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1	Running head:
2	Potato tuberization activities of JA related compounds
3	
4	Title:
5	Potato Tuber-inducing Activities of Jasmonic acid and Related-Compounds (II)
6	
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1 Abstract

2	New information is being accumulated for plant-derived oxylipins, such as JA amino
3	acid conjugates. However, these compounds have not being examined for their activity
4	in promoting potato tuber formation. It was found that (-)-JA had the highest activity
5	followed <i>cis</i> -(-)-OPDA, (+)-4, 5-didehydroJA, <i>cis</i> -(+)-OPDA-L-Ile, and (-)-JA-L-Ile,
6	-Leu, -Phe, -Val, although iso-OPDA and 3,7-didehydroJA did not exhibit activity.
7	
8	Keywords: jasmonic acid, jasmonoyl L-isoleucine, cis-OPDA, iso-OPDA,
9	3,7-didehydrojasmonic acid
10	
11	

2	Tuberization in potato plants is regulated predominantly by photoperiods. Short-day
3	conditions promote tuberization, whereas long-day conditions inhibit the tuberization
4	process. Using a grafting experimental procedure, the biological role of a specific
5	tuber-inducing stimulus in leaves exposed to short days was discovered to be
6	translocated from leaves into the stolon tip to stimulate potato tuber formation by
7	Gregory et al. (Gregory 1956) and Chapman et al. (Chapman 1958). An attempt was
8	made to isolate and identify this unknown factor, resulting in the discovery of
9	(+)-7- <i>iso</i> -12- O - β -D-glucopuranosyloxyjasmonic acid (12OGlcJA) from leaflets of
10	potato plant (Solanum tuberosum L.) (Koda and Okazawa 1988; Yoshihara et al. 1989),
11	and the aglycone moiety of the compound, (+)-7-iso-12-hydroxyjasmonic acid
12	(120HJA), was named as tuberonic acid. Subsequent studies showed that jasmonic acid
13	(JA) also possessed potato tuber inducing activity (Koda et al. 1991). It is generally
14	accepted that JA and its derivatives are important signalling compounds in plant
15	development and stress response pathways, such as senescence (Miyamoto et al. 1995),
16	wound response (Farmer and Ryan 1992) and reproductive development (Falkenstein et
17	al. 1991; McConn and Browse 1996). JA is biosynthesized from the α -linoleinic acid
18	released by lipase activity; the intermediate is converted by sequential peroxidation,
19	dehydration and cyclization to form <i>cis</i> -12-oxo-phytodienic acid (<i>cis</i> -OPDA).
20	cis-OPDA is converted to OPC 8:0 via OPR3 (Schaller et al. 2000; Strassner et al.
21	2002), which was named as OPDA reducing pathway (Figure 1), and furthermore, by
22	three successive reduction and β -oxidation steps that shorten the acid side chain to
23	produce (+)-7-iso-JA, which is spontaneously epimerized into (-)-JA. Different
24	biosynthetic pathways using OPR2 to reduce 4,5-didehydro-7-iso-JA to JA have also

1	been reported using opr3 mutant Arabidopsis thaliana (Chini et al. 2018). (+)-7-iso-JA
2	is enzymatically converted into many kinds of conjugates and derivatives, including
3	MeJA (Seo et al. 2001) and JA amino acid conjugates (Staswick and Tiryaki 2004).
4	Among the amino acid conjugates, jasmonoyl-L-isoleucine (JA-L-Ile) is considered as
5	the most important compound that shows biological activity, especially for wound
6	response (Chini et al. 2007). However, it was found that each jasmonate has its own
7	unique biological activity, thus cis-OPDA possesses its own unique biological activity
8	that is needed for withstanding the wound response (Taki et al. 2005) and for the
9	tendril-coiling response of Bryonia dioica Jacq. (Blechert et al. 1999). Furthermore,
10	new types of JA-related compounds have been reported, such as death acids from
11	Cochliobolus heterostrophus infected leaves of maize (Zea mays) (Christensen et al.
12	2015), cis-OPDA glutathione conjugates (Ohkama-Ohtsu et al. 2011), and cis-OPDA
13	amino acid conjugates form A. thaliana (Flokova et al. 2016; Uchiyama et al. 2018),
14	and wound response pathways involving interactions with COI1 proteins other than
15	JA-L-Ile have been reported, which are mediated via cis-dinor-OPDA, iso-dinor-OPDA
16	using Marchantia polymorpha as an experimental plant (Monte et al. 2018) and
17	(+)-7-iso-12-hydroxyJA-L-Ile in A. thaliana (Poudel et al. 2019). Recent studies have
18	also revealed the relationship between JA and cis-jasmone (Dabrowska and Boland
19	2007), and the details of their biosynthetic pathway have been clarified, but it is still
20	debated whether JA is a precursor that is converted <i>cis</i> -jasmone. The key compounds
21	for this topic are <i>iso</i> -OPDA and 3,7-didehydroJA (Koch, Bandemer and Boland 1997;
22	Matsui et al. 2017; Matsui et al. 2019; Matsui et al. 2020).
23	Therefore, from the above knowledge it can be concluded that new information is

