

# A glycolipid involved in flower bud formation of *Arabidopsis thaliana*

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**ABSTRACT.** We searched for bioactive substances involved in flower bud formation of *Arabidopsis thaliana*. Some significantly decreasing HPLC peaks were detected in the extract of flower buds-forming *A. thaliana* compared with that of the non-flower bud-forming stage. Compound **1**, which corresponded to the most decreased HPLC peak, was isolated from aerial parts of *A. thaliana*. From NMR and MS data, compound **1** was identified as one of the monogalactosyl diacylglyceride (MGDG). Compound **1** induced flower bud formation of *A. thaliana* exposed to long day condition for only 1 day. These results suggest that compound **1** as a precursor or a substrate of flower bud-forming substances plays important roles in the flower bud formation of *A. thaliana*.

**Keywords:** *Arabidopsis thaliana*; Bioactive substance; Flower bud formation; Long day condition; MGDG; Short day condition.

## INTRODUCTION

Flower bud formation is one of the most important physiological process for higher plants, and the flowering time is influenced by photoperiod, vernalization, drought stress, and so on. Chailakhyan demonstrated that flowering was regulated by the bioactive substances, which were produced in leaves that were subjected to favorable photoperiods, and the substances were transported to the shoot apex to induce flower bud formation. He named the substances “flower-inducing hormone” or “florigen” (Chailakhyan, 1936). Since then, studies on isolation of substances inducing flower bud formation have been carried out with a large number of plant species. For example, when the water solution prepared by immersing *Lemna paucicostata* exposed to drought, heat, or osmotic stress, were incubated with (-)-norepinephrine, the water solution showed strong flower inducing activity of *L. paucicostata* (Takimoto et al., 1994). They found that FN1, the tricyclic  $\alpha$ -ketol fatty acid derived from (-)-norepinephrine and 9, 10-ketol-octadecadienoic acid (KODA), induced flower formation of *Lemna* (Yamaguchi et al., 2001). On the other hand, to analyze the molecular processes that initiate flower bud formation and trigger the change from vegetative to reproductive growth, biologists have performed intensive genetic studies of flowering time in model plant *A. thaliana*. As a result, there was discovery of many

genes about the regulation of flowering time and the development of a lot of genetic models (Bastow and Dean, 2003). However, bioactive substances involved in flower bud formation of *A. thaliana* have been hardly reported. In this paper, we report the isolation and identification of a bioactive substance (compound **1**) involved in flower bud formation of *A. thaliana* and the flower buds-forming activity of compound **1**.

## MATERIALS AND METHODS

### Equipment

Optical rotations were measured with a JASCO DIP-370 polarimeter. <sup>1</sup>H and <sup>13</sup>C NMR spectra were measured and recorded on a Bruker AVANCE-500 in CD<sub>3</sub>OD. The resonances of CD<sub>3</sub>OD at  $\delta_H$  3.35 ppm and  $\delta_C$  49.8 ppm were used as internal standards for NMR spectra. ESIMS were recorded on a Waters platform LC. HPLC was performed using a system composed of a TOSOH DP-8020 pump and a TOSOH PD-8020 photodiodearray detector or a TOSOH RI-8021 refractive index detector.

### Plant materials

The seeds of *Arabidopsis thaliana* cv. Columbia were provided by the Sendai *Arabidopsis* Seed Stock Center (SASSC, Japan). The seeds were immersed in the water for 2 days before sowing on rock wool (Rock fiber, NITTOBO, Japan). They have been cultured in the growth container (24°C, ca. 3,800 lux) under short day condition (8 h-light and 16 h-dark, SD) for 26 or 30 days.

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## HPLC analyses of the extracts of groups I, II, and III

*Arabidopsis thaliana* were cultured at 24°C for 26 days under SD, and they were divided into groups I, II, and III. Group I was grown under long day conditions (16 h-light and 8 h-dark, LD, ca. 2,500 lux) until the flower bud formation, group II was grown under SD and exposed to LD for 3 days just before extraction, and group III was grown under SD throughout the course of this experiment.

