

DARWIN REVIEW

Unveiling the complexity of strigolactones: exploring structural diversity, biosynthesis pathways, and signaling mechanisms

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Abstract

Strigolactone is the collective name for compounds containing a butenolide as a part of their structure, first discovered as compounds that induce seed germination of root parasitic plants. They were later found to be rhizosphere signaling molecules that induce hyphal branching of arbuscular mycorrhizal fungi, and, finally, they emerged as a class of plant hormones. Strigolactones are found in root exudates, where they display a great variability in their chemical structure. Their structure varies among plant species, and multiple strigolactones can exist in one species. Over 30 strigolactones have been identified, yet the chemical structure of the strigolactone that functions as an endogenous hormone and is found in the above-ground parts of plants remains unknown. We discuss our current knowledge of the synthetic pathways of diverse strigolactones and their regulation, as well as recent progress in identifying strigolactones as plant hormones. Strigolactone is perceived by the DWARF14 (D14), receptor, an α/β hydrolase which originated by gene duplication of *KARRIKIN INSENSITIVE 2* (KAI2). D14 and KAI2 signaling pathways are partially overlapping paralogous pathways. Progress in understanding the signaling mechanisms mediated by two α/β hydrolase receptors as well as remaining challenges in the field of strigolactone research are reviewed.

Keywords: Arbuscular mycorrhizae, D14, α/β -hydrolase, KAI2, P450, root parasitic plants.

Introduction

Strigolactone (SL) is the collective name for compounds containing a butenolide as a part of their structure that induce hyphal branching of arbuscular mycorrhizal (AM) fungi and seed germination of root parasitic plants (Butler, 1994; Al-Babili and Bouwmeester, 2015). Over 30 SLs have been identified from

various plant species (Yoneyama, 2020). SLs were first discovered as the compound that induces seed germination of witchweed (*Striga lutea* Lour.), a root parasitic plant. The SL named strigol was isolated from root exudates of cotton (*Gossypium hirsutum* L.) (Cook *et al.*, 1966). It was suggested that strigol

functions as a plant hormone based on the finding that it is effective at low concentration and that stimulants similar to strigol are found in various plant species (Cook *et al.*, 1972). Before the discovery of SLs as a class of plant hormones in 2008 (Gomez-Roldan *et al.*, 2008; Umehara *et al.*, 2008), they were identified as the rhizosphere signaling molecules that induce hyphal branching of AM fungi (Akiyama *et al.*, 2005). Plant symbiosis with AM fungi started in the common ancestor of land plants and occurs in >80% of existing plant species (Rich *et al.*, 2021). Plants provide carbohydrates and lipids to AM fungi; in turn, AM fungi help plants obtain inorganic nutrients, such as phosphate (Pi). The symbiosis is fine-tuned by SL biosynthesis which is modulated by Pi availability (Balzergue *et al.*, 2011). SL biosynthesis is enhanced under low Pi conditions, probably to induce symbiosis with AM fungi, and suppressed upon recovery of Pi levels. The finding of SLs as a class of plant hormones indicated that the fine-tuning of growth by SL is more complicated. Pi availability is one of the major determinants of plant growth and development. For example, shoot branching is suppressed under low Pi conditions. It has been clearly shown that the suppression of shoot branching is due to Pi deficiency-induced SL biosynthesis rather than a direct consequence of the shortage of Pi as a nutrient (Umehara *et al.*, 2010). The dual function of SL as a rhizosphere signaling molecule to induce symbiosis with AM fungi and as a plant hormone constitutes an effective feedback system to optimize plant growth depending on the availability of nutrients.

The first two discoveries of SLs, as stimulants for seed germination in root parasitic plants and as rhizosphere signaling molecules, were achieved through natural product chemistry approaches (Cook *et al.*, 1966; Akiyama *et al.*, 2005). In contrast, their role as plant hormones was demonstrated through genetic analyses. A series of mutants exhibiting similar excess branching phenotypes were analyzed in *Arabidopsis*, pea, rice, and petunia (Beveridge *et al.*, 1994; Napoli, 1996; Stürnberg *et al.*, 2002; Ishikawa *et al.*, 2005). Before the discovery of SL as a plant hormone, genetic analyses revealed that causal genes of excess branching are likely to be involved in the synthesis or signaling of an unidentified hormone (Sorefan *et al.*, 2003; Johnson *et al.*, 2006; Stürnberg *et al.*, 2007). The isolation of receptors for karrikins, compounds found in burned plants that stimulate seed germination in certain plant species (Flematti *et al.*, 2004), led to the discovery that DWARF14 (D14), the receptor for SLs, originated from the duplication of KARRIKIN INSENSITIVE2 (KAI2), a receptor for karrikins (Waters *et al.*, 2012). It is assumed that KAI2 is a receptor of an unidentified hormone, tentatively called KAI2 ligand (KL) (Conn and Nelson, 2015). These discoveries attracted researchers from a wide range of research fields, including developmental biology, evolutionary biology, natural product chemistry, and structural biology, resulting in the rapid growth of SL research. Despite the growing interest in SL research, there are still many unanswered questions. This review summarizes what is known and unknown about the nature of SLs, their synthesis, and their signaling.

Chemical nature of strigolactones

SL is the collective name for related compounds (Butler, 1994). By definition, SLs are substances with a butenolide (D ring) linked by enol ether to a lactone (C ring) or a carboxylate ester as a common structure, which are produced by plants (Al-Babili and Bouwmeester, 2015). Unlike other plant hormones, SLs vary in structure between plant species, and multiple SL structures may exist within a single plant species. More than 30 SLs have been reported (Yoneyama, 2020). The biosynthetic intermediates of these SLs were identified as endogenous compounds, and most of the biologically active molecules are found in root exudates. SLs are unstable compounds that exist in the picomolar to nanomolar concentration range in plant tissues. They are more easily extracted and purified from root exudates (Al-Babili and Bouwmeester, 2015; Yoneyama, 2020).

Since the first isolated SL, named strigol, contains a four-ring structure (Cook *et al.*, 1966, 1972), SLs with a four-ring structure are collectively called canonical SLs (Waters *et al.*, 2017). Canonical SLs contain a 6-5-5 or 7-5-5 membered tricyclic lactone structure (ABC ring) bonded to a butenolide (D ring) by an enol ether bridge. The D ring of natural SLs is always in a 2' *R* orientation. Canonical SLs can be classified into two types, the orobanchol-type and the strigol-type SLs, based on the orientation at the BC-ring junction (α - and β -orientations, respectively) (Xie *et al.*, 2013). Recently, a variety of SLs lacking the basic ABC ring structure have been isolated; they are called non-canonical SLs (Yoneyama *et al.*, 2018b). Hence, the classification of canonical and non-canonical SLs is largely based on the history of their discovery. It is not known whether there are any differences in the function between canonical and non-canonical SLs.

