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Invited Review

Strigolactone, a key regulator of nutrient allocation in plants

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Abstract Strigolactones (SLs) are a group of terpenoid lactones that are derived from carotenoids. SLs have been found in a number of plant species and appear to serve several diverse physiological functions. SLs were first identified by their ability to stimulate seed germination of root-parasitic plants. Later, SLs were isolated as hyphal-branching inducers of arbuscular mycorrhizal fungi, which facilitate the uptake of soil nutrients by plants. Most recently, SLs (or their derivatives) were found to be a new class of plant hormones that inhibit shoot branching. Considering these three roles of SLs, it was unclear at first why communication signals in the rhizosphere would regulate shoot branching in the host plant. Recent reports, however, suggest that plants produce SLs in response to nitrogen and phosphorus deficiency, stimulating changes in plant shoot and root architecture that enable them to adapt to environmental conditions. Excess SLs produced in roots are released into the soil, where they stimulate the growth of arbuscular mycorrhizal fungi. These symbiotic fungi supply inorganic nutrients that can be used by the plant. This review paper focuses on the physiological roles of SLs as a key regulator of nutrient allocation in plants.
Key words: Arbuscular mycorrhizal fungi, leaf senescence, phosphorus deficiency, shoot branching, strigolactones.

Strigolactones (SLs) are a group of terpenoid lactones in which a tricyclic lactone (ABC ring) and a methyl butenolide (D ring) are connected by an enol ether bridge (Figure 1). SLs were initially detected because of their ability to stimulate seed germination of root-parasitic plants such as *Striga lutea,* which forms haustoria and take in nutrients via the haustoria from the host plant (Cook et al. 1966). Chemical identification of the germination stimulant was attempted, and strigol (Figure 1) and strigyl acetate were isolated from cotton root exudates, representing the first SLs to be identified (Cook et al. 1972). *Striga* species are serious weeds of important food crops in Africa, including sorghum, maize, millet, and rice. Another root parasitic plant species *Orobanche* attack dicotyledonous crops in Europe and North Africa, including tomato, tobacco, carrot, cucumber, sunflower, and legumes. Their impacts are severe: many millions of hectares are infected, and the losses annually amount to billions of dollars (US) in heavily infested areas (Parker 2009). In the 1950s it was known that the seeds of root-parasitic plants would germinate more frequently in the close vicinity of host plant roots, and germination-stimulating activity was found in root exudates from various plant species. Later, several types of SLs were isolated from the root exudates of diverse plant species (Yoneyama et al. 2010). Development of the synthetic SL analog GR24 (Figure 1) accelerated SL research (Johnson et al. 1981). However, it took many years to clarify why host plants had evolved to produce SLs despite the risk of parasitism

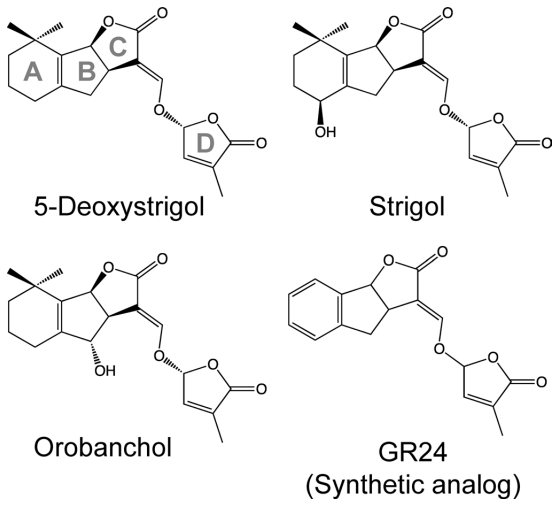

Figure 1. Chemical structures of representative SLs.

