Chapter 35

Strigolactones: Crucial Cues in the Rhizosphere

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35.1 INTRODUCTION

Strigolactones (SLs) are multifunctional molecules that have been recently classified as a new class of plant hormones regulating above- and belowground plant architecture (Gómez-Roldán et al., 2008; Umehara et al., 2008; Kapulnik et al., 2011a; Ruyter-Spira et al., 2011). However, they were initially identified as signaling molecules playing a dual role in the rhizosphere. There, SLs act as host detection cues for symbiotic arbuscular mycorrhizal (AM) fungi and root parasitic plants of the family Orobanchaceae (Akiyama et al., 2005; Bouwmeester et al., 2007; López-Ráez et al., 2011b; Fig. 35.1a; see Chapters 33, 34). SLs are mainly produced in the roots, although their biosynthesis in the lower part of the shoot has also been suggested (Dun et al., 2009). They are derived from the carotenoids through sequential oxidative cleavage by carotenoid cleavage dioxygenases (CCD7 and CCD8) (Matusova et al., 2005; López-Ráez et al., 2008a), thus belonging to the apocarotenoids as the phytohormone abscisic acid (ABA) (Ohmiya, 2009; see Chapter 33). However, the biosynthetic pathway of SLs remains largely unknown, and to date, only few genes encoding enzymes involved in their biosynthesis and signaling cascade have been identified (Xie et al., 2010; Domagalska and Leyser, 2011) (see Chapters 33, 34). All natural SLs isolated and characterized so far show a similar chemical structure (Fig. 35.1b) (Rani et al., 2008; Yoneyama et al., 2009; Zwanenburg et al., 2009). The structural core of SLs consists of a tricyclic lactone (the ABC rings) connected via an enol–ether bridge to a butyrolactone group (the D-ring). In addition, they have different substituents on the AB-rings that make them different. It has been suggested that the biological activity of SLs resides in the enol–ether bridge, which can be rapidly cleaved in aqueous and/or alkaline environments, indicating their short-lived and signaling character (Yoneyama et al., 2009; Zwanenburg et al., 2009; Akiyama et al., 2010; see Chapter 34).

SLs are produced and exuded into the rhizosphere in very low amounts, being active at pico- and nano-molar concentrations (Bouwmeester et al., 2007; Yoneyama et al., 2009). They have been detected in the root exudates of a wide range of monocotyledonous and dicotyledonous plant species, and it has been shown that each plant produces a mixture of different SLs, which suggests their broad action spectrum and importance in nature (Yoneyama et al., 2008; Xie et al., 2010; see Chapter 34).

SLs or their derivates were identified in 2008 as the elusive graft transmissible branching inhibiting signal regulating aboveground plant architecture, and therefore classified as phytohormones (Bainbridge et al., 2005; Gómez-Roldán et al., 2008; Umehara et al., 2008) (Fig. 35.1a). Since then, extensive efforts are being devoted to examining SL effects on plant growth and development, broadening our understanding of their functions in plant physiology. Thus, it has been recently shown that SLs also regulate belowground architecture by altering root development, root-hair elongation and adventitious rooting, and affecting reproductive development (Kapulnik et al., 2011a; Ruyter-Spira et al., 2011;

