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Control of adventitious root formation: Insights into synergistic and antagonistic hormonal interactions

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Plants have evolved sophisticated root systems that help them to cope with harsh environmental conditions. They are typically composed of a primary root (PR) and lateral roots (LRs), but may also include adventitious roots (ARs). Unlike LRs, ARs may be initiated not only from pericycle cells, but from various cell types and tissues depending on the species. Phytohormones, together with many other internal and external stimuli, coordinate and guide every step of AR formation from the first event of cell reprogramming until emergence and outgrowth. In this review we summarize recent advances in the molecular mechanisms controlling AR formation and highlight the main hormonal cross-talk involved in its regulation under different conditions and in different model systems.

Abbreviations – ABA, abscisic acid; ABCB19, ATP BINDING CASSETTE TYPE B 19; ACC, 1-aminocyclopropane-1-carboxylic acid; AR, adventitious root; ARI, adventitious root initiation; ARF, AUXIN RESPONSE FACTOR; ASA1, ANTHRANILATE SYNTHASE ALPHA 1; ASB1, ANTHRANILATE SYNTHASE BETA 1; BR, brassinosteroid; CK, cytokinin; ET, ethylene; ERF, ETHYLENE RESPONSE FACTOR; GA, gibberellic acid; GH3, Gretchen Hagen3; IBA, indole-3-butyric acid; JA, jasmonic acid; JA-Ile, (+)-7-iso-jasmonoyl-L-isoleucine; LR, lateral root; MeJA, methyl jasmonate; NAA, 1-naphthalene acetic acid; NPA, naphthylphthalamic acid; PAT, polar auxin transport; SA, salicylic acid; SL, strigolactone; TCL, thin cell layer; WEI2, WEAK ETHYLENE INSENSITIVE 2.

Introduction

Unlike most animals, plants have developed remarkable capacities of regeneration and propagation. Inter alia, they can propagate both sexually and vegetatively due to their ability to develop adventitious roots (ARs) from aerial organs, which leads to the development of new genetically identical clonal plants. AR formation is a post-embryonic process, which is an intrinsic element of the normal development of monocots, while in both monocots and dicots it may occur in response to diverse environmental and physiological stimuli, such as darkness, flooding, mechanical wounding or nutrient deprivation (reviewed in Bellini et al. 2014, Steffens and Rasmussen 2016). The process is a prime example of plants' evolution of sophisticated molecular machinery that precisely translates external cues and coordinates finely-tuned developmental responses that include de novo organogenesis (reviewed by Bellini et al. 2014, Xu 2018).

Vegetative or clonal propagation is exploited in horticulture and forest nurseries to produce large numbers of clones relatively quickly. However, some taxa (including economically important species) are difficult to root. For example, some *Eucalyptus* and *Pinus* species poorly develop AR without exogenous applications of phytohormones (Fett-Neto et al. 2001). Reasons for the wide variety in plants' capacity to form ARs are not yet clear.

It is now evident that the internal cues regulating AR initiation (ARI) are mainly integrated by the interactive effects of phytohormones (reviewed by Pacurar et al. 2014b). Auxin is the central player, but it acts with an array of other phytohormones through very complex crosstalk, modulating each other's levels and actions at every level: biosynthesis, metabolism, transport and signalling. In this review we summarize the most recent advances in our understanding of hormonal regulation of AR formation, particularly the initiation steps.

Adventitious root initiation and patterning

AR formation is a tightly controlled developmental program, which generally involves three steps. First, cell specification and reprogramming, in which differentiated cells acquire new cell fate programs leading to the specification of AR founder cells. Second, initiation, in which the AR founder cells undergo successive cell divisions leading to the formation of primordia. Third, primordia emergence and outgrowth. ARI may occur in various cell types, with distinct anatomical and molecular identities, depending on both the species and environmental stimuli involved (reviewed by Geiss et al. 2009). In *Arabidopsis thaliana* (Arabidopsis), ARs may be initiated from xylem pole pericycle cells in both intact and de-rooted hypocotyls (Sorin et al. 2005, Sukumar et al. 2013). Alternatively, they may be initiated from procambium, and probably from the adjacent parenchyma cells of leaf explants kept in the dark on hormone-free B5 medium (Liu et al. 2014). However, Bustillo-Avendaño et al. (2018) found that when a whole leaf including the petiole was used as a propagating system, ARs initiated from a pre-formed micro-callus. When the petiole is kept, vascular tissues including xylem and pericycle-like cells first undergo massive cell division, resulting in formation of a micro-callus, which subsequently undergoes a second step of reprogramming that specifies the AR founder cell (Bustillo-Avendaño et al. 2018). This process resembles the two-step mechanism during hormone-induced organogenesis (reviewed by Kareem et al. 2016). Histological studies of *Populus* and carnation (*Dianthus caryophyllus* L.) stem cuttings revealed that the first cell division leading to primordium formation occurs in cambial tissues (Rigal et al. 2012, Agulló-Antón et al. 2014). In monocots, serial cross sections in rice (*Oryza sativa*) have demonstrated that crown roots