Abbreviations: 5DS, 5-deoxystrigol; AMF, arbuscular mycorrhizal fungi; *BRC*, *BRANCHED*; CCD, carotenoid cleavage dioxygenase; *DAD*, *DECREASED APICAL DOMINANCE*; *D*, *DWARF*; *FC1*, *FINE CULM1*; *GID1*, *GIBBERELLIN INSENSITIVE DWARF1*; *HTD*, *HIGH-TILLERING DWARF*; LC-MS/MS, Liquid chromatography-tandem mass spectrometry; *MAX*, *MORE AXILLARY GROWTH*; NCED, 9-*cis*-epoxycarotenoid cleavage dioxygenases; Pi, inorganic phosphate; *RMS*, *RAMOSUS*; SL, strigolactone; SABP2, a salicylic acid binding protein.

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by root-parasitic plants.

In 2005, the natural SL 5-deoxystrigol (5DS) (Figure 1) was isolated as a factor that could stimulate branching of arbuscular mycorrhizal fungi (AMF) from root exudates of *Lotus japonicus* (Akiyama et al. 2005). AMF forms mutualistic, symbiotic associations with the roots of more than 80% of land plants. The fossil records from the Ordovician and Devonian eras indicate the existence of AMF symbioses more than 460 million years ago and suggest that the fungi played a crucial role in facilitating the colonization of land by plants (Remy et al. 1994; Redecker et al. 2000). AMF penetrate and colonize plant roots; there, they differentiate into highly branched structures known as arbuscules, which are thought to be the sites of nutrient exchange between AMF and plants. The fungi develop extraradical hyphae that provide the host with essential inorganic nutrients such as nitrogen and inorganic phosphorus (phosphate, Pi) from the soil (Govindarajulu et al. 2005; Harrison and Vanbuuren 1995). At the same time, AMF obtain carbohydrates from the host plants. This discovery led to the hypothesis that the SLs produced by plants result in stronger symbiotic interactions with AMF and thus provide the plant with a source of inorganic nutrients, although root-parasitic plants might use SLs to detect potential hosts (Akiyama and Hayashi 2006).

In addition to stimulating parasitic plants and AMF, SLs also induce seed germination of non-parasitic plants such as shepherd's purse, lettuce, and wild oats (Bradow 1986; Bradow et al. 1988; Bradow et al. 1990), and they are produced in Arabidopsis and white lupin, which are not hosts of AMF (Goldwasser et al. 2008; Yoneyama et al. 2008). These findings indicated that SLs have functions in plants unrelated to parasitism and fungal colonization. However, for many years it was difficult to investigate the functions of SLs in plants because of the apparent lack of SL-related mutants. As described in the next section, a third function of SLs was discovered through research on the regulation of shoot branching.

Discovery of SLs as a new class of plant hormone

The aerial architecture of plants is determined by the pattern of shoot branching. In agriculture and horticulture, the shoot branching pattern is important because it affects the number of flowers and thus the number of seeds. Shoot branching consists of two steps: the formation and the subsequent axillary bud outgrowth. The second step, axillary bud outgrowth, depends on both environmental and endogenous cues (McSteen and Leyser 2005). Nutrients and light conditions are the major environmental cues, and two classes of plant hormones, auxins and cytokinins, have important roles in shoot branching regulation as endogenous cues (Cline 1991). In addition, analysis of the enhanced shoot branching mutants *ramosus* (*rms*) of pea, *more axillary growth* (*max*) of Arabidopsis, *decreased apical dominance* (*dad*) of petunia, and *dwarf* (*d*) of rice had suggested the existence of a third class of hormones that inhibit shoot branching (Ongaro and Leyser 2008). Although the chemical identity of this third class of hormones had been unknown, our research group and a French research group finally found that SLs (or their downstream metabolites) are the shoot-branch-inhibiting hormones (Gomez-Roldan et al. 2008; Umehara et al. 2008). This finding also revealed that many of the shoot branching mutants were in fact mutants in SL production or perception/signaling.

