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REVIEW: PART OF A SPECIAL ISSUE ON MATCHING ROOTS TO THEIR ENVIRONMENT

Strigolactones activate different hormonal pathways for regulation of root development in response to phosphate growth conditions

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• *Background* Strigolactones (SLs) – a group of plant hormones and their derivatives – have been found to play a role in the regulation of root development, in addition to their role in suppression of lateral shoot branching: they alter root architecture and affect root-hair elongation, and SL signalling is necessary for the root response to low phosphate (Pi) conditions. These effects of SLs have been shown to be associated with differential activation of the auxin and ethylene signalling pathways.
• *Scope* The present review highlights recent findings on the activity of SLs as regulators of root development, in particular in response to low Pi stress, and discusses the different hormonal networks putatively acting with SLs in the root's Pi response.
• *Conclusions* SLs are suggested to be key regulators of the adaptive responses to low Pi in the root by modulating the balance between auxin and ethylene signalling. Consequently, they impact different developmental programmes responsible for the changes in root system architecture under differential Pi supply.

Key words: Strigolactones, root, phosphate, hormones, ethylene, auxin, root hairs, primary root, lateral root.

INTRODUCTION

Strigolactones (SLs) are now recognized as plant hormones (Gomez-Roldan *et al.*, 2008; Umehara *et al.*, 2008). These hormones were first identified over 40 years ago as stimulants of parasitic plant (*Striga* and *Orobanche*) germination (Cook *et al.*, 1966; reviewed by Xie *et al.*, 2010). Later, their activity as stimulants of hyphal branching was discovered in the symbiotic arbuscular mycorrhizal fungi (AMF; reviewed by Koltai *et al.*, 2012). As plant hormones, SLs have been shown to act as long-distance branching factors, suppressing the outgrowth of pre-formed axillary shoot buds (e.g. Gomez-Roldan *et al.*, 2008; Umehara *et al.*, 2008).

SLs are terpenoid lactones derived from carotenoid (Matusova *et al.*, 2005). Their presence has been demonstrated in a wide variety of plant species, including dicots, monocots and primitive plants, in which mixtures of several SL compounds have been found (reviewed by Xie *et al.*, 2010; Liu *et al.*, 2011; Proust *et al.*, 2011). They are synthesized in a few different plant parts, but roots are considered to be the main site of SL biosynthesis (reviewed by Xie *et al.*, 2010). There is also some evidence for the presence of the SL orobanchol in the xylem sap of arabidopsis (Kohlen *et al.*, 2011), suggesting that root-derived SLs are transported to the shoot. The movement of SLs, their metabolites or other unknown secondary messengers in the root-to-shoot direction might confer the observed reduction in shoot branching (reviewed by Dun *et al.*, 2009).

A number of SL-associated mutants have been found in several plant species. These include both SL-synthesis and SL-signalling mutants. Mutations in MAX1, a cytochrome P450, and in two carotenoid cleavage dioxygenase (CCD) enzymes (CCD7/MAX3 and CCD8/MAX4) result in a hyper-branching phenotype and reduced levels of SLs, suggesting that they catalyse SL biosynthesis (e.g. Liang *et al.*, 2010; Vogel *et al.*, 2010; reviewed by Dun *et al.*, 2009; Leyser, 2009). Rice mutants in the iron-binding protein Dwarf27 (D27) are also deficient in SL levels (Lin *et al.*, 2009). Recently, D27 has been suggested to be a β-carotene isomerase that converts all-*trans*-β-carotene into 9-*cis*-β-carotene. The latter may serve as a substrate for cleavage by CCD7, followed by CCD8 incorporation of oxygen: this produces carlactone, a compound with SL-like biological activities (Alder *et al.*, 2012). The GRAS-type transcription factors NSP1 and NSP2 have been suggested to be putative regulators of the SL biosynthesis pathways in rice and *Medicago* (Liu *et al.*, 2011).

