

1 **The effects of salt stress on ornamental plants: a review**

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9 **Abbreviations**

10 Dry weight (DW)

11 Electrical conductivity (EC)

12 Fresh weight (FW)

13 Light emitting diode (LED)

14 Pour Through (PT)

15

16 **Abstract**

17 Ornamental horticultural production is closely associated with a high water
18 consumption and yet the availability of freshwater is reducing. The irrigation of
19 ornamental plants with saline water may be an alternative, but an improvement in
20 knowledge of the effects on salinity on species used as ornamentals is essential. At high
21 salinities, plants exhibit a reduction of growth parameters such as biomass or leaf area
22 related to osmotic and ionic effects of salinity. Growth under saline conditions leads to
23 uptake of Na⁺ and Cl⁻ by plants, which can result in a nutritional imbalance due to the

24 antagonism between nutrients and saline ions with possible effects on the foliage.
25 Salinity can affect water relations in plants and photosynthetic capacity by stomatal
26 limitations. These negative effects can be counteracted by the plants through the
27 accumulation of compatible solutes or osmolytes and the activation of antioxidant
28 machinery. Nevertheless, the performance of these mechanisms is sometimes not
29 enough to avoid damage to the appearance of the plant and in consequence the
30 saleability of an ornamental species. In this review recommendations for the
31 establishment of new culture methods for nursery growers are made; these include
32 exogenous application of nutrients and osmolytes, enrichment with CO₂, and shading
33 treatments, in order to mitigate the damage caused by salt stress to ornamental plants.

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35 **Keywords:** Antioxidant responses, biomass, nutritional balance, osmolytes,
36 photosynthetic parameters, water relations.

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1. Introduction

39 Ornamental plants have an important place within the horticultural industry as
40 they are used in gardening, landscaping, and as cut flowers. The total turnover for all
41 aspects of floriculture is estimated to be more than 300 billion USD and cut flowers
42 make up about one-third of the global value of the ornamental plants market (Azadi et
43 al., 2016). Currently, the main constraint to ornamental plant production is water
44 consumption: it has been estimated that 100-350 kg of water are needed to produce 1 kg
45 of plant dry matter, although this can vary with species and variety, cultivation system
46 and plant growing season (Fornes et al., 2007). Growers have, over decades, used high
47 quality water to irrigate ornamental plants because of their high economic value.
48 Nowadays the increase in population and agricultural production together with the
49 diminishing sources of fresh water continue to intensify competition for good water

50 (Carter and Grieve, 2010). As a consequence, the use of saline water could be
51 considered an advisable source for the irrigation of ornamental plants since in
52 floriculture the products are not consumed.

53 Ornamental plants can be grown under field conditions and sold on as bare-rooted
54 plants or potted in containers filled with substrates such as peat moss, coconut fibre or
55 different kinds of mixtures with other materials (Reid and Jiang, 2012). The selection of
56 how plants are grown, whether under field conditions or in containers, will be
57 influenced by the salinity in the soil and the irrigation water available. There are
58 different causes of salinity in the soil and water. In the case of the soil, the main causes
59 are long-term natural accumulation of salts, deposition of sea-salt carried by wind and
60 rain and anthropogenic activities that disrupt the hydrologic balance of the soil between
61 water applied (irrigation or rainfall) and water used by crops (transpiration) (Singh,
62 2015). For the salinization of water, the main causes are overexploitation of ground-
63 waters, percolation of salts into the aquifers and seawater intrusion in aquifers (Payen et
64 al., 2016).

65 Soils are considered saline when they have an EC of 4 dS m^{-1} or higher, which
66 can be particularly problematic if the increased EC is the result of NaCl (Ghassemi et
67 al., 1995). Soil salinities of 50 mM NaCl (6 dS m^{-1}) are considered moderately saline,
68 whereas salinities greater than or equal to 150 mM NaCl (18 dS m^{-1}) are considered
69 highly saline by Cassaniti et al. (2013). They classified waters as slightly brackish with
70 an EC which ranges from 0.6 to 1.5 dS m^{-1} , brackish with an EC from 1.5 to 3.0 dS m^{-1} ,
71 moderately saline from 3 to 8 dS m^{-1} , saline from 8 to 15 dS m^{-1} and highly saline from
72 15 to 45 dS m^{-1} .

73 Plant growth response under saline conditions presents two phases. In the first
74 phase (osmotic phase), there is a growth reduction which starts immediately after

75 exposure of the roots to salt. This effect is associated with an osmotic impediment to
76 water uptake and consequent changes in water relations at a cellular level. The second
77 phase (ionic phase) results when old leaves are not able to compartmentalize sufficient
78 Na^+ and Cl^- concentrations to prevent effects on photosynthesis and consequently old
79 leaves die (Munns and Tester, 2008). However, plants differ considerably in the
80 concentration of salt that brings about these changes and species have been divided into
81 halophytes and glycophytes; the former can tolerate high concentrations of salt between
82 80 and 200 mM NaCl) while the latter are susceptible (see Flowers and Colmer, 2015).

83 The effect of saline irrigation on ornamental plants has been investigated to a
84 much lesser extent than other crops because ornamentals are normally irrigated with
85 high quality water. Nevertheless, there are many papers on the effects of the saline
86 stress in ornamental plants, describing the effects on one or more species (e.g. Valdes et
87 al., 2015 a; Garcia-Caparros et al., 2016) as well as comprehensive reviews (Niu and
88 Cabrera, 2010 a; Cassaniti et al., 2013). In this review we update information on the
89 effects of salinity on ornamental plants with material covering the last ten years,
90 tabulating effects on growth, nutritional status, water relations, photosynthetic
91 parameters, osmolytes accumulation and antioxidant activity, with the aim of allowing
92 the grower to make rational choices of plants and culture methods.

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2. The effects of salt stress on ornamental plants

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2.1. Growth (biomass, leaf area and number of flowers)

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Plant growth is affected by salinity as a result of the disruption of physiological
processes such as: 1) disturbed photosynthesis, 2) disturbed osmoregulation, 3) down-
regulation of aerial growth following a long distance signal, and 4) disturbance in
mineral supply to the aerial part (Negrao et al., 2017).

