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REVIEW

Hormone interactions at the root apical meristem

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Abstract Plants exhibit an amazing developmental flexibility. Plant embryogenesis results in the establishment of a simple apical–basal axis represented by apical shoot and basal root meristems. Later, during postembryonic growth, shaping of the plant body continues by the formation and activation of numerous adjacent meristems that give rise to lateral shoot branches, leaves, flowers, or lateral roots. This developmental plasticity reflects an important feature of the plant's life strategy based on the rapid reaction to different environmental stimuli, such as temperature fluctuations, availability of nutrients, light or water and response resulting in modulation of developmental programs. Plant hormones are important endogenous factors for the integration of these environmental inputs and regulation of plant development. After a period of studies focused primarily on single hormonal pathways that enabled us to understand the hormone perception and signal transduction mechanisms, it became obvious that the developmental output mediated by a single hormonal pathway is largely modified through a whole network of interactions with other hormonal pathways. In this review, we will summarize recent knowledge on hormonal networks that regulate the development and growth of root with focus on the hormonal interactions that shape the root apical meristem.

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Introduction: *when root grows*

The root meristem is an organ of well-defined structure with stereotypical patterns of cell types along radial and longitudinal axes. The radial pattern is organized in concentric rings of lateral root cap, epidermis, ground tissue (cortex and endodermis) and a pericycle surrounding a central stele (Dolan et al. 1993; van den Berg et al. 1998). The radial patterning is laid down during embryogenesis and maintained by stem cell niche activity consisting of four sets of initials: the lateral root cap/epidermal, the cortical/endodermal, the columella and the pericycle/vascular initials surrounding quiescent centre (QC) (Dolan et al. 1993; van den Berg et al. 1998). Stem cells have the capacity for prolonged self-renewal (Watt and Hogan 2000). Each stem cell undergoes an asymmetric division to produce one daughter cell that remains under the influence of a short-range signal from the QC, preventing differentiation and maintaining the stem cell status and the other daughter cell becomes part of differentiated tissues (van den Berg et al. 1998).

Along the longitudinal axis, the root meristem forms a distal root tip, including stem cell niche, columella and lateral root cap, proximal meristem with a population of rapidly dividing cells and elongation zone where cells leaving the root meristem undergo rapid elongation and mature (Dolan et al. 1993). The longitudinal root meristem organization is completed during the postembryonic development when the balance in the rate of generation of new cells in the proximal root meristem and the

differentiation of daughter cells leaving root meristem is established, resulting in the formation of the root meristem of stable size (Dello Ioio et al. 2007; Dolan et al. 1993).

The identification of mutants with defects in the root meristem organization has provided a basis for understanding the mechanisms of radial and longitudinal patterning in the root. Organization of root meristem along the longitudinal axis is primarily under the control of the plant hormone auxin and of the downstream auxin-acting family of *PLETHORA* (*PLT*) (AP2-like transcription factors) genes. The *PLT* expression follows the auxin gradient along the root meristem with its maxima in the stem cell niche region. *PLT* genes have been shown to act in a dosage dependent manner, high activity promotes stem cell identity and maintenance, whereas low levels promote mitotic activity of stem cell daughters; and even lower levels are required for cell differentiation (Aida et al. 2004; Galinha et al. 2007).

In parallel with the auxin and PLT pathway, the SHORTROOT/SCARECROW (SHR/SCR) pathway regulates the radial patterning, and they converge to specify and regulate function of the stem cell niche. Plants homozygous for the *scr* and *shr* mutations are defective in the division of the cortex/endodermis initial daughter cell, resulting in the formation of a single layer of ground tissue instead of two (Benfey et al. 1993; Scheres et al. 1995). Functional studies revealed that SHR, a transcription factor of the GRAS family, acts upstream of the SCR transcription factor (Helariutta et al. 2000). SHR moves from the central vasculature, place of its transcription, into the surrounding tissue layer, where after heterodimerization with SCR, it stimulates by a positive feedback loop the expression of *SCR* gene (Cui et al. 2007; Di Laurenzio et al. 1996; Nakajima et al. 2001). Ectopic expression experiments suggested that the SHR movement is limited to a single cell layer and that heterodimerization with SCR might be the mechanism to sequester the SHR protein in the nucleus and restrain its movement to a single cell layer adjacent to the stele (Cui et al. 2007). Recently, two zinc-finger proteins, MAGPIE (MGP) and JACKDAW (JKD), have been identified as factors required for radial patterning and contribute to refining the SHR and SCR action range (Welch et al. 2007).

Both auxin/PLT and SHR/SCR pathways are closely interconnected with the activities of several hormonal pathways. The PLT pathway acts downstream of the auxin signalling (Aida et al. 2004; Galinha et al. 2007), whereas among the eight direct targets of SHR, as elegantly identified by a set of microarray analyses (Levesque et al. 2006), one is involved in the brassinosteroid pathway (cytochrome P450/BRox62 regulating brassinosteroid biosynthesis; (Shimada et al. 2003)) and the other in the gibberellin signalling (SNEEZY/SLEEPY2 (SNE) F-box protein (Levesque et al. 2006)). Several other indirect targets are the molecular components of auxin biosynthesis *SUR2*(*SUPERROOT*) (Barlier et al. 2000), signalling *IAA12/BDL*(*BODENLOS*) and *ARF5/MP*(*MONOPTEROS*) (Hamann et al. 2002; Hardtke and Berleth 1998) and transport *PIN3* and *PIN7* (Friml et al. 2003a; Friml et al. 2002b); brassinosteroid perception *BRL3* (Cano-Delgado et al. 2004) and biosynthesis *Cyp90D1* (Kim et al. 2005) and gibberellin signalling R*GL1* and *RGL2* (Lee et al. 2002; Wen and Chang 2002); and *GA3* biosynthesis (Helliwell et al. 1998; Levesque et al. 2006). This clearly reflects that root development requires not only transcriptional network but also network of hormonal signalling.