The aerial parts of each group were frozen with liquid N<sub>2</sub>, and ground to a fine powder in a mortar, and then they were extracted with MeOH for 3 times. The MeOH extracts were evaporated to dryness *in vacuo* at 30°C and the residue was partitioned between EtOAc and H<sub>2</sub>O. The each equivalent amount of EtOAc-soluble material was analysed by a reversed-phase HPLC (ODS-80Ts,  $\phi$ 4.6×250 mm, TOSOH, UV detection at 195 nm) with H<sub>2</sub>O-CH<sub>3</sub>CN under linear gradient conditions at 0.8 ml/min (aqueous portion: 0 to 100% CH<sub>3</sub>CN at 1%/min, at 100% CH<sub>3</sub>CN for 10 min, EtOAc-soluble portion: 50 to 100% CH<sub>3</sub>CN at 1%/min, at 100% CH<sub>3</sub>CN for 30 min). Further HPLC analysis (same as above) was under the condition at 95% CH<sub>3</sub>CN (Figure 1).

## Isolation and structure identification of compound 1

The aerial parts of *A. thaliana* were extracted with MeOH (200 mL), and the MeOH extracts were evaporated to dryness *in vacuo* at 30°C. Then the residue was partitioned between EtOAc and H<sub>2</sub>O. The EtOAc-soluble portion was applied to a reversed-phase column (TOYOPAK ODS M, TOSOH, 100% CH<sub>3</sub>CN) to afford a glycolipids fraction, which was purified by a reversed-phase HPLC (ODS-80Ts,  $\phi$ 4.6×250 mm, TOSOH, 95% CH<sub>3</sub>CN at a flow rate of 0.8 ml/min, UV detection at 195 nm). From 0.78 g of aerial parts of *A. thaliana*, 0.3 mg of compound 1 was obtained.

The mass spectrum of compound 1 gave *m/z* 769 (M+Na)<sup>+</sup>. <sup>1</sup>H NMR (CD<sub>3</sub>OD):  $\delta$  1.03 (6H, t, *J* = 5.4 Hz), 1.38 (6H, m), 1.67 (2H, m), 2.13 (4H, m), 2.37 (2H, m), 2.86 (4H, m), 3.50 (1H, dd, *J* = 3.2 and 9.7 Hz, 3'-H), 3.55 (2H, m, 2', 5'-H), 3.75 (1H, dd, *J* = 5.2 and 10.7 Hz, *sn*-3-Hb, overlapped with 6'-H), 3.79 (2H, m, 6'-H), 3.86 (1H, d, *J* = 3.2 Hz, 4'-H), 4.04 (1H, dd, *J* = 5.5, 10.9 Hz, *sn*-3-Ha), 4.26 (1H, dd, *J* = 6.7 and 12.0 Hz, *sn*-1-Hb, overlapped with 1'-H), 4.27 (1H, d, *J* = 7.5 Hz, 1'-H), 4.49 (1H, dd, *J* = 2.8 and 12.0 Hz, *sn*-1-Ha), 5.31 (1H, m, *sn*-2-H), and 5.40 (12H, m, 7''-H, 8''-H, 10''-H, 11''-H, 13''-H, 14''-H, 9'''-H, 10'''-H, 12'''-H, 13'''-H, 15'''-H, 16'''-H). <sup>13</sup>C NMR (CD<sub>3</sub>OD):  $\delta$  105.8 (C-1'), 72.8 (C-2'), 75.3 (C-3'), 70.7 (C-4'), 77.3 (C-5'), 62.9 (C-6'), 64.5 (*sn*-1-C), 72.2 (*sn*-2-C), 69.2 (*sn*-3-C), 22.04, 22.17 (C-15'', C-17'''), 26.42, 26.53, 26.92, 27.04 (C-9'', C-11''', C-12'', C-14'''), 28.57, and 28.69 (C-6'', C-8''').

Enzymatic hydrolysis of compound 1. A solution of compound 1 (1 mg) and lipase type XI (0.72 units, Sigma) in boric acid – borax buffer [0.63 mL, containing Triton

X-100 (2.5 mg), pH 7.7] was stirred at 38°C for 12 h. The reaction was quenched with AcOH (0.1 mL) and then EtOH was added to the reaction mixture. The solvent was removed by N<sub>2</sub> gas and the residue was purified by a silica gel column (CHCl<sub>3</sub>/MeOH, 12:1→7:1) to afford linolenic acid and *sn*2-*O*-(hexadecatrienoyl)-monogalactosyl glyceride (Morimoto et al., 1995).

