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REVIEW

The role of strigolactone structural diversity in the host specificity and control of *Striga*, a major constraint to sub-Saharan agriculture

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Social Impact Statement

The parasitic weed *Striga* affects crops such as sorghum, maize, millet, and rice in over 40 countries on the African continent and negatively impacts the livelihood of over 300 million small-holder farmers. *Striga* seeds can remain dormant in the soil for many years until they are triggered to germinate by germination stimulants, called strigolactones, exuded from the roots of their host. Here, the current knowledge on the biosynthesis of the strigolactones, their structural diversity, and biological relevance are reviewed. This knowledge could improve *Striga* control and thus improve the livelihood of small-holder farmers.

Summary

The parasitic plant genus *Striga* causes major yield losses to several crops such as sorghum, millet, and rice in arid and semi-arid regions of the tropics. For *Striga* to successfully parasitize its host plant, two conditions should be fulfilled: suitable germination conditions and the presence of a host plant that exudes so-called germination stimulants, strigolactones, that are also as a signal to attract beneficial microorganisms such as arbuscular mycorrhizal (AM) fungi. Different plant species exude qualitatively and quantitatively different blends of strigolactones, and this plays a key role in determining *Striga* host specificity. Sorghum *lgs1* genotypes with a mutation in a sulfotransferase (SbSOT4A), for example, exude orobanchol and are resistant to *Striga*, while 5-deoxystrigol is the major strigolactone exuded by susceptible cultivars with wild type SbSOT4A. In this review, we discuss the current knowledge on the biosynthesis of the large diversity of strigolactones, how SbSOT4A may be involved in this, and how strigolactone diversity may contribute to microbiome recruitment. Finally, we discuss how knowledge on the importance of strigolactone diversity can contribute to *Striga* control.

KEYWORDS
arbuscular mycorrhizal fungi, microbiome, parasitic plants, sorghum, *Striga*, strigolactones, sulfotransferase

1 | INTRODUCTION

The production of strigolactones by plants and its role in the symbiosis with microorganisms played a significant role in land colonization during the Silurian (470 million years ago, MYA) by the first Embryophytes (land plants). Indeed, fossil evidence of the first mycorrhizal symbiosis with plants dates back to 407 MYA during the Devonian period (Rich et al., 2021; Strullu-Derrien et al., 2018). These fossils show that at that time, plant roots were already colonized by fungi belonging to the Glomeromycota, which also today is the major division of symbiotic fungi associated with plant roots, in over 80% of terrestrial plants.

Arbuscular mycorrhizal (AM) fungi, which also belong to the Glomeromycota, are obligate biotrophs that cannot complete their life cycle without colonizing a host plant. Strigolactones induce the initiation of the pre-symbiotic stage in AM fungi, which is characterized by hyphal branching of the germinated spores. In addition to hyphal branching, strigolactones may stimulate spore germination or act as a chemoattractant to direct the AM hyphae towards the roots (Akiyama et al., 2010). AM fungi form a hyphopodium on the host root where its hyphae emerge from and penetrate into the root cells. There, the fungus forms arbuscules, the major site for nutrient exchange between the fungus and the plant that is formed in the cells of the root cortex by repeated branching of the hyphae (Akiyama et al., 2010; Bücking et al., 2012). Inorganic phosphorous is taken up from the soil by the hyphae of the fungus and accumulates in its vacuole as polyphosphates (inorganic phosphate), which are later hydrolyzed to an available form of phosphate and delivered to the host plant through the arbuscule. In return, the host plant provides carbon, fixed in photosynthesis, to the fungus. Plants colonized by AM fungi contain up to four-fold higher levels of an inorganic oxidized form of phosphate than plants do to which phosphate fertilizer has been applied and that do not engage in symbiosis with AM fungi (Nouri et al., 2014).

The crucial role of strigolactones in facilitating this symbiosis explains why plants produce and exude strigolactones into the rhizosphere, even though the strigolactones were also shown to be a host cue (a germination stimulant) for root parasitic plants, such as the witchweeds and broomrapes (Bouwmeester et al., 2007; Cook et al., 1966). Parasitic plants parasitize the root or shoot of other plants and withdraw water, nutrients, and amino acids and assimilates from them. Some lack chlorophyl and are fully dependent on their host, such as dodder (*Cuscuta*) and broomrape (*Orobanche* and *Phelipanche* spp.), which are shoot and root parasites, respectively (Agrios, 2005; Nickrent & Musselman, 2004). There are around 200 broomrape species that can infect a wide range of crops such as oilseed rape, sunflower, tobacco, and tomato (Cartry et al., 2021; Parker, 2009). The witchweeds (belonging to the genus *Striga*) are obligate root parasites that do contain chlorophyll. The major weed in this genus, *Striga hermonthica*, called *Striga* from here on, causes significant losses in important cereal crops such as sorghum, maize, millet, and rice, mainly in sub-Saharan Africa (Musselman & Rodenburg, 2023).

The complex life cycle of *Striga* makes it difficult to control. *Striga* seeds stay dormant in the soil until they perceive a germination stimulant, as a cue for the presence of a suitable host. This is an important factor for the success of the parasitic plant to complete its life cycle. The failure to find a host plant in the close vicinity within few days after germination results in death of the seedling (Runo & Kuria, 2018). After germination, upon encountering a host root, the Striga seedling's radicle forms a haustorium, an organ that penetrates the host root cortex and endodermis within 6 to 72 h (Rich & Ejeta, 2007). Then, it establishes a xylem–xylem connection, enabling access to the nutrients from the host plant. After another 4–6 weeks, the *Striga* shoot will emerge from the ground (Pageau et al., 1998). Most damage to the host plant is already caused during the belowground period. Finally, to complete its life cycle, shoots develop and flower and set and shed seeds, thus increasing the number of seeds in the soil seed bank.

