

Plants Increase Photosynthesis Efficiency by Lowering the Proton Gradient across the Thylakoid Membrane

In chloroplasts, the pigments of the light-harvesting complex channel light energy to PSII and PSI. The light energy is used to separate an electron from PSII, starting its cascade through the electron transport chain. Accompanying the electron transfer, a proton gradient across the thylakoid membrane is established, with a higher concentration of protons and lower pH in the thylakoid lumen. The proton gradient (ΔpH) functions as an intermediate storage of the harvested light energy and drives ATP synthesis as protons pass across the membrane through the chloroplast cpATP synthase. Yet, the accumulation of positively charged protons on one side of the membrane also generates a gradient in charge or membrane potential ($\Delta\Psi$). Like the ΔpH , the $\Delta\Psi$ serves as a storage of the harvested light energy; it could be roughly imagined as an analog to a battery, with the negative pole on the stromal side of the membrane and the positive pole in the lumen. Consequently, protons are attracted to move from the lumen to the stroma. ΔpH and $\Delta\Psi$ combine to establish the proton motive force (also referred to as the proton electrochemical gradient) that drives the flux of protons through the cpATP synthase (Fig. 1; Allen, 2002; Armbruster et al., 2017).

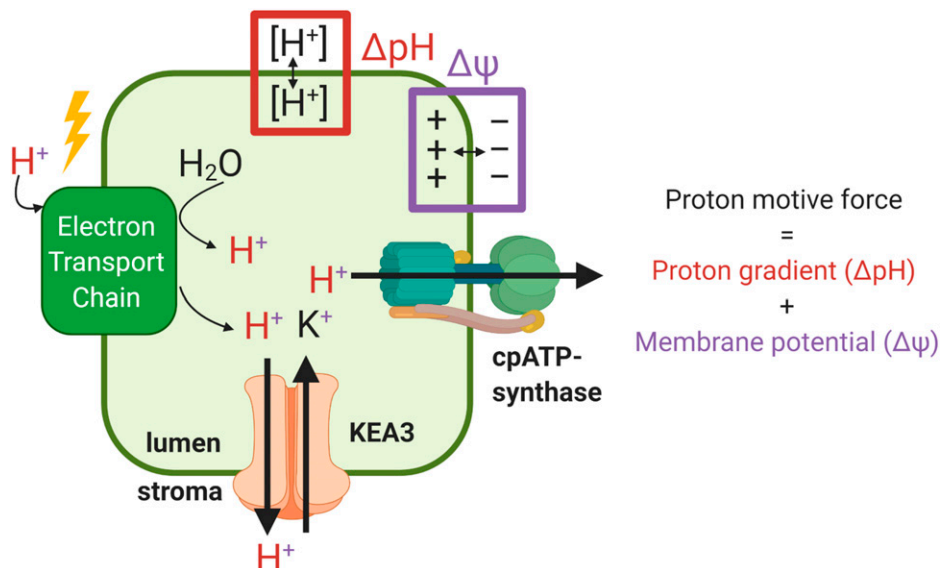
The chemical gradient or ΔpH is inseparably connected to protons, but $\Delta\Psi$ is a difference in charge, so any ion can replace the proton. Therefore, replacing protons in the lumen with another cation (or simultaneously removing protons and a negative charge) alters the relative contributions of ΔpH and $\Delta\Psi$ to the proton motive force. This currency exchange of charge substitution is particularly important under

nonoptimal conditions, such as low light, when energy available for biomass production is low and light needs to be harvested efficiently. The efficiency of the energy transfer from the harvested light into the electron transport chain depends on the lumen pH; at a low pH (i.e. a higher proton concentration), fewer electron acceptors are available. In these circumstances, more of the harvested light energy is dissipated as heat during nonphotochemical quenching, thereby decreasing photosynthetic efficiency.