Indeed, besides the plant hormone auxin, the key hormonal regulator of the root organogenesis, other plant hormones, e.g. cytokinin (Dello Ioio et al. 2007; Mahonen et al. 2006; Werner et al. 2003), ethylene (Ortega-Martinez et al. 2007; Swarup et al. 2007), brassinosteroids (Mouchel et al. 2006), gibberellin (Fu and Harberd 2003; Ubeda-Tomas et al. 2008) and abscisic acid (Achard et al. 2003) also participate in the regulation of different aspects of root organogenesis and activity. Lately, it became obvious that single hormone input is strongly modulated by other hormonal pathways acting in parallel. Characterization of these interactions and their impact on the root meristem development will be discussed in detail in the following sections.

Auxin: *the hormonal regulator of root development*

Auxin has been shown to regulate an extremely broad range of developmental processes, such as embryogenesis, organogenesis of leaves, flowers, ovules or lateral roots, gravitropic responses and apical hook formation. The whole process of root organogenesis, begining with the establishment of the root pole in embryos (Friml et al. 2003a; Weijers et al. 2006), positioning and formation of stem cell niche (Blilou et al. 2005; Sabatini et al. 1999), maintenance of mitotic activity in proximal meristem (Beemster and Baskin 2000; Dello Ioio et al. 2007; Galinha et al. 2007; Stepanova et al. 2008) and rapid elongation and differentiation of cells leaving the root meristem (Rahman et al. 2007) has been shown to be under the control of auxin. A real breakthrough in our understanding of how auxin molecule can lead to such a variety of developmental responses is the discovery of the instructive function of the auxin gradient formed along the longitudinal axis of the root meristem (Benkova et al. 2003; Friml et al. 2002a; Sabatini et al. 1999). The auxin gradient is generated by the concerted action of AUX/LAX auxin influx carriers (Bennett et al. 1996; Yang et al., 2006), PIN auxin efflux carriers (Galweiler et al. 1998; Luschnig et al. 1998; Friml et al. 2002a, b; Friml et al. 2003b; Petrášek

et al. 2006) and members of the multi-drug-resistant/P-glycoprotein (MDR/PGP) subfamily of ATP-binding cassette (ABC) proteins (Blakeslee et al., 2007). Interference with its establishment results in dramatic patterning and developmental defects in the root meristem (Blilou et al. 2005; Friml et al. 2002a; Sabatini et al. 1999).

It is still not precisely known how the auxin gradient achieves the specificity of the response required for the different aspects of the root meristem development by using the signal transduction pathway consisting of four TIR/AFB auxin receptors of the F-box protein family (Dharmasiri et al. 2005), 29 AUX/IAA negative regulators (Overvoorde et al. 2005) and 23 ARF (AUXIN RESPONSE FACTORS) transcription factors (Okushima et al. 2005), activating the expression of downstream auxin response genes. It has been proposed that certain combinations of AUX/IAAs and ARFs determine the response specificity (Hamann et al. 2002; Knox et al. 2003; Weijers et al. 2005). In the case of root development, the specific pair of IAA12/BDL and ARF5/MP was identified to determine the establishment of root pole in early embryogenesis (Hamann et al. 2002). Beside the *BDL-MP* pair, some other genes of the auxin signalling pathway (*SHY2/IAA3, AXR3/IAA17* and *AXR2/IAA7*) were shown to be involved in different aspects of root growth (Leyser et al. 1996; Nagpal et al. 2000; Tian and Reed 1999), although their direct ARF counterparts are still unknown. The *PLT* gene family seems to play an important role in the developmental interpretation of the auxin gradient. *PLT* genes respond in an auxin concentration-dependent manner to regulate stem cell identity and maintenance, mitotic activity of stem cells' daughters and cell differentiation (Galinha et al. 2007).

Auxin: universal partner in hormonal interactions?

Interestingly, many mutants in the auxin pathway exhibit not only auxin-related root phenotypes but also an altered sensitivity to other hormones. For example, root growth of the auxin transport mutants *aux1* and *pin2* is also ethylene resistant (Roman et al. 1995). Similarly, mutants in the auxin signalling *shy2-2/iaa3*, *axr2/iaa7* and *tir1* do not exclusively exhibit an auxin-resistant root phenotype, but also exhibit a changed sensitivity to other hormones such as cytokinins, abscisic acid or ethylene (Alonso et al. 2003; Tian and Reed 1999; Wilson et al. 1990). This promiscuous behaviour of mutants points out that auxin regulated events in root growth are tightly interconnected with other hormonal pathways and in many interactions auxin seems to act downstream of other hormonal pathways. From longstanding investigations on regulatory pathways in root development, auxin has emerged as one of the key factors involved in many very specific aspects of root organogenesis. Therefore, from practical reasons, auxin and its interactions will be discussed in the context of respective hormonal pathways (see Fig. 1).

Ethylene *is all around … and interacts*

Typically, seedlings germinated at high ethylene concentrations have short hairy roots, a phenotype in some aspects resembling auxin-treated roots. Detailed developmental studies revealed that ethylene affects root growth primarily by inhibiting the rapid expansion of cells leaving the root meristem (Le et al. 2001; Ruzicka et al. 2007; Swarup et al. 2007). More recently, ethylene has also been demonstrated to participate in the regulation of the cell division activity of the QC. Manipulation of the ethylene pathway by genetic or chemical tools affected the division activity of the QC suggesting its functions in maintenance of stem cell niche by regulating the balance between proliferation and quiescence of stem cells (Ortega-Martinez et al. 2007).

