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RESPONSE OF LISIANTHUS TO IRRIGATION WITH SALINE WATER: ION RELATIONS

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□ *Eustoma grandiflorum* (Raf.) Shinn. (lisianthus) is a moderately salt tolerant species that can be produced commercially under irrigation with saline wastewaters prevalent in two salt-affected areas of California. The objective of the present studies was to determine the effect of irrigation with saline waters of two different compositions on the ion accumulation and ion relations of lisianthus 'Pure White' and 'Echo Blue'. The ionic composition of irrigation waters simulated the compositions typical of i) seawater dilutions (SWD) and ii) concentrations of Colorado River water (CCRW). Electrical conductivities (EC) of SWD and CCRW were between 2 and 12 dS · m⁻¹. Plants irrigated with CCRW were higher in Ca²⁺ compared to plants irrigated with SWD water. Calcium was also higher in 'Pure White' than in 'Echo Blue'. Increasing EC of irrigation water caused a significant decrease in shoot and leaf Ca²⁺ concentration in 'Echo Blue', but had no effect on Ca²⁺ content of 'Pure White' shoots and leaves. Magnesium concentration in 'Echo Blue' was higher than in 'Pure White'. Electrical conductivity did not significantly affect Mg²⁺ concentration of either cultivar, despite the increasingly higher external concentration. Potassium concentration of young and mature leaves of 'Echo Blue' increased as EC increased from 2 to 8 dS · m⁻¹, then decreased significantly once EC exceeded 8 dS · m⁻¹. Potassium concentration of 'Pure White' leaves decreased over the range of salinity treatments tested, suggesting that the reduced potassium ion (K⁺) activity at EC levels of 8 dS · m⁻¹, or less, that resulted in lower leaf-K⁺ in 'Pure White' did not cause a decrease in K⁺ uptake in 'Echo Blue'. Increases in external Na⁺ caused a significant increase in Na⁺ in 'Pure White' leaves and these plants exhibited the best growth even when levels of Na⁺ were high enough to be considered detrimental for growth.

Keywords: cut flowers, nutrient accumulation, salinity, stress physiology, water reuse

INTRODUCTION

Salinity is a grave problem that adversely affects agricultural productivity worldwide by altering the physical and chemical properties of over 831

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million hectares (Martínez-Beltrán and Manzur, 2005). Plant growth is detrimentally affected by salinity due to the disruption of certain physiological processes that lead to reductions in yield and/or quality. Growth, yield, and quality reduction may occur via i) a decrease in the ability of plants to take up water from the soil solution, ii) the destruction of soil structure (Barrett-Lennard, 2003), and iii) toxicity due to excessive concentration of certain ions. Salinity also causes nutritional imbalances due to ion competition for uptake and/or transport, decreased nutrient activity, or partitioning within the plant (Grattan and Grieve, 1999).

Water for irrigation is one of the most important limiting factors in agricultural production because of decreasing availability and quality (Raviv and Bloom, 2001). Salinity of water is a problem because it introduces salts to the soil, which accumulate in the root zone if leaching is insufficient, hydraulic conductivity is low, or inadequate drainage (Rengasamy, 2006).

Cut flower growers rarely use saline water for irrigation because of the potential reduction in plant productivity and quality. However, they will eventually have to confront the dilemma by either moving their operations to sites in which water quality and quantity do not pose a problem, or by continuing production at their current site but at the same time, developing techniques to ameliorate the response of plants to irrigation with saline water. Due to these facts, in recent years, there has been an increasing interest as to the feasibility of commercial production using alternative waters (agricultural drainage waters, treated municipal wastewaters, saline groundwaters) for irrigation of ornamental species.

Lisianthus [*Eustoma grandiflorum* (Raf.) Shinn.] has become a consumer favorite in the cut flower market due to its exceptional blooms and long vase life. More than 40% of lisianthus operations in United States (US) are located in the coastal areas of California, where seawater intrusion is a problem, or in the southern inland valleys, where water quality and quantity issues are prevalent due to drainage of agricultural fields with high nutrient and salt concentrations (Carter et al., 2005a). Previous research has demonstrated that lisianthus can be grown profitably when irrigated with saline water with an electrical conductivity (EC) as high as $8 \text{ dS} \cdot \text{m}^{-1}$, without measurable impact in flower quality (Valdez-Aguilar et al., 2013). In the present study we report the ion accumulation of lisianthus in response to irrigation with two solutions differing in ionic composition that are typical of i) well waters contaminated with seawater dilutions (SWD) and ii) tailwaters prevalent in the inland valleys of southern California and essentially represent concentrations of Colorado River water (CCRW). The goal of this study was to achieve a better understanding of the effect of salinity in irrigation water on plant nutrient uptake and accumulation, which could be used to design nutritional programs that would attenuate its detrimental impact.

