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BRIEF REPORT

Discovery of strigol synthase from cotton (*Gossypium hirsutum*): The enzyme behind the first identified germination stimulant for *Striga*

Takatoshi Wakabayashi[1] | Megumi Nakayama[1] | Yurie Kitano[1] | Masato Homma[1] | Kenji Miura[2,3] | Hirosato Takikawa[4] | Masaharu Mizutani[1] | Yukihiro Sugimoto[1]

[1]Graduate School of Agricultural Science, Kobe University, Kobe, Japan

[2]Faculty of Life and Environmental Sciences, University of Tsukuba, Tsukuba, Japan

[3]Tsukuba-Plant Innovation Research Center, University of Tsukuba, Tsukuba, Japan

[4]Graduate School of Agricultural and Life Sciences, The University of Tokyo, Tokyo, Japan

Correspondence
Yukihiro Sugimoto, Graduate School of Agricultural Science, Kobe University, 1-1 Rokkodai, Nada, Kobe 657-8501, Japan.
Email: yukihiro@kobe-u.ac.jp

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Societal Impact Statement

Parasitic witchweeds (*Striga* species) pose a serious threat to food security in Africa, attacking cereal grains and legumes. Chemicals released from the host roots that initiate the life cycle of *Striga* are known as germination stimulants, predominantly strigolactones (SLs). Strigol, the first identified SL, was isolated from the root exudates of cotton (*Gossypium hirsutum*), a false host of *Striga*, over 50 years ago. The identification of strigol synthase in cotton establishes the complete biosynthesis pathway of this emblematic SL. This discovery has the potential to advance our understanding of SL-mediated rhizosphere interactions and enhance cotton's effectiveness as a trap crop.

KEYWORDS
biosynthesis, cytochrome P450, *Gossypium hirsutum*, strigol, strigolactone

1 | INTRODUCTION

Strigol, a plant specialized metabolite, was first discovered as a germination stimulant for the root parasitic weed *Striga lutea*, from root exudates of the cotton plants, *Gossypium hirsutum* (Cook et al., 1966) (Figure 1a). Cotton can induce germination of *Striga* seeds but not function as a host. This false host is employed as a trap crop to diminish the seed bank of *Striga*. The relative structure of strigol was determined using spectroscopic and X-ray crystallographic data (Cook et al., 1972). A racemic mixture of strigol (a mixture of two enantiomers, strigol and *ent*-strigol) was synthesized and optically resolved, enabling the unequivocal establishment of the absolute structure of natural strigol (Brooks et al., 1985). Following the discovery of strigol, structural analogs with the germination-stimulating activity for *Striga* were identified in the root exudates of host plants. Butler (1995) coined the term strigolactone (SL) to refer to these strigol analogs. SLs are now recognized as exhibiting diverse functions, including rhizosphere signaling that induces hyphal branching in arbuscular mycorrhizal fungi (Akiyama et al., 2005) and endogenous plant hormones that inhibit shoot branching (Gomez-Roldan et al., 2008; Umehara et al., 2008). The potential of

