

REVIEW

Auxin and the integration of environmental signals into plant root development

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- **Background** Auxin is a versatile plant hormone with important roles in many essential physiological processes. In recent years, significant progress has been made towards understanding the roles of this hormone in plant growth and development. Recent evidence also points to a less well-known but equally important role for auxin as a mediator of environmental adaptation in plants.
- **Scope** This review briefly discusses recent findings on how plants utilize auxin signalling and transport to modify their root system architecture when responding to diverse biotic and abiotic rhizosphere signals, including macro- and micro-nutrient starvation, cold and water stress, soil acidity, pathogenic and beneficial microbes, nematodes and neighbouring plants. Stress-responsive transcription factors and microRNAs that modulate auxin- and environment-mediated root development are also briefly highlighted.
- **Conclusions** The auxin pathway constitutes an essential component of the plant's biotic and abiotic stress tolerance mechanisms. Further understanding of the specific roles that auxin plays in environmental adaptation can ultimately lead to the development of crops better adapted to stressful environments.

Key words: Abiotic stress, arabidopsis, auxin, biotic stress, hormone crosstalk, lateral root development, plant hormones.

INTRODUCTION

Plants are extremely flexible organisms adaptable to a range of diverse environments. Their intrinsic ability to simultaneously inhabit both above- and below-ground domains makes them unique among most other living organisms, which occupy a single habitat at a given time. In response to diverse environmental signals, plants modify their development through the perception and integration of exogenous signals into the signalling pathways of plant hormones. Auxin is one of the most versatile plant hormones and plays essential roles in growth and development. The revelation of the existence of an auxin biosynthesis, signalling and transport apparatus in single-celled green algae is a clear indication that auxin has played an important evolutionary role during the adaptation of plants to diverse land environments (De Smet *et al.*, 2010). In recent years, significant progress has been made towards understanding how this hormone regulates plant growth and development. However, less is known about the roles of auxin as a regulator of biotic and abiotic stress responses. In this review, after a brief account of auxin biosynthesis, signalling and transport, interesting new insights into the role of auxin as an integrator of environmental signals are highlighted.

AUXIN BIOSYNTHESIS, SIGNALLING AND TRANSPORT

Auxin biosynthesis, signalling and transport processes, which are particularly relevant to the findings discussed in this article, have been extensively reviewed elsewhere (Vanneste

and Friml, 2009; Tromas and Perrot-Rechenmann, 2010; Zhao, 2010; Finet and Jaillais, 2012; Mano and Nemoto, 2012; Rosquete *et al.*, 2012; Swarup and Péret, 2012). Therefore, only a brief account of these processes will be presented here.

Auxin biosynthesis

As reviewed extensively elsewhere (Zhao, 2010; Mano and Nemoto, 2012; Rosquete *et al.*, 2012; Sauer *et al.*, 2013), auxin [indole-3-acetic acid (IAA)], is produced in meristematic tissues through tryptophan-dependent and -independent biosynthetic pathways. So far, three tryptophan-dependent auxin biosynthetic pathways, named after the intermediate compounds generated in each pathway, have been identified. These include the IPA (indole-3-pyruvic acid) pathway, the IAM (indole-3-acetamide) pathway, the TAM (tryptamine) pathway and the IAOx (indole-3-acetaldoxime) pathway. To maintain optimal concentrations and ratios of IAA and IAA derivatives in plant tissues, auxin homeostasis is regulated by processes such as degradation, conjugation to amino acids and transport. The apparent complexity and redundancy of auxin biosynthesis, signalling and transport seem to indicate the absolute requirement of this hormone for multiple plant processes.

Auxin signalling

In recent years, tremendous progress has been made towards dissecting the signalling pathway of auxin (reviewed by Vanneste and Friml, 2009; Tromas and Perrot-Rechenmann, 2010; Swarup and Péret, 2012). Briefly, at low auxin

concentrations, auxin responses are suppressed by AUX/IAA (AUXIN/INDOLE-3-ACETIC ACID) proteins. AUX/IAA proteins repress AUXIN RESPONSE FACTORS (ARFs), a class of transcription factors that regulate auxin-responsive gene expression. Auxin perception by TIR1 (TRANSPORT INHIBITOR RESPONSE 1) and related AUXIN F-BOX (AFB) proteins AFB1, AFB2 and AFB3 leads to the degradation of AUX/IAAs by the 26S proteasome and the subsequent release of ARFs from suppression. By binding to the auxin-responsive element (ARE) commonly found in the promoters of auxin-responsive genes, ARFs regulate (activate or repress) auxin-responsive gene expression, leading to a variety of auxin-mediated phenotypic alterations.

Auxin transport

Plant processes involved in auxin transport have also been extensively reviewed (Vanneste and Friml, 2009; Spalding, 2013). Briefly, auxin synthesized in aerial tissues (e.g. apical meristems) is transported locally and systemically throughout the plant. The cell-to-cell active movement of auxin is known as polar auxin transport (PAT), as opposed to the direct and rapid transport of auxin from shoots to roots through the phloem. Two general classes of transporters involved in PAT are auxin influx carriers such as AUX1 (AUXIN RESISTANT 1) and LAX1 (like aux1), which pump auxin into the cell, and auxin efflux carriers such as the PIN (PIN-FORMED) and ATP-binding cassette type B (ABCB) families [also known as the multidrug resistant proteins or P-glycoproteins (MDR-PGPs)], which pump auxin out of the cell. The specific localization of PIN proteins within the cell influences the direction of auxin transport (see below). More recently another class of auxin carriers, called PILS (PIN-LIKES), has been identified based on their structural similarity to the PIN family (Barbez *et al.*, 2012).