In this issue of *Plant Physiology*, Correa Galvis et al. (2020) demonstrate that the Arabidopsis (*Arabidopsis thaliana*) potassium exchange antiporter (KEA3), a K^+/H^+ antiporter, is a key component responsible for altering the composition of the proton motive force by decreasing the relative contribution of the ΔpH while increasing the contribution of the $\Delta\Psi$ (Fig. 1). Correa Galvis et al. (2020) use Arabidopsis mutant plants with limited ATP synthase capacity as a tool; these mutants store a higher proportion of the proton motive force as $\Delta\Psi$ (Davis et al., 2016). Combining these mutants with *kea3* knockouts, they demonstrate that KEA3 function improves photosynthetic capacity in plants that are dependent on storing a larger proportion of the proton motive force as $\Delta\Psi$, a situation that is found in wild-type plants under low light. They further show that the KEA3-dependent conversion of ΔpH to $\Delta\Psi$ is directly connected to the stability of several components of the electron transport chain, further contributing to enhanced photosynthetic efficiency.

The results presented by Correa Galvis et al. (2020), combined with previous results from Wang and

Figure 1. Light energy is harvested in chloroplasts and converted into an electron transport chain that establishes a ΔpH and a $\Delta\Psi$ at the thylakoid membrane. The ΔpH and the $\Delta\Psi$ combined establish the proton motive force, which drives the proton flux through the chloroplast cpATP synthase for ATP production. The K^+/H^+ antiporter KEA3 is a key regulator for altering the composition of the proton motive force. KEA3 decreases the ΔpH component of the proton motive force, which enhances photosynthesis efficiency. Adapted from Correa Galvis et al. (2020) and Wang and Shikanai (2019); image generated using bio-render (<https://biorender.com/>).



Shikanai (2019), elegantly demonstrate the important contribution of the K^+/H^+ antiporter KEA3. KEA3 is an excellent example of an ion transporter that is important for processes other than nutrient distribution in the plant. KEA3 activity is not connected to maintaining potassium nutrition; the movement of the proton is the important aspect of the transporter activity, and potassium acts as a general positive charge that is moved. Moreover, coupling proton and potassium transport contributes to ATP production rather than costing ATP. KEA3 could therefore be seen as an H^+/K^+ transporter as opposed to a K^+/H^+ transporter.

Proton/ion antiporters, particularly those in the plasma or vacuolar membrane, are often viewed from the point of the transported ion as opposed to the proton; a well-known example of this is the Na^+/H^+ transporter SOS1 (Shi et al., 2002). SOS1 uses the proton gradient across the plasma membrane (PM) to export sodium out of the cell, contributing to salinity tolerance. The proton gradient across the PM is mainly generated by the PM H^+ -ATPase or proton pump. Similar to the situation at the thylakoid membrane, establishing the proton gradient across the PM will also generate a membrane potential. SOS1 and KEA3 share the same antiporter transport mode; sodium exclusion via SOS1 therefore impacts the ATP-derived energy that is stored as the proton gradient but not the ATP-derived energy stored as the charge difference across the PM. This makes SOS1-dependent sodium exclusion less energy demanding than it would intuitively seem at first.

The role of KEA3 in chloroplasts highlights the interconnection of ion fluxes; other transport proteins might have equally complex and crucial roles in cells. It might be time to move away from viewing ion transporters solely as nutrient or osmolyte carriers and toward a more integrated approach of investigating ion and charge movement. The complex interconnectivity of all ion fluxes across all cellular membranes makes them challenging to investigate. In recent years, mathematical modeling of ion fluxes and the development of genetically encoded fluorescent ion sensors have emerged as essential tools for enhancing our understanding of these networks; in particular, they helped

to increase our knowledge of the regulation of cytosolic pH signaling events (Chen et al., 2012; Jezek and Blatt, 2017; Behera et al., 2018). Many more roles of ion transport proteins and ion flux networks are likely waiting to be discovered.

Stefanie Wege^{1,2}

ORCID ID: 0000-0002-7232-5889

Australian Research Council Centre of Excellence
in Plant Energy Biology, Plant Research Centre,
School of Agriculture, Food, and Wine,
Waite Research Institute, University of Adelaide,
Waite Campus, Glen Osmond,
South Australia 5064, Australia

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¹Author for contact: stefanie.wege@adelaide.edu.au.

²Senior author.

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