

## **Salinity tolerance of crops – what is the cost?**

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### **Summary**

Soil salinity reduces crop yield. The extent and severity of salt-affected agricultural land is predicted to worsen due to inadequate drainage of irrigated land, rising water tables, and global warming. The growth and yield of most plant species is adversely affected by soil salinity, but varied adaptations can allow some crop cultivars to continue to grow and produce a harvestable yield under moderate soil salinity. Significant costs are associated with saline soils: the economic costs to the farming community, and the energy costs of plant adaptations. We briefly consider mechanisms of adaptation and highlight recent research examples through a lens of their applicability to improving the energy efficiency of crops under saline field conditions.

Keywords: salinity, salt, tolerance, yield, cost, energy, mechanism, adaptation

1

## 2 *I. Soil salinity and its economic costs*

3 Soil salinity can reduce crop, horticulture and forage production in arid and semi-arid  
4 regions. Salt may arise naturally in the subsoil, or be introduced by brackish irrigation waters.  
5 Salinity is becoming more extensive due to land clearing and unsustainable irrigation  
6 practices, and through pressures for bringing marginal land into production. Agronomic and  
7 engineering solutions are being exhausted, so to minimise the impact of saline land on global  
8 food production the way forward is to breed greater salt tolerance into present crops, and to  
9 introduce new species for cultivation.

10 In this article we focus on the costs of soil salinity. One cost, relevant to farmers, is the  
11 economic cost of reduced yield (Box 1). The second cost – and the cause of the reduced yield  
12 that underpins the economic loss to the farmer – is the energy cost incurred by the plant when  
13 exposed to soil salinity. We briefly consider these two costs and highlight recent research  
14 with potential for improving crop salinity tolerance.

## 15 *II. Mechanisms of plant adaptation to saline soil and potential energy costs*

16 The majority of energy acquired by photosynthesis and fixed into carbon (C) compounds is  
17 used by plants in general maintenance (Amthor, 2000; Jacoby *et al.*, 2011). Only a small  
18 proportion (10-40%) is used directly for biomass accumulation even under optimal conditions  
19 (Figure 1). Stress can be defined in terms of energy costs; we consider stress to be occurring  
20 when the amount of energy acquired by plants is reduced (due to a reduction in  
21 photosynthetic rate or leaf area) and/or when energy is redistributed from growth into stress  
22 defence (Figure 1). By improving the energy efficiency of plant metabolism and physiology,  
23 especially during floral development and grain fill, more fixed C could be allocated to grain,  
24 improving yield. When crops are exposed to stress, the less energy plants need to use in  
25 tolerating salt the more will be available for grain yield (Figure 1).

26 Plants deploy a variety of traits to combat salt in soil solution. The most essential trait is  
27 osmotic adjustment – all cells must accumulate sufficient solutes to balance extra osmotic  
28 pressure in the soil solution to maintain turgor. To achieve this, plants use two strategies to  
29 varying degrees: (A) excluding  $\text{Na}^+$  and  $\text{Cl}^-$ , particularly from leaves, and relying on organic  
30 solutes for osmotic adjustment (“ion exclusion”); or, (B) ~~allowing accumulating uptake of~~  
31 sufficient  $\text{Na}^+$  and  $\text{Cl}^-$  to balance that in the soil solution but having strict ionic regulation in  
32 various cell compartments (“tissue tolerance”).