In addition to being a rhizosphere signal, strigolactones also are an *in planta* phytohormone that regulates plant development and architecture. One of the most well-known roles is as a branching-inhibiting hormone. Strigolactone-deficient mutants in pea, *Arabidopsis*, and rice display enhanced shoot branching (Gomez-Roldan et al., 2008; Sorefan et al., 2003; Umehara et al., 2008; Yuan et al., 2023). Strigolactones can serve as both growth promotor and inhibitor in different plant organs. For instance, above ground, strigolactones repress bud outgrowth but can stimulate secondary growth of the stem and promote internode elongation (Agusti et al., 2011; de Saint Germain et al., 2013). Below ground, strigolactones promote root hair elongation and lateral root formation (Ruyter-Spira et al., 2011; Wu et al., 2017). Strigolactones have also been demonstrated to play a role in biotic and abiotic stress responses. The best-studied example of this is their increased production during plant exposure to low nutrient conditions, especially of phosphate (Jamil et al., 2011; Yoneyama et al., 2007). This upregulation of strigolactone production under low phosphate conditions results in the repression of shoot branching and the adaptation of root architecture, with increased lateral roots and root hairs, allowing the plant to explore the soil for phosphate (Ezquerro et al., 2022; Gomez-Roldan et al., 2008; Kohlen et al., 2011; Ruyter-Spira et al., 2011; Sun et al., 2016; Umehara et al., 2010). Through this mechanism, plants can respond promptly to changing environmental conditions.

A large number of strigolactones have been identified in the root exudate of plants, and plant species produce different blends of strigolactones that may even vary among cultivars with in a species. This diversification in root exudate strigolactone composition has been shown to impact plant rhizosphere signaling (Awad et al., 2006; Gobena et al., 2017; Yoneyama et al., 2015, 2011, 2008). For instance, in sorghum, genotypes with high levels of 5-deoxystrigol and sorgomol show significantly higher germination stimulant activity in *Striga* than do genotypes producing mainly orobanchol (Gobena et al., 2017; Mohemed et al., 2018; Wakabayashi, Ueno, & Sugimoto, 2022). Under field conditions, this results in a higher *Striga* infection of the former genotypes (Gobena et al., 2017; Mohemed et al., 2016). In vitro studies confirm that strigol-type strigolactones,

such as 5-deoxystrigol, have a higher germination stimulant activity toward *S. hermonthica* than orobanchol-type strigolactones (Mohemed et al., 2018; Nomura et al., 2013). Interestingly, this stereochemically specific response is *Striga* species dependent. In contrast to *S. hermonthica*, *Striga gesnerioides* is more sensitive to orobanchol-type than strigol-type strigolactones (Nomura et al., 2013; Ueno et al., 2011; Vurro et al., 2019). On the other hand, the induction of hyphal branching activity in the AM fungus *Gigaspora margerita* seems less affected by the stereochemistry of strigolactones, while modifications in the ABC-part of the strigolactones do impact hyphal branching (Akiyama et al., 2010). Indeed, in sorghum, the colonization of the roots by three different species of AM fungi is not affected by the difference in root exudate composition of 5-deoxystrigol and orobanchol producing genotypes (Gobena et al., 2017). These different responses of different organisms to particular strigolactones can also be seen in bioassays with root exudates. Different HPLC fractions of root exudates collected from rice showed contrasting activity towards *Striga* germination and AM fungal hyphal branching (Cardoso et al., 2014).

Among the 40 *Striga* species reported worldwide, 33 species have been found in Africa infecting 11 major crops (Ejeta et al., 2007; Gethi & Smith, 2004; Reda & Verkleij, 2004). As a result, in sub-Saharan Africa alone, it is estimated to cause a yield loss valued at US $383 million per year (Woomer et al., 2008). Understanding the role of strigolactones in host specificity of parasitic weeds and in the recruitment of AM fungi will be key to combating this pernicious weed. In this review, we discuss the current knowledge on strigolactone biosynthesis and diversification in plants and how this could contribute to a better control of *Striga*.