initiate from the peripheral vascular cylinder. In conclusion, whatever the tissue or organ, ARs are initiated from cells with vascular associations.

Regardless of the cell type from which AR arise, phytohormones in coordination with environmental stimuli guide every step of AR formation. They usually act in complex interactions that provide the robust spatio-temporal cues required for AR development (Fig. 1), as outlined in the following sections.

Auxin: the master player and hub of any crosstalk

Indole 3-acetic acid (IAA), the most abundant natural auxin, is a weak organic acid that is mainly derived from L-tryptophan. IAA controls a plethora of developmental programs in plants, including AR formation. It has long been established that different types of auxins promote AR formation in different species (Bellini et al. 2014, Pacurar et al. 2014b). Indole-3-butyric acid (IBA) is the most frequently used natural auxin for clonal propagation in horticulture and forestry because of its stability and effectiveness in promoting AR from stem cuttings compared to other available auxins. IBA induces the auxin signalling machinery following conversion to IAA in planta (Strader et al. 2011). Thus, the double mutant, *ech2ibr10*, in which IBA to IAA conversion is impaired, produces very few LR and ARs compared to wild type counterparts (Strader et al. 2011, Fattorini et al. 2017). The conversion of IBA to IAA seems to be species and genotype dependent. This is significant, because (for example) the rooting capacity of elm (*Ulmus americana*) genotypes' stem cuttings is correlated with their ability to convert IBA to IAA (Kreiser et al. 2016). IBA-derived IAA also controls many other developmental processes (Frick and Strader 2017). For example, root cap-derived IBA plays a prominent role in lateral root pre-branch site establishment in Arabidopsis (Xuan et al. 2015).

In Arabidopsis, constitutively IAA-overproducing mutants such as *superroot1* (*sur1*), *superroot2* (*sur2*) and the activation tagged *YUCCA1* (*yuc1-D*) spontaneously form AR in the hypocotyl (Boerjan et al. 1995, Delarue et al. 1998, Zhao et al. 2001). Very early steps in ARI and most organogenesis include formation of an IAA gradient and its accumulation in specific cell types, via processes that include polar auxin transport (PAT) and local auxin biosynthesis, conjugation and degradation.

IAA biosynthesis has been found to be crucial for the cell fate transition of procambium cells to AR founder cells in leaf explants grown on (hormone-free) B5 medium in darkness (Liu et al. 2014, Chen et al. 2016). The cited authors showed that induction of *YUC* genes' expression in detached Arabidopsis leaves rapidly mediated increases in free IAA levels. Expression of *YUC1* and *YUC4* ubiquitously increased in the mesophyll after leaf detachment. The quadruple mutant *yuc1,2,4,6* was

unable to develop ARs and blocking the activity of YUC enzymes with the chemical yucasin severely affected adventitious rooting in leaf explants. In both cases, exposure to 0.1 μ M of IAA could restore AR formation. These results clearly indicate that YUC-mediated auxin biosynthesis is required to trigger cell reprogramming and/or cell fate transition in leaf explants (Chen et al. 2016). Therefore, a link between wounding-induced YUCs and de novo AR initiation has been proposed (Chen et al. 2016, Xu 2018). However, whether wounding induces expression of YUC genes directly or indirectly *via* jasmonate (JA) and/or ethylene (ET) remains to be resolved. Both JA and ET are highly induced during mechanical wounding and they may trigger expression of YUCs and possibly other IAA biosynthesis genes such as *ANTHRANILATE SYNTHASE ALPHA 1/WEAK ETHYLENE INSENSITIVE 2 (ASA1/WEI2)* (Stepanova 2005, Sun et al. 2009, Cai et al. 2014). As Chen et al. (2016) found that dark-grown leaf explants produced more ARs than light-grown counterparts, it would be interesting to elucidate the molecular link between darkness and wounding in promotion of IAA-induced de novo organogenesis. Several IAA biosynthesis genes have been identified in a suppressor screen of *sur2-1* AR phenotype, such as *ASA1/WEI2*, *ASB1/WEI7*, and *TRYPTOPHAN SYNTHASE BETA 1 (TSB1)* (Pacurar et al. 2014a). Loss of function of any of these genes reduced numbers of ARs produced by *sur2-1* mutants, confirming the pivotal role of IAA biosynthesis in AR formation (Pacurar et al. 2014a).

