009). For example, exogenous application of auxin promotes LR formation by activating division of the pericycle cells in *Arabidopsis* roots (Laskowski *et al.* 1995; Magidin *et al.* 2003). The mutants overproducing auxin or having an altered auxin distribution generate more LRs (Boerjan *et al.* 1995; Marchant *et al.* 2002). In contrast, gain-of-function *solitary-root 1* (*slr1/ iaa14*) and *iaa28* mutants have no or less LRs respectively (Fukaki *et al.* 2002; Dreher *et al.* 2006). It is clear now that during plant development, auxin can reactivate differentiated cells to form lateral meristems, promote additional vascular tissue development and regulate LR formation. The levels and locations of the auxin maximum determine the positions and quantity of LRs (Dubrovsky *et al.* 2008). Recently, Laskowski *et al.* (2008) discovered that stretching root cells initiates changes in auxin transport by up-regulation of auxin influx carrier (AUX1) and down-regulation of PIN, leading to LR initiation in plants. Furthermore, recent studies reveal the role of two RING-finger ligases SINAT5 and XBAT32 in LR initiation, indicating that multiple E3s, in addition to the $SCF^{TIR1/ABF1\text{-}5}$ E3, are directly involved in the action of auxin during LR initiation (Xie *et al.* 2002; Nodzon *et al.* 2004). SINAT5, ubiquitinates NAC1, a transcriptional activator that functions downstream of TIR1 to promote auxin-mediated lateral root development. The mechanism of protein degradation might allow rapid adjustments of the position and density of LR meristem initiation.

Auxin also controls root epidermal cell development in a concentration-dependent manner. The epidermal cell fate specification, initiation and outgrowth all require auxin. A recent study showed that AUX1-dependent transport through non-hair cells maintains an auxin supply to developing hair cells as they increase in distance from the root tip, and sustains root-hair outgrowth (Jones *et al.* 2009). Clearly, alterations in auxin localization and maximum can differentially modify growth of cells within an organ, thus influencing organ size and shape, and subsequent overall plant architecture.

In the last few decades, great progress has been made and many mutants have been isolated, ranging from auxin synthesis to auxin transport and auxin responses (Hobbie and Estelle 1995; Ottenschläger *et al.* 2003; Paponov *et al.* 2005; Mockaitis and Estelle 2008). With this increase in the determinants found, the auxin signal pathway is becoming much clearer. The most exciting finding is that auxin perception occurs through a novel mechanism, in which auxin binds to the auxin receptor transport inhibitor response 1 (TIR1), a F-box protein, and functions by directly regulating the ubiquitin (Ub) protein ligase SCF^{TIR1} (SKP1-Cullin1-F-box protein), in this case TIR1, resulting in AUX/ IAA ubiquitination and subsequent degradation (Dharmasiri *et al.* 2005; Kepinski and Leyser 2005). The degradation of AUX/IAA proteins releases the auxin-response factor (ARF) and actives the auxin response gene expression (Leyser 2002; Mockaitis and Estelle 2008).

Regulation of cell division, cell elongation and lateral organ development of plants by auxin may also involve interplays with other morphogens. It has been shown that auxin controls root cell proliferation and enlargement by modulating cellular responses to gibberellin (GA) (Fu and Harbred 2003; Fukaki and Tasaka 2009). The synergistic action of brassinosteroids (BR) and auxin on plant cell proliferation and enlargement was also reported (Nemhauser *et al.* 2004; Hardtke *et al.* 2007). BR influence plant development in part by affecting the distribution of auxin (Bao *et al.* 2004). Recent studies also demonstrate that interaction of BR biosynthesis and auxin signalling through a *BRX*-mediated feedback loop is required for optimal root growth both embryonically and post-embryonically (Mouchel *et al.* 2006). These findings suggest that the auxin signaling pathway is highly complex. A full understanding of the auxin pathway will still be a hot and challenging topic for the future.

AUXIN MEDIATES ROOT TROPISM

Plants grow in a permanently changing environment. In response to external signals, plants activate their protective/ defense systems and this eventually leads to the alteration of auxin, which subsequently binds to the receptors that activate transcriptional regulators downstream of responsive genes (Potters *et al.* 2007, 2009). By targeting many genes, auxin serves as a master switch in the control of network responses that underlie behavioral and morphological adaptation (Malamy and Ryan 2001; Malamy 2005; Potters *et al.* 2007, 2009).

One famous example of auxin-mediated plant behavioral adaptation to environmental stimuli is phototropism. This phenomenon was originally documented by Charles and Francis Darwin. They found that exposure to light in one area of a grass coleoptile causes bending towards light in another, suggesting the involvement of a transported signaling (Darwin 1880). The active molecules were later isolated and crystallized, and were named auxin. Recent studies showed that light promotes asymmetric auxin distribution in the stem causing asymmetric growth and eventually organ bending (Kimura and Kagawa 2006; Tanaka *et al.* 2006). Light-regulated orientation of shoot growth can optimize photosynthesis and plant survival. Gravity is another constant environmental stimulus. In response to the gravity vector, the shoot grows upward away from the stimulus (negative gravitropism), whereas the root always grows along with the gravity vector (positive gravitropism) (Sack 1991; Fukaki *et al.* 1996; Mano *et al.* 2006). When their growth direction changes, shoots and roots can rapidly reorient themselves and grow against and toward gravity respectively. Similar asymmetric distribution on either side of the organ is also observed.

