Aquaporins: exploring gating and function in the plant kingdom

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Aquaporins are small transmembrane proteins ubiquitously expressed in biological membranes that facilitates water exchange. Assembled as homo/hetero tetramers -and in contrast to ion channels- each monomer works as a functional transport unit. In the plant kingdom seven aquaporin subfamilies are described and, in particular, the plasma membrane intrinsic proteins (PIPs) seems crucial in controlling osmotic permeability (P_f) at the plasma membrane. These PIP aquaporins also represent a highly abundant and conserved subfamily that has been historically divided into two subgroups due to their differences: PIP1 and PIP2. In terms of their function, all PIPs show capacity to rapidly adjust the P_f by means of a gating response. A close state seems to prevail under certain stimuli as cytosolic pH decrease, intracellular Ca^{2+} concentration increase and dephosphorylation of specific Serines. Many PIP1s also show another feature that clearly distinguishes them from any PIP2. These PIP1 fail to reach the PM when expressed alone, but they can succeed if they are coexpressed with a PIP2. Therefore, in terms of activity, PIP aquaporins can rapidly adjust membrane water permeability by means of two mechanisms: channel gating and channel translocation of PIP subunits (PIP1 and PIP2, organized -or not- in mixed tetramers). Evidences indicate that these mechanisms are not only highly conserved among species but their juxtaposition enhances the dynamics of the response. In particular, we propose that heterotetramerization, serine phosphorylation status and pH sensitivity affects aquaporin gating and thus would rule the P_f of a membrane that express PIPs when fast responses are mandatory. The functional properties of this interaction and physiological consequences are addressed in order to understand the relevance of the cell to cell pathway in the hydraulics dynamics not only as a physiological challenge but also as a response to adverse plant environmental conditions.