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Review

AUXOLOGY: When auxin meets plant evo-devo

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ABSTRACT

Auxin is implicated throughout plant growth and development. Although the effects of this plant hormone have been recognized for more than a century, it is only in the past two decades that light has been shed on the molecular mechanisms that regulate auxin homeostasis, signaling, transport, crosstalk with other hormonal pathways as well as its roles in plant development. These discoveries established a molecular framework to study the role of auxin in land plant evolution. Here, we review recent advances in auxin biology and their implications in both micro- and macro-evolution of plant morphology. By analogy to the term 'hoxology', which refers to the critical role of *HOX* genes in metazoan evolution, we propose to introduce the term 'auxology' to take into account the crucial role of auxin in plant evo-devo.

Introduction

Body plan (or *Bauplan* in German) is essentially the blueprint for the way the body of an organism is laid out. It recapitulates the basic features for a phylum without precisely describing any one particular species of that division. Unlike animals, plants have an alternation of generations where the sporophyte (2*n*) and the gametophyte (*n*) are independent organisms that are characterized by a unique body plan. The patterning of the body plan mainly includes the establishment of axial properties (such as the apical–basal, the radial, and the proximal–distal axes) and the determination of cell fate by positional information.

In seed plants, the principal body axes of plants are patterned both early in embryonic development and during all the life cycle. Embryogenesis generates the apical–basal axis, the radial axis, the cotyledons (embryonic leaves) and the primary shoot and root meristems. During postembryonic development, these meristems produce lateral organs along the growing primary body axis and establish the proximal–distal axis. In contrast to animals, plants are thus able to develop reiterative morphological units throughout the entire lifespan. These modular units can also vary in form in response to variable environmental cues. Phenotypic plasticity in plant development might therefore constrain evolution in a very different way from animals insofar as the final shape of the whole plant is not so canalized.

In angiosperms, all these major patterning events involve the phytohormone auxin. Moreover, auxin mediates plant growth in response to environmental signals. Thus, the evolution of auxin homeostasis and response systems is thought to play a key role in the evolution of land plant architecture (Cooke et al., 2004, 2002).

Coincident with the increased understanding of the auxin signaling in model organisms has been the development of tools and data in non-seed plants. The recently sequenced genomes of the moss *Physcomitrella patens* (Rensing et al., 2008) and the lycophyte *Selaginella moellendorffii* (Banks et al., 2011) make comparative genomic approaches possible. In parallel, several tools for studying gene function have been developed in *P. patens*, such as RNAi, inducible promoters and gene targeting by homologous recombination.

It is therefore timely to review our understanding in the evolutionary genetics of development across the land plants. Here we attempt to survey a limited number of recent findings that investigate the extent to which changes in auxin signaling could have played a role in the radiation and diversification of the body plan in land plants. Due to the lack of functional data in most non-model species, this review mainly focuses on genes rather than on development, except when data about their role in development are available (e.g., *Arabidopsis* or *Physcomitrella*).

From auxin biosynthesis to signaling in the angiosperm *Arabidopsis thaliana*

Auxin pathway is controlled at many levels that include auxin biosynthesis, auxin metabolism, and auxin transport. Moreover,

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auxin was proposed to act as an integrator of the activities of multiple plant hormones, altogether suggesting a vast regulatory network of auxin during plant development (Jaillais and Chory, 2010).

Auxin biosynthesis

Indole-3-acetic acid (IAA) is the most potent naturally occurring member of the auxin family. High IAA levels are detected in shoot and root meristematic tissues, in cotyledons, as well as in young leaves that have the highest biosynthetic capacity (Ljung et al., 2001). In mature leaves and roots, IAA remains present but in smaller amounts.

The identification of molecular components of IAA biosynthesis revealed the existence of at least two separate major pathways. One is dependent on the precursor tryptophan (Trp) and the other is Trp-independent (see the review by Woodward and Bartel, 2005). Indeed, labeling experiments suggest that seedlings do not synthesize IAA solely from Trp (Normanly et al., 1993). Moreover, *trp2-1* and *trp3-1* mutants in Trp biosynthesis contain comparable levels of free IAA to that of wild-type plants, suggesting that a Trp-independent pathway occurs in plants. Analyses of the *trp2-1* mutant imply that IAA could be produced from indole-3-glycerol phosphate or indole (Ouyang et al., 2000).