24 being accumulated for plant-derived oxylipins, which is a general term for a group of

1	compounds originating from α linolenic acid (Figure 1). A paper regarding potato
2	tuber-inducing activities using several kinds of JAs was published (Koda et al. 1991),
3	although new types of JA were discovered after the report, such as JA amino acid
4	conjugates, which did not undergo tests regarding their ability to promote potato tuber
5	formation. In this paper, the structure-activity relationship activities for <i>cis</i> -(–)-OPDA,
6	(+)-OPDA-L-Ile, <i>iso</i> -OPDA, (-)-JA-L-Leu, (-)-JA-L-Phe, (-)-JA-L-Val, (-)-JA-L-Ile,
7	(+)-4,5-didehydroJA, and 3,7-didehydroJA promoting potato tuber formation are
8	evaluated.

10 JA was used for a positive control in this study, since it was reported that JA showed 11 potato tuber induing activity (Koda et al. 1991), and optically pure (-)-JA was isolated 12 from the culture filtrate of Lasiodiplodia theobromae (Aldridge et al. 1971). Optically 13 pure cis-(-)-OPDA (Figure 1) and cis-(+)-OPDA-L-Ile (Figure S1) were synthesized 14 according to the reported method (Kajiwara et al. 2012, Uchiyama et al. 2018) using 15 acetone powder prepared from flax seeds (Zimmerman and Feng 1978) and a 16 recombinant AOC derived from Physcomitrella patens (Stumpe et al. 2010). iso-OPDA 17 (Figure 1) was synthesized according to a previously reported method (Lauchli and 18 Boland 2003). Optically pure JA amino acid conjugates, (-)-JA-L-Ile, -Phe, Leu, and 19 Val (Figure S1), were obtained using (\pm) -MeJA as a starting compound, and (+) and (-)20 forms were separated at the final step by conventional silica gel column 21 chromatography (Kramell *et al.* 1988). Optically pure, (+)-4,5-didehydroJA (Figure 1) 22 was prepared according to the reported method (Monte et al., 2018) using (-)-JA as a 23 starting compound. (+)-3,7-DidehydroJA (Figure 1) was prepared according to the

reported method (Monte *et al.*, 2018) using (±)-MeJA as a starting compound. All data
 for synthesized compounds are given in Supplementary data.

