

1 **Plant responses to heterogeneous salinity: agronomic relevance and research priorities**

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33 **Abstract**

34 • **Background.** Soil salinity, in both natural and managed environments, is highly
35 heterogeneous and understanding how plants respond to this spatiotemporal
36 heterogeneity is increasingly important for sustainable agriculture in the era of global
37 climate change. While the vast majority of research on crop response to salinity
38 utilises homogenous saline conditions, a much smaller, but important, effort has been
39 made in the past decade to understand plant molecular and physiological responses to
40 heterogeneous salinity mainly by using split-root studies. These studies have begun to
41 unravel how plants compensate for water/nutrient deprivation and limit salt stress by
42 optimising root-foraging in the most favourable parts of the soil.

43

44 • **Scope.** This review provides an overview of the patterns of salinity heterogeneity in
45 rain-fed and irrigated systems. We then discuss results from split-root studies and the
46 recent progress in understanding physiological and molecular mechanisms regulating
47 plant responses to heterogeneous root-zone salinity and nutrient conditions. We focus
48 on mechanisms by which plants (salt/nutrient sensing, root-shoot signalling and water
49 uptake) could optimise the use of less-saline patches within the root-zone, thereby
50 enhancing growth under heterogeneous soil salinity conditions. Finally, we place
51 these findings in the context of defining future research priorities, possible irrigation
52 management and crop breeding opportunities to improve productivity from salt-
53 affected lands.

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60 INTRODUCTION

61 The world's population is expected to increase to 9.9 billion by 2050 (Liu et al., 2020a),
62 prompting a need to double annual food production within the next 30 years (Razzaq et al.,
63 2021). To achieve this production goal, agriculture will inevitably expand further into
64 marginal lands (Pancaldi and Trindade, 2020; Ahmadzai et al., 2021; Khanna et al., 2021;
65 Razzaq et al., 2021) which often suffer from poor soil structure and low fertility (Mantovani
66 et al., 2015; Shukla et al., 2017). Many of the marginal areas are also affected by the soil
67 salinity.

68 Soil salinity, both naturally occurring (i.e., primary salinisation) and as a consequence of
69 human activities (i.e., secondary salinisation), is a threat to agriculture and a major limitation
70 to food production. The salinisation of agricultural land commonly occurs as a result of using
71 irrigation water containing elevated levels of ions (e.g., Na^+ and Cl^-) without adequate,
72 periodic leaching of the accumulated salts from the soil. Secondary dryland salinisation can
73 also occur in non-irrigated areas due to changes in the hydrological balance of a landscape
74 and rising water tables (e.g. as a result of replacing deep-rooted vegetation with annual crop
75 and pasture species, which results in a higher proportion of incoming rain entering the
76 groundwater, Pannell and Ewing, 2006; McFarlane et al. 2016). The problem is often
77 exacerbated by decreases in soil permeability caused by sodicity (i.e., when the accumulation
78 of Na^+ exceeds that of other cations) and over-exploitation of groundwater, which exhaust
79 high quality water resources, resulting in water extraction from less favourable groundwater
80 that may be brackish or saline (Ruto et al., 2021). Increases in salinity can also be expected in
81 low-lying coastal areas associated with sea-level rises due to climate change and salinisation
82 of groundwater due to salt water intrusion into depleted aquifers (Vellinga and Barrett-
83 Lennard, 2021).

84 While the vast majority of research on crop response to salinity has been conducted under
85 homogenous saline conditions, root-zones of plants in both natural and managed
86 environments can commonly experience spatial and temporal heterogeneity in soil salinity
87 (Yakir and Yechieli, 1995; Bleby et al. 1996; Davidson et al. 1996; Silvestri et al. 2005; Xing
88 et al. 2019; Zhang et al. 2021). The nature of soils and irrigation practice, crop type and
89 phenology, climate-type and seasonal weather, and the duration of crop exposure, all together
90 determine the extent and impact of salinity and its heterogeneity on plant growth and crop
91 productivity (Bazihizina et al., 2012a; Northey et al., 2006; Bogunovic et al., 2017; Xing et

92 al., 2019; Xu et al., 2019). Despite this complexity, most experiments on the impacts of
93 salinity on plants have imposed homogeneous root-zone salinity, which does not represent
94 saline agricultural settings. The extent of the temporal heterogeneity in soil salinity in the
95 field is illustrated within an irrigated wheat trial in China (Fig. 1A) and a rain-fed wheat trial
96 in Western Australia (Fig. 1B). These patterns of saline heterogeneity can be contrasted with
97 the near homogenous conditions commonly imposed in controlled-environment research
98 trials (Fig. 1C). Since complex multi-faceted traits (developmental, physiological,
99 anatomical, morphological and biochemical) are involved in plant tolerance of salinity, this
100 raises the question of whether trials conducted under near uniform soil (or root-zone) salinity
101 are indeed optimal for identifying and selecting traits of most value to increasing plant
102 tolerance to the common reality of heterogeneous salinity.

103 The generic guidelines used to predict crop response to soil and water salinity, produced
104 under near homogeneous conditions, are generally described by crop yield curves that consist
105 of a threshold value at which salinity induced damage first occurs, and a linear % yield
106 reduction with every increment in the electrical conductivity of the saturated soil extracts
107 (EC_e) thereafter (Maas and Hoffman, 1977; Maas and Grattan, 1999). Such static diagnostic
108 criteria do not reflect soil salinity under realistic field conditions that are highly spatially and
109 temporally heterogeneous (Chen et al., 2019). Thus, the prevailing standard of describing
110 plant response to salinity is both inadequate and generally overestimates crop response (Tanji
111 et al., 2002), is not relevant nor easily interpreted under field reality and may not adequately
112 inform irrigation practice, crop selection or salinity mitigation strategies (Ayars, 2021). In the
113 following, we summarise the pattern of occurrence of salinity heterogeneity in rain-fed and
114 irrigated systems, and discuss results from studies of plant responses to heterogeneous root-
115 zone salinity. We then discuss the mechanistic understanding of root physiological and
116 morphological adaptations to heterogeneous conditions, and place these findings in the
117 context of defining future research priorities and possible management and crop breeding
118 opportunities to improve productivity in saline lands.

119

120 **SOIL SALINITY HETEROGENEITY**

121 In naturally saline environments, within the rooting zone of a single plant, non-saline patches
122 can coexist with nearby saline ones, ranging from few mM to several times seawater

123 (Bazihizina et al., 2012a). The magnitude of this heterogeneity varies in time and space
124 depending upon soil parent material, landscape position (Aldabaa et al., 2015), soil physical
125 and chemical characteristics (e.g., texture, sodicity and alkalinity, Hillel, 1980; Robbins et al.,
126 1980), surface runoff and subsurface lateral flow of water, intrusion by saline groundwaters
127 or seawater (Tiggeloven et al., 2020; Choukr-Allah, 2021), and root water extraction
128 (Heuperman, 1995; Barrett-Lennard and Malcolm, 2000; Alharby et al., 2014; Alharby et al.,
129 2018). Climatic conditions also affect temporal and spatial heterogeneity of soil salinity, with
130 rainfall leading to soil leaching events while droughts and heatwaves concentrate solutes
131 depending on soil features and topography, and differences in radiation and resulting
132 evaporation due to aspect and slope (Schwantes et al., 2018).

133 Irrigation also dramatically influences soil salinity (Fig. 2, 3). Irrigation induced
134 heterogeneity can commonly result in differences in soil EC_e greater than 10 fold (Bernstein
135 et al., 1955; Bernstein and Fireman, 1957; Bernstein, 1975). Extremely heterogeneous
136 distribution of salinity in irrigated systems makes it difficult to design a soil sampling regime
137 to determine the truly effective root-zone salinity (Bernstein et al., 1955). This effect is
138 highly relevant to modern drip and micro-irrigated agriculture (see Box 1 for term definition)
139 in arid regions (Fig. 2), which are the most common irrigation strategies in many areas of the
140 world. While micro-irrigation is generally considered a valuable way to improve water use
141 efficiency and allows controlled fertigation strategies, these systems may complicate salinity
142 management, generating highly non-uniform salt and disparate nutrient deposition patterns
143 below the irrigation emitter (Bar-Yosef, 1999). These salt/nutrient deposition patterns below
144 the micro-irrigation emitter directly impacts root growth, root activity, nutrient and salt
145 movement in the soil within the root zone, with effects strongly determined by crop
146 placement, soil preparation, irrigation design and management.

147 Bar-Yosef (1999) further discussed the risk of salt accumulation in the root-zone under drip
148 irrigation, suggesting that salts are not efficiently displaced to the periphery of the wetted soil
149 volume as might occur under a full surface irrigation system. Under drip irrigation, salts can
150 accumulate in the wetting front after several irrigation cycles but this wetting front will shrink
151 and swell with subsequent irrigation events and root water consumption. Varying the
152 frequency and volumes of irrigation events can manipulate this salt displacement and
153 represents a management strategy. Salts can also accumulate at the upper margin of the
154 wetted soil volume (close to the soil surface) due to capillarity driven by soil evaporation.

155 This effect is particularly marked with buried drip irrigation systems where the depth of
156 irrigation tubes, shape of the furrow, plant and environmental water use patterns (Fig. 3)
157 influence the ultimate salt distribution.

158 Based upon current understanding, irrigation system placement and operation could
159 theoretically be managed to ensure that the deposition of salinity is largely restricted to the
160 outer margins of the wetted root-zone, thereby providing a zone of lower inner salinity with
161 abundant plant root activity. Better understanding of soil processes and plant responses under
162 heterogeneous conditions may therefore allow us to mitigate the adverse effects of salinity
163 (Lycoskoufis et al., 2005). Although very few field experiments have tested this theory that
164 drip irrigation can be optimised to minimise impacts of salinity, several studies of split-root
165 plants showed greater plant growth under heterogeneous salinities than uniform salinity, at
166 the same average root-zone salinity (Sonneveld and Voogt, 1990; Zekri and Parsons, 1990;
167 Flores et al., 2002; Mulholland et al., 2002; Tabatabaei et al., 2004; Attia et al., 2009; Kong
168 et al., 2012; Sun et al., 2016; Zhang et al., 2020). This encourages us that further developing
169 these irrigation strategies should be fruitful. Understanding the nature of plant response to
170 heterogeneous salinity is therefore essential to develop and implement improved irrigation
171 practices for saline systems. In particular, this opens an excellent opportunity to improve
172 production by manipulating the heterogeneity in the salinity of the soil solution, thereby
173 harnessing the abilities of plants to make optimum use of less-saline patches within root-
174 zones.

175

176 **ROOT RESPONSES TO HETEROGENEOUS SOILS**

177 In naturally occurring and agriculturally induced salinity, plant growth is affected by the
178 salinity of the soil solution or the ratio of salt (of which the EC_e or $EC_{1.5}$ are measures) and
179 the water content of the soil. Soil salinities vary on spatial scales of microns to meters, and on
180 temporal scales ranging from seconds to seasonal changes (Bazihizina et al., 2012a; Rellán-
181 Álvarez et al., 2016; Dinnyeny, 2019). Thus, roots of a single plant will be exposed to a range
182 of soil water salinity levels that vary temporally and spatially, with differential effects
183 depending upon the stage of plant growth. Nevertheless, while heterogeneous salinities
184 typically occur in salt-affected soils, experiments have almost exclusively imposed
185 homogeneous salinity or highly manipulated experimental conditions such as split-root

186 systems, which expose a portion of a root system to salinity while the remainder receives
187 non-saline conditions. Although split-root experiments may not adequately mimic a complex
188 field condition, these have provided valuable insights by demonstrating how plant responses
189 to heterogeneous conditions differ markedly from those of homogeneous saline conditions.