The core pathway of SL biosynthesis has been rapidly elucidated using *Arabidopsis thaliana* and rice (*Oryza sativa*), since the discovery of SLs as a plant hormone in 2008 (Fig. 1) (Gomez-Roldan *et al.*, 2008; Umehara *et al.*, 2008). SLs are biosynthesized from all-*trans*- β -carotene, which is converted to the bicyclic precursor carlactone (CL) by a carotenoid isomerase encoded by DWARF27 (D27) and two carotenoid oxidative cleavage enzymes, CAROTENOID CLEAVAGE DIOXYGENASE 7 (CCD7) and CAROTENOID CLEAVAGE DIOXYGENASE 8 (CCD8) (Lin *et al.*, 2009; Alder *et al.*, 2012; Seto *et al.*, 2014). CCD7 and CCD8 are encoded by genes that were previously described as the RAMOUSUS genes (RMS5 and RMS1) in pea (*Pisum sativum*), the DECREASED APICAL DOMINANCE genes (DAD3 and DAD1) in petunia (*Petunia hybrida*), the MORE AXILLARY GROWTH genes (MAX3 and MAX4) in *Arabidopsis*, and the DWARF/HIGH-TILLERING DWARF genes (D17/HTD1 and D10) in rice (Sorefan *et al.*, 2003; Booker *et al.*, 2004; Foo *et al.*, 2005; Snowden *et al.*, 2005; Johnson *et al.*, 2006; Zou *et al.*, 2006; Arite *et al.*, 2007). CL is oxidized and converted to carlactonoic acid (CLA) by a cytochrome P450 (CYP711A) encoded by MORE AXILLARY GROWTH 1 (MAX1) (Booker *et al.*, 2005; Abe *et al.*, 2014). In some plant species, CLA is further modified by CYP711A or

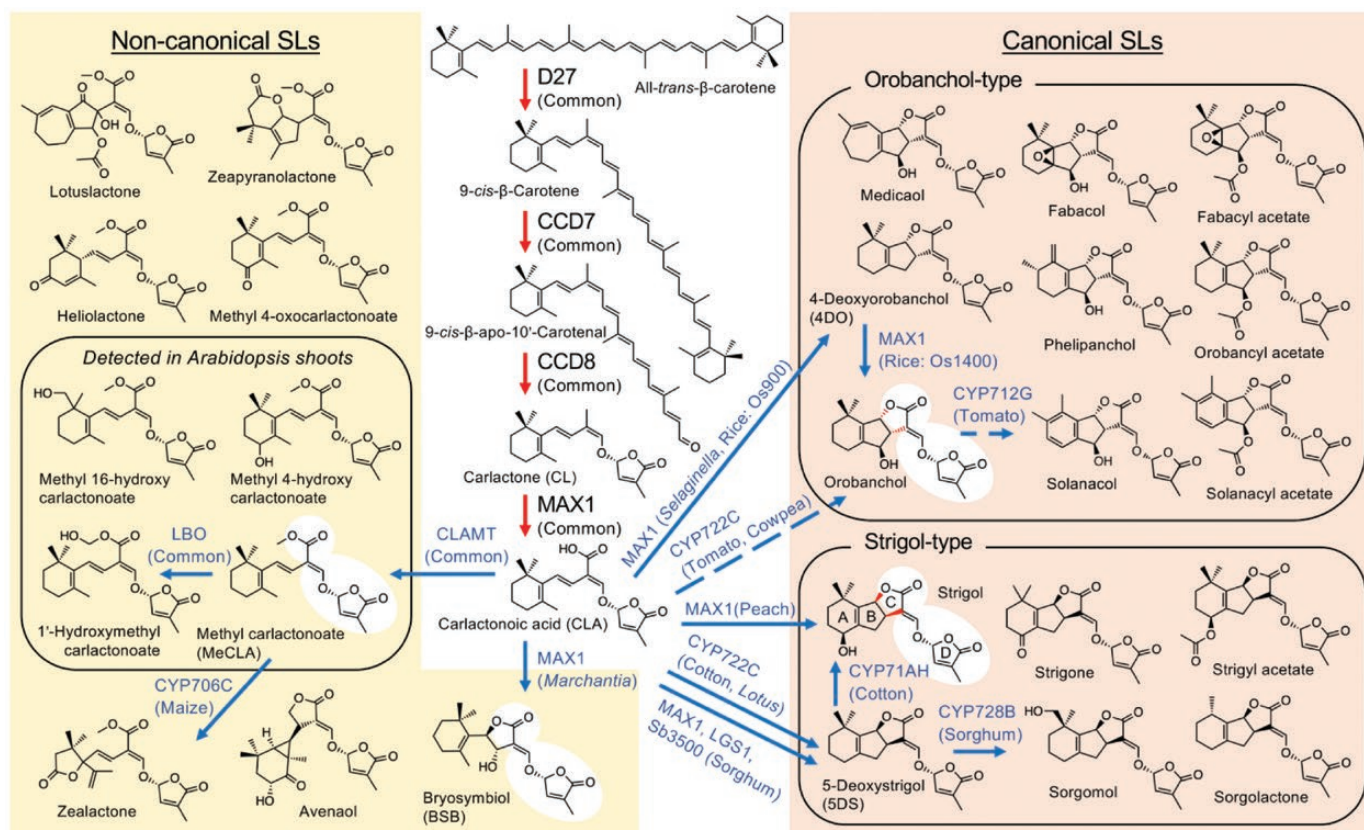


Fig. 1. Strigolactone biosynthetic pathways. SLs are biosynthesized from all-*trans*- β -carotene, which is converted to the bicyclic precursor carlactone (CL) by D27, CCD7, and CCD8. CL is converted to carlactonoic acid (CLA) by the cytochrome P450 MAX1 (CYP711A). The pathway up to CLA is common to all SLs, but multiple pathways branch out at CLA depending on plant species. SLs with a four-ring structure (collectively called canonical SLs) can be classified into orobanchol- and strigol-type based on stereochemistry at the BC-ring junction. Non-canonical SLs do not have an A, B, and/or C ring, but have a butenolide (D ring) linked by enol ether to carboxylate ester or lactone as canonical SLs. Most of the SLs isolated so far are rhizosphere signals exuded from host roots and not detected in above-ground tissues. Methyl carlactonoate (MeCLA) and its hydroxylated form are detected in above-ground tissues, suggesting that they may act as endogenous plant hormones. The white bubble indicates a conserved chemical structure in natural SLs.

other enzymes belonging to P450 families (Zhang *et al.*, 2014; Wakabayashi *et al.*, 2019, 2020; Kodama *et al.*, 2022; Li *et al.*, 2023; Wu *et al.*, 2023). Therefore, the pathway up to CLA is common in the biosynthesis of all SLs (Yoneyama *et al.*, 2018a), while the pathways after CLA diverge among plant species, leading to the generation of variable SL structures.

Diversification of biosynthetic pathways leading to the synthesis of variable strigolactones

Several enzymes involved in producing species-specific SLs were recently identified, but the mechanisms to produce different types of SLs after CLA are not fully understood.

Diversification of *MAX1* genes contributed to the production of variable SLs. Most dicotyledonous species contain one or two *MAX1* genes, while grass species tend to have more than three copies of the gene. *Japonica* rice (*Oryza sativa* ssp.

japonica) produces orobanchol, 4-deoxyorobanchol (4DO), and methyl 4-oxocaractonoate (4-oxo-MeCLA), and exudes these SLs from roots. It has been reported that rice produces the isomers of methoxy-5-deoxystrigol (Cardoso *et al.*, 2014a), and one of them was recently tentatively identified as 4-oxo-MeCLA (Ito *et al.*, 2022). *Japonica* rice contains five *MAX1* genes, including one pseudogene. Among the four functional *MAX1* genes, *Os900* encoding CYP711A2 produces 4DO from CLA via CLA (Zhang *et al.*, 2014; Yoneyama *et al.*, 2018a), and *Os1400*, encoding CYP711A3 hydroxylates 4DO at C-4 to produce orobanchol (Zhang *et al.*, 2014). *Os900* is also involved in the biosynthesis of 4-oxo-MeCLA (Ito *et al.*, 2022). *Indica* rice (*Oryza sativa* ssp. *indica*) does not have the *Os900* or *Os1400* genes, but 4DO and orobanchol were detected in their root exudates (Cardoso *et al.*, 2014b). This implies that diversification of the *MAX1* gene, which occurred in the lineage leading to *japonica* rice after diversification of *japonica* and *indica* rice, led to the development of a new pathway to synthesize orobanchol.