3 The synthesized compounds were subjected to a bioassay to evaluate potato 4 tuber-inducing activity using potato single node stems (Koda and Okazawa 1988) 5 accorging to the described method in Supplementary data, in which the concentrations 6 of test compounds and (-)-JA (positive control) were set at 10⁻⁴ M. Photographs 7 showing representative biological activities are given in Figure S2. In the control plants, 8 the stems extending from transplanted node stems had just grown out, and the 9 emergences of induced potato tubers were very rare. In contrast, the induced potato 10 tubers on the tip from transplanted node stems were observed in (-)-JA-treated stems, in 11 which case the length of the extending stems from transplanted node stems was less 12 than 1 cm. When the transplanted node stems were planted in agar medium containing (-)-JA at 10⁻⁴ M, the emergence of the stem from the transplanted stem was delayed 13 14 compared with that of the control, and stems already bearing potato tuber at the tip 15 suddenly appeared almost 12 days post-transplantation into the medium. The results of the bioassay using *cis*-OPDA were similar with that of (-)-JA at 10⁻⁴ M. However, the 16 17 length of the extending stem from transplanted node was slightly longer than those treated with (-)-JA at 10⁻⁴ M, although the lengths of the extending stems from 18 19 transplanted node stems were less than 1 cm. Similar to the trends of cis-OPDA, active 20 potato tuber inductions were observed in cis-(+)-OPDA-L-Ile and (+)-4,5-didehydroJA, 21 but the lengths of the extending stems from transplanted node stems were slightly 22 longer than those treated with *cis*-OPDA. In the case of testing (-)-JA amino acids, 23 potato tubers were able to be detected at the tips of the extending stems from 24 transplanted node stems, but in some cases, potato tubers were found to have formed in

1 the middle of the extending stems from transplanted node stems. Generally, the stem 2 length of (-)-JA amino acid-treated plants were over 1 cm but less than 2 cm. However, 3 it was very rare to observe the potato tuber-inducing activity using iso-OPDA and 4 3,7-didehydroJA as test compounds. The induced potato tubers, if observed at all, were 5 only found on stems that were more than 2 cm long. To evaluate the results of the 6 bioassay numerically, the degree of activity was quantified. Judged by the previous 7 description, the assessment of potato tuber-inducing properties can be roughly 8 determined by the lengths of the extending stems from transplanted node stems and the 9 location where the tuber arises. In accordance with this view, numerical values were 10 assigned to the following plant states: 10 points, potato tubers formed at the tip of the 11 extending stem less than 1 cm of the stem length; 6 points, potato tubers formed at the 12 tip of the extending stem less than almost 2 cm of the stem length; 3 points, potato 13 tubers formed on the extending stem more than 2 cm in length; and 0 points, potato 14 tubers were not formed on the extending stem (Figure S3). We evaluated the biological 15 activity of the potato tuber-inducing activity of each compound based on its numerical 16 values using the evaluation method shown in Figure S3, and the results are given in 17 Table I, and the schematic illustration to show relative activity for each compound is 18 given in Figure 2. The results were similar to those of the other two independent 19 experiments.

Since it was reported that JA showed potato tuber inducing activity (Koda *et al.*1991) and exogenously applied JA was converted into 12OHJA and 12OGlcJA using
potato single node stems (Matsuura and Yoshihara, 2003), it was hypothesized that
exogenously applied *iso*-OPDA and 3,7-didehydroJA would not be converted to afford
enough amounts of the compounds to induce potato tubers showing activity. Therefore,

1 the endogenous levels of those compounds in JA, (+)-4,5-didehydroJA, iso-OPDA, and 2 3,7-didehydroJA treated and the non-treated single node stems were evaluated 3 according to the described method in Supplementary data. It was cleared that the 4 endogenous levels of those compounds in iso-OPDA, 3,7-didehydroJA treated and the 5 non-treated single node stems were almost same (Table S1). 6 In this paper, potato tuber-inducing activities of (-)-JA and the related 7 compounds, cis-(-)-OPDA, (+)-OPDA-L-Ile, iso-OPDA, (-)-JA-L-Leu, (-)-JA-L-Phe, 8 (-)-JA-L-Val, (-)-JA-L-Ile, (+)-4,5-didehydroJA, and 3,7-didehydroJA, were evaluated, 9 which showed that (-)-JA gave the highest activity following *cis*-(-)-OPDA, 10 (+)-4,5-didehydroJA and (-)-JA-L-Ile, although iso-OPDA and 3,7-didehydroJA did not 11 show activity. Interestingly, the potato tuber-inducing activity of (-)-JA-L-Ile was 12 weaker than that of (-)-JA. Since (-)-JA-L-Ile is thought to be the active form for 13 JA-mediated biological activity, it was supposed that there might be a different mode of 14 action to induce potato tuber other than that of (-)-JA-L-Ile signaling system. However, 15 the weaker activity of (-)-JA-L-Ile might be due to the difference in physical properties 16 between (-)-JA and (-)-JA-L-Ile, such as permeability to cell membrane of plants, but 17 there is not enough accumulated knowledge to discuss this point. The involvement of 18 the FT homologue protein, SPL6 (Navarro et al. 2011) and the mobile mRNA, BELL5 19 (Lin *et al.* 2013) in potato tuber induction has been reported, although the relationship 20 between these mobile factors and the oxylipins has not been established yet. 21 Furthermore, there are no data or reports on the involvement of the COII-JAZ complex 22 in the regulation of tuber induction and real form of the compound to induce potato 23 tubers. To clarify the unclear points, further research is needed. 24

