



Review

The effects of salt stress on ornamental plants and integrative cultivation practices

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ABSTRACT

Ornamental horticultural production is closely associated with a high water consumption and yet the availability of freshwater is reducing. The irrigation of ornamental plants with saline water may be an alternative, but an improvement in knowledge of the effects on salinity on species used as ornamentals is essential. In this review, considering the references from the last decade, we summarized the main effects of salt stress on growth, nutrient, photosynthetic and physiological parameters in ornamental plants. At high salinities, plants exhibit a reduction of growth parameters such as biomass or leaf area related to osmotic and ionic effects of salinity. Growth under saline conditions leads to uptake of Na^+ and Cl^- by plants, which can result in a nutritional imbalance due to the antagonism between nutrients and saline ions with possible effects on the foliage. Salinity can affect water relations in plants and photosynthetic capacity by stomatal limitations. These negative effects can be counteracted by the plants through the accumulation of compatible solutes or osmolytes and the activation of antioxidant machinery. Nevertheless, the performance of these mechanisms is sometimes not enough to avoid damage to the appearance of the plant and in consequence the saleability of an ornamental species. In this review recommendations for the establishment of integrative cultivation practices for nursery growers are made; these include exogenous application of nutrients and osmolytes and enrichment with CO_2 , in order to mitigate the damage caused by salt stress to ornamental plants.

1. Introduction

Ornamental plants have an important place within the horticultural industry as they are used in gardening, landscaping, and as cut flowers. The total turnover for all aspects of floriculture is estimated to be more than 300 billion USD and cut flowers make up about one-third of the global value of the ornamental plants market (Azadi et al., 2016). Currently, the main constraint to ornamental plant production is water consumption: it has been estimated that 100–350 kg of water are needed to produce 1 kg of plant dry matter, although this can vary with species and variety, cultivation system and plant growing season (Fornes et al., 2007). Growers have, over decades, used high quality water to irrigate ornamental plants because of their high economic value. Nowadays the increase in population and agricultural production together with the diminishing sources of fresh water continue to intensify competition for good water (Carter and Grieve, 2010).

Ornamental plants can be grown under field conditions and sold on as bare-rooted plants or potted in containers filled with substrates such as peat moss, coconut fibre or different kinds of mixtures with other

materials (Reid and Jiang, 2012). The selection of how plants are grown, whether under field conditions or in containers, will be influenced by the salinity in the soil and the irrigation water available. There are different causes of salinity in the soil and water. In the case of the soil, the main causes are long-term natural accumulation of salts, deposition of sea-salt carried by wind and rain and anthropogenic activities that disrupt the hydrologic balance of the soil between water applied (irrigation or rainfall) and water used by crops (transpiration) (Singh, 2015). For the salinization of water, the main causes are over-exploitation of ground-waters, percolation of salts into the aquifers and seawater intrusion in aquifers (Payen et al., 2016).

Soils are considered saline when they have an EC of 4 dS m^{-1} or higher, which can be particularly problematic if the increased EC is the result of NaCl (Ghassemi et al., 1995). Cassaniti et al. (2013) (modified from Paranychianakis and Chartzoulakis, 2005) classified water salinity by EC as freshwater with lower values of 0.6 dS m^{-1} , slightly brackish with 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} , moderately saline from 3 to 8 dS m^{-1} , saline from 8 to 15 dS m^{-1} and highly saline from 15 to 45 dS m^{-1} .

Abbreviations: DW, dryweight; EC, electrical conductivity; FW, fresh weight; LED, light emitting diode; PT, pour through

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Plant growth response under saline conditions presents two phases. In the first phase (osmotic stress), there is a growth reduction which starts immediately after exposure of the roots to salt. This effect is associated with an osmotic impediment to water uptake and consequent changes in water relations at a cellular level. The second phase (ionic toxicity) results when leaves, becoming senescent, are anymore able to compartmentalize sufficient Na^+ and Cl^- to prevent effects on photosynthesis and consequently old leaves die (Munns and Tester, 2008). However, plants differ considerably in the concentration of salt that brings about these changes and species have been divided into halophytes and glycophytes. Some halophytes benefit from growing under saline conditions, whereas among glycophytes some species are more tolerant than others (see Munns and Tester, 2008). The main difference between the two groups of plants is the mechanism adopted to face the salinity stress (see Flowers and Colmer, 2015).

