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Strigolactone Signaling in Plants

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<http://dx.doi.org/10.5772/intechopen.68497>

Abstract

Strigolactones (SLs) are a new group of recently described phytohormones. They were found to be involved in the communication between plant roots and symbiotic bacteria or fungi, but also in the interactions between roots of host plants and germinating seeds of parasitic plants. Over the years, however, it has become clear that SLs play a regulatory role in many aspects of plant growth and development. Extensive studies on plant model species *Arabidopsis thaliana* L. and *Oryza sativa* L. have uncovered the molecular mechanisms of SL biosynthesis and signaling. In some aspects, the SL perception and signaling correspond to the already known mechanisms described for other phytohormones, but in other points, they seem to be unique in the plant kingdom. This chapter summarizes the recent discoveries in the signal transduction pathway of SLs and describes the model of SL perception and signaling.

Keywords: strigolactones (SLs), perception, signaling, degradation, SCF complex, receptor, repressor

1. Introduction

Strigolactones (SLs) are a class of carotenoid derivatives. They were first discovered in root exudates of cotton and found germinating to be potent stimulants for seed germination of the parasitic plant *Striga lutea* Lour. (witchweed) [1], for review, see [2]. Why plants should produce and secrete a signal molecule that is recognized by its parasites was revealed much later when SLs were identified as signal molecules involved in the establishment and maintenance of interactions with arbuscular mycorrhizal fungi (AMF) [3] and N-fixing bacteria [4]. This also marked the time when SLs were classified as a new class of phytohormones, based on the semi-dwarf and shoot-branched mutants of

Arabidopsis thaliana L. and *Oryza sativa* L. [5, 6]. In the following years, it was discovered that SLs are involved in additional aspects of plant development (**Figure 1**), that is, in the regulation of root system development by promotion of primary roots (PRs) elongation and inhibition of adventitious roots (ARs) formation. The SL effect on lateral roots (LRs) development was found to depend on the availability of nutrients, especially phosphorous (P) and nitrogen (N). Under optimal growth conditions, SLs will inhibit the elongation of LRs, but when plants are exposed to starvation stress SLs induce LR growth, for review see [7]. It thus became clear that SLs play a role in the complex plant response to nutrient stresses. Under both P and N deficiency conditions, the synthesis of SLs is increased and larger amounts of this hormone are secreted into the soil, probably to promote the symbiotic relations with AMF and bacteria. The elevated levels of SLs also influence the plant phenotype by suppressing shoot growth and stimulating root development, thus adapting the plant to starvation conditions, for review see [8, 9]. The contribution of SLs in plant adaptation to the other stresses such as drought is