33 In general, salt tolerant species have high  $\text{Na}^+$  and  $\text{Cl}^-$  concentrations in leaves – higher than  
34 the external solution. This is particularly true for halophytes and the more salt tolerant non-  
35 halophytes like barley, where the trait of tissue tolerance is clearly evident. Such plants must  
36 compartmentalise most of the leaf  $\text{Na}^+$  and  $\text{Cl}^-$  in vacuoles to keep the cytosolic and  
37 organellar concentrations below toxic levels, and use organic osmolytes (and  $\text{K}^+$ ) to balance  
38 the osmotic pressure in these cytoplasmic compartments (Shabala, 2013). The concentration  
39 where  $\text{Na}^+$  (or  $\text{Cl}^-$ ) becomes toxic in the cytoplasm is unclear, and is a priority area for  
40 research; cytosolic estimates are  $\sim 30$  mM  $\text{Na}^+$  (Munns & Tester, 2008; Conn and Gilliham,  
41 2010), whereas chloroplasts and mitochondria appear to tolerate 100–200 mM  $\text{Na}^+$  and  $\text{Cl}^-$   
42 (Flowers *et al.*, 2015). Estimates of osmotic adjustment costs using organic molecules versus  
43  $\text{Na}^+$  and  $\text{Cl}^-$  (Greenway & Munns, 1983; Raven, 1985; Yeo, 1983) indicate that the energy  
44 demands are significant and could restrict growth rates at high salinity, either in the diversion  
45 of C or N compounds from growth to storage pools, or in costs of controlling  $\text{Na}^+$  and  $\text{Cl}^-$   
46 transport across membranes. Table 1 indicates that 200 mM NaCl is the limit of growth for  
47 species that have low  $\text{Na}^+$  and  $\text{Cl}^-$  concentrations in leaves and rely on organic solutes for  
48 osmotic adjustment.

49 The more sensitive species tend to have low  $\text{Na}^+$  concentrations in leaves, lower than in the  
50 external solution, i.e. they rely on “ion exclusion” as the major adaptive trait. ~~Interestingly,~~  
51 ~~there is a paradox that seemingly contradicts the notion that “tissue tolerance” is the most~~  
52 ~~cost-efficient strategy.~~ Within any species, where significant genotypic variation in  $\text{Na}^+$   
53 accumulation in leaves exists, there is a correlation between salt tolerance and  $\text{Na}^+$  exclusion.  
54 This is true for sensitive species like rice and durum wheat (reviewed in Munns, 2005), but it  
55 may also be true for the more salt tolerant species like barley (e.g. Chen *et al.*, 2005). ~~This~~  
56 ~~presents~~ ~~Interestingly, there is a paradox that seemingly contradicts the notion that “tissue~~  
57 ~~tolerance” is the most cost-efficient strategy; it.~~ ~~This~~ indicates that there are significant costs  
58 of compartmentation of  $\text{Na}^+$  and or  $\text{Cl}^-$  in leaf cells, and that reducing the salt load on a leaf  
59 confers a benefit. This presumably becomes important over time when the initial osmotic  
60 adjustment has occurred, and salt toxicity threatens as ions continue to be transported to  
61 leaves.

62 Future work is needed to quantify the costs of the different traits for salt tolerance to test the  
63 limits of each strategy, and to provide new ideas for research approaches to increase the salt  
64 tolerance of crops.

### 65 ***III. New insights into salinity tolerance mechanisms***

66 Salinity research is predominantly performed on model systems. Very few fundamental  
67 research findings relevant to salinity tolerance have been applied to crop plants. An exception  
68 is the application of AtNHX1 (Na<sup>+</sup>/H<sup>+</sup> antiporter 1 proteins) to improve salt  
69 compartmentation in the vacuoles of tomato vegetative tissue, which improved yield without  
70 increasing salt in the tomato fruit (cited in Bassil & Blumwald, 2014). More recently,  
71 *AtCIPK16*, a SNF1-related kinase/CBL-interacting protein kinase underlying a QTL for Na<sup>+</sup>  
72 exclusion in the *Arabidopsis thaliana* Bay-0 x Shahadara mapping population, was expressed  
73 in barley and found to improve Na<sup>+</sup> exclusion and biomass in a saline field (Roy *et al.*, 2013).  
74 Here, we discuss recent research that has the potential for improving salt tolerance in the  
75 field, which is also summarised at both the cellular and organ level in Figure 2.

76

#### 77 ***Cellular mechanisms of salt tolerance***

78 Reactive oxygen species (ROS) act as a signal during salt stress but can also damage plant  
79 root and shoot tissue during salinity stress by perturbing enzyme, cell wall and membrane  
80 function. Several genes involved in ROS detoxification have been cloned from SR3 wheat  
81 which is a hybrid with a high level of salinity tolerance (e.g. Dong *et al.*, 2013).

82 Overexpression of genes involved in ROS scavenging have resulted in lower cellular damage,  
83 the maintenance of photosynthetic energy capture, and an improvement in shoot and root  
84 growth under saline conditions (Roy *et al.*, 2014). Many of these transgenics have reduced  
85 growth under non-saline conditions so the energetics of ROS detoxification is important to  
86 quantify, as are the implications of ROS detoxification on final grain yield.