As mentioned above mutations in many auxin transport or signalling components cause aberrant responses to ethylene, thus pointing to an ethylene–auxin interaction. Mutations in the auxin influx and efflux carrier genes *AUX1* and *EIR1/AGR/PIN2* (Luschnig et al. 1998; Pickett et al. 1990; Roman et al. 1995), several components of the auxin signalling cascade, including the auxin receptor *TIR1* (Alonso et al. 2003) and the AUX/IAA regulators *axr2/iaa7* (Wilson et al. 1990) and *axr3/iaa17* (Leyser et al. 1996; Swarup et al. 2007) confer ethylene insensitive root growth phenotypes. Stepanova et al. (2005) demonstrated that mutations in two *Arabidopsis* genes *ASA1* and *ASB1* encoding subunits of the anthranilate synthase enzyme that synthesizes an auxin precursor also confer ethylene insensitive root growth phenotypes. Gene interaction studies have positioned these auxin pathway components downstream of the ethylene signal transduction pathway (Roman et al. 1995; Stepanova et al. 2005), suggesting that ethylene inhibition of root growth requires auxin biosynthesis, transport and responses. The hypothesis is further corroborated by other findings. As indicated by Rahman et al. (2001), *aux1* root growth can be sensitized to ethylene when cultured in the presence of auxin. Accordingly, ethylene sensitivity of the ethylene response reporter EBS in roots depends on auxin (Stepanova et al. 2007). Measurements of the auxin biosynthesis rate upon ethylene treatment revealed a stimulatory effect of ethylene on the auxin biosynthetic pathway (Swarup et al. 2007). Indeed, several genes of the auxin biosynthesis pathways were isolated and found to be under transcriptional control of ethylene. Beside *ASA1* and *ASB1,* (Stepanova et al. 2005), recently, a small family of genes encoding a long-anticipated tryptophan aminotransferase, TAA1, regulating the indole-3-pyruvic acid branch of the auxin biosynthetic pathway (Stepanova et al. 2008; Tao et al. 2008) has been

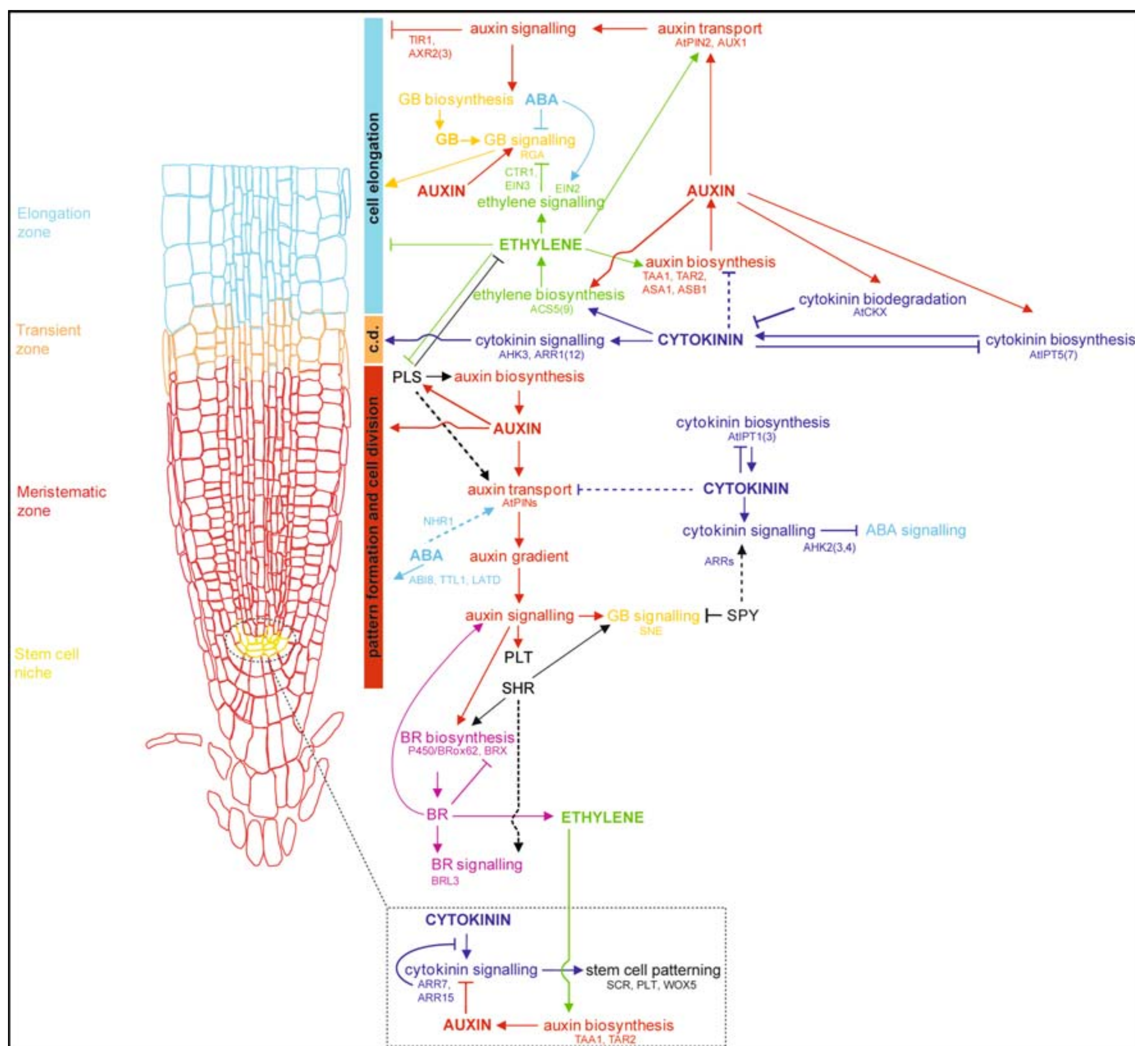

Fig. 1 Scheme of the hormonal cross-talk involved in the regulation of the root apical meristem growth and development. Selected regulators of the cross-talk are highlighted. Dashed lines correspond to not completely clear or mostly indirect regulations. c.d. is transition zone where differentiation starts

identified. Interestingly, *TAA1* and its close homologue *TAR2* are expressed in different organs including root meristem. Lack of their functions caused a drastic reduction in the meristem size and collapse of the root meristem, similar to mutants with reduced auxin levels due to a defective auxin transport (Benjamins et al. 2001; Blilou et al. 2005). Thus, analysis of *TAA1* and its homologues represents an important and for a long time missing link between local auxin production, tissue-specific ethylene effects and organ development, including root meristem (Stepanova et al. 2008).