Other mutants have been found to be insensitive to SLs. Mutations in MAX2 confer an over-shooting phenotype (Stirnberg *et al.*, 2002); this phenotype was not repressed by application of GR24 (a bioactive, synthetic SL; Johnson *et al.*, 1981; Umehara *et al.*, 2008) and was not associated with reduced levels of the SL orobanchol (Kohlen *et al.*, 2011). Hence, MAX2 was suggested to be a component of SL signalling (Umehara *et al.*, 2008) which encodes an F-box protein that might be part of the ubiquitin-mediated degradation of as-yet unknown protein targets (Stirnberg *et al.*, 2007). Another gene associated with the SL response was shown to be Dwarf14 (D14). Mutants in D14 of both rice and arabidopsis showed a hyper-branching phenotype and insensitivity to SLs (Arite *et al.*, 2009; Waters *et al.*, 2012).

Additional roles for SLs have been found in plants, including regulation of secondary growth (Agusti *et al.*, 2011) and

adventitious root formation (Rasmussen *et al.*, 2012). Importantly, SLs are also involved in the regulation of root development: they have been shown to alter lateral root (LR) formation and root-hair (RH) length (Kapulnik *et al.*, 2011*a*; Ruyter-Spira *et al.*, 2011).

Phosphorus (P) is one of the essential macronutrients required by plants. It plays vital roles as a structural component of cellular macromolecules and in major metabolic processes. Inorganic phosphate (Pi) is the P form that is most readily accessible to plants. The availability of P varies considerably in soils (Maathuis, 2009), whereas the concentration of Pi in soil solutions hardly ever exceeds 10 μM (Bieleski, 1973).

Plants have evolved strategies to cope with low P conditions. Roots are considered to be the main site of Pi absorption by the plant. Hence, among the functionally important structural changes undergone by plants under P deprivation are alterations in root development (Williamson *et al.*, 2001; López-Bucio *et al.*, 2002; Sánchez-Calderón *et al.*, 2005, 2006). Under low-Pi growth conditions, development of the root system architecture is altered by promotion of LR formation and elongation, and inhibition of primary root (PR) growth; in addition, RH number and length increase. These changes are suggested to promote topsoil foraging and increase the root surface for absorption, thereby increasing the plant's ability to absorb Pi (López-Bucio *et al.*, 2003; reviewed by Péret *et al.*, 2011).

Several studies have demonstrated a role for SLs in root and shoot responses to low Pi availability (Umehara *et al.*, 2010; Kohlen *et al.*, 2011; Ruyter-Spira *et al.*, 2011; Mayzlish-Gati *et al.*, 2012). The present review summarizes and discusses recent findings on the activity of SLs as regulators of root development, in particular in response to Pi conditions, and on the different hormonal networks putatively acting with SLs in the root's Pi response.

ROLE OF SLs IN ROOT DEVELOPMENT

Evidence from SL-mutant phenotypes and pharmacological studies suggests that SLs regulate the architecture of the root system. LR formation was shown to be negatively regulated by SLs in arabidopsis under conditions of sufficient Pi nutrition (Kapulnik *et al.*, 2011*a*). This is because mutants that are deficient in SL response (i.e. *max2*) or biosynthesis (i.e. *max3* and *max4*) had more LRs than the wild type (WT) (Kapulnik *et al.*, 2011*a*; Ruyter-Spira *et al.*, 2011). Accordingly, treatment of seedlings with GR24 affected LR formation (Kapulnik *et al.*, 2011*a*; Ruyter-Spira *et al.*, 2011). Moreover, an effect of exogenously supplied SLs on LR formation was found in the WT and SL-synthesis mutants, but was absent from the SL-response mutant; these results suggested that the effect of SLs on LR formation is mediated via the MAX2 F-box (Kapulnik *et al.*, 2011*a*; Ruyter-Spira *et al.*, 2011).

SLs have also been shown to regulate RH elongation: GR24 treatment led to an increase in RH length in the WT and SL-deficient mutants (*max3* and *max4*) but not in the SL-response mutant *max2*. Hence, SLs were suggested to have a positive effect on RH length, which is mediated via MAX2 (Kapulnik *et al.*, 2011*a*).