Lateral root development

One of the plant processes regulated by auxin is lateral root development, which has been extensively reviewed elsewhere (Osmont *et al.*, 2007; Nibau *et al.*, 2008; Péret *et al.*, 2009; Overvoorde *et al.*, 2010; Smith and De Smet, 2012; Petricka *et al.*, 2012) and will not be discussed here in detail. Briefly, upon germination, young seedlings contain only primary roots formed directly from the radicle present in the embryo. Lateral root primordia originate from pericycle cells located in front of the xylem of primary roots. Additional lateral roots reiteratively generated during root growth play essential roles in the water and nutrient uptake required to sustain proper plant growth and development. Auxin biosynthesis, signalling and transport are required for lateral root formation since auxin mutants show reduced or defective lateral root production, and exogenous treatment of pericycle cells with auxin promotes lateral root formation. Over recent years, research into lateral root development has introduced a new paradigm whereby the role of auxin as a key regulator of plant root architecture in response to environmental stimuli has been studied (Malamy, 2005). In this review I will briefly highlight some of the recent studies in this exciting research area.

AUXIN- AND NUTRIENT-DEPENDENT ALTERATIONS IN ROOT ARCHITECTURE

Given the importance of macro- and micro-nutrient elements for plant growth and development, it is not surprising that plant roots have developed unique capabilities to sense and respond to nutrients available in soil. Emerging evidence implicates auxin as one of the main players involved in this essential adaptive response. Since different plant species may respond differently to the lack or excess of a particular nutrient (Niu *et al.*, 2012), for consistency this review will discuss mainly examples from the dicot model plant *Arabidopsis thaliana*.

Nitrogen

Nitrogen (N) is an essential element taken up mostly in the form of nitrate (NO_3^-) from the soil solution. It has long been known that nitrogen deficiency leads to directional root growth towards nitrogen-rich regions of the soil (Zhang and Forde, 2000). Until recently how this nutritional signal is integrated into plant root development had remained elusive. So far, a number of plasma membrane-located transporters involved in nitrate uptake have been identified. One of such transporters, the *Arabidopsis* NITRATE TRANSPORTER1.1 (NRT1.1) protein (also known as CHL1), has dual functionality as a high-activity nitrate influx carrier and nitrate sensor (Ho *et al.*, 2009). At high nitrate concentrations, the *chl1/nrt1-1* mutant shows decreased lateral root proliferation relative to wild-type, suggesting that the nitrate-sensing mechanism is compromised in this mutant (Remans *et al.*, 2006). Remarkably, recent research has provided a mechanistic new insight into the role of NRT1.1 in lateral root development. It appears that under low NO_3^- concentrations NRT1.1 promotes basipetal auxin transport (from the lateral root tip shootward) to inhibit auxin accumulation in lateral root initials. At high NO_3^- levels, NRT1.1-dependent auxin transport out of the lateral roots is inhibited, leading to the accumulation of auxin in lateral root initials and promotion of lateral root growth (Krouk *et al.*, 2010; Gojon *et al.*, 2011; Bouguyon *et al.*, 2012). Therefore, it appears that auxin transport and nitrate uptake and sensing mechanisms are linked so that rapid alterations in root architecture can be achieved during adaptive responses to this essential nutrient.

Potassium

Similar to the dual roles of NRT1.1, the *Arabidopsis* *TRH1* (*TINY ROOT HAIR 1*) gene, which encodes a KT/KUP/HAK family protein, has been proposed to play a role in both auxin and potassium (K^+) transport (Vicente-Agullo *et al.*, 2004). *TRH1* is expressed in root-cap cells known to be involved in gravity perception and auxin redistribution (Vicente-Agullo *et al.*, 2004). The *Arabidopsis* *trh1* mutant shows defects in root hair development and gravitropism and a reduced ability to transport K^+ (Rigas *et al.*, 2001). These phenotypic defects could be restored by an exogenous auxin supply, suggesting that auxin is involved in TRH1-mediated root development (Vicente-Agullo *et al.*, 2004). Indeed, recent research has shown that TRH1 regulates auxin transport by influencing the localization of the auxin efflux protein PIN1 (Rigas *et al.*, 2013), although, as highlighted by Dolan (2013), additional research is required to further

dissect the possible roles of TRH1 in auxin and K^+ transport. Recent transcriptome analyses of rice roots during K^+ deficiency have also identified a large number of auxin-related genes (Ma *et al.*, 2012), further suggesting that auxin regulates root responses to this nutrient.

Phosphorus

Plants also alter their root development in response to low phosphate (Pi) (López-Bucio *et al.*, 2002, 2005; Nacry *et al.*, 2005; Svistoonoff *et al.*, 2007; Niu *et al.*, 2012). Such alterations include the reduction of primary root growth but promotion of lateral root development to facilitate exploration of the rhizosphere for new nutrient sources. The response to Pi deficiency of the auxin signalling mutant *axr1* is similar to that of wild-type plants (Williamson *et al.*, 2001). Also, in contrast to N deficiency, which alters lateral root development through alteration of auxin transport, no increase in free auxin levels or auxin transport was found in the roots of Pi-deprived seedlings (Pérez-Torres *et al.*, 2008). However, pericycle cells in the primary roots of Pi-deprived seedlings show increased sensitivity to exogenous auxin as determined by analysis of expression of the *DR5-GUS* synthetic auxin reporter in these cells (Pérez-Torres *et al.*, 2008). As mentioned above, lateral root primordium originates from pericycle founder cells and the increased sensitivity of these cells to auxin under low-Pi conditions suggests that Pi starvation primes these cells to produce lateral roots. The sensitivity of lateral root formation to Pi deficiency was reduced in the *tir1* mutant and nearly completely lost in the *tir1 afb2 afb3* triple auxin receptor mutant. Furthermore, in the absence of Pi, the AUX/IAA protein AXR3/IAA7 shows an increased degradation rate (Pérez-Torres *et al.*, 2008). Together, these findings suggest that functional auxin perception is required for proper root responses to Pi.