100 Ornamental plants subjected to salt stress exhibit a decrease in fresh weight (FW)
101 and dry weight (DW), especially in the aerial part, a reduction in total leaf area and
102 plant height and a reduction of the number and quality of flowers, which has been
103 recorded in previous reviews (Quist et al., 1999; Kucukahmetler, 2002) and can be seen
104 in the updated references in Table 1. The decrease in FW or DW is mainly due to a
105 reduction in the number of leaves or the formation of smaller and fewer leaves and
106 reduced plant height as reported by Acosta-Motos et al. (2017 a). This reduction of FW
107 and DW under saline conditions can be used for the classification of ornamental species
108 according to the degree of salt tolerance, essential information for the nursery grower in
109 order to choose which species is the most suitable for the soil and water available.
110 Species that are very sensitive to salinity include *Impatiens walleriana*, *Zinnia*
111 *angustifolia* and *Viola tricolor* with a high biomass decrease (90%), while *Chamaerops*
112 *humilis* and *Washingtonia robusta* can be grown with electrical conductivity of
113 irrigation water from 2 to 8 dS m⁻¹ (see Table 1).

114 For ornamental plants, exposure to saline conditions can involve not only a
115 decrease in plant weight, but also a consequent reduction of plant height (Zhang and
116 Shi, 2013). Nevertheless, this reduction in size could be an advantage from the grower's
117 point of view since consumers often require short, compact plants with good keeping
118 quality and ornamental value, but taking into account that the consumer should continue
119 with the irrigation with salt water in order to maintain the reduction in size.
120 Furthermore, smaller plants require less space in expensive production facilities, are
121 easier to handle, have reduced transportation costs and advantages for retailers (Lutken
122 et al., 2012). Nevertheless, the use of salt has not yet been used as a technique to
123 manage plant size.

124 A typical response to salt stress described in papers is a reduction in total leaf
125 area. The reduction in leaf area, a consequence of changes in cell wall properties, cell
126 water relations and a reduction in photosynthetic rate (Munns and Tester, 2008), has
127 been recorded (see Table 1) for *Paulownia* sp. (Ivanova et al., 2014), *Callistemon laevis*
128 (Alvarez and Sanchez-Blanco, 2015) and *Euonymus japonicus* (Gomez-Bellot et al.,
129 2013). A reduction of leaf area due to the salt stress could be beneficial for nursery
130 growers, especially when they want to produce compact plants without the use of plant
131 growth regulators.

132 In floricultural crops, under salt stress there can be a reduction of the number
133 and quality of flowers as was reported in previous literature (Wahome et al., 2000;
134 Shillo et al., 2002). This effect can be related to an alteration of the concentration of
135 hormones directly involved in flowering such as abscisic and jasmonic acids (Rogers,
136 2013). The reduction of number and quality of flowers can result in a decrease of sales
137 for floricultural crops which is not acceptable to growers. Therefore, one possible
138 solution to mitigate these effects could be the foliar application of hormones, following
139 the recommendations given in a comprehensive review on post-harvest biology and
140 technology in potted plants by Reid and Jiang (2012). To date, there is only information
141 about the foliar application of these hormones under non-saline conditions. For instance,
142 Jahanbazi et al. (2014) reported that the exogenous application of jasmonic acid in rose
143 resulted in an increase of number of flower and quality. Raviz et al. (2016) reported the
144 same effects in gerbera fumigated with methyl jasmonate.

145

146 2.2. *Nutritional balance*

147 Salt stress can affect the nutritional status of a plant through a complex net of
148 interactions, including a decrease of nutrient uptake and/or transport from root to shoot

149 (Munns and Tester, 2008). As can be seen in Table 2, ornamental plants grown under
150 saline conditions exhibited a decrease of N, P, K and Ca concentration in leaves related
151 to antagonisms with Cl and Na and an increase in Na and Cl concentration in leaves.

152 Under salt stress conditions, nitrogen uptake is often disrupted mainly due to the
153 antagonism between Cl^- and NO_3^- (Munns and Gilliam, 2015). Salinity stress also
154 reduces P availability because of the antagonism between Cl^- and H_2PO_4^- as reported by
155 Parihar et al. (2015). Reduced uptake of phosphorus under salt stress can also be a
156 consequence of the strong influence of sorption processes that control the concentration
157 of phosphorus in the soil and low solubility of Ca-P minerals (Marschner, 2011). The
158 inhibition of K^+ uptake in plant occurs primarily due to the physical and chemical
159 similarities between K^+ and Na^+ and the tendency of the latter to compete with K^+ for
160 major binding sites, including control of enzymatic activity that occurs at unfavourable
161 cytosolic K^+/Na^+ ratios (Adams and Shin, 2014; Benito et al., 2014). With respect to Ca,
162 the decrease in uptake is due to the to the antagonistic effect between Ca^{2+} and Na^+ ions,
163 which affects membrane properties, due to displacement of membrane-associated Ca^{2+}
164 by Na^+ , leading to dissolution of membrane integrity and selectivity (Kopittke, 2012).

165 In plants subjected to saline conditions, there is an increase of toxic elements
166 such as Na and Cl in leaves that can result in visual damage like tip and marginal burn,
167 with negative influences on decorative value (Cassaniti et al., 2009). The typical
168 symptoms of Na^+ accumulation are leaf burn, scorch and dead tissue along the leaf
169 margins, which first occur in the oldest leaves. As the severity increases, the drying
170 progresses towards the leaf centre until the entire tissue is dead. Injury due to Cl^-
171 toxicity, however, typically, starts at the extreme leaf tip of older leaves and progresses
172 from the tip back as the severity increases (Cassaniti et al., 2013).

173 The fact that water uptake by plants and relative exclusion of Na⁺ and Cl⁻ from
174 the transpiration stream can concentrate ions in the substrate leads to such aesthetic
175 damage in ornamental plants, so one possible solution for the displacement of these ions
176 is through the adjustment of the irrigation according to the electrical conductivity of the
177 substrate as reported by Valdes et al. (2015 b). The estimation of the electrical
178 conductivity in the substrate can be performed through three different methods: the
179 pour-through (PT) method, the saturated media extract, and the 1:2 water:substrate (v/v)
180 suspension test (1:2) (Camberato et al., 2009). The first method (PT) is a widely
181 accepted practice amongst nursery growers. This method is a bulk solution
182 displacement, simple, rapid, non-destructive, and cost effective means of monitoring EC
183 and nutrient availability in substrates (Torres et al., 2010).

