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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 *cis*-(-)-OPDA, (+)-4, 5-didehydroJA, *cis*-(+)-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

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1  
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-*iso*-12-*O*- $\beta$ -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 (12OHJA), 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  $\alpha$ -linoleinic acid  
18 released by lipase activity; the intermediate is converted by sequential peroxidation,  
19 dehydration and cyclization to form *cis*-12-oxo-phytodienic acid (*cis*-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  $\beta$ -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 from *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 *cis*-jasmone. The key compounds  
21 for this topic are *iso*-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  $\alpha$  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 *cis*-(-)-OPDA,  
6 (+)-OPDA-L-Ile, *iso*-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.

9

10 JA was used for a positive control in this study, since it was reported that JA showed  
11 potato tuber inducing 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

1 reported method (Monte *et al.*, 2018) using ( $\pm$ )-MeJA as a starting compound. All data  
2 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 according 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  
13 (-)-JA at  $10^{-4}$  M, the emergence of the stem from the transplanted stem was delayed  
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  
16 the bioassay using *cis*-OPDA were similar with that of (-)-JA at  $10^{-4}$  M. However, the  
17 length of the extending stem from transplanted node was slightly longer than those  
18 treated with (-)-JA at  $10^{-4}$  M, although the lengths of the extending stems from  
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.

20 Since it was reported that JA showed potato tuber inducing activity (Koda *et al.*  
21 1991) and exogenously applied JA was converted into 12OHJA and 12OGlcJA using  
22 potato single node stems (Matsuura and Yoshihara, 2003), it was hypothesized that  
23 exogenously applied *iso*-OPDA and 3,7-didehydroJA would not be converted to afford  
24 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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3 Faculty of Agriculture, Hokkaido University) in obtaining the spectroscopic data. We  
4 used UPLC MS/MS systems at the Research Faculty of Agriculture, Hokkaido  
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

Table I. Evaluation of the potato tuber inducing activities.

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

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

6

1 **Figure Legends**

2

3 **Figure 1.** Biosynthetic pathway of JA and its derivatives.

4 *cis*-OPDA: *cis*-12-oxo-phytodienoic acid, OPC 8:0:

5 3-oxo-2-(2'-[Z]-pentenyl)-cyclopentane-1-octanoic acid, 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-butanoic acid, LOX: lipoxygenase, AOS:

8 alene oxide synthase, AOC: alene oxide cyclase, OPR3: *cis*-12-oxophytodienoate