The effect of saline irrigation on ornamental plants has been investigated to a much lesser extent than other crops because ornamentals are normally irrigated with high quality water. Nevertheless, there are many papers on the effects of the saline stress in ornamental plants, describing the effects on one or more species (e.g. Valdés et al., 2015a; García-Caparrós et al., 2016) as well as comprehensive reviews (Niu and Cabrera, 2010; Cassaniti et al., 2013; Acosta-Motos et al., 2017a). In this review we update information on the effects of salinity on ornamental plants with material covering the last ten years, tabulating effects on growth, nutritional status, water relations, photosynthetic parameters, osmolytes accumulation and antioxidant activity, with the aim of allowing the grower to make rational choices of plants and culture methods.

2. The effects of salt stress on ornamental plants

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

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 (Negrão et al., 2017).

Roots are the most vulnerable part of the plant because they are directly exposed to salt, as a result, water absorption capacity, water use efficiency and other parameters and processes may be affected (Sánchez-Blanco et al., 2014). In general, root growth is inhibited by exposure to high salinity as a result of osmotic and toxic effects (Bañón et al., 2012), although this response depends on the species and salinity level. For instance, *Phlomis purpurea* plants irrigated with water of 4 dS m^{-1} reduced root DW, although *Callistemon citrinus*, *Evonimus* and *Pistacia lentiscus* plants irrigated with the same salt level did not show a reduction in root DW (Castillo, 2011; Álvarez et al., 2012b; Gómez-Bellot et al., 2013).

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

effects produced by saline irrigation, some researchers have proposed that arbuscular mycorrhizal fungi have positive effects on the growth of crops under saline conditions being a sustainable option that should be considered (Porcel et al., 2012; Estrada et al., 2013).

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

A typical response to salt stress described in literature is a reduction in total leaf area. The reduction in leaf area, a consequence of changes in cell wall properties, cell water relations and a reduction in photosynthetic rate (Munns and Tester, 2008), has been recorded (see Table 1) for *Paulownia* sp. (Ivanova et al., 2014), *Callistemon laevis* (Álvarez and Sánchez-Blanco, 2015) and *Euonymus japonicus* (Gómez-Bellot et al., 2013). A reduction of leaf area due to the salt stress could, again, be beneficial for nursery growers, especially when they want to produce compact plants avoiding the use of plant growth regulators (Rademacher, 2015). Also, reduced leaf area is an avoidance mechanism in order to minimise water loss via transpiration under saline conditions (Acosta-Motos et al., 2017a).

In floricultural crops, under salt stress there can be a reduction of the number and quality of flowers as was reported in previous literature (Wahome et al., 2000; Shillo et al., 2002). Thus, plants subjected to saline stress may reduce flowering intensity, bring forward or delay flowering and shortened the period of flowering (Fornes et al., 2007; Álvarez et al., 2012a). This effect can be related to an alteration of the concentration of hormones directly involved in flowering such as abscisic and jasmonic acids (Rogers, 2013). The reduction of number and quality of flowers can result in a decrease of sales for floricultural crops which is not acceptable to growers. Therefore, one possible solution to mitigate these effects could be the foliar application of hormones, following the recommendations given in a comprehensive review on post-harvest biology and technology in potted plants by Reid and Jiang (2012). For instance, Ashour and Sakr (2016) reported the application of ABA or salicylic acid on *Hamelia patens* plants to alleviate the effects of saline irrigations. On the same hand, Gad et al. (2016) noted an enhancement of growth and flowering in *Ixora coccinea* plants sprayed with salicylic acid.