The observation of asymmetric distribution of auxin in bending organs in response to light and gravity led to the formulation of the Cholodney-Went hypothesis, which hypothesized an unequal distribution of auxin between two sides of the curving organ as the cause of tropic growth (Went and Thimann 1937). Indeed, application of polar auxin transport inhibitors, such as naphthylphthalamic acid (NPA), inhibits auxin efflux and tropic growth curvature, but not auxin uptake. Recent analysis of *Arabidopsis* mutants with agravitropic roots identified the PIN2 and PIN3 proteins as individually required for root gravitropism (Chen *et al.* 1998; Luschnig *et al.* 1998; Müller *et al.* 1998; Friml *et al.* 2002). It has been shown that loss of PIN2 is sufficient to establish unequal distribution of auxin in the elongation zone, and the latest results demonstrate that the proteosome is involved in the control of PIN2 protein turnover, the subsequent asymmetric distribution of PIN2 at the upper and lower sides of the root, and in gravitropic responses (Abas *et al.* 2006). Mutants of AUX1 and PIN3 which expresses preferentially in columella cells also exhibit gravitropic defects (Bennett *et al.* 1996; Firml *et al.* 2002; Swarup *et al.* 2005). Moreover, auxin inducible genes, such as *AUX/IAA* genes, *SMALL AUXIN UP-REGULATED RNAs* (*SAUR*) and *GH3* were also found to be asymmetrically distributed during gravitropic growth, and the mutations in the corresponding genes resulted in alteration in gravitropic response (McClure and Guilfoyle 1989; Conner *et al.* 1990; Esmon *et al.* 2006). These molecular and genetic results provide convincing evidence that auxin transport and the auxin signaling pathway are essential for plant response to gravity stimulus.

In addition to light and gravity, other abiotic signals, such as moisture and ion gradients, can also induce tropic growth. The former, termed hydrotropism, is the response of roots to a moisture gradient. Hydrotropism is a common response for plants (Takahashi *et al.* 2009). Auxin transport inhibitor 2,3,5-triiodobenzoic acid (TIBA), blocked hydrotropic response of pea and cucumber roots, suggesting that auxin polar transport plays an important role in hydrotropism (Takahashi and Suge 1991; Takahashi *et al.* 1999; Mizuno *et al.* 2002). Interestingly, *Arabidopsis* plant does not require polar auxin transport for the induction of hydrotropism, because application of TIBA or NPA does not affect the tropic response of the roots to moisture gradients (Kaneyasu *et al.* 2007). It is proposed that auxin redistribution or action may function in a species-specific manner (Takahashi *et al.* 2008, 2009). Whether an unidentified mechanism regulates auxin functions and how gravitropism interferes with hydrotropism are still not clear. In response to ion gradients in the growth medium, *Arabidopsis* plants also showed negative halotropism mediated by auxin transport (Li and Zhang 2008; Sun *et al.* 2008). After perception of excess ions, plant roots activate the SOS (salt overly sensitive) signaling pathway, which regulates PIN2 expression at both transcriptional and posttranscriptional levels, resulting in asymmetric distribution of auxin and the subsequent negative halotropism. Both hydrotropic and negative halotropic growth are adaptive responses (avoidance-tropism), which protect plant cells against dehydration and ion toxicity through regulation of root orientation. Avoidance-tropism also includes obstacle avoidance through which the plant root curves vigorously away from a barrier in the soil. Clearly, a complex interaction between moisture/ion gradient, touch sensing and gravity sensing helps growing roots maintain efficient access to water and nutrients in the soil.

AUXIN AND PRIMARY ROOT GROWTH INHIBITION BY STRESSES

The primary root is formed during embryogenesis. Its growth status influences root system architecture and plant development. The primary root growth is controlled princepally by cell division in the root meristem and elongation and expansion of root cells.

Nitrogen availability

Nitrogen (N) is essential for plants. The levels of organic and inorganic N in soil are highly variable, and have pronounced effects on LR development (Zhang and Forde 1998; Linkohr *et al.* 2002; Boukcim *et al.* 2006; Nibau *et al.* 2008). N supply can affect root growth (Zhao *et al.* 2007; Tian *et al.* 2008). Recent studies show that high levels of nitrate substantially inhibit elongation of primary, seminal and crown roots of maize (*Zea mays* L.). At 20 mM nitrate, primary root growth was reduced by 17% compared with the untreated control during a 12-day treatment period (Tian *et al.* 2008). The crown roots were most sensitive with a 30% reduction in length. Further evidence shows that root inhibition caused by high nitrate is primarily caused by reduced cell elongation, because the sizes of root meristems remain largely unchanged (Tian *et al.* 2008).

Root growth retardation in response to high nitrate is closely related to reduction of IAA concentrations in roots, especially in the sections close to root tips. Exogenous NAA and IAA can restore primary root growth under high nitrate conditions (Zhao *et al.* 2007; Tian *et al.* 2008). Application of IAA also markedly enhanced endogenous NO levels in root apices grown in high nitrate (Zhao *et al.* 2007). The results suggest that auxin may control root cell elongation through regulation of NO levels in the roots in response to high nitrate stress.

When N is deficient in the growth conditions, plant root growth is also affected with varied rates among different plant species. *Arabidopsis thaliana* is sensitive to low N, and root growth is significantly inhibited by low N availability (Martin *et al.* 2002; Bi *et al.* 2007; Peng *et al.* 2007a, 2007b). In contrast, its wild relative *Thellungiella halophila* is tolerant to N deprivation (Kant *et al.* 2008). Growth of modern maize hybrids and wheat (*Triticum aestivum*) cultivars are less sensitive to N starvation than the old lines (McCullough *et al.* 1994; Ortiz-Monasterio *et al.* 1997; Ding *et al.* 2005). However, the molecular mechanisms that how plants adapt to and tolerate low N stress conditions and regulate N use efficiency are still not clear.