Genes involved in SL biosynthesis

Ishikawa et al. (2005) analyzed five tillering *dwarf* (*d*) mutants in rice (*d3*, *d10*, *d14*, *d17*, and *d27*) and showed that the axillary meristems are normally established in these mutants, but the dormancy of tiller bud activity is weakened. This series of highly tillered *d* mutants has several advantages as a research tool. One advantage is that *d* mutant plants can be classified easily and more rapidly than the Arabidopsis *max* mutants. Two outgrowing tillers are observed in hydroponic culture of 2-week-old seedlings of *d* mutants, whereas no tillers are observed in the wild type. Also, rice can be grown in small-scale hydroponic culture without aeration for use in bioassays. Another advantage of this mutant series is that additional candidates for SL-related mutants, *d14* and *d27*, have been isolated only in rice.

Experiments using carotenoid biosynthesis inhibitors and mutants suggested that carotenoid-cleaved products form the ABC ring of SLs through an oxidation and cyclization step (Humphrey and Beale 2006; Matusova et al. 2005). The carotenoid cleavage dioxygenases (CCDs) and 9-*cis*-epoxycarotenoid cleavage dioxygenases (NCEDs) in seed plants have been classified into six clusters: CCD1, NCED, CCD4, CCD7, CCD8, and a rice-specific enzyme (Bouwmeester et al. 2007). CCD1 is involved in the production of volatile compounds such as β-ionone and β-cyclocitral. Members of the NCED and CCD4 clusters contribute to abscisic acid biosynthesis and formation of flower pigments such as bixin and crocetin, respectively (Ohmiya 2009). CCD7 and CCD8 are involved in the biosynthesis of the branch-inhibiting hormone(s). When I started to look for a chemical that inhibits shoot branching, no SL-biosynthetic mutant had yet been found. Thus, I investigated whether SLs would suppress tiller bud outgrowth of *ccd7* and *ccd8* mutants.

Genes related to SL biosynthesis are shown in Figure 2. The rice *D10* gene encodes a CCD8-type enzyme and is an ortholog of the *MAX4*/*RMS1*/*DAD1* genes (Arite et al. 2007; Sorefan et al. 2003; Snowden et al. 2005). *D17* was found to be an allele of *HIGH-TILLERING DWARF1* (*HTD1*), an ortholog of *RMS5*/*MAX3*/*DAD3*,

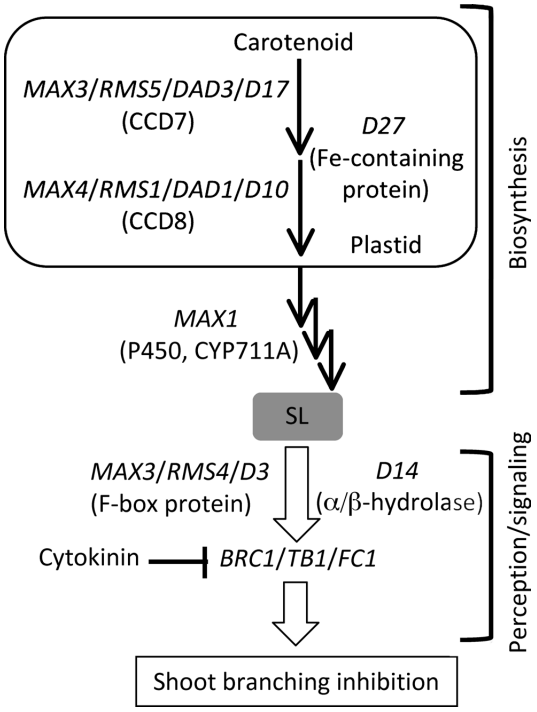

Figure 2. SL biosynthesis and perception/signaling pathway.

that encodes a CCD7-type enzyme (Booker et al. 2004; Drummond et al. 2009; Johnson et al. 2006; Umehara et al. 2008; Zou et al. 2006). Application of SLs to the roots of *d10* and *d17* mutant seedlings was found to inhibit tiller bud outgrowth, and the SL levels of these mutants were shown to be lower than those of the wild type by liquid chromatography-tandem mass spectrometry (LC-MS/MS) analysis and the *Striga* germination assay (Umehara et al. 2008). Similar results were obtained with Arabidopsis *max* and pea *rms* mutants (Gomez-Roldan et al. 2008; Umehara et al. 2008).

