Contribution of the IAM pathway to IAA pool in developing rice grains

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Abstract: A possible role for the indole-3-acetamide (IAM) pathway in the indole-3-acetic acid (IAA) production was investigated in developing rice grains. IAM-hydrolase proposed to convert IAM to IAA primarily through the identification of IAM and IAM-hydrolase activity in some plant species. Expression profiles of the two putative rice IAM-hydrolase genes, *OsAMI1&2*, were compared to the previously quantified IAA level. The abrupt increase in IAA level between 4 and 7 days after anthesis (DAF) was not found to correlate with changes in the expression of *OsAMI1* or *OsAMID2* suggesting that the IAM pathway may not contribute significantly to IAA pool in rice grains. Production of a biological compound other than IAA may explain the high activity of *OsAMI1&2* in developing rice grains. *OsAMI1* that reported to be conserved across the plant kingdom showed higher expression level in most analyzed reproductive rice tissues whereas *OsAMID2* showed more fluctuation in expression comparing to *OsAMI1*. Role of the IAM pathway in IAA production was also discussed in other plant systems and *Arabidopsis* seed was recommended as an ideal tissue to identify enzyme(s) convert(s) tryptophan to IAM as well as physiological effects of IAA produced via this pathway.
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Introduction

The phytohormone auxin is structurally a versatile group of chemicals. IAA is the predominant naturally occurring auxin. IAA acts as a regulator for many aspects of plant growth and development including cell division, elongation and differentiation as well as organ patterning, shoot architecture, vascular development, root growth, leaf expansion, and fruit development (reviewed by Woodward and Bartel 2005; Mockaitis and Estelle 2008). Several pathways of IAA synthesis have been proposed to be operated in plants including a Tryptophan (Trp)-independent as well as Trp-dependent pathways (Figure 1). The indole-3-acetaldoxime (IAOx), the tryptamine (TAM), the indole-3-pyruvic acid (IPA), and the indole-3-acetamide pathways were reported to synthesis IAA from Trp (Fig. 1). So far only the IPA pathway of IAA synthesis in plants has been completely elucidated in *Arabidopsis* (Mashiguchi, Tanaka et al. 2011; Stepanova, Yun et al. 2011; Won, Shen et al. 2011; Kriechbaumer, Wang et al. 2012), maize (Phillips, Skirpan et al. 2011) as well as *Pisum sativum* (Tivendale, Davidson et al. 2012). In this pathway, Trp aminotransferase (TAA) converts Trp to IPA whereas YUCCA, a flavin monooxygenase catalyses the conversion of IPA to IAA. The mutants in TAA or YUCCA of *Arabidopsis* and other plants are not lethal suggesting that other pathways together with the IPA are expected. The mutant in Vanishing tassel2, which encode grass-specific TAA, was reported to account for 60% reduction in IAA level (Phillips, Skirpan et al. 2011). This hormone in plant is crucial and two pathways of IAA production or more may be needed to ensure the efflux of enough amount of IAA. Moreover, multiple IAA biosynthetic pathways may contribute to regulation of IAA production.

As in the IPA pathway, the IAM pathway has been completely elucidated in bacteria and proposed to be operated in plants. In this pathway the IAM-hydrolase was proposed to catalyze the conversion of IAM to IAA whereas the enzyme or enzymes that convert Trp to IAM has not been identified so far in any plant members. The occurrence of IAM pathway in plants has been suggested due to firstly, the identification of endogenous IAM in a wide range of monocot and dicot plants including *Poncirus trifoliate* (Kawaguchi, Fujioka et al. 1993), aseptically grown *Cucurbita maxima* (Rajagopal, Tsurusaki et al. 1994), young fruit of *Citrus unshiu* (Takahashi, Yamaguchi et al. 1975), hypocotyls of *Prunus jamasakura* (Saotome, Shirahata et al. 1993), and epicotyls of *Pisum sativum* (Prinsen, Bercetche et al. 1992). Recently, the IAM has been detected in the model dicot plant *Arabidopsis* (Pollmann, Muller et al. 2002; Sugawara, Hishiyama et al. 2009), *Oryza sativa*, *Zea mays* (Sugawara, Hishiyama et al. 2009), as well as *Nicotiana tabacum* (Lemcke K, Prinsen E et al. 2000; Nemoto K, Hara M et al. 2009; Sugawara, Hishiyama et al. 2009). Secondly, the IAM-hydrolase activity was detected in rice calli (Kawaguchi, Kobayashi et al. 1991; Arai, Kawaguchi et al. 2004), crude extract

from young fruits of *Poncirus trifoliate* (Kawaguchi, Fujioka et al. 1993), *Arabidopsis* (Pollmann, Neu et al. 2003), *Nicotiana* (Nemoto, Hara et al. 2009). The importance of IAM as an intermediate in IAA synthesis was also stressed by the observation that IAM interferes with the conversion of $[^2H]_5$-Trp to $[^2H]_5$- IAA by the IAA synthase complex extracted from 14 different plant species (Pollmann, Düchting et al. 2009).