87 Ion transport can account for the majority of respiratory costs in plants (Van der Werf *et al.*,  
88 1988). Ion transporters (e.g. Osakabe *et al.*, 2014) and their localisation in key cell-types  
89 underpin plant salinity tolerance. Root xylem parenchyma cells represent ‘gatekeeper’ cell  
90 types for shoot NaCl exclusion as they have a physical location and unique protein circuitry  
91 primed for this role (Henderson & Gilliam, 2015). TaHKT1;5-D is responsible for  
92 maintaining high cytosolic K<sup>+</sup>/Na<sup>+</sup> ratios in bread wheat shoots; it underpins the *Kna1* locus,  
93 resides on the (PM) membrane of root xylem parenchyma cells and reduces Na<sup>+</sup> load in the  
94 xylem prior to entering the shoot (Byrt *et al.*, 2014). Orthologous proteins in sequence and  
95 function are found in *Arabidopsis*, durum wheat and rice (Henderson & Gilliam, 2015).

96 Introgression of the *Triticum monococcum* (*HKT1;5-A*) into durum wheat improved shoot  
97  $\text{Na}^+$  exclusion and improved grain yield in the field by 25% (Munns *et al.*, 2012). Other salt  
98 tolerance factors expressed in the root stele include the *salt overly sensitive* (*SOS*) pathway  
99 genes and *AtCIPK16* (Roy *et al.*, 2013). Root stelar cells also confer control shoot  $\text{Cl}^-$   
100 accumulation, which can induce salinity toxicity in crops, however, we know little about the  
101 proteins involved (Henderson *et al.*, 2014).

102 Aquaporin proteins, a large multigenic family that regulate a large proportion of water  
103 transport across membranes, are rapidly influenced both transcriptionally and post-  
104 translationally by salt (Chaumont & Tyerman, 2014). Overexpression of a PM intrinsic  
105 protein in soybean increased shoot  $\text{Na}^+$  exclusion and increased seed yield from a saline field  
106 (Zhou *et al.*, 2014). Wheat TIP2;2 is regulated by methylation following salt treatment (Xu *et al.*,  
107 2013), as is HKT1 in Arabidopsis (Sani *et al.*, 2013). The role of methylation and  
108 aquaporins in salt tolerance is worth further exploration.

### 109 ***The emerging role of the endomembranes and endosomes***

110 In salt-acclimated tobacco BY2 cells (Garcia de la Garma *et al.*, 2015) reported extensive  
111 vesicle trafficking of  $\text{Na}^+$  between the PM and the  $\text{Na}^+$ -rich vacuolar compartment. This  
112 novel mechanism of salt deposition presumably avoids raising cytosolic  $\text{Na}^+$ , so its  
113 application is worth further exploration. The role of RAB6 GTPase ARA6 and VAMP727-  
114 mediated endocytotic machinery in salt tolerance was also shown in Arabidopsis roots; when  
115 *ARA6* was overexpressed it improved salt tolerance whereas *ara6/vamp727* knockout plants  
116 were salt hypersensitive (Ebine *et al.*, 2011).

117 The CPA1 family of  $\text{Na}^+/\text{H}^+$  antiporters, NHX1 (tonoplast-localised) and NHX7/SOS1 (PM-  
118 localised) are often reported to confer  $\text{Na}^+$  compartmentation or exclusion under high salt  
119 loads but their role is less clear under moderate salinities. Double knockouts of *nhx1/nhx2* are  
120 not ~~salt~~-sensitive to moderate external  $\text{Na}^+$  concentrations, whereas they are sensitive to  
121 moderate external  $\text{K}^+$  concentrations (reviewed in Bassil & Blumwald, 2014). In contrast, the  
122 trans-golgi network-localised NHX double knockouts, *nhx5/nhx6*, are hypersensitive to  
123 moderate salinity and disrupt vesicle trafficking to the vacuole (Bassil & Blumwald, 2014).  
124 Another CPA family member, a cation/ $\text{H}^+$  exchanger (CHX), GmSALT3, improves shoot  
125  $\text{Na}^+$  exclusion and salt tolerance in soybean (Guan *et al.*, 2014). CHX proteins, including  
126 GmSALT3, have frequently been localised to the ER using fluorescent protein fusions. If  
127 these membrane localisations are to be trusted this is further evidence to suggest that

128 endosomal-localised transport proteins have crucial roles in salt tolerance – possibly in  
129 endosomal pH or cation homeostasis, or vesicle trafficking, but their exact roles are still to be  
130 determined.

