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DIAGEOTROPICA: news from the auxin swamp

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Abstract

Recently established links between the tomato cyclophilin A-type protein *DIAGEOTROPICA* and the regulation of polar auxin transport provide first mechanistic insights into the function of this enigmatic locus.

Keywords

DIAGEOTROPICA; polar auxin transport; cyclophilin A

Auxin: a field in flux

Plants have evolved a repertoire of molecular switches, allowing them to sense and cope with continuous environmental changes. Plant biologists struggle to identify these switches that could help establishing a solid foundation for a consecutive characterization of plant adaptation processes. Research on the phytohormone auxin (indole-3-acetic acid; IAA) represents an excellent example for these constant efforts, because it allowed for characterization of pathways exhibiting well-defined activities in plant development [1]. By contrast, work on auxin also yielded less comprehensive results, which nevertheless signify important cornerstones in our attempts trying to understand auxin biology.

From its initial characterization as growth-promoting substance, modulating diverse morphogenetic processes in plants, it took another fifty years until the first molecular building blocks required for perception and transmission of auxin signals could be identified [1]. Important discoveries involve identification of signaling pathways, whose function relies on activity of oligomeric SCF$^{TIR1/AFB}$ E3 ubiquitin ligases, required for auxin perception and regulation of down-stream transcriptional regulators [1]. Additional fundamental findings established different classes of membrane proteins responsible for intercellular, directional auxin transport throughout the entire plant body, and it is now widely accepted that subcellular distribution and activity of AUX/LAX, ABCB-type and PIN auxin transport proteins act in concert to define auxin signals via adjustments in polar auxin transport (PAT) [1].

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Enigmatic elements of auxin signaling

Apart from *bona fide* constituents of auxin action, additional elements implicated in transmission of auxin signals have been characterized, but their function remained incomprehensible. AUXIN BINDING PROTEIN 1 (ABP1), identified about 30 years ago as an auxin binding activity in higher plants, arguably represents the most prominent example. This is mainly because of recent findings, questioning earlier reports that characterized ABP1 as an additional auxin receptor [2].

The tomato (*Solanum lycopersicum*) *DIAGEOTROPICA* (*DGT*) gene represents another player in the auxin field with an amazingly long history. Originally described as *lazy-3*, a spontaneously occurring, segregating mutant, this genetic trait later has been redubbed *diageotropica*, owing to the horizontal growth characteristics of *dgt* stem axes [3]. Apart from these eponymous defects in directional growth, *dgt* displays additional phenotypes consistent with altered responsiveness to auxin. Most notably, *dgt* plantlets lack lateral roots, even upon treatment with excess hormone concentrations, conditions that efficiently promote lateral rooting in wild type plantlets [3]. Furthermore, *dgt* exhibits profound aberrations in auxin-controlled elongation growth and is less responsive to auxin effects on gene expression [4–6]. All this reflects a considerably reduced sensitivity to the hormone, which might also explain the fact that *dgt* shows resistance to inhibitors of PAT such as N-1-naphthylphthalamic acid (NPA) [5]. Auxin-related mutant phenotypes led to speculations about functions for *DGT*, possibly in perception of the growth regulator. Later on, when *DGT* was cloned, it turned out to encode a cyclophilin A-type protein, belonging to the immunophilin superfamily (Box 1) [4]. Moreover, a *DGT* orthologue has been identified as an auxin-resistant mutant in the moss *Physcomitrella patens*, strongly arguing for an evolutionary conserved role of cyclophilins in auxin signaling [7]. However, although cyclophilin action is well understood, its role in transmitting auxin signals remained mysterious.

A report by Ivanchenko and colleagues now sheds some first light onto mechanisms, by which DGT could influence auxin effects in plants [8]. By employing a combination of conventional auxin transport assays and utilization of an extremely sensitive IAA-specific microelectrode the authors demonstrate altered PAT in *dgt*. Specifically, upon assessing auxin flux rates in root meristems, the authors found a pronounced reduction in *dgt*, which altogether could feed back on auxin-controlled growth processes, giving rise to the mutant’s phenotypes [8]. The authors went on to determine *DGT* effects on auxin transport proteins and observed DGT-dependent reduction of PIN-dependent cellular auxin efflux upon co-expression in baker’s yeast, whereas no comparable effect was detected in yeast cells jointly expressing DGT and ABCB1 [8]. Could this indicate a specific function for DGT in controlling PINs, uncoupled from canonical auxin signaling? When assessing the results from transient expression assays in *N. benthamiana*, this seems indeed possible. In these assays the authors demonstrated DGT-dependent relocation of plasma-membrane localized PIN reporter signals to the interior of leaf pavement cells, whereas distribution of ABCB1 reporter signals appeared unaffected by DGT coexpression [8]. Notably, subtle alterations in PIN localization became also apparent in root epidermis cells of the *dgt* loss-of-function mutant, consistent with a function for *DGT* in PIN sorting control.

Further questions

Evidently, findings summarized by Ivanchenko and colleagues represent a promising launching pad for a detailed characterization of *DGT*-controlled pathways. This could reveal further analogies to activities of *Arabidopsis* (*Arabidopsis thaliana*) TWISTED DWARF 1 (TWD1), an FK506-binding protein implicated in auxin transport via interaction and possibly stabilization of ABCB-type proteins at the plasma membrane [9]. Such findings would argue for a scenario, in which different classes of immunophilins regulate PAT-mediated morphogenesis via modulation of distinct auxin transport activities. Reduced responsiveness of *twd1* and *dgt* mutants to PAT inhibitors would be consistent with this model. It remains to be tested though, if altered PIN functionality can be held responsible for the entire spectrum of *dgt* deficiencies. This for example, concerns the mutant's overall resistance to auxin, which at least in the *Physcomitrella Ppdgt* mutant appears to be related to auxin perception via AFB proteins [7]. Another puzzling observation has been made upon grafting *DGT* scions onto *dgt* rootstocks, resulting in a clear-cut reversion of *dgt* root phenotypes [3,8]. A hypothetical mobile signal, moving from wild type scions to mutant roots, causing such reversion, however, has not been identified. In this context it needs to be noted that photoaffinity labeling experiments revealed a loss of a membrane-associated auxin-binding activity, explicitly in the stems of *dgt*, whereas no corresponding changes were observed in root-derived material [10]. Neither the auxin binding protein's identity nor the significance of its differentially affected abundance in *dgt* stems and roots has been characterized so far. It seems that the auxin community will experience another surprise or two, once *DGT*-controlled signaling is fully revealed.

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Box 1

Immunophilins

Together with FK506-binding proteins (FKBP), cyclophilins belong to the immunophilins, a ubiquitous class of proteins, several of which, including DGT [4], have been demonstrated to function as peptidyl prolyl isomerases (PPIases), catalyzing peptidyl-bond isomerization at positions preceding prolines [11]. PPIases have been characterized in prokaryotes and eukaryotes and are associated with fundamental cellular processes, particularly protein folding in the course of protein biosynthesis and maturation. Consequently, activity of immunophilins has been associated with diverse pathways, important for signal transduction, metabolic activity, cell proliferation and differentiation, to name just a few. In plants, immunophilins function in an array of processes, ranging from stress responses to hormonal control of plant development [11]. Among plant immunophilins, some FKBPs and cyclophilins were found to impact on the control of vesicle trafficking and protein sorting ([11] and references therein). Based on recently published observations, a related function for DGT in controlling PIN protein trafficking seems feasible [8].