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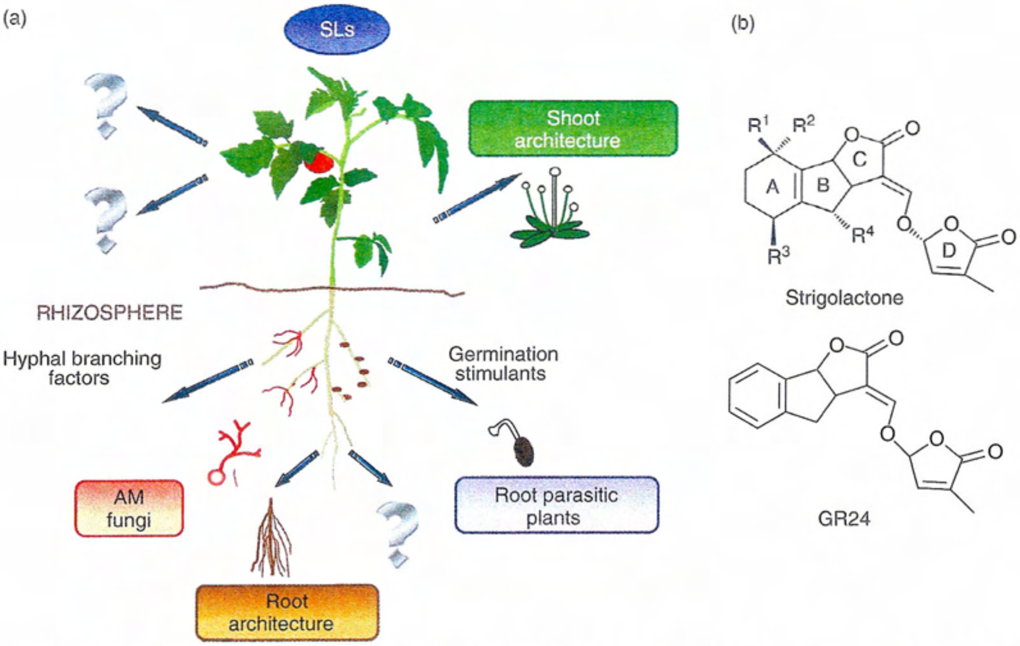

Figure 35.1 Roles of the strigolactones above- and belowground, and chemical structure. (a) Strigolactones (SLs) are plant hormones involved in plant architecture by inhibiting shoot branching and altering root system architecture. In the rhizosphere, strigolactones act as signaling molecules for symbiotic arbuscular mycorrhizal (AM) fungi and root parasitic plants. Question marks (?) indicate possible new functions for strigolactones above- and belowground. (b) General structure of natural strigolactones and the synthetic strigolactone analog GR24.

Kohlen et al., 2012; Rasmussen et al., 2012; see Chapter 33; Fig. 35.1a).

35.2 ROLE OF STRIGOLACTONES IN ROOT SYSTEM ARCHITECTURE

Root system architecture (RSA) is of great importance for plants. Roots are essential for different plant functions such as uptake of nutrients and water, anchorage in the substrate, and interaction with symbiotic organisms (Den Herder et al., 2010). RSA is altered under nutrient-deficient conditions such as phosphorous starvation. Phosphorous, which is taken up from the soil as inorganic phosphate (Pi), is one of the least available of all essential nutrients in the soil because of its low mobility. Moreover, the majority of the applied phosphorus may be fixed in the soil owing to the interaction with other ions, being unavailable to plants and resulting in phosphate depletion in the rhizosphere (Raghothama, 2000; Péret et al., 2011). Pi starvation results in an important negative impact on plant growth and development. As a consequence, plants have evolved sophisticated mechanisms to flexibly adapt themselves to overcome this kind of stress. Such adaptation takes place through a combination of growth and developmental and metabolic changes, resulting in an attenuated shoot development, a shorter primary root, more and longer lateral roots, and a greater density of root hairs, thus expanding the exploratory capacity of the root system (Sánchez-Calderón et al., 2005; Desnos, 2008; Rouached et al., 2010). These responses are regulated through a complex network of interconnected signaling pathways in which plant hormones, particularly SLs, play a key role (Fig. 35.1a) (Kapulnik et al., 2011a; Ruyter-Spira et al., 2011). Under Pi-sufficient conditions, SLs seem to negatively regulate lateral root formation. However, upon Pi starvation they promote lateral root development, whereas a negative impact was observed on the primary root (Ruyter-Spira et al., 2011; see also Chapter 33) (Fig. 35.2). A stimulatory effect of SLs in root hairs has also been suggested, as the application of the synthetic SL analog GR24 (Fig. 35.1b) induced root-hair elongation (Kapulnik et al., 2011a) (Fig. 35.2). According to this positive effect on root development under limited Pi conditions, SL biosynthesis is promoted under such stress condition (Yoneyama et al., 2007a; Yoneyama et al., 2007b; López-Ráez et al., 2008a). Consequently, it has been suggested that SLs play a pivotal role in plants as modulators of the coordinated development of roots and shoots in response to Pi starvation (Ruyter-Spira et al., 2011; see also Chapter 33).