The tomato (*Solanum lycopersicum*) genome contains only one *MAX1* gene coding for CYP711A21 which catalyzes the conversion of CL to CLA, but lacks the activity to further convert CLA to 4DO or orobanchol. Similarly, in Arabidopsis, CYP711A encoded by *MAX1* only catalyzes conversion from CL to CLA (Yoneyama *et al.*, 2018a; Zhang *et al.*, 2018). In tomato and cowpea (*Vigna unguiculata*), biosynthesis of orobanchol is catalyzed by CYP722C, another member of the cytochrome P450 family (Wakabayashi *et al.*, 2019). *In vitro* enzyme assays using a recombinant protein showed that CYP722C converts CLA to orobanchol and its diastereomer *ent*-2'-*epi*-orobanchol. However, *ent*-2'-*epi*-orobanchol is not detected in root exudates of tomato and cowpea, suggesting that other mechanisms exist for stereoselective production of orobanchol in plants. It was also reported that CYP722C stereoselectively produces 5-deoxystrigol (5DS), a diastereomer of 4DO, from CLA in cotton (*Gossypium arboreum*) and *Lotus japonicus* (Mori *et al.*, 2020; Wakabayashi *et al.*, 2020; Wu *et al.*, 2021). Therefore, there are two types of CYP722C, one catalyzes the stereoselective biosynthesis of the strigol-type 5DS, and the other catalyzes the biosynthesis of orobanchol but is non-stereoselective by itself. The *Solanaceae* plants produce solanacol, in which the A ring of orobanchol is converted to an aromatic ring. Production of an intermediate of solanacol from orobanchol and phelipanchol derived from a solanacol intermediate is catalyzed by CYP712G1, another P450 family member (Wakabayashi *et al.*, 2022; Wang *et al.*, 2022).

Exceptionally, in the *Rosaceae* family, such as in the case of peach (*Prunus persica*), there are three *MAX1* genes. CYP711A encoded by *PpMAX1c*, one of the three *MAX1* genes, produces strigol from CL via CLA (Wu *et al.*, 2023). Strawberry (*Fragaria × ananassa*), another *Rosaceae* species, also produces strigol (Yoneyama *et al.*, 2018a). However, CYP711A in *Fragaria vesca* only catalyzes the conversion of CL to CLA, but not of CLA to strigol (Wu *et al.*, 2023). This is also the case for apple (*Malus domestica*) (Wu *et al.*, 2023). Therefore, *PpMAX1c* in *Rosaceae* seems to have duplicated after the diversification of *Prunus* and acquired its unique function as a strigol synthase. There is another strigol biosynthetic pathway in which 5DS is produced from CLA by CYP722C, followed by the hydroxylation of C-5 by another P450 family member, CYP71AH (Iseki *et al.*, 2018; Wu *et al.*, 2021; Wakabayashi *et al.*, 2023). Most plants produce either strigol- or orobanchol-type SLs. However, both strigol and orobanchol are detected in peach where CYP722C functions as an enzyme for orobanchol biosynthesis in addition to CYP711A encoded by *PpMAX1c* (Wu *et al.*, 2023). In general, the *Solanaceae* plants produce the orobanchol-type SLs. However, both 5DS, which is a strigol-type SL, and orobanchol can be found in root exudates of tobacco (*Nicotiana tabacum*), which is another plant species belonging to the *Solanaceae* family (Xie *et al.*, 2013). We speculate that the allotetraploid tobacco may have CYP722C, which acts as a 5DS synthase in addition to orobanchol synthase.

Recently, *LOW GERMINATION STIMULANT 1* (*LGS1*), which encodes a sulfotransferase, was identified as a key gene in the pathway of SL biosynthesis in sorghum (Gobena *et al.*, 2017) which produces 5DS and sorgomol, a C-9 hydroxylated derivative of 5DS. Sorghum generates 5DS through the catalytic actions of *LGS1*, CYP711A31 encoded by *SbMAX1a*, one of the four *MAX1* genes, and a 2-oxoglutarate-dependent dioxygenase (2OGD) encoded by *Sobic.005G213500* (*Sb3500*) (Yoda *et al.*, 2023). The sulfate group added by *LGS1* is not retained in the final SL structure but becomes a leaving group and promotes cyclization of the BC ring (Wu and Li, 2021; Yoda *et al.*, 2021). Subsequently, 5DS is converted to sorgomol by hydroxylation at C-9 by another P450 family member, CYP728B35 (Wakabayashi *et al.*, 2021a). In a mutant sorghum line in which *LGS1* is deleted, the major SL is changed from 5DS to orobanchol (Gobena *et al.*, 2017). Sorghum CYP722B does not show CLA to 5DS or orobanchol conversion activity (Yoda *et al.*, 2021). CYP711A31 encoded by *SbMAX1a* catalyzes CL conversion to 18-oxocaractonoic acid, which is considered to be a direct precursor of orobanchol (Yoda *et al.*, 2023). Despite the occurrence of spontaneous conversion of 18-oxocaractonoic acid to orobanchol and *ent*-2'-*epi*-orobanchol under acidic conditions, only orobanchol is detected in the *lgs1* mutant. Thus, it is likely that sorghum has another factor that stereoselectively converts 18-oxocaractonoic acid to orobanchol (Yoda *et al.*, 2023). The reason why sorghum possesses a biosynthesis pathway for orobanchol that exclusively operates in the absence of *LGS1* remains unknown. Sulfotransferase with the same function as *LGS1* is not found in rice or maize (*Zea mays*) (Wu and Li, 2021). Since the *LGS1* pathway is present in a limited number of species, orobanchol might have been the major SL in sorghum before acquiring *LGS1*.

In contrast to the progress in elucidating the canonical SL biosynthesis pathways, those leading to non-canonical SLs are poorly understood. Non-canonical SLs have a butenolide (D ring) linked by enol ether to a lactone (C ring) or a carboxylate ester, but no tricyclic lactone structure (ABC ring) (Fig. 1). The non-canonical SL zealactone is the major SL in maize. Zealactone is a derivative of methyl caractonate (MeCLA), in which the carboxyl group of CLA is methyl esterified (Charnikhova *et al.*, 2017; Xie *et al.*, 2017). It is produced from CL through the catalytic actions of CYP706C37, CYP711A18 encoded by *ZmMAX1b*, one of three *MAX1* genes, and the methyltransferase CLA METHYLTRANSFERASE (*ZmCLAMT*) (Li *et al.*, 2023). These genes are adjacent on the maize genome (Li *et al.*, 2023). In sorghum, *LGS1* and the gene encoding 2OGD *Sb3500* are adjacent to each other, but *SbMAX1a* is located on a different chromosome (Yoda *et al.*, 2023). It is intriguing that genes encoding different families of enzymes align closely on the genome, and they have been selected to create a species-specific SL biosynthetic pathway. *Lotus japonicus* produces 5DS and lotuslactone. Lotuslactone,

a MeCLA derivative, is a species-specific non-canonical SL (Xie *et al.*, 2019). 2OGD LOTUSLACTONE-DEFECTIVE (LLD) has been identified as a biosynthetic enzyme for lotuslactone; however, its enzymatic function is unknown (Mori *et al.*, 2020). In the phylogenetic tree of 2OGDs, LLD belongs to the same DOXC55 family as Sb3500, which is involved in 5DS biosynthesis in sorghum. The biosynthetic pathways and enzymes for the other non-canonical SLs, such as avenaol, heliolactone, and zeapyranolactone, remain unknown (Kim *et al.*, 2014; Ueno *et al.*, 2014; Charnikhova *et al.*, 2018).