184 It is important to note that although growers supply standard nutrient solutions
185 for an adequate growth of ornamental plants, it is common to see nutritional
186 deficiencies of N, P, K and Ca in salt-affected plants (Table 2) as a consequence of the
187 antagonisms between nutrient and Na and Cl uptake. A shortage of nutrient reduces the
188 visual appearance and the quality in plants, thus decreasing their saleability. One culture
189 method that could be implemented by nursery growers is the application of
190 macronutrients via foliar spray, since the process of uptake via the leaves and the
191 distribution of nutrients in the plant organs is enhanced compared with fertigation,
192 resulting in a higher growth and better visual appearance as reported Kashif et al. (2014)
193 in *Dahlia hybrida*.

194 2.3. *Water relations*

196 Plant-water relations explain the behaviour of plants in terms of how they control
197 the hydration of their cells, which is essential in physiological and metabolic processes

198 that determine the quantity and quality of plant growth (Acosta-Motos et al., 2017 a).
199 One of the main problems for plants growing under saline conditions is the low water
200 potential in the soil solution due to the increase of solute concentration in the root zone,
201 therefore in order to ensure the water flow plants should adjust osmotically, decreasing
202 their water and osmotic potentials (Cassaniti et al., 2013).

203 Water potential and osmotic potential of plants become more negative with an
204 increase in salinity. Leaf water potential and osmotic potential decline depending on the
205 osmotic potential of the rooting medium and the mode of stress imposition (Parihar et
206 al., 2015). Consequently, it might be expected that ornamental plants grown under salt
207 stress will show a decrease of water and osmotic and potential, but the reality is that
208 each species behaves differently (Table 3). For instance, *Narcissus* sp., *Rose* sp. and
209 *Salvia hispanica* exhibited no variation of leaf osmotic potential under saline conditions
210 while *Teuchrium chamaedrys* showed an increase of leaf osmotic potential; the rest of
211 the species in Table 3 showed a decline of leaf osmotic potential. These results can be
212 related to the different degrees of salt tolerance and the time of salt exposure of each
213 species since the methodology used was the same in all experiments (Scholander
214 pressure chamber). Any change in water relations in ornamental plants can result in an
215 appearance of drought stress and a decrease of growth thus there is a reduction in the
216 saleability of plants with these symptoms. From the nursery grower's point of view, the
217 different trends between species can be solved with an irrigation-schedule based on the
218 evapotranspiration demands of each species under saline conditions in order to improve
219 their quality. Nevertheless, the applicability of this evapotranspiration-based irrigation
220 scheduling is difficult for growers, since it requires an exhaustive study over several
221 years. For instance, in an experiment conducted on *Forsythia intermedia*, *Photinia*
222 *fraseri*, *Prunus laurocerasus* L. and *Viburnum tinus* L. during the summer of four

223 consecutive years (2007–2010), Incrocci et al. (2014) determined the evapotranspiration
224 irrigation scheduling of these species according to the type of container used for the
225 growth. Carmassi et al. (2013) determined the rate of evapotranspiration of *Gerbera*
226 *jamesonii* grown under greenhouse conditions in a Mediterranean climate. Such
227 experiments need to be carried out under saline conditions if this methodology is to be
228 applied to the use of brackish water, in evapotranspiration-based irrigation.

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2.4. *Photosynthetic parameters*

231 The response of photosynthesis to salinity stress is highly complex because this
232 abiotic stress affects photosynthesis both in the short and long term. In the short term,
233 salinity can affect photosynthesis by stomatal limitations, leading to a decrease in
234 carbon assimilation. In the long term, salt stress can also affect the photosynthetic
235 process due to salt accumulation in young leaves and decreases in chlorophyll and
236 carotenoid concentrations (Acosta-Motos et al., 2017 a).

237

2.4.1. *Chlorophyll content*

239 Chlorophyll a, chlorophyll b and carotenoids are the main photosynthetic
240 pigments and they play important role in photosynthesis (Hagemman and Bauwe,
241 2016). Chlorophyll a functions as primary electron donor and chlorophyll b is consider
242 the primary accessory pigment for light harvesting and energy transfer (Li and Chen,
243 2015).

244 It is well-known that chlorophyll content in plants correlates directly to the
245 healthiness of plant (Barry, 2009). A decrease in chlorophyll concentration under salt
246 stress is a commonly reported phenomenon used as a sensitive indicator of the cellular
247 metabolic state. This decrease may be related to membrane deterioration (Silveira and
248 Carvalho, 2016). Nevertheless, it is also possible to find that under salt stress, plants

249 show an increase of chlorophyll concentration that can be due to an increase in the
250 number of chloroplast per unit area of leaf in the stressed plant leaves as reported by
251 Chaum and Kirdmanee (2009). For instance, in an experiment conducted on *Eugenia*
252 *myrtifolia* grown in pots filled with a mixture of coconut fibre, sphagnum peat and
253 Perlite (8:7:1) and irrigated with increasing NaCl concentrations, Acosta-Motos et al.
254 (2015) reported an increase in total chlorophyll concentration compared to the control
255 treatment.

256 A decrease of chlorophyll concentration in ornamental plants under saline
257 conditions has been recorded by many researchers (Table 4). This negative effect results
258 in the yellowing of leaves affecting the visual appearance and thus the sale value of
259 these ornamental species. One possible technique to counteract these negative effects
260 could be the use of shading since under low-light conditions, plants exhibit an increase
261 of chlorophyll concentration (Ashraf and Harris, 2013). Pires et al. (2011) carried out an
262 experiment with *Passiflora* cvs. grown under different light intensities and reported that
263 one of the main effects of shading was an increase of chlorophyll concentration in these
264 varieties. Lugassi-Ben-Hamo et al. (2010) reported the same effects in *Eustoma*
265 *grandiflorum* grown under 67% or 88% reduction in light intensity through shading.
266 Nevertheless, it is necessary to point out that these shading experiments were conducted
267 with plants grown under non-saline conditions, so need to be repeated with saline
268 irrigation.

