Quantitative modelling of the energy cost of Na^+ exclusion, transport and storage in plant roots under salt stress

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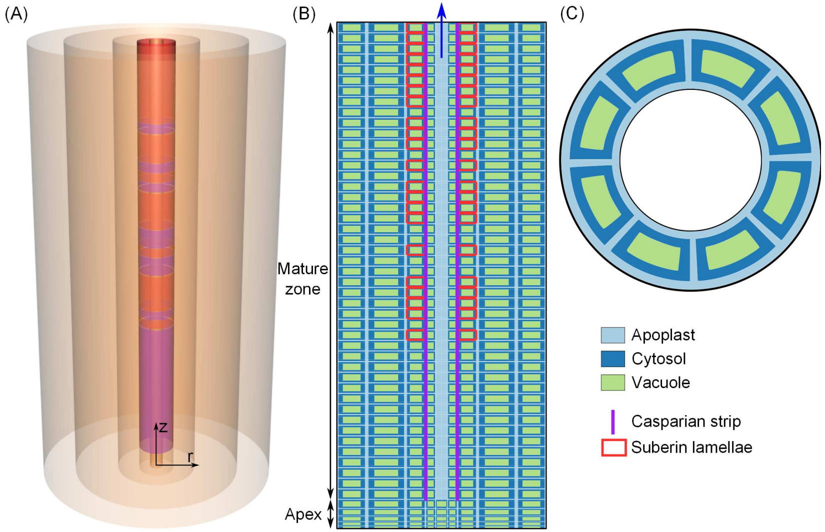
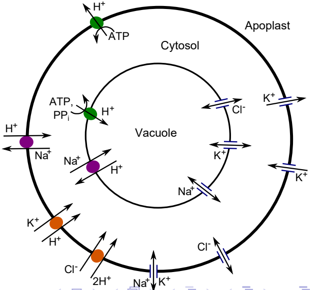
Schematics of our model root



Driving forces for ion and water transport

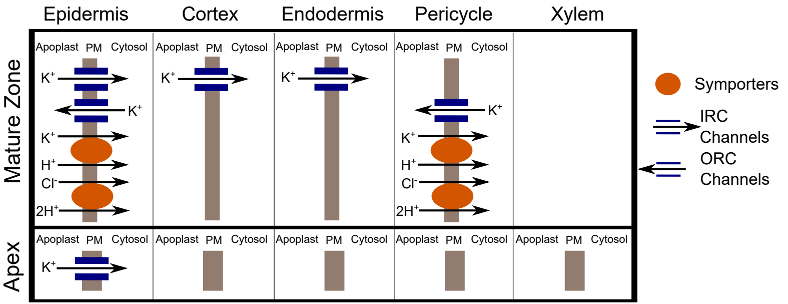
- Water transport is driven by hydraulic and osmotic pressure differences.
- Apoplastic and symplastic ion (Na^+, K^+, H^+ and Cl^-) transport is driven by electrochemical diffusion and convection.
- Transmembrane ion transport is driven by relevant ion concentrations and transmembrane potentials:

- Channels permeable to Na^+, K^+ (VIC, IRC and ORC) and Cl^-;
- K^+/H^+ symporters and Cl^-/H^+ symporters;
- H^+ pumps;
- Na^+/H^+ antiporters.



Spatial distributions of model transport proteins

- Spatial distribution of plasma membrane transport proteins:



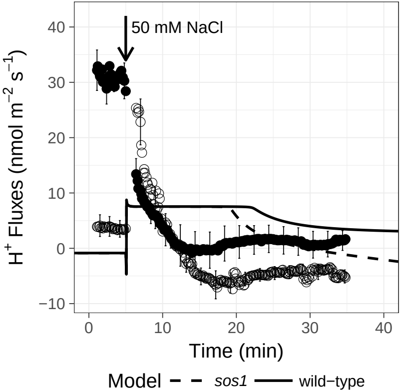
- PM VIC channels and H^+ pumps operating in all cells
- Plasma membrane Na^+/H^+ antiporters? We have simulated a range of spatial distributions.
- Tonoplast membrane transport proteins: No active storage of Na^+ in the apex.