In *in vitro* experiments, CCD7 and CCD8 in sequence cleaved β-carotene and produced an apo-carotenone named D'orenone (Schwartz et al. 2004; Schlicht et al. 2008). We expected that D'orenone might be an SL precursor, forming the SL ABC ring (Figure 1) by oxidation and cyclization of the side chain, but application of D'orenone did not rescue *d10* mutants and SLs were not detected in D'orenone-treated *d10* roots (our unpublished data). Since D'orenone is highly hydrophobic, *d10* may be unable to absorb it. Quantification of endogenous D'orenone is the next important step in understanding its role. Quantification of endogenous D'orenone is in progress.

The *max1* mutant is the only known mutant in Arabidopsis, not reported in other plant species. *MAX1* encodes CYP711A, a cytochrome P450 monooxygenase that functions downstream of CCD7 and CCD8 (Booker et al. 2005). The *max1* mutant could be rescued by SL treatment, indicating that *max1* is also likely to be an SL biosynthesis mutant (Gomez-Roldan et al. 2008; Crawford et al. 2010).

D27, a novel iron-containing protein, is found in the plastio of many plant species (Lin et al. 2009). Endogenous SL levels were undetectable in the rice *d27* mutant, which could be rescued by SL treatment. These results suggested that D27 is yet another protein involved in SL biosynthesis, but its biochemical function is still unknown. To produce the ABC portion of SLs from carotenoids, many steps (and therefore many genes) would be needed. In addition, little is known about the formation of the D ring, which part is found in all natural SLs and is necessary for their biological activity in root-parasitic plants and AMF (Akiyama et al. 2010; Zwanenburg et al. 2009). Further analysis of other branching mutants might lead to the discovery of new SL biosynthesis-related genes.

Genes related to SL perception and signaling

Genes related to SL perception/signaling are shown in Figure 2. Map-based cloning of *D3* revealed that it encodes an F-box leucine-rich repeat (LRR) protein and is an ortholog of *RMS4* and *MAX2* (Ishikawa et al. 2005; Johnson et al. 2006; Stirnberg et al. 2002). Several F-box proteins are involved in signal perception or transduction of plant hormones; these proteins include TIR1 (in auxin), SLY1/GID2 (in gibberellin), COI1 (in jasmonate), and EBF1 and EBF2 (in ethylene) (Lechner et al. 2006). The F-box proteins function as subunits of an SCF-type E3 ligase that polyubiquitinates and targets proteins for degradation by the 26S proteasome. Application of SLs to *d3/rms4/max2* mutants did not inhibit their excess shoot branching (Gomez-Roldan et al. 2008; Umehara et al. 2008). The SL levels in the shoot and roots of *d3* mutants were very low under Pi-sufficient conditions, but higher than those of the wild type under Pi-deficient conditions (Umehara et al. 2008; Umehara et al. 2010). This increase is correlated with the upregulation of *D10* (CCD8) transcript levels in *d3* and other tillering *d* mutants (Arite et al. 2007). The *rms4* mutants in pea also show similar transcriptional feedback regulation of *RMS1* (CCD8) (Foo et al. 2005).

D14 encodes a protein in the α/β-fold hydrolase superfamily (Arite et al. 2009; Gao et al. 2009; Liu et al. 2009). Endogenous SL levels are elevated in the *d14* mutant, and its excess tillering is not rescued by SL treatment. *d14/d88/htd2* mutants show feedback upregulation of the SL biosynthesis pathway (Arite et al. 2009; Liu et al. 2009). These findings demonstrate that D14 functions downstream of SL synthesis. Among the α/β-hydrolase superfamily of proteins, D14 shows significant sequence similarity to RsbQ of *Bacillus subtilis*, whose function depends on binding with a small molecule (Brody et al. 2001). This raises the intriguing idea that D14 might directly interact with SLs or