Auxin has also been implicated in nitrate uptake and the subsequent root growth regulation. For example, *Arabidopsis* AtNRT1.1 (CHL1), a dual-affinity nitrate transporter, is responsible for both low and high affinity nitrate uptake. *CHL1* is preferentially expressed in the root tips of primary and LRs (Guo *et al.* 2002). Interestingly, *CHL1* expression is highly inducible by exogenous auxin with a similar induction pattern as DR5 in wild type plants, and the mutants overproducing auxin (*yucca* and *rooty/superroot1*) show high levels of *CHL1* expression in the corresponding regions. These results suggest that auxin may be an important regulator which may improve N uptake and root growth by modulating CHL1 in root tips of *Arabidopsis*.

Phosphorus availability

Phosphorus (P) is another essential nutrient critical for plant growth and development, and it is primarily taken up via the root as inorganic P. Because of its low mobility in soil, low P availability often inhibits plant growth and reduces plant productivity (Holford 1997; Raghothama 1999). When growing under limiting phosphate conditions, primary root growth of *Arabidopsis* plants is dramatically retarded (Williamson *et al.* 2001; López-Bucio *et al.* 2002; Al-Ghazi *et al.* 2003; López-Bucio *et al.* 2005; Nacry *et al.* 2005). The studies show that primary root growth inhibition by low P is caused by a shift from an indeterminate to a determinate developmental program. Low P first reduces cell elongation, followed by progressive loss of meristematic cells and the ceasing of cell proliferation in the primary roots (Sánchez-Calderón *et al.* 2005; Jain *et al.* 2007). A further study using the cell cycle marker CycB1;1:*uidA* and the QC identity marker QC46:*GUS* indicates that low P induced-root developmental determination is related to alteration of the QC.

Under normal conditions, the distribution of auxin and auxin maxima play an important role in QC formation, which is required for meristem organization and activity. Disappearance of QC is associated with roots becoming determinate (Jiang and Fedman 2005). It is conceivable that auxin plays a role in the root growth inhibition. However, genetic, physiological and biochemical studies show that low-P-induced developmental determinate program of root growth and subsequent growth inhibition are auxin-independent (Williamson *et al.* 2001; López-Bucio *et al.* 2002; Al-Ghazi *et al.* 2003; López-Bucio *et al.* 2005; Jain *et al.* 2007). It has been proposed that modulation of the mitotic activity of the primary root by the P-specific local sensing pathway lies downstream of the auxin-mediated maintenance of the root meristem. More studies are needed to uncover the mechanism underlying developmental plasticity of primary root growth in response to low P.

Salt stress

Maintenance of ion homeostasis is very important to many biological progresses such as enzyme reaction, and potential modulation. When plants grow in conditions containing inappropriate concentrations of nutritional ions, disturbance of ion homeostasis can occur. Such disturbance in homeostasis will directly affect the physiology and morphology of plants. High salinity markedly inhibits primary root growth in various plant species (Lin and Kao 1995; Reinhardt and Rost 1995; Kouki *et al.* 2001). Kinematic analysis of *Arabidopsis* primary root growth shows that growth reduction of stressed roots is caused by reduced cell production and shortened cell length (Burssens *et al.* 2000; Fricke and Peters 2002). However, salt stress does not affect the average cell cycle duration; instead it decreases the number of dividing meristematic cells. The salt induced-changes in cell division are achieved by dynamically regulating activity of cyclin-dependent kinase, such as CDC2aAt, CycA2;1, CycB1;1 (Burssens *et al.* 2000), CDKA;1 and CDKB1;1 (Fricke and Peters 2002) and the downstream target genes. This process is adjustable and reversible and enables plant roots to grow at an appropriate rate under given growth conditions.

There is extensive evidence to show that ABA mediates regulation of adaptive responses of plants to high salinity, including root growth retardation (Mulhollanda *et al.* 2003; Khadri *et al.* 2007). Regulatory roles of auxin in the growth reprogram are much less known. Current evidence suggests that auxin may play a very important role in plastic development of plants under salt stress. When the ion concentration around the plants is high or low, changes in auxin synthesis, metabolism and sensitivity under salt stress has been noticed. Exogenous IAA mimics not only the inhibition of salt stress on primary root growth, but also the effects of salt stress on the enzymes of carbohydrate metabolism in chickpea seedlings (Kaur *et al.* 2003). These results suggest that salt stress signaling may modulate the auxin pathway to regulate the morphological adaptation of plants to salt stress. The auxin-resistant mutant *axr1-24* (*auxin resistant 1-24*) was more tolerant to inhibition of primary root growth by NaCl at concentrations less than 128 mM (Tiryaki 2007). The gain-of-function mutant in *GH3*, *wes1-D*, shows substantially increased salt tolerance (Park *et al.* 2007). PIN2 expression is repressed by salt stress at both transcriptional and posttranscriptional levels (Sun *et al.* 2008; Dinneny *et al.* 2008). The diminished expression pattern of PIN2 in *sos1* mutant under salt stress also supports this hypothesis.

Water status

Plant growth generally decreases when soil water is limiting. Maize root growth, including elongation and radial expansion, is greatly inhibited when the water potentials become low (Sharp *et al.* 1988). Therefore, the roots of stressed plants are shorter and thinner compared with those of untreated controls. This morphological change is likely a common phenomenon for the angiosperm roots. Although root growth is less sensitive to water stress than shoots, water stress clearly inhibits cell division and cell volume. The mechanisms of how cell division of meristematic cells in the root tips is modulated by various levels of water status and how the cell elongation and expansion is controlled remain to be studied.