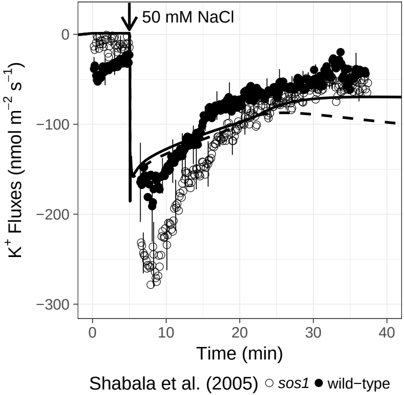
Energy cost calculations

- We assume:
  - 5 ATP synthesized per O_2 consumed in respiration.
  - 1 H^+ transported across PM per ATP hydrolysed.
  - 2 H^+ transporter across TM per ATP hydrolysed.
- There is a single 'composite' pump operating on the model TM, so we can only calculate an upper bound for the ATP cost of storage (assuming all TM H^+ fluxes are through the V-ATPase).
- Energy costs calculated:
  - Cost of active efflux of Na^+ across plasma membranes (based on H^+ flux through PM antiporters).
  - Cost of actively transporting all ions across plasma membranes (based on total H^+ flux through PM pumps).
  - Cost of actively transport of Na^+ across both PM and TM.
  - Cost of actively transporting all ions across PM and TM.

Model validation: MIFE fluxes and electric potentials

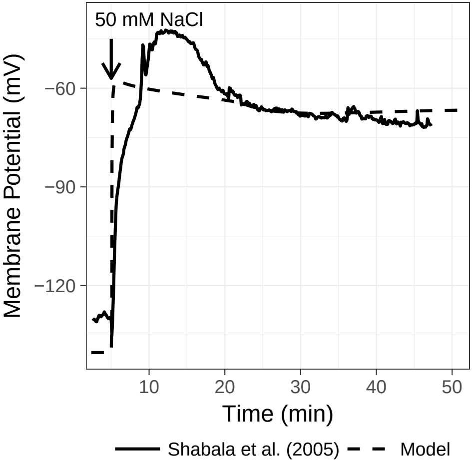
- Model parameters fitted using K^+ and H^+ flux measurements, and electric potential measurements from Shabala et. al. (2005) for wild-type *Arabidopsis* plants and *sos1* mutants.
- Mature zone fluxes:





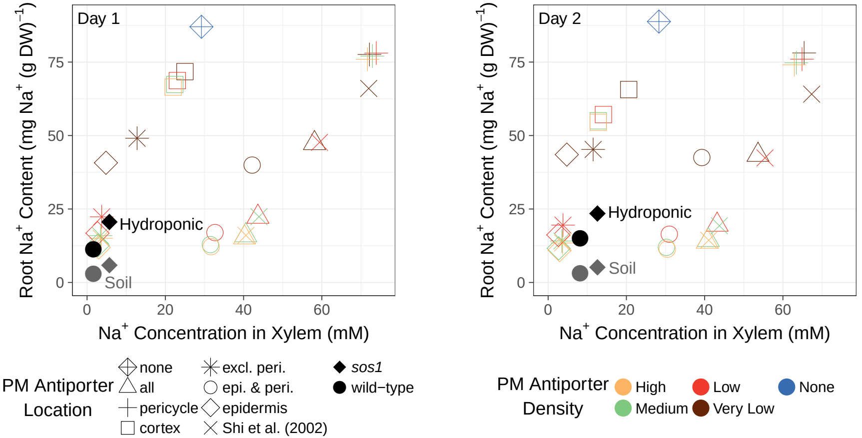
Model validation: MIFE fluxes and electric potentials

- Mature zone epidermal cell electric potential results:



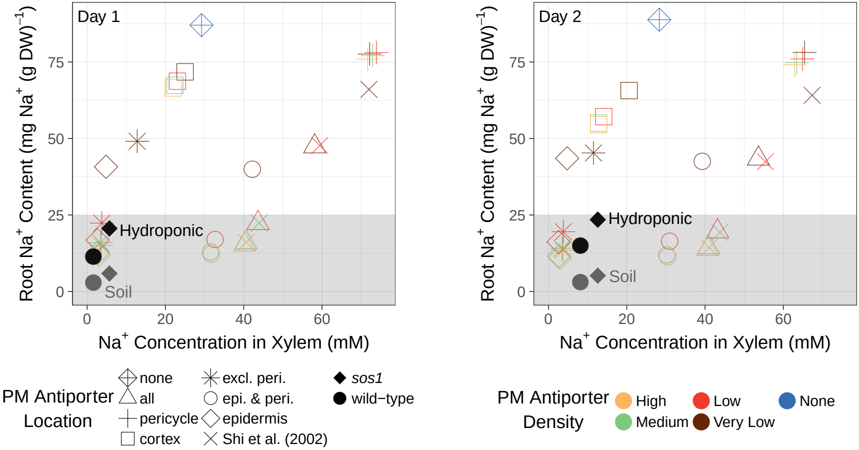
Model validation: Na^+ content and xylem concentrations

- We also compared our model with Na^+ root contents and Na^+ concentrations in the xylem of wild-type *Arabidopsis* and *sos1* mutants from Shi et al. (2002).



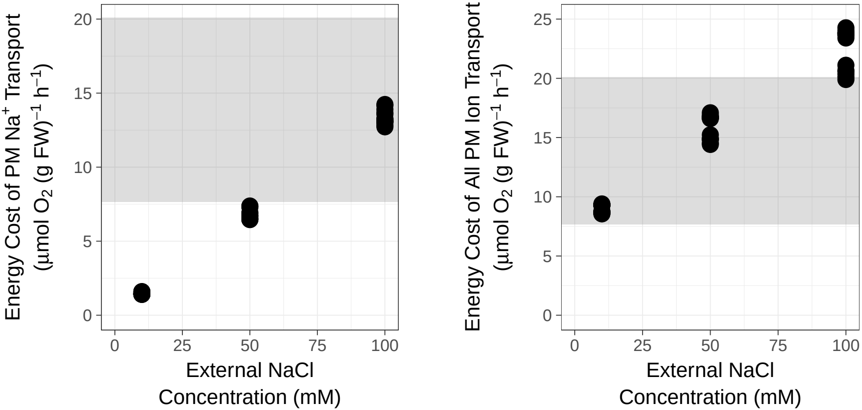
Model validation: Na^+ content and xylem concentrations

- Realistic Na^+ contents:



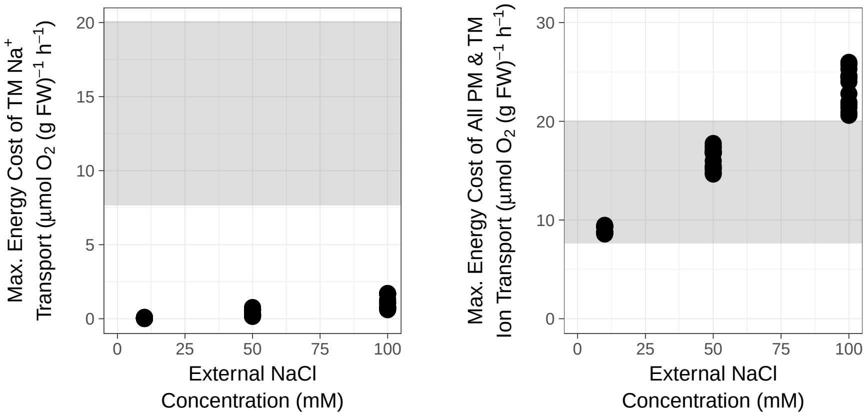
Magnitude of energy costs: PM ion transport

- The energy costs of transporting just Na^+ across just the plasma membranes are very high compared to available energy from respiration.