A mechanistic model integrating our recent knowledge on the auxin - ethylene cross talk in roots has been proposed (Ruzicka et al. 2007; Stepanova et al. 2007; Swarup et al. 2007). According to this model, ethylene stimulates auxin biosynthesis in different plant organs via its known signalling pathway. In addition, ethylene increases the auxin transport capacity by regulating the transcription of several auxin transport components, including *PIN1*, *PIN2* and *AUX1* (Ruzicka et al. 2007). The additionally produced auxin is redistributed by polar auxin transport towards the root tip. The major components of the auxin transport in these tissues, AUX1 and PIN2, mediate the auxin delivery into cells of the elongation zone, where auxin accumulates and induces local auxin responses that inhibit cell elongation and overall root growth (Ruzicka et al. 2007; Stepanova et al. 2007; Swarup et al. 2007). Thus, inhibition of auxin responses in several mutants of the auxin signalling results in ethylene insensitive root growth. As revealed by tissue targeted inhibition of auxin responses, ethylene inhibition of root growth requires auxin responses in multiple cell layers of the elongation zone tissues (Swarup et al. 2007). However, this mechanism can account for most, but not all, ethylene effects on the root

growth. Some of the auxin insensitive mutants, e.g. *slr/iaa14* (Fukaki et al. 2002), *shy2-2/iaa3* (Tian and Reed 1999) or *nph4-1/arf7, arf19* (Okushima et al. 2005) are strongly resistant to auxin, but not or weakly to ethylene (Li et al. 2006a; Ruzicka et al. 2007). In addition, auxin transport mutants *aux1* and *pin2* do not exhibit complete ethylene resistance. Based on the extensive gene expression analysis, Stepanova et al. (2007) predicted that besides an auxin-mediated ethylene response there are at least three other types of interactions between auxin and ethylene. Thus, although an important part of the ethylene effect on root growth is performed through the auxin pathway, there appears to be a direct ethylene-specific, auxin response-independent component for this regulation.

Maintenance of a proper ethylene–auxin concentration balance along the root meristem seems to be one of the important mechanisms involved in ethylene–auxin regulated root growth. Besides the previously described control of the auxin biosynthesis by ethylene, auxin control over ethylene biosynthesis is also well established (Bleecker and Kende 2000; Liang et al. 1992; Yang and Hoffman 1984). One of the rate-limiting enzymes in the ethylene synthesis pathway is 1-aminocyclopropane-1-carboxylate synthases (ACS). Numerous ACS genes are expressed in the root meristem in a tissue-specific manner (Tsuchisaka and Theologis 2004) and their expression is enhanced upon auxin treatment (Tsuchisaka and Theologis 2004). This complicated regulatory loop between auxin and ethylene biosynthetic pathways suggests the presence of a complex feedback mechanism involving components that tightly control the actual auxin–ethylene level in root cells. One of the candidates for such a component might be the *POLARIS* (*PLS*) gene encoding a short 36-amino acid peptide. Mutation in *PLS* results in an enhanced ethylene phenotype, repressed auxin transport and auxin accumulation (Casson et al. 2002; Chilley et al. 2006). *PLS* transcription itself is under the negative control of ethylene and is stimulated by auxin. The *pls* mutant phenotype can be restored by genetic and pharmacological inhibition of the ethylene action, implicating PLS as a negative regulator of ethylene responses. Chilley et al. (2006) proposed a model in which the *PLS* transcription is activated at the root tip by the relatively high auxin concentration that accumulates and is required for correct cell division at that position (Blilou et al. 2005; Friml et al. 2002a; Sabatini et al. 1999). Here, PLS acts as a negative regulator of ethylene signalling, which is inhibitory to cell division and expansion, and therefore root growth. Although some aspects of *pls* phenotype are seemingly in contradiction with previously shown stimulatory effect of ethylene on auxin biosynthesis, PLS might be an important component of the ethylene sensing mechanism for the tuning auxin pathway action during root development.

Cytokinin: *antagonist in root*

The negative role of cytokinin (CK) on root growth is a long-known phenomenon that has been proven by both exogenous CK application and overexpression of the bacterial *ISOPENTENYLTRANSFERASE* (*IPT)* gene (Hewelt et al. 1994; Kuderova et al. 2008; Li et al. 2006b; Medford et al. 1989; Smigocki 1991). Accordingly, decreased endogenous CK levels via overexpression of the *CYTOKININ OXIDASE/DEHYDROGENASE* (*CKX*) gene results in an opposite effect i.e. enhanced root meristem and the root growth (Werner et al. 2003; Yang et al. 2003).

Interestingly, studies on mutants of CK signalling revealed a positive role of CK in the root meristem. The root meristem was reduced in the triple cytokinin receptor mutant *ahk2,ahk3,ahk4* and multiple mutant in *ahp* members of the signal transduction cascade (Higuchi et al. 2004; Hutchison et al. 2006; Nishimura et al. 2004; Riefler et al. 2006; To et al. 2004). Based on the phenotypes of CK signalling mutants, the modulation of CK levels led to the hypothesis of "supraoptimal" CK concentration in the root meristem (Ferreira and Kieber 2005), according to which, downregulation of the endogenous CK levels to optimal levels via *CKX* overexpression enhances root growth. However, both complete absence of the CK signal in CK signalling mutants and its abundance after *IPT* overexpression and/or exogenous application, respectively, exert optimal levels and lead to inhibitory effects (Ferreira and Kieber 2005).

A role for CK during embryonal root formation has been suggested by the *wooden leg* (*wol*) mutant identified for its defect in the radial root patterning (Scheres et al. 1995). In the *wol* embryos, the last series of divisions in the stele is missing, leading to the formation of the pericycle with a reduced cell number (Scheres et al. 1995). In the postembryonal development, *wol* mutation affects the asymmetric division of the procambium, resulting in a defective vasculature without phloem and formed exclusively by the protoxylem (Mahonen et al. 2000; Scheres et al. 1995). *WOL* was found to be allelic to the CK receptor *AHK4/CRE1*, thus pointing to a role for CK as a negative regulator of the protoxylem differentiation from the procambium. CK inhibition of the protoxylem differentiation allows procambial cells to undergo another developmental pathway, leading to phloem formation. *AHP6*, the downstream component of the CK transduction pathway, has been revealed to act in a negative regulatory feedback loop, antagonizing the CK effects (Mahonen et al. 2006).