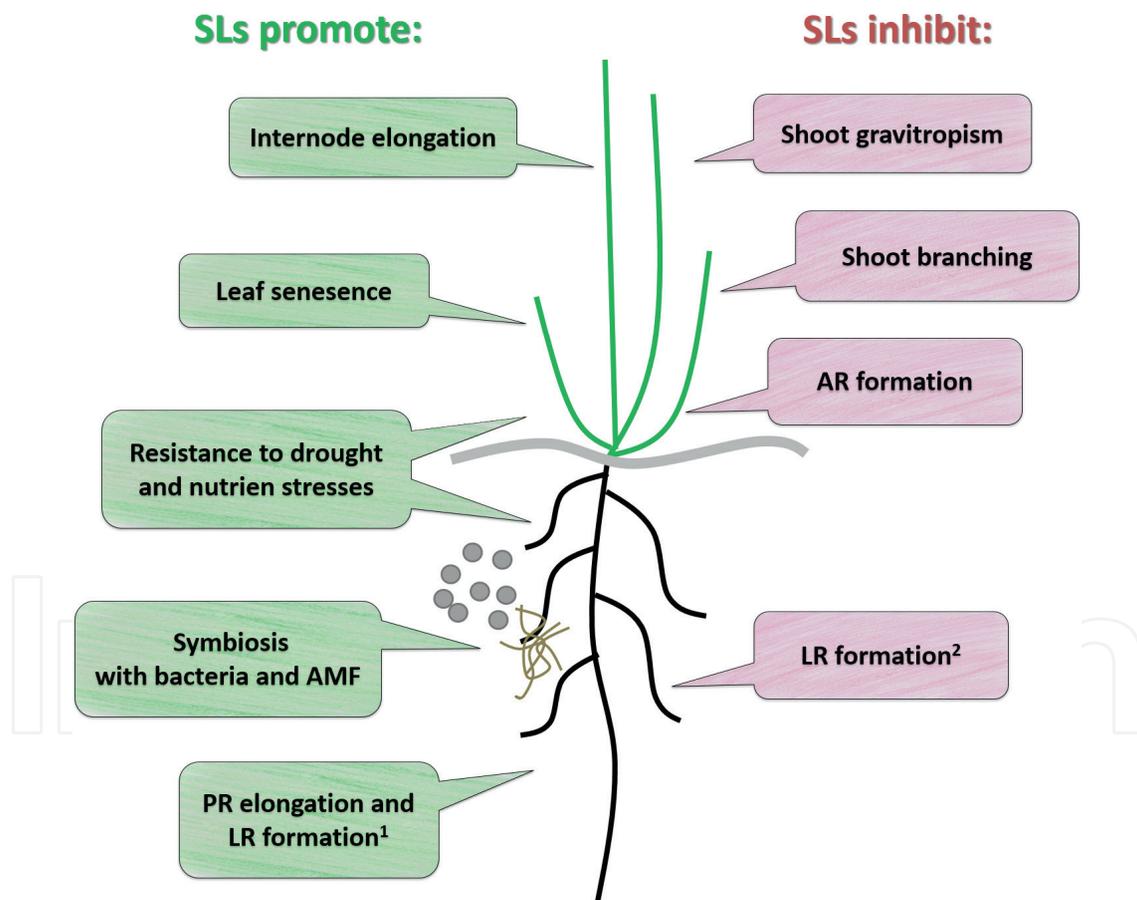


Figure 1. SLs regulate plant development by the promotion of internode elongation, leaf senescence, elongation of primary root (PR) and lateral root (LR)¹ or inhibition of shoot branching, shoot gravitropism, and formation of adventitious root (AR) and LR². Additionally, SLs promote the symbiosis with arbuscular mycorrhizal fungi (AMF) and N-fixing bacteria, and play a role in plant adaptation to drought and nutrient stresses. ¹SLs promote LR elongation under starvation stress and ²inhibit LR elongation under optimal growth conditions.

unclear. According to some recent studies, SL mutants of *A. thaliana* are more sensitive to drought stress in comparison to the wild-type plants [10, 11]. The results were not conclusive, however. In one study, the SL-signaling mutants, *max2-1* and *max2-2*, were found to be hypersensitive to drought, whereas the SL biosynthesis mutants, *max1*, *max3* and *max4*, were not [10]. In a second study, both groups of mutants, defective in SL-biosynthesis (*max3-11*, *max4-7*) or SL signaling (*max2-3*), were more sensitive to drought [11]. Additional studies on *Lotus japonicas* L. [12] and *Solanum lycopersicum* L. [13, 14] confirmed that SLs together with abscisic acid (ABA) play a role in plant adaptation to the limited water conditions. In response to drought, tomato plants show decreased SL biosynthesis in the roots but increased biosynthesis in the shoots [14]. Results like these feed the impression that SLs may well present a broad-spectrum class of phytohormones (**Figure 1**). Based on an *in silico* analysis of the genes involved in SL biosynthesis in *A. thaliana* and rice, it has been postulated that SLs may also participate in pathogen defense mechanisms and plant responses to wounding, cold stress or flooding [15]. Until now, the experimental evidences have confirmed the role of SLs in plant resistance to bacterial and fungal pathogens, reviewed by Marzec [16].

Up to now, more than 20 naturally occurring SLs, synthesized from the carlactone precursor, have been identified in the plant kingdom [17]. They share a similar structure, composed of a tricyclic lactone (ABC rings) connected to a butenolide group (D ring) by an enol-ether bond (**Figure 2**). SLs are divided into two groups based on the stereochemical differences at the junctions between B and C rings: the orobanchol group with an α -oriented C ring and the strigol group with a β -oriented C ring (**Figure 2**) [18]. SLs are mainly produced in roots and transported to the shoot *via* specific transporters [19]. Alternatively, they might be also produced in the above-ground parts of plants [20]. SLs biosynthesis started in plastids with the conversion of all-*trans*- β -carotene into 9-*cis*- β -carotene by the carotenoid isomerase Dwarf27 (D27), an iron-containing protein [21–23]. The following stages of SLs biosynthesis are conducted by the carotenoid cleavage dioxygenases (CCDs) CCD7 [24, 25] and CCD8 [26, 27] and first involve the transformation of 9-*cis*- β -carotene into 9-*cis*- β -apo-10'-carotenal which is subsequently converted into carlactone [23]. Carlactone, a precursor for all known SLs, has no activity attributed to SLs, until it is converted into carlatonic acid by more axillary growth (MAX1) that belongs to the cytochrome P450 family [23]. The final methylation of carlatonic acid is mediated by an as-yet unknown enzyme [28] (**Figure 3**).