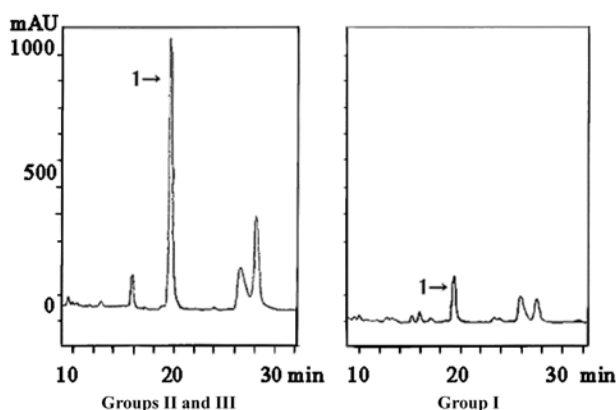
Determination of absolute configuration at C-2 in compound 1. A solution of compound 1 (9.6 mg) and NaOMe (10 equiv.) in anhyd. MeOH (0.1 mL) was stirred at room temperature for 1 h. The reaction mixture was partitioned between hexane and water and the water-soluble materials were purified by a C<sub>18</sub> column (Sep-Pak C<sub>18</sub> cartridge 12 CC, Waters, H<sub>2</sub>O) and HPLC (TSKgel amide-80,  $\phi$ 4.6×250 mm, TOSOH, 75% CH<sub>3</sub>CN, flow rate: 0.8 mL/min, RI detection) to give the  $\beta$ -galactosylglycerol (2, 1.75 mg, 54%). The absolute configuration of 2 was determined by comparison with the optical rotation (Son et al., 2001).

## Long day treatment under weak light

*Arabidopsis thaliana* were cultured at 24°C for 26 days under SD. Some plants were grown under SD throughout the course of the experiment. The others were cultured for several days under long day conditions (16 h-light and 8 h-dark, LD, ca. 2,500 lux), and then were grown under SD until flower bud formation. The days for forming flower bud was measured individually and averaged. Means  $\pm$  SE showed of 3 replicates of 5 plants.

## Bioassay

Thirty-day-old *A. thaliana* plants cultured at 24°C under SD were used for bioassay. Before application, one group of the assayed plants was exposed to LD for



**Figure 1.** HPLC chromatograms of groups I, II, and III. Group I: grown under long day conditions (16 h-light and 8 h-dark, LD, ca. 2,500 lux) until the flower bud formation, Group II: grown under SD and exposed to LD for 3 days just before extraction, and Group III: grown under SD throughout the course of the experiment. They were extracted with MeOH and partitioned between EtOAc and H<sub>2</sub>O. The EtOAc-soluble materials were analysed by HPLC. This experiment was repeated 3 times.

one day (LD-1). It was shown that exposing to long day condition for only 1 day (LD-1) give the plants only slight promotion of forming flower bud (Figure 1). Then, compound **1** in 50% aqueous acetone solutions of several concentrations was applied to the center of rosette leaves using microsyringe at intervals of 7 days. Twenty-days after the onset of application, the number of plants formed flower bud was counted. This experiment was repeated twice.

## RESULTS

The aerial parts of *A. thaliana* in groups I, II, and III were extracted with MeOH, and the extracts were partitioned between EtOAc and H<sub>2</sub>O. The EtOAc-soluble materials were analysed by HPLC. Some decreased peaks were observed in *t<sub>R</sub>* 50-80 min fraction of EtOAc-soluble materials obtained from group I in comparison with those of groups II and III, while no increased peaks were observed. As the result of further analysis, peak 1 was most decreased in HPLC chromatogram of group I (Figure 1).