190 Split-root experiments indicate a more nuanced plant response to saline environments than
191 commonly recognised. As summarised in Bazihizina et al. (2012a), key features of plants
192 exposed to heterogeneous salinities are: (1) shoot water potentials are determined by the
193 salinity level of the low-salinity zone; (2) water uptake occurs predominantly from the low-
194 salinity medium; and (3) greater maintenance of shoot growth even when a large proportion
195 of the root system is exposed to high NaCl concentrations that would greatly inhibit growth if
196 applied uniformly to the roots. Transcriptome profiling of plants exposed for 6-9 h to
197 heterogeneous salinities indicated that improved performance under heterogeneous conditions
198 compared to uniform salinities is related to the rapid activation of salt resistance genes and a
199 crosstalk between the non-saline and high-saline root sides (Kong et al., 2016; Xiong et al.,
200 2018; Zhang et al., 2020). This suggests that roots operate as the central hub that control: (i)
201 how stress is perceived; (ii) long-distance communication with the shoots; and (iii) the
202 integration of long-distance systemic signals with local root-based ones. Furthermore, salinity
203 heterogeneity is inevitably linked with temporal and spatial variation in the distribution and
204 biological availability of water, essential nutrients and soil pH (Li et al. 2011; Feng et al.
205 2018; Zhang et al. 2021), with the latter having a major impact on root membrane potential
206 thus affecting both plant ability to acquire essential nutrients and exclude toxic Na^+ and Cl^-
207 ions (Babourina et al. 2001; Zhang et al. 2018). Thus, responses at the root level also play a
208 critical role in: (iv) how plants compensate for water/nutrient deprivation and limit salt stress
209 by optimising root-foraging in the most favourable part of the soil. Understanding how roots
210 respond to heterogeneous salinities is therefore of utmost importance and is needed to
211 develop management strategies to optimise resource use and crop productivity in saline soils.
212 Different processes enable roots to integrate fluctuating soil conditions into appropriate
213 developmental and physiological responses that ultimately determine how efficiently
214 resources are captured. These are fundamentally controlled at variable spatial scales, from the
215 single cell to the entire organ.

216 **Salinity sensing**

217 Local patches of high salinity are sensed in individual cells, and then integrated into organ-
218 scale processes. After salinity increases, plants experience multiple constraints ranging from
219 reduced water availability, disturbance to cytosolic ion homeostasis, and dramatic increases
220 in ROS accumulation. The emerging picture suggests that more than one sensory mechanism
221 may operate in the same cell at the same time, with some common downstream signalling
222 pathway(s) (Shabala et al., 2015; Feng et al., 2018; Niu et al., 2018; Fichman and Mittler,
223 2020; Peck and Mittler, 2020; Fichman and Mittler, 2021).

224 Calcium and ROS signals are amongst the first signals commonly evoked upon biotic and
225 abiotic stressors. Ca^{2+} and ROS signals are established second messengers involved in most
226 (local) stress responses and increasing evidence suggests that these act in tandem, interacting
227 and amplifying each other during root salt sensing (Dodd et al., 2010; Choi et al., 2014;
228 Shabala et al., 2015; Evans et al., 2016; Niu et al., 2018; Pottosin and Zepeda-Jazo, 2018).
229 Several molecular components underlying Ca^{2+} and ROS signalling (including *MOCAI*,
230 *OSCAI*, and *RBOHs*) have been identified and are currently being considered as potential salt
231 sensors (Yuan et al., 2014; Jiang et al., 2019; Liu et al., 2020b). Interestingly, local salt stress
232 at the root apex triggers immediate cytosolic Ca^{2+} increases at the point of application;
233 leading to propagation of a *TPCI* ('two-pore channel 1') dependent Ca^{2+} wave to distal shoot
234 tissues, passing through cortical and endodermal cell layers (Choi et al., 2014). By combining
235 experimental analyses and mathematical modelling, Evans et al. (2016) also clearly linked the
236 $[\text{Ca}^{2+}]_{\text{cyt}}$ wave triggered by a localised salt application with systemic ROS waves. Additional
237 salt sensors (extensively reviewed in Shabala et al., 2015; Shabala et al., 2016; Byrt et al.,
238 2018; Rui and Dinneny, 2020; Gigli-Bisceglia et al., 2020) include: (i) cell walls, and in
239 particular the salt-induced alterations in cell wall integrity and composition that are sensed by
240 the receptor-like kinase, *FERONIA* (*FER*) (Feng et al., 2018); (ii) mechanosensory channels
241 and transporters (e.g. *OSCAI*, *MSLs*, *MCAs*) that sense the mechanical force exerted on the
242 plasma membrane due to the osmotic component of salinity and translate hydraulic cues into
243 chemical signals (Yuan et al., 2014; Yoshimura et al., 2021)); and (iii) Na^+ transport systems
244 and proteins with regulatory Na^+ binding sites (e.g., *MOCAI*, Jiang et al., 2019).

245 While it is becoming increasingly clear that plant cells sense and respond to salinity stress by
246 activating multiple sensing networks, much of our knowledge on root salt sensing and
247 signalling has utilised uniform conditions, with no such studies attempted for heterogeneous
248 salinities. Such experiments will generate valuable information on how salt sensing at the

249 single cell level is integrated into organ-scale processes, revealing how the signal propagates
250 and its effects on root system architecture, developmental trade-offs and root plasticity.

251 **Root foraging**

252 Scaling up to the whole root level, the root system is a highly dynamic physical network that
253 enables a plant to forage for resources and rapidly explore favourable soil patches. Under
254 spatially heterogeneous soil salinities, preferential root growth can occur in the least (or non)
255 saline compartment, compensating to different degrees for root growth inhibition in the saline
256 patches (Bazihizina et al., 2009; Bazihizina et al., 2012b; Feng et al., 2017; Sun et al., 2016;
257 Xiong et al., 2018; Table 1, Fig. 4). A split-root experiment that closely examined root
258 morphology under heterogeneous salinities revealed that compensatory root growth in the
259 non-saline areas was associated with increased lateral root growth, which doubled compared
260 to plants with both root halves in non-saline conditions (Feng et al., 2017). However, root
261 proliferation in the non-saline compartment does not always occur, with several studies
262 showing no differences, or even a decline, in root growth compared to measurements under
263 uniform non-saline conditions (see references in Table 1). This highlights the complexity of
264 interpreting how heterogeneous conditions alter root growth, because responses depend on
265 timescale, salt concentration, and species sensitivity to salinity.

266 To understand root foraging it will be necessary to determine whether heterogeneous
267 salinities (and the associated variability in water availability and nutrients distribution) affect
268 root anatomical features, in addition to any effects on root morphology. Section 3.3 considers
269 suberin deposition in root cell walls. Even when heterogeneous salinities do not alter root
270 architecture, it remains possible that traits that reduce the metabolic cost of soil exploration,
271 such as cortical cell enlargement and cortical senescence, could be beneficial. This has yet to
272 be tested. Nevertheless, these anatomical traits that reduce the metabolic cost of root soil
273 exploration are currently considered an advantage in water, nitrogen and O₂ limited soils as
274 these improve water and nutrient uptake per unit investment in roots (Colombi et al., 2021;
275 Lynch, 2018, 2019; Schneider and Lynch, 2020). This topic therefore merits greater research
276 efforts to identify key root traits that maximise soil resource capture under heterogeneous
277 salinity.

278 **Water uptake**

279 Irrespective of environmental heterogeneity within the root-zone, plant water uptake is
280 essential to maintain photosynthesis. Typically, water uptake from the non-saline side of the
281 root system significantly increases, which is not always accompanied by increased root
282 biomass (Fig. 4A). Roots can dynamically alter their water transport capacity to acclimate to
283 the ever-changing soil conditions and rapidly explore favourable soil patches. Under
284 heterogeneous salinity, preferential water uptake from the regions with the least negative
285 water potentials are mediated by changes in root hydraulic conductivity that occur within
286 hours of salt exposure (Kong et al., 2016). These are achieved through changes in the
287 abundance or activity of water channel proteins named aquaporins that facilitate water
288 diffusion across cell membranes (Maurel et al. 2008; Gambetta et al., 2017; Kong et al.,
289 2017; Maurel and Nacry, 2020). The activity of aquaporins is regulated at many levels,
290 including altered transcription levels, channel gating between an open/closed state by various
291 mechanisms including phosphorylation, pH, or Ca^{2+} , and changed cellular trafficking (Maurel
292 et al. 2008; Gambetta et al., 2017; Maurel and Nacry, 2020). Under heterogeneous
293 conditions, increased water uptake from the non-saline roots has largely been attributed to
294 changes in aquaporin expression levels (Kong et al., 2017). After applying 200 mM NaCl to
295 one root half in split-root cotton seedlings (with 0 mM NaCl to the other half), gene
296 expression profiling revealed several aquaporin genes were up-regulated within 3 h in the
297 non-salinised root half, resulting in 16% higher root hydraulic conductivity when measured
298 against NaCl-free controls (Kong et al., 2017). By contrast, both root hydraulic conductivity
299 and most of the differentially expressed aquaporin genes were largely inhibited in the high-
300 salinity side (Kong et al., 2017).

301 The deposition of hydrophobic lignin and suberin in the cell walls of the exo- and endodermis
302 also alters root hydraulic conductivity and restricts the free diffusion of solutes and water,
303 including restricting entry of Na^+ and Cl^- from the soil into the vascular stream with high
304 root-zone salinity (Krishnamurthy et al., 2011; Barberon et al., 2016; Cui et al., 2019; Wang
305 et al., 2019). Accordingly, dynamic regulation of root hydraulic conductivity under
306 heterogeneous salinities was also associated with altered expression of genes associated with
307 cutin, suberin and wax biosynthesis in the salinised root portions (Xiong et al., 2020). This
308 could potentially explain decreased endodermal and exodermal permeabilities, that limit
309 water and solute transport from the highly saline areas.

310 The ability of plant to acquire and transport water from the roots to the leaves also depends
311 on root anatomy and architecture, and the combined hydraulic conductivities among root
312 types and along the root length (Meunier et al., 2017; Ahmed et al., 2018). Thus, over the
313 longer term (days), increases in new root growth and altered root architecture (i.e. root
314 proliferation and increased lateral root formation) and anatomy may have a more significant
315 effect than localised changes in root hydraulic conductivity at the single root level.
316 Nevertheless, our understanding of the timescale and concentration dependent drivers of the
317 long- and short-term responses of roots to localised salinity are inadequate. As highlighted in
318 the following sections and above, responses are expected to become increasingly complex
319 when heterogeneous salinity interacts with other environmental factors, such as
320 heterogeneous nutrients as discussed below, and their impacts on plant nutrient and water
321 acquisition.

322 **Phytohormone root-shoot communication**

323 Heterogeneous salinity can induce variable degrees of stomatal closure, with stomatal
324 conductance similar to uniform salinity in some studies (Lycoskoufis et al., 2005, Fig. 5).
325 However, most split-root studies indicate greater plant water use under heterogeneous than
326 uniform salinity, at the same average root-zone salinity. This is mostly because plant water
327 uptake from the non-salinised part of the root system substantially increases, even exceeding
328 water uptake from roots of non-salinised plants (see section 3.3). Long-distance signalling *in*
329 *planta* is implicated in regulating these plant water relations under heterogeneous salinity by
330 modulating root hydraulic conductivity and stomatal conductance.

331 Although leaf water status is regarded as an important regulator of stomatal responses
332 (Christmann et al., 2007), it is generally determined by the non-salinised part of the root-zone
333 under heterogeneous salinities (Bazihizina et al., 2009, 2012a,b; Feng et al., 2021).
334 Considerable stomatal closure of these plants (Fig. 5) suggests non-hydraulic mechanisms of
335 stomatal closure. Homogeneous salinity induced multiple phytohormonal changes in salinised
336 roots, according to the duration of exposure, with phytohormones such as ABA, auxin and
337 cytokinins (Albacete et al., 2008), and their crosstalk, mediating the balance between growth
338 and salinity stress responses (Yu et al., 2020). The same applies to heterogeneous salinities.
339 In cotton grown with heterogeneous salinity (0/200 mM NaCl), 200 mM NaCl induced only
340 transient (within 3-12 h of treatment) increases in root ABA concentration. Root ABA levels
341 were similar to controls after 24 h, presumably as sustained up-regulation of ABA catabolism

342 (*CYP707A*) genes influenced root ABA concentrations more than concurrent up-regulation of
343 ABA biosynthesis (*NCED*) genes (Kong et al., 2016). Paradoxically, root ABA
344 concentrations of the non-salinised roots exceeded those of salinised roots throughout the
345 experiment, despite a limited and transient (3-6 h) up-regulation of (*NCED*) genes, implying
346 considerable ABA transport into these non-salinised roots. Further studies need to elucidate
347 the source of this additional ABA, since the shoot can regulate root ABA concentration
348 (Manzi et al., 2015; McAdam et al., 2016) which in turn upregulates root hydraulic
349 conductance (Thompson et al., 2007).