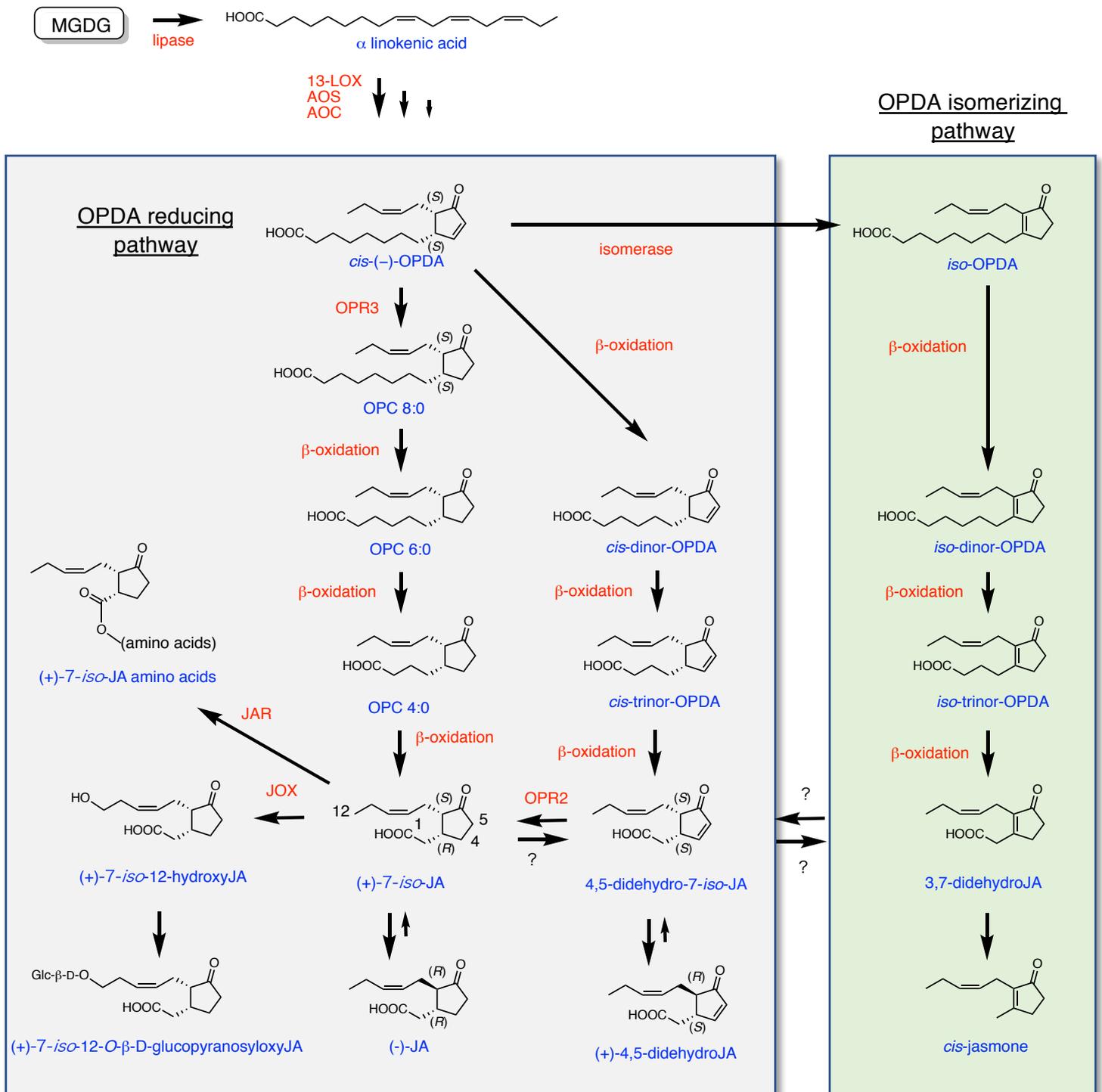
9 reductase 3, OPR2: *cis*-12-oxophytodienoate reductase 2, JA: jasmonic acid.

10

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

12

13



**Figure 1.** Biosynthetic pathway of JA and its derivatives.

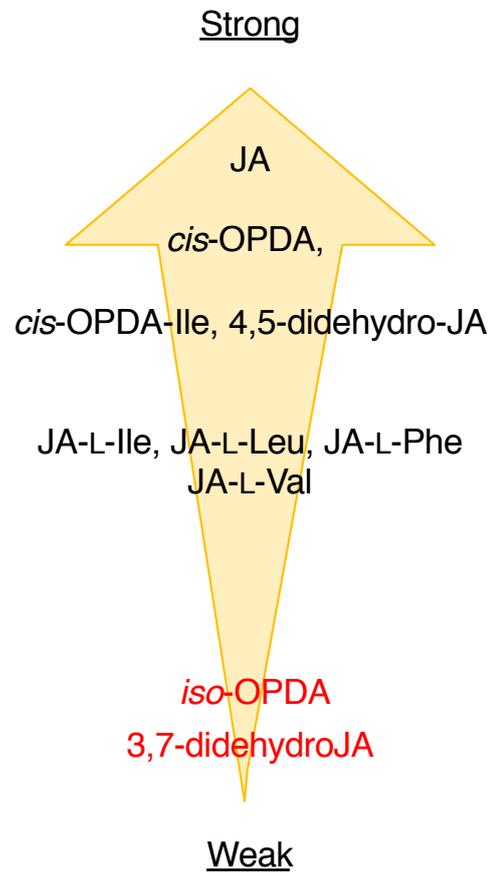
*cis*(-)-OPDA: *cis*-12-oxo-phytyldienoic acid, OPC 8:0: 3-oxo-2-(2'-[Z]-pentenyl)-cyclopentane-1-octanoic acid, OPC 6:0: 3-oxo-2-(2'-[Z]-pentenyl)-cyclopentane-1-hexanoic acid, OPC 4:0: 3-oxo-2-(2'-[Z]-pentenyl)-cyclopentane-1-butanoic acid, LOX: lipoxygenase, AOS: alene oxide synthase, AOC: alene oxide cyclase, OPR3: *cis*-12-oxophytyldienoate reductase 3, JA: jasmonic acid.



Active



Inactive



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