2.2. Nutritional balance

Salt stress can affect the nutritional status of a plant through a complex net of interactions, including a decrease of nutrient uptake and/or transport from root to shoot (Munns and Tester, 2008). As can be seen in Table 2, ornamental plants grown under saline conditions exhibited a decrease of N, P, K and Ca concentration in leaves related to antagonisms with Cl and Na and an increase in Na and Cl concentration in leaves.

Under salt stress conditions, nitrogen uptake is often disrupted mainly due to the antagonism between Cl^- and NO_3^- (Munns and Gilliam, 2015). Salinity stress also reduces P availability because of the antagonism between Cl^- and H_2PO_4^- as reported by Parihar et al. (2015). Reduced uptake of P under salt stress can also be a consequence of the strong influence of sorption processes that control the concentration of P in the soil and low solubility of Ca-P minerals (Marschner, 2011). The inhibition of K^+ uptake in plant occurs primarily due to the physical and chemical similarities between K^+ and Na^+ and the tendency of the latter to compete with K^+ for major

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>		DW reduction of 70-90%	
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>		DW reduction > 90%	
Euphorbiaceae	<i>Euphorbia hybrida</i>			
Lamiaceae	<i>Salvia splendens</i>			
Asteraceae	<i>Zinnia angustifolia</i>		100% mortality	Simón et al. (2010)
Violaceae	<i>Viola tricolor</i>			
Arecaceae	<i>Chamaerops humilis</i>	2-8 dS m ⁻¹ , 2 years	Total biomass decrease of 38%	
Arecaceae	<i>Washingtonia robusta</i>		Total biomass decrease of 48%	
Asparagaceae	<i>Hyacinthus orientalis</i>	0-600 mM NaCl, 15 d	Plant fresh weight reduction of 55%	
Adoxaceae	<i>Viburnum lucidum</i>	0-200 mM NaCl, 3 months	Roots and shoots dry weight reduction (29 and 37%; respectively)	
Lamiaceae	<i>Lavandula angustifolia</i>	0-100 mM NaCl, 21 d	Plant dry weight reduction of 55-80%	
Lamiaceae	<i>Salvia hispanica</i>	0.3-60 mM NaCl, 80 d	Plant dry weight reduction (90%)	
Asteraceae	<i>Stevia rebaudiana</i>	0.4-12 dS m ⁻¹ , 1 year	Plant fresh and dry weight reduction (75 and 50%; respectively)	
Asteraceae	<i>Tagetes erecta</i>	2-10 dS m ⁻¹ , 16 d	Plant height reduction of 20-25%	Valdez-Aguilar et al. (2009)
Euphorbiaceae	<i>Euphorbia pulcherrima</i>	0.5-1.2 g NaCl L ⁻¹ , 4 months	Plant height reduction of 10-20%	Gent et al. (2016)
Paulowniaceae	<i>Paulownia</i> sp.	50-200 mM NaCl, 58 d	Leaf area reduction of 80%	Ivanova et al. (2014)
Myrtaceae	<i>Callistemon laevis</i>	0.8-4 dS m ⁻¹ , 10 months	Leaf area reduction of 37%	Álvarez and Sánchez-Blanco (2015)
Celastraceae	<i>Euonymus japonicus</i>	0.9-4 dS m ⁻¹ , 20 wks	Leaf area reduction of 43%	Gómez-Bellot et al. (2013)
Iridaceae	<i>Freesia</i> sp.	1.5-6 dS m ⁻¹ , 7 months	Flower number reduction (30-45%)	Aydinsakir et al. (2010)
Rosaceae	<i>Rosa hybrida</i>	1.5-8.0 dS m ⁻¹ , 2 months	Flower number reduction (42-77%)	Cai et al. (2014)

binding sites, including control of enzymatic activity that occurs at unfavourable cytosolic K⁺/Na⁺ ratios (Adams and Shin, 2014; Benito et al., 2014). With respect to Ca, the decrease in uptake is due to the to the antagonistic effect between Ca²⁺ and Na⁺ ions, which affects membrane properties, due to displacement of membrane-associated Ca²⁺ by Na⁺, leading to dissolution of membrane integrity and selectivity (Kopittke, 2012).