350 Heterogeneous salinity also altered the concentrations of other phytohormones in the non-
351 salinised portion of split-root cotton plants: with IAA, iPA and ZR concentrations increasing
352 compared to their concentrations in plants that were not exposed to salinity (Kong et al.,
353 2016). In this case, increased root cytokinin concentrations correlated with increased
354 expression of *IPT* genes, which were maximal 3 hours after salinising the other part of the
355 root system. Measuring root water potential in a transpiring plant (Adeoye and Rawlins,
356 1981) may help determine whether this was a transient response to altered root water
357 relations in the non-salinised roots. Such measurements (along with root gene expression) are
358 required in girdled and non-girdled plants (since girdling at the root-shoot junction blocks
359 phloem transport to the roots) to determine whether local root water relations and/or a
360 cumulative message from other parts of the plant regulates gene expression. Under
361 heterogeneous salinity, Na⁺ accumulation in the non-salinised portion of the root system
362 doubled compared to roots from non-salinised controls. Such Na⁺ accumulation depended on
363 phloem transport from the salinised roots, as girdling prevented Na⁺ transport to these roots
364 (Kong et al., 2012). Whether girdling eliminates changes in root phytohormone concentration
365 in non-salinised roots, when the other part of the root system is exposed to salinity, needs to
366 be addressed.

367 Irrespective of whether changes in root phytohormone concentration occur, it is uncertain
368 whether they actually affect shoot phytohormone concentrations and physiological responses,
369 since root-to-shoot signalling under heterogeneous soil conditions depends on relative sap
370 flow from different parts of the root system (Dodd et al., 2008). Under heterogeneous
371 salinity, changes in root phytohormone concentration in the salinised root system may have
372 little impact on shoot physiology since these roots contribute relatively little to total
373 transpirational flow (Kong et al., 2012). Interestingly, changes in root phytohormone

374 concentration in the non-salinised roots may have a greater influence on shoot physiology,
375 since these roots contribute most of the total water flux. Grafting techniques allow the
376 relative contribution of different parts of the root system to root phytohormone export to be
377 evaluated (Dodd et al., 2008), but to date this has only been attempted in plants exposed to
378 different soil moisture levels and such experiments should be applied to plants with
379 heterogeneous root-zone salinity.

380

381 **HETEROGENEOUS SALINITY AND NUTRIENT DISTRIBUTION: THE MISSING** 382 **LINK?**

383 In both natural and managed systems, a variable distribution of nutrients (and salinity) in
384 soils is inevitable. This is associated with differential ion mobility and solubility, localised
385 decomposition of organic matter, or applying soluble nutrients through a fertigation system.
386 Furthermore, considerable evidence suggests that nutrient ‘patches’ can influence root
387 foraging, lateral root formation and root hair formation. Thus, the mutual effects of salinity
388 and nutrient heterogeneity are relevant.

389

390 **Root physiological responses to nutrient heterogeneity in fertigated crops**

391 Though likely a common occurrence in drip irrigated crops, very few studies have
392 simultaneously varied both salinity and nutrient distribution. The following discussion first
393 considers experiments with only nutrient heterogeneity, before discussing the integration of
394 nutrients with salinity heterogeneity in Section 4.3.

395 In tomato, preferential nitrate (NO_3^-) uptake occurred from areas of the root-zone with higher
396 (1.6- to 3.3-fold greater, with 10 dS m^{-1} being the highest EC) electrical conductivity (or
397 more negative osmotic potential) generated by locally high nutrient concentrations
398 (Sonneveld and Voogt, 1990) suggesting a local response of roots exposed to high
399 concentration likely due to their enhanced NO_3^- uptake kinetics. Mathematical simulations of
400 nutrient uptake under heterogeneous conditions of NO_3^- and phosphate (PO_4^{3-}) using the
401 Barber-Cushman model found a greater impact of soil heterogeneity and root plasticity, with
402 NO_3^- uptake increasing 7-20 times under heterogeneous conditions (Jackson and Caldwell,

403 1996). Root proliferation and increased uptake kinetics from the enriched root-zones
404 accounted for up to 75% of NO_3^- supply of a plant and over 50% of PO_4^{3-} acquired from
405 enriched soil patches. Simulations demonstrated that plants lacking plasticity of root growth
406 or uptake always acquired less nutrient under heterogeneous NO_3^- and PO_4^{3-} distribution.

407 In a split-root solution culture experiment on *Lolium multiflorum*, less than 24 h after
408 depriving NO_3^- from half the root volume, net NO_3^- influx to roots in the nitrate-rich area
409 increased, with root growth increments observed only after 1 week (Lainé et al., 1998).
410 *Brassica napus* responded similarly (Lainé et al., 1995). This rapid variation in NO_3^- uptake
411 was strongly associated with altered root hydraulic conductivities, with a sudden increase in
412 NO_3^- concentration around the roots almost simultaneously increasing root hydraulic
413 conductivity and preferential water uptake from the nitrate-rich patch (Gorska et al., 2008).
414 Split-root experiments applying NO_3^- to a portion of the root system demonstrated a localised
415 and reversible response, with N starvation on one side of the root system leading to
416 compensatory and enhanced NO_3^- uptake in the other root portion (Tabata et al., 2014).

417 Heterogeneous NO_3^- distribution to split-root *Acer rubrum* and *Betula papyrifera* plants
418 demonstrated a species-dependent response, with two times more fine roots measured for *B.*
419 *papyrifera* in the high NO_3^- portion than *A. rubrum*, yet similar total NO_3^- uptake rate (Gloser
420 et al., 2008). Under heterogeneous conditions, *A. rubrum* had smaller leaves and N deficiency
421 symptoms in the shoot portion directly above the nutrient-deficient root portion, while *B.*
422 *papyrifera* had regular leaves with no visible deficiency symptoms. Vascular system
423 architecture may explain this differential response (Orians and Jones, 2001). In species with
424 sectorised vascular systems (e.g. *A. rubrum*), in which contiguous and largely exclusive
425 vascular traces occur from a specific root to a specific branch, N deficiencies occurring in
426 isolated parts of the canopy reflect the nutritional status of the specific root that feeds that
427 branch. In contrast, other species (*B. papyrifera*) have an integrated vascular system allowing
428 nutrient transfer from an individual root to the canopy as a whole, avoiding the consequences
429 of patchy nutritional deficiencies.

430

431 **Root morphological responses to nutrient heterogeneity**

432 In *Betula pendula*, dry matter allocation to roots can be modified in three different ways
433 when the availability of mineral nutrients is limited: a) increased root growth in N-, P- or S-

434 limited soils; b) decreased root growth when K^+ , Mg^{2+} , and Mn^{2+} were limited; c) no effect
435 on root growth when Ca^{2+} , Fe^{2+} and Zn^+ were limited (Ericsson, 1995). Root growth
436 plasticity in patchy soil enhances the ability of plants to fill the soil volume rich in nutrients
437 and was the most important trait influencing species success (Hodge, 2006; Rajaniemi, 2007).
438 The ability of a plant to ‘find’ the nutrient-rich patch is essential if
439 morphological/physiological root responses are to be expressed. For instance, while nutrient
440 (N) heterogeneity in *Lolium perenne* did not lead to preferential root growth in the nutrient
441 rich soil patches (suggesting the patch was not explored to any greater extent than the bulk
442 soil), there were overall increases in specific root length (length/biomass) and root elongation
443 throughout the entire soil profile compared to the uniform N treatment (Nakamura et al.,
444 2008). This suggests that the overall plant N deficiency induced root elongation and not the
445 patchiness *per se*. The differential response of roots to nutritional patchiness is likely a
446 consequence of complex nutrient-specific signal transduction pathways (López-Bucio et al.,
447 2003).

448

449 **Impacts of simultaneous salinity and nutrient heterogeneity**

450 To investigate the effects of heterogeneous root salinity and nutrient conditions, several split-
451 root tomato experiments were conducted (Fig. 6; Valenzuela et al., 2022). Water uptake from
452 the saline root-zone dramatically decreased within 8 hours of treatment (Fig. 6A, B) in
453 contrast to the non-saline root-zone, with a more pronounced effect when nutrients were
454 provided only to the non-salinised root-zone (Fig. 6A, B). This reduction in water uptake did
455 not correlate with decreased root growth (which was maintained during Days 1-3), with the
456 saline root-zone only showing significantly less root growth towards the end of the
457 experiment (Day 9). The rapidity and consistency of decreased water uptake by roots in the
458 saline zone, from treatment imposition through to Day 9, suggests a primary physiological
459 response (possibly due to reduced aquaporin activity) was followed by a morphological
460 response.

461 To further explore the role of heterogeneous nutrient provision on root activity, complete
462 nutrient solutions were selectively depleted of either N or K^+ in the non-saline root half while
463 the other root half received a saline, complete nutrient solution (Fig. 6C, D). These treatments
464 provoked a ‘two-phase-response’. Immediately upon treatment application, the saline

465 conditions given to one side of the roots dominated, immediately decreasing water uptake of
466 those roots. Subsequently, water uptake from the saline-treated, nutrient-supplied roots
467 proportionally increased, likely in response to the nutrient deficiency induced by the omission
468 of the nutrient on the non-saline side. This effect was marked when K^+ was only present in
469 the saline root half and slight in the case of N. The presence of K^+ in the nutrient solution was
470 the most important determinant of root activity even when coinciding with salinity, resulting
471 in a notably higher shoot tissue Na^+ and Cl^- concentration when the sole source of K^+ was to
472 the saline root volume (Valenzuela et al., 2022).

473 This experiment and others described herein suggests that interpreting root responses to
474 heterogeneous conditions depends markedly on context, time, salinity concentrations and
475 plant nutrient status:

- 476 • Immediate (within hours) reductions in water uptake in salt-exposed root-zones commonly
477 occur and are expected to be determined by the relative difference in salinity between root
478 parts. Subsequently, relative nutrient availability affects root activity, with responses to K^+
479 depletion perceived within days. In the longer term, ionic stress and changes in relative root
480 growth may further alter relative root activity in each root-zone.
- 481 • Plant responses to the relative distribution of nutrients in the root-zone likely also depend
482 on plant nutrient status and the absolute concentrations of nutrients and salinity present in
483 each root-zone. Thus, a K^+ replete plant, provided low levels of K^+ in the non-saline root-
484 zone, or the presence of extreme salinity (>100 mM) would likely diminish the dramatic
485 response seen here (Fig. 6).
- 486 • All split-root systems or otherwise manipulated heterogeneous root-zone experiments do
487 not reflect the complexity of natural ecosystems, where soil heterogeneity is likely
488 significantly more complex in space and time. However, certain agricultural conditions may
489 closely resemble split-root studies, such as in substrate hydroponic systems, raised bed
490 vegetable production and micro-irrigated arid zone crops.

491 While these simple split-root experimental approaches cannot explain all potential nutrient
492 interactions, they do illustrate the rapidity and plasticity of plant responses and the
493 importance of considering nutrients when studying heterogeneous salinity. Furthermore, this
494 raises several important questions on the signalling pathways underlying root system
495 architecture and functions under heterogeneous saline conditions: (i) what is the relative
496 importance of the signal(s) under heterogeneous saline conditions (salt ions vs nutrients vs

497 water vs hormones)?; (ii) how variation in salt tolerance affects this response (e.g.,
498 halophytes vs non-halophytes)?; (iii) how the local conditions (salinity vs nutrient vs water
499 availability) and whole plant status (e.g. shoot Na^+ , Cl^- and/or nutrient concentrations)
500 modulate the response? Interestingly nutrient availability alters the endodermal specific ABA
501 signalling in roots that modulates lateral root formation and root system architecture in
502 response to salinity stress (Duan et al., 2013). As demonstrated above, this suggests that the
503 ‘nutrient signal’ might eventually override, or at least affect, the ‘salinity signal’ in regulating
504 root growth and functions under heterogeneous conditions.

505 **IMPLICATIONS FOR CROP MANAGEMENT**

506 When considering crop responses to salinity, two parameters define salt tolerance: (a) the
507 threshold salinity that causes the initial significant reduction in the maximum expected yield;
508 and (b) the rate of yield decline as salinity increases beyond the threshold (i.e., slope, Maas
509 and Hoffman, 1977; Maas and Grattan, 1999). However, the important underlying
510 assumption of the threshold model by Maas and Hoffman (1977) is that steady state
511 conditions exist in the root-zone, with water content and salt concentration remaining
512 constant in time and space. Since these conditions rarely exist in crop root-zones in the field
513 (e.g., Fig. 1), conclusions from steady-state analyses can be questionable (Letey and Feng,
514 2007). This has critical repercussions when defining the salinity experienced by the roots
515 when identifying breeding targets and soil management practices.

