Plant Cell Monogr (1)
J. Šamaj · F. Baluška · D. Menzel: Plant Endocytosis
DOI 10.1007/7089_010/Published online: 22 September 2005

MDR/PGP Auxin Transport Proteins and Endocytic Cycling

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Abstract Auxin is an essential regulator of plant growth and development. Polarized transport of auxin is responsible for apical dominance, tropic growth, and organ development. Previous studies have demonstrated that the polarized movement of auxin is dependent upon the action of polarly localized, endocytotically cycled PIN auxin efflux facilitator proteins. More recently, plant orthologs of mammalian multidrug-resistance (MDR)/P-glycoprotein (PGP) type ABC transporters have been shown to function in auxin transport. In this review, the PGP nomenclature/numbering system established by Martinoia et al., (*Planta* 214:345–355,2002) is used, as there is increasing evidence that in plants MDR/PGPs function as PGPs and not as multiple specificity MDR proteins. Defects in *PGP1* and *PGP19* (*MDR1*)genes result in decreased auxin transport and reduced growth phenotypes in *Arabidopsis* (*pgp1*, *pgp19*), maize (*br2*), and sorghum (*dw3*). Further, dwarf phenotypes are more severe in *Arabidopsis* double mutants, indicating that PGPs have overlapping functions. More recently, MDR/PGPs have been shown to function as ATP-activated hydrophobic anion transporters capable of auxin transport. Further, MDR/PGPs have been shown to stabilize PIN1 in detergent-resistant membrane microdomains, and synergistic MDR/PGP-PIN interactions have been shown to increase the rate and specificity of MDR/PGP-mediated auxin transport. Several lines of evidence indicate that, like their mammalian counterparts, *Arabidopsis* MDR/PGPs are regulated via endocytic cycling. Here we review the evidence for endocytic cycling of MDR/PGPs *in planta* and provide a model by which this cycling could occur.

1 Introduction to Auxin Transport

The plant hormone auxin is an essential regulator of plant growth and development. The primary auxin, indole-3-acetic acid (IAA), is synthesized primarily in young tissues at the shoot tip and transported to the root tip, where it is redirected basipetally through root cortical and epidermal tissues. Polarized auxin transport provides directional and positional information for developmental processes such as vascular differentiation, apical dominance, organ development and tropic growth (Benkova et al., 2003; Blancaflor and Masson, 2003; Blilou et al., 2005). The importance of auxin transport in normal plant growth is demonstrated by the severe developmental defects exhibited by plants treated with auxin transport inhibitors or carrying mutations that reduce auxin transport (reviewed in Friml, 2003) Polar transport of IAA is regulated at the cellular level, and is best described by a chemiosmotic

model in which plasma membrane (PM) ATPases generate an H^+ gradient between the neutral cytoplasm and the acidic extracellular space (Lomax et al., 1995; Swarup and Bennett, 2003). Lipophilic absorption of apoplastic IAAH into the PM is augmented by a tissue-specific, gradient-driven H^+ symport activity characterized by the AUX1 family of proteins (Lomax et al., 1995; Swarup and Bennett, 2003). In the neutral cytoplasm, IAA is found almost exclusively in the lipid insoluble anionic form and can only exit the cell via efflux carriers. The polar bias of IAA efflux is attributed to highly regulated, polarly localized efflux complexes characterized by the PIN family of proteins (Friml, 2003; Friml and Palme, 2002; Chen and Masson, this volume).

2 Auxin Efflux Inhibitors

Auxin efflux inhibitors (AEIs) are important tools for auxin transport studies. AEIs such as triiodobenzoic acid (TIBA) compete with IAA at the site of cellular efflux, while AEIs such as 1-*N*-naphthylpthalamic acid (NPA) and cyclopropyl propane dione are noncompetitive inhibitors that interact with regulatory sites of the auxin efflux complex (Muday et al., 2003). NPA has been used extensively to characterize auxin efflux from plant tissues and membrane vesicles (Muday et al., 2003). NPA binding is seen in all tissues and has long been used as a PM marker (Katekar and Geissler, 1979; Lomax et al., 1995). In etiolated zucchini hypocotyls, both integral and peripheral NPA-binding sites have been identified on the PM (Bernasconi et al., 1996; Dixon et al., 1996; Jacobs and Rubery, 1988). Other studies identified high- and low-affinity NPA-binding sites in these same membranes and noted that NPA binding correlates poorly with auxin transport inhibition, especially in the presence of observed *in planta* NPA amidase activity (Geissler et al., 1985; Michalke et al., 1992; Murphy and Taiz, 1999a,b). Further, some morphological changes observed in *Arabidopsis thaliana* seedlings exposed to NPA are only seen at levels of NPA treatment that are higher than those needed to inhibit auxin transport (Geissler et al., 1985, Michalke et al., 1992; Murphy and Taiz, 1999a, b). In *Arabidopsis thaliana* seedlings, NPA has been shown to accumulate and undergo light-dependent hydrolysis in the root/shoot apices and the root-shoot transition zone (Murphy and Taiz, 1999a, b). NPA hydrolysis was shown to be sensitive to aminopeptidase and ABC transporter inhibitors and requires two components: a high-affinity NPA-binding component and an NPA amidase activity (Murphy and Taiz, 1999a, b). High-affinity NPA binding was attributed to an integral membrane protein, while NPA amidase activity was found primarily in peripheral membrane fractions (Murphy and Taiz, 1999a, b). Studies demonstrating colocalization of flavonols in *A. thaliana* and displacement of NPA from microsomal vesicles by quercetin and kaempferol suggest that NPA mimics the activity of natural flavonoid in-