It is well known that polar auxin transport (PAT) plays a key role in IAA distribution and gradient establishment. Ahkami et al. (2013) found that free IAA levels increased quickly in the stem base of petunia (*Petunia hybrida*) cuttings in a biphasic manner, with IAA peaking 2 and 24 h after cutting. The second peak (24 h) was diminished when the plants were treated with naphthylphthalamic acid (NPA, an auxin transport inhibitor), confirming the importance of PAT in ARI (Ahkami et al. 2013). The increase in IAA at the base of petunia stem cuttings triggered the IAA signalling machinery, leading to a dramatic increase in expression of *GRETCHEN HAGEN3 (GH3)* auxin-inducible genes as well as increases in cell wall and vacuolar invertases (Ahkami et al. 2013). GH3 enzymes play crucial roles in the regulation of levels of active forms of IAA, JA and SA (Staswick et al. 2005, Gutierrez et al. 2012, Westfall et al. 2016). Interestingly it has been demonstrated that JA is an inhibitor of ARI in Arabidopsis hypocotyls, and that auxin induces ARI by decreasing the pool of active JA through its conjugation to amino acids by GH3 enzymes (Gutierrez et al., 2012). Therefore, we propose that the peaks of IAA that occur in petunia cuttings may prevent inhibition of ARI by wounding-induced accumulation of JA.

The *ATP-BINDING CASSETTE B19 (ABCB19)* and *PIN-formed 1 (PIN1)* seem to be the main IAA efflux carriers involved in auxin accumulation at the base of excised Arabidopsis hypocotyls and, thus, contributors to AR formation. Accordingly, Sukumar et al. (2013) found that de-rooted *abcb19-1* and *pin1-1* loss-of-function mutant seedlings produced fewer ARs than wild type counterparts, and the *ABCB19* gene was rapidly induced upon excision, especially in the hypocotyl epidermis and vascular tissues. *PIN6* is also involved in AR formation, as demonstrated by phenotypes of loss- or gain-of-function lines reported by Simon et al. (2016). The *pin6* knock-out mutant produced more ARs, whereas the over-expressing line *35:PIN6* produced very few ARs compared to wild type counterparts. These findings confirm the importance of rootward IAA transport during ARI.

Many mutants with IAA perception or signalling impairments have been identified in the last decade and their functional analysis has illuminated some of the molecular mechanisms controlling ARI downstream of IAA. In intact Arabidopsis hypocotyls, IAA acts through transcription factors from the *AUXIN RESPONSE FACTOR (ARF)* family. *ARF6* and *ARF8* have been identified as positive regulators of ARI, and *ARF17* as a negative regulator (Gutierrez et al. 2009, 2012). Interestingly, *ARF6* and *ARF8* genes were found to be specifically induced in the rooting-competent phloem parenchyma cells in stem cuttings of black walnut (*Juglans nigra* L.), while *ARF17* expression decreased during the same developmental stage (Stevens et al. 2018). This differential expression of the three *ARF* genes was observed before AR primordia formation (Stevens et al. 2018). Ruedell et al. (2015) found that expression of *ARF6* and *ARF8* was also induced in difficult-to-root *Eucalyptus globulus* donor plants treated with far-red enriched light, and after cutting. Moreover, this induction coincided with the promotion of AR formation under these conditions. These results suggest that *ARF6* and *ARF8*, which were identified as positive regulators of AR formation in Arabidopsis, may be key elements of an ARI mechanism that has been conserved across diverse taxa.