SLs have also been shown to be regulators of PR development. Under conditions of carbohydrate limitation, which usually lead to a reduction in PR length (Jain *et al.*, 2007), GR24 treatments at all concentrations had a positive effect, in a MAX2-dependent fashion, on PR elongation (Ruyter-Spira *et al.*, 2011). Accordingly, under these conditions, the PR lengths of the SL-deficient and SL-response mutants were shorter than those of the WT plant (Ruyter-Spira *et al.*, 2011). This reduction in PR length was accompanied by a reduction in cell number in the PR meristem that could be rescued by application of GR24 to SL-deficient, but not SL-response mutants (Ruyter-Spira *et al.*, 2011).

SLs ARE MEDIATORS OF THE ROOT RESPONSE TO PHOSPHATE CONDITIONS

Recently, SL biosynthesis and sensitivity have been shown to be important for the root's ability to sense or respond to low-Pi growth conditions (Ruyter-Spira *et al.*, 2011; Mayzlish-Gati *et al.*, 2012). It seems that mutants that are flawed in SL biosynthesis (e.g. *max4*) are unable to respond to low Pi conditions with respect to root architecture: induction of LR is reduced in the arabidopsis SL mutants compared with the WT under low-Pi growth conditions (Ruyter-Spira *et al.*, 2011). Moreover, the SL mutants were deficient in their ability to increase RH length and density under low Pi conditions relative to the WT, at least for the first 96 h post-germination under low-Pi growth conditions (H. Koltai, unpubl. res.; Mayzlish-Gati *et al.*, 2012; Fig. 1).

The number and length of RHs are thought to be directly associated with the plant's ability to absorb nutrients from the soil (Sánchez-Calderón *et al.*, 2005; reviewed by Gilroy and Jones, 2000). Therefore, the lack of RH density increase in the SL mutants following germination suggests that they may suffer from reduced internal P levels. This suggestion is strengthened by the finding that the expression of several Pi transporters is reduced in the SL mutants following germination (Mayzlish-Gati *et al.*, 2012). However, levels of P in the SL-insensitive mutant *max2* plants were found to be similar to those of the WT under diverse Pi conditions (Mayzlish-Gati *et al.*, 2012), suggesting that even in the absence of an SL response, the plant can acquire P. On the other hand, despite the WT-like, low levels of P in the SL mutant under low Pi conditions, it was not able to alter its root development. Taken together, the results suggest that root sensing of, or response to, low Pi is dependent on the SL pathway and requires the activity of MAX2 and WT levels of SLs.

With respect to the shoot, in both arabidopsis and rice, evidence has been brought showing that SLs contribute to regulation of the shoot architectural response to low-Pi growth conditions: at least one of the arabidopsis SLs (orobanchol) was detected in xylem sap and up-regulated under Pi deficiency, in correlation with the changes in shoot architecture observed under these conditions (Kohlen *et al.*, 2011). In rice, tiller bud outgrowth in WT rice seedlings was inhibited, whereas root SL (2′-epi-5-deoxystrigol) levels increased in response to Pi deficiency; the suppression of tiller bud outgrowth under low-Pi growth conditions was not evident in the SL-deficient or insensitive mutants (Umehara *et al.*, 2010;