516 **Re-defining soil salinity**

517 One valuable tool in categorising and quantifying genetic variation in salt tolerance has been
518 to define crop relative yield responses in terms of threshold salinities up to which yields are
519 unaffected and linear decreases in relative yield with increasing salinity thereafter (*c.f.* Maas
520 and Hoffman, 1977, and their successors). However, it is critical to recognise that these
521 relationships have generally always been presented in terms of variation in parameters like
522 EC_e (the electrical conductivity of the soil saturation extract) or more occasionally in terms of
523 variation in $\text{EC}_{1:5}$ (the electrical conductivity of a 1:5 soil:water slurry) that relate to the
524 salinity of the soil. However, it is not the salinity of the soil (a parameter that does not
525 account for variations in soil water content) that affects plant growth but the salinity of the
526 soil solution, and thus the ratio of salt to water in the soil. This means that the salinity stress
527 on a plant can be doubled by doubling the salt concentration in a soil or by halving the water

528 concentration of the soil. Furthermore, as soils become drier, plant growth becomes affected
529 by the increasingly negative matric potentials (Ψ_m values) that develop in soils because of the
530 adhesion of water by soil pores.

531 This view profoundly affects the whole idea of the heterogeneity of salinity stress in soils,
532 because heterogeneity arises because of variable: (a) leaching effects of irrigation or rainfall
533 on salt concentrations in soil; (b) hydrating effects of irrigation or rainfall on soil water
534 contents; (c) effects of surface soil evaporation increasing salt concentrations by capillarity
535 and decreasing water contents in the soil; and/or (d) water extraction rates of roots and the ion
536 uptake/exclusion capacity, which over time also influence ion and water abundances near the
537 roots.

538 One variable that captures variation in both salt and water concentrations in soil is solute
539 potential (Ψ_s ; units MPa). For soils salinised with NaCl, this can be calculated as:

$$540 \quad \Psi_s = -22.75 \times EC_{1.5}/W \quad \text{equation 1}$$

541 where the $EC_{1.5}$ of the bulk soil is in units of $dS\ m^{-1}$, and soil water content of the bulk soil
542 (W) has units of % dry mass.

543 Water potential of the soil (Ψ_{soil}) can be calculated (Slatyer, 1967) as:

$$544 \quad \Psi_{soil} = \Psi_m + \Psi_s \quad \text{equation 2}$$

545 Furthermore, a leaf's transpiration rate (E_t) can be related to its water potential (Ψ_{leaf}), the
546 water potential of the soil (Ψ_{soil}) and the resistance to flow (R) as follows (Nulsen and
547 Thurtell, 1980):

$$548 \quad E_t = (\Psi_{soil} - \Psi_{leaf})/R \quad \text{equation 3}$$

549 While theoretically sound, plants change these simple mathematical relationships. Firstly, salt
550 accumulates in the root-zone making Ψ_s more negative than can be calculated using the $EC_{1.5}$
551 and W measurements of the bulk soil. Passioura and Frere (1967) define the variable U as the
552 factor by which Ψ_s at the root surface is more negative than in the bulk soil. Experimental
553 approaches suggest that U can be around 2 in well hydrated soils (e.g. Sinha and Singh 1974,
554 1976), but modelling approaches suggest that U could increase to values around 10 as the soil
555 becomes drier (Passioura and Frere, 1967). Given this, equation 2 can be modified to:

556 $\Psi_{\text{soil}} = \Psi_m + U\Psi_s$ equation 4

557

558 Secondly, the resistance of water flow to the surface of the root increases as the soil pores
559 around the root become depleted of water (Stirzaker and Passioura, 1996). This increases the
560 variable R in equation 3.

561 Given this background, how should heterogeneity of salinity in the soil solution in the root-
562 zone be viewed? Unfortunately, very few of the critical experiments have been done under
563 uniform conditions in the root-zone, let alone variable ones. To our knowledge, no split-root
564 experiments have ever attempted to compare the effects of different (or even the same) Ψ_{soil}
565 values by manipulating the salt and water concentrations on each side of the root-zone of a
566 plant, even though the components of Ψ_{soil} (Ψ_m , Ψ_s and U) can all be determined
567 experimentally. Maintaining such treatments is technically challenging, requiring new
568 experimental protocols to be developed. In such experiments, there could be considerable
569 rewards by comparing plants of different salt tolerance.

570 **Opportunities to better manage irrigated agriculture**

571 All irrigation water introduces salts to the system (Hanson and Bendixen, 1995) and in
572 regions with high evapotranspiration and low rainfall, traditional salinity management
573 emphasises deliberate leaching of salts away from the root-zone while avoiding elevation of
574 the water table to prevent damage to crops (Hopmans et al., 2021). Leaching is usually
575 achieved by applying irrigation water in excess of crop evapo-transpirational demands. The
576 fraction of applied water that drains below the root-zone is referred to as the “leaching
577 fraction” and this value is used to coarsely gauge the extent of leaching (Hanson et al., 2009).
578 Larger leaching fractions generally result in larger zones with a low soil water salinity but
579 may necessitate disposal of large volumes of saline drainage water and may cause additional
580 salinisation through capillary rise of saline water by raising the water table (Corwin, 2021;
581 Grismer et al., 1988), as well as environmental impacts of drainage water disposal.

582 Designing the appropriate leaching fractions needed to avoid yield loss is context-specific
583 and will depend on the crop, soil texture, climate, irrigation system, irrigation schedule, and
584 the salinity of irrigation water being used (Assouline et al., 2015; Ayers and Westcot, 1985;
585 Hanson and Bendixen, 1995). Ayers and Westcot (1985) developed a simple approach to

586 calculate the leaching requirement based on salt mass balance calculations. This approach
587 estimates the leaching fraction required to keep the average root-zone salinity below the
588 salinity threshold of the crop assuming a specific root distribution and a strictly vertical,
589 continual water flow. Approaches like this neglect the spatial non-uniformity of irrigation
590 water application as well as the temporal dynamics of irrigation and water uptake during the
591 season (Letey et al., 2011) and assume that the average root-zone salinity determines the
592 impact of salinity on the crop (Letey and Feng, 2007).

593 While the physical principles underlying salinity management have not changed since Ayers
594 and Westcott developed these leaching guidelines, management goals have shifted over time
595 to better recognise environmental impacts of nutrient and salinity losses and develop more
596 advanced micro-irrigation and fertigation systems. This has given rise to both new challenges
597 and new opportunities in managing salinity.

598 *Challenge 1: Managing salinity under micro-irrigation systems*

599 Spatial patterns of salt accumulation are diverse and differ by irrigation system (Riaz et al.,
600 2018; Wallender and Tanji, 2011), with each irrigation system having specific challenges to
601 salinity management. In the simplest case, flood irrigation applies water uniformly across the
602 whole surface (although local topography and soil heterogeneity can cause spatially
603 heterogeneous infiltration). In this case, salinity distribution is approximately uniform in
604 horizontal direction, but a salinity gradient exists vertically (Fig. 2, 3). Assuming sufficient
605 leaching, salinity increases with depth in these systems (Ayers and Westcot, 1985) and
606 uniform leaching of salts below the root-zone causes the salinity within the root-zone to be
607 relatively homogeneous.

608 In contrast, applying water to only part of the surface causes strong horizontal salinity
609 heterogeneity, as in furrow irrigation and more advanced micro-irrigation systems. Micro-
610 irrigation aims to target water application to the root-zone, thereby improving water use
611 efficiency by applying less water to regions with low root density and providing an
612 opportunity to deliver water at a rate which matches crop demand. Flood and overhead
613 sprinkler irrigation manage soil moisture and salt content at the field-scale, while micro-
614 irrigation approaches management at the root-zone scale. Targeted water application results
615 in targeted leaching with micro-irrigation leaching salts in zones which are rich with plant
616 roots, while flood irrigation requires additional water to also leach salts from field zones
617 between plants with low root density, making micro-irrigation more efficient than

618 furrow/sprinkler irrigation for managing salinity (Hanson et al., 2009). When drip and furrow
619 irrigation were compared, drip irrigation sustained higher yields of salt sensitive crops
620 compared to furrow irrigation when saline groundwater is shallow, while using less water
621 than furrow irrigation (Hanson et al., 2009).

622 The economic incentive to install micro-irrigation systems is context-dependent, with the
623 advantage of micro-irrigation over conventional irrigation becoming less clear when growing
624 salt-tolerant crops or when irrigation water is abundant. Despite its potential to accumulate
625 salts in the root-zone, even subsurface drip can have advantages over salinity management
626 with traditional irrigation. While higher tomato yields justified the expense of installing a
627 subsurface drip irrigation system in California, the same was not true of cotton which
628 remained lucrative with furrow irrigation (Hoffmann and Johnsson, 2000; Hanson et al.,
629 2009), as such salt-tolerant crops tend to tolerate flood irrigation without yield loss provided
630 that irrigation is applied pre-planting to avoid stand establishment losses (Ayars et al., 1993;
631 Hanson et al., 2009).

632

633 In drip irrigation systems with strongly localised water application, salt is not only leached
634 downwards, but significant lateral water movement away from the drip emitter also leaches
635 salt horizontally (Raine et al., 2007) resulting in salt accumulation in the fringes of the wetted
636 volume (Fig. 2A). This leads to a strongly heterogeneous small-scale salt distribution where
637 soil salinity levels in the top 20 cm can vary by a factor of more than five within only 40 cm
638 of horizontal distance (e.g., May and Hanson, 2006). Although the extent of horizontal salt
639 movement depends on the soil texture and can be partially controlled by emitter spacing,
640 under micro-irrigation, salts concentrated between emitters near the surface generally have
641 little opportunity to intrude into the root-zone without precipitation, due to surface
642 evaporation and irrigation (Hanson and Bendixen, 1995; Hanson and May, 2011). For this
643 reason, it is recommended that crops be arranged close to emitters where salinity is low and
644 that new lines be installed as close as possible to where old lines existed to avoid the need for
645 pre-season reclamation leaching (Hanson and May, 2011).

646 Sub-surface drip irrigation results in a different pattern of water flow and salinity
647 accumulation. While water application at the soil surface causes salts to leach downward and
648 outward from the water source, sub-surface irrigation causes resident and irrigated salts to
649 flow upward through advection and accumulate above the dripline where plants are present
650 (Hanson and Bendixen, 1995; Hopmans et al., 2021). This accumulation pattern antagonises

651 the establishment of many row crops as germination is relatively sensitive to salt stress
652 (Bernstein et al., 1955). Such production systems rely on pre-season rain, sprinkler, or surface
653 irrigation to leach salts below the drip line where they may be leached downward by
654 subsurface irrigation (Hanson and Bendixen, 1995). Shallow installation of subsurface drip
655 lines is advantageous where sufficient pre-season rains are present as irrigating the soil
656 surface may be avoided altogether (Hanson and Bendixen, 1995). This issue can be
657 mechanically managed in processing tomato by adding soil to planting beds (Hanson *et al.*,
658 1995), followed by irrigation to accumulate salts into the uppermost zone of the bed, which is
659 subsequently removed and placed in the furrow between rows, where very little horizontal
660 salt movement occurs (Hanson and Bendixen, 1995).

661 The strong localisation of water application in drip irrigation questions the applicability of
662 historical steady-state leaching models to micro-irrigation systems (Letey and Feng, 2007).
663 These models insufficiently account for the highly local nature of micro-irrigation and
664 underestimate both the local leaching fraction experienced by plants and the tolerable EC of
665 irrigation water (Wallender and Tanji, 2011). Adequate management of heterogeneous
666 salinity patterns and localised leaching under drip or micro-sprinkler may allow sustainable
667 crop production in soils that would otherwise be deemed too saline for that species. Using
668 transient models like the HYDRUS model has been suggested as an alternative (Letey et al.,
669 2011). These models account for localised application of water and changes in flow rates
670 over time by explicitly simulating two-dimensional (or even three-dimensional) water and
671 solute transport in the root-zone by numerically solving mechanistic models. However,
672 although these models are very strong in depicting physical transport processes, they often
673 oversimplify the description of plant physiological processes governing water and solute
674 uptake. For example, the HYDRUS model neglects that the distribution of water uptake is
675 also affected by nutrient concentrations. Moreover, even if it was possible to perfectly
676 simulate the water, nutrient, and salinity dynamics for a given scenario, it would still be
677 unclear how the calculated heterogeneous salinity distribution would translate into plant
678 performance. Incorporating current knowledge of plant responses to heterogeneous
679 conditions (both salinity and nutrient) might make these models more suitable for evaluating
680 salinity management practices.

