Origin of plant auxin biosynthesis

Jipei Yue[1,2], **Xiangyang Hu**[1], and **Jinling Huang**[2]

[1] Key Laboratory for Plant Diversity and Biogeography of East Asia, Kunming Institute of Botany, Chinese Academy of Sciences, Kunming, China
[2] Department of Biology, East Carolina University, Greenville, NC 27858, USA

The recent finding of the tryptophan aminotransferase (TAA)/flavin monooxygenase (YUC) pathway as the principal route of auxin production in plants provides an opportunity to revisit the origin of plant auxin biosynthesis. Phylogenetic analyses of the *TAA* and *YUC* gene families provide very little evidence for the production of indole-3-acetic acid (IAA) in algae. Instead, horizontal gene transfer of *YUCs* from bacteria to the ancestral land plant suggests that the TAA/YUC pathway is a land plant innovation. In this Opinion article we postulate that the origin of tryptophan-dependent IAA biosynthesis in land plants might have evolved in response to interactions with microbes, particularly bacteria, allowing plants to counteract bacterial activities and control their own auxin signaling.

Auxin biosynthesis in plants and algae

Plants adapt to environments by regulating growth and development largely through signaling via phytohormones [1]. Auxins are a class of phytohormones that regulate apical dominance, cell elongation, xylem differentiation, abscission suppression, and many other developmental processes [2,3]. The study of auxins dates back to the time of Charles Darwin, who first described the phototropism of coleoptiles, later found to be caused by IAA (reviewed in [4]). Because IAA is the most abundant endogenous auxin in plants, the terms auxin and IAA are sometimes used interchangeably [5]. The effect of IAA on plant development is mainly dependent upon the IAA concentration gradient, which in turn is affected by several other processes such as IAA biosynthesis, conjugation, de-conjugation, degradation, and intercellular transport [1,4].

Despite the importance of auxins in plant development, and a long history of study, our knowledge about the evolution of plant auxin biosynthesis remains limited. The biosynthesis of IAA in plants is generally believed to be either tryptophan (Trp)-independent or Trp-dependent, but there is little molecular evidence for the Trp-independent pathway. Trp-dependent IAA biosynthesis also occurs widely in microbes such as bacteria and fungi [6–8], but it is not entirely clear whether and how the plant and microbial pathways are related; both similarities and differences in gene components were found between plant and bacterial pathways [4,9], and the details of fungal IAA biosynthesis remains elusive [10]. In addition, the distribution of auxin biosynthesis in photosynthetic eukaryotes continues to be controversial [11,12]. Machineries of IAA polar transport and response are conserved and appear to be specific to land plants [12,13]. However, homologs of several IAA biosynthetic genes are found in brown algae and green algae, suggesting that IAA is possibly produced in miscellaneous algal lineages [14–16].

Much of the above confusion stems from the lack of clear understanding of IAA biosynthesis itself in plants [17]. Traditionally, at least four Trp-dependent IAA biosynthetic pathways have been proposed [7,18]. Not only are these pathways interlinked but they are also either questionable or restricted to certain plant groups [18]. Furthermore, none of these proposed IAA biosynthetic pathways were fully defined until the recent finding of a simple two-step pathway, catalyzed by the TAA family of aminotransferases and the YUC family of flavin monooxygenases [19]. This new TAA/YUC pathway is also the principal route of IAA biosynthesis in land plants [20–22], thus allowing an opportunity to revisit some outstanding questions in plant biology: when did plant auxin biosynthesis evolve? How and why?

Revisiting IAA biosynthesis in algae

Auxins have long been thought to play a crucial role in the evolution of land plants and multicellular algae [14]. There are many, sometimes conflicting, reports on the production of auxin or auxin-like substances in algae [14,15], but concerns that these substances may be produced by algae-associated microbes have also been raised [11]. Detailed genome analyses of auxin signaling, including auxin biosynthesis, transport and response [23], provide no definite answer. Both auxin transport and response machineries are well studied and conserved in land plants. Homologs of auxin transporter and receptor genes (e.g., *PIN*, *ABP1*) are present in green algae [13,24]. However, components of the well-established auxin response machinery, including TRANSPORT INHIBITOR RESPONSE1-AUXIN SIGNALING F-BOX PROTEIN (TIR1-AFB), AUXIN RESPONSE FACTOR (ARF) and AUXIN-INDOLE-3-ACETIC ACID (AUXIN-IAA), are specific to land plants [12,25]. In addition, plasma membrane-localized PIN transporters, which mediate auxin polar transport and concentration gradients, have not been identified in any algal groups [13]. Therefore, it appears that auxin transport and response machineries likely are innovations of land plants. Nevertheless, homologs of several Trp-dependent IAA biosynthetic genes have been found in different algal lineages [15,16], supporting a much earlier origin of IAA biosynthesis.

Corresponding author: Huang, J. (huangj@ecu.edu).

Keywords: IAA biosynthesis; microbe–plant interaction; gene transfer; plant evolution.