35.2.1 Hormone Cross-Talk in RSA

Regulation of RSA by SLs seems to be mediated through cross-communication with other plant hormones (Fig. 35.2). It is well established that SLs interact with auxins through connected feedback loops, in which SLs inhibit auxin transport, and therefore shoot branching under nutrient-deficient conditions (reviewed

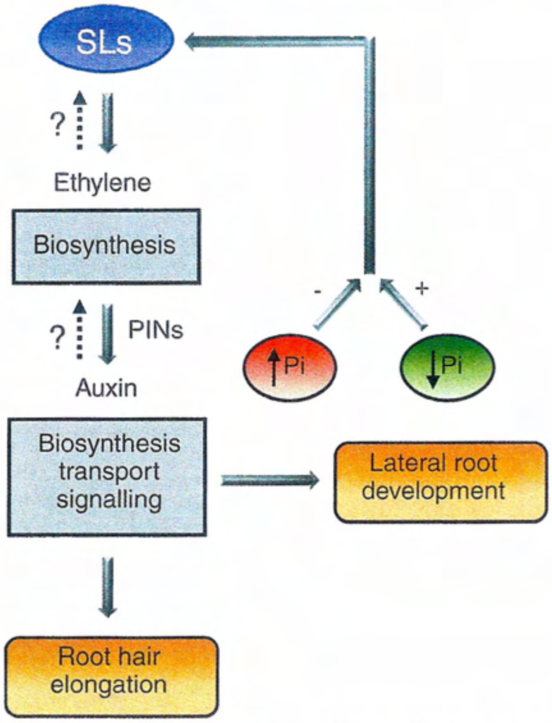

Figure 35.2 Proposed model for the role of strigolactones in root system architecture. SLs alter lateral root development and root-hair elongation, although a differential effect can be observed depending on phosphorous (Pi) content (and auxin levels) in the roots. Root system architecture regulation by strigolactones requires a cross-talk with ethylene and auxin signaling pathways.

in Domagalska and Leyser, 2011; see Chapter 33). A similar mechanism has been proposed for the regulation of RSA, which is dependent on the auxin status and/or sensitivity of the plant (Kapulnik et al., 2011a; Ruyter-Spira et al., 2011). Local auxin levels in the primary root tip are regulated by the combined action of the PIN auxin efflux transporters (Billou et al., 2005). In this scenario, SLs would act by inhibiting *PIN* expression, thus altering auxin allocation and affecting root development (Fig. 35.2). Ethylene is another important player in RSA. It has been proposed that SLs induce ethylene biosynthesis, which in turn promotes auxin production, transport, and signaling in the roots (Stepanova and Alonso, 2009). Therefore, SL and ethylene pathways would interact together in regulating root-hair elongation via modulation of auxin flux (Kapulnik et al., 2011b; see Chapter 33) (Fig. 35.2). As SLs are involved in other events within the plant, Kapulnik and coworkers suggested that this intimate cross-talk among the SLs, auxin, and ethylene may be valid for other SL-mediated processes.

In addition to increasing the root system exploratory capacity in the soil, plants have alternative strategies to cope with nutrient (mainly Pi) and water deficiencies. One of them is through the establishment of symbiosis with AM fungi (Péret et al., 2011), in which SLs also play a crucial role (see Chapter 43).