681 *Challenge 2: How to simultaneously optimise N efficiency and minimise the impact of*
682 *salinity.*

683 The necessity of a leaching fraction for long-term salinity management is coupled with the
684 issue of nutrient loss, especially for nitrate (NO_3^-) which exhibits similar leaching potential as
685 Cl^- . Any practice designed to remove Na^+ or Cl^- from the root-zone likely also leaches NO_3^-
686 (Assouline et al., 2015; Libutti and Monteleone, 2017; Vaughan and Letey, 2015). Although
687 a common problem, few studies have addressed the integrated nature of salinity and nutrient
688 management (Libutti and Monteleone, 2017). While NO_3^- and Cl^- are subject to very similar
689 transport mechanisms and rates in the soil, their distribution in the soil can nevertheless be
690 quite different, and high Na^+ and Cl^- concentrations do not necessarily coincide with high
691 NO_3^- concentrations. This is because: (i) in contrast to Na^+ and Cl^- , NO_3^- is preferentially
692 taken up by plant roots; and (ii) nitrogen fertiliser is deliberately added to the irrigation water
693 during fertigation and is to some degree independent of water (and therefore salt) application.
694 Understanding crop nitrogen demands and responses to spatially localised nutrients and
695 salinity may help manage fertigation systems to achieve the simultaneous goal of salinity
696 leaching and minimal nitrate loss.

697 By providing nutrients through fertigation in a manner (rate, duration and timing during a
698 fertigation event) that retains nutrients in the low-salinity zone adjacent to the drip-emitter,
699 roots can avoid exploring the saline fringes of the wetted zones, thus reducing salt exposure.
700 HYDRUS-based modelling suggests that high frequency applications of small amounts of
701 nitrate, timed toward the end of a fertigation event, can help retain NO_3^- in the root-zone
702 adjacent to the irrigation source while allowing salt (i.e. Na^+ and Cl^-) to be leached to the
703 peripheral root-zone. Scheduling low but frequent NO_3^- applications, attuned to crop demand,
704 allows the crop to take up most of the NO_3^- before it passes through the low-salinity zone into
705 the saline fringes. Figure 7 simulates continuous NO_3^- application and a scenario which
706 applies NO_3^- only every 10 days, while the total amount of NO_3^- applied is the same for both
707 simulations. High frequency applications of NO_3^- using drip irrigation increased N uptake
708 efficiency in some cases (e.g. Scholberg et al., 2002; Quiñones et al., 2007).

709 **Breeding targets**

710 Challenging as they are, modern irrigation systems provide some leeway for controlling
711 water and nutrient supply, to match plant demands. Nevertheless, genetic approaches to
712 enhance salt tolerance are also needed.

713 *Avenue 1: Breeding for root traits that facilitate water and nutrient uptake*

714 Do specific root traits facilitate resource foraging (water and nutrients) under heterogeneous
715 soil salinities? With the current (or lack of) knowledge it is very difficult to address this
716 question. As advocated for other marginal environments (Colombi et al., 2021; Lynch, 2018,
717 2019; Schneider and Lynch, 2020), root architectural traits and anatomical plasticity that
718 reduce the metabolic cost of soil exploration might be beneficial in saline environments.
719 Since heterogeneous salt distribution is likely associated with non-uniform water and nutrient
720 distribution, careful consideration is necessary. For example, under saline conditions plants
721 modify their root system architecture to reduce salt uptake (Julkowska et al., 2014) by
722 reducing the length and density of root hairs and thus the overall absorption surface area
723 (Shabala et al., 2003). However, marginal soils can also be highly deficient in phosphorus
724 (P), and root hairs would be critical to allow root exploration beyond the root depletion zones
725 and acquire P (and also other nutrients and water) from impoverished soil (Lynch, 2018,
726 2019, Rongsawat et al., 2021). Our ability to understand how plants could resolve such
727 dilemma, and identify which root traits might more favourable under heterogeneous
728 salinities, is hindered by the simplicity of the experimental systems employed to date.

729 *Avenue 2: Breeding for tissue tolerance*

730 Traditionally, crop breeding for salinity tolerance has targeted Na⁺ exclusion traits (Munns
731 (Genc et al., 2010; Munns et al., 2012; Wu et al., 2019). This strategy comes with a caveat of
732 a progressive build-up of Na⁺ in a root-zone (Liu et al., 2020a), thus further exacerbating
733 heterogeneity of Na⁺ distribution profiles in the rhizosphere and affecting water uptake and
734 ultimately growth (Alharby et al., 2014, 2018). Furthermore, this strategy requires a heavy
735 reliance on energetically expensive *de novo* synthesis of compatible solutes for osmotic
736 adjustment (Munns et al., 2020). A viable alternative may be to target crop halophytism, e.g.
737 a set of anatomical and physiological traits that allow plants to include significant amounts of
738 Na⁺ in their tissues, without compromising their metabolic activity (Flowers and Colmer,
739 2015; Munns et al., 2016). Amongst key traits conferring crop halophytism, vacuolar Na⁺
740 sequestration, ROS desensitisation, tissue succulence, and salt deposition in trichomes are
741 considered as promising targets in breeding programs (Liu et al., 2020a).

742 *Avenue 3: Understanding the nature of root to shoot signals*

743 Plant biomass is ultimately proportional to the amount of CO₂ assimilated by the shoot that,
744 in turn, is determined by the efficiency of stomata in balancing CO₂ gain and water loss via

745 leaf transpiration. Root-borne signals play a critical role in coordinating plant gas exchange
746 and optimising plant water use efficiency. The signalling between roots and shoots integrates
747 various signals (from electrical and hydraulic signals, Ca^{2+} and ROS waves to hormones,
748 peptides and RNA; Gilroy et al., 2016; Shabala et al., 2016; Li et al., 2021) that ultimately
749 determine plant's ability to adapt to saline conditions. Stress-induced elevations in ROS
750 levels is accelerated in halophytes compared to glycophytes (Ellouzi et al., 2011), and
751 NADPH oxidase-mediated root-borne ROS signals induce early stomatal closure in salt-
752 tolerant species (Niu et al., 2018). Although shoot ABA levels increase within 30 min of
753 salinity exposure, the magnitude of this increase appears to be species specific (Geilfus et al.,
754 2015; Hedrich and Shabala, 2018). While xylem sap ABA concentrations also increase
755 (Albacete et al., 2008), grafting experiments with ABA-deficient mutants indicate this is
756 shoot-mediated (Li et al., 2018). Nevertheless, grafting wild-type tomato scions onto an ABA
757 overproducing rootstock enhanced salt tolerance, even if it was difficult to establish
758 consistent evidence of root-to-shoot ABA signalling (Martínez-Andújar et al., 2021). As
759 discussed above, it remains uncertain how plants exposed to heterogeneous salinity integrate
760 signals from exposed and non-exposed roots to regulate stomatal aperture. Since a multitude
761 of signals interact during root-to-shoot communication, it is critical to understand how they
762 confer plant stress tolerance.

763 *Avenue 4: Understanding how water and ion transport are coupled*

764 Another emerging topic is a possibility of water and ion flow coupling by aquaporins.
765 Initially described as water and neutral solute channels, aquaporins can also transport ions
766 across various cellular membranes (Byrt et al., 2017; Qiu et al., 2020). This discovery
767 challenges current concepts that water and solutes move across membranes via separate
768 pathways and may account for situations where water movement into the xylem goes against
769 an apparent water potential gradient (Tyerman et al., 2021; Wegner, 2017). Such coupling
770 may be especially crucial for roots exposed to heterogeneous salinity as transcriptional
771 changes are likely too slow to account for the highly dynamic external ionic environment. In
772 this context, a phosphorylation-dependent switch between ion and water permeation in
773 aquaporins (and, specifically, *PIP2;1*) might enable plant cells to rapidly adjust to altered
774 ionic conditions in the rhizosphere and optimise ion transport at minimal energy cost. This
775 option implies that plants that rely on Na^+ accumulation for osmotic adjustment and thus

776 water uptake under hypersaline soil conditions can tolerate tissue Na⁺ loads thereby avoiding
777 cytotoxicity, requiring that halophytic traits be incorporated into modern elite varieties.

778 **CONCLUDING REMARKS**

779 There are several constraints in conducting experiments or genotypic selection of plants
780 under conditions that do not reflect real agricultural conditions of heterogeneous soil
781 environments. Homogeneous conditions limit more complex interactions between salinity
782 prevalence and plant responses such as exclusion of saline ions, nutrient and water uptake,
783 root architecture, or adjustment to varying pH within the root-zone. As highlighted above,
784 fundamental questions remain on plant responses to heterogeneous salinities and how this is
785 affected by the associated variations in water and nutrient distribution. We call for a greater
786 focus on understanding plant responses to heterogeneous soil salinity, which should be
787 considered as the next frontier for salinity research and land management. Understanding
788 responses to heterogeneous saline conditions holds significant promise for identifying new
789 breeding targets for crop salt tolerance and adequate management practices of saline
790 environments, which will accelerate the implementation of solutions to improve the
791 productive use of saline land.

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Table 1. Root distribution in different species under horizontally heterogeneous salinities as % of dry mass in control plants with low or no-salt media.

Species	Salinity (mM NaCl)	Duration	Root biomass (% control)		Ratio L:H	Reference
			L	H		
<i>Atriplex nummularia</i>	10/500	3 weeks	88	87	1.0	Bazhizina et al., 2012b
<i>Atriplex nummularia</i>	10/1500	3 weeks	153	32	4.8	Bazhizina et al., 2012b
<i>Hibiscus moscheutos</i>	0/200	2 months	72	57	1.3	Feng et al., 2021
<i>Hibiscus moscheutos</i>	0/200	2 months	79	20	4.0	Feng et al., 2021
<i>Medicago sativa</i>	0/200	15 days	140	56	2.5	Xiong et al., 2018
<i>Medicago sativa</i>	50/200	15 days	131	61	2.1	Xiong et al., 2018
<i>Medicago sativa</i>	0/75	9 days	99	90	1.1	Sun et al., 2016
<i>Medicago sativa</i>	0/150	9 days	113	82	1.4	Sun et al., 2016
<i>Medicago sativa</i>	0/225	9 days	118	56	2.1	Sun et al., 2016
<i>Medicago sativa</i>	75/150	9 days	82	60	1.4	Sun et al., 2016
<i>Medicago sativa</i>	75/250	9 days	72	55	1.3	Sun et al., 2016
<i>Sorghum bicolor</i>	0/200	2 weeks	100	49	2.0	Zhang et al., 2020

Box 1: Irrigation system terminology

	Term explanation
Surface Irrigation	<p>All formats of irrigation which rely on gravity (rather than pressurised conveyance systems) to distribute water across a field. Examples include flood and furrow irrigation. It is important to note that while these systems are collectively referred to as surface irrigation, they are not the only irrigation systems which apply water to the soil surface; overhead sprinkler, micro-sprinkler, and surface drip also irrigate the soil surface but are not generally categorised as traditional “surface irrigation.”</p>
Micro-irrigation	<p>Drip</p> <p>Highly local, small volumes of water emanating from points along a pressurised plastic pipe (“drip line”) which is installed either on the soil surface (surface drip) or buried beneath the crop (“subsurface drip”/“subirrigation”) with very little loss to evaporation.</p> <p>Micro-sprinkler</p> <p>Any small, stationary sprinklers which are installed near the soil’s surface and irrigate the soil’s surface without applying water to the canopy. Micro-sprinkler irrigation is more targeted than overhead sprinkler irrigation, particularly with orchard crops which are widely spaced and have high canopies which can lose large fractions of overhead irrigated water to evaporation.</p>

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FIGURE LEGENDS

Figure 1. Temporal variations in soil salinity measured in irrigated and rainfed wheat in saline land compared with the typical experimental setup used to assess salt tolerance. In (A) The crop was irrigated with water diverted from the Yellow River that had an average electrical conductivity of 0.75 dS m^{-1} . Crops were planted in a field with shallow saline groundwater. The electrical conductivity (EC) and depth of the groundwater varied from 0.5 to 3 dS m^{-1} and 80 to 200 cm , respectively. Irrigation events are indicated with black arrow. Red arrows indicate the crop harvest (date of crop harvest is assumed based on the maturation days generally required for spring wheat). Data modified from Xu et al. (2013). In (B) field trials to evaluate the salinity tolerance of wheat accessions under rain fed conditions were conducted on saline sites in Western Australia. Data modified from Setter et al. (2016). (C) Diagram showing a typical experimental protocol used to assess salt tolerance in irrigated sand culture in pots, where the salinity of the soil solution is increased gradually to achieve the desired concentration, which then remains constant throughout the experimental period (Hussain et al., 2021). After an initial trial in hydroponics to evaluate salt tolerance at the seedlings stage, the protocol shown in (C) was used to screen the salt tolerance in different wheat germplasm grown in sand irrigated with a saline Hoagland solution. Depending on the irrigation schedule (not indicated), it is to be expected that the salinity of the soil solution would have varied depending on the evapo-transpiration and the decline water content in the pots.