2 | STRIGOLACTONE BIOSYNTHESIS

Over 30 strigolactones have been identified from a wide range of different plant species (Yoneyama & Brewer, 2021). Strigolactone diversification arises from modifications such as hydroxylation, acetylation, methylation, and epoxidation. Canonical strigolactones share the common skeleton of a tricyclic lactone (ABC ring) connected to a butenolide D-ring in *2′R* configuration via an enol ether bridge. They can be grouped into two types based on the stereochemistry of the B-C ring junction: strigol-type, with β orientation, and orobanchol-type, with α orientation (Wang & Bouwmeester, 2018). In general, biosynthesis of strigolactones starts with the isomerization of all-*trans*-β-carotene to 9-*cis*-β-carotene by the β-carotene isomerase, DWARF27 (D27) (Alder et al., 2012; Sorefan et al., 2003). This 9-*cis*-β-carotene subsequently serves as a substrate for CAROTENOID CLEAVAGE DIOXYGENASE 7 (CCD7) that converts it into the C13 β-ionone and C27 9-*cis*-β-apo-10′-carotenal (Alder et al., 2012; Schwartz et al., 2004; Sorefan et al., 2003). Further cleavage of 9-*cis*-β-apo-10′-carotenal is catalyzed by CAROTENOID CLEAVAGE DIOXYGENASE 8 (CCD8), and this cleavage reaction results in the formation of carlactone (CL), which has the *2′R* configured D-ring (Alder et al., 2012; Seto et al., 2014). In *Arabidopsis*, the cytochrome P450 (CYP) MORE AXILLARY GROWTH 1 (MAX1) catalyzes the conversion of CL to carlactonoic acid (CLA), which is further converted to methyl carlactonoate (MeCLA) by a CLA methyltransferase (Abe et al., 2014; Mashiguchi et al., 2022). In rice, a MAX1 homolog, Os900, called carlactone oxidase, catalyzes the direct conversion of CL to 4-deoxyorobanchol, instead of via CLA as in *Arabidopsis*, which is subsequently converted to orobanchol by another MAX1 homolog, Os1400, called orobanchol synthase (Zhang et al., 2014). 4-Deoxyorobanchol and 5-deoxystrigol are the precursors of the orobanchol- and strigol-type strigolactones, respectively, through further modifications. For instance, 5-deoxystrigol has been shown to be the precursor of the strigol-type strigolactone, sorgomol (Motonami et al., 2013; Xie et al., 2010), through C9-hydroxylation by SbCYP728B35 (encoded by *Sobic.008G122800*) (Wakabayashi et al., 2021). Interestingly, convergent evolution of the biosynthesis of orobanchol was demonstrated in tomato and cowpea with a CYP722C (encoded by *Solyc02g084930.3* and *Vigun09g224400*, respectively), instead of MAX1 homologs as in rice, catalyzing the two-step oxidation of CLA to orobanchol (Wakabayashi et al., 2019). Recently, Wu et al. (2023) demonstrated that a *Prunus persica* cytochrome P450, CYP711c, encoded by *LOC18790989* can synthesize strigol directly from CL (Wu et al., 2023). CYP722C family members were shown to catalyze the production of 5-deoxystrigol from CLA in lotus and cotton (Mori et al., 2020; Wakabayashi et al., 2020). In tomato, double oxidation of orobanchol by CYP712G1 results in the formation of didehydroorobanchol (DDH) isomers (Wang et al., 2022). Wakabayashi, Moriyama, et al. (2022) and Wakabayashi, Ueno, and Sugimoto (2022) identified these three putative DDH isomers as 6,7-didehydroorobanchol, phelipanchol, and *epi*-phelipanchol. In maize, another cytochrome P450 was shown to be involved in the diversification of strigolactones. A single CYP, ZmCYP706C37, was shown to catalyze a series of oxidative steps in the biosynthesis pathway leading to the production of zealactone (Li et al., 2023).

Despite significant progress in the elucidation of strigolactone biosynthesis in a large number of plant species, the biosynthesis of many is still only postulated, and the genes encoding these putative enzymatic activities are still unknown. For instance, the genes catalyzing the production of strigone, strigyl acetate, fabacol, solonacol, and sorgolactone have not yet been identified. The high diversity in the pathways of different plant species makes it difficult to translate the knowledge gained from one plant species to another. An example of this is the biosynthesis of orobanchol in sorghum, a crop species of which yield in the African continent is strongly hampered by infection with *Striga hermonthica* (Ejeta, 2007; Mwangangi et al., 2023).

3 | STRIGOLACTONE BIOSYNTHESIS IN SORGHUM

To breed for *Striga* resistance in sorghum, an in vitro assay was developed that scores the distance between the root of a sorghum seedling and germinated *Striga* seeds co-cultured in agar to select for lines that induced less *Striga* germination (Hess et al., 1992). Indeed, the authors identified a low germination stimulant activity mutant and coined it

BOX 1 Sulfotransferases

Sulfotransferases (SOTs) are present in a wide range of organisms including plants. They catalyze the transfer of a sulfuryl group (-SO_3) from a donor, 3′-phosphoadenosine-5′-phosphosulfate (PAPS), to an alcohol or amine acceptor. As a result of this reaction, a sulfate conjugate, sulfate ester, or sulfamate and 3′-phosphoadenosine-5′-phosphate (PAP) is formed (Hirschmann et al., 2017). The role of SOT in plants is still poorly understood. They play a role in the detoxification of xenobiotics and the modification of secondary metabolites. Sulfation of xenobiotics such as herbicides and pesticides detoxify the latter, and this reduces the negative effect these compounds have on the growth and development of the plant. SOTs facilitate the transport or storage of compounds in a less toxic form (Baek et al., 2010). Sulfation also modulates signaling in response to stress. For instance, sulfated quercetin stimulates auxin transport from the apical tissues and promotes plant growth (Ananvoranich et al., 1994; Varin & Ibrahim, 1989). Interestingly, the same SOT was also shown to have a broader spectrum of substrates and play a role in detoxification by sulfating cycloheximide and toxins produced by bacteria (Chen et al., 2015).

The characterization of three SOTs from *Flaveria chloraefolia* sheds light on their possible role in the regulation of plant growth. All three FcSOTs were shown to catalyze the sulfation of the flavonoid quercetin. AtSOT12 (the product of *At2g03760*) that has SOT activity towards brassinosteroids was also shown to use salicylic acid (SA) and flavanone as substrates (Baek et al., 2010; Hashiguchi et al., 2014; Marsolais et al., 2007). The expression of three brassinosteroid SOTs from *Brassica napus* and two from *Arabidopsis thaliana* was shown to be induced by SA, which suggests they may have a role in plant defense against pathogens (Marsolais et al., 2007; Rouleau et al., 1999). In humans and animals, cytosolic SOTs have been shown to inactivate signal molecules such as steroids and thyroids or to play a role in the storage of some molecules, which later can be reactivated by sulfatases or be transported by transporters (Coughtrie, 2016; Reed et al., 2005). A good example of the latter is the *Arabidopsis* cytosolic SOT, AtSOT18, that sulfates glucosinolates (Graser et al., 2001; Klein et al., 2006). Salicylic acid sulfation is mediated by AtSOT12, which results in a less toxic form and was suggested to happen when the level of SA is high after the plant has been exposed to stress such as pathogen infection (Baek et al., 2010). In other cases, sulfation is a form of activation of metabolites. For instance, several studies on SOTs demonstrated their involvement in the plant response to biotic and abiotic stresses. Sulfation plays an important role in glucosinolate biosynthesis since the desulfoglucosinolates are not functional. It has been suggested that desulfoglucosinolates are a storage or transport form since they are less toxic to the plant (Klein et al., 2006; Mithen, 2001). Mutants in AtSot12, which is known to sulfate brassinosteroids, are hypersensitive to salt and display an increased level of ABA and higher susceptibility to pathogens (Baek et al., 2010; Hirschmann et al., 2014).