In plants subjected to saline conditions, there is an increase of toxic elements such as Na⁺ and Cl⁻ in leaves that can result in visual damage

like tip and marginal burn, with negative influences on decorative value (Cassaniti et al., 2009). The typical symptoms of Na⁺ accumulation are leaf burn, scorch and dead tissue along the leaf margins, which first occur in the oldest leaves. As the severity increases, the drying progresses towards the leaf centre until the entire tissue is dead. Injury due to Cl⁻ toxicity, however, typically, starts at the extreme leaf tip of older leaves and progresses from the tip back as the severity increases (Cassaniti et al., 2013).

The fact that water uptake by plants and relative exclusion of Na⁺

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

H	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			↓	↓	↑	↑	
Buxaceae	<i>Buxus sempervirens</i>	0-250 mM NaCl, 5 months					↑	↑	Caser et al. (2013)
Arecaceae	<i>Chamaerops humilis</i>	2-8 dS m ⁻¹ , 2 years	↓	↓	↓		↑	↑	Simón et al. (2010)
Arecaceae	<i>Washingtonia robusta</i>		↓	↓	↓	↓			
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>Escallonia exoniensis</i>	0.6-8 dS m ⁻¹ , 6 months			↓		↑	↑	Valdez-Aguilar et al. (2011)
Malvaceae	<i>Hibiscus rosa sinensis</i>						↑	↑	
Cupressaceae	<i>Juniperus chilensis</i>						↑		
Rosaceae	<i>Raphiolepis indica</i>				↓		↑	↑	
Buxaceae	<i>Buxus microphylla</i>				↓		↑	↑	
Brassicaceae	<i>Matthiola incana</i>	2.5-14 dS m ⁻¹ , 2 months			↓	↓	↑	↑	Grieve et al. (2006)
Liliaceae	<i>Cordylone fruticosa</i>	1.5-4.5 dS m ⁻¹ , 2 months		↓	↓		↑	↑	Plaza et al. (2012a,b)
Asteraceae	<i>Osteospermum hybrida</i>	1.5-5 dS m ⁻¹ , 14 wks			↓		↑	↑	Valdés et al. (2015a)
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. (2014)

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

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

2.3. Water relations

Plant-water relations explain the behaviour of plants in terms of how they control the hydration of their cells, which is essential in physiological and metabolic processes that determine the quantity and quality of plant growth (Acosta-Motos et al., 2017a). One of the main problems for plants growing under saline conditions is the low water potential in the soil solution due to the increase of solute concentration in the root zone, therefore in order to ensure the water flow plants should adjust osmotically, decreasing their water and osmotic potentials (Cassaniti et al., 2013).

Water potential and osmotic potential of plants become more negative with an increase in salinity. Leaf water potential and osmotic potential decline depending on the osmotic potential of the rooting medium and the mode of stress imposition (Parihar et al., 2015). Consequently, it might be expected that ornamental plants grown under salt stress will show a decrease of water and osmotic potential, but the reality is that each species behaves differently (Table 3). For instance, *Narcissus* sp., *Rose* sp. and *Salvia hispanica* exhibited no variation of leaf osmotic potential under saline conditions while *Teuchrium chamaedrys*

