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Auxin Transport and Recycling of PIN Proteins in Plants

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Abstract Polar transport of the phytohormone auxin is mediated by plasma-membrane and endosome localized carrier proteins. PIN proteins are the best studied auxin efflux components implicated in the establishment of the auxin gradient required for growth and patterning in plants. Emerging models postulate a role for vesicular trafficking and protein phosphorylation and dephosphorylation in the regulation of PIN protein subcellular localization and auxin transport activity, providing a conceptual framework for our understanding of auxin transport and its role in plant development.

1 Introduction

Long before the discovery of its chemical structure in the mid-1930s, indole-3-acetic acid (IAA), the prominent endogenous form of the plant growth regulator auxin, was implicated in tropic responses to light and gravity (reviewed by Lomax et al., 1995). It is widely accepted that foci of IAA biosynthesis are located in young leaves and developing leaf primordia, and in the meristematic region of the primary root tip as well as in the tips of emerged lateral roots (Ljung et al., 2005; for a recent review see Woodward and Bartel, 2005). IAA is polarly transported to other tissues where it plays a regulatory role in cell division, differentiation, and elongation. Increasing evidence suggests that this directional auxin movement/distribution is closely linked to the diverse effects of IAA on plant development (Leyser, 2001; Swarup and Bennett, 2003; Zazimalova and Napier, 2003; Berleth et al., 2004; Weijers and Jurgen, 2004, 2005; Kramer, 2004; Kepinski and Leyser, 2005). Both cellular uptake and efflux mediated by protein carriers are involved. This review provides an overview of a group of recently identified transmembrane proteins of the PIN family representing auxin efflux components. In particular, emphasis is placed on emerging models of how biological activities of PIN proteins are regulated. Notably, another class of proteins belonging to the multidrug resistance ABC-type transporters has been postulated to play a role in polar auxin transport (Muday and Murphy, 2002; Murphy et al., 2004). Involvement of this

type of protein in auxin transport is reviewed separately in the chapter by Blakeslee et al. in this volume.

Polar transport of auxin is a cell-to-cell process that has been best described in a modified chemiosmotic model for auxin transport (reviewed by Lomax et al., 1995). Due to differences in the acidity between apoplastic and intracellular space, IAA (mostly as the protonated form in the acidic apoplastic space) enters cells via passive diffusion and/or by the activity of a $2H^+$-IAA^- symporter (auxin influx carrier) driven by the proton motive force across the plasma membrane. Once inside cells where the pH is neutral, IAA is in the ionized form which is impermeable through the plasma membrane. The ionic form of IAA has to exit cells via auxin efflux carriers whose activity is driven by the membrane potential. This model postulates that the polarity of auxin transport is mediated by asymmetrical localization of auxin influx and efflux carriers on opposite ends of cells. Recent immunolocalization studies of the putative auxin influx and efflux component/facilitator proteins strongly support this model. Several candidates have been identified as the auxin influx carrier. Among them are AUX1 (for AUXIN RESISTANCE 1, Bennett et al., 1996) and members of the AUX1 amino acid/auxin:proton symport permease (AAAP) family (Swarup et al., 2000; Swarup and Bennett, 2003). On the other hand, PIN proteins have been identified as the auxin efflux component/facilitator proteins.

2
Pin-Formed (PIN) Protein Family

Molecular genetics studies have led to the discovery of two founding members (*pin-formed 1* and *agravitropic 1*; Okada et al., 1991; Bell and Maher, 1990, Fig. 1) of the putative auxin efflux component/facilitator PIN family (for reviews see Palme and Galweiler, 1999; Friml and Palme, 2002; Friml, 2003; Paponov et al., 2005). Facilitated by the completed genome sequence information of *Arabidopsis thaliana* and the availability of sequence-indexed T-DNA insertional mutants (http://www.arabidopsis.org), six more closely related PIN proteins and seven PIN-like proteins have been identified (Table 1). Biological functions of five PIN proteins have been recently characterized while functions of others remain to be elucidated.

2.1
PIN1 (Pin-Formed 1)

When *Arabidopsis* plants are grown in the presence of polar auxin transport (PAT) inhibitors, such as 1-naphthylphthalamic acid (NPA), inflorescence stems develop into pin-shaped structures lacking flowers and other lateral organs (Okada et al., 1991; Fig. 1). The lack of lateral organ development is likely