Like ABA, auxin, such as IAA (Havlová *et al.* 2008) and indole-3-butyric acid (IBA) (Ludwig-Müller 2007) accumulates in *Arabidopsis* and tobacco roots and shoots upon exposure to water stress. Increased levels of auxin in the stressed maize roots were also observed (Ribaut and Pilet 1994; Xin *et al.* 1997). The function of auxin during the drought-stress response of roots remains to be elucidated. The application of high ABA concentrations promoted IBA synthetase activity and IBA contents in the same way as water stress and it was hypothesized that an increase of endogenous ABA induced by water stress may promote IAA and IBA synthesis and modulates plant growth (Ludwig-Müller 2007; Havlová *et al.* 2008). In addition, comparable studies on two-dimensional protein patterns of *Arabidopsis* wild type and *axr1* mutants suggest an interaction between auxin signaling and drought signals in plant root morphogenesis (Leymarie *et al.* 1996). Further physiological and molecular analysis of the *axr1-3* mutant of *Arabidopsis* reveals that functional auxin signaling is required for the induction of stress-related protein RD29B in roots and in drought-induced rhizogenesis (Bianchi *et al.* 2002).

Heavy metal toxicity

Heavy metals are toxic to plants resulting in reduced agricultural productivity. Heavy metals, such as chromium (Cr), aluminum (Al) and lead (Pb) in the growth medium/soil cause great growth inhibition of primary roots (Castro *et al.* 2007; Kozhevnikova *et al.* 2007; Rounds and Larsen 2008). The most important discovery for the heavy metal-induced inhibition of primary roots is that various heavy metals severely affect cell division, the function of QC and organization of root tips. For example, after entering plant cells, Pb inhibits cell division in the root cap, and activates cell division of QC, resulting in a defective root meristem structure (Kozhevnikova *et al.* 2007). Recently, Rounds and Larsen (2008) provide evidence that Al toxicity-induced inhibition of primary root growth is also caused by DNA damage and subsequent arrest of the cell cycle and impaired QC. This might be a common response of plants to toxic heavy metals though the mechanisms of uptake and transport of the heavy metals are different.

Analysis of the responses of wild type *Arabidopsis* and the auxin-resistant mutants *axr2* and *aux1–7* to Cr (VI) indicates that auxin is not involved in root growth regulation. Instead, increase in the sulfate, phosphate or nitrate concentrations in the growth media dramatically alleviates the growth inhibition caused by Cr (VI) (Castro *et al.* 2007). However, the most recent results showed that the primary root growth inhibition by increased levels of Ni^{2+} or Mn^{2+} is modulated by altered auxin response, which is regulated by the vacuolar cation/H^+ antiporter CAX4 (Mei *et al.* 2009). Under metal stresses, CAX4 was induced in root apex and lateral root primordia, the loss of function mutant displayed altered responses to heavy metals, Ni^{2+}, Mn^{2+} and Cd^{2+}, auxin, as well as root growth. Auxin redistribution through auxin influx and efflux in the stressed roots was also shown to mediate Al^{3+}-mediated root growth arrest (Sun *et al.* 2009). Genetic and biochemical analysis indicate that ethylene may function upstream of auxin signaling in the Al^{3+} induced root growth inhibition. The results suggest that auxin signaling plays an important role in root growth of the seedlings grown under heavy metal stress conditions.

AUXIN AND REPROGRAM OF LATERAL ROOT FORMATION

Plant architecture is largely determined by lateral organ development along roots and shoots. Lateral organs are initiated postembryonically, therefore their development is highly plastic in response to environmental cues. Since roots are required for the acquisition of water and nutrients, for experiencing alterations in soil moisture, salinity and nutrient availability, and for anchoring the plant in the ground, much attention has been paid to how LRs are modified in response to various abiotic stresses and what the underlying molecular mechanisms are.

Nitrogen availability

It has been well documented that localized high nitrate in low-nitrate conditions results in local stimulation of LR growth, whereas global high concentrations of nitrate inhibits LR initiation and elongation of emerged LRs (Drew and Saker 1975; Zhang and Forde 2000). This appears to be a common feature among many plant species (Robinson 1994; Hodge 2004). However, different species show different patterns of nitrate-induced modification in LR development. For example, localized nitrate supplies increased both the number and growth rate of the LRs in barley plants (Drew and Saker 1975), whereas the primary response of Arabidopsis plant roots to localized nitrate supplies was increased elongation of the existing LRs (Zhang and Forde 1998; Linkohr *et al.* 2002). Nitrate-induced LR elongation is mainly due to increasing cell production rather than cell expansion (Zhang *et al.* 1999). As *ANR1* and *AtNRT1* (*Arabidopsis thaliana NITRATE TRANSPORTER 1*) are key regulators in the local nitrate response of LR development, down-regulation of *ANR1* and up-regulation of *AtNRT1* by local high nitrate application are directly related to localized stimulation of LR growth (Zhang and Forde 1998; Muños *et al.* 2004; Gan *et al.* 2005). In contrast, inhibition of LR development by uniform treatment with high nitrate is caused by retarded growth of the emerged LRs (Zhang *et al.* 1999). How these responses are regulated and how auxin is involved in plastic development are both currently unknown. Preliminary evidence indicates that the nitrate levels might affect auxin biosynthesis (Caba *et al.* 2000; Walch-Liu *et al.* 2006). In soybean, IAA contents in the plant roots grown in high nitrate conditions (8 mM NO_3^-) were approximately 4 times lower than those in the roots grown in the presence of 1 mM NO_3^- (Caba *et al.* 2000). In Arabidopsis, IAA levels in roots were substantially increased after they were transferred from high nitrate to low nitrate conditions (Walch-Liu *et al.* 2006). Recently, Gifford *et al.* (2008) provided strong evidence for the link between auxin response and plant response to N. They found that root N response is in a cell specific pattern, and expression of six auxin response factors (*ARFs*) and seven *Aux/IAA* genes was within the largest cell-specific response clusters in pericycle and LR cap. By analysis of cell specific and N induced expression pattern of *microRNA167* (*miR167*) and its target gene *ARF8*, a link between auxin signaling and LR plastic development in response to N availability was further established (Gifford *et al.* 2008).

