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Origin of plant auxin biosynthesis

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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.

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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
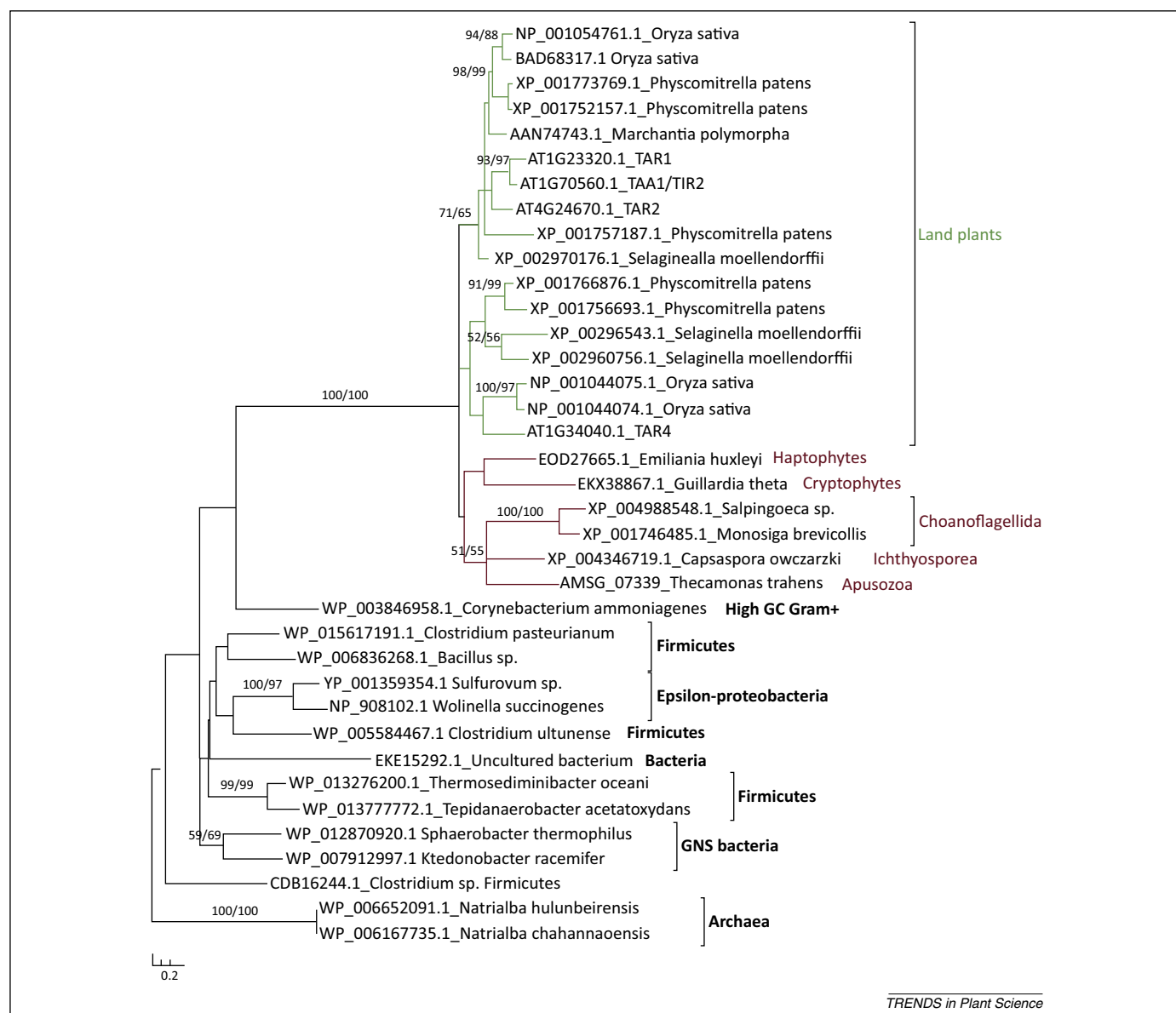

Figure 1. Molecular phylogeny of tryptophan aminotransferases (TAAs) and their homologous sequences in different lineages. Numbers above branches show bootstrap support values inferred from maximum likelihood and distance analyses, respectively. Bootstrap values below 50% in both methods are not shown.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

that NCBI dbEST database contains sequences from multiple charophyte species [e.g., *Chlorokybus atmophyticus* (23 716 sequences), *Klebsormidium spp.* (60 125 sequences), *Mesostigma viride* (15 972 sequences), *Nitella hyalina* (88 280 sequences), *Chaetosphaeridium globosum* (59 098 sequences), and *Coleochaete spp.* (9813 sequences)]. Brown algal and chlorophyte *YUC* homologs are more closely related to sequences from animals, fungi, and other eukaryotes (including several other remote land plant homologs that are not involved in IAA biosynthesis) (Figure 2). Therefore, it is doubtful that these algal *YUC* homologs are functionally related to IAA biosynthesis. Admittedly, such a gene tree topology can almost always be explained by multiple scenarios, such as differential gene loss, intracellular gene transfer (IGT) from mitochondria, or insufficient taxonomic sampling. However, the most parsimonious explanation is that *YUCs* essential to IAA biosynthesis are derived from an horizontal gene transfer (HGT) event from bacteria to the most recent common ancestor of land plants [26] (Figure 2). This HGT event also suggests that the TAA/YUC main IAA biosynthetic pathway is an innovation of land plants.