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5	University.
6	
7	Supplementary material
8	Supplementary material is available at Bioscience Biotechnology and Biochemistry
9	*************
10	
11	Data availability
12	The data underlying this article will be shared on reasonable request to the
13	corresponding author.
14	
15	Author contribution
16	H.M. shared the responsibility of writing the manuscript with K.M., S.I. and N.K. All
17	authors were responsible for the study concept and design. K.M., S.I. performed all the
18	experiments. All authors contributed to the critical revision of the manuscript.
19	
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23	
24	Declaration of Competing Interests

1	No potential conflict of interest was reported by the authors.
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5	

Entry	Average \pm STDEV
(–)-JA	29.0 ± 1.7^{a}
(-)-cis-OPDA	25.5 ± 3.6^{a}
cis-(+)-OPDA-L-Ile	25.3 ± 1.3^{a}
(+)-4,5-didehydroJA	$24.0 \pm 4.0^{\ a)}$
(–)-JA-L-Ile	18.8 ± 1.6 ^{b)}
(–)-JA-L-Phe	17.3 ± 1.3^{a}
(–)-JA-L-Leu	16.8 ± 1.5 ^{b)}
(–)-JA-L-Val	16.2 ± 1.5 b)
iso-OPDA	6.8 ± 2.5^{a}
3,7-didehydroJA	3.6 ± 2.9^{a}
control	3.8 ± 1.3^{a}

Table I. Evaluation of the potato tuber inducing activities.

1 Three node stemstems of *S. tuberosum* L. cv Dansyaku were transplanted in one flask,

2 and the mean and standard deviation values were calculated from the points given

3 according to Figure S3.

4 a) n=4, b) n=5.

5

1 Figure Legends

2

3	Figure 1	. Biosynthetic	pathway of	of JA	and its	derivatives.
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- 4 *cis*-OPDA: *cis*-12-oxo-phytodienoic acid, OPC 8:0:
- 5 3-oxo-2-(2'-[Z]-pentenyl)-cyclopentane-1-octanoicacid, OPC 6:0;
- 6 3-oxo-2-(2'-[Z]-pentenyl)-cyclopentane-1-hexanoic acid, OPC 4:0:
- 7 3-oxo-2-(2'-[Z]-pentenyl)-cyclopentane-1-butanoicacid, LOX: lipoxygenase, AOS:
- 8 alene oxide synthase, AOC: alene oxide cyclase, OPR3: *cis*-12-oxophytodienoate
- 9 reductase 3, OPR2: *cis*-12-oxophytodienoate reductase 2, JA: jasmonic acid.

10

11 Figure 2. Order of strength of biological activity to induce potato tubers.

12



Figure 1. Biosynthetic pathway of JA and its derivatives.

cis-(–)-OPDA: *cis*-12-oxo-phytodienoic acid, OPC 8:0: 3-oxo-2-(2'-[*Z*]-pentenyl)cyclopentane-1-octanoicacid, OPC 6:0; 3-oxo-2-(2'-[*Z*]-pentenyl)-cyclopentane-1-hexanoic acid, OPC 4:0: 3-oxo-2-(2'-[*Z*]-pentenyl)-cyclopentane-1-butanoicacid, LOX: lipoxygenase, AOS: alene oxide synthase, AOC: alene oxide cyclase, OPR3: *cis*-12-oxophytodienoate reductase 3, JA: jasmonic acid.



Figure 2. Order of strength of biological activity to induce potato tubers.