35.3 STRIGOLACTONES ARE SIGNALING MOLECULES IN THE RHIZOSPHERE

The rhizosphere is the narrow soil zone surrounding plant roots and constitutes a very dynamic environment, harboring many different organisms (Bais et al., 2006; Badri et al., 2009). Plants continuously communicate with these organisms through the production and release of a large variety of signaling compounds into the rhizosphere (Bais et al., 2006; Badri et al., 2009; see Chapters 11, 12). They use these metabolites not only to defend themselves against soil-borne pathogens, which can adversely affect plant growth and fitness, but also to establish mutualistic associations with beneficial soil micro-organisms. Despite their important regulatory functions as plant hormones above- and belowground, SLs were first identified as signaling molecules in the rhizosphere. They are produced and exuded by the plant roots in very tiny amounts. In agreement with their function as signaling molecules, they are short-lived in watery environments and in alkaline soils (Bouwmeester et al., 2007; Yoneyama et al., 2009; Zwanenburg et al., 2009). In the rhizosphere they play a pivotal role acting as host detection signals for symbiotic AM fungi and for root parasitic plants of the Orobanchaceae (Akiyama et al., 2005; Bouwmeester et al., 2007; López-Ráez et al., 2011b; see also Chapter 33) (Fig. 35.1a). More recently, it has been shown that SLs are also regulators of root nodulation by rhizobia, another beneficial group of micro-organisms forming mutualistic symbiosis with legumes (see Chapter 44) (Soto et al., 2010; Foo and Davies, 2011). Unlike AM symbiosis, here SLs would not act as host detection cues (Soto et al., 2010), but they would be required for optimal nodule number (Foo and Davies, 2011). Interestingly, no response after GR24 application was observed in other beneficial fungal species such as ectomycorrhizal fungi, *Trichoderma*, and *Piriformospora indica* nor in soil-borne pathogens such as *Rhizoctonia solani*, *Fusarium oxysporum*, or *Verticillium dahliae* (Steinkellner et al., 2007), suggesting that SLs are rather specific signaling molecules. Altogether, experimental evidence illustrates the multifunctionality as well as the biological and ecological importance of SLs in the rhizosphere.

35.4 ROLE OF STRIGOLACTONES IN AM SYMBIOSIS: A CRY FOR HELP

AM symbiosis in one of the best studied beneficial plant–microorganism associations (Barea et al., 2005; Parniske, 2008; Smith and Read, 2008; Bonfante and Genre, 2010) (see Chapters 4 and 43). It is a mutualistic association between fungi of the phylum Glomeromycota and the vast majority of land plants, including most agricultural and horticultural crop species (Parniske, 2008;

Smith and Read, 2008). AM fungi are obligate biotrophs and depend entirely on the host plant to obtain carbon and complete their life cycle. They colonize the root cortex of the host plant and form specialized tree-like structures called *arbuscules*, which are involved in nutrient exchange between the two partners. In the soil surrounding the roots, AM symbiosis gives rise to the formation of hyphal networks that facilitate the uptake of nutrients beyond the area of nutrient depletion, thereby assisting the plant in the acquisition of mineral nutrients and water (Harrison, 2005; Parniske, 2008; see Chapter 43).

AM symbiosis establishment and functioning requires a high degree of coordination between the host plant and the AM fungi based on a finely regulated molecular dialogue that orchestrates complex symbiotic programmes (Paszkowski, 2006; Hause et al., 2007; Requena et al., 2007; López-Ráez et al., 2010). This molecular communication between the two partners starts with the production and exudation into the rhizosphere of SLs by the host plant. SLs are perceived by the AM fungi, inducing extensive hyphal branching (Akiyama et al., 2005; Besserer et al., 2006; Parniske, 2008) (Fig. 35.3), increasing the probability to contact the root and establish symbiosis. Spores of AM fungi can germinate spontaneously and undergo an initial asymbiotic stage of hyphal growth from the germ tube. Asymbiotic growth can be maintained for 1 or 2 weeks; but if during this period hyphae do not find a host to be colonized, their growth is arrested. On the contrary, if a partner producing SLs is nearby, hyphae grow and ramify intensively (Bouwmeester et al., 2007). It has been suggested that SLs may also act as the chemoattractant that directs the growth of the AM hyphae to the roots (Sbrana and Giovannetti, 2005). In addition, a Myc factor (by analogy with the Nod factors) is produced by the metabolically active fungus. This fungal-derived cue induces molecular responses in the host plant required for a successful colonization (Bucher et al., 2009; see Chapters 43, 45). The chemical nature of the elusive Myc factor remained unknown for a long time. However, it has been recently shown that AM fungi produce and secrete a mixture of sulfated and nonsulfated simple lipochitooligosaccharides, which have structural similarities with rhizobial Nod factors (Maillet et al., 2011). Despite the importance of SLs in the initiation of AM symbiosis, it is unknown whether they also play a role in subsequent steps of the symbiosis.