showed an increase of leaf osmotic potential; the rest of the species in Table 3 showed a decline of leaf osmotic potential. Although the results showed in Table 3 are mainly referred to leaf osmotic potential it is necessary to point out that according to Álvarez and Sánchez-Blanco (2014), stem water potential (Ψ_s) is a good indicator of the osmotic stress resulting from salinity since Ψ_s identify differences between treatments earlier than leaf water potential (Ψ_l), which did only when the salt stress became more severe. Any change in water relations in ornamental plants can result in an appearance of drought stress and a decrease of growth thus there is a reduction in the saleability of plants with these symptoms. From the nursery grower's point of view, the different trends between species can be solved with an irrigation-schedule based on the evapotranspiration demands of each species under saline conditions in order to improve their quality, but it is also necessary to prevent the salt accumulation in the substrate considering an adequate percentage of leaching fraction and the maintenance of constant substrate humidity (Bañón et al., 2011). Nevertheless, the applicability of this evapotranspiration-based irrigation scheduling is difficult for growers, since it requires an exhaustive study over several years. For instance, in an experiment conducted on *Forsythia intermedia*, *Photinia fraseri*, *Prunus laurocerasus* L. and *Viburnum tinus* L. during the summer of four consecutive years (2007–2010), Incrocci et al. (2014) determined the evapotranspiration irrigation scheduling of these species according to the type of container used for the growth. Carmassi et al. (2013) determined the rate of evapotranspiration of *Gerbera jamesonii* grown under greenhouse conditions in a Mediterranean climate. Such experiments need to be carried out under saline conditions if this methodology is to be applied to the use of brackish water, in evapotranspiration-based irrigation.

2.4. Photosynthetic parameters

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

2.4.1. Chlorophyll content

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

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 Rodríguez (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 , 11wks	Decline of leaf osmotic potential	Niu and Rodríguez (2006b)
Lamiaceae	<i>Teucrium chamaedrys</i>		Increase of leaf osmotic potential	
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	Valdés et al. (2014a)
Amaryllidaceae	<i>Narcissus</i> sp.	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	Álvarez et al., Álvarez et al. (2012a)
Rosaceae	<i>Rose</i> sp.	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)
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)

It is well-known that chlorophyll content in plants correlates directly to the healthiness of plant (Barry, 2009). A decrease in chlorophyll concentration under salt stress is a commonly reported phenomenon used as a sensitive indicator of the cellular metabolic state. This decrease may be related to membrane deterioration (Silveira and Carvalho, 2016). Nevertheless, it is also possible to find that under salt stress, plants show an increase of chlorophyll concentration that can be due to an increase in the number of chloroplast per unit leaf area in the stressed plant leaves as reported by Chaum and Kirdmanee (2009). For instance, in an experiment conducted on *Eugenia myrtifolia* grown in pots filled with a mixture of coconut fibre, sphagnum peat and Perlite (8:7:1) and irrigated with increasing NaCl concentrations, Acosta-Motos et al. (2015) reported an increase in total chlorophyll concentration compared to the control treatment.

A decrease of chlorophyll concentration in ornamental plants under saline conditions has been recorded by many researchers (Table 4). This negative effect results in the yellowing of leaves affecting the visual appearance and thus the sale value of these ornamental species. One relatively cheap possibility to increase the chlorophyll concentration in leaves in these species is through the foliar application of magnesium, since its concentration is essential to the generation of chlorophyll. For instance, in an experiment conducted on strawberry grown under saline conditions, Yildirim et al. (2009) reported an increase of chlorophyll concentration in plants treated with magnesium nitrate as foliar fertilizer. Even though this result was on strawberry it might be used as a practical application in ornamentals too.

2.4.2. Photosystem II photochemical efficiency

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

(Ruban, 2016).