Evolution of strigolactone biosynthesis pathways

Since symbiosis with AM fungi is found in >80% of terrestrial plants, it must have started in the common ancestor of terrestrial plants, but it has been unknown whether bryophytes—basal land plants—use SLs for AM symbiosis. There have been several reports of SLs detected in liverwort, in moss, and in charophyte algae; however, since those lack biosynthetic enzyme genes for SL, these findings had been unreliable (Proust *et al.*, 2011; Delaux *et al.*, 2012; Yoneyama *et al.*, 2018b).

Genes such as *D27*, *CCD7*, *CCD8*, and *MAX1* involved in the fundamental biosynthesis of SLs are conserved in bryophytes (Rensing *et al.*, 2008; Bowman *et al.*, 2017; Li *et al.*, 2020; J. Zhang *et al.*, 2020). Bryosymbiol (BSB) was identified as an endogenous SL in *Marchantia paleacea*. BSB is a non-canonical SL, which lacks the B ring, and is produced by *MAX1*. *Marchantia paleacea* has two *CCD8* genes, and loss of both genes blocks BSB production and AM symbiosis, indicating that BSB acts as a symbiosis signal for AM fungi (Kodama *et al.*, 2022). BSB was also detected in thalli and exudates of the *Marchantia* relatives, *M. emarginata* and *M. pinnata*, but not in the model liverwort species *M. polymorpha* (Kodama *et al.*, 2022). Consistent with the absence of AM symbiosis, *M. polymorpha* lacks the *CCD8* and *MAX1* genes and does not produce BSB, which is exceptional in liverworts (Radhakrishnan *et al.*, 2020). The model moss species, *Physcomitrium patens*, does not form AM symbiosis. Indeed, *P. patens* lacks the *MAX1* gene, and BSB is not synthesized. However, intriguingly, biologically active SLs, the nature of which is unknown, are produced and regulate colony extension in *P. patens* (Proust *et al.*, 2011; Decker *et al.*, 2017; Kodama *et al.*, 2022). Elucidation of the chemical nature of SLs in *P. patens* is an important issue from the viewpoint of hormone evolution. BSB and its diastereomer *ent*-2'-*epi*-BSB (stereochemistry is tentative) were detected in *Phaeoceros carolinianus*, a hornwort species, the most basal lineage of bryophytes (Kodama *et al.*, 2022).

The *D27*, *CCD7*, *CCD8*, and *MAX1* genes are conserved in ferns and lycophytes (Banks *et al.*, 2011; Fang *et al.*, 2022; Huang *et al.*, 2022). The existence of SLs was examined in nine fern species from six families (Kodama *et al.*, 2022). BSB and

tentative *ent*-2'-*epi*-BSB were detected in the root exudates of two fern species, *Dryopteris erythrosora* and *Matteuccia struthiopteris*, respectively (Kodama *et al.*, 2022). However, no known SL, including BSB or its isomer, was detected in the other fern species. On the other hand, the lycophyte *Selaginella moellendorffii*, which diverged from land plants before ferns, produces 4DO containing the basic chemical structure of orobanchol-type SLs (Yoneyama *et al.*, 2018a). The CYP711A17 encoded by *MAX1* of *S. moellendorffii* converts CL into 4DO via CLA, similar to the function of rice Os900 (Yoneyama *et al.*, 2018a). 4DO is also produced in seed plants and is one of the natural SLs with strong hyphal branching activity in AM fungi (Akiyama *et al.*, 2010). We speculate that, in *S. moellendorffii*, the function of *MAX1* may have evolved to produce 4DO with a more stable tricyclic (ABC ring) structure which confers higher AM hyphal branching activity than BSB.

The biosynthesis pathways of SLs have been mainly studied in angiosperms, such as Arabidopsis and rice. Although there are no detailed reports on the structure and biosynthesis of SLs in gymnosperms, recent genome sequencing data indicate that the SL biosynthesis genes are conserved in gymnosperms (Liu *et al.*, 2021; Liu *et al.*, 2022; Kodama *et al.*, 2023). *Ginkgo biloba*, *Cryptomeria japonica*, and *Pinus thunbergii* seem to produce 4DO and orobanchol (Yoneyama *et al.*, 2018b). On the other hand, SLs with various structures, including BSB, were isolated from root exudates of angiosperms. Root exudates from 27 species belonging to 17 families of angiosperms were analyzed, and BSB and tentative *ent*-2'-*epi*-BSB were found in asparagus (*Asparagus officinalis*), a monocot, and groundnut (*Arachis hypogaea*), a dicot species, respectively (Kodama *et al.*, 2022). The presence of BSB in ferns and seed plants clearly demonstrates that BSB or its isomer is an ancestral SL produced by the common ancestor of land plants. Besides the conserved function to convert CL to CLA, CYP711A encoded by *MAX1* works at the branching point of diverse SL biosynthesis pathways (Abe *et al.*, 2014; Yoneyama *et al.*, 2018a). Dicot species probably developed biosynthesis pathways from CLA to canonical SLs, which display strong hyphal branching activity towards AM fungi, by acquiring the P450 CYP722C family (Wakabayashi *et al.*, 2019, 2020; Mori *et al.*, 2020). On the other hand, CYP722C genes were lost in some dicot species, such as *Brassicaceae* species, including *A. thaliana*. *Brassicaceae* species do not produce canonical SLs, which is why they do not form symbiosis with AM fungi. Exceptionally among legumes, groundnut does not contain the gene encoding CYP722C. We speculate that the loss of CYP722C activity may have triggered a new pathway to produce BSB in groundnut.

Diversification of SL structures in host plants may have evolved as countermeasures against parasitic organisms in the rhizosphere. Since SLs are ideal signals to indicate the presence of roots, other unknown parasitic, mutualistic, or commensal organisms may recognize SLs. Indeed, SL compositions affect the microbiome and AM fungi in the rhizosphere (Carvalhais

et al., 2019; Nasir *et al.*, 2019; Liu *et al.*, 2020; Kim *et al.*, 2022). To escape parasites, it is believed that host plants may need to modify the structure and composition of SLs while maintaining a mutually beneficial relationship with AM fungi. This process probably led to changes in the enzymatic functions of MAX1 and the recruitment of the activity of other enzymes, such as CYP722C, CYP706C, CYP712G, CYP728B, 2OGD, and sulfotransferase in the SL biosynthesis pathways, resulting in the production of a wide variety of SL structures.

The chemical structure of strigolactones which act as a plant hormone *in planta* is still unknown

So far, the SLs isolated have been chemical signals that are exuded from host roots, and none of them was detected in above-ground tissues. While SLs isolated from root exudates exhibit the ability to inhibit shoot branching when applied exogenously to plants, there is no evidence to suggest that they are identical to active forms functioning *in planta* (Boyer *et al.*, 2012; Umehara *et al.*, 2015). However, recent studies have started unveiling the structure of SLs as a plant hormone.