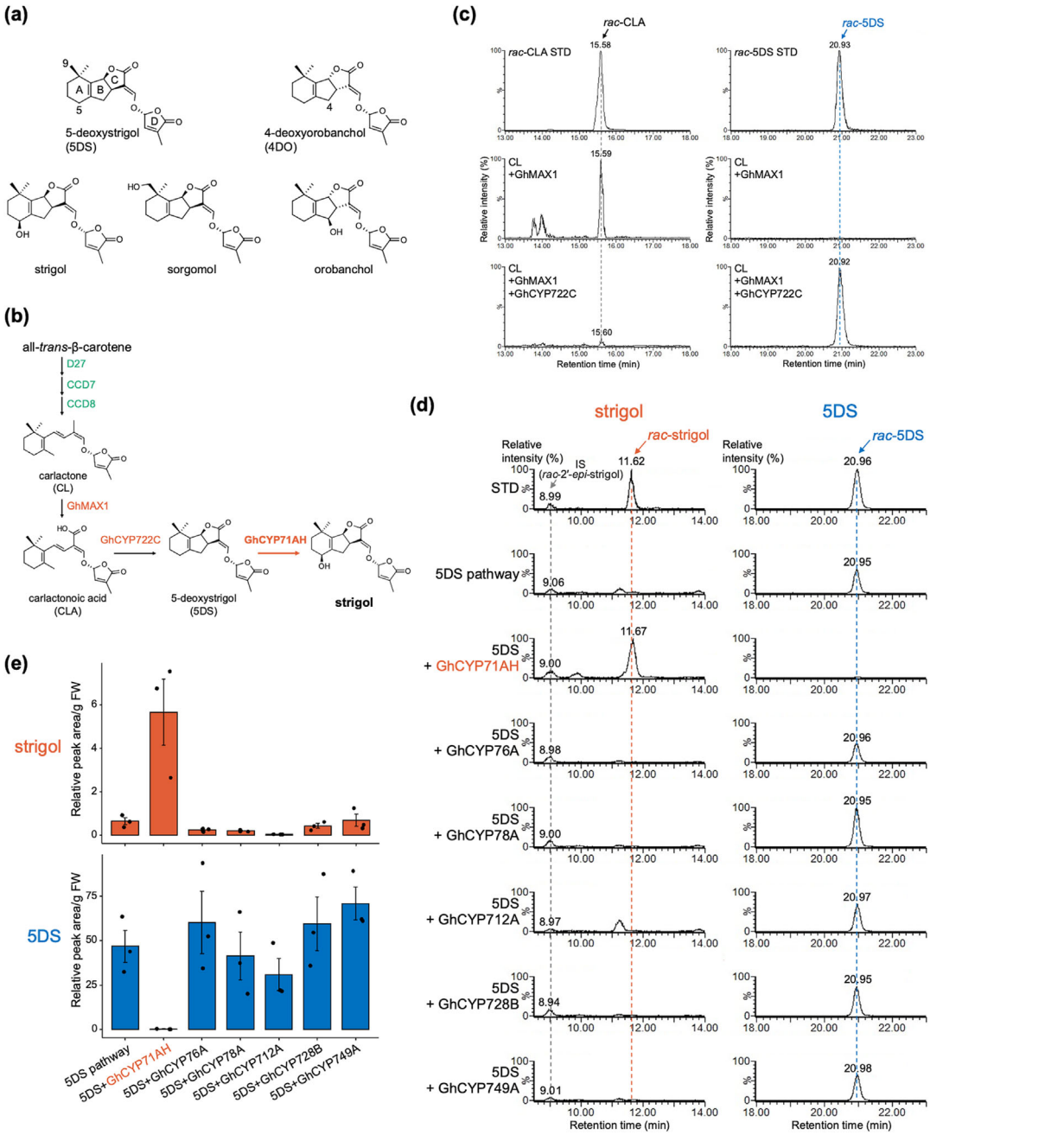

FIGURE 1 Screening of strigol synthases and identification of GhCYP71AH as a potential candidate. (a) Structures of canonical strigolactones (SLs). (b) Proposed pathway for SL biosynthesis in *Gossypium hirsutum*. Enzymes catalyzing the reactions shown with red arrows were confirmed in this study. CCD, CAROTENOID CLEAVAGE DIOXYGENASE; MAX1, MORE AXILLARY GROWTH 1; Gh, *Gossypium hirsutum*. (c) The reconstruction of the 5-deoxystrigol (5DS) biosynthesis pathway in *Nicotiana benthamiana* leaves. The transient expression of carlactone (CL) biosynthesis genes (*AtD27*, *AtCCD7*, and *AtCCD8*) from Arabidopsis and *GhMAX1* (*Gh_D05G044100*) from *G. hirsutum* produced carlactonoic acid (CLA). In addition, co-expression of *GhCYP722C* (*Gh_A12G067300*) resulted in the formation of 5DS. The signal intensity of each chromatogram is 1.25×10^4 and 5.60×10^5 for CLA and 5DS, respectively. STD, authentic standard. (d and e) Screening for strigol synthase. Each candidate cytochrome P450s was co-expressed with the reconstructed 5DS pathway in *N. benthamiana* leaves. Representative chromatograms of SL analysis by LC–MS/MS (d) and the results of SL quantification (e) are shown. (d) The signal intensity for each chromatogram is 5.20×10^5 and 2.40×10^6 for strigol and 5DS, respectively. IS, internal standard; STD, authentic standard. (e) The SL content of *N. benthamiana* leaves was represented as the relative peak area per fresh weight of roots. The relative peak area was calculated by measuring the peak area of peak appearing at the respective retention time for the authentic *rac*-strigol and *rac*-5DS, and dividing by the peak area of the internal standard, *rac*-2′-*epi*-strigol. Error bars represent means ± SE ($n = 3$ biologically independent replicates).