Whereas the *A. thaliana* genome contains only one MAX1 gene, different rice varieties were characterized from two to five MAX1 homologs, which are involved in the synthesis of different SLs [29]. Still the open question remains if *A. thaliana* MAX1 mediates in the production of all SLs or only in the specific ones. The enzyme involved in the subsequent steps of SLs specialization, lateral branching oxidoreductase (LBO), converts methylated carlatonic acid into an as-yet unidentified strigolactone-like compound [30]. Characterization of the product of LBO activity and identification of additional enzymes involved in the last stages of SLs biosynthesis will be essential to compare the production pathways of this hormone in mono- and dicot species.

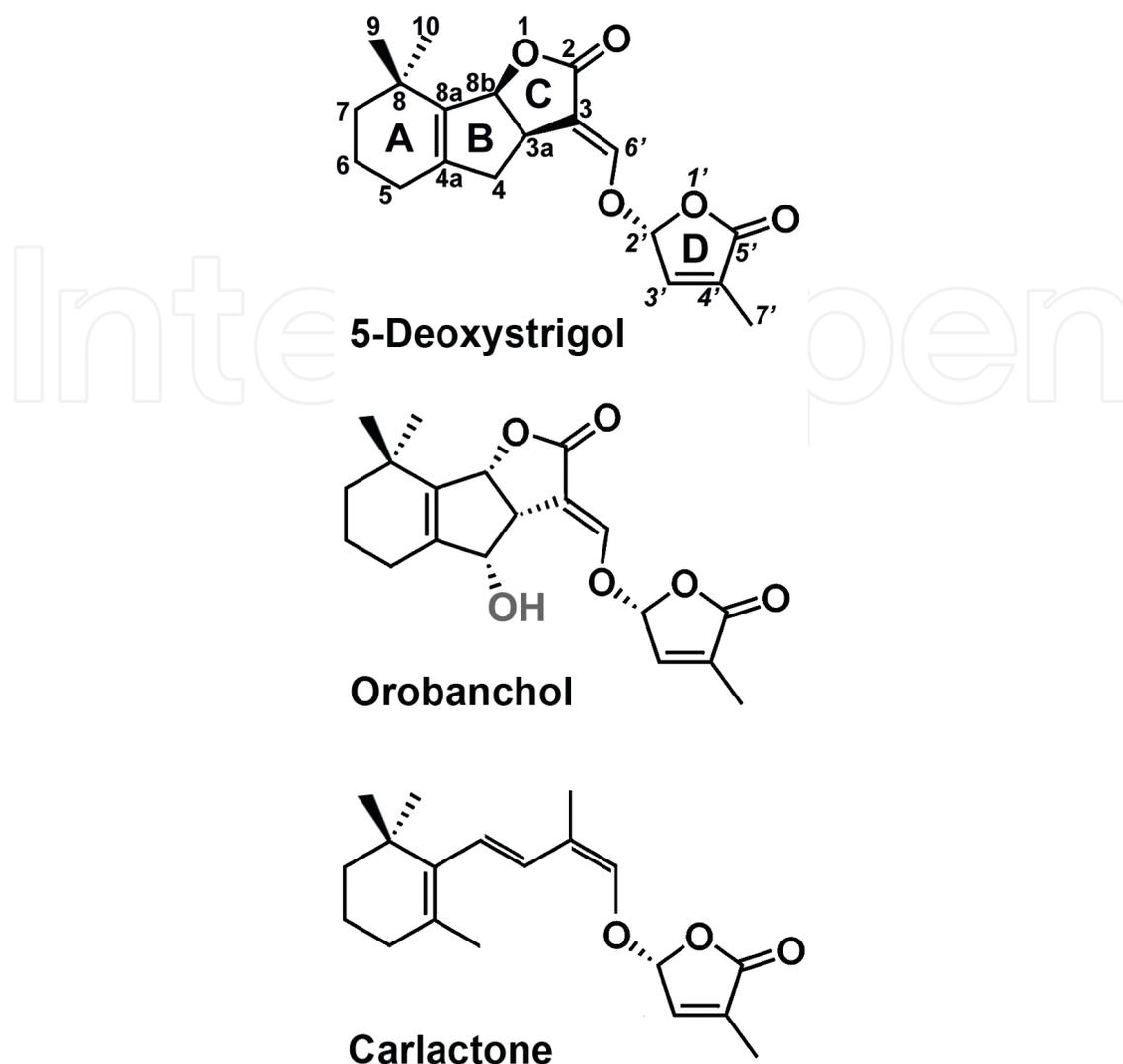


Figure 2. Structures of SL precursor carlactone and SLs represent two main stereochemical groups: strigol-type SL with a β -oriented C ring – 5-deoxystrigol and orobanchol type with an α -oriented C ring – orobanchol. Differences are present at the 8b and 3a positions between B and C rings.

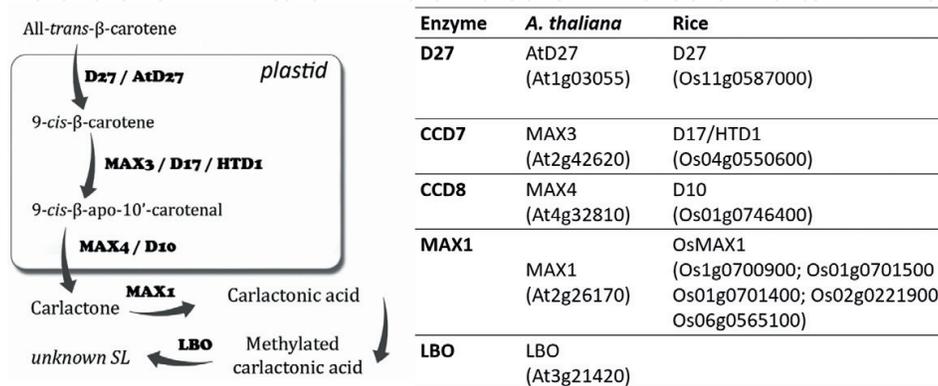


Figure 3. Scheme of SLs biosynthesis and a list of enzymes involved in this process. Descriptions are given in the text.

2. Perception of SLs

The Dwarf14 (D14) protein is the only known receptor of SLs. This protein was originally identified in rice [31] and later on found in other species, such as *A. thaliana* (AtD14) [32], petunia (DAD2) [33], *Hordeum vulgare* L. (HvD14) [34] or *Populus trichocarpa* Torr. & A. Gray (PtD14) [35]. All D14 proteins belong to the α/β -hydrolase family and exhibit enzymatic activity, which is unusual for hormone receptors. D14 proteins can not only bind SL molecule but also hydrolyze the ligand, which is crucial for the next steps of the signaling cascade [36]. The entry to the active site pocket of D14 is surrounded by four helices, and mutation in which the size of this aperture is reduced causes an insensitivity to SLs (Figure 4) [34]. When a ligand is docked to the receptor, a nucleophilic attack separates the ABC part of the SL molecule from the D ring [37]. The hydrolyze activity of D14 depends on the presence of a highly conserved catalytic Ser/His/Asp triad. Replacement of these amino acids results in a loss of D14 activity and sensitivity to SLs [33]. It was also shown