Another link between auxin transport and Pi-mediated lateral root development has recently been uncovered through the analysis of the arabidopsis *siz1* mutant. *SIZ1*, which encodes a SUMO E3 ligase, was previously identified as a negative regulator of lateral root development under Pi-deficient conditions (Miura *et al.*, 2005). The *siz1* mutant displays extreme sensitivity to Pi deficiency with a reduction in primary root but an increase in lateral root development. This response appears to occur through earlier accumulation of auxin in *siz1* roots (Miura *et al.*, 2011). *N*-1-naphthylphthalamic acid (NPA), a chemical inhibitor of auxin (efflux) activity, reverses the phenotypes caused by the *siz1* mutation under Pi-deficient conditions. This suggests that *SIZ1* is a negative regulator of auxin transport and lateral root development in plants grown under Pi-deficient conditions (Miura *et al.*, 2011).

Other nutrient elements

Metal ions such as copper (Cu^{2+}), aluminium (Al^{3+}), iron (Fe), boron (B) and cadmium (Cd) also cause drastic alterations in lateral root development, elongation and overall plant root architecture (Lequeux *et al.*, 2010; Aquea *et al.*, 2011; Martín-Rejano *et al.*, 2011; Peto *et al.*, 2011; Giehl *et al.*, 2012; Hu *et al.*, 2013; Yuan *et al.*, 2013). Altered auxin biosynthesis, signalling and/or transport seem to have an underlying effect on these alterations as transcriptional activation of auxin-related genes and increased auxin levels were observed in roots

exposed to various concentrations of these metals (Mattiello *et al.*, 2010; Lequeux *et al.*, 2010; Giehl *et al.*, 2012). For instance, genetic analyses show that root growth is inhibited less by Al^{3+} in *aux1* and *pin2* mutants than in wild-type plants. Chemical inhibition of auxin transport also reduces the negative effects of Al^{3+} on root growth (Sun *et al.*, 2010). Similarly, the AUX1 auxin transporter is required for Fe-triggered lateral root elongation (Giehl *et al.*, 2012). Sulphur (S) deficiency also suppresses lateral root development in wild-type arabidopsis, while this response is compromised in the *axr1-3* mutant (Dan *et al.*, 2007).

Together, these findings are consistent with the view that auxin signalling and transport play important roles in regulating root responses to soil nutrients.

AUXIN-MEDIATED ALTERATIONS OF ROOT ARCHITECTURE DURING ABIOTIC STRESS ADAPTATION

Low-temperature stress

During gravitropic responses, asymmetrical localization of auxin to one side of the cell through the action of auxin transport proteins, in particular PINs, redirects the root growth towards the centre of gravity (Friml, 2010). Exposure of roots to cold inhibits such gravity responses in arabidopsis (Rahman, 2013). In cold-exposed root cells, trafficking and lateral localization of the auxin efflux proteins PIN2 and PIN3 is inhibited until the seedlings are returned to normal growth temperatures (Shibasaki *et al.*, 2009). Possible roles of auxin as a regulator of cold stress responses of arabidopsis have recently been reviewed (Rahman, 2013) and will not be discussed here in detail.

Water stress

The importance of roots during water stress has been studied in much less detail compared with above-ground parts. Nevertheless, plant roots are capable of sensing and responding to the presence of moisture in soil, a phenomenon known as hydrotropism. The auxin response pathway, but not auxin transport, appears to play a role in hydrotropism (Kaneyasu *et al.*, 2007). The gravitropic and hydrotropic responses are antagonistic, and the overall involvement of auxin in hydrotropism is predicted to be less than that on gravitropism (Cassab *et al.*, 2013). Hydrotropic root responses seem to be mainly regulated by abscisic acid (ABA) signalling, which can overcome the effect of auxin-mediated responses (e.g. gravitropism) when these two forces are at odds to facilitate the extension of roots towards moist regions of the soil profile (Taniguchi *et al.*, 2010). Under moderate water stress conditions, ABA is required for maintaining primary root and root hair growth by modulating auxin transport in both arabidopsis and rice. This response is also accompanied by an enhanced proton secretion process through the action of plasma membrane-located H-ATPases, which are essential for maintaining root elongation (Xu W *et al.*, 2013). Further research is needed to dissect the complex interactions between auxin and other plant hormones that may be at play during water stress- or drought-mediated alterations in root architecture.

Recently, an important role for arabidopsis IAR3 (IAA-Ala Resistant3) as a modulator of root architecture during osmotic stress has been shown (Kinoshita *et al.*, 2012). IAR3 is a hydrolase capable of generating free auxin by hydrolysing an inactive auxin form such as an IAA–amino acid conjugate (e.g. IAA-Ala) (Rampey *et al.*, 2004). It was therefore proposed that, under drought stress, IAR3 generates bioactive auxin which then stimulates lateral root development and contributes to survival under drought stress (Kinoshita *et al.*, 2012).