Organic N compounds, such as the amino acid L-glutamate and carnitine also affect LR development (Walch-Liu *et al.* 2006; Lelandais-Briere *et al.* 2007). Exposure of *Arabidopsis* plants to L-glutamate resulted in increased LR density but shorter LRs (Williamson *et al.* 2001). Whether L-glutamate acts a signaling molecule or a nutritional cue remains in question. Gifford *et al.* (2008) compared the expression of *ARF8* in pericycle cells treated with nitrate and methionine sulfoximine (MSX), which blocks the assimilation of nitrate into glutamine. MSX treatment blocked the induction of *ARF8* and its target genes by nitrate, and the inhibitory effects of MSX were restored by addition of glutamine (Gifford *et al.* 2008). These results suggest that *ARF8* and the target genes in the pericycle cells are responsive to glutamine or a downstream metabolite but not nitrate itself; in other words, glutamine/glutamate may act as a predominant signal regulating modification of root system architecture (RSA) in response to N.

Phosphorus deficiency

Induction of initiation and elongation of LRs by low P is considered as an important adaptive trait, which contributes to the successful exploration of nutrients in the upper layer of the soil (López-Bucio *et al.* 2000; Williamson *et al.* 2001; López-Bucio *et al.* 2002). To achieve this goal, plant species such as *Arabidopsis* form more LRs near the origin of the primary root following the arrest of PR growth (Williamson et al. 2001; López-Bucio *et al.* 2002); some plants (e.g. the bean *phaseolus vulgaris*) shift the root growth direction from downward to outward to maximize P absorption (Bonser *et al.* 1996); the strategy for the N-fixing white lupin to adapt to a low P environment is to form proteoid (cluster) roots that solubilize P by secreting organic acids and phosphatases into the soil (Schulze *et al.* 2006).

Low P is sensed at the primary root tip and the signal is transduced to reprogram the LR development (Svistoonoff *et al.* 2007). Currently, the molecular mechanism of the signaling pathway from signal perception to reprogramming of RSA remains unknown. However, recent molecular and genetic studies have identified several important genes, such as *PHR1* (*PHOSPHATE STARVATION RESPONSE 1*) and *WRKY75* (*WRKY DNA-BINDING PROTEIN 75*), which may play important roles in developmental plasticity induced by phosphate deficiency (Rubio *et al.* 2001; Devaiah *et al.* 2007). However, there is no direct evidence for *PHR1* in LR regulation under P deficiency. What we know is that *PHR1*encoding a MYB-like transcription factor regulates many genes responsive to P deficiency (Rubio et al. 2001), and mutation in its regulator *AtSIZ1*, the small ubiquitin modifier (SUMO) E3-ligase, exhibited dramatic alterations in lateral formation in response to P deficiency (Miura *et al.* 2005). Whether *PHR1* is directly responsible for LR formation and how *AtSIZ1* and its target gene *PHR1* regulate P-deficient induced root developmental plasticity is still not clear.

Involvement of auxin in the alterations of LRs under P deprived conditions has been proved (López-Bucio *et al.* 2002; Jain *et al.* 2007). In *Arabidopsis*, exogenous application of low concentrations of IAA and the synthetic auxin 2,4-D significantly increased LRs under low P (1 µM), suggesting that auxin is required for the stimulation of lateral formation by low P (Lopez-Bucio *et al.* 2002). Addition of TIBA markedly reduced low-P induced LR formation, indicating that polar auxin transport is critical for LR formation in the P-deprived plants. Further evidence to support the notion is that mutations in *BIG* (formerly *DARK OVER-EXPRESSION OF CAB 1/TIR3/ASA1*), which is required for auxin transport, causes reduced numbers of LRs under low P conditions (López-Bucio *et al.* 2005). Analysis of the *lpr1-1* to *lpr1-3* mutants of in *LOW PHOSPHATE-RESISTANT ROOT*, which are allelic to BIG further revealed that BIG is required for activation of pericycle cells and subsequent LR primordia formation. Phenotypic analysis of the auxin related mutants, such as *axr4-1*, *aux1-7*, and *eir1-1* (*ETHYLENE INSENSITIVE ROOT 1*) mutants, suggest that auxin sensitivity andredistribution of auxin play a very important role in plastic development of LRs under low-P (Nacry *et al.* 2005; Jain *et al.* 2007). Most recently, Pérez-Torres *et al* (2008) showed that pericycle cells of P-deprived *Arabidopsis* seedlings are more sensitive to exogenous auxin, and the specific responses of the plant to low P are TIR1 dependent. Loss-of-function in *TIR1* confers significantly reduced promotion effects in LRs in response to low P availability. Based on their results, it is proposed that P deprivation increases the expression of *TIR1* in Arabidopsis plants, which promotes degradation of AUX/IAA protein (e.g. AXR3) and unshackling of ARFs (e.g. ARF19) which eventually modulate LR formation and outgrowth by controlling the downstream target genes (Pérez-Torres *et al.* 2008). Most recently, Pérez-Torres *et al.* (2009) show that low Pi-induced plastic development of root system is mediated by modulation of cell cycle in the stressed seedlings, which is dependent on auxin sensitivity in the root but not the auxin transport (Pérez-Torres *et al* 2009).