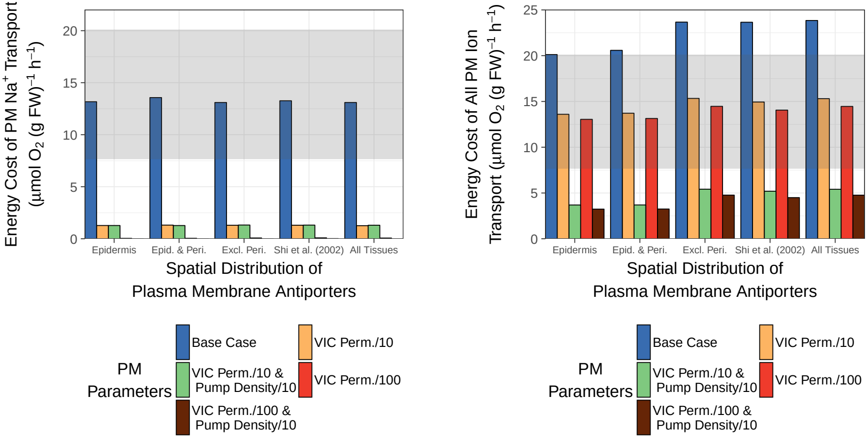
Magnitude of energy costs: Tonoplast ion transport

- The energy costs of transporting Na^+ across tonoplast membranes are relatively minor.



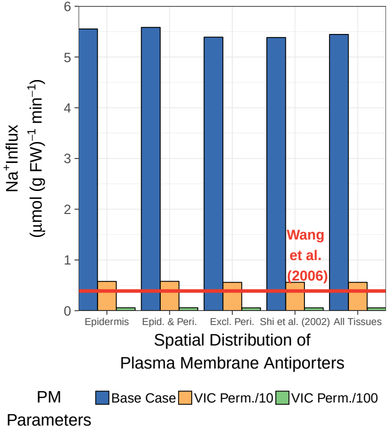
Possible explanations for high energy costs

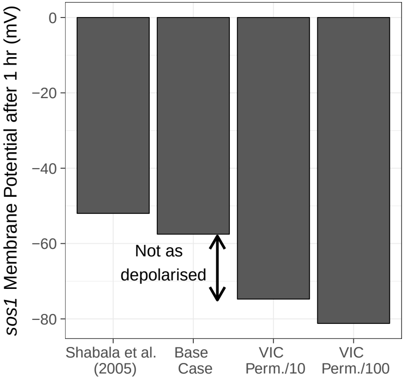
- The model energy costs are very high.
- Possible explanations:
  - Overestimated passive plasma membrane Na^+ permeability.



Possible explanations for high energy costs

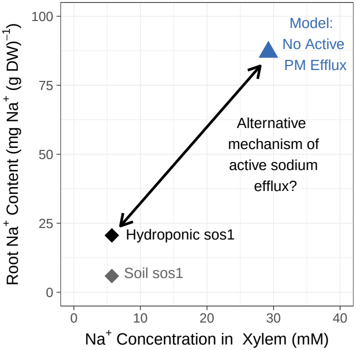
- Overestimated passive plasma membrane Na^+ permeability.
  - Further experimental evidence:





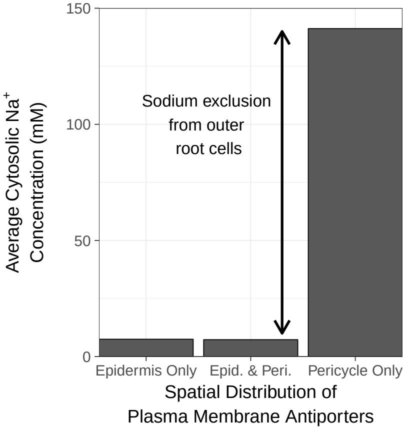
Possible explanations for high energy costs

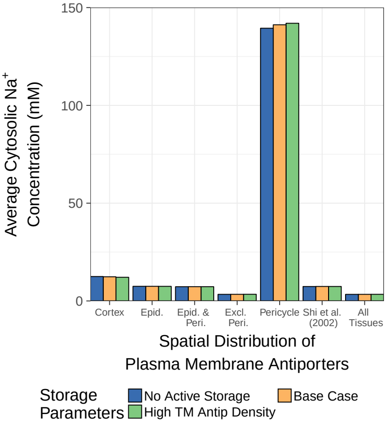
- The model energy costs are very high.
- Possible explanations:
  - There is a transport mechanism missing from the current model of Na^+ transport in roots, i.e. active Na^+ efflux through a transporter other than SOS1.
  - A much more energy efficient mechanism would be required.