SOTs are classified as soluble/cytosolic or membrane-associated (Chapman et al., 2004). Cytosolic SOTs preferably sulfate small molecules such as hormones while the membrane-associated SOTs are mainly involved in the post-translational modification of macromolecules, such as carbohydrates, proteins, proteoglycans, and glycolipids (Chapman et al., 2004). SOT family proteins contain four highly conserved regions with critical residues for binding of the cofactor 3′-phospho-adenosyl-5′-phosphosulfate (PAPS) (Driscoll et al., 1995; Komatsu et al., 1994; Marsolais & Varin, 1995). The N-terminal Region I contains a 5′-phosphosulfate binding loop (PSB). Region II contains a 3′-phosphate binding loop (PB) and starts with a highly conserved catalytic histidine. This region is important for proton acceptance during sulfuryl transfer (Kakuta et al., 1998). Regions II and III contain important residues that form a parallel stack with the adenine group of PAPS (Hernàndez-Sebastiá et al., 2008). Region IV, located at the C-terminal of SOTs, contains GxxGxxK and KxxxTVxxxE motifs, with the latter being important for dimerization (Komatsu et al., 1994; Petrotchenko et al., 2001). As shown in Figure 1, these four regions are conserved in SbSOT4A.

So far, AtSOT18 of *Arabidopsis thaliana* is the only plant SOT with a complete structure published. AtSOT18 is a cytosolic sulfotransferase that catalyzes the sulfation of desulfoglucosinolates. In vitro, AtSOT18 was shown to sulfate a broad spectrum of substrates but with a preference for 7-methylthioheptyl and 8-methylthiooctyl glucosinolates (Klein & Papenbrock, 2009).

lgs1. Using recombinant inbred lines derived from the *lgs1* genotype, SRN39, and the high *Striga* seed germination stimulant genotype Shanqui Red, the *LGS1* locus was mapped to Chromosome 5. The region was fine-mapped to 400 kb, which based on the sorghum genome sequence and comparative analysis of the rice genome encompassed about 30 genes (Satish et al., 2012). One of these genes, *Sobic.005G213600* encoding a sulfotransferase, SbSOT4A, was determined to be the gene underlying the QTL (Gobena et al., 2017). The predominant strigolactone exuded by the roots of *lgs1* mutants is orobanchol, the C-ring of which is in α-orientation, while high germination stimulant, *Striga* susceptible, sorghum lines exude mainly 5-deoxystrigol, with a β-oriented C-ring. Since then, other *lgs1*

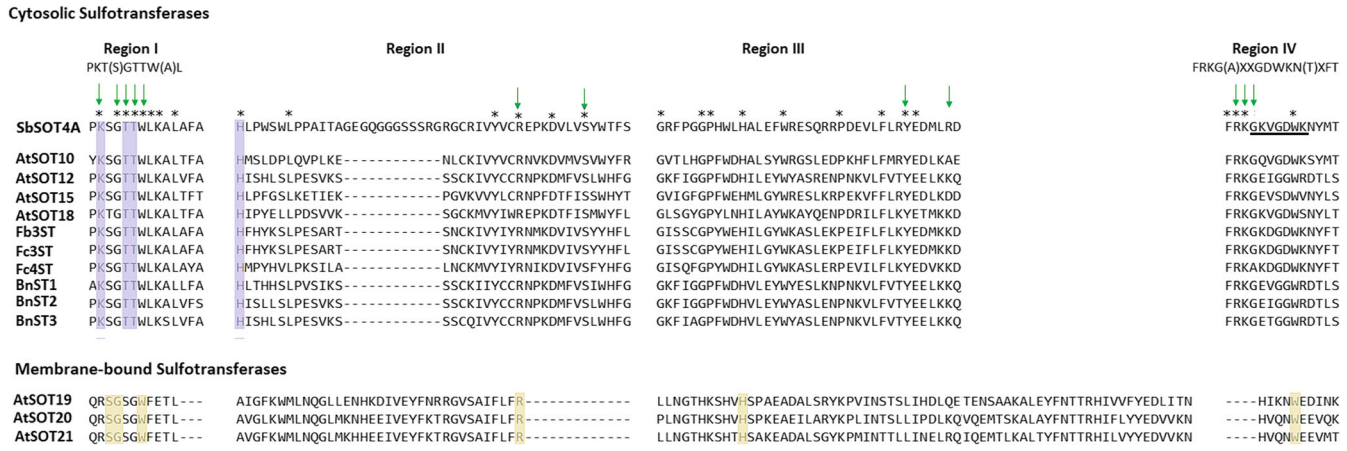

FIGURE 1 Partial amino acid sequence alignment of *Sorghum bicolor* sulfotransferase 4A (SbSOT4A) with functionally characterized or annotated plant sulfotransferases (SOTs). AtSOT10 (product of At2g14920, *Arabidopsis thaliana*), AtSOT12 (from At2g03760, *Arabidopsis thaliana*), AtSOT15 (At5g07010, *Arabidopsis thaliana*), AtSOT18 (At1g74090, *Arabidopsis thaliana*), Fb3ST from *Flaveria bidentis*, Fc3ST and Fc4ST from *Flaveria chlorifolia*, BnST1, BnST2, and BnST3 (the respective products of AF000305, AF000306, and AF000307 from *Brassica napus*), AtSOT19, AtSOT20, and AtSOT21 (from At3g50620, At2g15730, and At4g34420 of *Arabidopsis thaliana*). The four known conserved regions (I–IV) are indicated on top of the alignment. Residues that are also conserved with membrane-associated SOTs are shaded in gray. The 3′-phospho-adenosyl-5′-phosphosulfate (PAPS) binding residues are indicated with green arrows, and the catalytic residues are indicated with purple highlighting.

mutants have been identified among sorghum diversity panels that also predominantly exude orobanchol as the major strigolactone (Bellis et al., 2020; Mutinda et al., 2023). These genotypes display resistance towards *Striga* both under laboratory and field conditions (Mutinda et al., 2023).