downstream metabolites and function as a receptor. GIBBERELLIN INSENSITIVE DWARF1 (GID1), a receptor of gibberellin, is also a member of the α/β-hydrolase superfamily. GID1 does not possess enzymatic activity; instead, it binds to bioactive GAs and activates an associated F-box protein that degrades negative regulators and allows GA signaling to proceed (Ueguchi-Tanaka et al. 2005). In contrast with GID1, SABP2, a salicylic acid–binding protein, is an enzyme that converts methyl salicylate to salicylic acid, and included in the α/β-fold hydrolase superfamily (Kumar and Klessig 2003; Forouhar et al. 2005). D14 contains three invariant amino acids called the catalytic triad: a nucleophilic residue, an acidic residue, and histidine. The presence of this triad indicates that D14 might have an enzymatic function. To determine whether D14 acts as a component of SL signaling or as an enzyme to convert SLs to a bioactive form of branch-inhibiting hormones, further biochemical analysis of the D14 protein will be required.

In addition to the five tillering *d* mutants, *fine culm1* (*fc1*) is another increased-tillering mutant in rice. *FC1* is an ortholog of maize *TEOSINTE BRANCHED1* and encodes a member of the TCP family of transcription factors (Doebley et al. 1997; Takeda et al. 2003). The *fc1* mutant is not rescued by SL treatment and its endogenous SL levels are not significantly different from those of the wild type (Minakuchi et al. 2010). *FC1* expression is negatively regulated by cytokinins, but unaffected by SL treatment. The relationships between *FC1* and SL in rice are still unclear. In Arabidopsis, *TB1* homologs *BRANCHED1* (*BRC1*) and *BRC2* encode TCP proteins that act to inhibit shoot branching (Aguilar-Martinez et al. 2007; Martin-Trillo and Cubas 2010). *BRC1* expression is decreased in *max* mutants (Aguilar-Martinez et al. 2007) and induced by SL treatment in both wild type and *max* mutants (Mashiguchi et al. 2009), indicating that *BRC1* might function downstream of SLs in shoot branching inhibition. Thus, *FC1* and *BRC1* are thought to be integrators of multiple signaling pathways downstream of SLs.

SL production and inhibition of shoot branching in response to nutrient deficiency

Why do SLs function both as plant hormones that inhibit shoot branching and as communication signals in the rhizosphere? One possible answer is suggested by the observation that SL levels are increased in response to inorganic nutrient deficiency such as nitrogen and Pi deficiency (Lopez-Raez et al. 2008; Umehara et al. 2008; Yoneyama et al. 2007a; Yoneyama et al. 2007b). AMF can supply both Pi and nitrogen to the host plant (Govindarajulu et al. 2005). Some leguminous plants including red clover and *Lotus japonicus*, which can have a symbiotic interaction with root nodule bacteria, produce SL only in response to Pi deficiency, and other plants depend on AMF to acquire both nitrogen and Pi at times of deficiency (Table 1). There are several patterns of SL production in response to nutrient deficiency, but enhancement of SL levels in response to Pi deficiency is common among many plants.

Table 1. Strigolactone (SL) production in response to nutrient deficiency and symbiotic relations.

	Enhanced SL production[a]		Symbiosis[b]	
	Low N	Low Pi	RNB	AMF
Red clover	−	+	+	+
Lotus japonicus	−?	+	+	+
Tomato	−	+	−	+
Rice	+?	+	−	+
Sorghum	+	+	−	+
Arabidopsis	−?	+	−	−
White lupin	−	−	−	−

[a] Relative to nutrient-sufficient condition. [b] Indicates whether the plant is a host of the indicated microorganism. AMF, arbuscular mycorrhizal fungi; Pi, inorganic phosphate; RNB, root nodule bacteria.

Pi is a structural component of nucleic acids and membrane lipids and also takes part in regulatory pathways involving phospholipid-derived signaling molecules or phosphorylation reactions (Amtmann and Armengaud 2009), so whole-plant growth is generally inhibited by Pi deficiency. The presence of high endogenous SL levels under Pi deficiency implies that SLs may play an important role in efficient utilization of Pi in plants. I suggest that SL minimizes shoot branching, which reduces the nutrient needs of the plant, and maximizes the symbiotic interaction with AMF, thus facilitating the uptake of inorganic nutrients (Umehara et al. 2008).