Genetic screens designed to identify mutants compromised in hydrotropism have also identified *MIZU-KUSSEI* (*MIZ1*), encoding a novel protein in arabidopsis. Roots of *miz1* mutants grow vertically towards gravity, but do not show curved growth towards moisture (Kobayashi *et al.*, 2007). *MIZ1* over-expression lines show earlier and more pronounced growth curvature towards moisture and reduced primary root elongation, lateral root development and auxin levels (Miyazawa *et al.*, 2012).

Genome-wide expression analyses of plants under water stress often reveal differentially expressed auxin-responsive genes. For instance, genes encoding various members of the ARF transcription factor family are differentially expressed during dehydration stress in soybean roots, leading to the suggestion that these genes may be potential candidates for the generation of soybeans with increased drought tolerance (Ha *et al.*, 2013).

Salt stress

Salinity is an abiotic stress that severely affects plant and root development. A mild salt stress results in a drastic reduction of lateral root elongation but an increase in lateral root numbers, while higher salt levels completely inhibit root elongation (Zolla *et al.*, 2010). Increased lateral root numbers due to salt stress were reduced in auxin signalling mutants *axr1*, *axr4* and *tir1*, and completely blocked in the auxin influx mutant *aux1* (Wang *et al.*, 2009; Zolla *et al.*, 2010).

As stated above, uneven distribution of auxin efflux carriers, in particular PIN2, in the cells of the root elongation zone is known to control gravitropic root responses through the regulation of basipetal auxin transport (reviewed by Vanneste and Friml, 2009). Salt stress, in addition to altering PIN2 cellular localization, inhibits PIN2 expression (Sun *et al.*, 2008). Therefore, like cold stress, salt stress interferes with root gravitropism, which appears to be an adaptive response to reduce the damaging effects of salt stress (Galvan-Ampudia and Testerink, 2011).

The SOS (SALT OVERLY SENSITIVE) pathway characterized by molecular genetic analysis of several mutants (e.g. *sos1*, *sos2* and *sos3*) is required for salt tolerance in arabidopsis (Ji *et al.*, 2013). The tolerance provided by this pathway seems to occur at least partly through the promotion of lateral root development as transgenic plants over-expressing *SOS* genes show both increased salt tolerance and lateral root development under salt stress (Yang *et al.*, 2008). Lateral root development in the *sos3* mutant shows increased inhibition (salt sensitivity) at low salt concentrations, accompanied by reduced auxin levels in lateral root primordia. The reduced lateral root emergence observed in *sos3* appears to be due to the reduced shoot-to-root (acropetal) auxin transport as well as reduced basipetal auxin transport within the roots. The reduced expression

of the auxin efflux protein PIN2 in the roots of *sos3* plants supports this proposal (Zhao *et al.*, 2011). These findings indicate that auxin signalling and influx are both required for lateral root development under salt stress.

pH

Soil acidity or pH directly and indirectly influences root development. Plant roots respond to changes in soil pH with massive transcriptional alterations in the expression of a large number of auxin-responsive genes, suggesting that pH-mediated changes in root architecture are at least partly mediated by auxin (Lager *et al.*, 2010). Plant roots grown under alkaline conditions (e.g. pH 8) show increased auxin transport activity mediated by PIN2 (Xu W *et al.*, 2012). PIN2-transported auxin is also required for the activation of plasma membrane H⁺-ATPase-mediated proton secretion from the root tips. This process appears to be essential in acidifying the environment around the roots and maintaining primary root growth (Xu W *et al.*, 2012). Additional studies are certainly required to dissect the effect of pH on root development and the potential roles of auxin signalling and transport in the integration of pH-mediated effects into root architecture.

Waterlogging

Submergence or waterlogging is another abiotic stress factor that negatively affects root development by restricting the O₂ supply to the roots. Plants tend to develop adventitious roots when submerged to alleviate the negative effects of this stress on plant growth and development. The accumulation of auxin in the base of the stem promotes adventitious root formation. In the tomato, adventitious root formation requires auxin sensitivity as the formation of these roots is inhibited in submerged tomato plants compromised in auxin sensing (Vidoz *et al.*, 2010). In addition, chemical inhibition of PAT inhibits adventitious root formation, suggesting that auxin transport is required for their formation (Vidoz *et al.*, 2010). Furthermore, recent evidence discussed by Muday *et al.* (2012) indicates that the stress hormone ethylene, which accumulates in waterlogged plants, can contribute to the regulation of lateral and adventitious root formation in a complex crosstalk with auxin.

Redox status/reactive oxygen

The redox status of cells is altered during biotic and abiotic stress responses and affects auxin signalling and lateral root development. The arabidopsis triple mutant *ntra ntrb cad2*, which lacks the key components of the thioredoxin and glutaredoxin signalling involved in redox regulation, shows compromised auxin transport (Bashandy *et al.*, 2010). Nitric oxide accumulates in response to auxin treatment during lateral root formation and chemical inhibition of nitric oxide accumulation abolishes lateral root formation. Nitric oxide is also required for normal operation of auxin signalling by promoting the degradation of AUX/IAAs (Terrile *et al.*, 2012). During cadmium stress, rice root growth is regulated by an interplay between reactive oxygen species (ROS) (H₂O₂) and auxin signalling, in which increased ROS alters the expression of key auxin signalling components (Zhao *et al.*, 2012). Together, these findings point to an

essential link between the signalling pathways of auxin and ROS during the adaptive responses to stress.