As discussed above, orobanchol biosynthesis in rice and tomato is catalyzed by two CYP711As and a CYP722C, respectively (Wakabayashi, Moriyama, et al., 2022; Zhang et al., 2014). There is, however, no CYP722C ortholog in sorghum (Yoda et al., 2021), and instead of the involvement of CYP711A, analogous to rice, mutation of *LGS1* (*Sobic.005G213600*) leads to the production of orobanchol in sorghum, while the presence of wild-type *LGS1* results in 5-deoxystrigol production. This makes the biosynthesis of these two strigolactones in sorghum surprisingly different compared with other plant species; no ortholog of *LGS1* has been found in other Poaceae (Yoda et al., 2021). Indeed, according to Wu and Li (2021), the four sorghum MAX1 homologs are involved in different steps of the strigolactone biosynthesis pathway than their counterparts in rice. For instance, SbMAX1a (encoded by *Sobic.003G269500*) catalyzes up to four steps of oxygenation converting CL to 18-hydroxy-CLA and a negligible amount of orobanchol (Wu & Li, 2021). All this suggests that sorghum evolved a different mechanism for the biosynthesis of orobanchol and the involvement of SbSOT4A in this is puzzling.

4 | SULFOTRANSFERASES

Sulfotransferases (SOTs) may be cytosolic or membrane-bound (see Box 1), and Shimels (2019) showed that SbSOT4A is cytoplasmic. This cytosolic localization of SbSOT4A seems to rule out an alternative explanation for its function, a role in post-translational protein (e.g., of strigolactone biosynthetic enzymes) modification, which is carried out by membrane-associated SOTs (see Box 1).

In general, cytosolic SOTs sulfate a wide range of substrates (Hirschmann et al., 2014). To explore the substrate preference of SbSOT4A, Shimels (2019) performed a BLASTp search with the amino acid sequences of all known SOTs from *Arabidopsis* and rice in several online databases such as Phytozome and NCBI. This resulted in retrieval of 25 non-redundant sorghum AA sequences with a known SOT domain, including SbSOT4A (Shimels, 2019). Alignment of the sorghum SOTs with those of *Arabidopsis*, *Brassica napus*, maize, rice, and other species that were previously functionally characterized was consistent with earlier work (Hernàndez-Sebastiá et al., 2008). However, of the SOTs that cluster with SbSOT4A, none had been functionally characterized, and this thus gave no hint on the possible substrate of the latter.

Therefore, Shimels (2019) used a homology model approach using MODELLER, version 9.18 (Šali & Blundell, 1993) and the X-ray structure of *Arabidopsis thaliana* SOT18 (AtSOT18), co-crystallized with the substrate sinigrin (which was sulfated) and the (desulfated) 3′-phospho-adenosyl-5′-phosphosulfate (PAPS), as a template (Shimels, 2019). SbSOT4A displays only 33% sequence identity with AtSOT18, but the PAPS binding site displays a high level of identity, with the key residues for cofactor binding and catalytic activity being well conserved (Table 1; Figure 2). In contrast, the substrate binding sites of the two SOTs are very different, suggesting the two enzymes have a different substrate specificity (Table 1; Figure 2). On the other hand, Lys93, Thr96, and His155, which are involved in the coordination of the sulfate moiety, are also conserved in SbSOT4A (Lys103, Thr106, and His171), further

TABLE 1 Partial alignment of the protein sequences of *Arabidopsis thaliana* sulfotransferase 18 (AtSOT18) and *Sorghum bicolor* sulfotransferase 4A (SbSOT4A) to illustrate differences in affinity to substrates with different polarity.

Residues involved in PAPS binding																										
	92	93	94	95	96	97	98	125	177	185	243	247	282	283	284	287	311	312	313	314	315	316				
AtSOT18	P	K	T	G	T	T	W	H	R	S	Y	R	C	S	F	L	Y	F	R	K	G	K				
SbSOT4A	P	K	S	G	T	T	W	H	R	S	Y	L	C	S	L	L	F	F	R	K	G	K				
	147	148	149	150	151	152	153	180	254	262	341	345	384	385	386	389	410	411	412	413	414	415				
Residues involved in substrate binding																										
	51	54	65	68	92	93	96	125	130	132	133	134	155	186	189	193	215	216	217	299	302	303	304	305	306	311
AtSOT18	R	E	L	L	P	K	T	H	Y	E	I	D	H	M	F	E	S	G	Y	R	R	P	G	V	Y	Y
SbSOT4A	-	-	A	L	P	K	T	H	F	E	L	M	H	Y	F	A	F	P	G	T	V	L	G	V	T	F
			114	117	147	148	151	185	189	191	192	193	220	263	266	270	313	314	315	399	402	403	404	405	406	411

Note: Only residues important for 3′-phospho-adenosyl-5′-phosphosulfate (PAPS) and substrate binding are shown. - denotes missing amino acids.

supporting the sulfation catalytic activity of the enzyme. In AtSOT18, a network of hydrogen bonds exists between the sulfated sinigrin and the polar sidechains of the substrate binding site. Sinigrin binding to AtSOT18 is further facilitated by hydrogen bonds with the side chains of Arg51, Glu54, Glu193, and Tyr306. However, none of these amino acids are present in SbSOT4A making it unlikely that SbSOT4 can form analogous hydrogen bonds with its substrate. Overall, through several polar to apolar changes, SbSOT4A has a much more hydrophobic substrate binding cavity than AtSOT18, suggesting that the substrate of SbSOT4A has a hydrophobic character, such as possibly a strigolactone-like molecule.