In rice, Pi deficiency was found to reduce shoot and tiller growth (Luquet et al. 2005), but it was unknown at that time whether endogenous SL elevated by Pi deficiency would inhibit tiller bud outgrowth. Under Pi-sufficient conditions, tiller bud outgrowth was observed in 3-week-old wild-type rice seedlings, so we grew rice seedlings were grown in hydroponic culture media containing various Pi concentrations (Umehara et al. 2010). When wild-type rice seedlings were grown under Pi-deficient conditions, tiller bud outgrowth was inhibited and SL levels were elevated, but tiller bud growth was not inhibited in the *d3* and *d10* mutants (Umehara et al. 2010). When wild-type seedlings in Pi-deficient medium were transferred to Pi-sufficient medium, tiller bud outgrowth increased and endogenous SL levels in roots decreased. The decrease in SL levels was very rapid and could be detected within one day after Pi was supplied to the Pi deficient seedlings. To investigate which gene(s) in the SL pathway contributed to the Pi-induced decrease in root SL levels, the transcript levels of several *D* genes and *MAX* gene homologs were analyzed. *D10*, *D17*, and *D27* mRNA levels in roots decreased within 1 day after transfer to the

Pi-sufficient medium and showed a similar pattern of change in SL levels (Umehara et al. 2010). Among the five *MAX1* homologs (*OsMAX1*) in rice (Nelson et al. 2004), transcript levels of two (*Os01g0700900* and *Os02g0221900*) decreased within 1 day after supplying sufficient Pi, as was seen for *D10*, *D17*, and *D27*. These results suggest that down-regulation of multiple SL biosynthesis genes by Pi might decrease the SL levels in roots. In contrast, transcript levels of *D14* doubled after roots were transferred to Pi-sufficient medium, and *D3* mRNA levels were unchanged by changes in the level of Pi (Umehara et al. 2010).

Recently, similar results were reported in Arabidopsis, a non-host of AMF (Kohlen et al. 2011). When Arabidopsis was grown under Pi deficiency, SL levels increased and the outgrowth of secondary rosette branches in the wild type was strongly suppressed, but no suppression was observed in the *max* mutants. Thus, it appears that Arabidopsis became independent of AMF and acquired the ability to absorb inorganic nutrients during the evolutionary process. Furthermore, Kohlen et al. (2011) applied the SL synthetic analog GR24 to the roots of hydroponically grown Arabidopsis and later detected GR24 in the shoots. Kohlen et al. (2011) also detected natural SLs in the xylem sap of Arabidopsis. These results indicate that SLs can be transported from roots to shoots.

Altogether, these results support the idea that endogenous SL levels elevated by Pi deficiency in roots contribute to the suppression of shoot branching. However, a small wild-type hypocotyl segment grafted between a root and a shoot of a mutant such as *max3*/*ccd7* is sufficient to restore a wild-type branching habit (Booker et al. 2004). Further analysis will be required to better understand the contribution of SL biosynthesis in the shoot.

In addition, shoot branching is generally suppressed under nitrogen deficiency. However, whether SL production in response to nitrogen deficiency affects to shoot branching is still unknown. To explore the relationships between shoot branching and SL production under nitrogen deficiency, further analysis using rice *d* mutants is in progress.