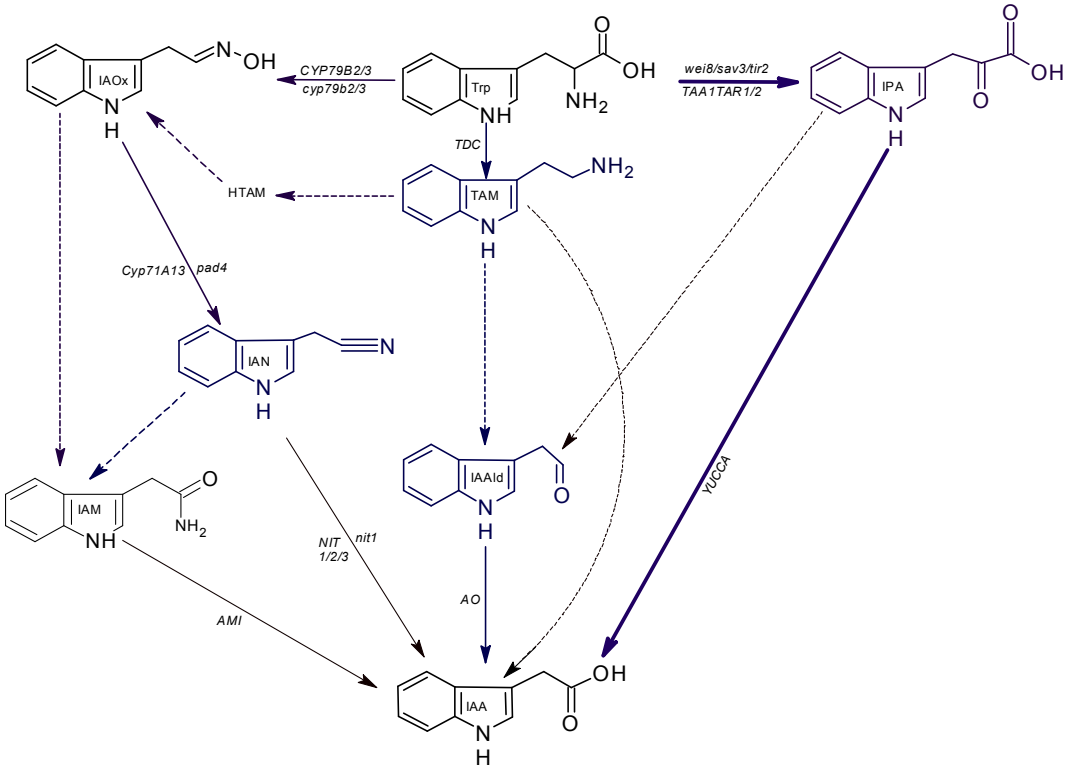

Figure 1: Proposed routes from tryptophan to IAA in plants. Bold lines refer to the first complete dissected pathway of IAA synthesis in plants. Dashed lines indicate that neither a gene nor enzyme activity has been identified in any member of plants. Trp: tryptophan; IAOx: Indole-3-acetaldoxime; IAM: indole-3-acetamide; IAA: indole-3-acetic acid; IPA: indole-3-pyruvic acid; TAM: tryptamine; HTAM: N-hydroxyl tryptamine; IAAld: indole-3-acetaldehyde; IAN: indole-3-acetonitrile; TAA: tryptophan aminotransferase; AMI: amidase; NIT: nitrilase; AO: aldehyde oxidase; YUCCA: a flavin monooxygenase. References for mutant phenotypes are described in (Stepanova, Robertson-Hoyt et al. 2008) *wei8*; (Tao, Ferrer et al. 2008)(*sav3*); (Yamada, Greenham et al. 2009) *tir2*; (Zhao, Hull et al. 2002) *cytp79b2/3*; (Nafisi, Goregaoker et al. 2007) *pad4*; and (Normanly, Grisafi et al. 1997) *nit1*. Gene abbreviations are given in upper case italics. Mutant alleles are given in lower case italics.