SLs to mitigate the adverse effects caused by root parasitic weeds on plant production prompted the development of synthetic strigol analogs, including GR compounds (Johnson et al., 1981). It is noteworthy that most of these structural developments had been accomplished soon after the identification of strigol. These analogs have had a tremendous impact on SL research, not only for the management of root parasitic weeds, but also for the study of plant–microbe communication in the rhizosphere and the control of plant architecture.

Over 30 distinct naturally occurring SLs have been identified in a variety of plants. Their common biosynthetic precursor carlactone (CL) is synthesized from β-carotene through the core SL biosynthesis pathway involving sequential reactions of DWARF27 (D27), CAROTENOID CLEAVAGE DIOXYGENASE 7 (CCD7), and CCD8 (Alder et al., 2012). The biosynthesis of SLs downstream of CL has become increasingly clear. In Arabidopsis, cytochrome P450 (CYP) AtCYP711A1, encoded by MORE AXILLARY GROWTH 1 (MAX1), catalyzes the conversion of CL to carlactonoic acid (CLA) (Abe et al., 2014; Seto et al., 2014). This enzymatic conversion was found to be a conserved function of CYP711A/MAX1 homologs in various plants (Yoneyama et al., 2018). In rice (*Oryza sativa*), two MAX1 homologs convert CL to 4-deoxyorobanchol (4DO) via CLA and 4DO to orobanchol (Yoneyama et al., 2018; Zhang et al., 2014). The cotton plants, *G. hirsutum* and *G. arboreum*, produce 5-deoxystrigol (5DS) (Iseki et al., 2018), a stereoisomer of 4DO. In *G. arboreum*, the conversion of CLA to 5DS is catalyzed by another CYP family enzyme, GaCYP722C (Wakabayashi et al., 2020). The conversion to 5DS is also catalyzed by the CYP722C subfamily in other 5DS-producing dicot plants (Wu et al., 2021). SLs sharing the same planar carbon skeleton as 4DO and 5DS have a characteristic tricyclic lactone (ABC-ring) that connects to a butenolide D-ring through an enol ether bridge. These are collectively known as canonical SLs. Both strigol and sorgomol are hydroxylated compounds of 5DS, and contain a hydroxy group at C-5 and C-9, respectively (Figure 1a). In sorghum (*Sorghum bicolor*), SbCYP728B35 catalyzes the introduction of a hydroxy group at C-9 of 5DS to form sorgomol (Wakabayashi et al., 2021); however, the complete biosynthesis pathway for strigol, a prototypical canonical SL, in *G. hirsutum* remains elusive, despite more than half a century since its discovery.

In the present study, we selected candidate strigol synthase genes in a transcriptome analysis of *G. hirsutum* roots by identifying upregulated genes under conditions that promote SL production. Screening of candidate genes via heterologous expression in the *Nicotiana benthamiana* transient expression system revealed GhCYP71AH as a promising candidate. Enzyme assays were performed using purified recombinant GhCYP71AH expressed in *Escherichia coli* to determine its substrate specificity and stereoselective hydroxylation of 5DS. These results confirm the function of GhCYP71AH as a strigol synthase (Figure 1b).