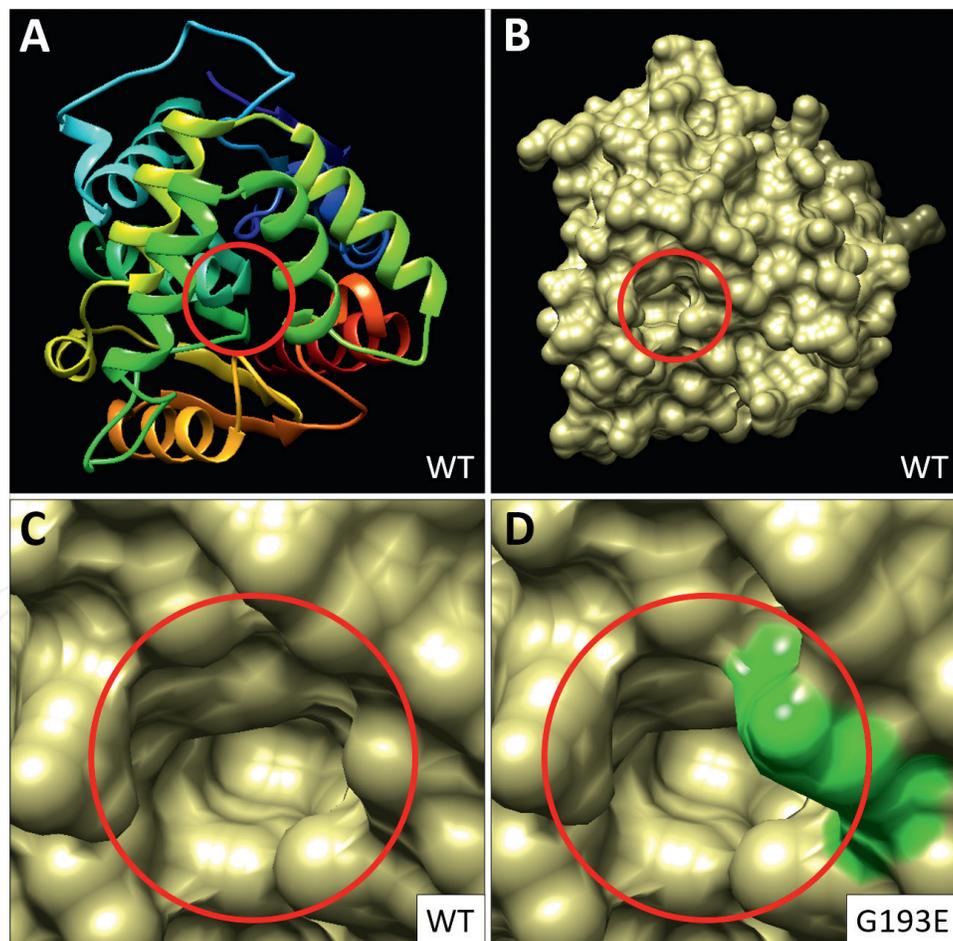


Figure 4. Visualization of SL receptor HvD14. (A) Structure of HvD14. Circle indicates entry to the active site pocket, surrounded by four helices. (B) 3D structure visualization of HvD14. (C) Detailed view of the entry to the active site pocket of the wild-type protein and (D) mutated protein with smaller aperture, resulting in insensitivity to SLs.

that serine from the catalytic triad is involved in docking of SLs into D14 [38]. With an average rate of 0.3 molecule/min, D14-mediated hydrolysis of SLs into non-active derivatives is very slow, indicating that this is not the main function of D14 [33, 36]. Crystallographic analysis indicates that the degradation of SL molecules by D14 brings about a change in receptor conformation, which is necessary for the interaction between D14 and other components from SL-signaling pathway [39]. After nucleophilic attack and release of the ABC part, the D ring remains within the receptor that now assumes a “closed” state unable to bind further molecules, reviewed by Waters [7]. This change in conformation destabilizes the D14 receptor, thus initiating its own degradation [40] (**Figure 5**). This is the first known case where hormone hydrolysis by a receptor causes the degradation receptor as well.

Since SLs are involved in the regulation of the development of different organs, it was expected that D14 will be located in almost all plant tissues. Expression analysis of *Atd14* in *A. thaliana*, however, showed markedly higher levels in vascular tissues of roots and shoots [41]. The discrepancy between expression and distribution pattern of the D14 protein was explained, when the intercellular transport of D14 *via* the phloem was uncovered. This transport is SL-independent and also in the SL biosynthesis mutants it was observed that D14 was delivered into axillary buds [42] leaving the question by what mechanism D14 is transported and how it is been used by plants to regulate the development and adaptation to different stresses.