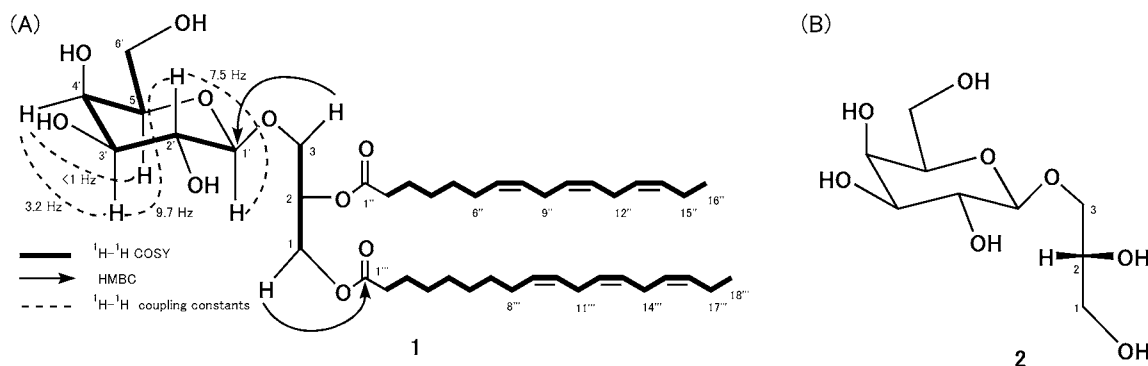
To identify the structure of compound **1** corresponded to peak 1, the aerial parts of *A. thaliana* were extracted with MeOH, and the extract was partitioned between EtOAc and H<sub>2</sub>O. The EtOAc-soluble portion was separated by a reversed-phase column and C<sub>18</sub> HPLC to afford compound **1**.

The ESIMS of compound **1** showed a pseudomolecular ion peak at *m/z* 769 (M+Na)<sup>+</sup>. The gross structure of compound **1** was deduced from detailed analysis of the <sup>1</sup>H and <sup>13</sup>C NMR data aided with 2D NMR experiments (<sup>1</sup>H-<sup>1</sup>H COSY, HMQC, and HMBC). The <sup>13</sup>C NMR data of compound **1** indicated that the molecule possessed two ester carbonyl carbons, six disubstituted olefins, one acetal carbon, five oxymethines, three oxymethylenes, eighteen methylenes, and two methyl groups. The <sup>1</sup>H-<sup>1</sup>H COSY connectivities of C-1 to C-3 and C-1' to C-6' indicated the presence of a glycerol and a sugar component. The sugar was assigned to be galactose by NOESY correlations of H-1' to H-3' and H-5' and H-4' to H-3' and H-5' and the

<sup>1</sup>H-<sup>1</sup>H coupling constants (*J*<sub>1',2'</sub> = 7.3 Hz, *J*<sub>2',3'</sub> = 7.4 Hz, *J*<sub>3',4'</sub> = 2.5 Hz, *J*<sub>4',5'</sub> = ~0 Hz). HMBC correlations of H-1' to C-3 (δ<sub>C</sub> 69.2) and H-3a and H-3b to C-1' (δ<sub>C</sub> 105.8) and the coupling constant (*J*<sub>1',2'</sub> = 7.3 Hz) of the anomeric proton (H-1') at δ<sub>H</sub> 4.27 revealed that compound **1** possessed a β-galactosyl glycerol moiety.

The <sup>1</sup>H-<sup>1</sup>H COSY connectivities of C-2'' to C-16''' and C-2''' to C-18''' indicated the presence of two fatty acids which contained three double bonds, respectively. Z-Genometries of six double bonds at C-7''-C-8'', C-10''-C-11'', C-13''-C-14'', C-9'''-C-10''', C-12'''-C-13''', and C-15'''-C-16''' were deduced from the carbon chemical shifts (δ<sub>C</sub> < 30) of allylic carbons (Gunstone et al., 1977). The two fatty acids were presumed to be octadecatrienoic acid and hexadecatrienoic acid judging from ESIMS of compound **1**. HMBC correlations of Ha-1 and Hb-1 to ester carbonyl carbon (δ<sub>C</sub> 175.5 or 175.1) and chemical shifts (δ<sub>H</sub> 5.31; δ<sub>C</sub> 72.2) of C-2 indicated that the linolenic acid and hexadecatrienoic acid connected to C-1 and C-2. In order to define the locations of these fatty acids in the β-galactosyl glycerol moiety of compound **1**, we applied enzymatic hydrolysis. The lipase type XI (Sigma)-catalyzed hydrolysis of compound **1** afforded *sn*2-*O*-(hexadecatrienoyl)-monogalactosyl glyceride and linolenic acid (Morimoto et al., 1995). Therefore, compound **1** was identified as *sn*1-*O*-(octadecatrienoyl)-*sn*2-*O*-(hexadecatrienoyl)-monogalactosyl diglyceride (Figure 2). The absolute configuration at C-2 in the β-galactosylglycerol (**2**), which was derived from compound **1** with NaOMe presumed to be *R*, from the basis of comparison of the optical rotation ([α]<sub>D</sub> -8°) of **2** with the reported values ([α]<sub>D</sub> -7° for C-2 *R* and [α]<sub>D</sub> +2° for C-2 *S*) (Son et al., 2001).