MATERIALS AND METHODS

Experiment 1. Effect of Irrigation with Sea Water Dilutions or Concentrations of Colorado River Water Compositions

This experiment was conducted in a greenhouse at the US Salinity Laboratory in Riverside, CA. Experimental conditions were as described for experiment 1 by Valdez-Aguilar et al. (2013). Daily air temperature ranged from 19.9 to 41.6°C (average 23.1°C) while night temperature ranged from 10.7 to 20.2°C (average 17.8°C). Relative humidity ranged from 43.6 to 47.5% (average 44.6%) and average daily photosynthetically active radiation (PAR) was 355.5 $\mu\text{mol m}^{-2} \text{s}^{-1}$, while noontime average PAR was 761.8 $\mu\text{mol m}^{-2} \text{s}^{-1}$.

Lisianthus 'Pure White' plugs were transplanted in 360 L tanks containing washed sand with volumetric water content of 0.34 $\text{m}^3 \cdot \text{m}^{-3}$ at saturation. Plants were allowed to establish by irrigating them twice daily with a complete nutrient solution containing 3 mM potassium nitrate (KNO_3), 0.34 mM monopotassium phosphate (KH_2PO_4), 50 μM iron diethylenetriaminepentaacetic acid (Fe-DTPA), 23 μM boric acid (H_3BO_3), 5 μM manganese sulfate (MnSO_4), 0.4 μM zinc sulfate (ZnSO_4), 0.2 μM copper sulfate (CuSO_4), and 0.1 μM molybdic acid (H_2MoO_4) ($\text{EC} = 2 \text{ dS} \cdot \text{m}^{-1}$). Riverside municipal water ($\text{EC} = 0.6 \text{ dS} \cdot \text{m}^{-1}$) was used for nutrient solution preparation. Each irrigation lasted 15 minutes and then drainage solution was retrieved in 765 L subsurface reservoirs for reuse every irrigation.

The treatments consisted of two different water compositions and five salinity levels (Table 1). Ionic composition 1 was typical of coastal well waters contaminated with seawater, i.e. SWD. Composition 2 mimicked the ionic content of tailwaters present in the inland valley areas of southern California and is essentially CCRW. In both cases, the ion content of the irrigation

TABLE 1 Ion concentration of irrigation waters simulating the composition of sea water dilutions (SWD) and concentrations of Colorado River water (CCRW), in California

Salinity Type	EC $\text{dS} \cdot \text{m}^{-1}$	Concentration $\text{meq} \cdot \text{L}^{-1}$				
		Ca^{2+}	Mg^{2+}	Na^+	SO_4^{2-}	Cl^-
SWD	2	5.0	1.6	12.9	0.5	14.5
	5	8.1	5.7	34.0	2.2	43.1
	7	10.1	8.0	47.8	3.2	60.6
	10	12.0	11.6	70.8	3.6	88.4
	12	15.0	14.1	84.3	5.6	107.0
CCRW	2	5.1	6.0	10.5	6.6	13.3
	5	9.6	15.4	26.6	16.6	34.8
	7	13.4	22.2	38.0	23.6	49.6
	10	18.9	32.1	55.2	34.5	72.5
	12	22.7	38.8	66.9	72.5	87.8

waters were calculated from predictions based on simulations of what long-term compositions of the waters would be upon further concentration due to plant water extraction and water evaporation (Suarez and Simunek, 1997). Salinization of the solutions commenced 1 week after transplant, and was incrementally increased over 8 days to avoid osmotic shock to the young plants. The pH of the solutions was not controlled, ranging from 7.8 and 8.4. Constant EC was maintained by replenishing water lost by evapotranspiration on a daily basis.

Shoots were harvested when one flower was completely mature and were washed twice in deionized water and dried in a forced air oven at 70°C for 72 h. Once dried, the shoots were ground to pass a 60-mesh screen. Total sulfur (S), total phosphorus (P), calcium (Ca²⁺), magnesium (Mg²⁺), sodium (Na⁺), and potassium (K⁺) were analyzed on nitric-perchloric acid digests of the shoot tissue by inductively coupled plasma-optical emission spectrometry. Chloride was analyzed on acid-acetic extracts by coulometric-ampereometric titration.