In seed plants, defects in *D27*, *CCD7*, *CCD8*, or *MAX1* cause excessive shoot branching (Sorefan *et al.*, 2003; Booker *et al.*, 2004, 2005; Snowden *et al.*, 2005; Zou *et al.*, 2006; Arite *et al.*, 2007; Drummond *et al.*, 2009; Lin *et al.*, 2009). In tomato, the loss of activity of CYP722C, which acts downstream of MAX1-encoded CYP711A21 and produces orobanchol, resulted in the reduction of orobanchol and solanacol levels in root exudates, while shoot branching was not affected (Wakabayashi *et al.*, 2019). In *japonica* rice, loss of *Os900*, one of the MAX1 genes, reduces the endogenous levels of 4DO, orobanchol, and 4-oxo-MeCLA in roots, but does not show an increase in tillering (Ito *et al.*, 2022). In maize, defective mutants of *ZmMAX1b*, one of the MAX1 genes, or *CYP706C37* show a reduction in zealactone level but no defects in tillering (Li *et al.*, 2023). On the other hand, the double mutant of *Os1900* and *Os5100* encoding CYP711A5 and CYP711A6, respectively, in *japonica* rice, which belong to different clades from *Os900*, showed an increase in tillering, suggesting that chemicals synthesized by these enzymes or their metabolic products may have the potential to function as endogenous hormones in rice (Cui *et al.*, 2023). Both CYP711As encoded by *Os1900* and *Os5100* catalyze the conversion of CL to CLA (Yoneyama *et al.*, 2018a), and these genes are conserved in grass species, including *indica* rice. Since their orthologs in maize, *ZmMAX1a* and *ZmMAX1c* encoding CYP711A13 and CYP711A19, respectively, are not involved in the biosynthesis of zealactone (Li *et al.*, 2023), we speculate that they may also be enzymes of the biosynthetic pathway of SLs that act as an endogenous plant hormone.

Recent studies clearly showed that the chemical structure of SLs that function as rhizosphere signals are different from those

that act as plant hormones *in planta*, and their biosynthesis pathways diverge after MAX1. Currently, MeCLA and its metabolites are candidates for acting as plant hormones. It was reported that CLA, which is a common product of MAX1, does not interact with SL receptor D14, but its methyl ester form, MeCLA, does (Abe *et al.*, 2014). Recently, a methyltransferase (CLAMT) of CLA was identified (Wakabayashi *et al.*, 2021b; Haider *et al.*, 2023; Li *et al.*, 2023), and the loss of CLAMT showed a phenotype of increased branching (Mashiguchi *et al.*, 2022). LATERAL BRANCHING OXIDOREDUCTASE (LBO), encoding a 2OGD that uses MeCLA as a substrate, has been identified (Brewer *et al.*, 2016). LBO hydroxylates the methyl group of the methyl ester of MeCLA to produce hydroxymethyl carlactonoate (1'-HO-MeCLA) (Yoneyama *et al.*, 2020). However, 1'-HO-MeCLA is unstable and is easily converted to CLA by demethylation in *in vitro* experiments (Yoneyama *et al.*, 2020). Although LBO is a single-copy gene in Arabidopsis, the *lbo* mutant phenotype, characterized by an increased shoot branching, is weaker than in mutants of other SL biosynthesis genes (Brewer *et al.*, 2016). In addition to MeCLA, the *lbo* mutant has increased amounts of hydroxylated MeCLA at C-4 or C-16, which may also be substrates for LBO (Yoneyama *et al.*, 2020). A possible reason for the weak phenotype of the *lbo* mutant may be that MeCLA and its hydroxylated forms have some branching-inhibitory activity *in planta* (Abe *et al.*, 2014). Biologically active SLs are anticipated to accumulate in the *d14* mutant due to a lack of feedback regulation. Indeed, hydroxylated MeCLAs were below the level of detection in the wild type, while they were detected in above-ground tissues of the *d14* mutant in Arabidopsis (Yoneyama *et al.*, 2020). This supports the possibility that a hydroxylated MeCLA is the plant hormone. Whether hydroxylated MeCLA is the active form or hydroxylated MeCLA is further converted to other metabolites to function as a plant hormone *in planta* remains to be established.

Strigolactone signaling mechanism mediated by α/β hydrolase receptor D14

The SL signaling pathway includes a ubiquitination-dependent protein degradation system, which is often seen in other plant hormone signaling pathways (Takeuchi *et al.*, 2021). The SL receptor, D14, belongs to the α/β -hydrolase superfamily of proteins (Arite *et al.*, 2009). In the absence of SLs, the negative regulator protein, D53 (rice) or SUPPRESSOR OF MAX2 1 (SMAX1) LIKE6 (SMXL6)/7/8 (Arabidopsis), suppresses the expression of the downstream target genes (Jiang *et al.*, 2013; Zhou *et al.*, 2013; Soundappan *et al.*, 2015; Wang *et al.*, 2015). In the presence of SLs, D14 [or Arabidopsis D14 (AtD14)] forms a complex with D53 (or SMXL6/7/8), and induces the proteasome-mediated degradation of D53/SMXL6/7/8 in a manner that requires the F-box protein D3 in rice or MAX2 in Arabidopsis (Fig. 2). D14, which has the conserved catalytic

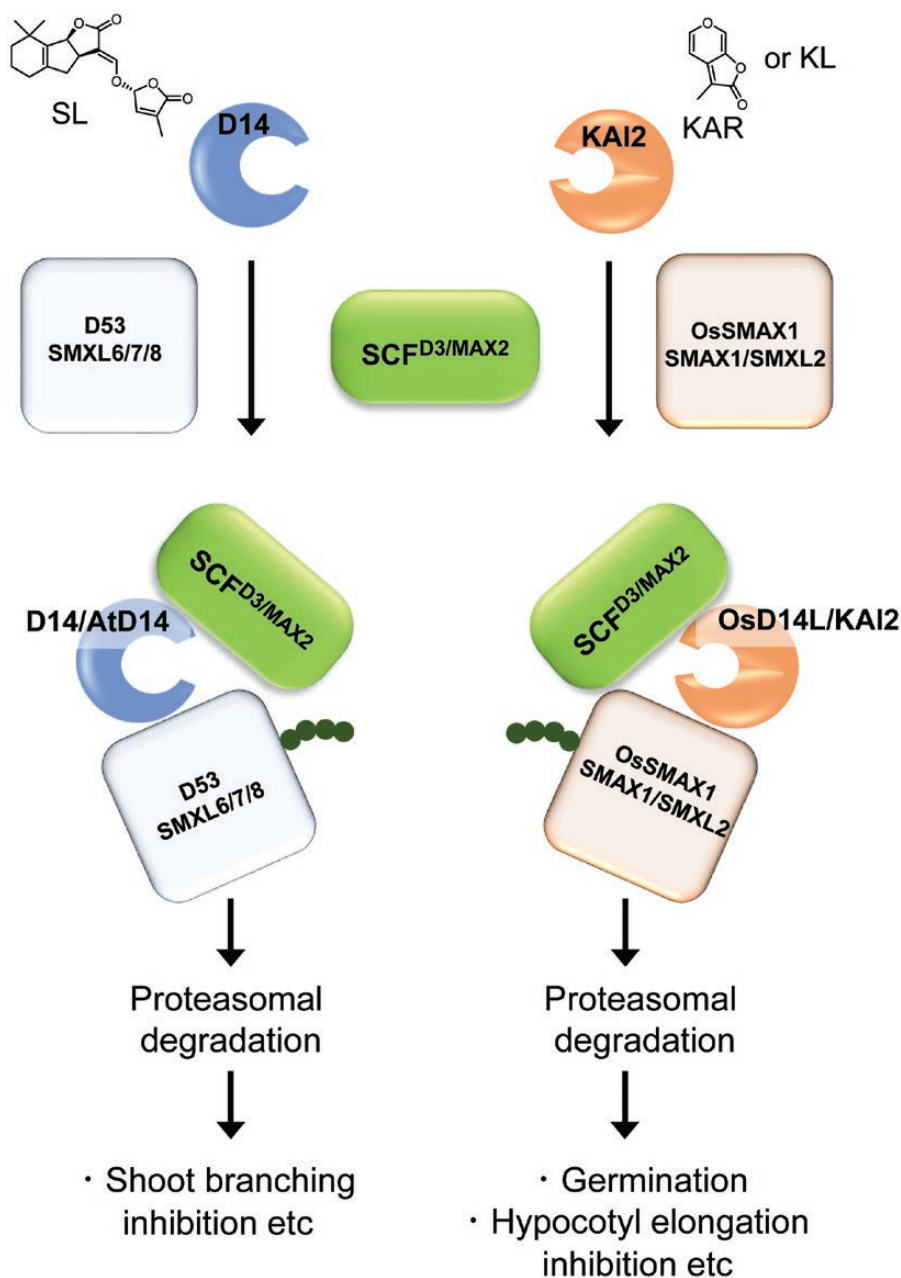


Fig. 2. Overviews of the signaling mechanisms of the D14 and KAI2 pathways. (D53, D3, D14 OsSMAX1=rice; AtD14, KAI2, MAX2, SMXL6/7/8, SMAX1, SMXL2=Arabidopsis).