131 ***Can we better exploit beneficial soil micro-organisms to improve salinity tolerance?***

132 Rhizospheric fungi and plant growth promoting rhizobacteria (PGPR) can increase plant  
133 yield under stressed and non-stressed conditions (De-la-Pena & Loyola-Vargas, 2014;  
134 Nadeem *et al.*, 2014). Salt tolerant PGPR populations can reduce Na<sup>+</sup> content of shoots,  
135 increase the expression of stress responsive transcription factors, induce greater proline  
136 synthesis, enhance ROS scavenging, and improve plant biomass under salinity stress (De-la-  
137 Pena & Loyola-Vargas, 2014; Nadeem *et al.*, 2014). Arbuscular mycorrhizal fungal  
138 colonisation of roots can improve plant salt tolerance by increasing water acquisition and  
139 shoot K<sup>+</sup> whilst decreasing shoot Na<sup>+</sup> concentration content (Auge *et al.*, 2014). Therefore,  
140 treatment with rhizospheric organisms is an attractive option to improve crop yields under  
141 saline conditions, so the quantification of their costs and expansion of trials to the field  
142 should be encouraged.

143 ***How does root system architecture ~~(RSA)~~ influence salinity tolerance of cereals?***

144 Root systems are key to improving crop salt tolerance through their potential for improving  
145 access to water and nutrients and limiting salt acquisition (Jung & McCouch, 2013). Salt,  
146 reportedly through its osmotic effects, decreases root epidermal cell division and elongation  
147 rates reducing primary root growth but initiating lateral root development in Arabidopsis and  
148 wheat (Rahnama *et al.*, 2011; Jung & McCouch, 2013). This would assist plants to mine non-  
149 saline areas for water and minerals until exploitation of saline areas is necessary. In the field,  
150 soil salinity is always heterogeneous and usually increases with depth. A complex set of  
151 intersecting hormone-mediated pathways control RSA-root system architecture in  
152 Arabidopsis (Jung & McCouch, 2013), with the mechanisms little explored in crops (Rogers  
153 & Benfey, 2015). Arabidopsis roots exposed to a band of high NaCl in sterile culture exhibit  
154 negative halotropism, i.e. they grow away from salt. This asymmetric root growth response is  
155 initiated by a rise in cytosolic Na<sup>+</sup> mediated by clathrin-mediated endocytosis of the PIN-  
156 FORMED 2 (PIN2) auxin efflux carrier, and an active redistribution of the auxin gradient to  
157 the side of the root facing the salt (Galvan-Ampudia *et al.*, 2013). Whether halotropism exists  
158 in crops, rather than root growth being inhibited purely by decrease water potential of the  
159 soil, is yet to be reported and the costs of changing RSA-root architecture are unexplored.

160 ***IV. Better yield under non-saline conditions equals better salt tolerance?***

161 Elite cultivars that perform particularly well under optimal conditions are also often best  
162 yielding under water-limited conditions (Richards *et al.*, 2014), and this principle may apply  
163 to saline conditions as long as the enhanced yields are due to energy-efficient processes.  
164 Overexpression of the Arabidopsis vacuolar proton pumping pyrophosphatase (H<sup>+</sup>-PPase)  
165 improves the salinity tolerance of various crop species under controlled conditions and was  
166 shown by Schilling *et al.* (2014) to increase growth and yield of transgenic barley under  
167 saline conditions in both greenhouse and field. Notably, the *AtAVP1* overexpressing barley  
168 also produced greater shoot biomass and grain yield *under non-saline conditions*. The  
169 mechanism for these improvements were unclear and is the source of further research  
170 (Schilling *et al.*, 2014). The transgenic manipulation of a crop to improve yield under both  
171 control and saline conditions is an exciting development and warrants further exploration.