The insights from molecular phylogenies of the *TAA* and *YUC* gene families are consistent with available data, such as the concurrent appearance of auxin polar transport and response systems in land plants [12,13]. Although the possibility of alternative auxin biosynthetic pathways cannot be ruled out, there appears to be very little phylogenetic evidence for the presence of the TAA/YUC pathway in any algal group. In fact, the suggestion of IAA biosynthesis in different algal groups can be difficult to reconcile with available data. For instance, brown algae are only distantly related to primary photosynthetic eukaryotes (red algae, glaucophytes, and green plants), and their plastids were acquired secondarily through endosymbiosis with a red algal cell [27,28]. If the TAA/YUC pathway indeed exists in brown algae, it would likely be present in (i) the common ancestor of all eukaryotes, or (ii) the common ancestor of primary photosynthetic eukaryotes, followed by a transfer from the red algal endosymbiont to brown algae [14]. Although not entirely impossible, both scenarios require losses of the TAA/YUC pathway in numerous eukaryotic taxa, which not only is less parsimonious, but also lacks sufficient evidence.

Mosaic nature of plant Trp-dependent IAA biosynthesis
Given that the TAA/YUC pathway most likely evolved during the transition of plants from aquatic to terrestrial environments, it is useful to understand the underlying genetic mechanisms for the origin of this major land plant novelty. Trp, as a common precursor of IAA biosynthesis, is produced in many prokaryotes and eukaryotes [29]. In plants, Trp biosynthesis occurs strictly in plastids [29]. Because of the lack of sufficient phylogenetic signal, the evolutionary origin of most Trp biosynthetic genes in plants cannot be pinpointed. However, several other genes are closely related to homologs from cyanobacteria, chlamydiae, or other bacteria (see the supplementary material online). For instance, genes encoding both subunits of Trp synthase (*TSA* and *TSB*) in red algae and green plants are

derived from cyanobacteria (plastids). The PR-anthranilate transferase gene (*PAT1*) in plastid-containing eukaryotes appears to be derived from chlamydiae. The cyanobacterial or chlamydial ancestry of these plant Trp biosynthetic genes is somewhat expected, considering the cyanobacterial origin of plastids [30] and the recent findings of chlamydial contribution to plastid establishment [31–33]. In addition, it has been shown that many plastid-derived nuclear genes perform plastidial functions [34]. Therefore, the origin of plant Trp biosynthesis was possibly associated with the origin of plastids and eukaryotic photosynthesis.

The subcellular localization of IAA biosynthetic enzymes has not been fully determined [35]. Of the two gene families (*TAAs* and *YUCs*) essential for plant IAA biosynthesis, neither appears to be derived from cyanobacteria (plastids) or chlamydiae. *TAAs* are only distantly related to bacterial homologs, whereas *YUCs* were possibly acquired from other bacterial groups (Figures 1 and 2). Clearly, plant Trp-dependent IAA biosynthesis has been shaped by gene recruitment from different sources, including plastids and bacteria. It has long been known that plant genomes contain numerous genes derived from organelles (plastids and mitochondria). Although many of these genes are functionally related to the original organelles, some have contributed to the evolution of various other important features or processes of plants, such as hemoglobins [36], mechanosensitive channels [37], cell wall [38,39], and stress response [40]. By contrast, HGT in multicellular eukaryotes is often debated, but an increasing amount of data point to its widespread impact on land plant evolution and adaptation [26,41–43]. For instance, the *ILR2* gene regulating auxin conjugate sensitivity and metal homeostasis in mustard family Brassicaceae and other flowering plants was reportedly acquired from viruses [44,45]. The mosaic nature of Trp-dependent TAA/YUC IAA biosynthetic pathway in land plants provides additional evidence for the important role of lateral genetic transmission in generating and optimizing evolutionary novelties in eukaryotes [46].