Figure 2: Irrigation induced heterogeneity in root-zone salinity. (A) Typical salt accumulation patterns in surface soils for various methods of water application. Salinity ranges from low (unshaded) to high (darkened). Arrows indicate the direction of soil water flow. Reproduced with permission from Ayers and Westcot (1985). (B, C) Examples of sloping bed irrigation style and their impact on localised salt deposition around sloped furrow irrigation. Reproduced with permission from Zaman et al. (2018).

Figure 3: Depiction of salt accumulation patterns from subsurface irrigation in a lettuce crop in the Santa Maria Valley (California, USA). While a low EC zone is formed beneath the emitter, salts can accumulate above and require rain or other surface irrigation to percolate salts beneath the emitter for leaching. Soil types were a clay loam and a fine sand. Reproduced with permission from Hanson and Bendixen (1995).

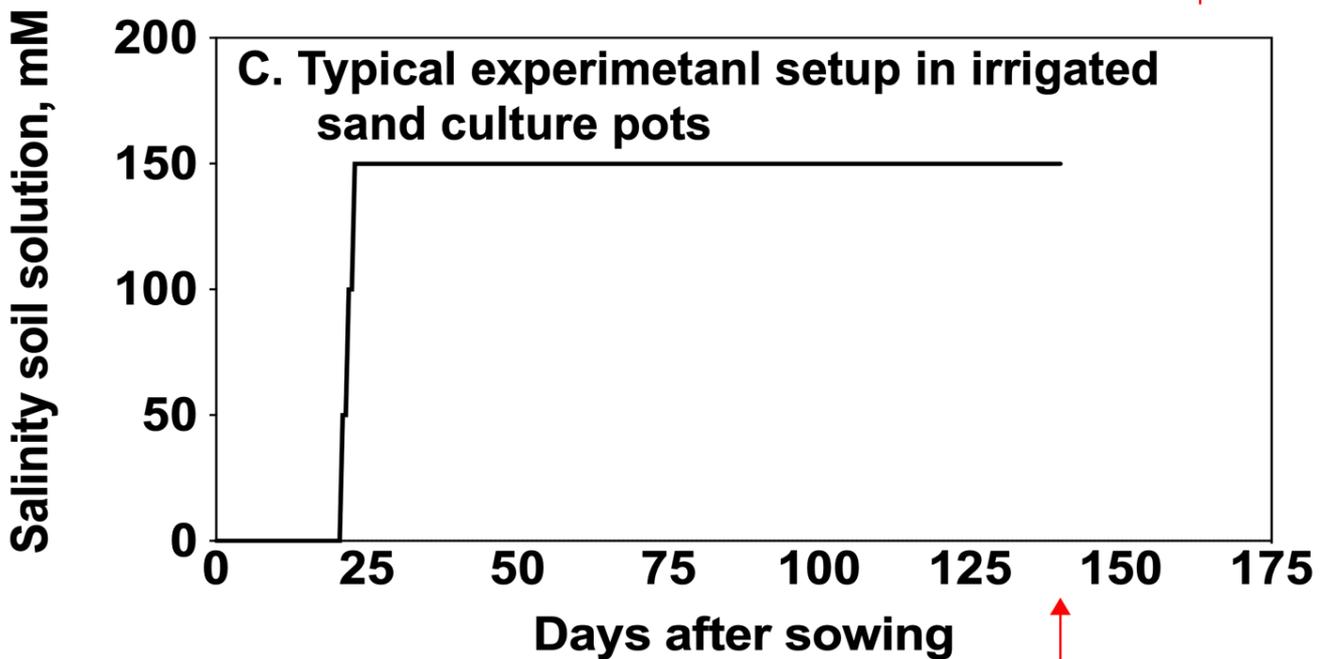
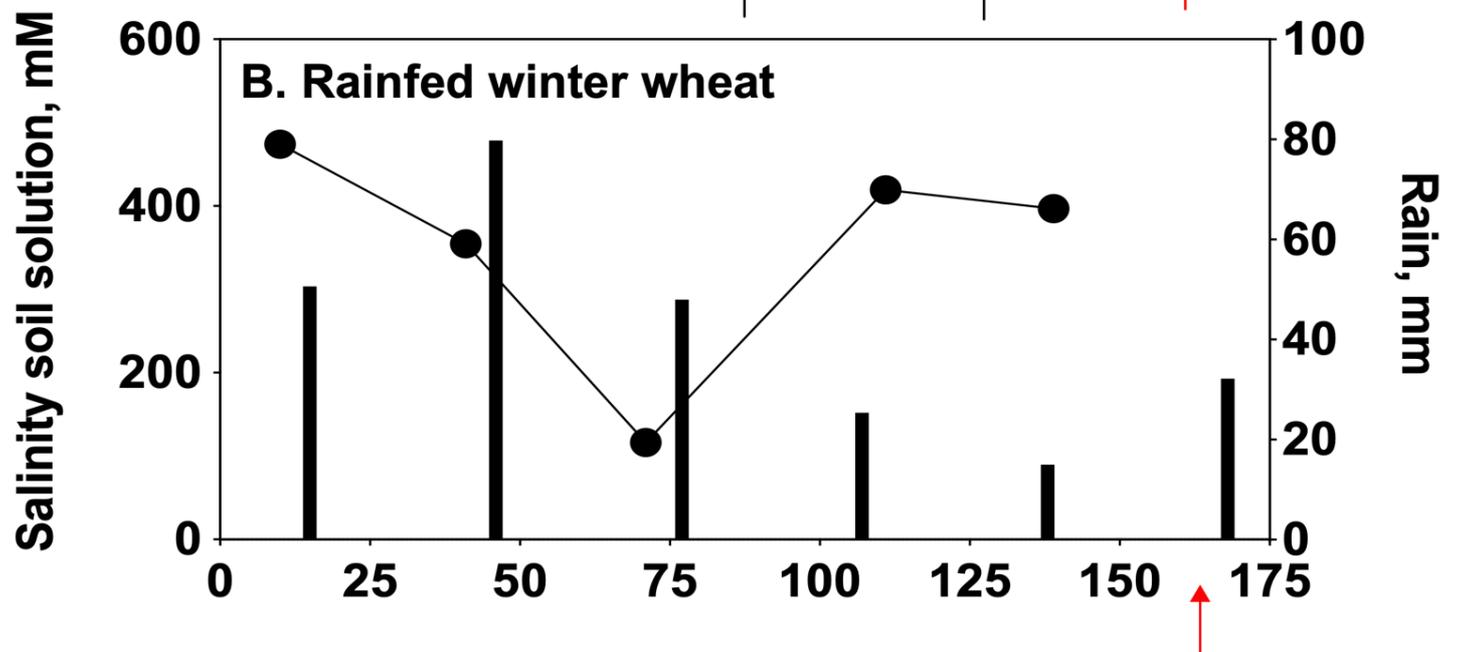
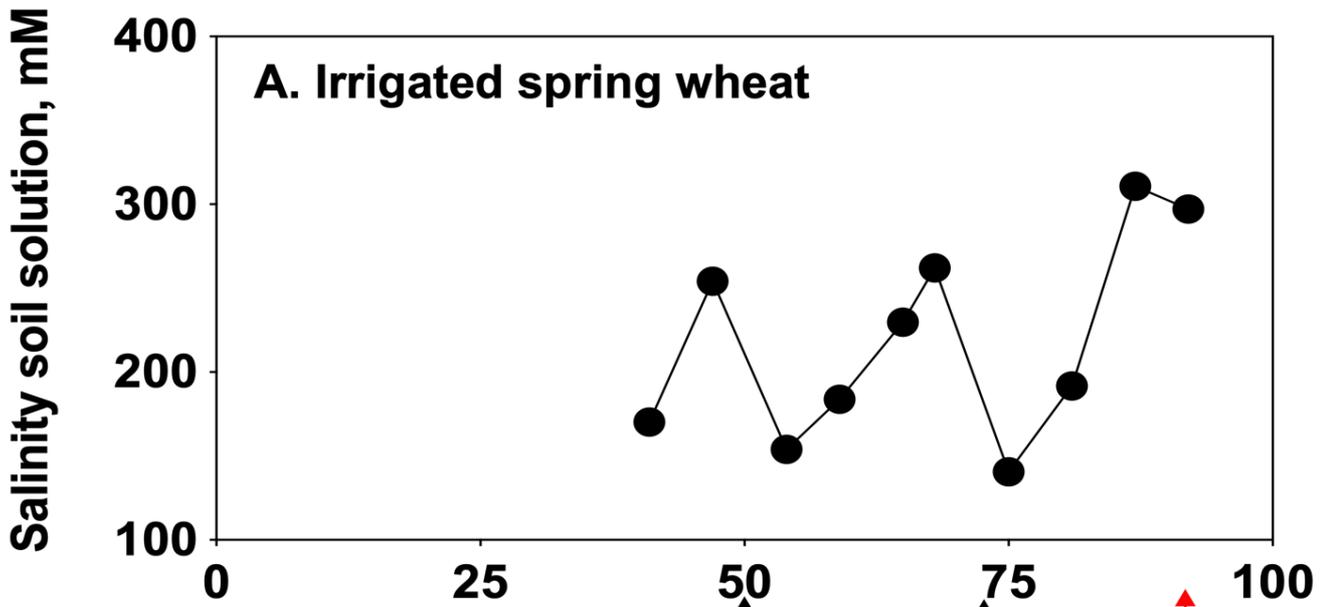
Figure 4. Taking advantage of the patch - Plants use the most accessible water source under spatially and temporally variable salinity. The datasets in (A) show water uptake and root growth in the non-halophytic almond rootstock “Nemaguard” (*Prunus persica* x *P. davidiana*) and the halophyte *Atriplex nummularia*, after 28 d and 21 d of heterogeneous salinity treatment respectively. The data shown for almond rootstock and *Atriplex nummularia* is modified from Valenzuela (2018) and Bazihizina et al. (2009), respectively. Values are mean (n=4) ± SE and different letters indicate a significant difference (P < 0.05) between treatments and root sides. The dataset in (B) shows temporal changes in soil water potentials and number of new roots in *Melaleuca halmaturorum* in response to fluctuating saline groundwater. The data shown in the upper two panels refer to soil water potentials and new roots observed at the end of summer, while those shown in the bottom two panels refer to soil water potentials and new roots at the end of winter. The red asterisks indicate location of main water uptake (based on the uptake of stable isotope data). The figure is modified from Mensforth and Walker (1996).