Interestingly, the *wol* defect in the vasculature formation is rescued by the *fass* (*fs*) mutation (Scheres et al. 1995), allelic to *TONNEAU2* that codes for the putative novel protein phosphatase 2A regulatory subunit (Camilleri et al.

2002). It seems that additional cell layers in the radial pattern of the *fs* mutant (Torres-Ruiz and Jurgens 1994) allow phloem differentiation while the reduced number of cells in the stele of *wol* is "used up" by xylem pole-directed protoxylem differentiation (Scheres et al. 1995). However, missexpression of *AHP6* in *wol* embryos (Mahonen et al. 2006) suggests that positional, CK-mediated information rather than the cell number is critical for the proper vascular specification. As demonstrated also by the conditional expression of *CKX*, phenocopying *wol*, CK is a sufficient and necessary signal to provide this information during both embryonal and postembryonal root meristem development (Mahonen et al. 2006). That *fs* mutation is accompanied with increased levels of auxin and ethylene (Fisher et al. 1996) might imply a hormonal origin of *wol* complementation and suggest a role for CK/auxin/ethylene interplay during embryonal radial root pattern specification.

The role of CK in the embryonal specification of the root meristem stem cells was recently described (Muller and Sheen 2008). In the set of elegant experiments using CK-responsive synthetic reporter, authors have shown that output of CK signalling is antagonized by auxin. This effect is mediated by auxin-inducible expressions of *ARR7* and *ARR15* type-A response regulators acting as negative regulators of CK signalling. In the absence of auxin, expression of *ARR7* and *ARR15* are balanced with CK signalling levels (CK induce expression of type-A ARRs, which in turn inhibit CK signalling phosphorelay). However, auxin-mediated local expression of *ARR7* and *ARR15* bypasses the CK feedback loop and counteracts CK signalling. In conditional *arr7* and *arr15* double mutants, ectopic CK phosphorelay output was detected, accompanied with defects in root stem cell region and misexpression of *SCR, PLT1* and *WUSCHEL_RELATED-HOMEOBOX 5* (*WOX5*) genes (Muller and Sheen 2008). These results provide insight into the molecular mechanism of long-known antagonistic effects of CK and auxin interaction and introduce the role of these interactions in root meristem establishment during the early embryogenesis.

Biometric analysis on root growth (Beemster and Baskin 2000) demonstrated that CK reduces the relative elongation rate and blocks the increase of the meristem size. In some aspects, CK regulated root growth resembles typical ethylene-induced inhibition. CK was found to stimulate ethylene production and root growth of ethylene insensitive mutants to be CK resistant (Cary et al. 1995). Moreover, inhibitors of ethylene signalling and biosynthesis partially relieve roots from CK inhibition. These results suggest that part of the CK effects on root growth is mediated through ethylene. Molecular characterization of the *ACS5* and *ACS9* genes in *ethylene overproduction* (*eto2 and eto3*) mutants revealed that dominant *eto2* mutation does not increase the specific activity of the ethylene biosynthesis ACS5 enzyme, rather it increases the half-life of the protein. Similarly, CK treatment was shown to enhance the stability of ACS5 by a mechanism that is at least partially independent of the *eto2* mutation (Chae et al. 2003).

Altogether, rapid expansion of cells in the root transition zone seems to be under the control of at least three hormonal pathways—cytokinin, ethylene and auxin downstream of this regulatory chain. Importantly, feedback loop mechanisms comprising control of the CK biosynthesis by auxin (Eklof et al. 1997; Nordstrom et al. 2004), or the ethylene biosynthesis by auxin (Tsuchisaka and Theologis 2004; Yang and Hoffman 1984) represent an important part of the homeostatic mechanism.

Recently, Dello Ioio et al. (2007) have analysed the role of CK in the root meristem formation and have demonstrated that CK does not interfere with specification of the QC and stem cell function, nor with the overall division rate in the proximal meristem. CK affects primarily the rate of meristematic cell differentiation, resulting in shortening of the meristematic zone. Accordingly, depletion of CK by overexpression of *CKX* or by mutation of three *Arabidopsis* cytokinin biosynthesis genes *ipt2,ipt3,ipt7* increases the root meristem size (Dello Ioio et al. 2007; Werner et al. 2003). The role of CK signalling in longitudinal root patterning has been further confirmed by the expansion of the root meristem in the *ahk3* and response regulator mutants *arr1* and *arr12*.

Important knowledge on the CK control mechanism on the root meristem development has arisen from the targeted depletion of CK in different root meristem tissue layers. Depletion of CK restricted to the vasculature of the transition zone was sufficient to reduce the rate of cell differentiation of all other tissues and, thus, to diminish the root meristem size. Such a type of non-cell autonomous effect suggests that CK acts by antagonizing other signals. As proposed by Dello Ioio et al. (2007), a candidate for such a signalling molecule would be auxin, which as described above, is critical for the control of cell division and root meristem size. Application of auxin at low concentrations causes an increase in the meristem size (Beemster and Baskin 2000; Dello Ioio et al. 2007). On the other hand, depletion of CK by CKX has no additional effects on the meristem size in the auxin efflux carrier triple mutant *pin2,pin3,pin7*. Thus, the balance between the auxin and cytokinin pathways regulates important aspects of root development and establishment and maintenance of the meristem size. The molecular mechanisms are so far illusive, although several modes of interaction are conceivable.