In transgenic tobacco infected with *Agrobacterium rhizogenes*, Trp can be converted to IAM and then to IAA by expression of the 2 integrated genes *AUX1* and *2* respectively (Nemoto K, Hara M et al. 2009). Interestingly, overexpression of the *AUX1* gene alone is sufficient to allow the rapid growth of tobacco cell lines in the absence of auxin and at lower concentration of IAM (10^{-5} M) whereas growth of these cell lines were found to be completely inhibited in the RNAi-mediated suppression of *NtAMI1* in IAM-containing medium (Nemoto, Hara et al. 2009). Moreover, phylogenetic analysis showed that that the IAM-hydrolase is a common component of cells in a wide array of monocot and dicot plants as well as the non-seed plant, *Selaginella moellendorffii,* and the moss *Physcomitrella patens* (Mano and Nemoto 2012; Abu-Zaitoon In Press). *Arabidopsis* genome was reported to have 4 putative IAM-hydrolase genes, one of them *Arabidopsis* amidase 1 (*AtAMI1*, At1g08980) was found to be the only *Arabidopsis* sequence to specifically converts IAM to IAA (Pollmann, Neu et al. 2003). In (2009) Nemoto, et al. isolated the AtAMI1 homologue in *Nicotiana tabacum* (NtAMI1) that showed IAM-hydrolase activity.

Rice has been chosen as a plant of study because it is the most popular crop in the world. The completion of sequencing rice genome is considered the first step to explore and develop traits of this crucial crop plant and ultimately all cereals. The abundance of genetic information derived from microarrays, expressed sequence tags, massively

parallel signature sequencing make rice an ideal monocot plant to explore genes involved in the IAM pathway of IAA synthesis. Rice was reported to accumulate large amount of IAA during grain's development (Abu-Zaitoon, Bennett et al. 2012). The largest increase in IAA was detected between 4 and 7 DAF. In a previous study (Abu-Zaitoon In Press), rice proteome was found to have 2 putative IAM-hydrolase enzymes Os04g02780 (OsAMI1) and Os04g02754 (OsAMI2). OsAMI1 was reported to be conserved across the plant kingdom and found in the same clade as AtAMI1 and NtAMI, the two isolated and well characterized IAM-hydrolase enzymes in plants (Pollmann, Neu et al. 2003; Nemoto, Hara et al. 2009). Moreover, All IAM-hydrolase sequences of the conserved clade were reported to encode amidase with significant sequence similarity to the IAM-hydrolyzing bacterial ones. Therefore OsAMI1 was concluded to have a major role in IAA synthesis or other primary process in plant growth and development (Abu-Zaitoon In Press).

The importance of IAM pathway in IAA synthesis has been highlighted primarily by the identification of IAM as well as IAM-hydrolase activity in species across the plant kingdom. Nevertheless, major questions regarding the IAM pathway need to be answered. The enzyme or enzymes converting Trp to IAM has not been identified in any plant. Contribution of the IAM pathway to IAA pool and associated phenotypes as well as interaction with other pathways of IAA synthesis was not determined. Physiological effects of IAA produced by the IAM pathway in plants remains elusive. The major aim of this research was to find out whether the IAM pathway is operated in developing rice grains. Therefore, correlation if any between the expression of *OsAMI1* and *OsAMI2* genes and changes in IAA level in the developing rice grains was explored. Expression profiles of IAM-hydrolase genes were also investigated in a group of reproductive rice organs.

Expression profiles of the *OsAMI1&2* were analyzed using Public microarray data downloaded from PLEXdb data base (Dash S, Van Hemert J et al. 2012) (http://www.plexdb.org). RNA samples from various organs of rice were harvested and hybridized on Affymetrix microarrays to investigate developmental and temporal expression of IAM-hydrolase genes. Data were downloaded from the following experiments: OS5 (Jain, Nijhawan et al. 2007), OS8, OS16 (Li M, Xu W et al. 2007), and OS89 (Gao and Xue 2012).

Results and discussion

In this study the expression profiles of *OsAMI1* and *OsAMI2* were studied in various reproductive rice tissues (Figure 2). The highest expression level of *OsAMI1* was found in Y leaf, inflorescence (6 DAF), seedling shoot, endosperm (9 DAF), and embryo (3 DAF) whereas peaks of expression level for *OsAMI2* were detected in Y leaf, inflorescence (6 DAF), seedling root, embryo (12 DAF), and endosperm (16 DAF). The lowest expression level of the 2 IAM-hydrolase genes was detected in the first 3 developmental stages of inflorescence. Generally, expression of *OsAMI1*is high in most tested tissues and changes in the expression is very limited comparing to that of *OsAMI2*. In *Arabidopsis*, transcripts for *AtAMI1* were detected in all analyzed tissues. The highest expression levels were detected in inflorescence, young leaves, and germinating seeds (Pollmann, Neu et al. 2006). High amount of the *Arabidopsis* amidase (at the translational level, protein) was only detected in young leaves. Discrepancy in the expression level of amidase from the same tissue in different plants suggests the multiphysiological effects of this enzyme in plant life.