ARF6 and *ARF8* genes regulate expression of the well-known auxin responsive genes *GH3.3*, *GH3.5* and *GH3.6* and the triple null mutant *gh3.3gh3.5gh3.6* reportedly produces fewer ARs than wild-type counterparts, highlighting a paradox (Gutierrez et al. 2012). The three corresponding GH3 proteins were initially described as auxin conjugating enzymes (Staswick et al. 2005), but knocking out *gh3.3*, *gh3.5* and *gh3.6* had no apparent effect on endogenous IAA contents, instead it resulted in higher production of free JA and its bioactive form (+)-7-iso-jasmonoyl-L-isoleucine (JA-Ile) (Gutierrez et al. 2012). These findings prompted the conclusion that auxin acted through the GH3 proteins by controlling levels of active JA, which was demonstrated to be a negative regulator of AR formation (Fig. 1) (Gutierrez et al. 2012).

Additional components of the IAA signalling machinery were identified in a genetic screen for suppressors of the AR phenotype of the auxin-overproducing mutant *sur2-1* (Pacurar et al. 2014a). For example, the *COP9 SIGNALOSOME SUBUNIT 4* (*CSN4*), which controls de-neddylation of CULLIN1 in the SCF complex, acts on the *ARF6/8* regulatory module and likely at the crossroads of IAA, JA and/or light signalling pathways involved in the control of both AR and LR formation (Pacurar et al. 2017). Intriguingly, phenotypic characterization of available viable *csn* mutants indicated a possible differential role of the COP9 signalosome in AR and LR formation (Pacurar et al. 2017). Moreover, the gain-of-function mutants *crane-2* and *solitary root-1* (*slr-1*), which harbour mutations in domain II of IAA18 and IAA14, respectively, that confer resistance to degradation by the proteasome, were also shown to be affected in ARI (Bustillo-Avendaño et al. 2018).

Wounding-induced IAA accumulation at the base of leaf blades triggers expression of the homeobox genes *WUSCHEL RELATED HOMEBOX11* and *12* (*WOX11* and *WOX12*), which are putatively key players in cell fate reprogramming during de novo organogenesis (Liu et al. 2014, Chen et al. 2016). *WOX11*, redundantly with *WOX12*, controls transition of competent cells into AR founder cells by activating *BOUNDARY LATERAL DOMAIN16* and *29* (*LBD16* and *LBD29*) genes in leaf cuttings (Liu et al. 2014). Although expression of *WOX11* was previously associated with ARI (Liu et al. 2014), a more recent study of whole leaf explants, including the petiole, revealed that it was not expressed at the site of ARI but in the proliferating vascular tissues, suggesting it participates in callus formation (Bustillo-Avendaño et al. 2018). This indicates that *WOX11* controls either very early events of cell reprogramming during ARI or callus formation, depending on the system.

The *OsWOX11* gene is specifically expressed in AR primordia and the corresponding protein interacts physically with ETHYLENE RESPONSE FACTOR (ERF3) in promotion of AR formation. The *ERF3* gene is rapidly and transiently induced by exogenously applied synthetic auxin (2-4 D) and cytokinin (6-BA) (Zhao et al. 2015). Comparative analyses of transcripts in root tips of *wox11* mutant and wild type plants revealed that *OsWOX11* regulates the expression of many genes in the cytokinin and auxin signalling pathways, suggesting that OsWOX11-OsERF3 dimers mediate complex crosstalk between different hormones during ARI (Zhao et al. 2015, Jiang et al. 2017). The *Populus* (cultivar Nanline895') genome contains two *WOX11* paralogs: *PeWOX11a* and *PeWOX11b*. Xu et al. (2015) found that constitutive overexpression of *PeWOX11* in transgenic lines not only enhanced the rate of rooting, but also increased numbers of ARs per cutting. In conclusion, the closely-related homologs of *AtWOX11* in rice and *Populus* are required for proper AR formation, suggesting that *WOX11* likely

mediates a conserved evolutionary mechanism of adventitious rooting in monocots and dicots, including woody species (Zhao et al. 2009, Xu et al. 2015).

Jasmonic acid: a positive or negative regulator of adventitious root initiation?

Jasmonic acid (JA) is an oxylipin-derived phytohormone, usually associated with mechanical wounding and plant defence against pathogens. However, during the last decade it has attracted the attention of many researchers and shown to be a key hormonal player in normal plant growth and development. JA participates in diverse developmental processes, such as apical hook formation, hypocotyl elongation, flower development (inter alia its timing), primary root elongation, AR and LR formation (reviewed by Wasternack and Song 2017).