269 The establishment of different shading regimes could be expensive, so another
270 cheaper possibility to increase the chlorophyll concentration in leaves in these species is
271 through the foliar application of magnesium, since its concentration is essential to the
272 generation of chlorophyll. For instance, in an experiment conducted on *Epipremnum*
273 *aureum*, Metwally et al. (2015) reported an increase of chlorophyll concentration in

274 plants treated with magnesium sulphate as foliar fertilizer. The results of foliar
275 application of Mg^{2+} in ornamental plants has not been tested in the presence of salinity,
276 but might be particularly effective given the competition in uptake of nutrients by Na^+
277 (and Cl^-) mentioned above. Therefore, as for the use of shading already mentioned, it
278 would be necessary to study the effects of foliar application of Mg^{2+} in species where
279 salinity has a particularly detrimental effect on the appearance.

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2.4.2. *Photosystem efficiency*

282 Chlorophyll fluorescence is a valuable tool to monitor the physiological status of
283 plants under different abiotic stresses like salinity. Under saline conditions, there is a
284 general decrease in PSII efficiency and photochemical quenching parameters (F_v/F_m)
285 and an increase in non-photochemical quenching parameters (Acosta-Motos et al., 2017
286 a). The F_v/F_m ratio is an important ratio for the determination of the maximum
287 quantum efficiency of PSII and the level of tolerance or sensitivity of a plant to stress
288 (Zhao et al., 2015). Decrease in F_v/F_m is a clear indication that PSII was affected by
289 salt and photoinhibition was occurring. In healthy leaves, F_v/F_m value is usually close
290 to 0.8 in most plant species, therefore a lower value indicates that a proportion of PSII
291 reaction centres is damaged or inactivated, a phenomenon, termed as photoinhibition,
292 commonly observed in plants under stress (Kalaji et al., 2016). Non-photochemical
293 quenching (NPQ) is a photoprotective mechanism in photosynthesis which protects the
294 components of PSII by dissipating excess energy as heat when plants were exposed to
295 stress (Ruban, 2016).

296 Few papers have analysed the effect of salinity on chlorophyll fluorescence in
297 ornamental plants. From the general responses of plants to salinity, the most common
298 trend in chlorophyll fluorescence would be predicted to be a decrease of PSII efficiency
299 and photochemical quenching parameters (F_v/F_m) and an increase in non-

300 photochemical quenching parameters as has been previously reported (Jimenez et al.,
301 1997) in an experiment conducted in roses. However, there is a great variability in the
302 effects of salinity on the chlorophyll fluorescence in ornamental plants (Table 5), but the
303 response of each species is related to its degree of salt tolerance, confirming that
304 chlorophyll fluorescence is a good indicator of which species to grow with saline water.
305 The changes in chlorophyll fluorescence in ornamental plants involves a reduction of
306 the photosynthetic capacity in leaves causing physiological changes that result in a loss
307 of sale capacity for the growers. These negative effects could be mitigated through the
308 use of light-emitting diode (LED) lamps at different wavelengths according to the
309 requirement of each species. In an experiment carried out under non-saline conditions
310 with different ornamental species such as *Impatiens walleriana*, *Petunia hybrida*,
311 *Tagetes patula* and *Salvia splendens*, Wollaeger and Runkle (2013) reported that under
312 red light conditions (600-700 nm), these species exhibited an improvement in the
313 photosynthetic efficiency. Bergstrand and Schussler (2012) also reported that
314 supplementary lighting, supplied by white LED and red/blue LED improved the
315 photosynthesis in *Euphorbia pulcherrima*. Such experiments now need to be carried out
316 under saline conditions.

317

318 2.4.3. Net photosynthesis and stomatal conductance

319 It is assumed that under saline conditions, plants suffer a decrease of net
320 photosynthesis and stomatal conductance. The reduction in photosynthetic rate in plants
321 under salt stress may be due to several factors: a) dehydration of cell membranes, which
322 reduces their permeability to CO₂, b) salt toxicity, c) reduction of CO₂ supply because
323 of hydroactive closure of stomata, d) enhanced senescence induced by salinity and e)
324 changes of enzyme activity induced by changes in cytoplasmic structure (Gururani et
325 al., 2015). Under salt stress there is a reduction in stomatal conductance which restricts

326 the availability of CO₂ for carboxylation reactions. Moreover, this stomatal closure
327 minimizes loss of water through transpiration and this affects light-harvesting and
328 energy-conversion systems thus leading to alteration in chloroplast activity (Chaves et
329 al., 2011).

330 The recent literature suggests ornamental plants subjected to saline conditions
331 exhibited a decrease of net photosynthesis and stomatal conductance (Table 6). The
332 consequence of these changes in photosynthesis is a reduction of saleable plants,
333 therefore the enrichment of atmospheric CO₂ for ornamental plants with a high
334 profitability could be an appropriate technology to overcome the negative effects of
335 salinity. However, although a common practice in commercial horticulture, the
336 establishment of this technique is expensive. Zhang et al. (2012) and Xu et al. (2014)
337 conducted experiments on *Gerbera jamesonni* and *Impatiens hawkeri* and reported that
338 the enrichment of CO₂ at levels of 800 μmol·mol⁻¹ resulted in a growth increase of these
339 species. These studies were not, however, conducted under saline conditions so that it
340 would be necessary to investigate the interaction of salinity and enrichment of CO₂ on
341 the growth of ornamentals.

342 343 2.5. Osmolytes

344 Under salt stress, plants accumulate low-molecular-mass compounds termed
345 compatible solutes to adjust the osmotic potential of the cytoplasm because they do not
346 interfere with normal biochemical reactions (Fahad et al., 2015). Nevertheless, the
347 production of sufficient osmotica is metabolically expensive, potentially limiting plant
348 growth by consuming significant quantities of carbon that could otherwise be used for
349 growth (Flowers and Colmer, 2015).

350 Compatible solutes include compounds such as proline, sugars, glycine-betaine
351 and other related quaternary ammonium compounds (Szabados and Savoure, 2010;

352 Slama et al., 2015), but due to the lack of information on the effects of salt stress on the
353 accumulation of solutes in ornamental plants, we will focus on two of them: proline and
354 soluble sugars.

355 The main roles of proline under salt stress include osmotic adjustment, protection
356 of enzymes and membranes, as well as acting as a reservoir of energy and nitrogen for
357 utilization (Amini et al., 2015). The accumulation of proline is a well-known adaptive
358 mechanism in plants against salt stress conditions. It has also been suggested that
359 proline accumulation can serve as a selection criterion for the salt tolerance because the
360 increase in proline content was positively correlated to the level of salt tolerance (Kaur
361 and Asthir, 2015).