Few papers have analysed the effect of salinity on chlorophyll fluorescence in ornamental plants. From the general responses of plants to salinity, the most common trend in chlorophyll fluorescence would be predicted to be a decrease of PSII efficiency and photochemical quenching parameters (Fv/Fm) and an increase in non-photochemical quenching parameters as has been previously reported in an experiment conducted in roses (Jiménez et al., 1997). However, there is a great variability in the effects of salinity on the chlorophyll fluorescence in ornamental plants (Table 5), but the response of each species is related to its degree of salt tolerance, confirming that chlorophyll fluorescence is a good indicator of which species to grow with saline water. The changes in chlorophyll fluorescence in ornamental plants involve a reduction of the photosynthetic capacity in leaves causing physiological changes that result in a loss of sale capacity for the growers. These negative effects could be mitigated through the use of light-emitting diode (LED) lamps at different wavelengths according to the requirement of each species. In an experiment carried out under non-saline conditions with different ornamental species such as *Impatiens walleriana*, *Petunia hybrida*, *Tagetes patula* and *Salvia splendens*, Wollaege and Runkle (2013) reported that under red light conditions (600–700 nm), these species exhibited an improvement in the photosynthetic efficiency. Bergstrand and Schussler (2012) also reported that supplementary lighting, supplied by white LED and red/blue LED improved the photosynthesis in *Euphorbia pulcherrima*. Such experiments now need to be carried out under saline conditions.

2.4.3. Net photosynthesis and stomatal conductance

It is assumed that under saline conditions, plants suffer a decrease of net photosynthesis and stomatal conductance. The reduction in photosynthetic rate in plants under salt stress may be due to several factors: a) dehydration of cell membranes, which reduces their permeability to CO₂, b) salt toxicity, c) reduction of CO₂ supply because of hydroactive closure of stomata, d) enhanced senescence induced by salinity and e) changes of enzyme activity induced by changes in cytoplasmic structure (Gururani et al., 2015). Under salt stress there is a reduction in stomatal conductance which restricts the availability of CO₂ for carboxylation reactions. Moreover, this stomatal closure minimizes loss of water through transpiration and this affects light-harvesting and energy-conversion systems thus leading to alteration in chloroplast activity (Chaves et al., 2011).

The recent literature suggests ornamental plants subjected to saline conditions exhibited a decrease of net photosynthesis and stomatal conductance (Table 6). The consequence of these changes in

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)	Valdés 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)	Bañón et al. (2011)
Polygalaceae	<i>Polygala myrtifolia</i>		No variations of photosystem II efficiency, maximum quantum yield of PSII (Fv/Fm) and non-photochemical quenching (NPQ)	Fernández-García et al. (2014)
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)	Bañón et al. (2012)
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)	
Adoxaceae	<i>Viburnum lauristinus</i>		Decrease of photosystem II efficiency and no variations of maximum quantum yield of PSII (Fv/Fm) and non-photochemical quenching (NPQ)	
Lamiaceae	<i>Phlomis purpurea</i>	1–4 dS m ⁻¹ , 26 wks	No variations of maximum quantum yield of PSII (Fv/Fm)	Álvarez et al., Álvarez et al. (2012b)
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 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)

photosynthesis is a reduction of saleable plants, therefore the enrichment of atmospheric CO₂ for ornamental plants with a high profitability could be an appropriate technology to overcome the negative effects of salinity. However, although a common practice in commercial horticulture, the establishment of this technique is expensive. Zhang et al. (2012) and Xu et al. (2014) conducted experiments on *Gerbera jamesonni* and *Impatiens hawkeri* and reported that the enrichment of CO₂ at levels of 800 μmol·mol⁻¹ resulted in a growth increase of these species. These studies were not, however, conducted under saline conditions so that it would be necessary to investigate the interaction of salinity and enrichment of CO₂ on the growth of ornamentals.

2.5. Osmolytes

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

Compatible solutes include compounds such as proline, sugars, glycine-betaine and other related quaternary ammonium compounds (Szabados and Savoure, 2010; Slama et al., 2015), but due to the lack of information on the effects of salt stress on the accumulation of solutes in ornamental plants, we will focus on two of them: proline and soluble sugars.

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

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

In the recent literature on the effect of salt stress on ornamental plants, it is clear that the proline concentration in leaves is commonly increased (Table 7), suggesting that the exogenous application of this osmolyte could be a useful tool for nursery growers to produce plants of better quality using saline irrigation water. Zheng et al. (2015) carried out experiments in *Eurya emarginata* plants grown under different levels of salinity and reported that the exogenous application of proline resulted in an improvement of the salinity tolerance in this species. This relatively simple procedure could be evaluated for other ornamentals. It is necessary to point out that another cheaper solution to overcome the effects of salt stress could be the exogenous application of glycine-betaine since the commercial price is much lower than proline price.