35.4.1 Biological Relevance of Strigolactones in the AM Symbiosis: Phosphate Availability

As mentioned earlier, the availability of Pi in the soil is very limited in many areas of the world, limiting plant growth and fitness (Rouached et al., 2010; Péret et al., 2011). Pi starvation induces a series of adaptive changes in the plant to increase the exploratory capacity of the root system (Sánchez-Calderón et al., 2005; Desnos, 2008; Rouached et al., 2010). In addition, Pi limitation induces alternative strategies to cope with such deficiency in the soil, including the establishment of AM symbiosis (Péret et al., 2011). In agreement with the important role of AM fungi in the acquisition of mineral nutrients, and specially Pi, it was observed that root exudates produced by plants grown under Pi-limited conditions

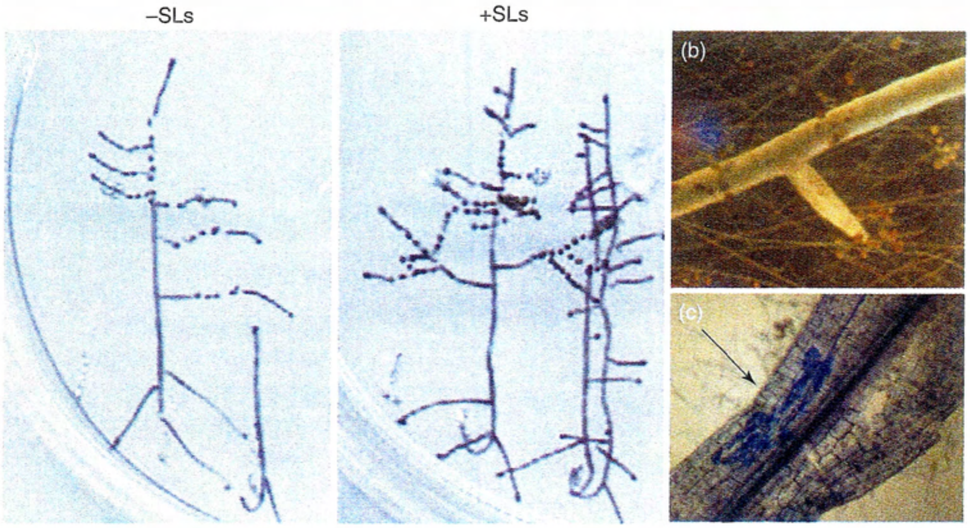

Figure 35.3 Role of strigolactones as signaling molecules in arbuscular mycorrhizal symbiosis. (a) SLs are hyphal branching factors for germinating spores of arbuscular mycorrhizal fungi. Effect of tomato strigolactones on hyphal branching of *Gigaspora margarita* germinating spores. (b) Spores and hyphal branching of *Glomus mosseae* in the vicinity of a tomato root. (c) Tomato root colonized by the AM fungus *G. mosseae* showing arbuscules within the root cortex.

were more stimulatory in AM fungi hyphal branching than exudates produced under sufficient Pi nutrition (Nagahashi and Douds, 2004). Accordingly, a significant increase in the production and exudation of SLs by the roots under Pi deficiency have been extensively reported in different plant species such as sorghum, red clover, rice, pea, Arabidopsis, and tomato (Yoneyama et al., 2007a; Yoneyama et al., 2007b; López-Ráez et al., 2008a; Umehara et al., 2010; Balzergue et al., 2011; Kohlen et al., 2011). Therefore, it is generally accepted that under these stressful conditions, the host plant increases the production and exudation of SLs into the rhizosphere to promote AM fungal development and symbiosis establishment, thus acting as a "cry for help" (see also Chapter 33).