And next, we applied compound **1** to *A. thaliana* to examine its affection in flower bud formation. Before assay, we measured how long it took for forming flower buds of *A. thaliana* under light conditions described in materials and methods. As shown in Figure 3, *A. thaliana* under LD for one day acquired about 23 days for forming flower buds, but the plants exposed LD for 3 days longer took about 15 days (Figure 3). When the solution of



**Figure 2.** 2D NMR correlations of compound **1** (A) and β-galactosyl glycerol (**2**) derived from compound **1** (B).

compound **1** in 50% aqueous acetone solutions of several concentrations applied to the center of rosette leaves of assayed plants, which were exposed to LD for one day just before onset of the bioassay, the 58% of the plants applied compound **1** at 1,000 ppm formed flower bud, whereas only 14% and 20% of the plants applied for nothing or 50% acetone have flower bud (Table 1). On the other hand, flower bud of the plants not exposed to LD were not promoted by compound **1** (data not shown).

## DISCUSSION

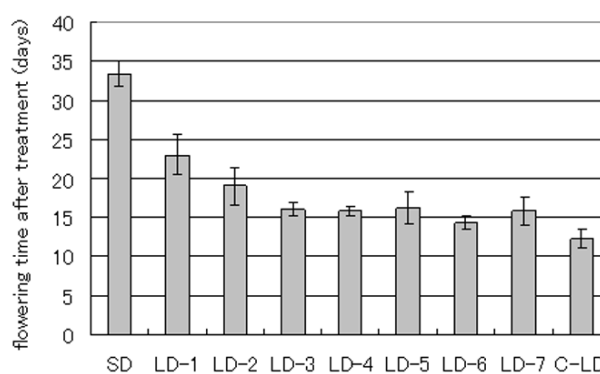
In *Arabidopsis thaliana*, large amount of studies on flower bud formation from genetic point of view have been carried out. However, bioactive substances involved in flowering of *A. thaliana* have been hardly reported. In this study, therefore, we exhibited the isolation of bioactive substances involved in flower bud formation of *A. thaliana*.

The aerial parts of *A. thaliana* in groups I, II, and III were extracted with MeOH, and the extracts were partitioned between EtOAc and H<sub>2</sub>O. The EtOAc-soluble materials were analysed by HPLC. Some decreased peaks were observed in *t<sub>R</sub>* 50-80 min fraction of EtOAc-soluble materials obtained from group I in comparison with those of groups II and III, while increased peaks weren't observed. The decrease of peak **1** after flower bud formation suggested that the substance including peak **1** was metabolized to bioactive substance (s) when flower bud was formed and in groups II and III, the peak **1** was not decreased as they were not formed flower bud. Therefore, we further separated the fraction to afford the substance of peak **1**, which was named compound **1** (Figure 1). As a result, *sn1-O*-(octadecatrienoyl)-*sn2-O*-(hexadecatrienoyl)-monogalactosyl diglyceride (**1**), which corresponded to the most decreased HPLC peak, was isolated from EtOAc-soluble materials of *A. thaliana* (Figure 2).

And next, we measured how long it took for forming flower buds of *A. thaliana* under light conditions described in materials and methods. It took about 23 days until the flower buds under LD for one day were formed, but the flower buds under LD for 3 days longer were formed after about 15 days from the start of LD treatment (Figure

3). It suggested that exposing to LD for one day was not enough for *A. thaliana* to change from vegetative to reproductive growth under the long day conditions, and slightly promoted the flower buds formation. Therefore we assayed compound **1** to the plants exposed LD for one day.

