13 Potassium Homeostasis in Salinized Plant Tissues

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13.1 Introduction

Potassium is an essential cation, comprising ~6% of a plant's dry weight and is involved in numerous functions such as osmo- and turgor regulation, charge balance, and control of stomata and organ movement. K^+ activates over 50 enzymes critical for numerous metabolic processes, including photosynthesis, oxidative metabolism and protein synthesis (Marschner 1995). Within the cytosol, K^+ neutralizes the soluble and insoluble macromolecular anions and stabilizes the pH at the level optimal for most enzymatic reactions (pH ~7.2). Thus, cytosolic K^+ homeostasis is crucial to optimal cell metabolism.

In contrast to K^+, Na^+ is not essential for plants (Marschner 1995). For the majority of crop species, Na^+ is toxic at mM concentrations in the cytosol. With cytosolic K^+ concentrations being around 150 mM (Leigh and Wyn Jones 1984; Leigh 2001) and cytosolic Na^+ in a lower mM range (Carden et al. 2003), the cytosolic K^+/Na^+ ratio is high, enabling many K^+-dependent metabolic processes to proceed (Rubio et al. 1995; Maathuis and Amtmann 1999). Under saline conditions, cytosolic Na^+ levels increase dramatically, estimates varying from 10 to 30 mM, up to 200 mM (Koyro and Stelzer 1988; Flowers and Hajibagheri 2001; Carden et al. 2003). At the same time, cytosolic K^+ content decreases dramatically. An almost 2-fold decrease in cytosolic K^+ activity was measured in salinized roots of barley (Carden et al. 2003), and cytosolic K^+ activity as low as 15 mM in epidermal leaf cells has been reported (Cuin et al. 2003). Thus the cytosolic K^+/Na^+ ratio falls dramatically under saline conditions, severely impairing cell metabolism (Maathuis and Amtmann 1999; Flowers and Hajibagheri 2001; Munns 2002). Not surprising, the ability to maintain a high cytosolic K^+/Na^+ ratio has often been cited as a key feature in plant salt tolerance (Gorham et al. 1990; Maathuis and Amtmann 1999; Tester and Davenport 2003; Chen et al. 2005).

Within the vacuole, K^+ mediates osmoregulation, and within specialized cells, stomatal movements and tropisms. Here the K^+ concentration is much more flexible and can be more readily replaced by other cations, including

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Na^+ (Leigh et al. 1986). However, the vacuolar PP-ase is critically dependent on K^+ for both hydrolytic activity and H^+ pumping (White et al. 1990). Thus, even in this organelle, maintenance of a minimal level of K^+ is vitally important for optimal plant performance. How is this achieved?

Molecular and ionic mechanisms of K^+ transport have been the subject of a large number of comprehensive reviews in recent years (Maathuis and Amtmann 1999; Maathuis and Sanders 1999; Tyerman and Skerrett 1999; Schachtman 2000; Mäser et al. 2001; Véry and Sentenac 2002, 2003; Shabala 2003) so are only briefly revised in our review. Many important questions, however, remain to be answered. It is not clear how the levels and ratios of K^+ to Na^+ are maintained within the plant, and why these ratios are different in cells within various plant tissues. It is also remains to be answered how plants distinguish between K^+ and Na^+, both at the root and cellular levels. This latter problem is not trivial, due to the similarity in ionic radius and ion hydration energies for K^+ and Na^+ (Hille 1992), factors which determine both the ion transport mode and the competition for enzyme binding sites within the cytosol. Despite a recent plethora of research (Apse et al. 1999, 2003; Hasegawa et al. 2000; Zhu 2000, 2003; Zhang and Blumwald 2001), we are still lacking full knowledge of the signal-transduction pathways involved in K^+ homeostasis and maintenance of the critical K^+/Na^+ ratios under salt stressed conditions.

This review addresses some of the above issues and summarizes molecular and electrophysiological evidence regarding mechanisms regulating K^+ homeostasis in salinized plant tissues. The main emphasis is made on the integration of K^+ transport mechanisms at various levels of plant structural organization.

13.2 Potassium acquisition and distribution in plants

Potassium enters the root symplast via the cell plasma membrane (PM). From there, it can travel through the symplast to the vascular tissues, where it is unloaded from the xylem parenchyma into xylem vessels for long-distance transport to leaves. K^+ is reabsorbed from the xylem into leaf cells. Being a highly mobile element (Marschner 1995), it can be easily loaded into the phloem for translocation to actively growing sink tissues (e.g. shoot and root apices) where it can be unloaded by way of symplasmic or apoplastic pathways. K^+ can also cross the tonoplast membrane for storage in vacuoles of both root and shoot cells. The integration and regulation of K^+ transport systems at different sites along the long-distance pathway allows the plant to direct the partitioning and circulation of K^+. Such an integrated system plays a central role in plant growth and development and in the allocation of mineral nutrients in response to changes in nutrient availability. This section