Microbe–plant interactions and the origin of plant auxin biosynthesis
The ability to produce IAA is also widely distributed in bacteria and fungi, including not only many plant pathogens, symbionts, and rhizobacteria but also bacteria that are not commonly associated with plants [6,8]. Although fungal IAA biosynthetic pathways remain largely unclear, it is known that Trp is utilized in both bacteria and fungi as the main precursor for IAA production through intermediates such as IPA, indole-3-acetamide (IAM), and tryptamine (TAM) [10,47]. In particular, the IPA and IAM pathways are common among rhizobacteria and plant pathogens, respectively [6]. Because bacterial IAA biosynthetic pathways are relatively simple and better understood, their genes have traditionally been used to search for homologs in plants to understand plant IAA biosynthesis. These bacterial IAA biosynthetic genes, however, are often absent from plants or are only distantly related to their plant homologs [6,7,16]. A similar scenario also exists for genes essential to plant IAA biosynthesis because plant
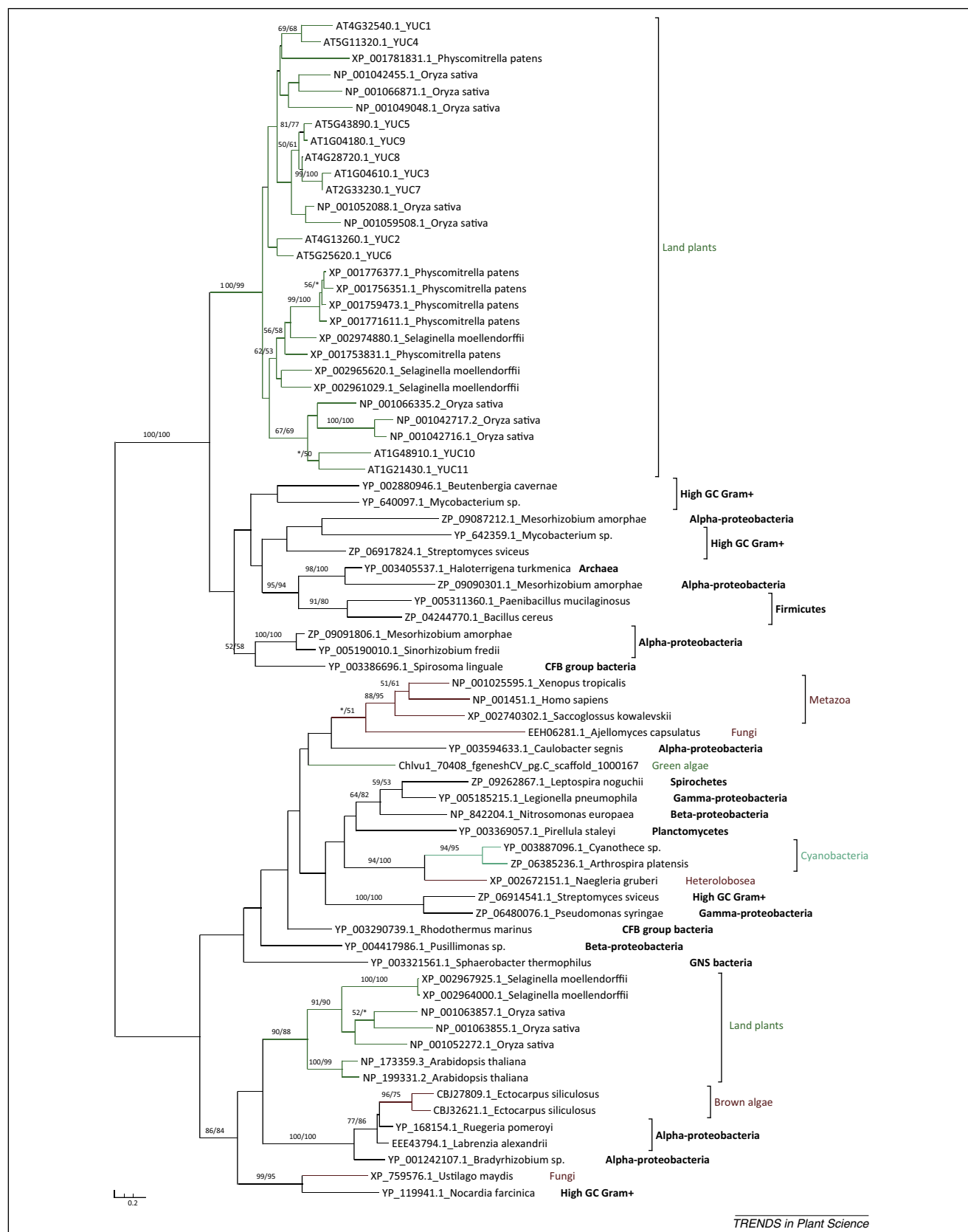
Figure 2. Molecular phylogeny of flavin monooxygenases (YUCs) and their homologous sequences in different lineages. YUCs essential to plant IAA biosynthesis are shown in the upper part of the tree. Numbers above branches show bootstrap support values inferred from maximum likelihood and distance analyses, respectively. Asterisks indicate values lower than 50%. Other bootstrap values below 50% in both methods are not shown. Taxonomic affiliations are shown after species names. Green: green plants; brown: other eukaryotes.