JA inhibits primary root elongation and promotes LR formation. In LR development, JA enhances IAA biosynthesis via transcriptional activation of *ASA1*, *YUC2*, *YUC8* and *YUC9* genes. Sun et al. (2009) and Cai et al. (2014) found that *asa1*, *yuc2*, *yuc8* or *yuc9* loss-of-function mutants produced far fewer LRs than wild type counterparts when treated with methyl jasmonate (MeJA). These results suggest that IAA biosynthesis is required for MeJA to promote LR formation. Cai et al. (2014) demonstrated that *ERF109*, which is highly induced by JA, binds directly to the promotor of *ASA1* and *YUC2* genes, activating their transcription and subsequently inducing IAA production, thereby providing the missing link between JA and IAA biosynthesis. MeJA has also been shown to be a positive regulator of AR formation in tobacco (*Nicotiana tabacum*) and Arabidopsis thin cell layers (TCLs) cultured on a root-inducing medium (Fattorini et al. 2009). However, this positive effect was not observed when the TCLs were cultured in hormone-free medium (Fattorini et al. 2009). The cited authors used a high concentration of IBA and low concentration of kinetin to induce AR formation. MeJA only had an ARI-promoting effect under these conditions, and it should be mentioned that exogenous application of phytohormones dramatically changes the balance of the internal signalling machinery. This is not surprising as regeneration and/or de novo organogenesis requires tight feedback systems and integration of multiple signalling cues (via complex interactions of endogenous phytohormones in natural conditions) that involve and affect multiple cell types and developmental stages.

JA is rapidly and transiently induced after cutting or mechanical wounding. It accumulates at the site of wounds, where it induces responses that protect plants from pathogen attacks. Because JA rapidly and transiently accumulates at the base of petunia leafy stem cuttings, before ARs emerge, it was proposed to be a positive regulator of AR formation (Ahkami et al. 2009). This hypothesis was

corroborated by findings that downregulation of *ALLENE OXIDE SYNTHASE* (*AOS*), which catalyses a critical step leading to formation of cis-12-oxo-phytodienoic acid (OPDA), reduced formation of ARs in petunia cuttings (Lischweski et al. 2015). Nevertheless, the same authors showed that when leafy stem cuttings of petunia were continuously treated with exogenous JA, JA-Ile or OPDA they produced significantly fewer ARs than controls (Lischweski et al. 2015). These results conflict with the hypothesis that JA could be a positive regulator of ARI, suggesting that long-term treatment with JA inhibits ARI. The latter hypothesis is strongly supported by the genetic characterization of Arabidopsis mutants with impairments in JA biosynthesis, perception and signalling, which prompted the conclusion that COI1-dependent JA signalling inhibits AR through *MYC2*, *MYC3* and *MYC4* transcription factors, downstream of IAA (Gutierrez et al. 2012). In conclusion, recent studies have shown that JA is a major regulator of AR formation, probably as an inhibitor of ARI, although its role could be more complex and species-dependent. JA strongly inhibits cell division and elongation (Swiatek et al. 2002, Pauwels et al. 2008), but we still have too little information about JA's mode of action in the specific phases of AR development. Future investigations of JA's effects on the formative cell divisions during ARI should be highly illuminating.

Ethylene: the gas that matters

Ethylene (ET) is a stress-related phytohormone that is rapidly induced in response to several environmental stimuli, inter alia mechanical wounding, darkness or flooding. The ethylene precursor 1-aminocyclopropane-1-carboxylic acid (ACC) seems to have species-dependent effects on AR production. Etiolated tomato (*Solanum lycopersicum*) seedlings and petunia stem cuttings treated with ACC reportedly produce more ARs than controls (Negi et al. 2010, Druege et al. 2014) suggesting ET promotes AR formation. This is supported by findings that the ET-insensitive tomato mutant *Never ripe* (*Nr*), which has impaired ET perception, produced fewer ARs than wild type counterparts (Negi et al. 2010). Similarly, flooding-induced AR formation is mediated by ET biosynthesis and signalling in rice and tomato (Lorbiecke and Sauter 1999, Vidoz et al. 2010). Vidoz et al. (2010) found that treatment with the ET biosynthesis inhibitor aminoethoxyvinylglycine (AVG) suppressed flooding-induced AR formation in tomato hypocotyls and *Nr* mutants produced fewer ARs than wild type plants following flooding, confirming the positive role of ET in AR formation. Accordingly, darkness-induced AR emergence in rice stem cuttings is promoted by ET signalling because treatment with 1-methylcyclopropene (1-MCP, an ET perception inhibitor) is sufficient to inhibit this process (Lin and Sauter 2018). It has been suggested that ET promotes ARI in de-rooted hypocotyls of Norway spruce

(*Picea abies*) by enhancing CK degradation (Bollmark and Eliasson 1990). ET also seems to have ARI-promoting effects on IAA transport (Negi et al. 2010).