To shed more light on the role of SbSOT4A in the biosynthesis of strigolactones, a protein modelling/substrate docking approach is attractive. The AlphaFold model of SbSOT4A suffers from structural predictions that are not very reliable in the areas surrounding the main substrate binding domain. For example, a loop of amino acids 395 to 411 that is part of the binding site is predicted with a low confidence score (which could indicate that the loop is flexible), and this makes it less ideal for docking simulations. The PDB structure of 5MEX, however, shows this loop in a ready-to-bind state with sinigrin, providing a more accurate template for modelling of SbSOT4A and ligand docking.

Protein-ligand docking using GOLD (CCDC, version 5.2) (Jones et al., 1997) was used to evaluate the docking of hydroxylated CL-like and strigolactone-like substrates into the active site of SbSOT4A (Table S1) (Shimels, 2019). Substrates with a hydroxy group at different positions served to explore positional preference in sulfate formation. Since SbSOT4 has been shown to play a role in the production of 5-deoxystrigol while a deletion of this enzyme results in the production of orobanchol (Gobena et al., 2017), also docking of these two strigolactones was evaluated as well as a number of stereoisomers and further functionalized strigolactones derived from these. Of the CL derivatives investigated (Table S1), 19-hydroxy-CL has been shown to be generated by AtMAX1 as an intermediate in the conversion of CL to CLA (Abe et al., 2014). 18-Hydroxy-CL and 18-hydroxy-CLA were postulated to be (likely enzyme-bound) intermediates in the biosynthesis of 4-deoxyorobanchol from CL by the rice MAX1 homolog Os900 (Zhang et al., 2014). All compounds were successfully docked into the substrate cavity and displayed a common binding mode, with the sulfate moiety binding deep at the catalytic site, whereas the rest of the molecule extends to the edge of the binding site (Figure 3).

Of all the possible substrates, 18-hydroxy-CL gave the best docking score. Figure 4 shows the substrate binding site of the homology model of SbSOT4A with sulfated 18-hydroxy-CL docked in comparison with the binding site of the protein structure of AtSOT18 with sulfated sinigrin. The sulfate group of the sulfated C18-hydroxy-CL is coordinated by Lys103, Thr106, and His171, corresponding to the conserved Lys93, Thr96, and His155 in AtSOT18 involved in the coordination of the sulfate group of sinigrin.

Considering the high docking score for 18-hydroxy-CL, Shimels postulated that sulfation of 18-hydroxy-CL is how SbSOT4A modifies strigolactone stereochemistry. This implies that CL in the presence of

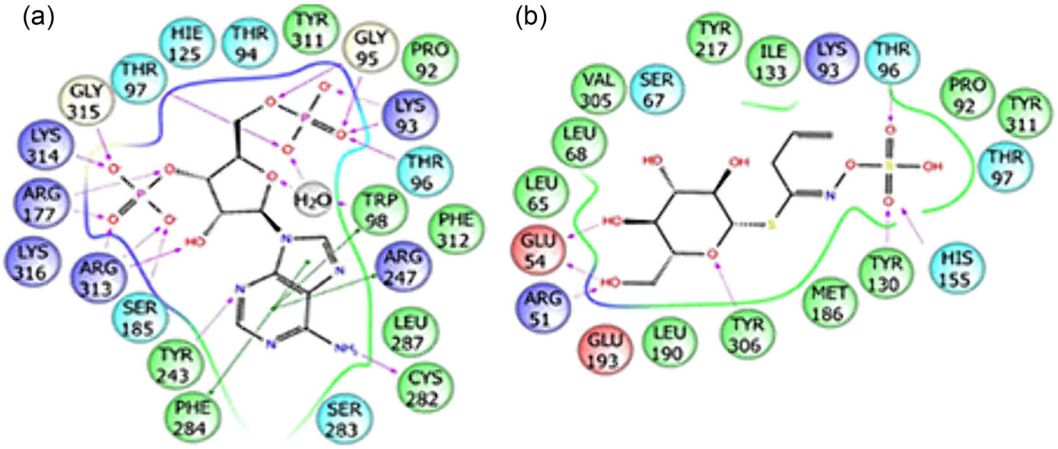

FIGURE 2 Residues in *Arabidopsis thaliana* sulfotransferase 18 (AtSOT18) that are involved in (a) cofactor (3′-phospho-adenosyl-5′-phosphosulfate [PAPS]; desulfated) and (b) substrate (sinigrin; sulphated) binding (Shimels, 2019).

