Genes and proteins for solute transport and sensing

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INTRODUCTION

Transport processes are required for nutrient acquisition, translocation in the plant and for compartmentation within the cells. The weed Arabidopsis occurs in many environmentally distinct locations around the world, and a significant proportion of the genome of this small plant encodes membrane proteins, especially transport proteins and putative sensors that cope with these conditions. Many of these proteins are homologous to transporters from other organisms including bacteria, fungi and animals. This chapter provides an overview of the components and mechanisms responsible for solute transport and sensing. Described are the basic principles of transport processes and the transporters of the pump and carrier classes found in Arabidopsis. Transport of the most prominent solutes that are taken up and distributed within the plant such as nitrogenous compounds (ammonium, nitrate, amino acids, peptides) and carbohydrates such as sugars (sucrose, glucose) or sugar alcohols (e.g. mannitol) are discussed in some detail.

General characteristics of transport processes

Cellular plasma membranes demark the interface between life and death: they protect the highly structured and organized plant cellular interior, the cytosol, from the hostile external environment. This creates a compartment which permits biochemical reactions to be carried out within a protected domain. Such a barrier, however, aside from its protective role, must at the same time allow passage of nutrients and solutes to allow cellular functions to proceed. Acquisition of ions, transfer of metabolites and excretion of waste products, but also transport of chemoattractants, kairomones (chemicals that convey information about interactions), hormones and substances that help mobilizing nutrients (e.g. protons, organic acids and phytosiderophores), establish homeostasis between the interior and the exterior. Furthermore, the plasma membrane represents the interface to the environment and thus must play a crucial role in relaying information about the external environment. Depending on the position of a cell in the plant, this may either be the soil, or the cell wall space as the interface to adjacent or distant cells of the same or a different organism (e.g. pathogenic or symbiotic bacteria and fungi).

The plasma membrane itself is composed of membrane lipids and integral and peripheral proteins (for a detailed discussion see Gennis, 1989). Protein composition within the plasma membrane can vary in wide ranges between 20% and 80% (dry weight). Furthermore membranes may contain carbohydrates in the form of glycolipids or glycoproteins. In the aqueous environment of living cells, the hydrophobic hydrogen-carbon tails of membrane lipids avoid water contact and, although lacking attracting forces, self-assemble and cluster together into an energy minimized state. The polar headgroups orient to the surrounding water on both sides, whereas the hydrophobic tails orient towards each other on the inside leading to the formation of a bilayer consisting of two leaflets with a thickness of ~4nm (Fig. 1). Biological membranes are characterized by an asymmetric distribution of lipids between the two leaflets, i.e. restriction of phosphatidylserine to the inner leaflet (Boon & Smith, 2002; Manno et al., 2002). The lipid asymmetry may have a variety of important biological functions and a loss of asymmetry can be used as a measure for cell death (Schliegel and Williamson, 2001).

Besides the plasma membrane, the eukaryotic cell also contains intracellular compartments surrounded by internal membranes, which enclose specialized organelles and vesicles, separating functional units within a single cell. Such lipid bilayers form a diffusion barrier preventing free exchange of molecules between the in- and outside of the cellular compartments. The lipids composition of the various membranes in a plant cell can vary significantly leading to differences in the membranes properties. Furthermore the phospholipid, glycolipid and sterol composition of cellular membranes is acclimated in different environments, especially due to altered temperature in order to maintain fluidity and functionality.

The lipid bilayer forms a lipid “sea”, in which molecules can normally move freely in lateral direction. In other words, individual lipid molecules and peripheral, integral and lipid anchored proteins may diffuse and distribute randomly, whereas an asymmetrical distribution of lipids