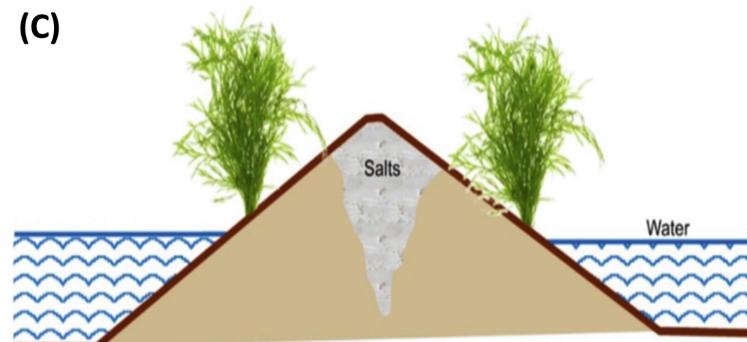
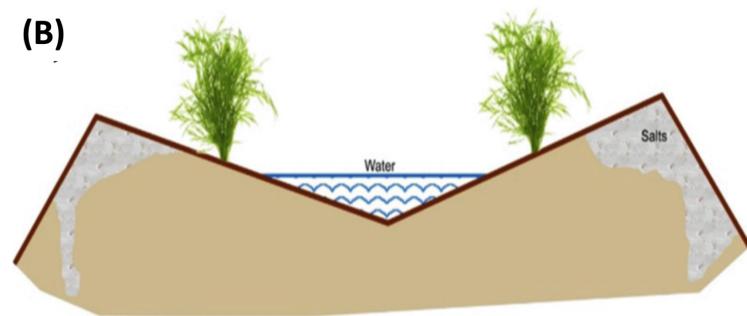
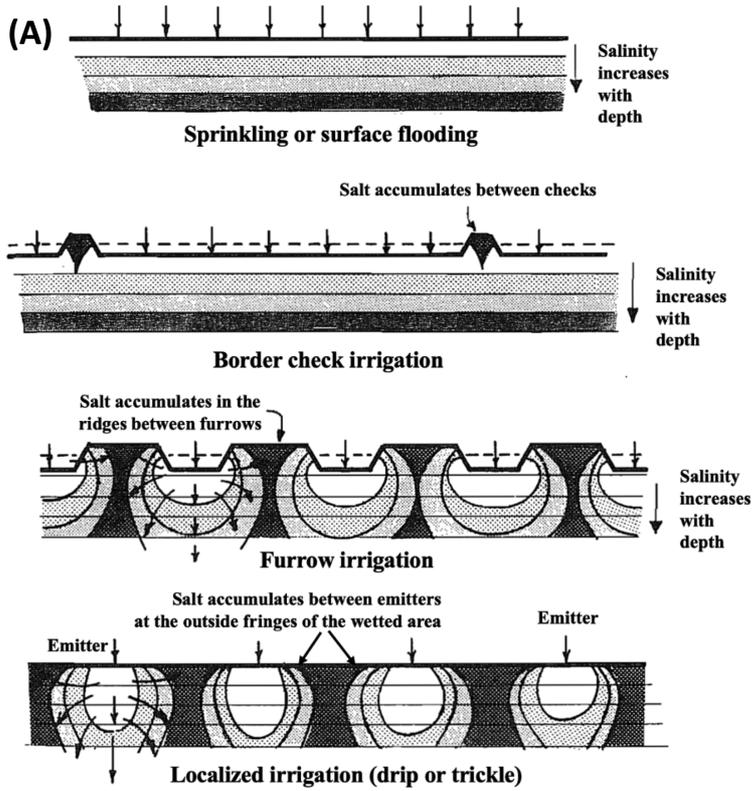
Figure 5. Stomatal conductance of salinised plants (expressed as a percentage of non-salinised controls) exposed to heterogeneous (hollow symbols) and homogeneous (filled symbols) salinity at the same average root-zone salinity. Original papers were from: *Solanum lycopersicum* (Wang et al., 2021), with plants grown with uniform (0 and 50 mM NaCl) and heterogeneous salinity (17/85 mM NaCl); *Hibiscus moscheutos* (Feng et al., 2021), with plants grown with uniform (0 and 200 mM NaCl) and heterogeneous salinity (0/400 mM NaCl); *Sorghum bicolor* (Zhang et al., 2020), with plants grown with uniform (0 and 100 mM NaCl) and heterogeneous salinity (0/200 mM NaCl); *Lycium chinense* (Feng et al., 2017), with plants grown with uniform (0 and 170 mM NaCl) and heterogeneous salinity (0/340 mM NaCl); *Gossypium hirsutum* (Kong et al. 2012), with plants grown with uniform (0 and 100 mM NaCl) and heterogeneous salinity (0/200 mM NaCl); and *Atriplex nummularia* (Bazihizina et al., 2009), with plants grown with uniform (10 and 230 mM NaCl) and heterogeneous salinity (10/450 mM NaCl).

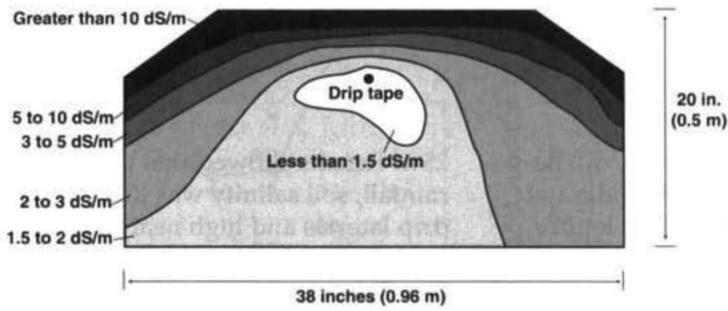
Figure 6: Daily measurement of the percentage of water consumption per root side in a split-root system under hydroponics. The vertical dashed line (- -) shows the time when salinity application was initiated. Dots (•) represent treatments applied to side A and triangles (◻) to side B. The saline agent was NaCl with a concentration of 50 mM. Bar graphs, at the right,

show the root biomass allocation for each treatment. In these experiments, tomato (*Lycopersicon esculentum*) seedlings were grown in a hydroponic split-root method for nine days under heterogeneous saline and nutritional conditions applied separately and in combination. Root activity was monitored by directly measuring root uptake of water and nutrients, biomass allocation and total nutrient uptake. The short experimental time frame and modest salinity concentrations were selected to minimise ionic toxicity and plant growth effects. Reproduced with permission from Valenzuela et al. (2022).

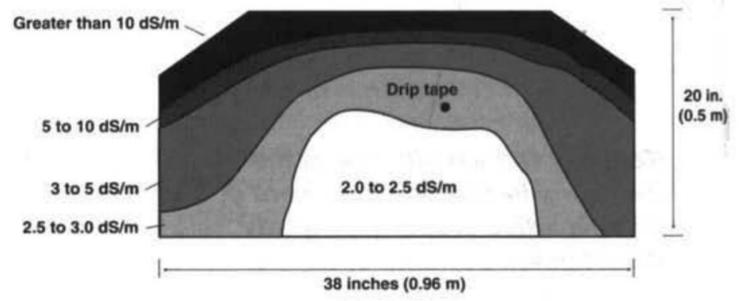
Figure 7: Simulated spatial distributions of salinity and nitrate following a growing season with an equal amount of nitrate applied (A) continuously and (B) once every 10 days for 8 hours. The density of black dots represents the concentration of nitrate in the soil and the isolines indicate volumetric water content (-). This simulation accounts for plant uptake of nitrate and water over the growing season. The simulation was done using the software HYDRUS 2D (Šimunek et al., 2012) assuming a constant transpiration rate of 8 mm/d and no surface evaporation over a period of 75 days (Reineke et al., 2021, unpublished).