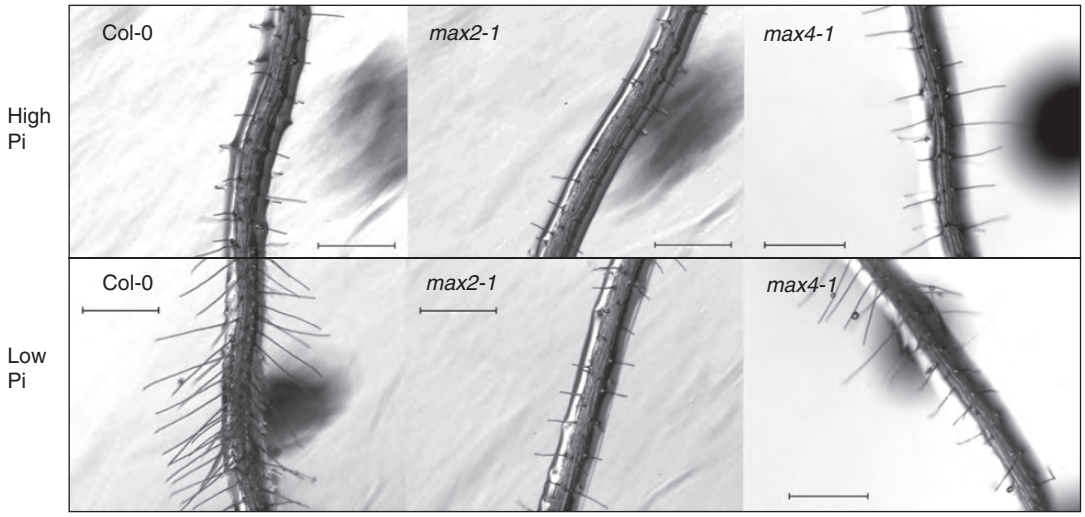

FIG. 1. Effects of high and low Pi conditions on root hair (RH) length and density of the WT, and *max2-1* and *max4-1* mutants. Examples of RH phenotype in Col-0, *max2-1* and *max4-1* under low (1 μM) and high (2 mM) Pi conditions at 48 h post-germination. Scale bars = 500 μm.

reviewed by Umehara, 2011). Due to their proposed role in both shoots and roots, SLs might be considered mediators of root development and architecture in response to external growth conditions, in addition to their role in regulating shoot development.

However, it is likely that, in order to mediate plant response to Pi levels, SL pathways must be regulated by Pi levels. Indeed, SL production has been found to be induced under low Pi conditions in several plant species (e.g. Yoneyama *et al.*, 2007; López-Ráez and Bouwmeester, 2008; Kohlen *et al.*, 2011). This induction was correlated with the inhibition of tiller or lateral bud outgrowth in WT rice and WT arabidopsis (Umehara *et al.*, 2010; Kohlen *et al.*, 2011). As SLs are suggested to regulate the root's response to Pi growth conditions, and possibly to internal P levels in the plant, the Pi-induced elevation of SL levels suggests a negative feedback loop between SLs and internal P levels, for fine regulation of the associated root response.

CROSS-TALK OF SLs WITH AUXIN AND ETHYLENE TO CONTROL ROOT DEVELOPMENT UNDER DIFFERENT PHOSPHATE GROWTH CONDITIONS

Other plant hormones are known to regulate root development (reviewed by Osmont *et al.*, 2007). Moreover, other plant hormones are known to regulate plant responses to nutritional conditions, including Pi deficiency (reviewed by López-Bucio *et al.*, 2002; Chiou and Lin, 2011). Hence, it is likely that SLs exert their function via a carefully controlled network with other plant hormones.

It has been shown that polar auxin transport is modulated by SLs in the control of shoot branching, that SLs reduce the basipetal transport of auxin and that in the presence of auxin, SLs enhance competition between two branches on a common stem. It was therefore suggested that SLs enhance competition between branches by dampening the shoot's capacity for polar auxin transport (Crawford *et al.*, 2010). On the other hand, in pea (*Pisum sativum*), exogenously applied SL inhibited shoot bud outgrowth even when plants were decapitated and thus auxin-depleted, whereas SL application was not associated with blocking auxin transport in the bud. Application of SL was also able to reduce shoot branching in auxin-response mutants of arabidopsis. Moreover, contrary to the auxin transport model predictions, WT and SL-biosynthesis mutants of both pea and arabidopsis were capable of transporting exogenously supplied auxin. These results suggested that repression of bud outgrowth is due to auxin-dependent production of SLs, rather than to the effect of SLs on auxin transport from the buds (Brewer *et al.*, 2009). Moreover, auxin has been shown to induce SL synthesis in the root via induction of CCD7 and CCD8 expression, indicating a feedback loop between auxin and SLs (reviewed by Beveridge and Kyozuka, 2010).

In the root, SLs have been suggested to interfere with auxin-efflux carriers: only 2,4-D, a synthetic auxin that is not secreted by efflux carriers, restored normal root growth in the presence of SLs (Koltai *et al.*, 2010). In agreement with this, the intensities of the auxin transporters PIN1-, PIN3- and PIN7-GFP decreased in the provascular tissue of the PR tip upon GR24 treatment (Ruyter-Spira *et al.*, 2011). Together, these results suggest that in the root, similar to the shoot, SLs have an effect on polar auxin transport.

