

Auxin Biosynthesis

The naturel auxin molecule is an indole-derived compound, indole-3-acetic acid, IAA. It is produced either from, or independently of, Tryptophan (Trp). Illustrated here are the known pathways of Trp-dependent IAA production in plants.

In chloroplast, Trp is produced from shikimate to chorismate, then to anthranilate by the anthranilate synthases WEI2/7 (or ASA1/ASB2) enzymes (Stepanova et al, 2005). WEI2 and WEI7 were uncovered in a genetic screen for identifying ethylene-mediated root growth regulators. Anthranilate is then converted into indole-3-glycerol phosphate (IGP) by multiple enzymes including IGS (Indole-3-glycerol phosphate synthase, Ouyang et al, 2001). Further conversion to indole and Trp is done by Trp synthase α (TSA1) and Trp synthase β (TSB1) (Tzin et al, 2010). The pathways for Trp-independent IAA production use IGP and Indole as substrates.

Four characterized pathways use Trp as precursor for IAA production. One of them, producing indole-3-acetaldoxime (IAOx), indole acetonitrile (IAN) and indole glucosinolate (IG), is specific to the Brassicaceae family (Sugawara et al, 2009). It is involved in the production of secondary metabolites such as glucosinolates and camalexin. IAOx is produced from Trp by cytochromes P450 CYP79B2 and CYP79B3 (Zhao et al, 2002). Glucosinolates biosynthetic genes include SUPERROOT SUR1 and SUR2, CYP71A13 and UGT74B1 (Douglas Grubb et al, 2004; Seo et al, 1998).

The first characterized enzymes in auxin biosynthesis were the iaaH and iaaM enzymes discovered in *Pseudomonas* and *Agrobacterium*. These enzymes encode a Trp-2-monooxygenase that converted Trp into indole-3-acetamide (IAM) and a hydrolase that modifies IAM into IAA. Orthologs of iaaH and iaaM have not be found in plants. The Trp-IAM-IAA pathway is catalized by a Trp-2-monooxygenase and the IAM hydrolase AMI1 (Pollmann et al, 2003). IAM may also be produced from IAOx and IAN.

The most prominent pathway for plant development is the two-step pathway involving indole-3-pyruvic acid (IPyA) as intermediate. The enzymes catalysing these reactions were isolated from genetic screens aiming at identifying regulators of organ development, ethylene response and shade avoidance. The first step is converting Trp into IPyA by the action of tryptophan aminotransferases (TAA1 and TARs). TAA1 was identified as WEAK ETHYLENE INSENSITIVE8 (WEI8, Stepanova et al, 2008), SHADE AVOIDANCE3 (SAV3, Tao et al, 2008) and TRANSPORT INHIBITOR RESPONSE2 (TIR2, Yamada et al, 2009). The second step is rate-limiting, catalyzed by the flavin-containing monooxygenases of the YUCCA proteins (YUC1-11, Zhao, 2012).

The last putative pathway involves tryptamine (TAM), as intermediate based on experiments performed in *Avena* (Lehman et al, 2010). The first step of the pathway is catalyzed by tryptophan decarboxylase (TDC), found in several plant species, but not yet in *Arabidopsis*. TAM is converted into N-hydroxytryptamine by hydroxylation of the amino group of TAM, supposedly by members of the YUCCA family (Zhao et al, 2001). However, N-hydroxytryptamine has not been detected in plants so far. Other research indicate that TAM may be directly converted into indole-3-acetaldehyde (IAAId) (Quittenden, 2009). Besides, IAAId may be also produced from IPyA by the YUCCAs as observed in rhizobacteria (Mano and Nemoto, 2012). IAAId is finally oxidized by aldehyde oxidases (AO) into IAA.



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