Regulation of root development by SLs

Plant hormones control most of the characteristics of root systems, including primary root growth and formation of lateral roots and root hairs. Many plants respond to exogenously applied auxins by reducing primary root growth and producing a large number of lateral roots, and respond to a combination of an auxin and ethylene by increasing the density and length of root hairs (Lopez-Bucio et al. 2003). Recent reports indicate that SLs regulate root branching as well as shoot branching. The primary roots of Arabidopsis *max* mutants were shorter than those of wild-type plants, and the number of meristematic cells in the primary roots was reduced (Ruyter-Spira et al. 2011). The short primary roots of *max1* and *max4*, but not *max2*, are rescued by SL treatment. Under Pi deficiency, the endogenous SL levels in roots are elevated (Kohlen et al. 2011), but the primary root length is shortened because of reduced cell elongation, indicating that primary root growth is more strongly influenced by Pi deficiency than by SLs (Williamson et al. 2001). Exogenously applied SL can suppress lateral root development under Pi-sufficient conditions, whereas SL stimulates lateral root development in the presence of exogenous auxin (Ruyter-Spira et al. 2011). Under Pi-deficient conditions, the auxin sensitivity of root cells in *Arabidopsis* is increased (Perez-Torres et al. 2008). It is therefore likely that endogenous SL levels in roots are elevated under Pi deficiency, and stimulate lateral root development through the modulation of local auxin sensitivity. SLs affect not only lateral root development but also root hair elongation in Arabidopsis (Kapulnik et al. 2011). Exogenously applied SLs can induce root hair elongation in the wild type, and in *max3* and *max4*, but not in *max2*. Under Pi deficiency, SLs in Arabidopsis appear to increase the surface area of roots by stimulating the formation of lateral roots and root hairs, giving the plant greater capacity to absorb limited inorganic nutrients from the soil.

White lupin (*Lupinus albus*) develops cluster roots (proteoid roots), which resemble the lateral roots in Arabidopsis, in response to Pi deficiency (Johnson et al. 1994). Exogenously applied auxin can induce cluster roots even under Pi-sufficient conditions, and this rooting can be inhibited by the presence of the auxin transport inhibitors, 2,3,5-triiodobenzoic acid, and naphthylphthalamic acid (Gilbert et al. 2000). Unlike the case in Arabidopsis, SL levels do not increase in white lupin under Pi deficiency (Table 1) (Yoneyama et al. 2008). In both Arabidopsis and white lupin, auxins play an important role in the formation of lateral roots and cluster roots, but SL production during Pi deficiency is quite different between the two species, both of which are non-hosts of AMF. To fully characterize the effects of SLs on the regulation of root architecture, changes in AMF host plants such as rice and pea will need to be explored.

The relationship between SL production and AMF colonization

As described above, SLs are produced at high levels in the roots of many plant species under Pi-deficient conditions (Lopez-Raez et al. 2008; Umehara et al. 2008; Yoneyama et al. 2007a; Yoneyama et al. 2007b). SLs stimulate hyphal branching of AMF, which supply the host with essential inorganic nutrients, especially Pi

(Akiyama et al. 2005). Thus, reduction of SL levels leads to a reduction in the rate of AMF colonization. In an SL-defective mutant in pea, the percentage of root colonization was lower than that of wild-type roots under low-Pi conditions, but could be increased by exogenously applied SLs (Gomez-Roldan et al. 2008). In contrast, SL levels and AMF colonization in wild-type pea decrease under high-Pi conditions, but colonization cannot be increased by exogenous SL treatment, indicating that SLs are not the only factor involved in the regulation of AMF colonization (Balzergue et al. 2011). In tomato, symbiosis with AMF decreases SL production (Lopez-Raez et al. 2011). In this case, the host plant might have the ability to block symbiosis with AMF, limiting the amount of carbon absorbed by the fungi.

In addition, when the root system of pea is divided into two parts, with one part placed in low-Pi solution and the other in high-Pi solution but both still connected to the same shoot, both root parts show low levels of SL and AMF colonization comparable to those of roots under high-Pi conditions (Balzergue et al. 2011). This indicates that the higher Pi side of these split-root plants negatively regulated SL production on the lower Pi side through systemic signaling. Interestingly, the Pi content in the leaves of such split-root plants is higher than that in the roots. These results suggest that plants respond to Pi content in the shoot.