An increase in local auxin levels or enhanced auxin sensitivity in pericycle cells regulate LR formation through a mechanism involving PIN1 (Benkova *et al.*, 2003; reviewed by Péret *et al.*, 2009). Treatment of seedlings with GR24 resulted in a decrease in PIN1-GFP intensity in LR primordia, suggesting involvement of PIN1 in the GR24-mediated reduction of LR formation. However, GR24 application induced, rather than reduced, LR formation when auxin levels were increased by exogenous application. Under those conditions, there was no reduction in PIN1-GFP intensity (Ruyter-Spira *et al.*, 2011).

Based on these findings, Ruyter-Spira *et al.* (2011) suggested that SLs, as modulators of auxin flux, might alter the auxin optima for LR formation: SLs reduced auxin import to

the root under relatively low auxin levels, resulting in inhibition of LR formation. In contrast, under high auxin levels, this SL-mediated reduction allowed the generation of auxin optima, and induction of LR formation. Along the same lines, in both tomato and arabidopsis, an effect of GR24 treatments on asymmetric root growth (Koltai *et al.*, 2010; Ruyter-Spira *et al.*, 2011) might be explained by asymmetric auxin distribution, or be a consequence of distorted expression of the PIN auxin efflux carriers (Ruyter-Spira *et al.*, 2011). Similarly, decreased GUS staining from the auxin-response reporter DR5-GUS in the aerial parts of GR24-treated plants might indicate SL reduction of auxin sensitivity or levels (Ruyter-Spira *et al.*, 2011).

Another indication that auxin is downstream of SLs in the signal transduction pathway comes from an examination of mutants' root responses. SL signalling was shown not to be necessary for the RH elongation induced by auxin, because the SL-insensitive mutant *max2* was responsive to auxin. However auxin signalling was needed, at least in part, for the RH-elongation response to SLs: the auxin-receptor mutant *tir1-1* (Dharmasiri *et al.*, 2005) showed reduced sensitivity to SLs relative to the WT (López-Bucio *et al.*, 2003; Kapulnik *et al.*, 2011*b*).

Root development, including a positive effect on RH elongation and a negative one on LR formation, has been shown to be regulated by ethylene as well (reviewed by López-Bucio *et al.*, 2002). Accordingly, the involvement of ethylene signalling in the SL response has been suggested under sufficient-Pi growth conditions. This suggestion was based on the markedly reduced SL response in the ethylene-signalling mutants *etr* and *ein*, on the negative effect of aminoethoxyvinylglycine (an ethylene-synthesis inhibitor) on the RH response to SLs, and on the ability of SLs to induce transcription of the 1-aminocyclopropane-1-carboxylic acid (ACC) synthases, involved in ethylene biosynthesis (Kapulnik *et al.*, 2011*b*). Accordingly, SLs were shown to induce ethylene biosynthesis in seeds of the parasitic plant *Striga*, leading to their germination (Sugimoto *et al.*, 2003). Therefore, the effect of SLs on the plant may involve ethylene biosynthesis.

Ethylene has been suggested in several studies to be involved in the response to low Pi (e.g. Lei *et al.*, 2011; Nagarajan *et al.*, 2011). Analysis of the root architecture of ethylene-signalling mutants and ACC-treated plants suggested that ethylene is involved in the process of RH formation and meristem exhaustion activated by Pi starvation, but not in the promotion of LR formation under these conditions (reviewed by Sato and Miura, 2011). In other studies, it was suggested that low P does not act via ethylene in its effect on RH density (Ma *et al.*, 2001). Indeed, ethylene was shown not to mediate the low-Pi response of SLs, at least with respect to RH density: ethylene was not able to compensate for the deficiency in the response of *max2* to low Pi. Therefore, the MAX2-regulated RH-density response to low Pi conditions is suggested to be downstream or independent of the ethylene pathway (Mayzlish-Gati *et al.*, 2012).

However, under Pi deprivation, addition of indole-3-acetic acid (IAA) to SL-insensitive and SL-biosynthesis mutant roots led to complementation of the mutants' phenotypes to that of the WT, suggesting that auxin is part of the SL-response pathway to low-Pi growth conditions (Mayzlish-Gati *et al.*, 2012). Indeed, auxin signalling is associated with alterations in root system architecture as a result of Pi deprivation, whereas Pi-deprived plants are more sensitive to exogenous auxin than Pi-nourished plants with regard to the induced formation of LR and arrest of PR growth (reviewed by López-Bucio *et al.*, 2002; Chiou and Lin, 2011).