It has been reported that IAA is produced in high amount in rice kernels compared to vegetative tissue. Abu-Zaitoon, et al. (2012) showed that IAA levels in kernels increase from undetectable limit at 4 DAF to 2µg/g FW during 14 days from anthesis. The greatest change in auxin synthesis occurs from 4 to 7 DAF. This period of grain development was investigated to find out whether the expression of *OsAMI1* and *OsAMID2* correlate with this change in IAA level and therefore to suggest a role for amidase in IAA synthesis.

Figure (3) shows change in expression level of *OsAMI1* and *OsAMI2*. The expression of the two IAM-hydrolase genes was not found to change significantly ($p=0.04$ and 0.3 respectively) between 3-4 and 5-10 DAF. Due to lack of correlation between change in the expression level of rice amidases and IAA level during the active period of IAA synthesis (4-7 DAF), a significant role if any for *OsAMIs* and ultimately the IAM pathway in IAA synthesis in the developing rice grains is not expected. High expression levels of *OsAMI1* and *OsAMI2* in developing rice grains may be linked to a biological activity other than IAA synthesis such as hydrolysis of IAA conjugates. The same conclusion was drawn by Arai, et al., (2004) who partially purified IAM-hydrolase from rice calli. The *Km* value of the isolated rice enzyme (0.96 mM) was found to be considerably higher for IAM comparing to that of the *Agrobacterium tumefaciens* (1.2 µM) (Kemper, Wafenschmidt et al. 1985). Additionally, no endogenous IAM was detected from various rice organs including shoots, roots, calli and young fruits (Arai, Kawaguchi et al. 2004).