triad of amino acids Ser (S), His (H), and Asp (D) characteristic of α/β -hydrolase proteins, can catalyze hydrolase reactions toward its ligand SLs (Hamiaux *et al.*, 2012; Yao *et al.*, 2016; Seto *et al.*, 2019). GID1, a soluble receptor of the plant hormone gibberellin (GA), also belongs to the α/β -hydrolase family (Ueguchi-Tanaka *et al.*, 2005). However, the catalytic triad is not conserved in GID1, and thus it does not have hydrolase catalytic activity (Ueguchi-Tanaka *et al.*, 2005). D14 is the first example of a plant hormone receptor with catalytic activity toward its ligand. Due to this feature, the analysis of the

SL signaling mechanism has become more complex compared with other plant hormones, and different signal transducing models have been proposed (Mashiguchi *et al.*, 2021). In the models, whether enzymatic activity is required for signal transduction is controversial. Structural analysis of the apo-form of the D14 family proteins suggests the presence of a V-shaped lid structure composed of four α -helices, and a possible ligand-binding pocket exists within this lid structure (Hamiaux *et al.*, 2012; Kagiya *et al.*, 2013; Nakamura *et al.*, 2013; Zhao *et al.*, 2013) (Fig. 3A). In 2016, the crystal structure of the signaling

complex composed of AtD14 and D3, which is formed in an SL-dependent manner, was solved (Yao *et al.*, 2016). Intriguingly, the AtD14 structure in this complex has conformational changes compared with the apo structure. In particular, the V-shaped lid structure is in a closed state. Moreover, small electron density predicted to originate from a covalently bound hydrolysis reaction intermediate (covalently linked intermediate molecule=CLIM) was detected in the ligand-binding pocket. These results suggest that the conformational change is critical to trigger the interaction between AtD14 (Arabidopsis protein) and D3 (rice protein), and the formation of a hydrolytic reaction intermediate between AtD14 and the SL D-ring part plays a critical role in inducing the conformational change of AtD14 (Fig. 3B). Following this report, the crystal structure of D3, the F-box protein, was reported (Shabek *et al.*, 2018). The D3 structure was solved in two different conformations, in one of which the electron density for the C-terminal helix (CTH) was not observed, suggesting that the CTH region has a flexible structure. Interestingly, the CTH domain of D3 (rice protein) interacts with AtD14 (Arabidopsis protein) in an SL-dependent manner, and the complex crystal structure of AtD14 and D3 CTH was successfully solved (Fig. 3C). AtD14 did not show notable structural changes compared with its apo structure in this complex structure. Moreover, the authors proposed that the entire SL molecule is present in the binding pocket of AtD14 in this complex. Therefore, the authors proposed a model in which the conformational change in AtD14 is not critical for signal transduction, and the entire SL molecule

has a significant role in inducing the complex formation with D3. In another model, it was proposed that the entire SL molecules induce the conformation change of AtD14 and trigger the complex formation with the signaling partners (Seto *et al.*, 2019). This model was proposed partly based on the genetic complementation tests in which a catalytically inactive AtD14 D218A mutant complemented the Arabidopsis *atd14* mutant phenotype in an SL-dependent manner. Moreover, another single substitution mutant of AtD14 (R183H) was shown to have hydrolytic activity, but did not complement the *atd14* mutant phenotype. Overexpression of this mutant version of AtD14 (R1183H) in the Arabidopsis wild-type (Col-0) background resulted in an increase in shoot branching, possibly due to hydrolytic degradation of the endogenous SL. These results imply that the hydrolytic degradation of SL contributes to the deactivating step of bioactive SLs. Based on these results, it was proposed that the initiation of the signal transduction does not require SL hydrolysis by D14. Further studies are needed to understand the relationship between hydrolysis and signal transduction of SLs. Structural analysis of the complex that integrates all signal transduction factors involved (the receptor, the repressor, and the F-box protein) is critical to uncover the whole picture of the signal transduction mechanism. However, the D53/SXMLs protein has a high molecular weight in the region of 100 kDa. Moreover, structural prediction using an AI system, such as alphafold2, predicted the presence of several disordered regions, which might be the reason for the instability of this family of proteins. Furthermore, the enzymatic

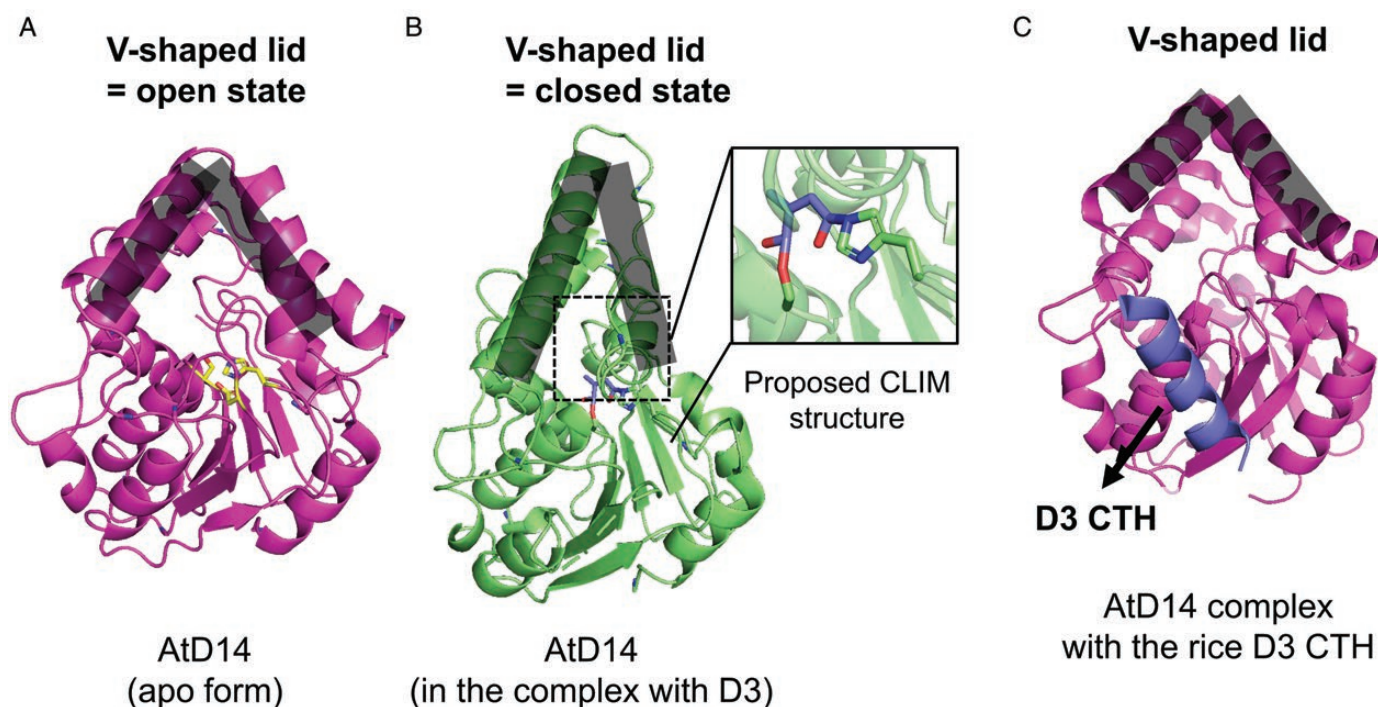


Fig. 3. The crystal structure of *Arabidopsis thaliana* D14. (A) AtD14 apo form. (B) Conformationally altered form in the signaling complex with D3. (C) AtD14 (Arabidopsis protein) complex with the C-terminal helix (CTH) of D3 (rice protein, blue).

function of D14 makes elucidating the structure of the receptor complex very difficult.