Moreover, under these conditions of Pi-deprivation, *max2* also displayed reduction rather than induction of *TIR1* transcription (Mayzlish-Gati *et al.*, 2012). In the WT, the auxin pathway and induction of *TIR1* transcription were suggested to play a fundamental role in the modifications of root architecture by P availability (López-Bucio *et al.*, 2003; Pérez-Torres *et al.*, 2008). Thus, the deficiency in the response of the *max2* mutant to low Pi might be associated with a reduction in *TIR1* transcription in comparison with the WT (Mayzlish-Gati *et al.*, 2012). However, due to the relatively high levels of auxin in the *max2* mutants (Bennett *et al.*, 2006), this lack of induction is probably not directly associated with reduced activity of the auxin pathway. Accordingly, the *tir1* mutant showed a reduced response to low Pi in comparison with the WT (Pérez-Torres *et al.*, 2008), which could not be restored by GR24 application. Hence, the deficiency in the response of *tir1* to low Pi is probably downstream of the SL signalling pathway (Mayzlish-Gati *et al.*, 2012).

Taken together, these studies suggest that different SL-related hormonal pathways are activated under different Pi conditions (Fig. 2). Under conditions of Pi sufficiency, the SL pathway, through MAX2, might activate ethylene

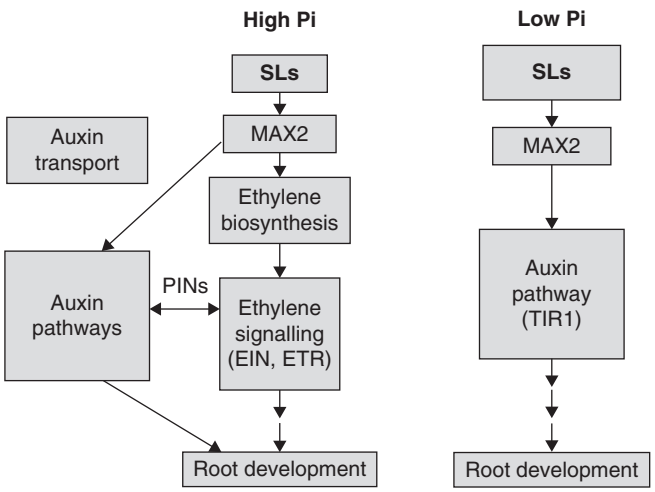

FIG. 2. Schematic illustration of the hormonal pathways activated by SLs in response to different Pi growth conditions. Under sufficient Pi, the SL pathway, via MAX2, is suggested to act mainly through the ethylene pathway (Kapulnik *et al.*, 2011*b*). This response is suggested to be mediated by ethylene-insensitive (EIN) and ethylene-resistant (ETR) proteins (Kapulnik *et al.*, 2011*b*; Koltai, 2011). Auxin synthesis, transport (including PIN Formed protein (PIN) expression) and signalling are positively affected by ethylene signalling (Stepanova and Alonso, 2009, and references therein). In addition, SLs have been suggested to dampen auxin transport (Crawford *et al.*, 2010). Hence, the auxin pathway may be activated either by the ethylene pathway or directly by SLs, to regulate root development for sufficient-Pi growth conditions. However, under conditions of Pi depletion, during the first few hours of seedling development, the SL pathway, through MAX2, is suggested to activate mainly the TIR1-dependent auxin signalling pathway (Mayzlish-Gati *et al.*, 2012), thereby regulating root development to suit those growth conditions.

biosynthesis as well as the auxin pathway, to regulate root development (Koltai, 2011). Under conditions of Pi depletion, the SL pathway, through MAX2, might mainly activate auxin signalling, and thus regulate root development such that it will be suited to those growth conditions (Fig. 2).