2 | EXPLORATION OF CANDIDATE CYPs FOR STRIGOL SYNTHASE

In a previous study, we demonstrated that the respective administration of CL, CLA, and 5DS in hydroponic solutions of *G. hirsutum* resulted in the formation of strigol (Iseki et al., 2018). The conversion of the immediate precursor 5DS to strigol was inhibited by the CYP inhibitor uniconazole-P in a dose-dependent manner (Ueno et al., 2018), suggesting that CYP catalyzes the introduction of a hydroxy group at C-5 of 5DS. We also demonstrated that under phosphate-deficient conditions, the expression of SL biosynthesis genes was upregulated in *G. arboreum*, another *Gossypium* sp., resulting in increased SL production (Iseki et al., 2018; Wakabayashi et al., 2020). In the present study, we confirmed high strigol exudation from the roots of *G. hirsutum* grown hydroponically under phosphate-deficient conditions (Figure S1), which is consistent with our previous report (see Method S1 for the detailed methods employed in this study) (Iseki et al., 2018). We hypothesized that the expression of the biosynthesis gene responsible for the conversion of 5DS to strigol is also induced by phosphate deficiency in *G. hirsutum*. To identify candidate CYP genes involved in the synthesis of strigol, we performed a comparative transcriptome analysis by RNA-seq using the above-mentioned *G. hirsutum* roots grown under phosphate-rich and phosphate-deficient conditions (Figure S1). Eleven transcripts, annotated as encoding CYP, were differentially up-regulated under phosphate-deficient conditions (Table S1). These transcripts include *GhCYP722C* (Gh_A12G067300.1), an ortholog of *GaCYP722C* in *G. arboreum* which converts CLA to 5DS (Wakabayashi et al., 2020). As described below, we confirmed the same function of GhCYP722C as GaCYP722C. Accordingly, 10 transcripts, excluding *GhCYP722C*, were selected as candidates for strigol synthase.

3 | EVALUATION OF THE CONVERSION ACTIVITY OF 5DS TO STRIGOL BY CANDIDATE CYPs IN *N. benthamiana*

Reconstruction of the SL biosynthesis pathway in *N. benthamiana* through the transient co-expression of relevant genes represents a robust approach to determine the function of additional unknown biosynthesis genes (Wang et al., 2022). Prior to pathway reconstruction, we confirmed the function of GhMAX1 (Gh_D05G044100) (Tian et al., 2022), a homolog of MAX1, using an in vitro enzyme assay as previously reported (Wakabayashi et al., 2020). Recombinant GhMAX1, which was expressed in a baculovirus-insect cell expression system, catalyzed the conversion of CL to CLA (Figure S2), thus verifying its conserved function (Yoneyama et al., 2018). In the reconstruction of the 5DS biosynthesis pathway in *N. benthamiana*, we co-expressed the Arabidopsis genes *AtD27*, *AtCCD7*, and *AtCCD8*, which are necessary for CL biosynthesis, along with the *G. hirsutum* genes, *GhMAX1* and above-mentioned *GhCYP722C*. LC–MS/MS analysis of leaf extracts co-expressing these genes revealed 5DS production, which confirmed the successful reconstruction of the 5DS biosynthesis pathway (Figures 1c and S3). The generation of 5DS by *GhCYP722C* provides further evidence of the function of CYP722C in 5DS-producing dicot plants.

We successfully cloned six of the 10 CYP candidates (Gh_D07G061000.1, GhCYP71AH; Gh_D04G121500.1, GhCYP76A;