362 Proline accumulation under salt stress can be explained by the higher inhibitory
363 rate of proline dehydrogenase and proline oxidase (Kaur and Asthir, 2015).
364 Nevertheless, it is also possible to find a depletion in the accumulation of proline in
365 plants due to its rapid breakdown upon relief of stress. The breakdown products provide
366 reducing agents that support mitochondrial oxidative phosphorylation and generation of
367 ATP for recovery from stress and repairing stress-induced damage (Fichman et al.,
368 2015). For instance, plants of *Catharanthus roseus* irrigated with salt solutions from 0
369 to 250 mM NaCl during 21 days showed a decline of proline concentration in leaves,
370 which may be due to its breakdown to reduce the effect of salt stress (Chang et al.,
371 2014).

372 In the recent literature on the effect of salt stress on ornamental plants it is clear
373 that they commonly increase the proline concentration in leaves (Table 7), suggesting
374 that the exogenous application of this osmolyte could be a useful tool for nursery
375 growers to produce plants of better quality using saline irrigation water. Cirillo et al.
376 (2015) and Zheng et al. (2015) carried out experiments with ornamental plants grown

377 under different levels of salinity and reported that the exogenous application of proline
378 resulted in an improvement of the salinity tolerance in these species. This relatively
379 simple procedure could be evaluated for other ornamentals.

380 As far as soluble sugars are concerned, it is assumed that under saline stress
381 there is an increase of concentration of soluble sugars in plants as sugars play a central
382 role in osmoprotection, osmotic adjustment, carbon storage and radical scavenging
383 under salt stress (Sami et al., 2016). The increase of soluble sugars under salt stress may
384 be related to a decrease of sucrose phosphate synthase activity and a decrease of starch
385 phosphorylase activity as reported by Ruan (2014). The increase of soluble sugars under
386 increasing NaCl concentration in ornamental plants has been recorded only by a few
387 researchers (Table 7). In previous literature there are reports of the value of exogenous
388 application of soluble sugars in order to improve the postharvest longevity of, for
389 instance, cut flowers: Ahmad et al. (2013) and Arrom and Munne-Bosch et al. (2012)
390 carried out experiments with *Rosa hybrida* and *Eustoma grandiflorum*, respectively,
391 where they reported that the application of sucrose resulted in an improvement of post-
392 harvest longevity of cut flowers. However, there are no reports on the use of exogenous
393 soluble sugars to increase the salt tolerance in ornamental plants. Nevertheless, we
394 suggest that nursery growers might evaluate the exogenous application of soluble sugars
395 in ornamental plants as a possible tool for the improvement of the salinity tolerance, as
396 occurs with the exogenous application of proline. It is necessary to point out that the use
397 of this technique can result in growth increase of pathogens and attraction of insects,
398 therefore additional measures should be considered.

399

400 *2.6. Antioxidant responses*

401 Under saline conditions, one of the common responses of plants is the accelerated
402 generation of reactive oxygen species (ROS), which include the superoxide radical
403 ($O_2^{\bullet-}$), singlet oxygen (1O_2), hydroxyl radical (OH^{\bullet}) and hydrogen peroxide (H_2O_2), all
404 of which are cytotoxic to plants (De Gara and Foyer, 2017). The main sources of ROS
405 generation in the cell are mitochondria, chloroplasts and peroxisomes (Pucciarello and
406 Perata, 2017). These reactive oxygen species are involved in different process such as
407 the DNA damage, lipid peroxidation and protein oxidation (Mittler, 2017).

408 In order to overcome the negative effects of ROS at the cellular level, plants
409 show a mechanism of scavenging of these species through the antioxidative machinery
410 composed by enzymatic and non-enzymatic components such as superoxide dismutase
411 (SOD), ascorbate peroxidase (APX), peroxidase (POX) and catalase (CAT) (Sewelam et
412 al., 2016). In the recent literature, there are a few references to the effect of salt stress on
413 the antioxidant activity in ornamental plants (Table 8). These publications report an
414 increase in the antioxidant machinery. As a consequence of oxidative stress due to the
415 exposure to saline conditions, plants suffer serious injuries which can depreciate their
416 economic value. Nevertheless, these injuries can be mitigated through the exogenous
417 application of antioxidant compounds via foliar sprays, resulting in the use of this
418 technique as an advisable tool for nursery growers. Hashish et al. (2015) conducted an
419 experiment on gladiolus plants grown under saline conditions and reported that the
420 foliar application with glutathione (100 and 200 ppm) resulted in an enhancement of salt
421 tolerance in this species. In a similar vein, Badawy et al. (2015) showed an increase in
422 yield and physiological enhancement of *Celosia argentea* sprayed with increasing
423 concentrations of α -tocopherol (from 200 to 600 ppm).

424

425 **3. Conclusions**

426 Salt stress involves a growth reduction, nutritional imbalances, changes in water
427 relations and photosynthesis and physiological changes that reduce the visual quality of
428 ornamental plants and as a consequence their saleability. Nevertheless, the high water
429 consumption associated with growing ornamental plants in a world with decreasing
430 fresh water availability suggests the use of saline waters by nursery growers for the
431 production these plants. where brackish water is used, the establishment of new culture
432 methods by nursery growers is advocated, methods such as irrigation based on the water
433 demands of each species, the exogenous application of nutrients and osmolytes, shading
434 and the enrichment of CO₂, all of which might mitigate damage caused by the salinity
435 and at the same time improve the visual quality and the profitability of growing these
436 ornamental species.

437

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441

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Table 1. Effects of salt stress on growth parameters in different ornamental species.