1360-1385/

http://dx.doi.org/10.1016/j.tplants.2014.07.004

In the TAA/YUC pathway, Trp is first converted by TAAs to indole-3-pyruvate (IPA), which is then converted to IAA by YUCs. Given that the TAA/YUC pathway represents the main and best-defined IAA biosynthetic pathway in land plants [20,21], its distribution may provide pivotal insights into the origin of auxin biosynthesis. Several earlier studies reported homologs of *TAAs* and/or *YUCs* in brown algae (e.g., *Ectocarpus siliculosus*) and green algae (e.g., *Chlorella*) based on pairwise sequence similarity comparisons [15,16]. The caveat of such an approach is that sequence similarity does not always translate into evolutionary relatedness and/or functional equivalent. In fact, both *TAAs* and *YUCs* belong to large gene families distributed in many prokaryotic and eukaryotic groups, possibly participating in various biological processes. To investigate the relationships of algal *TAA* and *YUC* homologs to other members of the gene families, we performed phylogenetic analyses with samples from representative lineages of the three domains of life (Bacteria, Archaea, and Eukaryotes). Clearly, land plant *TAAs* are most closely related to homologs from secondary photosynthetic eukaryotes, choanoflagellates and their close relatives apusozoans and ichthyosporeans (Figure 1). No choanoflagellates, apusozoans, or ichthyosporeans reportedly produce IAA, which is consistent with their lack of *YUC* homologs specifically related to IAA biosynthesis (discussed below). It is very likely that *TAA* gene homologs in these organisms are involved in activities other than IAA biosynthesis. Homologs of the *YUC* gene family are also present in bacteria and miscellaneous eukaryotes, including brown algae and chlorophyte green algae [15,16]. However, no *YUC* homologs were found in charophytes, a green algal group closely related to land plants, in our search of the US National Center for Biotechnology Information (NCBI) expressed sequence tag database (dbEST) and other databases. This is notable considering

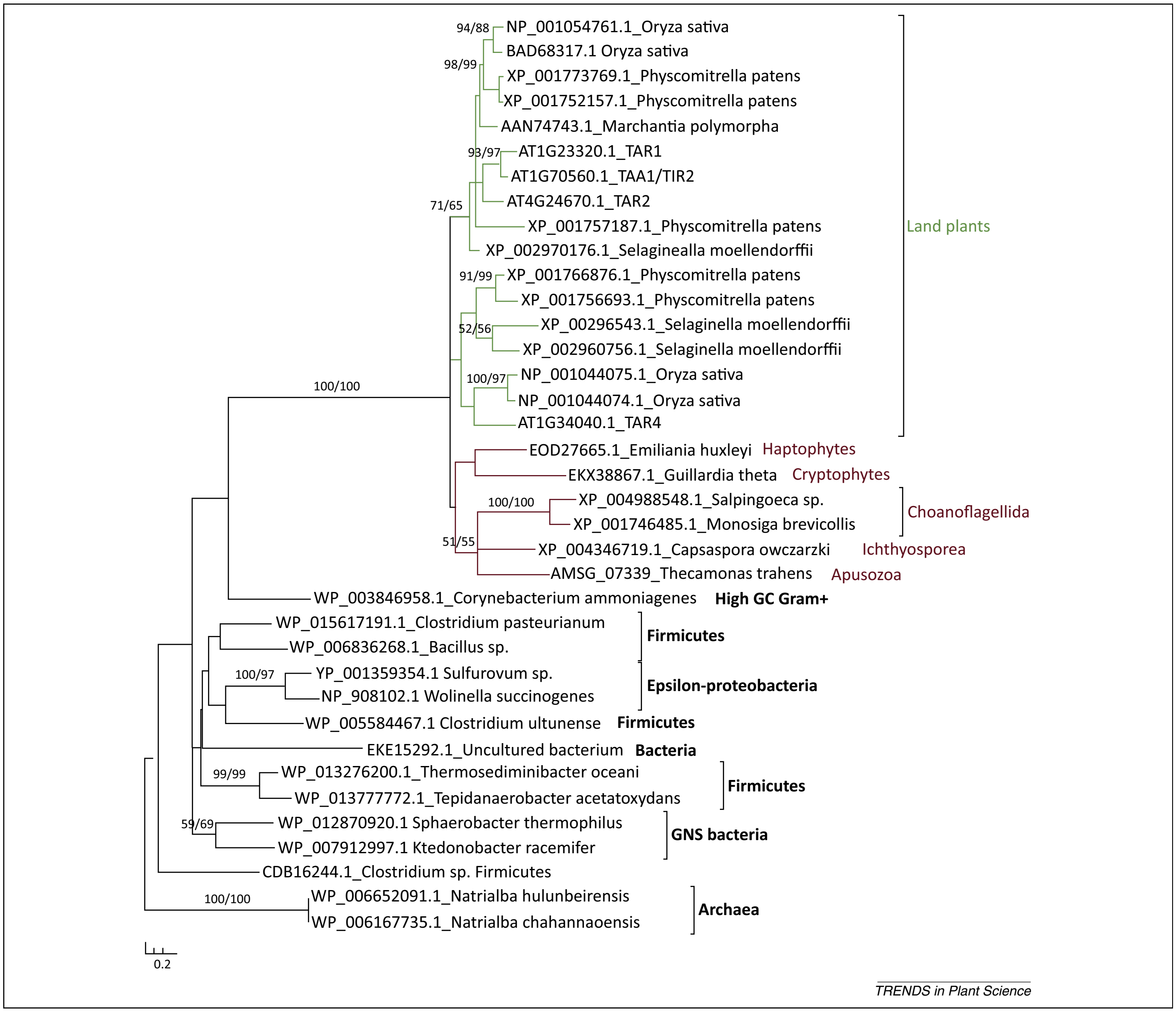

Figure 1. Molecular phylogeny of tryptophan aminotransferases (TAAs) and their homologous sequences in different lineages. Numbers above branches show bootstrap support values inferred from maximum likelihood and distance analyses, respectively. Bootstrap values below 50% in both methods are not shown. Taxonomic affiliations are shown after species names. Green: green plants; purple: other eukaryotes.