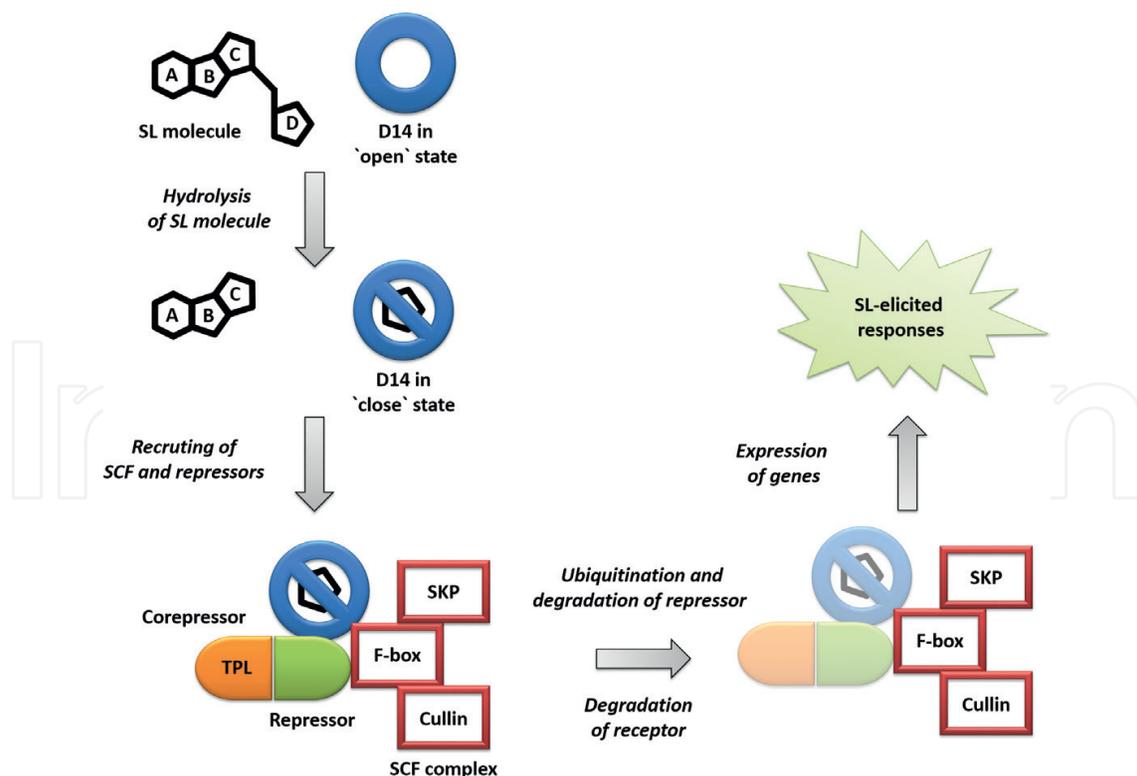


Figure 5. Overview of SL-signaling cascade including hydrolysis of SL molecules by receptor and change of the receptor conformation, which allows the interaction with the SCF complex and repressor. Ubiquitination of the repressor, mediated by the SCF complex, results in the expression of genes from the TCP family.

It has to be highlighted that D14 protein is specific receptor only for SLs. There are close D14 homologs, such as receptor for Karrikins (KARs): Karrikin-Insensitive2 (KAI2) that also belongs to the α/β -hydrolase. However, it was experimentally confirmed that D14 and KAI2 exhibit the different ligand specification [32].

3. Transduction of SL signal

The common mechanism for transducing phytohormone signals is the degradation of proteins called repressors. This degradation is mediated by a SKP1-Cullin-F-box complex (SCF), composed of three proteins that upon binding to repressors mark them for proteasomal degradation *via* ubiquitination. Cullin is a main structural part of the SCF complex controlling the connection of the whole complex to the ligase E3. The SKP1 component is responsible for the binding of the specific F-box protein which designates the protein for degradation [43]. In theory, the F-box protein renders specificity to the whole SCF complex and should be specific for different hormones. In practice, however, evidence shows that other components interacting with the SCF complex can influence its specificity.

An F-box protein which was part of an SCF complex and involved in SL signaling was identified in the *A. thaliana*-mutant *max2* and the rice-mutant *d3* that were insensitive to treatment with SLs [44, 45]. For the long time that mutants were used to describe the role of SLs in the plant growth and development, recently MAX2/D3 has been found to be involved in both SL- and KAR-signaling pathways, reviewed by Waters [7]. For this reason, the phenotype of *max2/d3* mutants cannot be directly linked to the function of SLs. Evidence showing that MAX2-guided degradation of transcription factors that is dependent also on the other phytohormone class of brassinosteroids (BRs) indicates that this F-box protein fulfills a wide range of this F-box protein in hormone signaling [46].