Botanical family	Species	Salt threshold	Observations	References
Plantaginaceae	<i>Antirrhinum majus</i>	0-80 mM NaCl, 5 wks	DW reduction of 50-70%	Villarino and Mattson (2011)
Solanaceae	<i>Petunia hybrida</i>			
Begoniaceae	<i>Begonia hiemalis</i>	0-80 mM NaCl, 5 wks	DW reduction of 70-90%	Villarino and Mattson (2011)
Onagraceae	<i>Fuchsia hybrida</i>			
Lamiaceae	<i>Solenostemon scutellarioides</i>			
Asteraceae	<i>Tagetes patula</i>			
Apocynaceae	<i>Catharanthus roseus</i>			
Verbenaceae	<i>Verbena hybrida</i>			
Geraniaceae	<i>Pelargonium hortorum</i>			
Balsaminaceae	<i>Impatiens walleriana</i>	0-80 mM NaCl, 5 wks	DW reduction >90%	Villarino and Mattson (2011)
Euphorbiaceae	<i>Euphorbia hybrida</i>			
Lamiaceae	<i>Salvia splendens</i>			
Asteraceae	<i>Zinnia angustifolia</i>	0-80 mM NaCl, 5 wks	100% mortality	Villarino and Mattson (2011)
Violaceae	<i>Viola tricolor</i>			
Arecaceae	<i>Chamaerops humilis</i>	2-8 dS m ⁻¹ , 2 years	Total biomass decrease of 38%	Simon et al. (2010)
Arecaceae	<i>Washingtonia robusta</i>	2-8 dS m ⁻¹ , 2 years	Total biomass decrease of 48%	Simon et al. (2010)
Asparagaceae	<i>Hyacinthus orientalis</i>	0-600 mM NaCl, 15 d	Plant fresh weight reduction	Koksal et al. (2014)
Adoxaceae	<i>Viburnum lucidum</i>	0-200 mM NaCl, 3 months	Roots, stems and shoots dry weight reduction	Sifola et al. (2017)
Lamiaceae	<i>Lavandula angustifolia</i>	0-100 mM NaCl, 21 d	Plant dry weight reduction	Cordovilla et al. (2014)
Lamiaceae	<i>Salvia hispanica</i>	0.3-60 mM NaCl, 80 d	Plant fresh and dry weight reduction	Raimondi et al. (2017)
Asteraceae	<i>Stevia rebaudiana</i>	0.4-12 dS m ⁻¹ , 1 year	Plant fresh and dry weight reduction	Reis et al. (2015)
Asteraceae	<i>Tagetes erecta</i>	2-10 dS m ⁻¹ , 16 d	Plant height reduction	Valdez-Aguilar et al. (2009)
Asteraceae	<i>Tagetes patula</i>			
Euphorbiaceae	<i>Euphorbia pulcherrima</i>	0.5-1.2 g NaCl L ⁻¹ , 4 months	Plant height reduction	Gent et al. (2016)
Paulowniaceae	<i>Paulownia sp.</i>	50-200 mM NaCl, 58 d	Leaf area reduction	Ivanova et al. (2014)
Myrtaceae	<i>Callistemon laevis</i>	0.8-4 dS m ⁻¹ , 10 months	Leaf area reduction	Alvarez and Sanchez-Blanco (2015)
Celastraceae	<i>Euonymus japonicus</i>	0.9-4 dS m ⁻¹ , 20 wks	Leaf area reduction	Gomez-Bellot et al. (2013)

Iridaceae	<i>Freesia</i> sp.	1.5-6 dS m ⁻¹ , 7 months	Flower number reduction	Aydinsakir et al. (2010)
Rosaceae	<i>Rosa hybrida</i>	1.5-8.0 dS m ⁻¹ , 2 months	Flower yield reduction	Cai et al. (2014)

Table 2. Effects of salt stress on nutrient concentrations in leaves in different ornamental species.

Botanical family	Species	Salt threshold	Nutrients						References
			N	P	K	Ca	Na	Cl	
Scrophulariaceae	<i>Antirrhinum majus</i>	2.5-14 dS m ⁻¹ , 2 months		↓	↓		↑	↑	Carter and Grieve (2008)
Ericaceae	<i>Arbutus unedo</i>	0.85-9.45 dS m ⁻¹ , 16 wks			↓	↓	↑		Navarro et al. (2008)
Buxaceae	<i>Buxus sempervirens</i>	0-250 mM NaCl, 5 months					↑	↑	Caser et al. (2013)
Buxaceae	<i>Buxus microphylla</i>	0.6-8 dS m ⁻¹ , 6 months			↓		↑	↑	Valdez-Aguilar et al. (2011)
Arecaceae	<i>Chamaerops humilis</i>	2-8 dS m ⁻¹ , 2 years	↓	↓	↓		↑	↑	Simon et al. (2013)
Asteraceae	<i>Cichorium spinosum</i>	2-12 dS m ⁻¹ , 56 d			↓		↑	↑	Ntatsi et al. (2017)
Caryophyllaceae	<i>Diantus caryophyllus</i>	1-6 dS m ⁻¹ , 3 months	↓	↓	↓	↓	↑	↑	Navarro et al. (2012)
Escalloniaceae	<i>Escalonia exoniensis</i>	0.6-8 dS m ⁻¹ , 6 months			↓		↑	↑	Valdez-Aguilar et al. (2011)
Malvaceae	<i>Hibiscus rosa sinensis</i>	0.6-8 dS m ⁻¹ , 6 months					↑	↑	Valdez-Aguilar et al. (2011)
Cupressaceae	<i>Juniperus chilensis</i>	0.6-8 dS m ⁻¹ , 6 months					↑		Valdez-Aguilar et al. (2011)
Brassicaceae	<i>Matthiola incana</i>	2.5-14 dS m ⁻¹ , 2 months			↓	↓	↑	↑	Grieve et al. (2006)
Asteraceae	<i>Osteospermum hybrida</i>	1.5-5 dS m ⁻¹ , 14 wks			↓		↑	↑	Valdes et al. (2015 a)
Rosaceae	<i>Raphiolepis indica</i>	0.6-8 dS m ⁻¹ , 6 months			↓		↑	↑	Valdez-Aguilar et al. (2011)
Rosaceae	<i>Rosa hybrida</i>	1.4-6.4 dS m ⁻¹ , 7 wks			↓	↓	↑	↑	Niu et al. (2013)
Asteraceae	<i>Tagetes erecta</i>	0-200 mM NaCl, 25 d			↓		↑		Koksal et al. (2016)
Arecaceae	<i>Washingtonia robusta</i>	2-8 dS m ⁻¹ , 2 years	↓	↓	↓	↓			Simon et al. (2013)

Table 3. Effects of salt stress on leaf water relations in different ornamental species.