Accordingly, the auxin and ethylene signalling pathways have been suggested to be differentially activated under diverse Pi growth conditions and to regulate different aspects of the root response to these conditions. It was suggested that acclimation of the root system to P deficiency is achieved by changing ethylene sensitivity (Ma *et al.*, 2003). On the other hand, reduced Pi availability was shown to increase auxin sensitivity and to lead to induction of *TIR1* transcription, thereby conferring a Pi-deprivation root response associated with LR development (López-Bucio *et al.*, 2003; Pérez-Torres *et al.*, 2008). Moreover, Schmidt and Schikora (2001) suggested that the signal from a P-deficiency-specific stress might act directly on components of an ethylene-independent pathway to confer RH elongation under conditions of Pi deprivation. Accordingly, SL may be one of the signals of P-deficiency stress, and activation of its signalling pathway might be an important component of the root's response to low-Pi growth conditions, when it acts mainly via auxin signalling.

CONCLUDING REMARKS

An increasing number of studies are suggesting the involvement of SLs in shoot and root development. On the one hand, shoot-derived auxin has been shown to positively regulate the biosynthesis of root-derived SLs. On the other, SLs have been shown to contribute to the regulation of both shoot and root architecture in response to Pi growth conditions as well.

In roots, developmental SL-regulation might be carried out via the activation of alternative signalling pathways: under conditions of Pi sufficiency, SLs act mainly through the ethylene signalling pathway, and under low Pi conditions, they act mainly through the auxin pathway. This may position SLs as an important element in the plant's ability to sense or respond to low Pi conditions, and modify shoot and root growth and development accordingly. SLs might adjust the balance between auxin and ethylene signalling pathways to activate different developmental programmes in response to changes in soil Pi, thereby controlling their own biosynthesis via a positive feedback loop: increased SL levels under low Pi conditions might lead to increased sensitivity to shoot-derived auxin, and therefore to increased SL biosynthesis in roots under these conditions.

Moreover, Pi signalling and the plant's response are known to rely on local and systemic signalling in both root and shoot, and to require fine-tuned communication between them (reviewed by Chiou and Lin, 2011). Perhaps some of the shoot–root communication in response to Pi conditions is conveyed via the SL-biosynthesis and signalling systems. Several genes are known to act in the plant response to Pi starvation. Some of them, such as those encoding PDR2 (Phosphate Deficiency Response 2), LPI (Low Phosphorus Insensitive) and LPR (Low Phosphate Root), might be acting locally, at the root tip, to regulate Pi response (López-Bucio *et al.*, 2005; Sánchez-Calderón *et al.*, 2006; Svistoonoff *et al.*, 2007; Ticconi *et al.*, 2009; reviewed by Chiou and Lin, 2011). In contrast, the gene encoding PHR1 (Phosphate Starvation Response 1) acts systemically to positively regulate miR399 expression under Pi starvation (Chiou and Lin, 2011, and references therein). Studies examining SL involvement in the activity of such genes may promote insight into the local and/or systemic activity of SLs in both root and shoot under Pi starvation. Moreover, because LPR1 has been suggested to participate in vesicular targeting of auxin transporters and to have a positive role in pericycle cell activation to form LR primordia and RH elongation (López-Bucio *et al.*, 2005), interaction of this protein with the SL pathway might explain the positive effects of SLs on RH elongation (Kapulnik *et al.*, 2011*a*) and LR formation under low Pi conditions (Ruyter-Spira *et al.*, 2011).

Another aspect of the role of SLs in roots is their involvement in signalling in the rhizosphere. SLs were initially identified as signalling molecules that are exuded from plants and necessary for parasitic plant germination. They are also known to be important signals for hyphal branching in plant-symbiotic AMF (reviewed by Xie *et al.*, 2010; Koltai *et al.*, 2012). Interestingly, as AMF promote the plant's ability to acquire Pi (e.g. Bucher, 2007), and because SL secretion and production have been shown to increase under low Pi conditions (Yoneyama *et al.*, 2007), SLs may benefit plants under Pi-deprived conditions by promoting the mycorrhizal association, in addition to their role as regulators of root development. However, the agricultural potential of SLs as modulators of plant development, and perhaps as a means of promoting AMF symbiosis, remains largely unexplored. Site, timing and concentrations of SL application still have to be optimized for their practical application.

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