172 In semi-arid regions, phenology is a primary factor determining grain yield. Worryingly,  
173 climate change models predict increased temperature and decreased rainfall in certain semi-  
174 arid regions (Anwar *et al.*, 2015). This may leave crops susceptible to terminal droughts, and  
175 very high salt concentrations in the soil during grain filling, which reduces grain size.  
176 Planting and flowering time is therefore crucial to maximise opportunities for photosynthetic  
177 capture and translocation of photosynthate to grain. Salinity affects flowering time, and can  
178 delay or advance it according to species and level of salinity (Munns & Rawson, 1999; Kim  
179 *et al.*, 2013). Research that has recently highlighted novel genes that have an impact on this  
180 salinity-flowering time interaction are summarised in Supporting Text S1. Further  
181 understanding of the molecular controls of flowering time and their interaction with soil  
182 salinity is needed to explain and exploit the difference in the salt-induced phenology  
183 responses between genotypes and species.

184 Whilst the salinity tolerance of many cereals remains poor, breeders are still producing yearly  
185 incremental improvements in grain yield. It has been suggested that the narrowing crop  
186 genetic diversity following domestication and intensive breeding has reduced the potential for  
187 large gains in stress tolerance (Munns *et al.*, 2012). Useful natural variation clearly exists in  
188 'exotic' cereals, for instance many Tibetan wild barley lines show higher than normal levels  
189 of salt tolerance in terms of biomass accumulation (Wu *et al.*, 2011). Exploiting such  
190 germplasm has great potential for improving crop salt tolerance.

191 ***V. What does the future hold for stress tolerance research?***



192 This insight has highlighted mechanisms with potential for improving crop stress tolerance. It  
193 has also highlighted that we lack basic information on the energy costs of salinity tolerance.  
194 There is a rationale for revisiting questions posed over thirty years ago and quantify the costs  
195 of salt to plants. The challenge is to gain quantitative data for the role of specific salt  
196 tolerance mechanisms at the genetic level through to single cells and whole plants so we can  
197 develop models that predict which pathways lead to energy gains. The desired outcome will  
198 be the informed selection of crops with lower energy costs and greater yields. A rigorous  
199 understanding of the plant economy when faced with salt, and the natural variation that exists  
200 in this economy will provide a foundation for a targeted approach to crop breeding for  
201 stressful environments that has not yet been possible.

202 A role of pre-breeding is to provide germplasm to breeders that produces significant increases  
203 in yield in stressful environments (e.g. Schroeder *et al.*, 2013). Fundamental research on  
204 Arabidopsis has led to interesting insights into salt tolerance mechanisms, but how much of  
205 this can be applied to crop plants in the field? (Figure 2). Affordable next generation  
206 sequencing and novel transformation techniques now allow fundamental research to be  
207 performed on crops. The greater available natural variation within crops, and their more  
208 complex genomes, will likely lead to greater yield improvements than has been possible with  
209 model plants, providing tangible research impacts towards food security targets.