Botanical family	Species	Salt threshold	Observations	References
Asteraceae	<i>Achillea millefolium</i>	0.8-4 dS m ⁻¹ , 70 d	Decline of leaf osmotic potential	Niu and Rodriguez (2006a)
Lamiaceae	<i>Agastache cana</i>			
Lamiaceae	<i>Salvia coccinea</i>			
Ericaceae	<i>Arbutus unedo</i>	0-105 mM NaCl, 16 wks	Decline of leaf water and osmotic potential	Navarro et al. (2007)
Aizoaceae	<i>Delosperma cooperi</i>	0.8-12 dS m ⁻¹ , 11 wks	Decline of leaf osmotic potential	Niu and Rodriguez (2006b)
Celastraceae	<i>Euonymus japonicus</i>	1.8-9 dS m ⁻¹ , 5 months	Decline of leaf water potential	Miralles et al. (2012)
Asteraceae	<i>Gaillardia aristata</i>	0.8-4 dS m ⁻¹ , 3 months	Decline of leaf osmotic potential	Niu et al. (2007)
Asteraceae	<i>Gerbera hybrida</i>	1.5-3 dS m ⁻¹ , 6 months	Decline of leaf water potential	Valdes et al. (2014 a)
Amaryllidaceae	<i>Narcissus sp.</i>	0-300 mM NaCl, 4 months	No variation in leaf osmotic potential	Veatch-Blohm et al. (2014)
Onagraceae	<i>Oenothera elata</i>	1.50-7.30 dS m ⁻¹ , 45 d	Decline of leaf osmotic potential	Niu et al. (2012a)
Lamiaceae	<i>Salvia farinacea</i>			
Asteraceae	<i>Zinnia grandiflora</i>			
Lamiaceae	<i>Phlomis purpurea</i>	1-4 dS m ⁻¹ , 26 wks	Decline of leaf osmotic potential	Alvarez et al. (2012 a)
Rosaceae	<i>Rose sp.</i>	1.6-9.0 dS m ⁻¹ , 15 wks	No variations of leaf osmotic potential	Niu et al. (2008)
Lamiaceae	<i>Salvia hispanica</i>	0.3-60 mM NaCl, 80 d	No variations of leaf water and osmotic potential	Raimondi et al. (2017)
Lamiaceae	<i>Teucrium chamaedrys</i>	0.8-12 dS m ⁻¹ , 11 wks	Increase of leaf osmotic potential	Niu and Rodriguez (2006 b)
Asteraceae	<i>Zinnia marylandica</i>	1.40-8.20 dS m ⁻¹ , 4 wks	Decline of leaf osmotic potential	Niu et al. (2012b)

Table 4. Effects of salt stress on pigments concentration in different ornamental species.

Botanical family	Species	Salt threshold	Observations	References
Fabaceae	<i>Acacia cultriformis</i>	0-15 g NaCl/L, 6 wks	Decrease of total chlorophyll concentration	Vernieri et al. (2010)
Myrtaceae	<i>Callistemon citrinus</i>			
Apocynaceae	<i>Carissa edulis microphylla</i>			
Onagraceae	<i>Gaura lindheimeri</i>			
Oleaceae	<i>Jasminum sambac</i>			
Lamiaceae	<i>Westringia fruticosa</i>			
Rosaceae	<i>Alchemilla mollis</i>	0-400 mM NaCl, 21 d	Decrease of total chlorophyll concentration	Eom et al. (2007)
Lamiaceae	<i>Nepeta faassenii</i>			
Polemoniaceae	<i>Phlox subulata</i>			
Asteraceae	<i>Solidago cutleri</i>			
Lamiaceae	<i>Thymus praecox</i>			
Apocynaceae	<i>Catharanthus roseus</i>	0-100 mM NaCl, 90 d	Decrease of chlorophyll a and b and total chlorophyll concentration	Jaleel et al. (2008)
Asteraceae	<i>Chrysanthemum morifolium</i>	2-16.9 dS m ⁻¹ , 60 d	Decrease of total chlorophyll concentration	Lee and van Iersel (2008)
Solanaceae	<i>Petunia hybrida</i>	0-125 mM NaCl, 1 month	Decrease of chlorophyll a and b concentration	Arun et al. (2016)
Asparagaceae	<i>Polianthes tuberosa</i>	0.7-4.3 dS m ⁻¹ , 47 d	Decrease of total chlorophyll concentration	Bahadoran and Salehi (2015)
Geraniaceae	<i>Pelargonium hortorum</i>	0-3 g/L NaCl, 3 months	Decrease of chlorophyll a and b concentration	Bres et al. (2016)
Asteraceae	<i>Stevia rebaudiana</i>	0-90 mM NaCl, 25 d	Decrease of chlorophyll a and b and total chlorophyll concentration	Cantabella et al. (2017)

Table 5. Effects of salt stress on fluorescence parameters in different ornamental species.

Botanical family	Species	Salt threshold	Observations	References
Celastraceae	<i>Euonymus japonicus</i>	1.8-9.0 dS m ⁻¹ , 6 months	Decrease of photosystem II efficiency and no variations of maximum quantum yield of PSII (Fv/Fm) and non-photochemical quenching (NPQ)	Miralles et al. (2016)
Moraceae	<i>Ficus benjamina</i>	1-5 dS m ⁻¹ , 5 months	No variation of photosystem II efficiency and decrease of maximum quantum yield of PSII (Fv/Fm) and non-photochemical quenching (NPQ)	Valdes et al. (2012)
Verbenaceae	<i>Lantana camara</i>	2-5 dS m ⁻¹ , 5 months	Decrease of photosystem II efficiency, maximum quantum yield of PSII (Fv/Fm) and non-photochemical quenching (NPQ)	Bañon et al. (2011)
Lythraceae	<i>Lawsonia inermis</i>	0-150 mM NaCl, 2 months	Decrease of photosystem II efficiency, maximum quantum yield of PSII (Fv/Fm) and non-photochemical quenching (NPQ)	Fernandez-Garcia et al. (2014)
Myrtaceae	<i>Metrosideros excelsa</i>	2-6 dS m ⁻¹ , 6 months	No variations of photosystem II efficiency, maximum quantum yield of PSII (Fv/Fm) and non-photochemical quenching (NPQ)	Bañon et al. (2012)
Lamiaceae	<i>Phlomis purpurea</i>	1-4 dS m ⁻¹ , 26 wks	No variations of maximum quantum yield of PSII (Fv/Fm)	Alvarez et al. (2012 b)
Polygalaceae	<i>Polygala myrtifolia</i>	2-5 dS m ⁻¹ , 5 months	No variations of photosystem II efficiency, maximum quantum yield of PSII (Fv/Fm) and non-photochemical quenching (NPQ)	Bañon et al. (2011)
Rosaceae	<i>Rosa hybrida</i>	1.5-8.0 dS m ⁻¹ , 2 months	Decrease of maximum quantum yield of PSII (Fv/Fm)	Cai et al. (2014)
Adoxaceae	<i>Viburnum lauristinus</i>	2-6 dS m ⁻¹ , 6 months	Decrease of photosystem II efficiency and no variations of maximum quantum yield of PSII (Fv/Fm) and non-photochemical quenching (NPQ)	Bañon et al. (2012)
Adoxaceae	<i>Viburnum odoratissimum</i>	0-60 mM NaCl, 4 months	No variations of photosystem II efficiency, maximum quantum yield of PSII (Fv/Fm) and non-photochemical quenching (NPQ)	Cacini et al. (2013)