Functionally diversified receptors in the D14 and its paralog KAI2 families

The SL receptor D14 has a paralog called HYPOSENSITIVE TO LIGHT (HTL), KARRIKIN INSENSITIVE 2 (KAI2), or DWARF14LIKE (D14L) (Arite *et al.*, 2009; Waters *et al.*, 2012). HTL/KAI2 (referred to as KAI2 hereafter) in Arabidopsis is involved in the perception step of the smoke-derived germination inducer, karrikin (KAR). The Arabidopsis *kai2* mutant shows delayed germination and a longer hypocotyl phenotype. Interestingly, KAI2 has a signaling mechanism quite similar to that of D14. In the KAI2 signaling pathway, SMAX1 and SMXL2, homologs of SMXL6/7/8, act as the repressors, and the common F-box protein, MAX2, mediates the ligand-dependent ubiquitination of the repressor proteins (Fig. 2) (Nelson *et al.*, 2011; Stanga *et al.*, 2013). A series of cross-species complementation experiments using AtD14 and KAI2 revealed that they could not functionally replace each other, suggesting that these two pathways independently regulate plant growth and development (Waters *et al.*, 2015). Although recent studies have revealed partial overlapping of these two pathways (Wang *et al.*, 2020; Li *et al.*, 2022), D14 and KAI2 transmit their physiologically distinct signals through SMXL6/7/8 and SMAX1/SMXL2, respectively, in Arabidopsis. In addition to the specific interaction of D14 and KAI2 with cognate repressors, these receptors distinguish their own ligand molecules. The presence of an endogenous KAI2 ligand molecule (KAI2 ligand=KL) has been proposed (Conn and Nelson, 2015), but the chemical structure of this molecule has not yet been identified. However, experiments using a series of stereoisomers of SL synthetic analogs demonstrated that KAI2 can physically interact with the non-natural type stereoisomers of SLs (Scaffidi *et al.*, 2014). In the case of a commonly used SL analog, GR24, (+)-GR24, which has the same stereochemistry at the D-ring (C-2' position) compared with the naturally existing SLs, is specifically recognized by D14, whereas KAI2 interacts with its enantiomer, (−)-GR24. More recently, the desmethyl type SL analogs, in which the methyl group in the SL D-ring is lacking, were found to be specifically recognized by not only Arabidopsis KAI2 but also its orthologs in other plant species such as a liverwort, *Marchantia polymorpha*, suggesting that this ligand specificity is a conserved feature of the KAI2 family of receptors (Yao *et al.*, 2021). It is still unclear how the two homologous receptors distinguish different ligands. The crystal structures of D14 and KAI2 have been solved, and detailed comparisons of their structures suggested that the ligand-binding pocket size of KAI2 is narrower than that of D14 (Kagiyama *et al.*, 2013) (Fig. 4A). This observation is consistent with the difference in the ligand size

between KAR and SL, and also supports the idea that KAI2 prefers desmethyl-type SLs.

As mentioned above, SLs were initially discovered as germination stimulants for root parasitic plants such as *Striga* and *Orobancha*. In 2015, the SL receptors in *S. hermonthica* were identified (Conn *et al.*, 2015; Toh *et al.*, 2015; Tsuchiya *et al.*, 2015). The characterized receptors belong to the KAI2 family; however, they are classified into a specific clade that has diverged from the non-parasitic plants KAI2 (Conn *et al.*, 2015). Phylogenetic analysis has revealed that the root parasitic plants possess multiple genes in this specific clade which is called KAI2 divergent (KAI2d) to distinguish it from the conserved KAI2 (KAI2c) and intermediate (KAI2i) clades. There are at least 11 KAI2 genes in *S. hermonthica*. Interestingly, one of them (*ShHTL7*) is highly sensitive to SL when expressed in Arabidopsis (Toh *et al.*, 2015). More recently, the function of five KAI2d proteins in another parasitic plant, *Orobancha minor*, was analyzed, and it was demonstrated that OmKAI2d3 is as highly sensitive to SL as ShHTL7 (Takei *et al.*, 2023). Therefore, it is interesting that the sensitivity of each KAI2d receptor to SL is different among highly duplicated SL receptors in root parasitic plants. The molecular mechanisms underlying the high sensitivity of ShHTL7 or OmKAI2d3 have not yet been elucidated. A report showed that ShHTL7 has an ability to interact with the Arabidopsis MAX2 protein more efficiently compared with other ShHTLs, as examined by yeast two-hybrid experiment or pull-down assay, indicating that this might be the reason for the high sensitivity of ShHTL7 (Y. Wang *et al.*, 2021). On the other hand, recent studies using SL synthetic analogs with different levels of hydrolyzability suggested that hydrolyzability by ShHTL7, or in other words the ability to form a covalently bound hydrolysis intermediate, is correlated with the seed germination-inducing activity for *S. hermonthica*. Moreover, the physiological importance of the multiple receptors with different levels of sensitivity in one plant species is also not clear. Root parasitic plants possess not only the KAI2d clade receptors but also D14, KAI2i, and KAI2c. Therefore, how parasitic plants use the diversified receptors properly to distinguish both exogenous and endogenous SLs, and KL is an important unresolved issue.

Structural modeling of KAI2d in root parasitic plants suggested that the enlargement of the ligand-binding pocket is due to amino acid substitutions around the ligand-binding pocket (Conn *et al.*, 2015). The crystal structure of ShHTL5, an *S. hermonthica* SL receptor, was solved, and it showed that the ligand-binding pocket is indeed larger than that of KAI2c (Toh *et al.*, 2015) (Fig. 4A). Later, the structures of ShHTL4, ShHTL7, ShHTL8, and OmKAI2d4 were also solved. All these receptors have larger cavities than KAI2c (Shahul Hameed *et al.*, 2018; Xu *et al.*, 2018; Y. Zhang *et al.*, 2020; Takei *et al.*, 2023) (Fig. 4A). Thus, the larger pocket size is one of the critical features for the KAI2d clade SL receptors in root parasitic plants. Recently, it was reported that the introduction of only three amino acid substitutions in the Arabidopsis KAI2c, relative to