On the other hand, it was reported that AM colonization itself influences RSA of the host root (Harrison, 2005; Olah et al., 2005; Gutjahr et al., 2009). An increase in lateral root number and length, which are generally the most highly colonized roots by AM fungi, has been shown for a number of species during AM symbiosis (Harrison, 2005; Gutjahr et al. 2009). It seems that AM fungi trigger alterations in root architecture to create the most favored sites of interaction with the host plant. Interestingly, this AM symbiosis-induced RSA modulation takes place even before physical contact between the two partners. It was shown that in Medicago, perception of a diffusible signal released by AM fungi during the presymbiotic stage was sufficient to induce lateral root formation (Olah et al., 2005), and a similar mechanism has been proposed in rice (Gutjahr et al., 2009). Accordingly, Maillet and coworkers showed that the Myc factors produced by metabolically active AM fungus are not only symbiotic signals that stimulate AM establishment but also plant growth regulators affecting root development (Maillet et al., 2011; see Chapters 43, 45).

35.5 STRIGOLACTONES ARE GERMINATION STIMULANTS OF ROOT PARASITIC PLANTS

Long before the discovery of their function as plant hormones and AM hyphal branching signals, SLs were described as germination stimulants of seeds from root parasitic plants of the family Orobanchaceae, including the genera *Striga* (witchweeds), *Orobanche*, and *Phelipanche* (broomrapes) (Figs. 35.1a and 35.4a) (Cook et al., 1972; Bouwmeester et al., 2003). These parasitic weeds are some of the most damaging agricultural pests, affecting important crops such as rice, maize, sorghum, legumes, tobacco, sunflower, and tomato worldwide, and causing devastating losses (up to 70%) in crop yields (Gressel et al., 2004; Joel et al., 2007; Parker, 2009). Root parasitic plants are obligate parasites that need to attach to a plant host to complete their life cycle. Upon attachment, they acquire nutrients and water from their host through a specialized organ called *haustorium*, negatively affecting plant fitness and crop yield (Estabrook and Yoder, 1998;

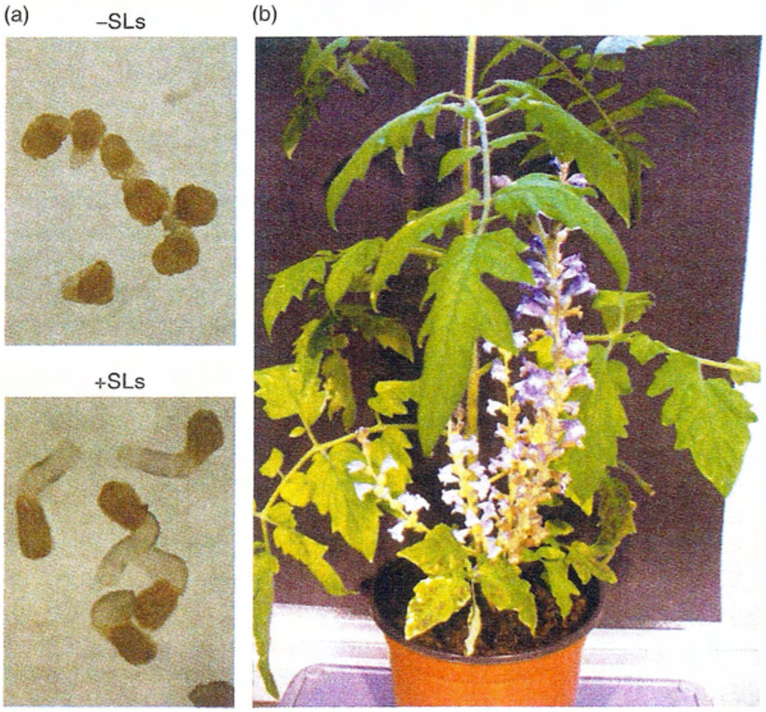

Figure 35.4 Role of strigolactones as signaling molecules for root parasitic plants. Strigolactones (SLs) are germination stimulants of seeds of root parasitic plants of the Orobanchaceae. (a) Germination of *Phelipanche ramosa* seeds after application of tomato strigolactones. (b) *P. ramosa* growing on tomato plants (photograph taken by Wouter Kohlen).