Table 6. References to a decrease of net photosynthesis and stomatal conductance in different ornamental species.

Botanical family	Species	Salt threshold	References
Myrtaceae	<i>Callistemon laevis</i>	0.8-4 dS m ⁻¹ , 10 months	Alvarez and Sanchez-Blanco (2015)
Myrtaceae	<i>Callistemon citrinus</i>	0.8-4 dS m ⁻¹ , 13 months	Alvarez and Sanchez-Blanco (2014)
Myrtaceae	<i>Eugenia myrtifolia</i>	0.3-12 dS m ⁻¹ , 30 d	Acosta-Motos et al. (2015)
Celastraceae	<i>Euonymus japonicus</i>	0.9-4 dS m ⁻¹ , 20 wks	Gomez-Bellot et al. (2013)
Euphorbiaceae	<i>Euphorbia pulcherrima</i>	1.5-4.5 dS m ⁻¹ , 2 months	Valdes et al. (2014 b)
Myrtaceae	<i>Myrtus communis</i>	0.8-8 dS m ⁻¹ , 2 months	Acosta-Motos et al. (2014)
Geraniaceae	<i>Pelargonium hortorum</i>	1.6-6.5 dS m ⁻¹ , 3 months	Valdes et al. (2015 b)
Fabaceae	<i>Sophora secundiflora</i>	0-6 dS m ⁻¹ , 6 months	Niu et al. (2010)
Adoxaceae	<i>Viburnum tinus</i>	0.9-4 dS m ⁻¹ , 6 months	Gomez-Bellot et al. (2015)

Table 7. Changes in proline and concentration of soluble sugars in leaves of different ornamental species.

Botanical family	Species	Salt threshold	Observations	References
Asteraceae	<i>Calendula officinalis</i>	50-100 mM NaCl, 36 d	Increase of proline concentration	Lacramioara et al. (2015)
Myrtaceae	<i>Eugenia myrtifolia</i>	0.3-12 dS m ⁻¹ , 30 d	Increase of proline concentration	Acosta-Motos et al. (2015)
Asteraceae	<i>Gerbera jamesonii</i>	0-40 mM NaCl, 6 months	Increase of proline concentration	Don et al. (2010)
Iridaceae	<i>Iris hexagona</i>	0-100 mM NaCl, 5 months	Increase of proline concentration	Wang et al. (2008)
Asparagaceae	<i>Polianthes tuberosa</i>	0.7-4.3 dS m ⁻¹ , 47 d	Increase of proline concentration	Bahadoran and Salehi (2015)
Geraniaceae	<i>Pelargonium hortorum</i>	0-3 g L ⁻¹ NaCl, 3 months	Increase of proline concentration	Bres et al. (2016)
Lamiaceae	<i>Rosmarinus officinalis</i>	0-150 mM NaCl, 4 wks	Increase of proline concentration	Tounekti et al. (2011)
Lamiaceae	<i>Lavandula multifida</i>	10-200 mM NaCl, 60 d	Increase of soluble sugars concentration	García-Caparrós et al. (2017)
Apocynaceae	<i>Cataranthus roseus</i>	50-200 mM NaCl, 4 months	Increase of soluble sugars concentration	Elfeky et al. (2007)
Boraginaceae	<i>Echium amoenum</i>	0-12 dS m ⁻¹ , 6 wks	Increase of soluble sugars concentration	Ramezani et al. (2011)

Table 8. Effects of salt stress on the antioxidant activity in different ornamental species.

Botanical family	Species	Salt threshold	Observations	References
Simaroubaceae	<i>Ailanthus altissima</i>	0-300 mM NaCl, 2 d	Increase of SOD and CAT activity	Filippou et al. (2014)
Asteraceae	<i>Calendula officinalis</i>	50-100 mM NaCl, 36 d	Increase of SOD, POX and CAT activity	Lacramioara et al. (2015)
Apocynaceae	<i>Catharanthus roseus</i>	0-100 mM NaCl, 2 months	Increase of SOD, POX and CAT activity	Misra and Gupta (2006)
Apocynaceae	<i>Catharanthus roseus</i>	0-100 mM NaCl, 90 d	Increase of APX activity and decrease of SOD, POX and CAT activity	Jaleel et al. (2007)
Myrtaceae	<i>Myrtus communis</i>	0.8-8 dS m ⁻¹ , 2 months	Decrease of APX activity and increase of SOD and POX activity	Acosta-Motos et al. (2014)
Solanaceae	<i>Petunia hybrida</i>	0-125 mM NaCl, 1 month	Decrease of CAT and POX activity	Arun et al. (2016)
Myrtaceae	<i>Eugenia myrtifolia</i>	0.9-7 dS m ⁻¹ , 23 wks	Decrease of APX activity and increase of SOD, POX and CAT activity	Acosta-Motos et al. (2017 b)
Apocynaceae	<i>Nerium oleander</i>	0-800 mM NaCl, 30 d	Increase of SOD, CAT and APX activity	Kumar et al. (2017)
Asteraceae	<i>Stevia rebaudiana</i>	0-90 mM NaCl, 25 d	Decrease of APX activity and increase of SOD, POX and CAT activity	Cantabella et al. (2017)