To obtain detailed insights into the key players involved in specific steps of AR formation in petunia stem cuttings, Druege et al. (2014) performed an extensive time course microarray analysis. This revealed that many *ACC SYNTHASE (ACS)* and *ACC OXIDASE (ACO)* genes were rapidly induced after cutting, suggesting that ET biosynthesis is required for ARI. In addition to ET biosynthesis genes, many *APETALA2/ETHYLENE RESPONSE FACTOR (AP2/ERF)* genes were differentially expressed at various stages during the process. Several *AP2/ERF* genes have been recently identified as potent players in regulation of tissue repair, *de-novo* organogenesis and regeneration (Heyman et al. 2017), indicating possible roles of the ET-induced *AP2/ERF* genes in AR formation.

In attempts to elucidate ET's role in ARI, Rasmussen et al. (2017) analysed several Arabidopsis ET biosynthesis and signalling mutants. Both *ethylene overproducing 2-1 (eto2-1)* and *eto3-1* mutants, and *constitutive triple response1-1 (ctr1-1)* mutants, which have constitutive ET signalling, produced more ARs, while *ethylene insensitive2-1 (ein2-1)* and *ein3-1* mutants produced fewer ARs, than wild type controls. To the same end, Rasmussen et al. (2017) showed that at very low concentration (0.01 μ M) ACC induced slightly higher AR densities, but higher concentrations (0.1-1 μ M) had no significant effect. These results clearly indicate that ET biosynthesis and signalling promote AR formation. The effect of ET on ARI is likely independent of strigolactone (Rasmussen et al. 2017).

However, contrasting results were obtained in another study using the same system and concentration of ACC by Veloccia et al. (2016), who found that treatment with 0.01 μ M ACC had no significant effect and higher (0.1-1 μ M) concentrations tended to suppress AR formation. These contrasting results might be due to differences in growth conditions and/or high concentrations of ACC affecting other physiological processes of the Arabidopsis seedlings, which might cause aberrant and pleiotropic developmental defects. Veloccia et al. (2016) assumed that ET inhibits AR formation in Arabidopsis by repressing the transcription of *WEI2*, *WEI7* and *YUC6* genes by an unknown mechanism. This would be surprising because of previous findings that ET induces expression of *WEI2* and *WEI7*, which leads to increases in IAA biosynthesis and signalling in the Arabidopsis root tip (Stepanova et al. 2005). Because *wei2* and *wei7* mutations strongly suppressed the *sur2-1* phenotype, Pacurar et al. (2014a) proposed that ET might have a positive role in early stages of AR formation, by inducing IAA biosynthesis, but a negative role in later stages.

In conclusion, several studies have provided indications that ET is involved in AR formation, but its mode of action is still far from clear. Identifying its downstream targets and acquiring direct evidence about its specific spatiotemporal regulatory role would be helpful for elucidating its mode of action.

Cytokinins: the required inhibitors

Like IAA, cytokinins (CKs) have been extensively studied and characterized. They are adenine-derived phytohormones that were called cytokinins because of their ability to promote cell division (cytokinesis). In hormone-induced de novo organogenesis systems, the balance between CK and IAA is the main determinant of cell fate reprogramming mechanisms. High concentrations of CKs promote shoot formation but inhibit root formation. Thus, CKs have long-known roles in AR and LR formation (reviewed by Kareem et al. 2016).

Ramirez-Carvajal et al. (2009) found that upregulating CK signalling by overexpressing an active version of the *RESPONSE REGULATOR type B* transcription factor *PtRR13* in *Populus* reduced numbers of ARs formed at the base of stem cuttings, and formation of callus. In rice, CKs inhibit crown root formation downstream of the IAA-induced *CROWN ROOTLESS 5* transcription factor (Kitomi et al. 2011).