Bouwmeester et al., 2003; see Chapter 33). Although these parasitic weeds parasitize different hosts in different parts of the world, their lifecycles are broadly similar and include seed germination in response to a host root stimulus—SLs—(Fig. 35.4a); radicle growth toward the host root; and attachment and penetration through the haustorium (Bouwmeester et al., 2003; López-Ráez et al., 2009). After emergence from the soil, parasitic plants will flower (Fig. 35.4b) and produce new ripe seeds that are scattered, increasing the seed bank (Bouwmeester et al., 2003; López-Ráez et al., 2009).

A wide number of approaches such as hand weeding, crop rotation, sanitation, fumigation, solarisation, and improvement of soil fertility are being used to control these root parasites without the desirable success (Joel et al., 2007; Rispail et al., 2007; Scholes and Press 2008), and the most efficient control method—fumigation—is environmentally hazardous. Therefore, new methods for a more effective control against these agricultural pests are required.

35.6 CONTROL STRATEGIES AGAINST ROOT PARASITIC PLANTS BASED ON REDUCED PRODUCTION OF STRIGOLACTONES

Root parasitic weeds are difficult to control because most of their life cycle occurs belowground. Moreover, they exert the greatest damage prior to their emergence aboveground. Thus, new control strategies for pest management should focus on the initial steps of infection, and particularly on those related to seed germination, which is triggered by SLs (Bouwmeester et al., 2003; López-Ráez et al., 2009; Cardoso et al., 2011).

Breeding for cultivars with low SL production and/or exudation could be an interesting control strategy against these parasitic weeds. It has been shown that the tomato mutant *Sl-ORT1*, unable to produce and secrete SLs, was more resistant to the infection by different *Orobanche* and *Phelipanche* species than the corresponding wild type (Dor et al., 2011). In agreement with this observation, the tomato mutant *high pigment-2* (*hp-*2^{dg}), an important mutant line marketed as lycopene-rich tomato (LRT), was less susceptible in the field to *Phelipanche aegyptiaca* infection than the corresponding wild type. In addition, we showed that this reduced susceptibility correlated with a lower SL production by the mutant (López-Ráez et al., 2008b). Genetic variation for low germination stimulant production has also been described in other important crops such as sorghum and rice (Ejeta, 2007; Jamil et al., 2011). In rice, this lower SL production was associated with a reduced germination, and attachment and emergence of *Striga hermonthica* both *in vitro* and *in situ* (Jamil et al., 2011). In the case of sorghum, this genetic variation was used to breed for *Striga*-resistant varieties and introduce them into high yielding cultivars in several African countries (Ejeta, 2007). Thus, selecting programs to breed for cultivars with low SL production seems to be a valid and promising strategy for root parasitic plant management.

Another attractive approach to obtain plants with a reduced production of SLs is through genetic modifications targeting one or more of the rate-limiting genes from the SL biosynthetic pathway. Indeed, *ccd7* and *ccd8* mutants of several plant species show a reduced production of SLs (Gómez-Roldán et al., 2008; Umehara et al., 2008; Drummond et al., 2009; Ledger et al., 2010; Vogel et al., 2010; Kohlen et al., 2012). Genetic engineering using RNAi technology on the tomato gene CCD7 induced a significant reduction in SLs, which correlated with a lower germination of *Phelipanche ramosa* seeds (Vogel et al., 2010). Similarly, we have recently shown that by silencing the *SlCCD8* gene in tomato, a mild reduction in SL biosynthesis strongly reduced root parasitism by *P. ramosa* without excessively compromising AM symbiosis (Kohlen et al., 2012). Therefore, molecular biotechnology targeting key SL biosynthetic genes is a promising and exciting control strategy. However, the limited knowledge on SL biosynthesis and signaling pathways (see Chapter 33), as well as their multifunctional properties, render the application of these strategies in the field at short-term difficult.