Perspectives—Shoot branching and leaf senescence

SL-related mutants have other phenotypes in addition to those already described. The *oresara* (*ore*) mutants in Arabidopsis have a delayed leaf senescence phenotype (Lim et al. 2007). Among the SL-related mutants in Arabidopsis, *max2* was originally isolated as a delayed leaf senescence mutant, but then renamed as *ore9* (Woo et al. 2001). Rice *d3* mutants also show a delayed leaf senescence phenotype (Yan et al. 2007). In addition, SL biosynthesis-related mutants exhibit delayed senescence symptoms (Snowden et al. 2005; our unpublished data). SL-related mutants retain green color in their leaves for a long time, which at first looks healthy for the plants. However, when leaves senesce, nutrients such as nitrogen, phosphorus, and metals are relocated to other parts of the plants such as developing seeds and leaves. Under poor nutrient conditions, the limited supply of mineral nutrients is needed for new leaf development or seed production, but SL-related mutants cannot preferentially supply nutrients to these tissues because of their delayed leaf senescence.

Taken together, the physiological roles of SLs are thought to be key for efficient nutrient allocation in plants, especially Pi acquisition (Figure 3, Table 2). Under Pi-sufficient conditions, plants absorb Pi through their roots and transport it to other tissues. SL levels remain low, and the axillary buds can grow using the Pi translocated from the roots. In contrast, SL levels in roots are highly elevated under conditions of Pi deficiency, which causes the inhibition of tiller bud outgrowth in shoots. Senescence of old leaves is activated, and nutrients such as carbon and Pi are translocated to seeds, flowers, and young tissues. Lateral roots and root hairs increase in size and number to acquire limited nutrients from the soil. SLs released into the soil enhance symbiotic interactions with AMF by stimulation of hyphal branching. AMF supply Pi to the host plants and obtain carbon from them. Root-parasitic plants also recognize the SL signals and take carbon from the host plants. Thus, a mechanism which initially appeared to be detrimental actually benefits the plant in a variety of ways.

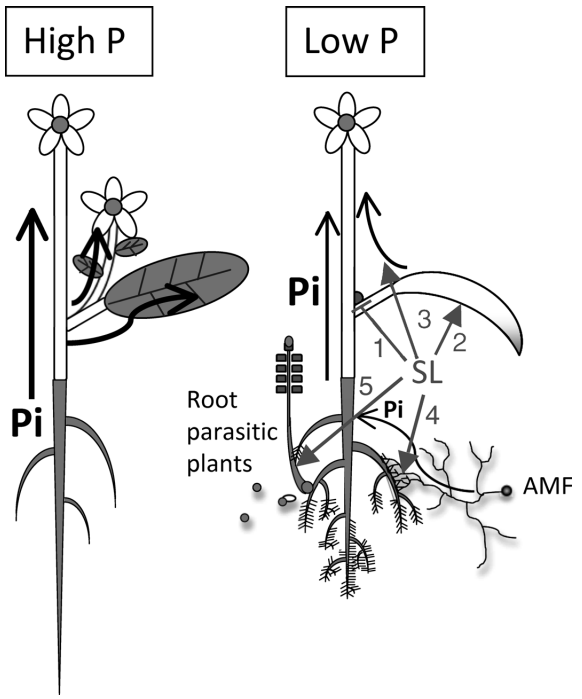

Figure 3. Model for the role of SL elevation in response to Pi deficiency. (Left) When Pi is sufficient, plants can absorb Pi through their roots. SL levels are low in roots, and outgrowth of axillary buds is not inhibited. Black arrows indicate the flow of Pi, which is distributed from the roots to the leaves, outgrowing axillary buds, and apical meristem. (Right) Under low-Pi conditions, SL levels in roots are highly elevated, inhibiting bud outgrowth in shoots (1). Senescence of old leaves is activated (2), nutrients such as Pi are translocated and concentrated within the apical meristem and young tissues (3), and supplied by AMF in soil (4). Root-parasitic plants might respond to SLs to detect potential hosts (5). Black arrows indicate the flow of Pi; gray arrows indicate the flow and action of SLs.

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