Very recently, Bustillo-Avendaño et al. (2018) suggested that in hormone-free medium de novo ARI at the base of petioles of detached leaves, involves a two-step mechanism in which CK synthesis and signalling play crucial roles. In this system, ARI involves two distinct reprogramming events. First, vascular-associated cells in the petiole proliferate, forming a micro-callus. Subsequently, a few cells in the micro-callus undergo another reprogramming event leading to AR founder cell specification and subsequently ARI. This mechanism has previously been proposed as an indirect ARI in difficult-to-root species such as of *Pinus* and *Eucalyptus* (Rasmussen et al. 2009). To confirm this interesting observation, cell lineage tracing and single cell transcriptomic analyses are needed to confirm that the proliferating cells have lost their original vascular identity and shifted towards callus identity. CKs seem to promote the first step i.e. cell proliferation but inhibit the second step i.e. cell reprogramming leading to specification of AR founder cells from the pre-formed micro-callus.

Several indications of CKs' roles in AR formation have been obtained from analyses of CK perception and signalling mutants, including *wol* (*wooden leg*), which carries a mutation of the CK receptor *ARABIDOPSIS HISTIDINE KINASE4* (*AHK4*) and *arr1arr10arr12*, a triple loss-of-function of *ARABIDOPSIS RESPONSE ELEMENT type B* genes mutant. Bustillo-Avendaño et al. (2018) found that vasculature proliferation or micro-callus formation was reduced in these mutants but,

interestingly, the petioles that developed a micro-callus generated higher numbers of ARs. Accordingly, downregulation of *arr1arr10arr12*, using oestradiol-inducible artificial microRNA, reportedly resulted in production of ARs rather than shoots by root explants incubated in CK-rich shoot induction medium (CIM) (Meng et al. 2017). *ARR1*, *ARR10* and *ARR12* directly bind to the promoter of *YUC4* and inhibit its transcriptional activity, suggesting that CKs likely inhibit ARI by repressing YUC-mediated IAA biosynthesis (Meng et al. 2017). Knowledge of the role of CKs in callus and shoot formation has provided important steps towards understanding their mechanistic mode of action, but accounts of their role in ARI are still descriptive and fragmentary. Mechanical wounding appears to locally enhance CK biosynthesis and signalling in Arabidopsis (Bustillo-Avendaño et al. 2018, Ikeuchi et al. 2017), thus it would be interesting to check whether there is a link between CKs and other wounding-induced hormones, such as JA because both hormones seem to be negative regulators of ARI.

Strigolactones: the newcomers to the club

Strigolactones (SL) are carotenoid-derived phytohormones, which participate in regulation of many developmental programs, including root architecture development (reviewed by Waters et al. 2017). Their roles in the control of AR formation are not clearly understood, but they were recently shown to participate interactively in this process with other hormones in various species.

SLs promote crown root elongation in rice via effects on cell division in the meristematic zone (Arite et al. 2012). Recently, it has also been shown that SLs positively control crown root formation in rice. In addition, Sun et al. (2015) found that the SL-deficient rice mutant *dwarf10* (*d10*), in which the key gene of SL biosynthesis is impaired, produced fewer ARs than wild type counterparts. AR production was also reduced in the SL-insensitive mutant *d3*, in which the F-box protein (a key component of the SCF complex involved in SL signalling) is affected. However, treating plants with GR24, a synthetic SL analogue, complemented the *d10* phenotype but not the *d3* phenotype (Sun et al. 2015). SLs apparently promote AR formation in rice via the D4-dependent pathway, probably by modulating IAA transport (Sun et al. 2015). However, they seem to inhibit AR formation in tomato (*Solanum lycopersicum*), pea (*Pisum sativum*) and Arabidopsis (Kohlen et al. 2012, Rasmussen et al. 2012, 2017). Kohlen et al. (2012) found that AR numbers were significantly increased in *CAROTENOID CLEAVAGE DIOXYGENASE 8* (*SICCD8*) *RNAi* transgenic lines, suggesting that SL-mediated AR formation is species-dependent. Moreover, SLs inhibit AR formation independently from the IAA, CK and ET pathways (Rasmussen et al. 2012, 2017). The contrasting effects of SL in AR formation

between monocots (rice) and dicots (pea, tomato, Arabidopsis) raise intriguing questions that remain to be answered.