The involvement of auxin signalling in salt and oxidative stress tolerance seems to occur, at least in part, through modulation of the cellular redox status. The primary root growth of *tir1afb2* seedlings show reduced sensitivity to salt (Iglesias *et al.*, 2010). Similarly, *tir1afb2* and *tir1afb3* double receptor mutants exhibit a higher percentage of primary root elongation and reduced H₂O₂-induced cell death than wild-type roots under oxidative stress. To explain this phenomenon, it was proposed that the mutant seedlings may have reduced levels of endogenous ROS. Indeed, higher levels of anti-oxidant enzymes such as CAT (CATALASE) and APX (ASCORBATE PEROXIDASE) were detected in salt-stressed *tir1afb2* plants. Increased activities of these ROS-degrading enzymes also correlated with transient induction of *GST1*, encoding glutathione S-transferase 1 (GST1), *APX1*, encoding a cytosolic ascorbate peroxidase, and *ZAT12*, encoding a zinc finger transcription factor in response to salt stress (Iglesias *et al.*, 2010). These findings have led to the suggestion that under stress conditions auxin signalling promotes the production of ROS, which potentiates tissue damage. Therefore, an attenuated auxin signalling pathway may be a strategy employed by plants to enhance tolerance to ROS-generating abiotic stresses (Iglesias *et al.*, 2010).

BIOTIC FACTORS AND AUXIN-MEDIATED ALTERATIONS OF PLANT ROOT ARCHITECTURE

In a complex environment like soil, plant roots encounter many living organisms, such as symbiotic/endophytic bacteria and fungi as well as bacterial and fungal pathogens, nematodes, insects and even parasitic plants. In the following sections, recent findings on how diverse biotic signals alter root development by directly or indirectly modifying auxin signalling and transport will be briefly reviewed.

Beneficial microbes

Many plant species establish symbiotic relationships with fungi such as arbuscular mycorrhiza (AM). AM enter plant roots through lateral roots and manipulates the plant's root system architecture, at least partly through the host auxin signalling pathway (Hanlon and Coenen, 2011; Sukumar *et al.*, 2013). Arabidopsis is not susceptible to infection by AM and therefore the interaction between AM and plant roots has been mostly studied in species other than arabidopsis. Nevertheless, arabidopsis roots can recognize the signals generated by AM. For instance, the mycorrhizal fungus *Laccaria bicolor* can induce lateral root development after indirect contact with arabidopsis roots (Felten *et al.*, 2009). Chemical or genetic inhibition of PAT through NPA treatment or the use of the *pin2* mutant leads to a dramatic reduction in *L. bicolor*-mediated lateral root induction during this interaction. Similar results were also reported for the interaction between arabidopsis roots and the mycorrhizal fungi known as truffles (*Tuber borchii* and *T. melanosporum*) (Splivallo *et al.*, 2009). Furthermore, *Trichoderma virens*, a plant-beneficial fungus, promotes lateral root growth in arabidopsis through an auxin signalling- and

transport-dependent mechanism. The lateral root-promoting ability of *T. virens* is attenuated in the auxin transport or signalling mutants *aux1*, *big1*, *eir1/pin2* and *axr1* (Contreras-Cornejo *et al.*, 2009). It should be noted that AM can also produce auxin and/or auxin-like compounds that can potentially contribute to the alterations observed in root development. For instance, the growth-promoting effects of the beneficial fungus *Piriformospora indica* on arabidopsis appears to be mediated through a highly branched root system promoted by fungally produced auxin (Sirrenberg *et al.*, 2007).

Root inoculation of arabidopsis with the rhizobacterium *Phyllobacterium brassicaceae* leads to a 50 % increase in lateral root growth, while this effect is abolished in *aux1* and *axr1* mutants, again suggesting that auxin signalling and transport are both required for this effect (Contesto *et al.*, 2010). Similarly, beneficial *Pseudomonas*, which promotes plant growth, inhibits primary root elongation while promoting lateral root formation in arabidopsis in an auxin-dependent manner, as the auxin receptor mutant *tir1afb2afb3* mutant shows insensitivity to *Pseudomonas*-stimulated lateral root formation (Zamioudis *et al.*, 2013). The nitrogen-fixing nodules formed during the interaction of plant roots with the beneficial soil bacterium *Frankia* are structurally and developmentally related to lateral roots (Pawlowski *et al.*, 2011). The involvement of auxin in the formation of root nodules in legumes by rhizobia has recently been reviewed (Mathesius, 2010) and will not be discussed here.

Pathogenic microbes

Plant roots are constantly exposed to a variety of soil-inhabiting organisms, including pathogenic bacteria and fungi that modify the plant's root architecture in an auxin-dependent manner. The root-infecting pathogenic bacterium *Ralstonia solanacearum*, for instance, reduces the formation of lateral roots in petunia (Zolobowska and Van Gijsegem, 2006). Similarly, the soil-borne fungal pathogen *Fusarium oxysporum* infects arabidopsis through lateral root initials (Kidd *et al.*, 2011). Several arabidopsis auxin signalling and transport mutants in which lateral root development is known to be altered show increased resistance to *F. oxysporum*, indicating the possible involvement of the host's auxin signalling and transport pathways in the infection process (Kidd *et al.*, 2011).