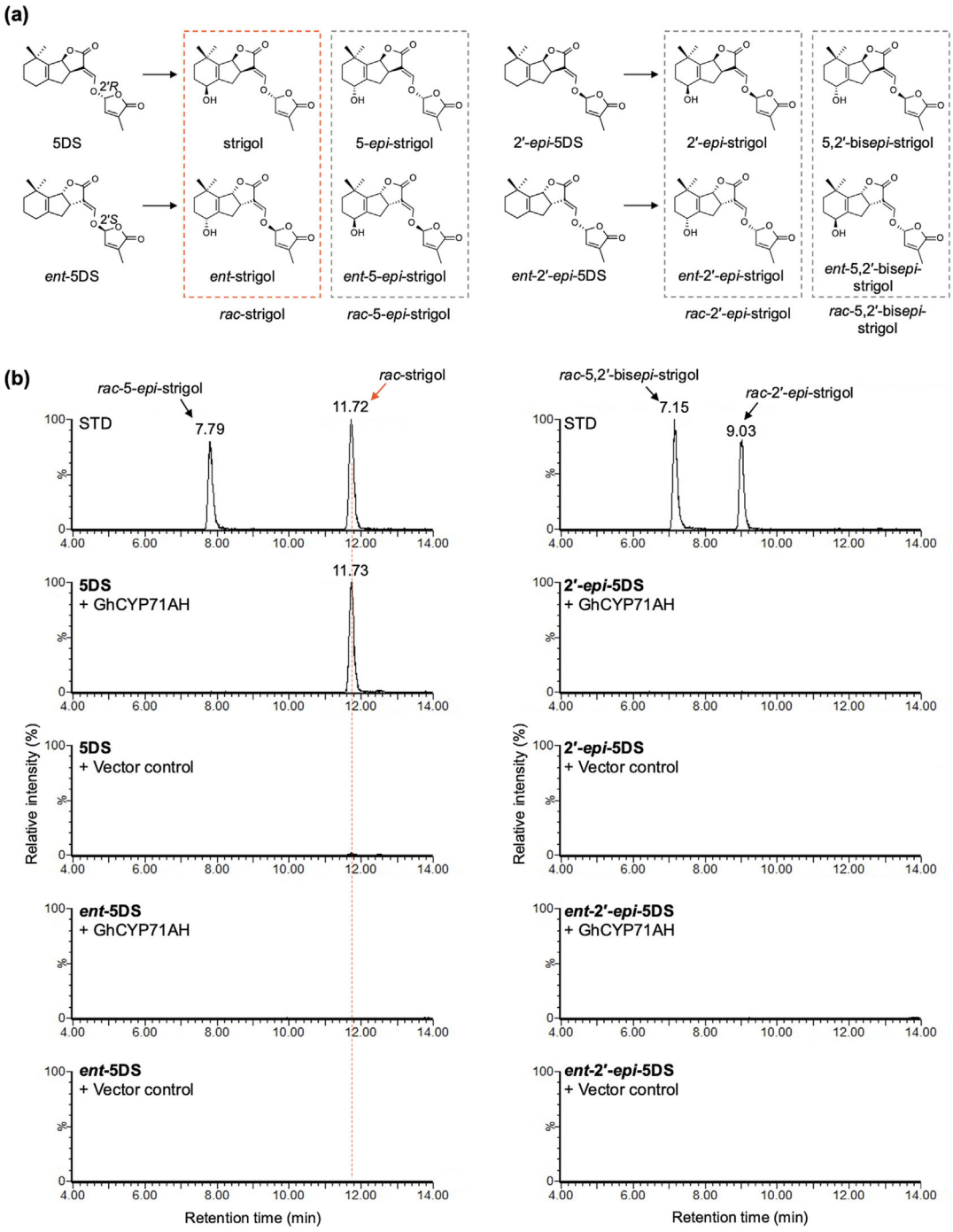

FIGURE 2 Stereospecific introduction of hydroxy group into 5-deoxystrigol (5DS) catalyzed by GhCYP71AH. (a) Structures of the 5DS stereoisomers used as substrates and the strigol stereoisomers considered the enzyme reaction products. (b) In vitro enzyme assay of recombinant GhCYP71AH with each of the 5DS stereoisomers as substrates. An enzyme reaction product consistent with the corresponding strigol stereoisomer standard was confirmed only when 5DS was used as a substrate. STD, authentic standard.

