



Research article

Potassium retention in leaf mesophyll as an element of salinity tissue tolerance in halophytes



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ABSTRACT

Soil salinity remains a major threat to global food security, and the progress in crop breeding for salinity stress tolerance may be achieved only by pyramiding key traits mediating plant adaptive responses to high amounts of dissolved salts in the rhizosphere. This task may be facilitated by studying natural variation in salinity tolerance among plant species and, specifically, exploring mechanisms of salinity tolerance in halophytes. The aim of this work was to establish the causal link between mesophyll ion transport activity and plant salt tolerance in a range of evolutionary contrasting halophyte and glycophyte species. Plants were grown under saline conditions in a glasshouse, followed by assessing their growth and photosynthetic performance. In a parallel set of experiments, net K⁺ and H⁺ transport across leaf mesophyll and their modulation by light were studied in control and salt-treated mesophyll segments using vibrating non-invasive ion selective microelectrode (the MIFE) technique. The reported results show that mesophyll cells in glycophyte species loses 2–6 fold more K⁺ compared with their halophyte counterparts. This decline was reflected in a reduced maximum photochemical efficiency of photosystem II, chlorophyll content and growth observed in the glasshouse experiments. In addition to reduced K⁺ efflux, the more tolerant species also exhibited reduced H⁺ efflux, which is interpreted as an energy-saving strategy allowing more resources to be redirected towards plant growth. It is concluded that the ability of mesophyll to retain K⁺ without a need to activate plasma membrane H⁺-ATPase is an essential component of salinity tolerance in halophytes and halophytic crop plants.

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1. Introduction

Soil salinity remains a major threat to global food security (Shabala, 2013; Shahbaz and Ashraf, 2013). Despite significant breakthroughs in our understanding mechanisms of Na⁺ transport and signalling in plants (Yamaguchi et al., 2013; Adams and Shin, 2014; Deinlein et al., 2014; Maathuis, 2014; Benito et al., 2014; Britto and Kronzucker, 2015), no major improvements in the salinity tolerance of commercial crops has been achieved so far. It has become more and more evident that manipulating the

expression level/function of merely one gene has little chance to make a significant change in overall salinity stress tolerance, and a “pyramiding approach” was advocated (Flowers and Yeo, 1995; Yamaguchi and Blumwald, 2005; Tester and Lanridge, 2010; Shabala, 2013). The question remains as to which traits should be combined, especially because some of the favourable traits are mutually exclusive.

Possible clues may come from studying natural variation in salinity tolerance among plant species and, specifically, from exploiting mechanisms of salinity tolerance in halophytes (Flowers et al., 2010; Shabala, 2013; Shabala et al., 2014; Volkov, 2015). Once these mechanisms are revealed, plant breeders may exploit them to produce tolerant crops. Importantly, the differences in tolerance between naturally salt tolerant plants (halophytes) and salt sensitive plants (glycophytes) comes from physiological differences rather than from unique anatomical features (Shabala and Mackay,

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2011). One such physiological hallmark of halophytes is the means by which plants achieve their osmotic adjustment under saline conditions.

Most glycophytes (conventional crops) are selected for their ability to exclude Na^+ from uptake and synthesise compatible solutes (low molecular weight organic compounds such as polyols and amino acids that do not interfere with metabolic processes in the cell) to maintain cell turgor under hyperosmotic saline conditions (Munns and Tester, 2008). This comes with substantial yield penalties because for the production of one mol of compatible solute, plants spend between 50 and 70 mol of ATP (Raven, 1985), at the expense of other metabolic and growth-related processes. Munns and Gilliam (2015) estimated that for plants grown under 200 mM NaCl salinity 70% of their dry matter should be comprised of sucrose (predominant organic osmolyte in cereals) to be used for osmotic adjustment purposes, assuming they rely exclusively on organic osmolytes. This leaves little if any carbon to be allocated for any other (metabolic/growth) purposes. On the contrary, all halophytes are Na^+ includers; they generally have higher Na^+ contents than other plants in non-saline environments, and in saline environments they further increase their Na^+ concentration to maintain shoot turgor using Na^+ as a cheap osmolyte (Santa-Cruz et al., 1999; Flowers and Colmer, 2008; Shabala and Mackay, 2011). For example, 95% of osmotic adjustment in quinoa plants is achieved by the accumulation of inorganic ions (Hariadi et al., 2011). This mechanism of osmotic adjustment, however, comes with strict control over cytosolic Na^+ and K^+ homeostasis in a trait termed as “tissue tolerance”.