Recognition of the conserved molecules collectively known as microbe-associated molecular patterns (MAMPs) by pattern recognition receptors (PRRs) elicits developmental alterations that may be executed through the auxin pathway. For instance, flg22, a conserved MAMP from the flagellin of the bacterial pathogen *Pseudomonas syringae*, inhibits root growth in arabidopsis (Gómez-Gómez *et al.*, 1999). This effect is most likely mediated by flg22-responsive microRNA393, a known inhibitor of auxin receptors *TIR1*, *AFB2* and *AFB3* (Navarro *et al.*, 2006). As expected, the inhibition of auxin receptor gene expression leads to the stabilization of IAA/AUX repressors, which act as repressors of auxin-responsive genes, including those involved in lateral root development.

Oligogalacturonides, elicitors derived from plant cell wall hydrolysis during parasitism, reduce primary root cell elongation and development but promote lateral root formation in an auxin-dependent manner (Hernández-Mata *et al.*, 2011). Interestingly, in contrast to flg22-mediated effects, the stabilization of

IAA/AUX repressors is not required for the antagonistic interaction between oligogalacturonides and auxin signalling (Savatin *et al.*, 2011). It was proposed that the effect of oligogalacturonides on auxin signalling is at least partly due to the promoting effects of oligogalacturonides on flavonoids (Savatin *et al.*, 2011), known inhibitors of auxin transport (Brown *et al.*, 2001). Supporting this view, auxin signalling (e.g. *tir1*) and transport (e.g. *doc1*, *pgp1*, *pgp4*, *pgp19* and *tt4*) mutants show altered responses to oligogalacturonides (Hernández-Mata *et al.*, 2011).

Nematodes

Nematodes are soil-dwelling organisms that cause significant damage to many crop plants. Root-knot nematodes (*Meloidogyne* spp.) induce multinucleated giant cells in infected roots while cyst nematodes (e.g. *Heterodera* sp.) modify root cells to form specialized cells called syncytia. Like lateral roots, these nematode-induced root cells originate from pericycle cells, and their formation requires components of the host's auxin signalling and transport pathways (Grunewald *et al.*, 2009a). Indeed, nematode infectivity is compromised in auxin signalling and transport mutants (Grunewald *et al.*, 2009b). Numbers of the infected beet cyst nematode (*Heterodera schachtii*) are significantly reduced in the *aux1 lax3* double mutant, suggesting that this nematode takes advantage of the host's auxin transport process during the colonization of arabidopsis roots (Lee *et al.*, 2011). Supporting this view, Hs19C07, an effector of *H. schachtii*, physically interacts with the arabidopsis auxin influx transporter LAX3, a close relative of the better known auxin influx protein AUX1 (Lee *et al.*, 2011). A possible mechanism for the reduced nematode infectivity observed in the mutant would be that LAX3-mediated auxin transport may be required for the activation of the cell wall-loosening enzymes (e.g. expansins) required for both lateral root formation (Swarup *et al.*, 2008) and syncytium development.

Other arabidopsis auxin transport proteins are also known to have roles in nematode susceptibility. Based on the analysis of single and double mutants of the PIN auxin efflux family, it was shown that PIN1 is required for the initiation and PIN3 and PIN4 are required for the expansion of nematode feeding sites in arabidopsis (Grunewald *et al.*, 2009b). Whether nematode effectors are involved in this phenomenon is not known; however, this finding further supports the view that nematodes can exploit the host's auxin transport process for their benefit (Gheysen and Mitchum, 2011; Haegeman *et al.*, 2012).

TRANSCRIPTIONAL AND POSTTRANSCRIPTIONAL REGULATION OF ENVIRONMENT- AND AUXIN-MEDIATED ROOT SYSTEM ARCHITECTURE

Transcription factors

So far, a few transcriptional regulators involved in the environmental regulation of lateral root development have been identified. For instance, the *Medicago truncatula* HD-Zip I transcription factor HB1 is required for the inhibition of lateral root emergence under salt stress (Ariel *et al.*, 2010). HB1

represses *LBD1*, which encodes an auxin-responsive lateral organ boundaries (LOB) domain-containing transcription factor (reviewed by Majer and Hochholdinger, 2011) by directly binding to the promoter of this transcription factor (Ariel *et al.*, 2010). Several members of the *LBD* gene family (e.g. *LBD18/ASL20*, *LBD16/ASL18* and *LBD29/ASL16*) regulate lateral root formation and the expression of these genes is directly regulated by ARFs (Okushima *et al.*, 2007; Lee *et al.*, 2009). More recently, the involvement of *LBD18* in the regulation of *EXPANSINA 14* (*EXPA14*) and *EXPA17* genes, which encode the cell wall-loosening expansin enzymes implicated in lateral root formation, has been shown (Lee *et al.*, 2012; Lee and Kim, 2013). Indeed, knocking down *EXPA17* expression delays lateral root emergence while *EXPA17* over-expression promotes lateral root density in the presence of exogenous auxin (Lee and Kim, 2013). Another member of the *LBD* gene family, *JAGGED LATERAL ORGAN* (*JLO*), is required for all auxin responses in the root (Bureau *et al.*, 2010). Identification of environmental signals that activate root-specific expression of these transcription factors may lead to new insights into the regulation of root architecture.

The arabidopsis transcription factor MYB77 is proposed to be a positive regulator of lateral root development under low IAA or low nutrient levels. MYB77 interacts with ARF7 and promotes auxin-responsive gene expression (Shin *et al.*, 2007). MYB77 expression is negatively regulated by K⁺ deprivation and the lateral root density of the *myb77* mutant is lower than that of wild-type plants under K-deprived conditions. The response of *myb77* to N and P remains unchanged, suggesting that MYB77 is required for correct responses to K⁺.