In *A. thaliana*, MAX2 interacts with AtCullin1 and Arabidopsis Serine/Threonine Kinase1 (ASK1) [47], whereas in rice D3 is part of a SCF complex together with OsCullin1 and *O. sativa* SKP1-Like 1/5/20 (OSK 1/5/20) [48]. Although these complexes indicate a conserved mechanism for SL signal transduction in both mono- and dicots, the presence of three different OSKs in rice may suggest that complexes with OSK1/5/20 recognize different substrates and are involved in different SL-dependent processes [48]. MAX2/D3 show nuclear localizations and SL-dependent interactions between F-box protein D3 with SL receptor D14 were reported in rice. Obtained results indicate that this interaction is mediated by the presence of SLs, and it depends on the concentration of SLs and it is also stereoisomer-specific. In a "closed" state, D14 is able to interact with D3 (**Figure 5**), while the version of D14 with mutations in or near the active pocket site shown reduced interactions with D3. This suggests that after SL-mediated changed conformation of D14, D3 can bind D14 close to the active pocket side entry [40].

Based on the similarity of MAX2/D3 protein to other hormone receptors such as jasmonate receptor Coronatine Insensitive1 (COI1) [49] or auxin receptor Transport Inhibitor Response1 (TIR1) [50], it was predicted that MAX2/D3 may also be involved in SL perception. Although

there is no evidence that MAX2/D3 can interact with SLs, there are reasons to assume that MAX2/D3 may act as a receptor for other signaling molecules.

For a long time, it was not known which proteins are recognized by the SCF^{MAX2/D3} complex, but recently the SL repressors degraded during SL signal transduction were identified in rice (D53) [51, 52] and in *A. thaliana* (Suppressor of MAX2-Like 6 to 8, SMXL 6 to 8) [53–55]. Gain-of-function mutation in D53 resulted in semi-dwarf plants with increased tillering, a phenotype which is characteristic for SL mutants. Similar effects were observed after overexpression of *D53*, whereas reduced expression of *D53* in a *d53*-mutant background inhibited tiller formation [52]. D53 shows the nuclear localization and it was confirmed that in the presence of SL molecules degradation of D53 occurs. This degradation proceeds through the proteasome-dependent pathway and requires the presence of D14 and D3 proteins [51, 52]. There are evidences that D53 may also interact with D3 in the absence of D14, although this interaction is less efficient. In contrast to rice, where only one SL repressor has been identified, *A. thaliana* contains three proteins—SMXL 6 to 8—that may act redundantly. First reports indicated that only a triple mutant *smxl6/7/8* will result in a phenotype with reduced number of tillers [54]. Later on, it was found that the phenotype characteristic for SL mutants could be produced by the expression of the non-degradable form of SMXL 7 under a native promoter [55]. All three SMXLs interact with D14 and are degraded in an SL-dependent manner in the presence of MAX2 and D14 [53, 54]. It still remains an open question whether SMXLs 6 to 8 do act redundantly or they are involved in different responses to SLs.

The SL repressors of both *A. thaliana* and rice contain the conserved amino acid sequences (F/L-D-L-N-L) which is known as an ethylene-responsive element-binding factor-associated amphiphilic repression (EAR) motif. This motif plays a key role in interactions with transcriptional corepressors from Topless (TPL) and Topless-Related Proteins (TPR) families [52, 53]. TPL and TPR regulate the expression of genes in response to different classes of hormones, such as auxin or jasmonates [56]. The presence of an EAR motif in SL repressors suggests that D53/SMXLs may bind TPL/TPR corepressors. An ensuing degradation of these corepressors may then result in the expression of transcriptional factors, previously suppressed by TPL/TRP. Interactions between SMXL6 to 8 and proteins from the TPR family were already confirmed using a yeast-two hybrid and co-immunoprecipitation assays [54].