Sulfur deficiency

Sulfur (S) deficiency promotes early development of LRs and increases the LR density leading to an increase in total root surface area for greater ability of absorption of S, in the form of sulphate (Kutz *et al.* 2002). Several lines of evidence link auxin to the reprogramming of RSA in S-deprived plants. Firstly, S-limiting conditions activate the transcription of the *NIT3* (*NITRILASE 3*) gene, which encodes a nitrilase, the enzyme converting indole-3-acetonitrile to IAA, resulting in increased auxin levels in the S-deprived roots (López-Bucio *et al.* 2003). Secondly, SURE regions, conserved in the upstream regions of various sulphate-deficient response genes, contain ARF consensus sequences (Maruyama-Nakashita *et al.* 2004). Thirdly, the expression of auxin responsive *AUX/IAA*, especially *IAA18* (*INDOLEACETIC ACID-INDUCED PROTEIN 18*) and *IAA28*, and the gene encoding tryptophan synthase beta chain are all upregulated by S starvation. The results suggest that auxin may be involved in the modulation of plant responses to S deficiency (Nikiforova *et al.* 2003, 2005).

Salt stress

Excess ions, such as Na^+, which produce ionic toxicity and osmotic stress have also been shown to affect LR development in *Arabidopsis*. Under moderate and severe salt stress, auxin redistribution was dramatically changed in the stressed root tip by analyzing of DR5::GUS, resulting in altered lateral root initiation and emergence (Wang *et al.* 2009). Under mild salt stress, lateral root initiation was markedly stimulated by increased auxin accumulation in developing primordia (Zolla *et al.* 2009). It has been shown that the transgenic plants overexpressing *SOS1*, *SOS2* or *SOS3* were more tolerant to salt stress than the wild type plants; the transgenic plants had more lateral roots (Yang *et al.* 2009). These results suggest that the SOS signal pathway is involved in the phenotypic plasticity of LRs under salt stress. Overexpression of *NAC2*, an ABA responsive gene, resulted in increased salt tolerance of transgenic Arabidopsis plants with more LRs (He *et al.* 2005). Interestingly, the *NAC2* gene is also inducible by auxin, and the upregulation of NAC2 gene expression is reduced in the auxin-insensitive mutant *tir1-1*, suggesting that auxin might be involved in salt stress-induced LR induction (He *et al.* 2005; Munns and Tester 2008). Recently, CIPK6, a CBL-interacting protein kinase has also been shown to be involved in root system development and salt tolerance (Tripathi *et al.* 2009a, 2009b). Overexpression of the constituively active mutant of CaCIPK6 resulted in increased basipetal auxin transport, sensitivity to auxin and subsequently altered lateral root development. Direct evidence of involvement of auxin in LR initiation and growth under salt stress conditions is still lacking.

In contrast, K^+ deprivation significantly inhibits LR elongation (Armengaud *et al.* 2004). Characterization of *Arabidopsis* MYB77 transcription factor reveals that auxin signaling is directly related to altered LR development (Shin *et al.* 2007). *MYB77* regulates plant responses to auxin by interacting with ARFs, and interaction between MYB77 and ARF7 controls lateral initiation. Knockout plants of *myb77* have reduced numbers of LRs responding specifically to potassium-deprived conditions.

Water status

Water stress affects RSA pronouncedly. As soon as the stress occurs, plant roots can sense the signal and respond immediately. In *in vitro* assays, reduction in water availability represses LR emergence, with the initiation largely unaffected (van der Weele *et al.* 2000; Deak and Malamy 2005). When plants are exposed to progressive drought in soil, newly formed LRs are short and tuberized. These LRs have different structures from the normal LRs formed before water stress. Importantly, these drought-induced roots can immediately resume growth when the plants are rehydrated, and form normal LRs.

Auxin has been shown to mediate this process because the auxin-resistant *axr1-3* mutant plants exhibit impaired root responses to water stress compared with those of the wild type plants (Vartanian *et al.* 1994). Most recent results showed that the R2R3-type MYB transcript factor plays very important role to link the ABA and auxin crosstalk in plastic lateral development and subsequent drought tolerance (Seo *et al.* 2009). The mutant overexpressing MYB96 resulted in increased GH3 gene expression, reduced lateral roots and drought tolerance. In contrast, the loss of function mutants were more susceptible to drought with increased number of lateral roots (Seo *et al.* 2009; Seo and Parks 2009). The results provide novel insight into how auxin homeostasis interplayed with ABA signaling to modulate lateral root development in response to drought stress.

AUXIN AND REMODELING OF ROOT HAIR DEVELOPMENT

Root hairs are important parts of RSA which provide most of the surface area for absorption of water and nutrients. In the past decade, considerable progress has been made in unraveling the mechanisms of root hair cell fate specification and outgrowth. The results show that cell fate determination of root epidermal cells, root hair initiation, and elongation are precisely controlled through temporally and spatially regulating genes such as *GL2* (*GLABRA* 2), *WER* (*WEREWOLF* 1), *TTG* (*TRANSPARENT TESTA GLABRA* 1), *CPC* (*CAPRICE*) and *RHD*s (*ROOT HAIR DEFECTIVE*). *GL2*, which encodes a homeodomain protein (Rerie *et al.* 1994), is expressed predominantly in hairless cell files and might be a negative regulator of root-hair development (Masucci *et al.* 1996). The WD40 domain protein TTG regulates *GL2* positively (Larkin *et al.* 2003). *WER* and *CPC*, which encode Myb transcription factors (Wada *et al.* 1997; Lee and Schiefelbein 1999) and cross regulate each other in a feedback loop (Lee and Schiefelbein 2002), positively and negatively regulate the position-specific expression of *GL2*, respectively. The *RHDl* gene is necessary for proper initiation of root hairs, whereas the *RHD2*, *RHD3*, and *RHD4* genes are required for normal hair elongation (Schiefelbein and Somerville 1990). And the *RHD6* gene is possibly involved in directing the selection of the root hair initiation site through a process involving auxin and ethylene (Masucci and Schiefelbein 1994).