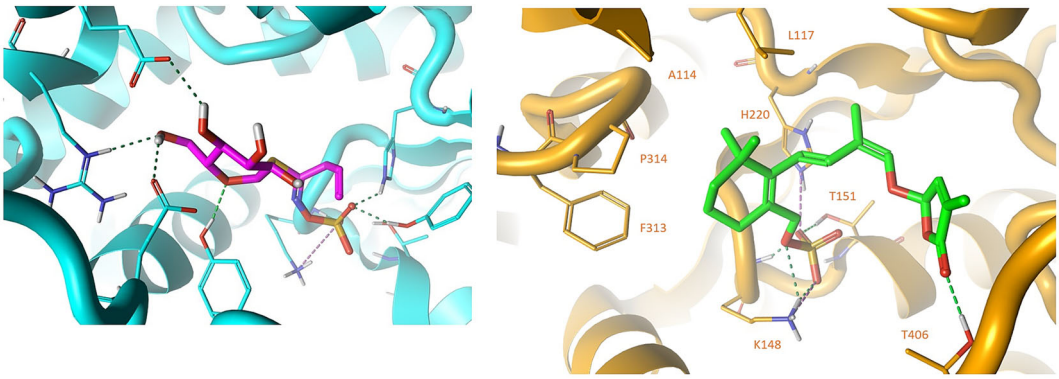

FIGURE 3 Partial models of the substrate binding region of *Arabidopsis thaliana* sulfotransferase 18 (AtSOT18) (left, cyan) with its substrate sinigrin (purple) and *Sorghum bicolor* sulfotransferase 4A (SbSOT4A) (right, brown) with 18-hydroxy-carlactone (18-hydroxy-CL) (green), which showed the highest docking efficiency of all tested putative substrates. Note the difference in polarity of the amino acids in the binding sites of the two enzymes that might correlate with their specificity for different substrates, with very different polarity. Homology models were constructed using MODELLER (Šali & Blundell, 1993) (version 9.18) using the X-ray structure of AtSOT18, Protein Data Bank (PDB) ID 5MEX, Uniprot ID Q9C9C9, co-crystallized with the substrate sinigrin (which was sulfated) and the (desulfated) cofactor PAPS as template.

wild type SOT4A is first hydroxylated at C18. C19 of this sulfated 18-hydroxy-CL is subsequently oxidized to form a carboxy group, likely by one of the MAX1 homologs, which favors ring closure with the loss of the sulfate group to the β-orientation resulting in 5-deoxystrigol. Recently, Yoda et al. (2023) suggested that SbSOT4A sulfates a C18 peroxide, instead of a C18 alcohol as proposed by Shimels (2019), although they do not provide proof for this. A 2-oxoglutarate-dependent dioxygenase (*Sobic.005G213500*, Sb3500) was suggested to subsequently catalyze the stereoselective production of 5-deoxystrigol from this sulphated peroxide.

Loss of SbSOT4A function, and thereby lack of a sulfated intermediate, favors the further oxidation of the C18 hydroxy to a carbonyl, and—upon oxidation of C19 to an acid by a MAX1 homolog—ring closure occurs to an α-orientation resulting in orobanchol (Figure 4). Although we do not know what drives the stereoselectivity of the ring closure, it is analogous to orobanchol formation in rice, which is also fully stereoselective (Zhang et al., 2014).

5 | IMPLICATIONS FOR RHIZOSPHERE COMMUNICATION

Considering the vast abundance of microbes in soil, plants have evolved sophisticated mechanisms to preferentially associate with beneficial, non-pathogenic microbes. Several studies have demonstrated that microbiome assembly is driven by the chemical composition of root exudates. Metabolites such as strigolactones and isoflavones recruit beneficial microbes such as arbuscular AM fungi and nitrogen-fixing rhizobia, respectively (Akiyama et al., 2005; Sugiyama & Yazaki, 2012). Phenolics and benzoaxzinoids have also been shown to modify the root microbiome composition (Cotton et al., 2019; Stringlis et al., 2018; Voges et al., 2019). As described above, the loss of sulfation causes a change in the stereochemistry of the strigolactones produced by sorghum. What would be the driving force for the evolution of this mechanism in sorghum? On the one hand, this could result from a selection pressure for *Striga* resistance.