Control points for Na^+ transport: Cytosolic Na^+

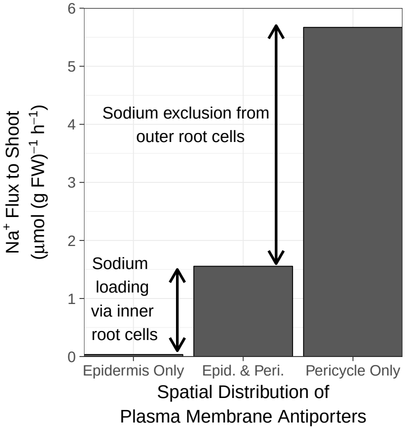
- What are the most important control points for maintaining low Na^+ levels in root cell cytosols?
  - Outer root cells.
  - NOT: Inner root cells or storage.

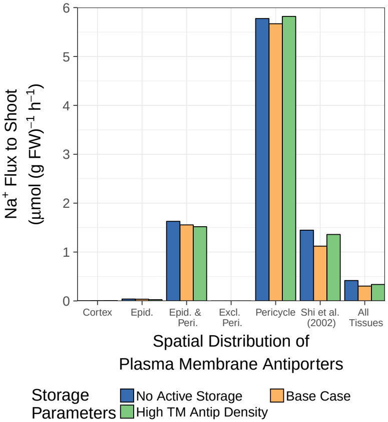




Control points for Na^+ transport: Na^+ flux

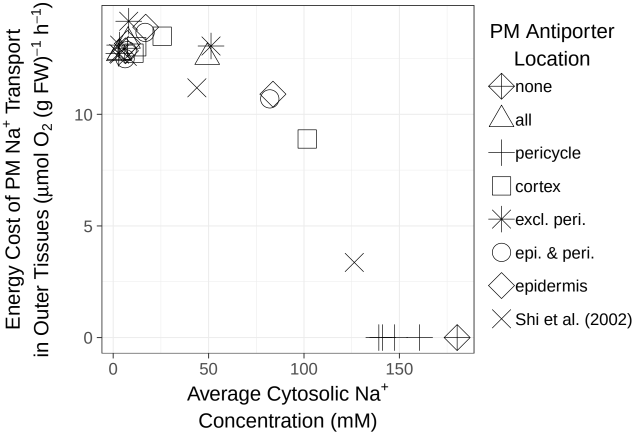
- What are the most important control points for Na^+ accumulation in the shoot?
  - Outer root cells (active efflux reduces Na^+ flux).
  - Inner root cells (active efflux increases Na^+ flux).





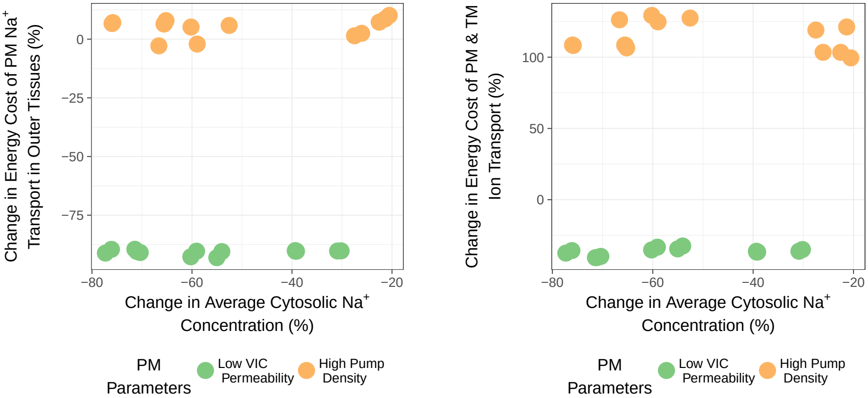
Na^+ exclusion from the outer root: Energy costs

- There are significant energy costs associated with the exclusion of Na^+ from the outer root cells.