210

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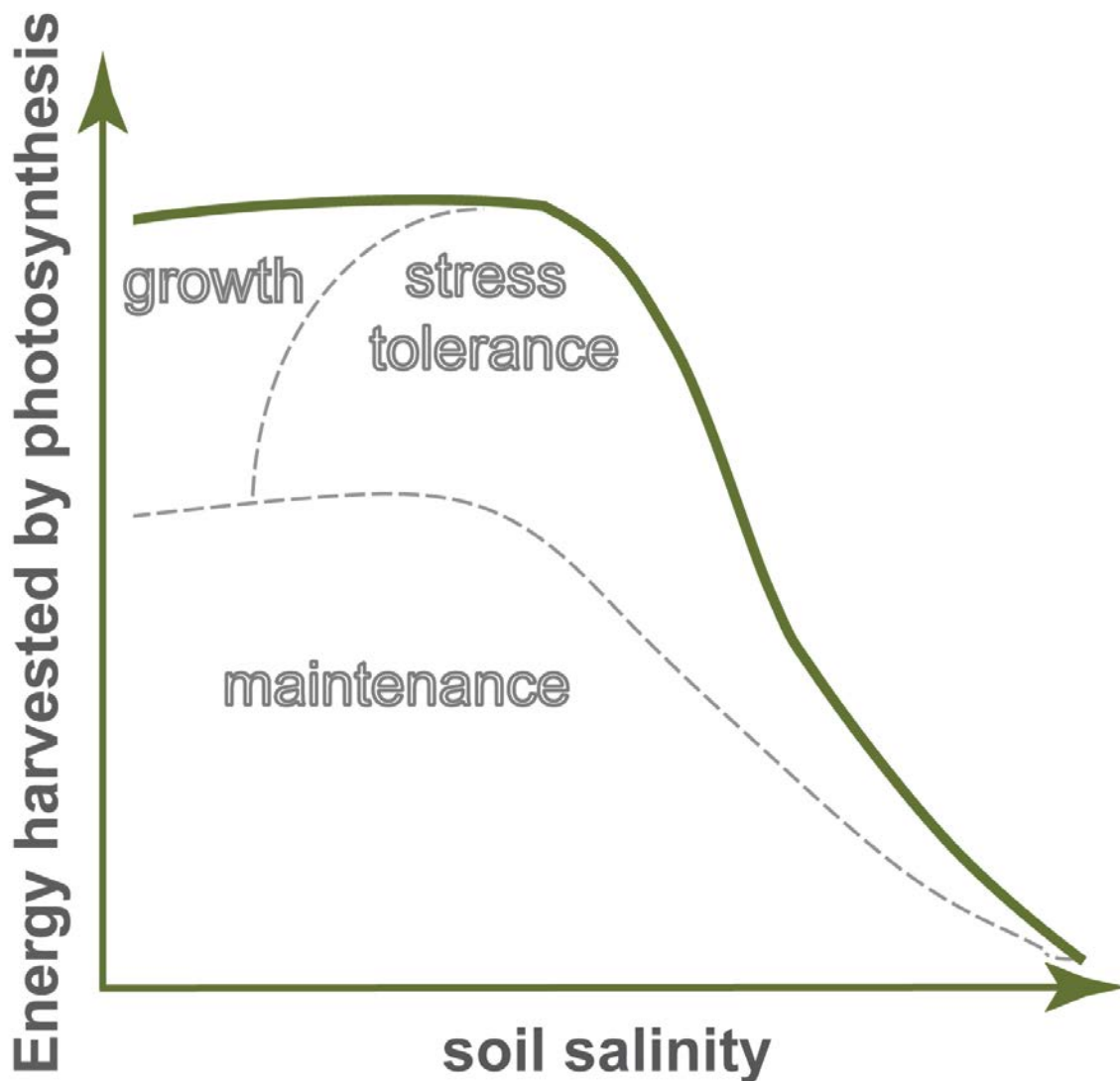
**Table 1. Demand for organic solutes (in hexose units) versus Na<sup>+</sup> and Cl<sup>-</sup> for osmotic adjustment (OA).** The contribution of osmotica to the dry weight is calculated from the concentration needed to balance the osmotic pressure of the external solution and the water content of a typical cereal leaf. (Note that 1 mole of NaCl is equivalent in osmolarity to 2 moles of hexose, and the molecular weight of hexose and NaCl is 180 and 60 respectively.) Most plants accumulate sucrose as the preferred organic osmotica, which has twice the mass as does hexose, thus setting 200 mM NaCl has an upper limit for growth in saline soil as it would comprise 70% of the dry weight.

<b>NaCl<sub>ext</sub></b>	Leaf H <sub>2</sub> O/DW	<b>Hexose for OA</b>		<b>NaCl for OA</b>	
		g/L H <sub>2</sub> O	g/g DW	g/L H <sub>2</sub> O	g/g DW
<b>50</b>	6	18	0.102	3	0.018
<b>100</b>	5.5	36	0.198	6	0.033
<b>200</b>	5	72	0.360	12	0.060
<b>300</b>	4.5	108	0.486	18	0.072

331 **Box 1. The economic cost of salinity**

332 The major economic cost of salinity is the reduced income to farmers caused by the reduced  
333 yield. Areas where salinity occurs are always arid or semi-arid, so crops are always limited  
334 by water, but they can also be limited by the salt concentration in the soil especially when  
335 rainfall is below average.