Over-expression of NAC2, a NAC (NAM-ATAF1/2-CUC2) domain-containing transcription factor whose salt-responsive induction is dependent on the auxin receptor TIR1, promotes lateral root development under salt stress, although the exact mechanism(s) of NAC2-mediated salt tolerance is currently unknown (He *et al.*, 2005). NTM2, another NAC transcription factor of arabidopsis, integrates auxin and salt signals during seed germination (Park *et al.*, 2011) while NAC4, acting downstream from the auxin receptor AFB3, controls nitrate-mediated lateral root development, most likely by directly or indirectly regulating the expression of other transcription factors, such as the zinc finger protein *OCS ELEMENT BINDING FACTOR 4* (*OBF4*) (Vidal *et al.*, 2013). The arabidopsis *WRKY75* transcription factor is induced by Pi deprivation. *wrky75* knockdown plants were more sensitive to Pi deprivation and exhibited increased lateral root length and numbers under both normal or Pi deprivation conditions. It was proposed that this transcription factor might exert its effect on lateral root development by regulating the genes involved in auxin transport (Devaiah *et al.*, 2007). GbWRKY1, a novel cotton (*Gossypium barbadense*) transcription factor, also positively regulates Pi deprivation tolerance by altering auxin sensitivity when over-expressed in arabidopsis (Xu L *et al.*, 2012). OsWRKY72, the rice orthologue of WRKY75, has also recently been associated with auxin transport (Yu *et al.*, 2010). Finally, the role of OsARF16, a positive regulator of auxin responses, in primary root, lateral root and root hair development under Pi deficiency, has recently been shown (Shen *et al.*, 2013). *OsARF16* and rice *PIN* genes such as *OsPINb*, *OsPIN4* and *OsPIN9* are co-regulated, suggesting that OsARF16-mediated effects occur through altered auxin transport (Shen *et al.*, 2013).

More recently, the involvement of three PLETHORA (PLT3, PLT5 and PLT7) transcription factors, which seem to act downstream from ARF7 and ARF19, in lateral root development was shown (Hofhuis *et al.*, 2013). It is unknown, however, whether these transcription factors regulate environmentally related root responses.

MicroRNAs

Over the years, a number of microRNAs that target plant genes involved in the regulation of root architecture have been identified (reviewed by Khan *et al.*, 2011). The mode of action of some of these microRNAs, which can also be responsive to signals such as nutrient deficiency or other stresses, clearly involves auxin. For instance, arabidopsis plants over-expressing miR393, a microRNA that downregulates the expression of the AFB3 auxin receptor, resemble *afb3* mutant plants, which

show compromised primary root and lateral root growth in response to nitrate (Vidal *et al.*, 2010). Interestingly, drought stress activates miR393. The miR393-dependent degradation of *TIR1* and *AFB2* transcripts contributes to osmotic stress-mediated inhibition of lateral root growth by attenuating auxin signalling (Chen *et al.*, 2012a). These findings indicate that diverse signals converge on these microRNAs, which in turn regulate the expression of key genes involved in auxin signalling and lateral root development. More recently, IAR3 has been identified as a target of miR167. As discussed above, IAR3 regulates lateral root development and contributes to osmotic stress tolerance in arabidopsis. miR167 also controls the expression of *ARF8* and modulates N-responsive lateral root initiation (Kinoshita *et al.*, 2012). Other stress-responsive microRNAs regulating lateral root development by targeting the auxin pathway have been reported. For instance, miR164 affects lateral root development by targeting NAC1, which in turn regulates auxin signalling in arabidopsis (Guo *et al.*, 2005).