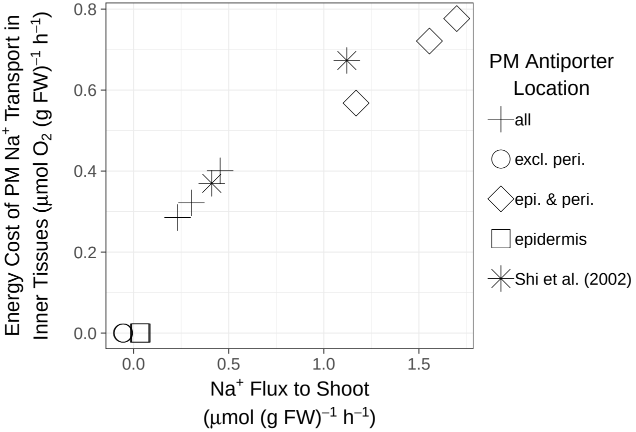
Na^+ exclusion from the outer root: Energy efficiency

- Increasing the plasma membrane H^+ pump density lowers the cytosolic Na^+ concentration but increases the energy costs.
- Reducing the passive Na^+ permeability of the plasma membranes significantly reduces the energy costs.



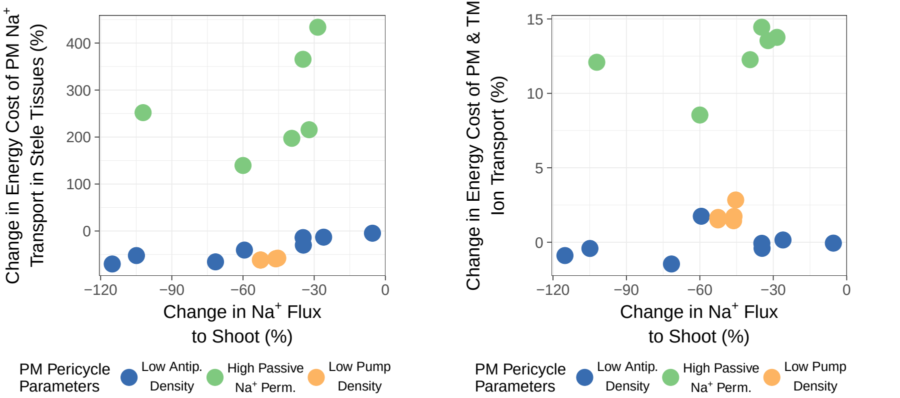
Minimising net Na^+ flux into the xylem: Energy costs

- Lower Na^+ flux requires *less* energy at the pericycle.
- Energy costs for Na^+ transport across pericycle plasma membranes are relatively small.



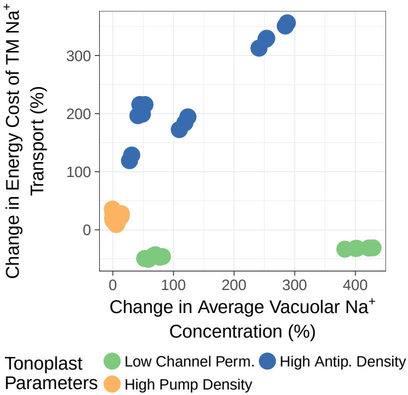
Minimising net Na^+ flux into the xylem: Energy efficiency

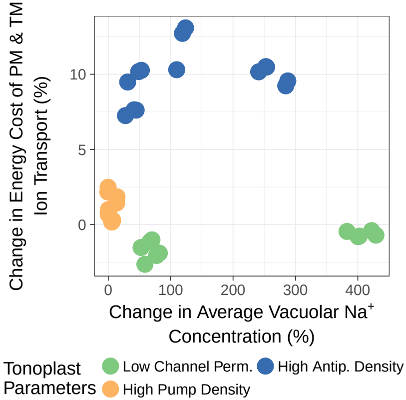
- Reducing active loading of Na^+ is more energy efficient than increasing the passive unloading of Na^+.