The “classical” component of tissue tolerance is vacuolar Na^+ sequestration mediated by tonoplast Na^+/H^+ NHX exchangers (Apse and Blumwald, 2007; Munns and Tester, 2008). However, higher NHX expression levels by themselves do not always result in increased salinity tolerance (Adem et al., 2015). At the very least, these NHX exchangers should be energized by the tonoplast H^+ -pumps (Shabala, 2013). Two major types of such pumps are known: tonoplast H^+ -ATPases that use ATP (Schumacher and Krebs, 2010) and H^+ -PPases that use inorganic pyrophosphate (Gaxiola et al., 2007) to acidify the vacuole to provide the driving electrochemical force for Na^+ transport across the tonoplast membrane against concentration and electrochemical gradients. Given reduced ATP availability under saline conditions (Shabala, 2013), it is reasonable to suggest H^+ -PPase should play a major role in fuelling tonoplast Na^+/H^+ exchangers. Indeed, under conditions of salt stress the expression and activity of H^+ -PPase increase (Colombo and Cerana, 1993; Zingarelli et al., 1994; Fukuda, 2004). Increased H^+ -PPase and NHX expression on their own induce salinity tolerance, however when these genes are co-expressed greater salinity tolerance is observed (Bhaskaran and Savithramma, 2011; Bao et al., 2014; Shen et al., 2014). H^+ -ATPase expression has also been shown to increase under salt stress (Popova and Gollidack, 2007) this up regulation H^+ -ATPase is linked to the SOS pathway (Batelli et al., 2007) and is likely to be a key determinant of salinity tolerance.

Type 1 H^+ -PPase activity is strongly dependent on K^+ activity in the cytosol (Belogurov and Lahti, 2002; Gaxiola et al., 2007), implying the importance of cytosolic K^+ retention as a component of the tissue tolerance mechanism. Salt-tolerant barley varieties have a greater ability to retain K^+ in mesophyll with increased apoplastic salinity (Wu et al., 2013). Increased apoplastic salinity causes a rapid and sustained K^+ efflux from bean mesophyll resulting in a dramatic decline in cytosolic K^+ concentrations from an estimated 150 mM–59 mM (Percey et al., 2014). This decline in cytosolic K^+ concentration results in reduced photosynthetic performance in chloroplasts (unpublished data). Thus, the differences between halophytes and glycophytes abilities to handle high NaCl

concentrations could be ultimately related to their ability to retain K^+ in the cytosols of mesophyll cells. This hypothesis, however, is yet to be tested in direct experiments.

The majority of Na^+ induced K^+ efflux from bean mesophyll occurs through outward rectifying depolarisation-activating KOR channels (Percey et al., 2014). KOR channels are voltage gated (Hedrich, 2012) and as such are initially activated by plasma membrane depolarisation under salinity stress due to the rapid entry of Na^+ into the cytosol (Shabala and Cuin, 2008). Another pathway for K^+ leak is via K^+ -permeable non-selective cation channels (NSCC) activated by reactive oxygen species (ROS) produced in plants under saline conditions (Demidchik et al., 2002, 2010; Percey et al., 2014). It remains to be answered, however, if the same scenario is applicable to halophytes, and the relative contribution of KOR and NSCC in salt-induced K^+ leak from mesophyll in this species.

Fluctuations in light intensity modulate ion transport across a variety of cellular membranes in leaves including the plasma membrane of epidermal (Elzenga et al., 1995; Shabala and Newman, 1999; Živanović et al., 2015), mesophyll (Elzenga et al., 1995; Shabala and Newman, 1999) and guard cells (Schroeder, 1988; Kinoshita and Shimazaki, 1999), as well as across the chloroplast envelope (Kreimer et al., 1985) and thylakoid membranes (Spetea and Schoefs, 2010). These changes were shown to be causally related to both photosynthetic (Checchetto et al., 2013; Carraretto et al., 2013) and developmental (Dodd et al., 2010) processes, as well as to leaf expansion growth (Blum et al., 1992; Staal et al., 1994; Živanović et al., 2005). In bean, the ability to respond to light with ion fluxes was diminished by salinity stress (Percey et al., 2014) and, thus, could be used as an indicator of adverse salinity effects on cell metabolism.

In this work, the non-invasive MIFE technique was used to fill some of the above gaps in our knowledge by linking growth and photosynthetic parameters with ion transport in mesophyll. Specifically, two hypotheses were tested: that salt tolerant plants (i) have a better ability to retain potassium in mesophyll and (ii) their ability to respond to light is less affected by salinity treatment.

2. Materials and methods

2.1. Growth experiment plant material

Three glycophyte and three halophyte species were used in this study (see Table 1 for details). All plants except *Mesembryanthemum* were grown from seeds under controlled greenhouse conditions (temperature between 19 °C and 26 °C; day length 12–14 h; average humidity ~65%) at the University of Tasmania in

Table 1
Details of plant species used in this study.

Latin name	Common name	Supplier
GLYCOPHYTES		
<i>Vicia faba</i> L	Broad beans	Hollander Imports, Hobart, Australia
<i>Beta vulgaris</i> L	Sugar beet	Hollander Imports, Hobart, Australia
<i>Pisum sativum</i> L	Pea	Hollander Imports, Hobart, Australia
HALOPHYTES		
<i>Chenopodium quinoa</i>	Quinoa	Prof SE Jacobsen, Univ. Copenhagen
<i>Mesembryanthemum purpureus</i>	Pig face	Bunnings, Hobart, Australia
<i>Disphyma crassifolium</i>	Noon-flower	Wildseed Tasmania, Sorell

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