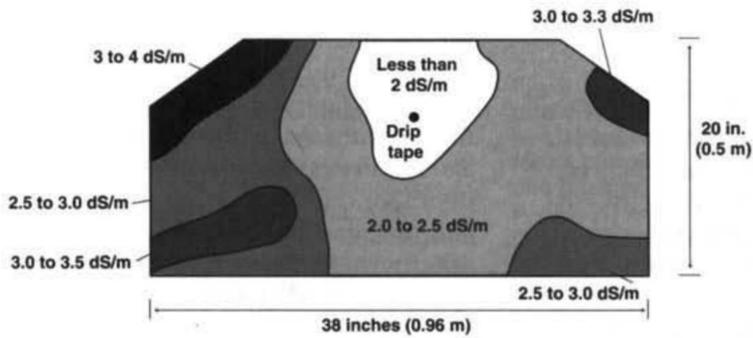




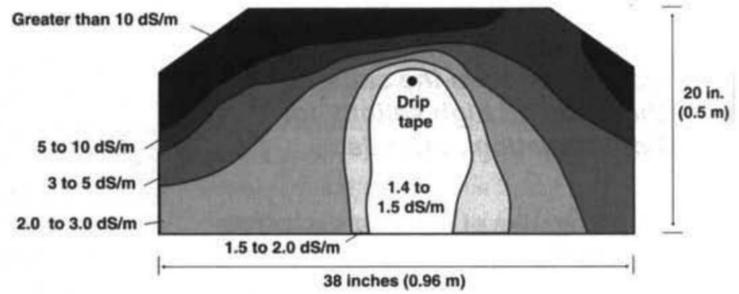
Salt pattern, August 1992



Salt pattern, October 1992



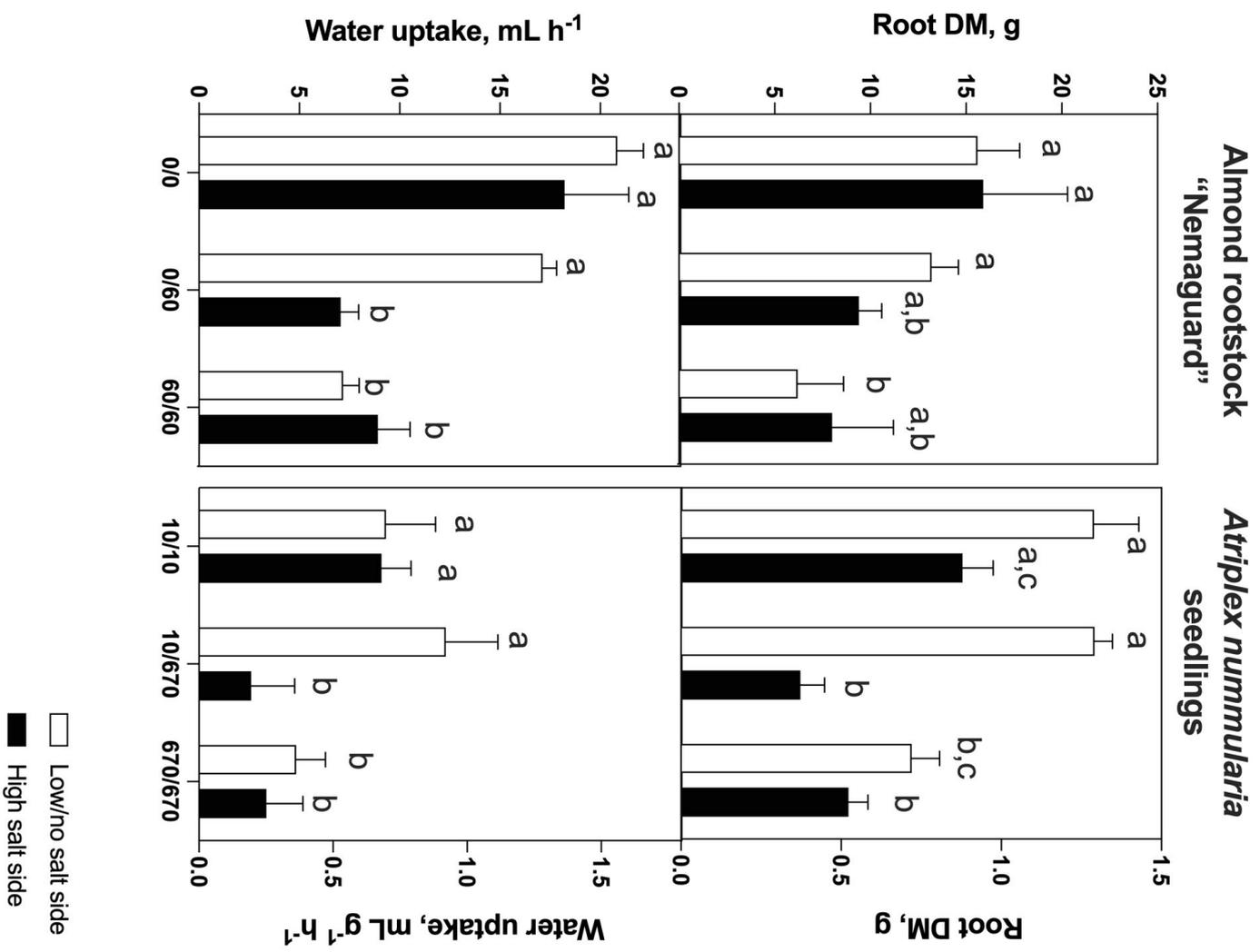
Soil salinity after 356 mm of rainfall



Salt pattern, September 1993

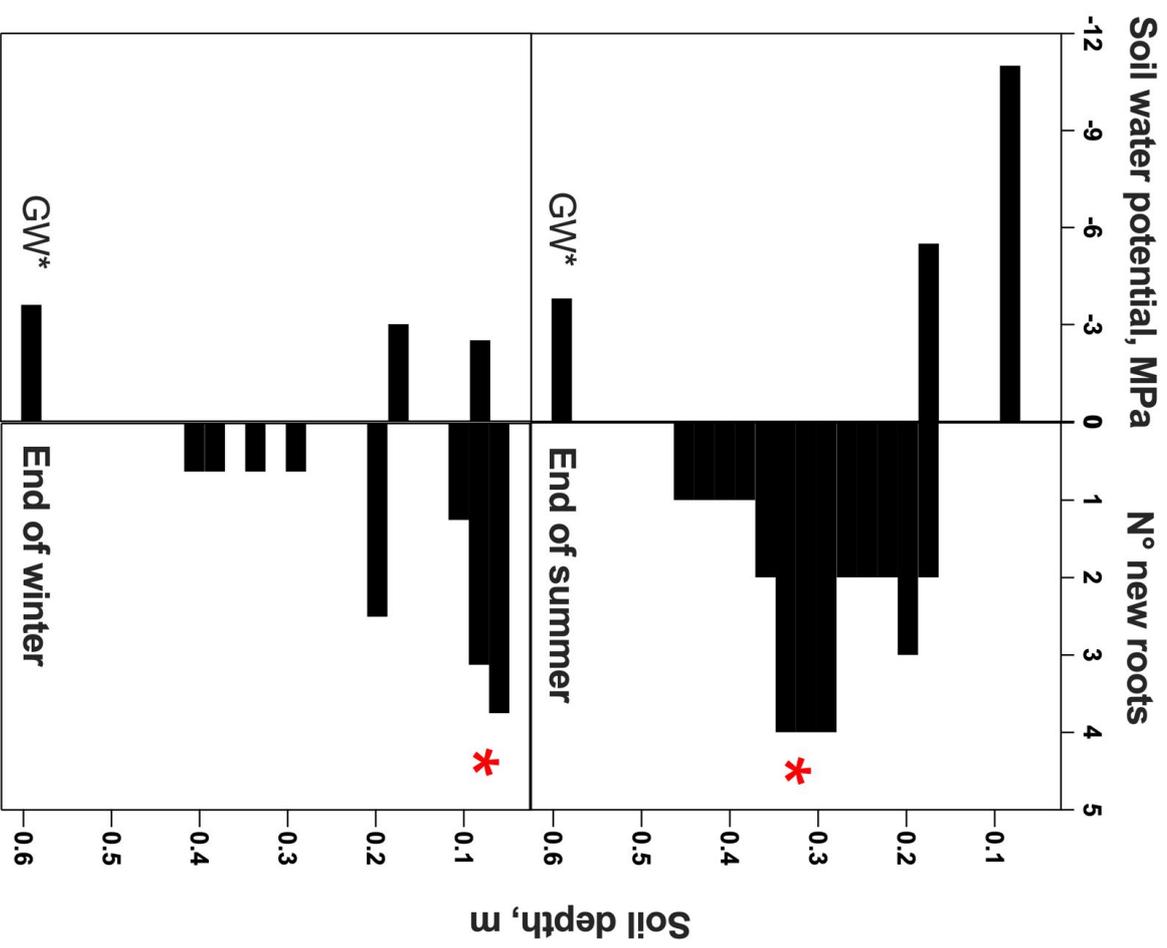
(A)

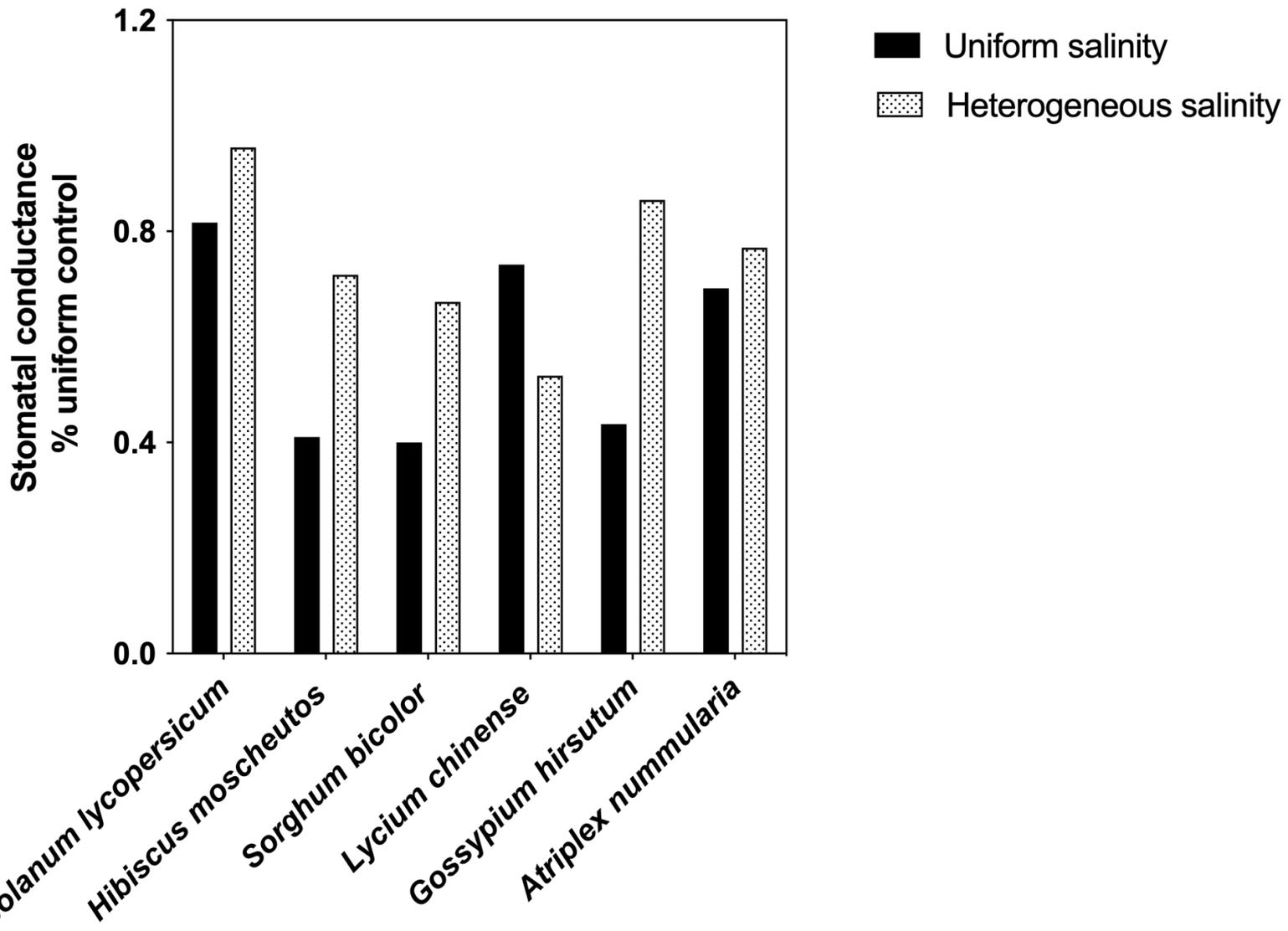
Spatial heterogeneity

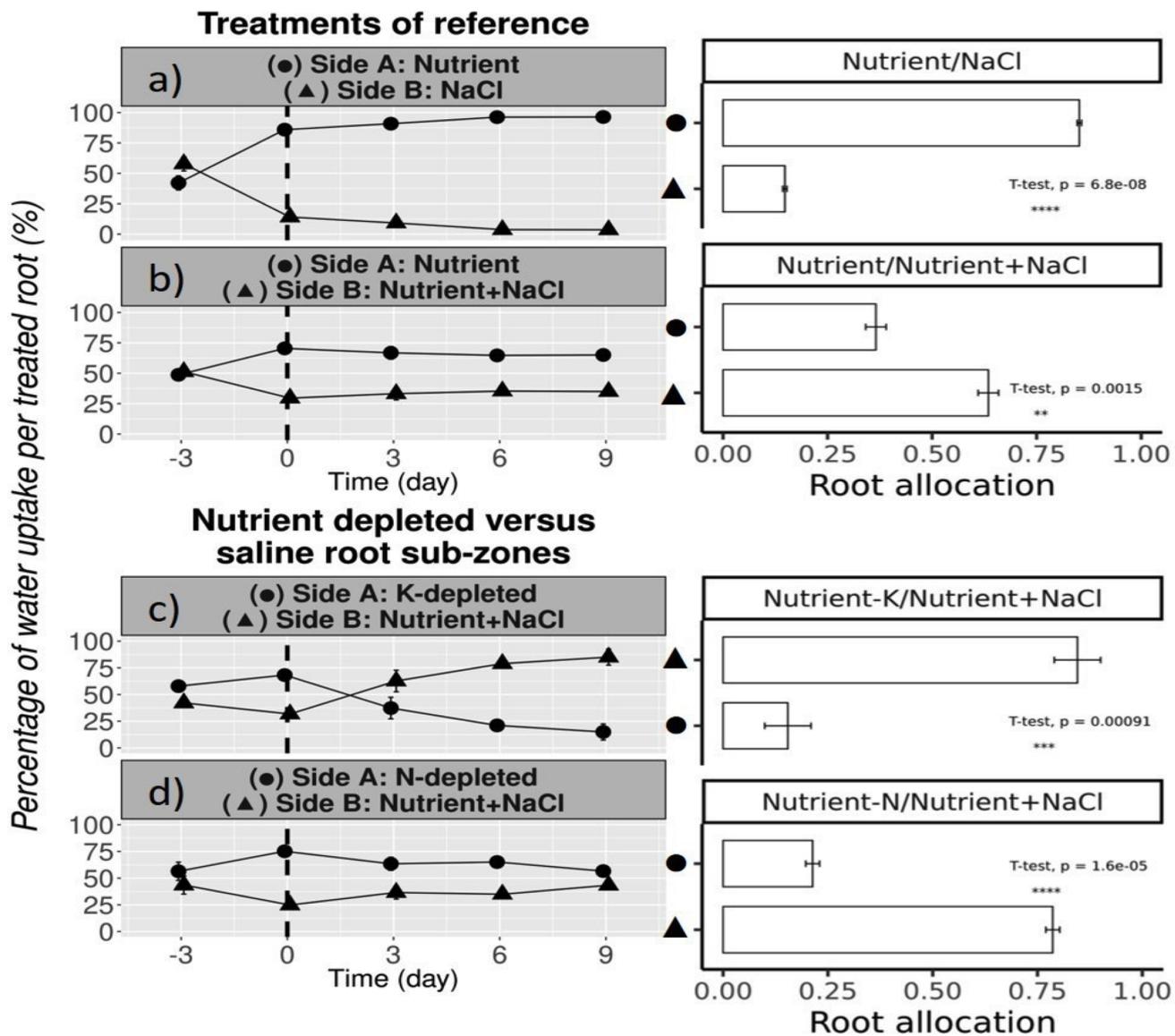


(B)

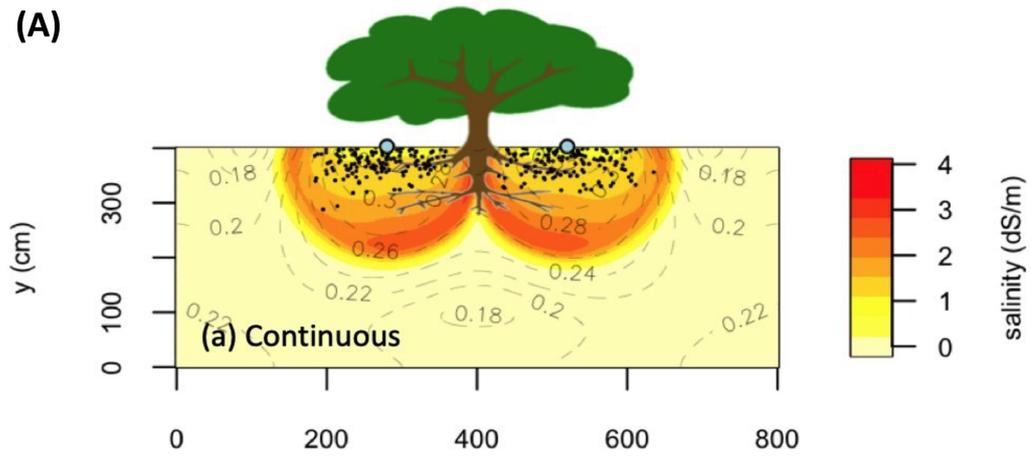
Temporal heterogeneity







(A)



(B)