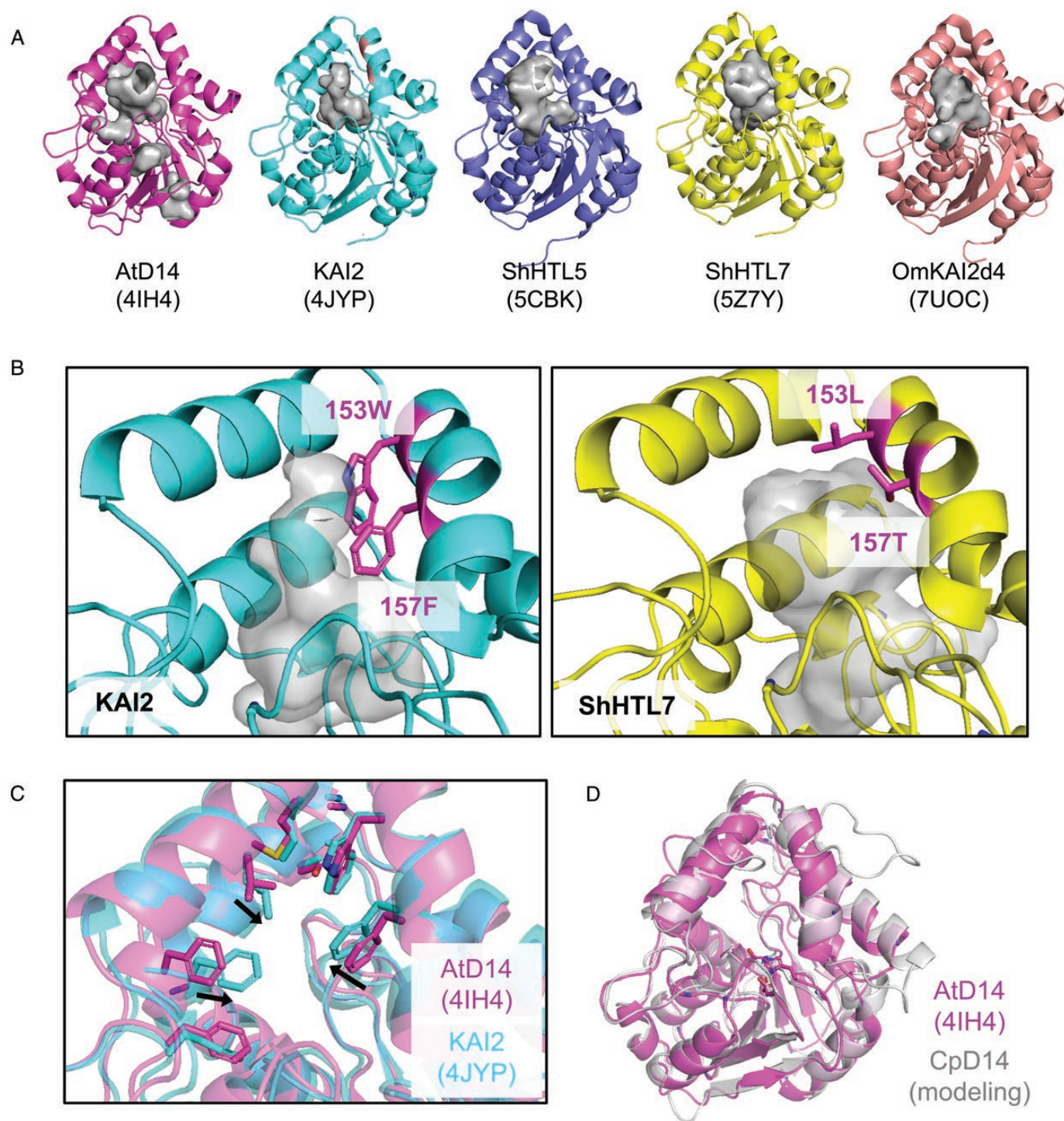


Fig. 4. Structure of the D14 and KAI2 proteins. (A) Structure of AtD14, KAI2, and the parasitic plant divergent clade KAI2/HTL. The cavity in the molecule is highlighted in gray. The PDB codes are in parentheses. (B) Structural comparison of Arabidopsis KAI2 and *S. hermonthica* HTL7 proteins. The key amino acid residues that may determine the ligand specificity are indicated by magenta. (C) Structural comparison of AtD14 and KAI2. KAI2 has a smaller binding pocket due to the shift of some amino acids surrounding the binding pocket surface. (D) Structural comparison of AtD14 and a fungal D14 homologue (CpD14).

the parasitic plants' KAI2d, can change its function into an SL receptor (Arellano-Saab *et al.*, 2021). These mutations include pocket surface amino acid substitutions such as Trp into

Leu and Phe into Thr, suggesting that the expansion of the pocket size is partly due to substitutions from bulky to small amino acids (Fig. 4B). As mentioned above, the pocket size of

D14 is also larger than that of KAI2c. However, the comparison of the pocket surface amino acids between KAI2c and AtD14 suggests that they are highly conserved between these two receptors. However, some surface amino acids in KAI2c locate much closer to the inside, resulting in a decrease in the pocket size (Kagiya *et al.*, 2013) (Fig. 4C). Currently, the factors that make such a difference are unknown. Interestingly, the model moss *P. patens* possesses >10 KAI2 genes in its genome, like root parasitic plants. However, all of these genes do not fall into the KAI2d clade, but they are close to the KAI2c clade. Biochemical and genetic analyses of these PpKAI2s have suggested that some of them are involved in the perception of the uncharacterized SL-like molecule(s), biosynthesized via CCD7 and CCD8 (Lopez-Obando *et al.*, 2021). On the other hand, it is likely that other PpKAI2s are involved in the KL signaling pathway. Therefore, *P. patens* might have developed unique mechanisms for the KAI2-mediated signaling pathway, and it will be interesting to study how these functionally diverse receptors are established in *P. patens*.

The SL receptors in fungi

In addition to their functions *in planta*, plant-derived SLs are also sensed by AM fungi as signals to detect host plants for symbiosis. AM fungi belong to the subphylum Glomeromycota, which includes many different species of plant symbiont fungi. As mentioned above, the activity of SLs on hyphal branching has been mostly evaluated using *Gigaspora margarita*, and it was suggested that *G. margarita* can respond to most naturally occurring SLs derived from various plant species. Although information about the structural requirement for AM fungi is increasing, the SL receptor in AM fungi has not yet been identified. AM fungi are obligate symbionts that require the host plant to complete their life cycle. The difficulty in culturing them in the absence of the host is one major barrier to performing basic research, such as SL receptor characterization. Recently, a candidate SL receptor was identified in the phytopathogenic fungus *Cryphonectria parasitica* (Fiorilli *et al.*, 2022). Although it has a low sequence similarity to D14, it belongs to the α/β -hydrolase family, and structural modeling suggested a similar structure to D14 (Fig. 4D). Based on this structural similarity, the potential SL receptor was named CpD14. Intriguingly, CpD14 hydrolyzes the synthetic SL analog GR24. Moreover, GR24 treatment inhibited the growth of the *C. parasitica* wild-type strain, whereas the *cpd14* knockout mutant was more resistant to GR24. Although functional analyses have yet to be conducted, the presence of a CpD14 homolog in AM fungi is a promising advance toward isolating the SL receptor in AM fungi.

Conclusions and perspectives

Remarkable progress in understanding SL's chemical structure, biosynthesis, and signaling has been made and the research

field of SL is still expanding. The variation of SLs identified in root exudates is likely to be part of the diverse SL structures. Many aspects of SLs, their biosynthesis processes, control of plant traits, and evolution still need to be clarified. Notably, the structure of SLs acting as endogenous plant hormones is not known. In addition, the identification of the endogenous ligand of KAI2 will be a challenging but indispensable issue to address in this field of research. D14 originated by gene duplication of KAI2 in the common ancestor of the seed plants (Waters *et al.*, 2012). Recent genome analysis revealed that KAI2 originated from a horizontal gene transfer of the *RsbQ* gene from bacteria (Q. Wang *et al.*, 2021). Thus, studies in bacteria will provide the key to understanding the origin of SL/KL signaling. A complete understanding of the SL and KL signaling pathways will uncover the relationship between these two homologous signaling pathways. Answering these questions will raise new questions and lead to further developments in our understanding of SLs.

Conflict of interest

The authors have no conflict of interest.

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