First, CK and auxin biosynthesis are dependent on each other and perturbation in the abundance of one affects the other. An increase in auxin concentration leads to a decrease in the CK level (Eklof et al. 1997; Nordstrom

et al. 2004), and slow inhibitory effect of CK on auxin biosynthesis was described (Nordstrom et al. 2004). Auxin has also been shown to contribute to the CK degradation via stimulation of the CKX activity (Palni et al. 1988). In contrast, expression of two genes for CK biosynthetic enzymes AtIPT5 and AtIPT7 in *Arabidopsis* is induced by exogenous auxin (Miyawaki et al. 2004).

Second, the activity of the polar auxin transport machinery, the principal director of the auxin distribution in the root meristem, might be modulated by CK. Recently, CK has been shown to affect the local auxin gradient formation and expression of *PIN* auxin efflux carriers during lateral root development (Kuderova et al. 2008; Laplaze et al. 2007).

Third, auxin and cytokinin can regulate a common set of genes. A promising candidate for the downstream molecular component is *PROPORZ1* (*PRZ1*). This putative transcriptional adaptor protein has been shown to be essential for the developmental switch from cell proliferation to differentiation in response to variations in auxin and CK concentrations (Sieberer et al. 2003). Expression of several other genes was found to be under control of auxin and cytokinin. For example, transcription of the root-specific putative homeobox gene *ATHB53* is differentially regulated by auxin and CK (Son et al. 2005), and interestingly, CK regulates also expression of genes of the auxin signalling pathway (*SHY2-2/IAA3*, *AXR3/IAA17* or *SAUR-AC1*) (Rashotte et al. 2005).

Brassinosteroid: *forget-me-not*

Typically, effects of brassinosteroids (BRs) on root growth strongly depend on the BR concentration used. Exogenous BRs stimulate root growth at low concentrations, but have an inhibitory effect at higher BR levels (Mussig et al. 2003). BR-deficient mutants, such as *dwarf1-6*/(*dwf1-6*) and *cabbage3*/(*cbb3*) (allelic to *cpd*), defective in brassinosteroid biosynthesis (Kauschmann et al., 1996; Szekeres et al., 1996), show shorter roots than wild-type plants (Mussig et al. 2003). Root-specific BR-deficiency in *brevis radix*/(*brx*) mutant causes reduced root growth due to reduction in the meristem size, and mature cell size as well (Mouchel et al. 2004). *BRX,* isolated as quantitative trait locus affecting root growth in the *Arabidopsis* accession Umkirch-1 (Uk-1), is a member of a small gene family representing most probably a novel class of transcriptional factors involved in the regulation of expression of a rate-limiting enzyme in brassinosteroid biosynthesis (Mouchel et al. 2006).

Transcriptome profile analyses in roots of two BR mutants, *dwf1-6* and (Mussig et al. 2003) and *brx* (Mouchel et al. 2006), revealed a link between BR and the auxin pathway in root development. Test of auxin response in *brx* via microarray analysis showed that almost none of tested auxin response genes responded normally to auxin in the BR-deficient *brx* mutant, but this auxin responsiveness was largely restored by brassinollide treatment. Accordingly, expression of the auxin reporter *DR5* (Sabatini et al. 1999; Ulmasov et al. 1997) in *brx* was fully sensitized to auxin by BR supply (Mouchel et al. 2006). Altogether, these results suggested that optimal BR levels are rate limiting for auxin-induced transcriptional responses. BR does not seem to act through regulation of endogenous auxin content, because as shown by Nakamura et al. (2003), BR did not increase the endogenous auxin levels of either the control plant or the BR-deficient mutant *deetiolated2*/*det2*. Furthermore, the levels of *AUX/IAA* transcripts were lower in the *det2* mutant than in the control, even though endogenous auxin levels were elevated in the *det2* background (Nakamura et al. 2003).

Accordingly, negative regulators of auxin signalling *IAA14* and *IAA2* showed weaker expression in roots of *dwf1-6* (Fukaki et al. 2002; Mussig et al. 2003) and the *NIT3* gene, encoding enzyme involved in IAA biosynthesis (Kutz et al. 2002) exhibited higher transcript level in the *dwf1-6* mutant background (Mussig et al. 2003).

Brassinosteroids are known to stimulate the production of ethylene in shoots and roots (Arteca and Arteca 2001; Schlagnhaufer and Arteca 1985; Yi et al. 1999). In line with these observations, expression data point to a positive BR effect on genes involved in ethylene biosynthesis and ethylene response in roots (Mussig et al. 2003). Thus, part of the BR inhibitory effect on root growth might be mediated through ethylene. More detailed studies are needed to dissect the ethylene effects in the context of BR action. However, analysis of the auxin and ethylene resistant mutants *axr1* points to the existence of ethylene-independent BR-regulated root growth (Clouse et al. 1993). A direct BR-ethylene feedback loop might exist that specifically interferes with BR transport, BR biosynthesis, or BR responses.

Also another mutant in BR biosynthesis, *sax1* (*hypersensitive to abscisic acid and auxin*), with roots oversensitive to auxin and ABA suggests that BR interacts with multiple hormonal pathways (Ephritikhine et al. 1999).

Gibberellins: *you have to beat me*

Although gibberellin (GA) has been recognized for a long time mainly as a regulator of shoot growth, its important role in the regulation of root growth has been demonstrated as well. The GA-deficient mutant *ga1-3* exhibits shorter roots. Loss of DELLA proteins GAI and RGA, negative inhibitors of GA signalling, suppress the *ga1-3* root phenotype, showing that GA pathway acts in the regulation of root growth (Fu and Harberd 2003). An elegant set of

experiments has recently been performed to map the site of GA action for regulating root growth (Ubeda-Tomas et al. 2008). When gai, a mutant non-degradable DELLA protein, was expressed in selected root tissues, the root growth was retarded specifically when *gai* was expressed in endodermal cells. These results demonstrated that the endodermis represents the primary GA-responsive tissue and that endodermal cell expansion is rate limiting for elongation of other tissues and, therefore, of the root as a whole (Ubeda-Tomas et al. 2008). In work of Paquette and Benfey (2005) also a role of GA in radial patterning of root meristem has been revealed and GA shown to act as negative regulator of the middle cortex formation—the third layer of the root ground tissue rapidly differentiating to cortex.