4. Transcription response to SL signal

Phytohormones induce a change in gene expression. This response is usually mediated by transcription factors. Until now, only one family of transcription factors has been identified as a downstream component in SL signaling, namely the TEOSINTE BRANCHED1/CYCLOIDEA/PROLIFERATING CELL FACTOR1 family (TCP). In different species, single transcription factors from this family, related to SL signal, were already characterized: Branched1 (BRC1) in *A. thaliana* [57], Fine Culm1/Teosinte Branched1 (FC1/OsTB1) in rice [58], TB1 in *Zea mays* L. [59] and PsBRC1 in *Pisum sativum* L. [60]. Expression of these genes is particularly strong in axillary buds, and mutations in these genes lead to an increased branched phenotype, which

cannot be reverse by treatment with SLs. Elevated levels of *AtBRC1* expression were found after SL treatment and in the triple *smxl6/7/8* mutant, whereas decreased levels were found in SL biosynthesis mutants [53, 54]. Similar results were obtained for the *AtBRC1* target gene *Homeobox-Leucine Zipper Protein 53 (HB53)* [54], confirming that the transcription factors from TCP family act as elicitors in the SL-signaling cascade. There remain, however, some differences between mono- and dicot species. In *A. thaliana* and pea, the expression of *AtBRC1/PsBRC1* is upregulated by SL treatment [60], whereas in rice and maize, the expression of *FC1/OsTB1* and *TB1* is not elevated by SL treatment [61, 62]. This difference is sometimes explained by assuming that monocots contain additional, still unknown, transcription factors that may act as *AtBRC1/PsBRC1* in dicots.

5. SL versus KAR signaling

The unique features of SLs signaling have been discussed elsewhere [7, 63]. Here, the similarities and differences between SLs and KARs will be summarized. Though SLs and KARs play different roles in plant development [64], there are some striking similarities in the signal transduction mechanisms of these two classes of plant growth regulators [65] what might be crucial in understanding the mechanisms of their actions in plants. As already mentioned, the signal transduction of SL and KAR is mediated by the same F-box protein MAX2. However, since the signals generated by SLs and KARs are not interchangeable these phytohormones must be recognized by different receptors. Indeed, the D14 receptor has found to be specific for SLs, whereas the KAI2 receptor is specific for KARs and based on the differences in the size of active pocket site they cannot recognize the signal from second group of plant growth regulators [66, 67]. Both D14 and KA12 display a conserved catalytic triad, but only in case of D14 its catalytic activity was confirmed [33, 37]. Not only has a catalytic function of KAI2 never been proven, modeling studies of the KAR-KAI2 complex indicate that the distance between the KAR molecule and the catalytic Ser from KAI2 prohibits nucleophilic attack [67, 68]. Nevertheless, since mutation in the catalytic triad of KA12 can abolish the function of this receptor [69], the catalytic triad of the KA12 receptor may be essential for ligand binding. Similar observations have been made for D14 [38]. The second similarity between both receptors is their degradation during perception, though in the case of KAI2 the presence of MAX2 is not required for its degradation [70].

MAX2 is a component of SCF complexes which are involved in the conversion of SL and KAR signals. Therefore, the phenotypic effects caused by a mutation of MAX2 are due to an insensitivity to both plant growth regulators.

Due to the presence of different receptors, the respective SCF complexes guide the degradation of different suppressors: SMXL6 to 8 in the case of D14-SL-Max2 and Suppressor of Max2 1 (SMAX1) in the case of KAI2-KAR-MAX2 [71]. *SMAX1* and *SMXL6/7/8* show similar patterns of expression in *A. thaliana* seedlings and all four proteins may interact with TPL corepressors *via the EAR* motif [53] which indicates that ultimately SLs and KARs may regulate gene expression by a similar mechanism.

6. Conclusions

Since their classification as phytohormones, great progress has been made uncovering the mechanisms of SL signaling, and identifying the main components of the SL signal transduction pathway in both mono- and dicots. Certain aspects of SL perception have been found to be unique among plant hormones, requiring additional research to understand these phenomena in more detail. SLs share a number of the signaling components with the KARs group of plant growth regulators. Attention should also be paid to the respective receptor molecules since they represent the crucial element separating both signal cascades. Presently, our knowledge about the transcriptional responses to treatment with SLs and KARs is limited and information on the targets of SMAX1 and SMXLs is still meager. It also remains to be elucidated by what mechanism the different SL stereoisomers exert different plant responses. Answering this question will require detailed investigations on the binding of the different SL stereoisomers by D14. Additional insights may be gained by the adaptation of *in vivo*-developed SL receptors and by screening for mutants in the SL-signaling pathway.

Acknowledgements

The author thanks Dr. Michael Melzer and Dr. Twan Rutten for critical reading of the text. The author is supported by scholarships funded by the Ministry of Science and Higher Education (424/STYP/10/2015 and DN/MOB/245/IV/2015).

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