35.7 USE OF AM SYMBIOSIS AS A BIOCONTROL STRATEGY

The dual role of SLs in the rhizosphere as signaling molecules for AM fungi and root parasitic plants points to potential interactions between the two biosystems. In this sense, it was shown that AM fungal inoculation of the cereal crops maize and sorghum led to a decrease in *S. hermonthica* infection in the field (Lendzemo et al., 2005). It was proposed that this reduced infection was caused, at least partially, by a reduction in the production of SLs in mycorrhizal plants (Lendzemo et al., 2007). Similarly, AM colonization in pea induced less germination of seeds of *Orobanche* and *Phelipanche* species compared to noncolonized plants (Fernández-Aparicio et al., 2010). We have recently shown that AM colonization in tomato plants also leads to a reduced germination of *P. ramosa* seeds. Moreover, we demonstrated that such reduction was caused by a decrease in the production of SLs and that this AM-associated decrease in SLs depends on a fully established mycorrhizal association (López-Ráez et al., 2011a). However, the mechanisms regulating SL production during AM symbiosis remain unknown.

The results with maize, sorghum, pea, and tomato suggest that the reduction in SL production and/or exudation induced by AM symbiosis is conserved across the plant kingdom. Because AM fungi colonize roots of most agricultural and horticultural species, and are widely distributed around the globe, AM symbiosis could be used as an environmentally friendly biocontrol strategy for economically important crops that suffer from these root parasitic weeds. Interestingly, these crops would also take advantage of all the other well-known benefits of the symbiosis, such as the positive effect on plant fitness and higher tolerance/resistance against biotic and abiotic stresses. However, as SLs are AM hyphal branching factors, the consequences on the AM fungal community, as well as in other micro-organisms present in the soil, should be analyzed. In addition, SLs are also involved in plant architecture. Therefore, the effect of reducing SL production and/or exudation should be carefully evaluated before following these approaches to avoid possible unwanted side-effects on plant physiology.

35.8 STRIGOLACTONE SPECIFICITY

As aforementioned, SLs are multifunctional molecules playing different roles both within the plant and in the interactions with other organisms in the rhizosphere. There is multiple evidence showing that plants produce a mixture of different SLs and that these mixtures may be different even among cultivars within the same plant species (Yoneyama et al., 2009; Xie et al., 2010; see Chapter 34). However, there is practically no information regarding the structural requirements for the different functions. Extensive studies on the structure–activity relationships of SLs have revealed that the CD-ring moiety (Fig. 35.1b) is the essential structure for the activity (Zwanenburg et al., 2009; Akiyama et al., 2010). In general, structural requirements for AM hyphal branching activity are very similar to those for germination stimulation of root parasitic plant seeds in all natural SLs identified so far. However, the activity intensity varies depending on the substitutions on the AB-rings (Fig. 35.1b) (Yoneyama et al., 2009; Akiyama et al., 2010). Interestingly, in the case of AM fungi, it was shown that the different SLs not only differed in the active concentration but also in the hyphal branching pattern induced (Akiyama et al., 2010). A role of SLs in host specificity regarding seed germination has also been shown in root parasitic plants of the broomrape genera *Orobanche* and *Phelipanche* (Fernández-Aparicio et al., 2011). The authors reported that weedy broomrapes species were less specialized in germination requirements than nonweedy species.

Altogether, these findings suggest that the different SLs produced by a plant might be involved in different signaling processes in the rhizosphere and probably also within the plant (see Chapter 33). A better understanding of the specificity and biological activity of the individual SLs seems essential to develop plants *à la carte* that could better cope with parasitism without compromising AM symbiosis or affecting plant physiology.

35.9 CONCLUSIONS

SLs are a new class of plant hormones regulating plant architecture and development that were originally identified as signaling molecules in the rhizosphere. Nevertheless, despite their importance in plant fitness, little attention has been devoted to them, probably because they can be analyzed only by highly sensitive analytical methods. Their multifunctional character makes SLs key molecules in both plant physiology and ecology, thus opening multiple potential biotechnological applications in agriculture. Unraveling new roles and functions for the different SLs is definitively exciting and promising. In addition, further research on their biosynthesis and regulatory mechanisms is required to manipulate their production on demand.

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