GA stimulates growth by promoting the destruction of DELLA proteins, a subfamily of the GRAS family of putative transcriptional regulators (Dill et al. 2001; Fu and Harberd 2003). Thus, DELLA proteins restrain the plant growth, whereas GA relieves the DELLA-mediated growth inhibition by targeting the DELLA proteins for destruction. GA-mediated destabilization of DELLA proteins involves GA-stimulated phosphorylation, polyubiquitination via a specific SCF E3 ubiquitin ligase complex and subsequent destruction in the 26S proteasome (Fu et al. 2002; McGinnis et al. 2003; Sasaki et al. 2003).

As demonstrated by several laboratories, GA-regulated root growth involves interaction with other hormonal pathways, e.g. auxin (Fu and Harberd 2003), cytokinin (Greenboim-Wainberg et al. 2005), ethylene (Achard et al. 2006) or ABA (Achard et al. 2006) and the regulation of DELLA proteins stability might represent an important cross-point.

GA and auxin pathways converge in roots to regulate cell expansion and tissue differentiation. GA-induced root elongation was inhibited by the removal of the shoot apex, which is a major auxin source, and this effect was reversed by auxin application suggesting that GA stimulation of root elongation requires auxin. Moreover, application of the auxin-transport inhibitor 1-*N*-naphthylphthalamic acid (NPA), or a mutation in the auxin efflux carrier *PIN1* attenuated the effect of GA on root elongation and on RGA degradation in root cells. GA-induced RGA degradation was also inhibited in the auxin resistant mutant *axr1*. These observations indicate that auxin promotes the growth of roots by enhancing the GA-induced destabilization of some of the DELLA proteins (Fu and Harberd 2003). Thus, the DELLA protein RGA seems to act as integrator of GA and auxin signals in the root.

Positive regulation of GA biosynthesis by auxin might be involved in these interactions. A stimulatory effect of the auxin on GA biosynthesis was demonstrated and several components of auxin signalling pathway seem to be included in this regulation (Frigerio et al. 2006).

GA has been shown to antagonize ethylene inhibitory effects on root growth (Achard et al. 2003). Ethylene insensitive root growth of the *gai rga* GA-insensitive mutant indicates that ethylene regulates root growth in a DELLA-dependent manner. In agreement with this observation, ethylene counteracted GA-induced destabilization of the RGA protein in root cell nuclei. The effect of ethylene on RGA stability was mimicked by the loss of its signalling suppressor CONSTITUTIVE TRIPLE RESPONSE1 (CTR1) (Guo and Ecker 2004), suggesting that the ethylene's RGA stabilizing signal is transduced via a CTR1-dependent pathway (Achard et al. 2003).

Analysis of *SPINDLY* (*SPY*) gene revealed antagonistic interaction of GA and CK in root growth (Greenboim-Wainberg et al. 2005). Mutation of *SPY* results in phenotypes resembling that of wild-type plants treated with exogenous GA and overexpression of *SPY* produced phenotypes consistent with a reduced GA action (Izhaki et al. 2001; Swain et al. 2001). This suggests that SPY functions as a negative regulator of the GA-signal transduction. Inhibition of root elongation by CK was greatly suppressed in the *spy* mutant background, and accordingly, exogenous application of GA antagonized the inhibitory effect of CK on root growth. Both GA and *spy* interfered with the induction of CK primary response gene *ARR5*. Thus, SPY is a potential molecular component that integrates GA and CK pathways in root growth and acts as a repressor of GA responses and a positive regulator of CK signalling. Based on the comparison of GA and CK sensitivities of *spy* mutants, it seems that GA suppresses CK responses at least partially via SPY (Greenboim-Wainberg et al. 2005).

In the shoot apical meristem *KNOTTED*-like homeobox genes were shown to play an important role in the establishment of the hormonal balance between CK and GA. They activate CK biosynthesis and repress *GA 20-oxidase* gene expression and, hence, GA biosynthesis, thus promoting meristem activity (Jasinski et al. 2005; Yanai et al. 2005). Several members of this gene family were shown to be expressed in distinct domains and cell types of the main root (Truernit et al. 2006), but their role in the hormonal interactions and its relevance for root growth regulation remains to be examined in detail.

Abscisic acid: *not only stress*

The role of abscisic acid (ABA) in the regulation of root growth is still not completely clear. However, recent genetic and molecular studies started to unravel the importance of ABA regulation in root meristem formation and root growth. An example of genes involved in ABA-mediated control of the root meristem is the *TETRATRICOPEPTIDE-REPEAT THIOREDOXIN-LIKE 1* (*TTL1*) gene. Mutation in *TTL1* causes reduced root

elongation and disorganization of the root meristem. TTL1 mediates the sensitivity to ABA and to osmotic stress and is supposed to participate in ABA signalling in *Arabidopsis* (Rosado et al. 2006). ABA has been shown to rescue the root meristem phenotype of *Medicago* mutant *latd*. *latd* roots have disorganized root tip that is defective in meristem organization, columella root cap formation and root growth (Liang et al. 2007). *latd* mutants exhibit normal ABA levels, but reduced sensitivity to ABA, suggesting that LATD functions in the ABA signalling.