The solution of compound **1** in 50% aqueous acetone of several concentrations was applied to the center of rosette leaves of assayed plants that exposed to LD for one day just before onset of the bioassay, and their effects on flower bud formation was tested (Table 1). Compound **1** induced significantly flower bud formation, whereas flower bud formation of the plants applied for nothing or 50% acetone wasn't promoted. On the other hand, flower bud of the plants not exposed to LD was not induced by compound **1** (data not shown). These results suggest that compound **1** is metabolized to the bioactive substance (s) inducing flower bud by exposed to LD, and which compound **1** was not metabolized to those by not exposed to LD. So it envisaged that compound **1** is the precursor



**Figure 3.** The effects of long day treatment related to flower buds formation. SD: grown under short day conditions (8 h-light and 16 h-dark, SD, ca. 3,800 lux) throughout the course of the experiment, LD-1~7: cultured for 1-7 days under long day conditions (16 h-light and 8 h-dark, LD, ca. 2,500 lux), and were backed to SD, C-LD: cultured under LD until forming flower bud. The days for forming flower bud was measured individually and averaged. Means  $\pm$  SE showed of 3 replicates of 5 plants.

**Table 1.** The effect of compound **1** on flower bud formation.

	Flower-bud forming plants <sup>a</sup>	Assayed plants
Control <sup>b</sup>	3 (14%)	21
50% acetone <sup>b</sup>	4 (20%)	20
Compound <b>1</b> (10 ppm)	7 (47%)	15
Compound <b>1</b> (100 ppm)	8 (53%)	15
Compound <b>1</b> (1,000 ppm)	11 (58%)	19

<sup>a</sup> Number of flower-bud forming plants at twenty-days after the application of test solution to the assayed plants.

<sup>b</sup> Control cultures were applied for nothing, an equal volume of 50% acetone (as negative control).

or the substrate of flower bud-inducing substance (s). Compound **1** may play important roles in flower bud formation of *A. thaliana*.

Compound **1** is one of monogalactosyl diglycerides (MGDG), which are major constituents of the chloroplast membrane in plants and recently, they were draw much attention because of their various biological activity. For example, MGDG is the stores of fatty acids that are substrates of various bioactive substances, such as jasmonic acid, 9, 10-ketol-octadecadienoic acid (KODA), *sn*1-*O*-(12-oxophytodienoyl)-*sn*2-*O*-(hexadecatrienoyl)-monogalactosyl glyceride (MGDG-O), and arabidopsides A and B (Vick and Zimmerman, 1984; Yokoyama et al., 2000; Stelmach et al., 2001; Hisamatsu et al., 2003). Jasmonic acid is one of the phytohormone which stimulates or inhibits several events in plant growth and development, while KODA was known to related to flower induction of *Lemna paucicostata* and *Pharbitis nil* (Miersch et al., 1999; Suzuki et al., 2003). MGDG-O and arabidopsides A and B are rare MGDG containing OPDA and/or dn-OPDA, which are precursors of jasmonic acid (Baertschi et al., 1988; Weber et al., 1997). Furthermore, as compound **1** induced flower bud of the plants exposed to LD-1, it suggested bioactive substances regulating flower bud formation of *A. thaliana* is also one of the metabolites of MGDG. We are now studying the substances derived from MGDG and their effect for flower bud formation.

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## 一種糖脂涉及阿拉伯芥之花芽形成

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我們追尋阿拉伯芥 (*Arabidopsis thaliana*) 涉及花芽形成之生理活性物質。比較花芽形成- 及未發芽形成- 之發育階段的抽取液於 HPLC 檢測時發現前者有下降之若干峯值。化合物 **1**，此乃減少最明顯之峯值，係單離自阿拉伯芥之地上部。從核磁共振儀及質譜儀之數據得知化合物 **1** 乃單半乳糖-雙酸甘油 (MGDG)。當阿拉伯芥暴露於長日照只一天時，添加化合物**1** 可誘導花芽形成。這些結果顯示：化合物 **1** 可能為花芽形成物質之前驅體或基質，因此乃阿拉伯芥花芽形成之一重要成份。

**關鍵詞：**花芽形成；阿拉伯芥；短日照；長日照；單半乳糖-雙酸甘油；生理活性物質。