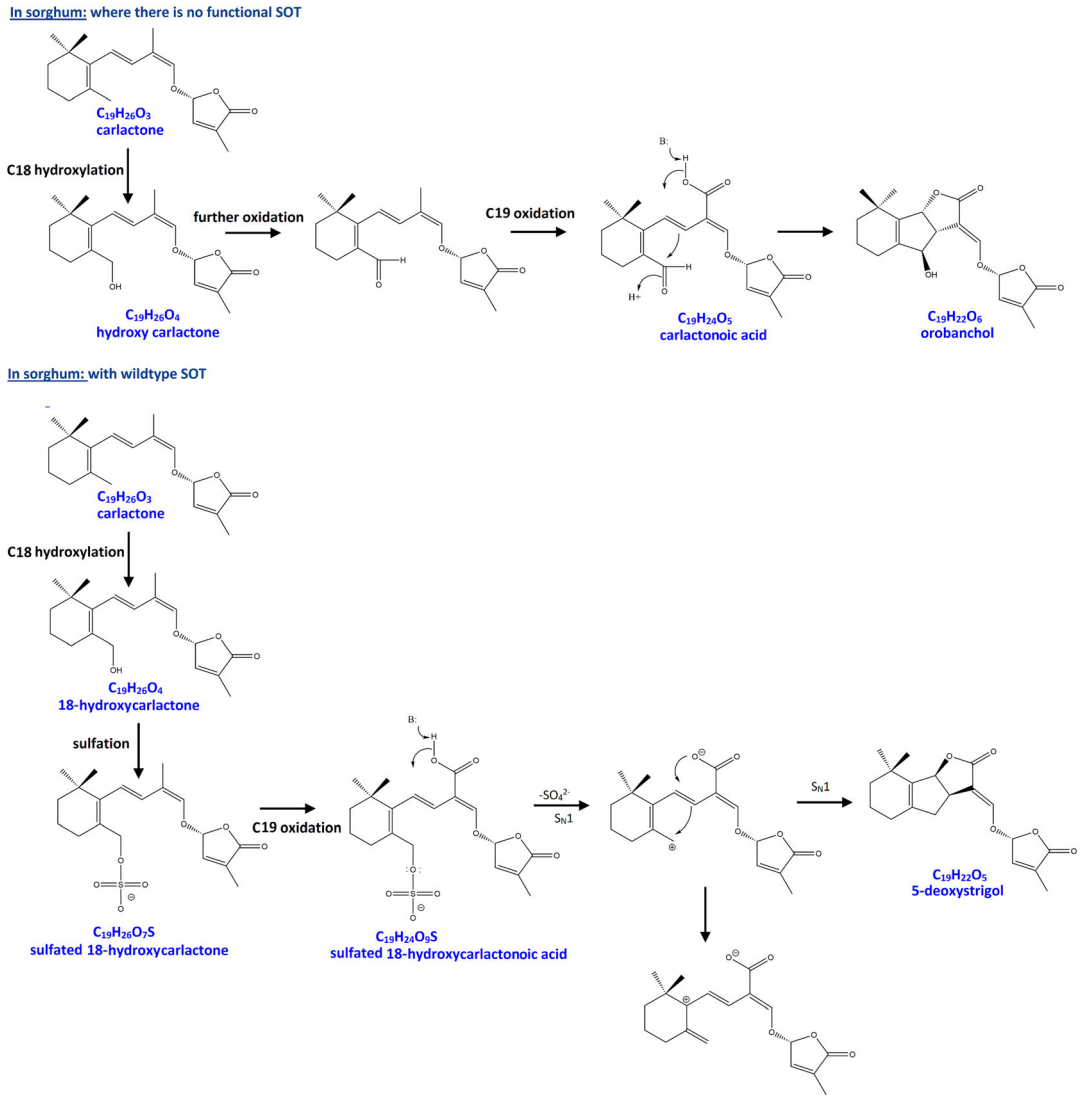

FIGURE 4 Overview of the putative biosynthesis pathway, including putative reaction intermediates, of orobanchol and 5-deoxystrigol in sorghum and the possible role of SbSOT4A in this.

Indeed, orobanchol has much lower *Striga* germination stimulant activity than 5-deoxystrigol, and therefore, the absence of SOT activity results in *Striga* resistance (Gobena et al., 2017). On the other hand, strigolactones are signaling molecules for soil micro-organisms. Orobanchol and 5-deoxystrigol are equally active hyphal branching factors in AM fungi (Akiyama et al., 2010), and as discussed above, indeed, there seems to be no effect of the SOT mutation on AM fungi colonization (Gobena et al., 2017). However, in a metabarcoding study on the recruitment of the bacterial microbiome in sorghum SRN39 and Shanqui Red, the rhizosphere microbiome composition differed between the two genotypes with the abundance of *Acidobacteria* GP1, *Burkholderia*, *Cupriavidus* (Burkholderiaceae), *Acidovorax*, and *Albidiferax* (Comamonadaceae) being higher in the orobanchol producing SRN39 (Schlemper et al., 2017). In rice, also, Kim et al. (2022) reported the strongest effect of orobanchol on microbiome recruitment, including of *Bulkholderia* as reported by Schlemper for sorghum.

Changes in the root microbial community have been shown to contribute to resistance against a range of pathogens (Liu et al., 2020; Trivedi et al., 2020; Vannier et al., 2019), and it has been speculated this may also hold for *Striga* (Masteling et al., 2019). In theory, thus, the change in the microbiome of SRN39 could also be responsible for or at least contribute to the *Striga* resistance of *lgs1* sorghum. In a recent study, Kawa et al. (2023) showed that the microbiome indeed protects sorghum against *Striga* infection, through degradation of haustorium inducing factors and suberin formation (Kawa et al., 2023).

6 | CONCLUSION

Striga is a major global constraint to sub-Saharan agriculture, blighting the lives of millions of African farmers. Elucidating the biosynthesis of the many different strigolactones, their structural diversity, and their biological role could contribute to the control of Striga. The

biosynthesis of strigolactones in sorghum represents an interesting case in which strigolactone biosynthesis affects *Striga* host specificity. Selection for resistance to the root parasitic weed *Striga* resulted in the identification of genotypes that display reduced *Striga* germination stimulant activity. The latter is the result of a change in the type of strigolactone exuded into the rhizosphere (Gobena et al., 2017; Mohemed et al., 2018; Mutinda et al., 2023). Resistant genotypes have a mutation in *LGS1*, a gene encoding the sulfotransferase, SbSOT4A, and exude orobanchol, while 5-deoxystrigol is the major strigolactone exuded by susceptible cultivars with wildtype *LGS1*. Aside from a hydroxy group, these strigolactones differ in the stereochemistry of the B- and C-ring junction. In the present review, we discuss the possible mechanism by which SbSOT4A could bring about this change in stereochemistry. Protein modelling and substrate docking show that of a range of alternative substrates, 18-hydroxy-CL docks with the best docking score into SbSOT4A. A model is proposed for how SbSOT4A, through sulfation of 18-hydroxy-CL, might contribute to the sorghum strigolactone phenotype. The difference in strigolactone stereochemistry between genotypes with and without a functional SbSOT4A does not seem to affect AM fungi colonization but did affect the recruitment of certain bacterial species. The functional consequences of the latter will need to be investigated as it could potentially contribute to the *Striga* resistance of *lgs1* lines. A better understanding of the role of SbSOT4A in the creation of strigolactone stereochemistry, and the potential role of the latter in microbiome recruitment, would help in the selection of *Striga-resistant* sorghum genotypes in breeding programs and thus potentially in improved control of this parasitic weed that is negatively affecting the livelihood of millions of African farmers.

AUTHOR CONTRIBUTIONS

Mahdere Z. Shimels conducted the literature review and drafted the manuscript. The other authors, Stefano Rendine, Patrick Rich, Carolien Ruyter-Spira, Gebisa Ejeta, and Harro Bouwmeester, contributed to the writing and all reviewed and approved the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no known conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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