As far as soluble sugars are concerned, it is assumed that under saline stress there is an increase of concentration of soluble sugars in plants as sugars play a central role in osmoprotection, osmotic adjustment, carbon storage and radical scavenging under salt stress (Sami et al., 2016). The increase of soluble sugars under salt stress may be related to a decrease of sucrose phosphate synthase activity and a decrease of starch phosphorylase activity as reported by Ruan (2014). The

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	Álvarez and Sánchez-Blanco (2015)
Myrtaceae	<i>Callistemon citrinus</i>	0.8–4 dS m ⁻¹ , 13 months	Álvarez and Sánchez-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	Gómez-Bellot et al. (2013)
Euphorbiaceae	<i>Euphorbia pulcherrima</i>	1.5–4.5 dS m ⁻¹ , 2 months	Valdés et al. (2014b)
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	Valdés et al. (2015b)
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	Gómez-Bellot et al. (2015)

increase of soluble sugars under increasing NaCl concentration in ornamental plants has been recorded only by a few researchers (Table 7). In previous literature there are reports of the value of exogenous application of soluble sugars in order to improve the postharvest longevity of, for instance, cut flowers: Ahmad et al. (2013) and Arrom and Munné-Bosch (2012) carried out experiments with *Rosa hybrida* and *Eustoma grandiflorum*, respectively, where they reported that the application of sucrose resulted in an improvement of post-harvest longevity of cut flowers. However, there are no reports on the use of exogenous soluble sugars to increase the salt tolerance in ornamental plants. Nevertheless, we suggest that nursery growers might evaluate the exogenous application of soluble sugars in ornamental plants as a possible tool for the improvement of the salinity tolerance, as occurs with the exogenous application of proline. It is necessary to point out that the use of this technique can result in growth increase of pathogens and attraction of insects, therefore additional measures should be considered.

Some authors also suggest that the paclobutrazol minimizes the absorption of toxic ions such as Na⁺ and Cl⁻, which eliminates the negative effects of NaCl. Paclobutrazol reduced saline stress symptoms and mortality in *Nerium oleander* stressed plants by promoting organic solutes synthesis and by reducing the availability of saline ions in the medium (Bañón et al., 2005).

2.6. Antioxidant responses

Under saline conditions, one of the common responses of plants is the accelerated generation of reactive oxygen species (ROS), which include the superoxide radical (O₂⁻), singlet oxygen (¹O₂), hydroxyl radical (OH[•]) and hydrogen peroxide (H₂O₂), all of which are cytotoxic to plants (De Gara and Foyer, 2017). The main sources of ROS generation in the cell are mitochondria, chloroplasts and peroxisomes (Pucciariello and Perata, 2017). These reactive oxygen species are involved in different process such as the DNA damage, lipid peroxidation and protein oxidation (Mittler, 2017).

In order to overcome the negative effects of ROS at the cellular

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

3. Conclusions

High water consumption associated with growing ornamental plants in a world with decreasing fresh water availability suggests the use of saline waters by nursery growers for the production of these plants. However, salt stress involves among others growth reduction, nutritional imbalances, changes in water relations and photosynthesis, oxidative stress that reduce the visual quality of ornamental plants and as a consequence their saleability. Therefore, where brackish water is used, the establishment of new cultivation methods by nursery growers is advocated; methods such as efficient irrigation management, the exogenous application of nutrients and osmolytes, shading and the enrichment of CO₂, all of which might mitigate damage caused by the salinity and at the same time improve the ornamental value and the profitability of these species.

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)
Liliaceae	<i>Cordylone fruticosa</i>	1.5–4.5 dS m ⁻¹ , 2 months	Increase of proline concentration	Plaza et al. (2009)
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. (2017b)
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)

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