Multiple ABA effects are associated with ethylene action. There are several hints that functional ethylene signalling is necessary for root responses to ABA. The ABA effect on the root growth was restrained by inhibitors of the ethylene perception, but not by reduced ethylene biosynthesis, suggesting that, in contrast to CK, ABA does not operate through ethylene biosynthesis, as confirmed by the measurements of ethylene production upon ABA treatment. Vice versa, ethylene seems to inhibit root responsiveness to ABA (Ghassemian et al. 2000). Close interplay of ABA and ethylene in root development indicates *era3* mutant identified in a screen for ABA hypersensitive germination mutant. The *era3* mutation was found to be allelic to the ethylene insensitive *ein2* mutant (Beaudoin et al. 2000; Ghassemian et al. 2000). Interestingly, the *era3* roots are not only resistant to CK and ethylene as previously shown for the *ein2* mutant in ethylene signalling (Cary et al. 1995) but also to ABA. Moreover, they are sensitive to auxin and accumulate more ABA (Ghassemian et al. 2000). Thus, *era3* represents an important candidate to investigate ABA and ethylene signalling interaction in the root development. The *abi8/eld1/kob1* mutant with altered ABA-responsive gene expression was shown to be necessary for the meristematic activity in the root (Brocard-Gifford et al. 2004). *ABI8/ELD1/KOB1* encodes a protein of unknown function and, in contrast to most of the other ABA insensitive mutations, the *abi8* phenotype cannot be suppressed by inhibition of the ethylene pathway. Thus, ABI8 might function in parallel or downstream of the EIN2 and EIN3 components of the ethylene signalling pathway (Brocard-Gifford et al. 2004).

The *nhr1* mutation uncovers interaction between ABA and auxin (Eapen et al. 2003). Semi-dominant *nhr1* mutation was identified in a screen for lack of hydrotropic root responses. *NHR1* affects root meristem formation via regulation of the QC, columella initials and root cap specification and affects cell proliferation in the root meristem. *nhr1* shows reduced sensitivity to ABA, NAA and to the auxin efflux inhibitor NPA. Authors hypothesize that NHR1 is involved in the ABA-dependent mechanism of efflux mediated auxin redistribution, allowing positive hydrotropic response of the root (Eapen et al. 2003).

Similarly to ethylene, salt stress-induced ABA increases the stability of DELLA negative regulators of the GA pathway (Achard et al. 2006; Fu and Harberd 2003; Vriezen et al. 2004). The quadruple DELLA mutant *gai,rga,rgl1,rgl2* is resistant to the growth-inhibitory effects of ABA. Furthermore, EIN3, a negative regulator of the ethylene signalling, was found to promote salt tolerance via enhancement of the DELLA function (Achard et al. 2006). Thus, DELLA proteins integrate ABA and ethylene signalling in the regulation of the root growth. As ABA and ethylene signalling are involved in different abiotic and biotic responses, this mechanism might mediate environmental regulation of the root growth response (Achard et al. 2006).

Recently, important connection between CK and ABA signalling was described in *Arabidopsis*. Homologue of CK receptors, sensory histidine kinase AHK1, was found to be a positive regulator of drought and salt stress responses and ABA signalling. In contrast, CK receptors AHK2, AHK3 and AHK4 were identified to be negative regulators of the ABA signalling, acting in case of AHK2 and AHK3 via negative regulation of many stress- and/or ABA-inducible genes (Tran et al. 2007).

Conclusion

The current status of knowledge on root development indisputably points out that a complex hormonal network participates in the regulation of root formation and growth from the moment of its initiation in the embryo. Essentially, all hormonal pathways are involved and control different developmental aspects of the root meristem formation. Auxin seems to be the most universal factor acting in all root developmental events (Dinneny and Benfey 2008; Galinha et al. 2007). CK has been shown to be a critical factor in radial root patterning (Mahonen et al. 2006; Scheres et al. 1995), establishment of root stem cells during early embryogenesis (Muller and Sheen 2008) and establishment of the root meristem size by controlling the balance between cell division and differentiation of cells leaving the root meristem (Dello Ioio et al. 2007). Ethylene and GA act primarily on the rapid elongation of cells leaving the root meristem (Fu and Harberd 2003; Ruzicka et al. 2007; Swarup et al. 2007; Ubeda-Tomas et al. 2008). BR deficiency affects both the division activity of the root meristem and rapid cell elongation (Mouchel et al. 2004), and ABA mediates the environmental regulation of root growth responses (Achard et al. 2006). Importantly, each hormonal pathway functions in the context of the whole hormonal network and they mutually modulate their actions. Thus, for example, auxin regulated processes require a minimal level of BR (Mouchel et al. 2006). Maintenance of the root meristem size is balanced by antagonistic activities of CK and auxin (Dello Ioio et al.

2007), and the gibberellin pathway is differently modulated by auxin and ethylene (Achard et al. 2003; Fu and Harberd 2003). Although our knowledge on the molecular components and pathways that mediate developmental responses to hormones has improved enormously in recent years, molecular mechanisms standing behind their interactions are poorly understood. However, from most of the recent studies, it became obvious that diverse mechanisms of hormonal interactions have evolved to coordinate activity of hormonal pathways in certain developmental processes. There are several examples of mutual regulations on the level of hormone metabolism and distribution (Laplaze et al. 2007; Stepanova et al. 2005; Stepanova et al. 2008; Tsuchisaka and Theologis 2004). Transcriptional or post-translational control over the key molecular components of signal transduction pathways by other hormonal signals is another example of a cross-talk strategy (Fu and Harberd 2003; Chae et al. 2003; Muller and Sheen 2008). There are rare cases in which activation of one hormonal pathway might branch and stimulate transduction component of another pathway (Hass et al. 2004). Hormonal signalling pathways might also differentially regulate expression or activity of common target gene (Chilley et al. 2006; Son et al. 2005). Several other modes of hormonal interactions could be predicted. Although we have no real evidence for their existence today, they might be revealed in the future years. In this context, we would like to note that although sometimes experimental findings might lead to contradictory conclusions on the mode of hormonal interactions (Ferreira and Kieber 2005), these "inconsistencies" might point to a very important feature of the hormone behaviour—its action is extremely dependent on concentration and developmental stage (Kuderova et al. 2008; Mussig et al. 2003). It has been nicely demonstrated by Kuderova et al. (2008) that the strength of the effects of temporal pulses of endogenous CK via regulated expression of the bacterial *IPT* depends on the developmental status of the root. Consequently, the same hormone can, during one developmental process, set up different interactions in relation to the actual concentration and developmental stage.

Recent investigations have created a good outline of different possible modes of interactions between hormones, which in combination with the fast progress in understanding single hormonal pathways represents a promising start to reveal concrete cross-talk molecular components, which is the challenge of future research.

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