336 The economic costs differ from one country to another, and are influenced largely by the cost  
337 of farmer inputs versus the profit they can make in the seasons with average rainfall. In  
338 broad-acre dryland farming, the inputs to the crop (including off-farm subsidies) may cost as  
339 much as \$300 ha<sup>-1</sup>. The water-limited yield may be 3 tonnes ha<sup>-1</sup>, and at a good market price  
340 (say \$200 per tonne) the crop will return a gross income of \$600 ha<sup>-1</sup> with a net return of 300  
341 ha<sup>-1</sup>. If the yield is reduced by salinity to 2 tonnes ha<sup>-1</sup>, the gross income drops to \$400 ha<sup>-1</sup>  
342 and the net return is only \$100 ha<sup>-1</sup>. Consistent losses to salinity due to climate change or  
343 rising water tables may mean that cropping is impossible, and the land usage reverts to  
344 pasture production, using salt-tolerant grasses or other species including halophytes. This  
345 usually brings a much lower return to farmers, but the inputs are fewer, so farming may still  
346 be viable. Farmers have many other expenses on the farm and are always living close to the  
347 margin of profit or loss, and a small decrease in yield or an enforced change in land use may  
348 have devastating economic consequences.

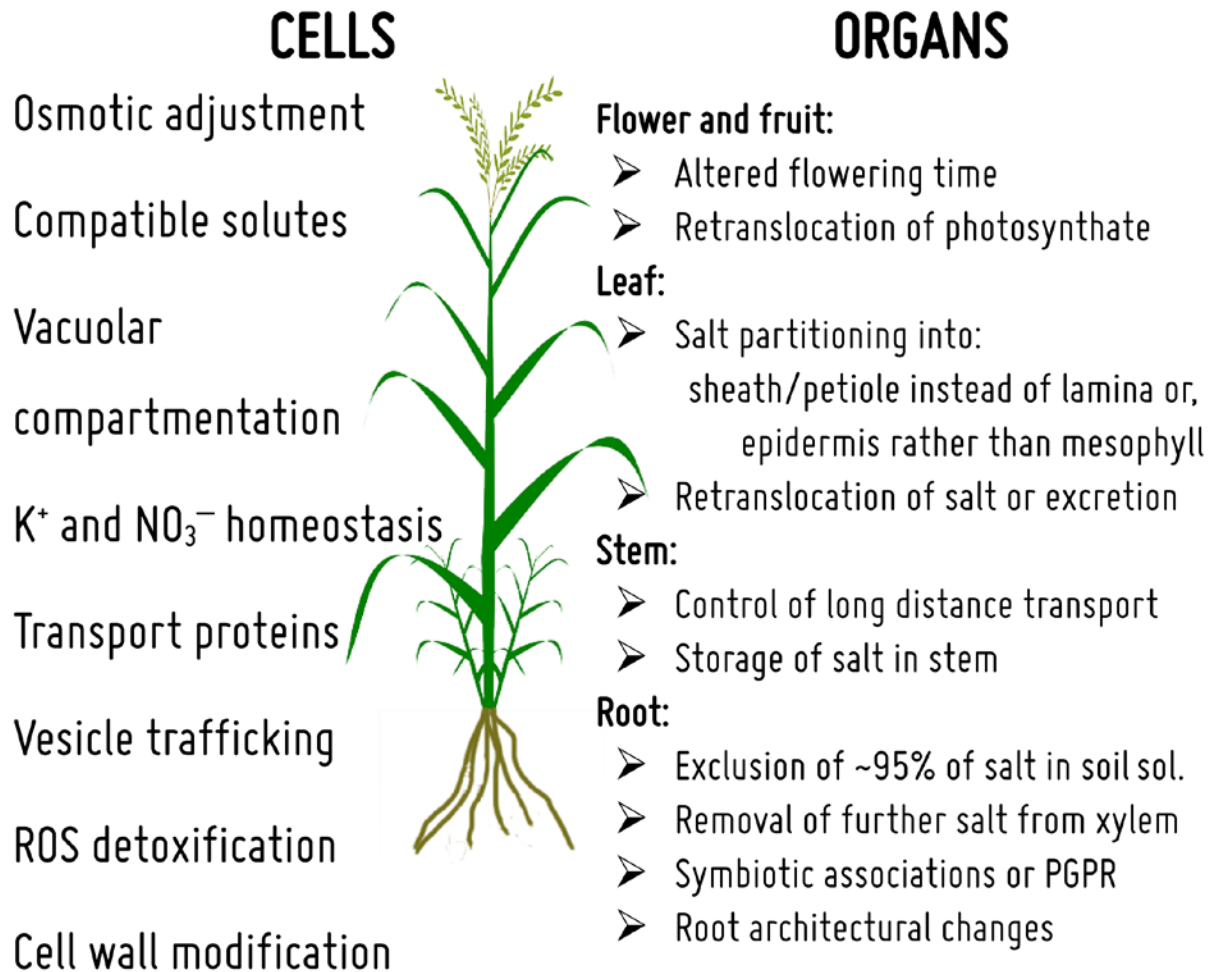


**Figure 1. Schematic of energy gain and use of a crop plant under salinity stress.** At any given time there is a finite amount of energy that can be harvested by the plant through photosynthesis. Plants use the majority of this energy in processes necessary for maintenance of biomass including protein turnover, synthesis of lipids and carbohydrates, maintaining ion gradients, gaining nutrients and source to sink transfer. Growth also requires the investment of energy in these processes, whether this is biomass accumulation or grain yield depends on the developmental stage of the plant. The proportion of energy used in maintenance, growth and stress defence is portrayed under the dotted lines. The relative proportions will change depending on the developmental stage of the plant – maintenance costs will be greater when plants are larger. Total energy gain will decrease with greater salinity by decreasing photosynthetic rate following induced closure of stomata and damage to cellular and photosynthetic machinery. Stress tolerance mechanisms represent additional costs to the plant

required to deal with the salt load in the soil (for example but not limited to greater costs in ion exclusion or compartmentation, and ROS detoxification). At high salinity there will be zero growth as the total costs to the plant equal energy gain, when costs exceed energy gained then tissue will senesce. Adapted from concept by A.H. Millar and H. Lambers, based on data and reasoning of Amthor, 2000 and van der Werf *et al.*, 1988.