Abscisic acid (ABA), gibberellic acid (GA) and brassinosteroids (BRs): the least investigated hormones in adventitious rooting

Roles of ABA, GA and BRs in AR formation are largely unclear, but there are interesting indications that they participate. For example, GA stimulates AR formation in deepwater rice via a mechanism that requires the presence of ET (Steffens et al. 2006). Treatment with GA3 alone was reportedly ineffective, but in combination with ET it significantly stimulated AR emergence (Steffens et al. 2006). In contrast, Busov et al. (2006) found that treatment with GA3 inhibited AR formation in *Populus* stem cuttings. This negative effect was corroborated by the finding that constitutive overexpression of *RGL1* (*REPRESSOR OF GA1-3-LIKE 1*) or *GAI* (*GIBBERELIC ACID INSENSITIVE*) genes without the DELLA domain, making them resistant to GA, increased numbers of ARs, indicating that GA is a negative regulator of AR formation in *Populus* (Busov et al. 2006). Similarly, Mauriat et al. (2014) showed that a treatment with GA4 inhibited AR formation in etiolated Arabidopsis hypocotyls and *Populus* stem cuttings, and that transgenic lines of both Arabidopsis and *Populus* with enhanced GA biosynthesis or perception produced fewer ARs than wild type counterparts. In the cited study, GA inhibited AR formation independently of SL biosynthesis and JA signalling, but probably interfered with establishment of an IAA gradient at the base of the stem cuttings by perturbing expression of IAA auxin efflux carrier genes.

ABA, which is a stress-related hormone, has been shown to inhibit AR emergence in deepwater rice, possibly by interfering with ET and GA signalling pathways (Steffens et al. 2006). Similarly, shoot-derived ABA inhibits LR and AR formation in tomato, likely via effects on ET and IAA pathways (McAdam et al. 2016).

Last, but not least, brassinosteroids (BRs) have been shown to stimulate ARI in Arabidopsis hypocotyls (Maharjan et al. 2014). The cited authors showed that treating weakly IAA-overproducing *gulliver1/sur2-7* mutants with exogenous brassinolide induced them to form ARs from light-grown hypocotyls, which they do not normally do, likely by enhancing IAA biosynthesis. BR and IAA synergistically promote cell elongation in Arabidopsis hypocotyls through a mechanism that involves *BRASSINAZOLE-RESISTANT 1* (*BZR1*), *ARF6*, *ARF8* and *PHYTOCHROME INTERACTING FACTOR* (*PIF4*). These transcription factors interact with each other physically and genetically in regulation of common targets including *GH3.3* and *GH3.6* (Oh et al. 2014). It is possible that BR

signalling acts synergistically with the *ARF6/ARF8* signalling module identified by Gutierrez et al (2012) in ARI promotion.

Conclusion and perspectives

AR formation is a developmental program that is controlled by complex hormonal crosstalk with strongly non-linear effects (Fig. 1). Numerous studies with model species such as *Arabidopsis*, rice and petunia, have provided information about the complex interactions involved. However, despite remarkable advances in molecular-level understanding of the process in the model species, little is still known about it in woody species such as *Populus*, *Pinus*, and Norway spruce. Checking whether the mechanisms identified in the model species are evolutionarily conserved is important, but challenging. Fortunately, the availability of genome sequences of increasing numbers of species and rapid development of genome editing techniques such as TALEN and CRISPR-Cas9 will greatly facilitate elucidation of AR formation in diverse taxa (particularly ecologically and economically important species) and the evolution of associated developmental machinery.

While efforts have focused on elucidating this process in single linear hormonal pathways, advances in modelling and integrative system biology approaches, including hormonomics, should be exploited to acquire more insights into the complex hormonal interactions involved and their final outcomes. It would also be interesting to discover how plants couple the intrinsic and extrinsic stimuli that guide and shape AR architecture. Further knowledge is required of how the external stimuli are perceived, transmitted and translated into tight internal signalling cues, as well as how specific subsets of cell types are targeted by these cues and transformed into AR founder cells.

• Author contributions

- A.L. wrote the manuscript, A.L. and C.B. edited it.

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Figure legend

Fig. 1. Overview of hormonal crosstalk during adventitious root initiation (ARI): Auxin (IAA) is the central modulator. Besides IAA, ethylene (ET) and brassinosteroids (BRs) promote ARI, while cytokinins (CKs), jasmonic acid (JA), gibberellic acid (GA), strigolactone (SL) and abscisic acid (ABA) are negative regulators. Continuous and dashed lines indicate proven and possible links, respectively. Blue and red colors indicate positive and negative regulators, respectively.

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