Gh_D12G259300.1, GhCYP78A; Gh_A01G219900.1, GhCYP712A; Gh_D01G076100.1, GhCYP728B; Gh_A02G027800.1, GhCYP749A) (see Table S2 for primer sequences used for cloning). Sequencing results showed that the translated amino acid sequences of cloned GhCYP78A and GhCYP728B matched with those recorded in the database, but the others were found to be, in part, different from the database sequences (Figure S4). We transiently co-expressed each of them together with the 5DS biosynthesis pathway. Of these six CYPs, the co-expression of only GhCYP71AH resulted in a significant reduction in 5DS. The generation of a product with a retention time of 11.67 min was observed, which was consistent with that of authentic *rac*-strigol (Figure 1d,e). These results suggest that GhCYP71AH is a potential candidate for strigol synthase in *G. hirsutum*. Sorgomol was not detected in the leaf extracts of

N. benthamiana co-expressing GhCYP728B (Figure S5), which belongs to the same subfamily as SbCYP728B35 catalyzing the conversion of 5DS to sorgomol in sorghum (Wakabayashi et al., 2021).

4 | IDENTIFICATION OF GhCYP71AH AS STRIGOL SYNTHASE

To confirm the function of GhCYP71AH as strigol synthase, we performed an in vitro enzyme assay using purified recombinant GhCYP71AH. Recombinant GhCYP71AH was expressed in *E. coli* as a truncated form of the *N*-terminal transmembrane domain and purified (Figure S6). For the enzyme assay, we focused on the substrate specificity and stereoselectivity of the C-5 hydroxylation of 5DS. The 5DS stereoisomers, 5DS, *ent*-5DS, 2′-*epi*-5DS, and *ent*-2′-*epi*-5DS (4DO), were used as substrates. Eight stereoisomers of strigol were considered as enzyme reaction products, depending on the configuration of the introduced hydroxy group at C-5 of each 5DS stereoisomer (Figure 2a). When 5DS was used as a substrate, a peak with a retention time consistent with that of authentic *rac*-strigol (mixture of strigol and *ent*-strigol) was observed. In contrast, no products consistent with the corresponding strigol stereoisomer standards were detected with the other substrates. (Figure 2b). Because 5DS contains a C-2′*R* configuration in the D-ring, the enzyme reaction product consistent with *rac*-strigol using 5DS as a substrate must be identical to strigol (Figure 2). The results indicate that GhCYP71AH catalyzes the stereoselective introduction of a hydroxy group at C-5 of 5DS to form strigol.

In the present study, the identification of strigol synthase signifies a noteworthy advancement in understanding the complete biosynthesis pathway of strigol, a prototypical and emblematic SL, at the molecular and biochemical levels. Enhancing the strigol biosynthesis pathway in cotton may confer useful traits as a trap crop, producing high levels of SL resulting in more *Striga* suicidal germination. On the other hand, it should be noted that the possibility that four uncloned candidates, whose inability to be cloned remains obscure, encode strigol synthase cannot be ruled out. These findings will further advance the use of strigol in SL research and increase our understanding of the rhizosphere interaction between plants and neighboring organisms.

AUTHOR CONTRIBUTIONS

Takatoshi Wakabayashi, Masaharu Mizutani, and Yukihiro Sugimoto planned and designed research. Takatoshi Wakabayashi, Megumi Nakayama, Yurie Kitano, and Masato Homma conducted experiments. Kenji Miura helped to construct the plasmids for the transient expression experiment. Hirosato Takikawa performed the synthesis of SLs. Takatoshi Wakabayashi and Yukihiro Sugimoto wrote the manuscript. All authors have read and approved the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no competing interest.

DATA AVAILABILITY STATEMENT

The methods applied in this study are described in Supporting Information. Primary RNA-seq data were deposited to the DDBJ (DNA Data Bank of Japan) Sequence Read Archive (accession number DRA016503). The accession numbers for the sequences of the *GhMAX1*, *GhCYP722C*, and *GhCYP71AH* are LC770317, LC770318, and LC770319, respectively. The data that support the findings of this study are available from the corresponding author upon reasonable request.

ORCID

Takatoshi Wakabayashi https://orcid.org/0000-0001-7065-6839
Masato Homma https://orcid.org/0009-0005-1836-128X
Kenji Miura https://orcid.org/0000-0003-1262-2176
Hirosato Takikawa https://orcid.org/0000-0002-3668-8834
Masaharu Mizutani https://orcid.org/0000-0002-4321-0644
Yukihiro Sugimoto https://orcid.org/0000-0002-8767-9671

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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