Auxin is a key regulator in controlling root epidermal cell development including their initiation and outgrowth in a concentration-dependent manner (Sabatini *et al.* 1999; Blilou *et al.* 2005). As mentioned above, recent evidence shows that high AUX1 auxin transport activity through non-hair cells is crucial for supplying auxin to adjacent developing hair cells and sustainable outgrowth (Jones *et al.* 2009). Plants have evolved adaptive mechanisms to protect plant cells from damage caused by nutrient starvation or excessive ion toxicity by adjusting the surface area. Therefore, root hair development is highly plastic in response to environmental cues.

Nitrogen availability

Root hairs play a very important role in N uptake. Firstly, they can transport NH_4^+ and NO_3^-. One NH_4^+ and two putative low-affinity NO_3^- transporters have been cloned from tomato; among them, the expression of genes *LeNRT1-2* and *LeAMT1* is root-hair-specific and regulated by an external N supply (Lauter *et al.* 1996). The NH_4^+ transporter

LeAMT1 is constitutively expressed and is down-regulated by the presence of NO_3^-. NH_4^+ uptake occurs instantly after the addition of NH4+ to N-starved roots (Kosegarten *et al.* 1997). By contrast, the putative low-affinity NO_3^- transporters encoded by *LeNRT1-1* and *LeNRT1-2* are both up-regulated by NO_3^-. The high-affinity NO_3^- transporter in *Arabidopsis* root hairs is greatly up-regulated under NO_3^- deficiency (Meharg and Blatt 1995). Recently, a new *PLD* (*PHOSPHOLIPASE D*), *PLDepsilon*, has been shown to be associated with the plasma membrane. Increased expression of *PLDepsilon* promotes root hair elongation and primary root growth under severe N deprivation, providing evidence that a lipid signaling process may mediate transmission of the membrane's sensing of nutrient status (Hong *et al.* 2009).

In addition, Shin *et al.* (2005) showed that root hair cells in *Arabidopsis* have a sensing pathway for N deprivation by analyzing root hair mutants in response to N deprivation. These results suggest that root hairs have a complete signal sensing and transduction cascade to regulate adequate N uptake for plant survival under N deficiency. Auxin is involved in plant response to N deprivation; however, we still lack an understanding of hormonal regulation of root hair development under N deprivation conditions.

Phosphorus deficiency

Under low P conditions, longer and denser root hairs have proved to be a less-input strategy that enables plants to survive better (Bates and Lynch 1996; Gahoonia and Nielsen 1998; Ma *et al.* 2001). In P-deficient soil, the root hair length and density of *Arabidopsis* plant increase massively, expanding the root's surface area up to approximately 7 times that under P-sufficient conditions (Bates and Lynch 1996). The low P-induced 5-fold increase in root hair density is due to an increase in the number of epidermal cells that differentiate into trichoblasts, suggesting that cell fate of root epidermal cells has been modified by P deprivation (Ma *et al.* 2001). In addition, root hair growth under low P conditions accelerates twice as fast as that grown under normal conditions.

Genetic and physiological analysis of *aux1*, *axr1* and *axr2* mutants indicates that auxin signaling is involved in controlling root hair development in response to P starvation, and auxin may function through interaction with the ethylene signaling pathway (Lynch and Brown 1997; Schmidt and Schikora 2001). Furthermore, phenotypic analyses of the mutants harboring defects in the genes responsible for cell specification, root hair initiation and elongation indicate that after perception of the low P signal by plant cells, the P response signaling pathway may directly modulate the regulatory genes that control root hair formation, such as *GL2/WER/TTG*, and downstream genes, such as *RHD1* and *RHD6*, which regulate initiation and outgrowth of the root hairs (Müller and Schmidt 2004). However, how the intrinsic signaling and external cues integrate to increase the density and the size of root hairs for efficient uptake of the limiting P remains largely unclear.

Low iron availability

When iron (Fe) becomes a limiting factor for plant growth, plants also exhibit similar phenotypic responses to those induced by P-deficiency, including longer and more dense root hairs (Müller and Schmidt 2004). Therefore, alterations in epidermal cell specification, root hair initiation and elongation under P- and Fe-starvation and the underlying mechanisms are usually studied in parallel. However, the increased root hair density in P-starved plants was largely achieved by the formation of extra hairs from non-hair cells, while roots of Fe-starved plants were characterized by a high percentage of extra hairs with two tips. Besides, hairs of P-deficient plants were markedly longer than those formed in response to Fe starvation or under control conditions.

Comparative studies on the aspects of root hair development between P- and Fe-starvation conditions using the auxin response mutants and the mutants controlling various stages of root hair development suggest that changes in root-hair morphology in response to Fe deficiency are mediated by a different signal transduction pathway from that which is employed for P starvation (Müller and Schmidt 2004). For example, the Fe-free medium, unlike P deficiency, does not change the phenotypes of *arx2* that has almost no root hairs under normal conditions.

Salt stress

Under salt stress conditions, root hair elongation and cytosolic calcium at the apex was reduced (Halperin *et al.* 2003), and root hair length and density decreased in a dose-dependent manner (Wang *et al.* 2008). High salinity changes the anatomical structure of roots, leading to a decrease in cell number in N positions and enlargement of the cells. Salt stress-induced alteration in epidermal cell fate also contributes to the reduction in root hairs. Analysis of the overly salt sensitive mutants indicated that salt-induced root hair response is caused by ion disequilibrium and appears to be an adaptive mechanism that reduces excessive ion uptake. *WER*, *GL3*, *EGL3* (ENHANCE OF GLABRA 3), *CPC*, and *GL2* genes were proposed be involved in cell specification of the root epidermis in stressed plants (Wang *et al.* 2008). Recent salt-stress microarray data showed that many of the repressed genes encode structural components of the cell wall or genes that are involved in trichoblast (hair cell precursor) differentiation (Dinneny *et al.* 2008). Furthermore, *Arabidopsis sos4* mutant, which was originally identified by screening for NaCl-hypersensitive growth, is defective in root hair development. The results show that *Arabidopsis SOS4* encodes a pyridoxal (PL) kinase that is involved in the biosynthesis of PL-5-phosphate (PLP), an active form of vitamin B6 which is required for root hair initiation and tip growth (Shi *et al.* 2002). The findings reveal the close relationship between root hair development and salt tolerance of plants. However, the regulatory mechanism for this salt stress-induced root hair developmental plasticity is not known.