In *Arabidopsis*, it is possible to distinguish two Trp-dependent pathways: the indole-3-acetaldoxime (IAOx) pathway and the indole-3-pyruvate (IPA) pathway. The IAOx pathway is carried out by the two P450 monooxygenases CYP79B2 and CYP79B3. Overexpression of CYP79B2 leads to an increase in free auxin levels and displays auxin overproduction phenotypes (longer hypocotyls, epinastic cotyledons), whereas *cyp79B*-deficient mutants have reduced levels of IAOx and IAA associated with shorter petioles and smaller leaves (Zhao et al., 2003). The intermediate IAOx can be converted to IAA either by the enzyme aldehyde oxidase protein AAO1 or indirectly by entering the indolic glucosinolates pathway in which the last step consists in hydrolyzing indole-3-acetonitrile (IAN) to IAA. The P450 monooxygenase CYP83B1, the C-S lyase SUR1 and the IAN nitrilases NIT1-3 have been shown to be involved in the latter pathway (Bak et al., 2001; Mikkelsen et al., 2004; Normanly et al., 1997). However, *CYP79B* genes are not conserved outside of Brassicales and IAOx intermediates are not found in rice, maize and tobacco, suggesting that the IAOx pathway is clade-specific and therefore might not be relevant at a macroevolutionary scale (Sugawara et al., 2009) (Table S1).

Recently, two independent genetic screens revealed the importance of IPA in auxin biosynthesis (Fig. 1A). Both screens identified mutants in a tryptophan aminotransferase called TAA1 that converts IPA into indole-3-acetaldehyde (Stepanova et al., 2008; Tao et al., 2008). Multiple mutants that disrupt three genes from the TAA1 family are severely impaired in both embryonic and post-embryonic development and they have phenotypes reminiscent of auxin signaling or transport mutants (Stepanova et al., 2008). The IPA pathway was recently shown to be very short, as IPA is directly converted into IAA by flavin monooxygenases from the YUCCA family (Fig. 1A) (Mashiguchi et al., 2011). Plants overexpressing YUCCA genes contain elevated levels of free auxin and display auxin overproduction phenotypes, a phenotype that is dependent on TAA1 activity (Stepanova et al., 2011; Won et al., 2011; Zhao et al., 2001). *yuc1yuc4yuc10yuc11* quadruple mutants lack a hypocotyl, a root meristem and floral organs, a phenotype very similar to some signaling or transport mutants (Cheng et al., 2007a). YUCCAs are rate-limiting enzymes in auxin biosynthesis and their expression is highly regulated by both environmental and developmental pathways. For example, the PIF transcription factors, which are master regulators of light-mediated development, control elongation by directly regulating *YUCCA* genes transcription (Hornitschek et al., 2012; Li et al., 2012; Sun et al., 2012). Besides, the transcriptional activator STYLISH1 promotes leaf and flower development by directly binding to the *YUCCA4* promoter (Eklund et al., 2010a).

Auxin transport

In plants, two distinct pathways are known to play a role in auxin transport: a passive distribution through vascular tissue and an active cell-to-cell polar transport. This polar auxin transport is fundamental for auxin distribution over both short and long distances. This transport occurs in a cell-to-cell manner and depends on specific influx and efflux carrier proteins that facilitate the uptake and release of auxin from/to the apoplast (Fig. 1B). Many auxin carriers are well characterized: the PIN-FORMED (PIN) proteins (Galweiler et al., 1998) and several proteins of the ABCB and ABCG transporter family (Cho et al., 2007; Geisler et al., 2005;

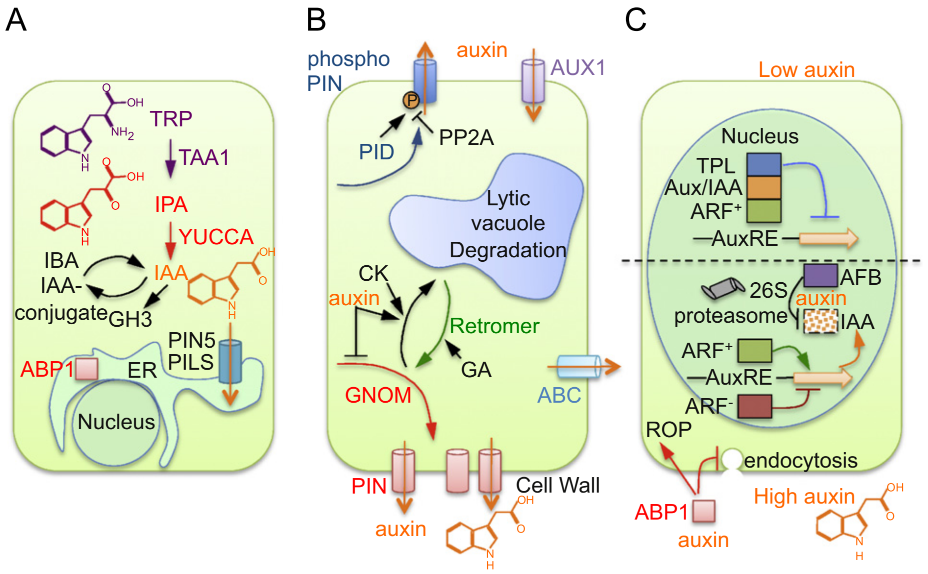

Fig. 1. Schematic representation of auxin signaling: (A) biosynthesis and homeostasis, (B) polar auxin transport and (C) perception. GA, gibberellin; CK, cytokinin; auxRE, Auxin Response Element.