Storage of Na^+ in vacuoles: Energy efficiency

- Reducing the passive Na^+ permeability of the tonoplast reduces the energy costs.
- Energy costs for Na^+ transport across tonoplast membranes are relatively small.

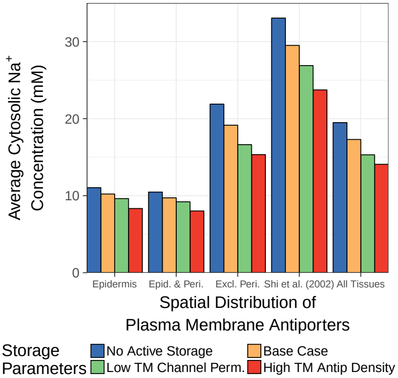


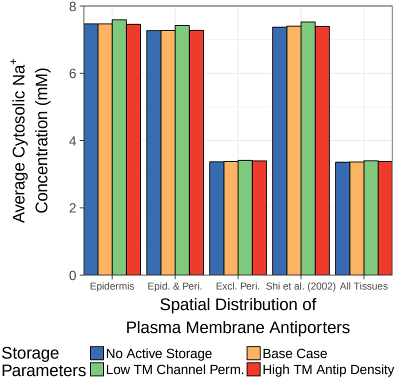


Storage of Na^+ in vacuoles: Benefits

- *Temporary* reduction in cytosolic Na^+ concentrations

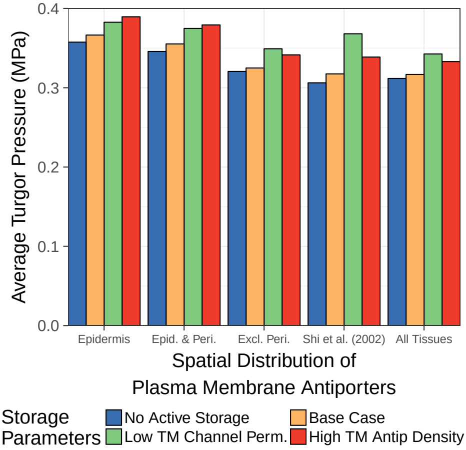
- 8 hrs after 100 mM NaCl
- 15 days after 100 mM NaCl





Storage of Na^+ in vacuoles: Benefits

- Increase in turgor pressure



Summary: Magnitude of energy costs

- The energy cost of ion transport under salt stress, based on the current model of Na^{+} transport in roots, is unrealistically high.
- Possible explanations for this:
  - Na^{+} influx is restricted by relatively low passive plasma membrane permeabilities.
  - There is an alternative transport mechanism effluxing Na^{+}.
- Key model assumptions:
  - Ca^{2+} transport is not included in the model.
  - Cl^{-} is the only mobile anion.
  - H^{+} transport across the tonoplast membrane is simulated using one 'composite pump' that represents the combined transport of H^{+} via V-ATPase and H^{+}-PPase.

Summary: Energy efficiency

- Exclusion of Na^+ from the outer root tissues:
  - Is very energetically expensive.
  - Can be most efficiently achieved by reducing the passive uptake of Na^+.
- Na^+ loading/unloading of the xylem:
  - It is more efficient to minimise net Na^+ transport into the xylem by reducing the active loading of Na^+ rather than by increasing the passive unloading of Na^+.
- Active Na^+ storage in vacuoles:
  - Can be most efficiently achieved by reducing the passive leak of Na^+ across the tonoplast.
  - Benefits?

References

- Experimental comparisons:

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  - Shi, H., Quintero, F. J., Pardo, J. M., Zhu, J., 2002. The putative plasma membrane Na^+/H^+ antiporter *SOS1* controls long-distance Na^+ transport in plants. The Plant Cell Online 14 (2), 465-477.
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References

- Spatial distribution of transport proteins:

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