Water status

Root hair development is very sensitive to water stress (Vartanin *et al.* 1983; Schnall and Quatrano 1992). When the water potentials become low enough, the mature root hairs of stressed plants, such as *Sinapis alba* L. and *Arabidopsis*, wilt. The tip growth of developing root hairs is greatly inhibited or ceased, causing root hairs to become short and bulbous. The epidermal cells, including trichoblasts and atrichoblasts, become dehydrated (Vartanin *et al.* 1983). However, the epidermal cells on the newly formed short and tubulized roots under drought conditions are turgid. The pattern of the trichoblasts and atrichoblasts is different to that on normal roots. When the plants are watered, trichoblast cells can immediately swell and absorb water. The epidermal cell specification and root hair development become normal. These results suggest that an adaptive regulatory mechanism exists to modulate cell fate decision and differentiation which enable plants to cope with the changing water status.

Hormonal regulation of root epidermal cell specification and root hair initiation and growth in response to water status is largely unknown. Genetic and phenotypic analysis indicates that ABA may mediate the response of root hairs to water stress because *abi1* (*ABA insensitive 1*) and *abi2* mutants did not display the root hair response (Schnall and Quatrano 1992). However, whether auxin is involved in the above process and how auxin signaling interacts with the water status signal and ABA pathway to regulate root hair remodeling needs to be studied.

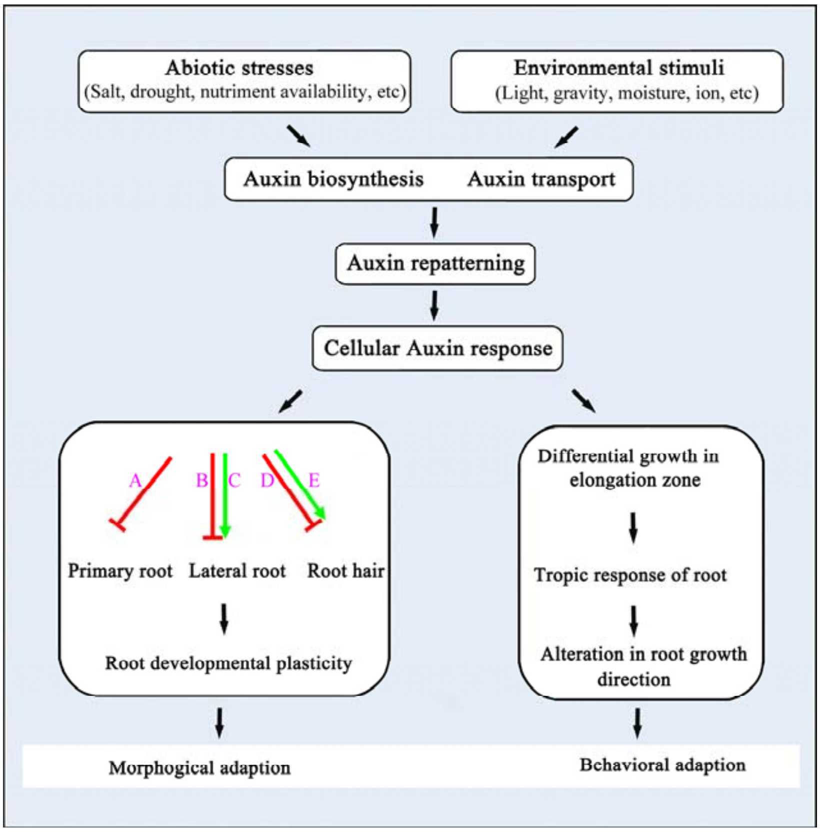

Fig. 2 Simplified models depicting the role of auxin in adaptation of plant root system architecture to abiotic stress. a, Auxin-mediated morphological plasticity of root system architecture under various abiotic stresses: A represents high N, low P, salt stress, water stress, heavy metals; (B) globle high N, K+ deprivation and drought; (C). low P, localized high N and low S, salinity; (D). drought; and (E). low P or low Fe. b, Behavioral adaptation of plant root mediated by auxin.

CONCLUSION

Plants live in a complicated and rapidly changing environment. Plant cells perceive internal and external signals, perform an integrated analysis of the vast amount of information received, then make an immediate decision on what to do to deal with the current status, and take quick actions to protect themselves from the stress conditions. These actions include activating or repressing the related signal pathways and networks, modulating the physiological changes, and generating the behavioral and morphological outcomes, such as root growth inhibition, stimulation of LR formation and altered root hair development. Thus, the developmental plasticity of plants plays a central role in tracking environmental change. As summarized in the review, auxin is a key player in plant phenotypic plasticity in response to various environmental cues (**Fig. 2A, 2B**). However, what we have learned about a plant's adaptation to the environment is very limited, and a number of critical questions from risk perception to proper response need to be answered in the future. We need to uncover how auxin finely rebuilds stressed plants and how the multiple regulatory networks are integrated to ensure their successful growth and reproduction. We must make use of the wealth of available genomic information, varieties/germplasm and new technologies to elucidate the evolutionary mechanisms underlying developmental plasticity. To predict what will happen and identify the critical factors/cues that will affect plant growth ahead of time will be an important future challenge. Of course, transformation and incorporation of our knowledge into breeding programs for new crops with enhanced stress tolerance, better fitness and high yield will be our ultimate goal.

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