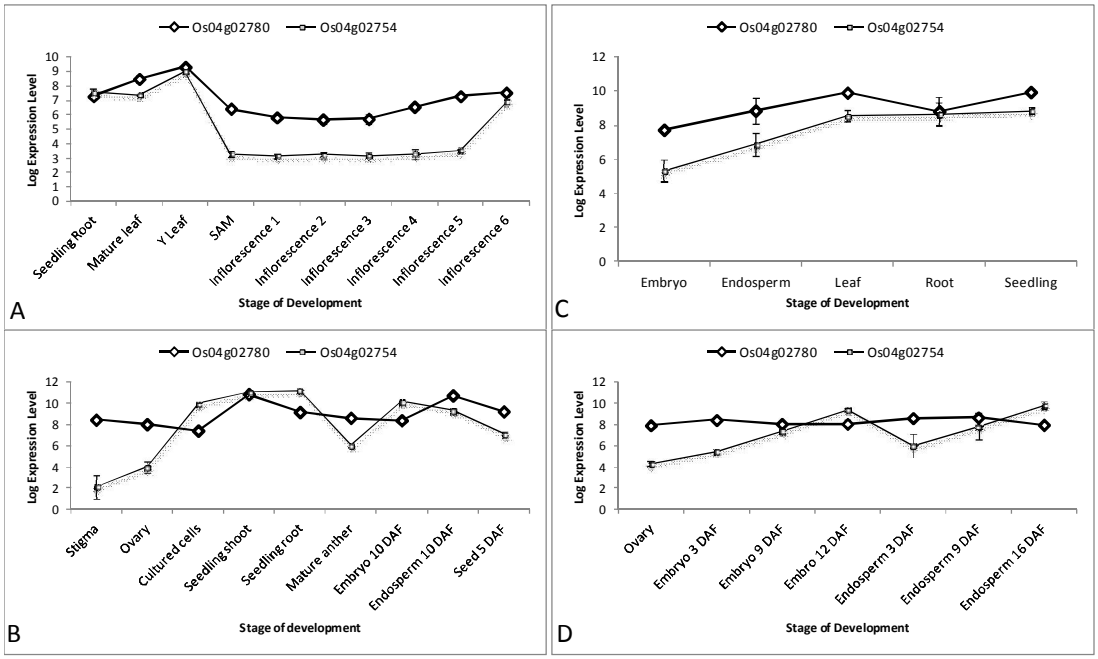

Figure 2: Expression profiles of *OsAMI* (Os04g02780) and *OsAMI2* (Os04g02754) as downloaded from PLEXdb data base (http://www.plexdb.org). Each point represents the mean ±standard error of 3 biological replicates for (A & stigma and ovary for C), 2 biological replicates for (B & D). All data were normalized by RMA from Rice 57k genechip at the experiment OS5 (A), OS8 (B), OS16 (C), OS89 (D). (A) Inflorescence 1 (1-3 cm), inflorescence 2 (3-5 cm), inflorescence 3 (5-10 cm), inflorescence 4 (10-15 cm), inflorescence 5 (15-22 cm), inflorescence 6 (22-30 cm), SAM (shoot apical meristem), seedling root (7-days old). (B) Embryo and endosperm (6 DAF), seedling. (D) Ovary (0 DAF).

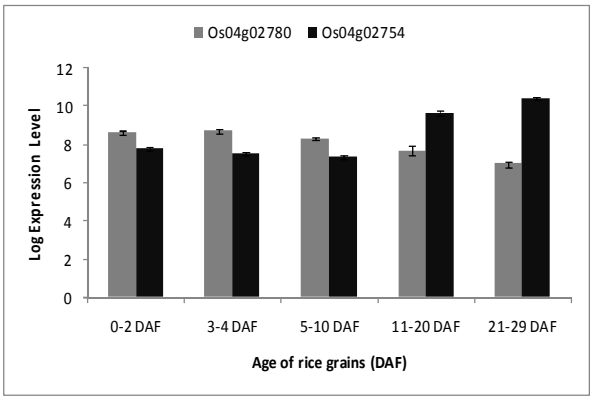

Figure 3: Expression profiles of Os04g02780 *(OSAMI)* and *OsAMI2* (Os04g02754) as downloaded from PLEXdb data base (http://www.plexdb.org). Each point represents the mean ±standard error of 3 biological replicates normalized by RMA from Rice57k genechip at the experiment OS5 (Jain, Nijhawan et al. 2007; Wise, Caldo et al. 2007).

Unlike the IAM pathway, the IPA pathway was reported by our research group to have a pivot role in IAA synthesis in rice grains (Abu-Zaitoon, Bennett et al. 2012). Changes in the expression of *OsYUCCA9*, *OsYUCCA11* as well as *OsTAA1*were found to significantly correlate with the abrupt and large change in IAA synthesis in the active period of IAA accumulation (between 4 and 7 DAF). A minor role if any for the IAM pathway is also expected in the maize endosperm. A 95% reduction in IAA level was reported in the *de-18* mutant that results from a mutation in the *YUCCA1* gene of maize endosperm (Bernardi, Lanubile et al. 2012). As in the developing rice grains, most IAA in the maize endosperm was reported to be obtained through the IPA pathway (Bernardi, Lanubile et al. 2012). IAM was also excluded as an intermediate in IAA synthesis in seeds of pea (*Pisum sativum*). Labeled IAM was not detected after injection the liquid endosperm of pea seed with deuterated Trp and the endogenous IAM was below the detection limit (Tivendale, Davidson et al. 2012). In *Brassica rapa* (turnip), correlation between amidase activity and free IAA level were not detected in a group of studied tissues including leaves, hypocotyls and roots (Ishikawa, Kuroda et al. 2007).

However, this may not be the case in other systems including *Arabidopsis thaliana*. Correlation between free IAA and IAM levels were found in imbibed seeds and sterile-grown seedlings. The amount of IAA and IAM were found to be 270 and 40-fold higher in imbibed seeds comparing to the 2-week old seedlings (Pollmann, Muller et al. 2002).

Interestingly, IAM were found to be parallel to IAA level in this system. The 2 metabolites were also found to largely decrease and at the same rate during the 2 weeks after seed imbibition. This system is ideal to follow the expression level of *AtAMI1* and to generate knock out as well as overexpression amidase mutants to detect effects on *de novo* IAA level as well as auxin phenotypes. After that, Microarray or real-time PCR analysis of any changes in the expression level of genes in these mutants may be enough to identify gene (s) catalyze(s) the conversion of Trp to IAM. The 2 weeks interval after seed imbibition will be also valuable to screen *AtYUCCAs* expression level and therefore the contribution of both pathways in IAA level. To sum up unlike the IPA, the IAM is not expected to be a ubiquitous pathway and seems to have a very limited role in IAA synthesis in plant tissues. Even though IAM and IAM-hydrolase activity has been identified in a group of monocot and dicot plants, correlation between IAA level and the expression of IAM-hydrolase genes were not found most studied plants.

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