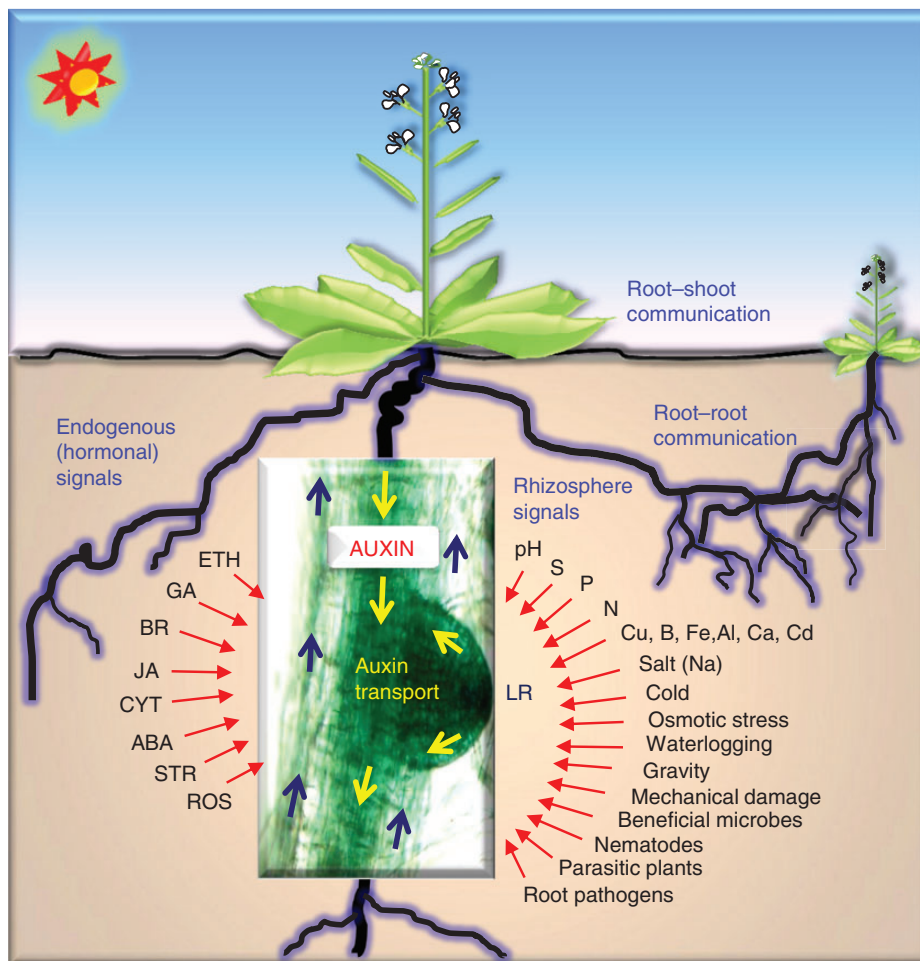


FIG. 1. Auxin plays an essential role in the integration of diverse biotic and abiotic environmental signals to plant root development. Auxin signalling interacts with the signalling pathways of all other known plant hormones. Auxin is also proposed to have roles in regulating the communication both within the same plant (root–shoot communication) and between different plants (root–root communication). The central image is a β -glucuronidase (GUS)-stained section of a primary root with emerging lateral root from a *DR5-GUS*-expressing arabidopsis seedling (Ulmasov *et al.*, 1997) and the intensity of GUS staining correlates with increased auxin activity. The arrows indicate an effect but do not necessarily suggest a positive interaction. ABA, abscisic acid; LR, lateral root; ETH, ethylene; GA, gibberellin; BR, brassinosteroid; STR, strictolactones; JA, jasmonate; CYT, cytokinins; ROS, reactive oxygen species. See the text for additional details.

CONCLUDING REMARKS: IS AUXIN A COMPONENT OF THE OVERALL BIOTIC AND ABIOTIC STRESS TOLERANCE MECHANISM OF PLANTS?

Better understanding of how plant roots integrate environmental signals can lead to the development of potential remedies to improve crop productivity, such as the use of soil microbes to optimize plant growth in stressful environments (Remans *et al.*, 2012; Schenk *et al.*, 2012). Although this review article has mainly focused on the role of auxin as an integrator of environmental signals in plant root development, emerging evidence also implicates auxin as an integral part of the plant's overall biotic and stress tolerance mechanism (see for instance Zhang *et al.*, 2008, 2012; Kazan and Manners, 2009; Shen *et al.*, 2010; Wang *et al.*, 2010; Stirnberg *et al.*, 2012). For instance, the arabidopsis activation-tagged *yuc7-1D* mutant, with constitutively elevated auxin levels, shows increased expression of the stress-associated genes *RD29A* (*RESPONSIVE TO DESSICATION 29A*) and *COR15A* (*COLD-REGULATED 15A*) and increased drought tolerance (Lee *et al.*, 2012). A similar role in drought tolerance has been shown for another arabidopsis *YUCCA* gene implicated in auxin production when expressed in potato (*Solanum tuberosum*) (Kim *et al.*, 2012). In rice, a novel *YUCCA* protein, *CONSTITUTIVELY WILTED1*, is involved in maintaining water homeostasis and an appropriate root-to-shoot ratio (Woo *et al.*, 2007). A role in drought tolerance has also recently been shown for the putative auxin efflux carrier *OsPIN3t* in rice (Zhang *et al.*, 2012).

In their natural environments, plants also encounter strong competition from nearby plants. The auxin pathway has long been known to be an essential part of the plant's shade-avoidance mechanism, an evolutionarily important response triggered by reduced red:far red light ratios under light-limiting conditions (Morelli and Ruberti, 2000; Keuskampa *et al.*, 2010). New evidence also suggests extensive communication between roots of different plants in the rhizosphere (Cahill *et al.*, 2010; Chen *et al.*, 2012b; Faget *et al.*, 2013; Falik *et al.*, 2013). Although possible mechanisms involved in this phenomenon are not yet clear, root tips seem to function as sensors for detecting the presence of other roots from nearby plants (Fang *et al.*, 2013). Given the prominent role of auxin in root adaptive responses, it would not be surprising if auxin also plays a role in regulating root–root communication. In fact, auxin is known to play a role in root–shoot communication, a process that can be critical for survival during environmental adaptation (Kabouw *et al.*, 2012).

The extensive interplay reported between auxin and other plant hormones might be at least partly responsible for some of the stress-related developmental alterations in auxin biosynthesis, signalling or transport mutants (Ivanchenko *et al.*, 2008; Teale *et al.*, 2008; Seo and Park, 2009; Fukaki and Tasaka, 2009; Gou *et al.*, 2010; Blomster *et al.*, 2011; Lewis *et al.*, 2011; Gutierrez *et al.*, 2012; Bielach *et al.*, 2012; Durbak *et al.*, 2012; Muday *et al.*, 2012; Shani *et al.*, 2013; Löfke *et al.*, 2013; Rahman, 2013). In addition, as reviewed here, auxin also crosstalks with other stress-responsive signalling pathways, such as those of Ca^{2+} and ROS, produced in the plant during adaptive responses to various biotic and abiotic stresses. Despite all these complexities, different stresses appear to induce an overlapping set of plant responses, called

the 'stress induced morphogenic response' (SIMR) (Potters *et al.*, 2007, 2009), which helps the plant to reallocate available resources between defence and development (Fig. 1). An improved understanding of the role of auxin during plants' adaptation to environmental signals will help in the design of future strategies aimed at improving biotic and abiotic stress tolerance in crop plants.

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