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Integrating membrane transport, signaling and physiology

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Membranes constitute a barrier that compartmentalizes cells and organelles from their surrounding environment. Transport across these barriers, mediated in the most part by channels, transporters and pumps, is essential for many aspects of cellular function. In plants, approximately 7% of the encoded proteins host at least four transmembrane spans and are potentially involved in membrane transport. Membrane transport plays key roles in including nutrition, cellular homeostasis, signaling and development, and is a vital component of responses to biotic and abiotic stresses. This Focus Issue brings together updates and research articles that address some of most exciting and recent advances in our understanding of the molecular mechanisms underlying membrane transport, its integration with signaling, and its roles in homeostasis. Here, we highlight the contents of the 14 Updates presented in this Focus Issue.

Transport integration in signal generation and plant development

Plants have evolved many more ATP-binding cassette transporters (ABC) than other organisms. Youngsook Lee's group, that has worked on ABC transporters for more than two decades, comprehensively summarizes the recent developments on ABC transporters, including newly identified functions and regulatory mechanisms (Do et al, 2021). The Update outlines those transport functions that have been deciphered using physiological data and those which have been verified by functional assays in heterologous cell systems. The authors discuss a number of

40 outstanding questions such as how ABC transporters play such diverse roles in
41 plants and why so many ABC transporter genes have been retained in plant genome.

42

43 Metalloids are mineral elements that are often widely present in soils. In
44 their update, Yamaji and Ma (2021) focus on Boron (B), Silicon (Si) and Arsenic (As),
45 covering the range of metalloids relevant to plants, whether essential, beneficial, or
46 biotoxic. These three metalloids share overlapping transport pathways for uptake
47 and distribution throughout plants. Central to these pathways is the metalloid
48 influx mediated by highly specialized aquaporins of the NIP subfamily. The NIPs
49 operate with specific efflux transporters displaying distinct polar localizations.
50 Understanding the mechanisms by which substrate specificity of these localizations
51 is determined and their functional divergence among tissues or even plant species
52 (monocots vs. dicots) will provide novel insights into the molecular physiology of
53 metalloids in plants.

54

55 γ -aminobutyric acid (GABA) is a key signaling molecule in animals, but less is
56 known about the roles and actions of GABA in plants. Xu, Sai and Gilliam (2021)
57 update us on the physiological impact of GABA in plants summarizing the current
58 evidence for the roles of aluminum-activated malate transporters (ALMTs) being
59 the targets of GABA signaling in guard cells to regulate water use efficiency, as well
60 as in pollen to regulate fertility. They speculate on other potential targets of GABA in
61 plants, such as H⁺-ATPase, potassium channels, and 14-3-3 proteins. They also
62 discuss the link of GABA to glutamate and hormones, as well as the potential role of
63 GABA for long-distance signaling.

64

65 Cellular phosphate (Pi) homeostasis is regulated by inositol pyrophosphates
66 (PP-InsP), which act as intracellular messengers and are perceived by the SPX
67 domains of various proteins involved in Pi transport and signaling. In their Update,
68 Wang et al. (2021) explore the dynamics of Pi and PP-InsP metabolism. They
69 describe the role of PP-InsP as ligands to modulate the interactions between SPX
70 proteins and transcriptional activators in the phosphate starvation response,
71 thereby ultimately coordinating cross-membrane Pi transport and cellular Pi
72 homeostasis.

73

74 ***Integrating Transport within and between cellular membranes***

75

76 Membrane nanodomains are defined as submicron protein and/or lipid
77 assemblies, whose structural characterization has greatly profited from recent
78 advances in microscopy techniques. The Update by Martinière and Zelazny (2021)
79 illustrates the role of membrane nano-organization in regulating of molecule

80 transport in plants. They focus on plasma membrane nanodomain formation, which
81 arises from functional assembly of sterols, sphingolipids, and specific proteins,
82 thereby regulating internalization of transporters in response to stimuli or effecting
83 co-clustering of proteins with their regulators.

84

85 The Update from Mehlhorn, Asseck and Grefen (2021) sets out the
86 background to our understanding of protein maturation and insertion into the lipid
87 bilayers with a particular emphasis on tail-anchored proteins. As they note, the
88 textbook models of protein insertion mechanisms lack credibility for those
89 secretory or membrane proteins which lack an amino-terminal signal sequence or
90 transmembrane domain. They review our current state of knowledge about tail-
91 anchored proteins, harboring a single carboxy-terminal transmembrane domain,
92 and they address potential alternative, post-translational insertion routes into the
93 endoplasmic reticulum membrane.

94

95 In recent years, the technologies for exploring the subcellular mechanics of
96 Ca^{2+} signaling have greatly expanded with sensors that can be targeted to specific
97 locations within a plant cell. Two Updates in this Focus Issue evaluate these tools
98 and the information that they yield. The review by He et al (2021) examines
99 transporters likely to be involved in Ca^{2+} signal transmission, as well as those of
100 another divalent (Mn^{2+}), their transport across membranes, and their notable
101 association with glutamate receptor-like proteins (GLRs) and several linked pumps
102 and coupled transporters. Taking an organelle-focused perspective of the
103 interactive mechanics behind Ca^{2+} signaling, Resentini et al. (2021) address
104 questions about how unique characteristics of these signals may have arisen and
105 how the divalent ions are resequenced. They include examples of how latencies in
106 stomatal responsiveness to light and CO_2 have evolved (Jezek et al 2021), as well as
107 temporal properties of Ca^{2+} oscillations.