# ADAPTATIVE MECHANISMS OF SALT TOLERANCE



**Figure 2. Adaptive mechanisms of salt tolerance.** On the left are listed the cellular functions that would apply to all cells within the plant. On the right are the functions of specific tissues or organs. Exclusion of at least 95% (19/20) of salt in the soil solution is needed as plants transpire 20 times more water than they retain (Munns, 2005). Most of these functions are explained in the text. Omitted for space, and lack of recent advances, is limitation that  $Cl^-$  can impose on growth through its antagonistic accumulation against the nitrogen form  $NO_3^-$  ( $NO_3^-$  homeostasis) (Henderson *et al.*, 2014) and the differential capacity and sensitivity of different cell types and tissues to accumulate  $Na^+$  and  $Cl^-$  e.g. NaCl accumulation within photosynthetic cells incurs a larger cost than accumulation in root cortical cells (Conn and Gilliam, 2010).

## Supporting Text S1.

### *The impact of flowering time on salinity tolerance*

349 In Arabidopsis, salinity has been shown recently to delay flowering through at least two  
350 mechanisms. Salt-induced protein degradation of GIGANTEA (GI) resulting in delayed  
351 activity of the *Flowering Locus (FT)* (Kim *et al.*, 2013) and activated expression of *Brother*  
352 *of Flowering Time Locus (BFT)* with the resulting protein competing with FT for binding to  
353 the bZIP transcription factor (FD), which is required for floral initiation (Ryu *et al.*, 2014).  
354 Interestingly, Kim *et al.* (2013) also found that GI interacts with SOS2 (salt overly  
355 sensitive)/CIPK24 and upon salt degradation of GI, SOS2 is released to activate the plasma  
356 membrane Na<sup>+</sup>/H<sup>+</sup> antiporter SOS1, which results in greater cytoplasmic Na<sup>+</sup> exclusion. This  
357 provides a link between flowering and a key mechanism of salt tolerance first found in  
358 Arabidopsis, which appears to also be active in wheat. TdSOS1 in wheat (Feki *et al.*, 2014)  
359 was upregulated by salt – as is *AtSOS1* – and can complement the mutant phenotype of the  
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