TAAs and *YUCs* are only distantly related to bacterial and/or fungal homologs (Figures 1 and 2). In addition, neither *TAA* nor *YUC* homologs are known to participate in bacterial IAA biosynthesis. Therefore, the available data suggest that IAA biosynthesis evolved independently in bacteria, fungi, and land plants.

Microbe–host interactions have played a pivotal role in the evolution of many eukaryotic groups, including plants [48,49]. Such interactions often are mutualistic or pathogenic, characterized by complementary or competing biological needs, respectively. The convergent evolution of IAA production in plants, bacteria, and fungi points to an important biological role of IAA in the three groups and their interactions. Indeed, IAA is a common signaling molecule affecting many physiological processes of bacteria. It allows bacteria to meet their nutritional and habitat needs by stimulating root growth and carbohydrate exudation, facilitating host plant colonization, and inducing environmental stress responses [6,50–52]. Importantly, IAA is also involved in quorum-sensing [53,54], which regulates bacterial activities based on local population density. Not only is bacterial quorum-sensing intimately associated with the formation of rhizosphere [55], but also with infection of plants by pathogenic bacteria [56]. Likewise, IAA produced by fungi has been known to induce mycorrhizal formation or oncogenesis in host plants [10,57]. Presumably, the versatile role of bacterial and fungal IAA may either benefit or damage host plants. For instance, while rhizobacteria often produce IAA to promote plant growth and development, pathogenic bacteria generate the same molecule to increase the susceptibility of host plants, thus circumventing plant defense [47,50]. Furthermore, many bacteria and fungi also are able to degrade IAA or transfer it to plant tissues [52,58]. As such, bacteria and fungi could potentially hijack host plants by manipulating IAA production.

We postulate that plant auxin biosynthesis, or the TAA/YUC main IAA biosynthetic pathway, might have evolved in response to interactions with microbes, particularly bacteria, during the early stages of plant colonization of land. The ability to produce IAA by many bacterial groups, including those not associated with plants, suggests that IAA is a very ancient signaling molecule in bacteria. Many eukaryotes have evolved mechanisms to interact with microbes encountered in the environment [59,60]. These mechanisms frequently target microbial signaling pathways and, therefore, either interrupt or regulate microbial activities [61,62]. Plants may not only mimic or inhibit bacterial quorum-sensing as a defense response against infection, but they also produce precursors of quorum-sensing molecules to promote association with beneficial bacteria [59,63,64]. In addition, given the role of IAA as a common molecule important to both plants and bacteria, it is conceivable that plants need to maintain an independent system of IAA metabolism (biosynthesis, storage, and degradation), transport, and response. The production of IAA by plants essentially transforms IAA into a reciprocal signaling molecule in bacteria–plant interactions [65], allowing plants to counteract the behaviors of bacteria. Indeed, plant immunity is closely linked to signaling by auxin and other hormones [66–68]. Repressing IAA signaling leads to better resistance to pathogenic bacteria [69]. Crucially, an independent system of IAA metabolism also allows plants to exercise control of their own IAA concentration within cells and/or among tissues, thus providing autonomy in auxin regulation and plant development.

Available data show that the origin of Trp-dependent IAA biosynthesis was concurrent with the origins of plasma membrane-localized PIN transporters and the auxin response pathway in land plants [12,13]. Many genes related to these systems were subject to rapid duplication and functional differentiation [13,25,70], enabling plants to fine-tune the regulation of growth and development in response to environmental and internal cues [1,70]. Such an enhanced ability might have ultimately permitted plants to adapt to a broad spectrum of terrestrial habitats, thus facilitating their rapid diversification on land.

Concluding remarks and future directions

Knowledge about the origin of plant auxin biosynthesis is crucial for understanding the evolution of land plants and other multicellular photosynthetic eukaryotes. Phylogenetic evidence suggests that the TAA/YUC main IAA biosynthetic pathway most likely evolved in land plants. Such evidence is consistent with the available data about plant auxin transport and response systems, although it does not rule out the possibility that different systems of auxin signaling may exist in miscellaneous algal groups. Clearly, the evolution of plant Trp-dependent IAA biosynthesis has been shaped by lateral genetic transmission, gene duplication, and functional differentiation. We hypothesize that IAA biosynthesis evolved in land plants initially as a mechanism to regulate or counteract the activities of microbes, particularly bacteria, encountered in the environment. This hypothesis is largely tied to the role of IAA in microbial life. To test this hypothesis, future work is necessary to investigate how plant IAA production affects the activities of microbes such as rhizobacteria and plant pathogenic bacteria.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.tplants.2014.07.004.

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