108 Finally, Tomkins, Hughes and Morris (2021) revisit the fundamentals of ion
109 and solute diffusion, emphasizing on the physics of passive transport systems and
110 the driving forces that give rise to diffusive and bulk flow processes in and out of
111 cells.

112

113 ***Transport integration in environmental interactions***

114

115 Kv (potassium voltage) channels in plants are important for nutrition by
116 mediating potassium uptake from the soil and distribute it through the whole plant,
117 and also for stomata movements. The Update review by Lefoulon (2021) focuses on
118 how Kv channels work with an emphasis on their mechanistics, our knowledge of
119 plant Kv channel structure, and the structures of closely-related channels in other

120 organisms. Lefoulon (2021) addresses issues from the selectivity of the Kv channels
121 to their gating by voltage, and finally how auxiliary proteins can regulate their
122 function in the face of environmental stress and how the gating properties may be
123 manipulated to affect plant growth and physiology.
124

125 Plasma membrane H⁺-ATPases and Ca²⁺-ATPases are autoregulated by
126 cytoplasmic concentrations of H⁺ and Ca²⁺, respectively, to generate steep gradients
127 across membranes as a prerequisite for substrate transport and cellular signaling.
128 The Update by Fuglsang and Palmgren (2021) highlights the role of phosphorylated
129 sites in the terminal regulatory domains of these pumps. Although some of these
130 phosphosites appear to be constantly phosphorylated and may function as major
131 switches, others appear to be dynamically phosphorylated to enable gradual
132 reductions in their activity.
133

134 Kim et al. update us on transport processes, in which sugars and amino acids
135 are secreted from plant cells by SWEET-type and UmamiT-type exporters,
136 respectively. Supported by instructive illustrations, key aspects relate to their cell
137 type-specific expression in phloem parenchyma and companion cells to govern the
138 distribution of assimilates in plants, as well as to their function in roots and other
139 organs to feed beneficial or pathogenic microbes.
140

141 Apart from their fascinating and unique biology, carnivorous plants have
142 been highly relevant model systems for exploring long distance electrical signaling
143 in plants, since the early work of Charles Darwin. Böhm and Scherzer (2021) review
144 this topic, including their own research on signaling events in Venus flytrap
145 (*Dionaea muscipula* L.) and results from other research groups. The ion channel
146 activities underlying action potentials, their interaction with calcium and links to
147 downstream jasmonate signaling now provide a strong framework for
148 understanding the trap closure mechanism. Many other processes related to trap
149 biomechanics and the respective roles of growth and membrane transport during
150 slow trap reopening remain exciting topics for future research.
151

152 Plants sense the concentration of the major photosynthetic substrate CO₂
153 within their leaves and, consequently, alter atmospheric connectivity by opening or
154 closing their stomatal pores. Dubeaux et al. (2021) update a current understanding
155 of how plants sense and respond to changing levels of CO₂, focusing on signaling
156 mechanisms that are known or might be involved in stomatal aperture responses to
157 low or high CO₂ concentrations. They also include a brief topical perspective on the
158 effects of rising atmospheric CO₂ concentrations in terms of stomatal densities and
159 their potential impact on crop productivity.

160

161 Water may constitute up to 98% of the weight of fully turgid plant tissues.
162 Cross-membrane water transport mediated by aquaporins is critical to plant
163 expansion/growth, dehydration and germination of pollen and seeds, stomatal
164 closure etc. Accordingly, aquaporins represent central membrane targets of diverse
165 environmental and intrinsic signals. Maurel et al (2021) update us on how
166 aquaporins are regulated by drought, salinity, cold, nutrients, hormones, and other
167 biotic factors to maintain the plant water status. Interestingly, the multiple results
168 on the role of aquaporins in stomatal movement are discussed with explanations
169 proposed: due to their H₂O₂ transport activity, guard cell aquaporins function both
170 as players and targets of ABA and flagellin signalling during stomatal closure.

171

172 The combined and considerable efforts of the editorial team over two years
173 have culminated in this Focus Issue. We hope you enjoy reading it as much as we
174 have enjoyed assembling it. Much of the contents of this Focus Issue arise from the
175 open discussions and interactions that took place at the 18th International
176 Workshop in Plant Membrane Biology, in Glasgow in 2019. This Focus Issue serves
177 as a bridge leading you to the next International Workshop in Plant Membrane
178 Biology, scheduled for October 17-21 of 2022 in Taiwan, where all of the latest
179 advances in the above areas will be showcased. If nothing else, these Updates and
180 the Workshop show how rapidly the field is now evolving.

181

182

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