Treatments with three replications were randomly distributed in 30 sand tanks in the greenhouse. Each replication consisted of one tank containing 20 plants. The study was designed as a factorial experiment and established as a completely randomized design. Data were analyzed with SAS (SAS Institute, Cary, NC, USA 2001).

Experiment 2. Effect of Irrigation with CCRW on *Lisianthus* 'Pure White' and 'Echo Blue'

This experiment was conducted under conditions similar to those described for experiment 1. Plugs of 'Pure White' and 'Echo Blue' were transplanted in tanks of similar dimensions as in experiment 1. Daily air temperature ranged from 14.1 to 35.5°C (average 28.2°C) while night temperature ranged from 8.9 to 30.0°C (average 22.6°C). Relative humidity ranged from 43.6 to 47.5% (average 44.6%) and average PAR was 339.2 $\mu\text{mol m}^{-2} \text{s}^{-1}$ and average PAR at noontime was 689.3 $\mu\text{mol m}^{-2} \cdot \text{s}^{-1}$. Treatments consisted of six salinity levels of CCRW. Table 2 shows the target EC and the ion composition of the irrigation waters.

Experimental design and plant measurements recorded were performed as described in experiment 1. Shoots were harvested when one flower was completely mature. The leaves were separated by age, i.e., leaves from the bottom one-third of the shoot (mature leaves) and those from the top two thirds of the shoot (young leaves). Then, leaves were washed twice in deionized water, bagged and placed in a forced air oven at 70°C for 72 h. Once dried, the leaves were ground to pass a 60-mesh screen. Ion analyses and data analysis were carried out as described for experiment 1.

TABLE 2 Ion concentration of irrigation water simulating the typical composition of concentrations of Colorado River water

EC dS · m ⁻¹	Concentration meq · L ⁻¹				
	Ca ²⁺	Mg ²⁺	Na ⁺	SO ₄ ²⁻	Cl ⁻
2	5.0	5.0	8.0	5.0	13.0
4	7.8	12.1	20.9	13.1	27.5
6	11.4	18.7	32.3	20.0	42.0
8	15.1	25.3	43.6	27.2	57.2
10	18.8	32.6	55.0	34.6	72.5
12	22.8	38.8	66.9	41.8	74.8

RESULTS AND DISCUSSION

Shoot ion concentration data from experiment 1 was analyzed to assess the effects of increasing EC and the composition of irrigation water in lisianthus ‘Pure White’ (Figure 1). In experiment 2, ion concentration was determined on leaf tissues, and data were analyzed to determine the effect of increasing EC and leaf position (young and mature leaves) in lisianthus ‘Echo Blue’ and ‘Pure White’ (Figure 2). The effects of salinity and water types on plant growth were reported in Valdez-Aguilar et al. (2013).

Calcium

In experiment 1, plants of ‘Pure White’ irrigated with CCRW exhibited significantly higher Ca²⁺ shoot concentration compared to plants irrigated with SWD (Figure 1A), however, increasing salinity of water had no effect when EC was ≥ 8 dS · m⁻¹ in plants irrigated with CCRW and ≥ 5 dS · m⁻¹ in plants irrigated with SWD. In experiment 2, ‘Pure White’ exhibited similar trends when EC of water was ≥ 6 dS · m⁻¹ (Figure 2A). The non-significant decrease in Ca²⁺ concentration in ‘Pure White’ is in contrast to many reports that associate increasing salinity to a decline in internal Ca²⁺ (Grieve et al., 2004; Tuna et al., 2007). The reduction of Ca²⁺ in tissues of plants grown in high salinity has been related to: a) the displacement of Ca²⁺ from extracellular binding sites induced by the higher concentrations of Na⁺ in saline water (Cramer et al., 1985), b) the decreased activity of Ca²⁺ associated with the higher ionic strength of the external saline solution (Grattan and Grieve, 1999; Hu and Schmidhalter, 2005), and c) the decreased transpiration rate associated to the lower water extraction capacity of plants (Cuartero and Fernández-Muñoz, 1999). The capacity to maintain high internal Ca²⁺ in lisianthus was cultivar dependent since ‘Echo Blue’ showed a significant reduction, which was more pronounced in mature leaves (Figure 2B).

Calcium concentration was higher in younger leaves of both lisianthus cultivars, which was more obvious at high EC (Figure 2A-B). The higher

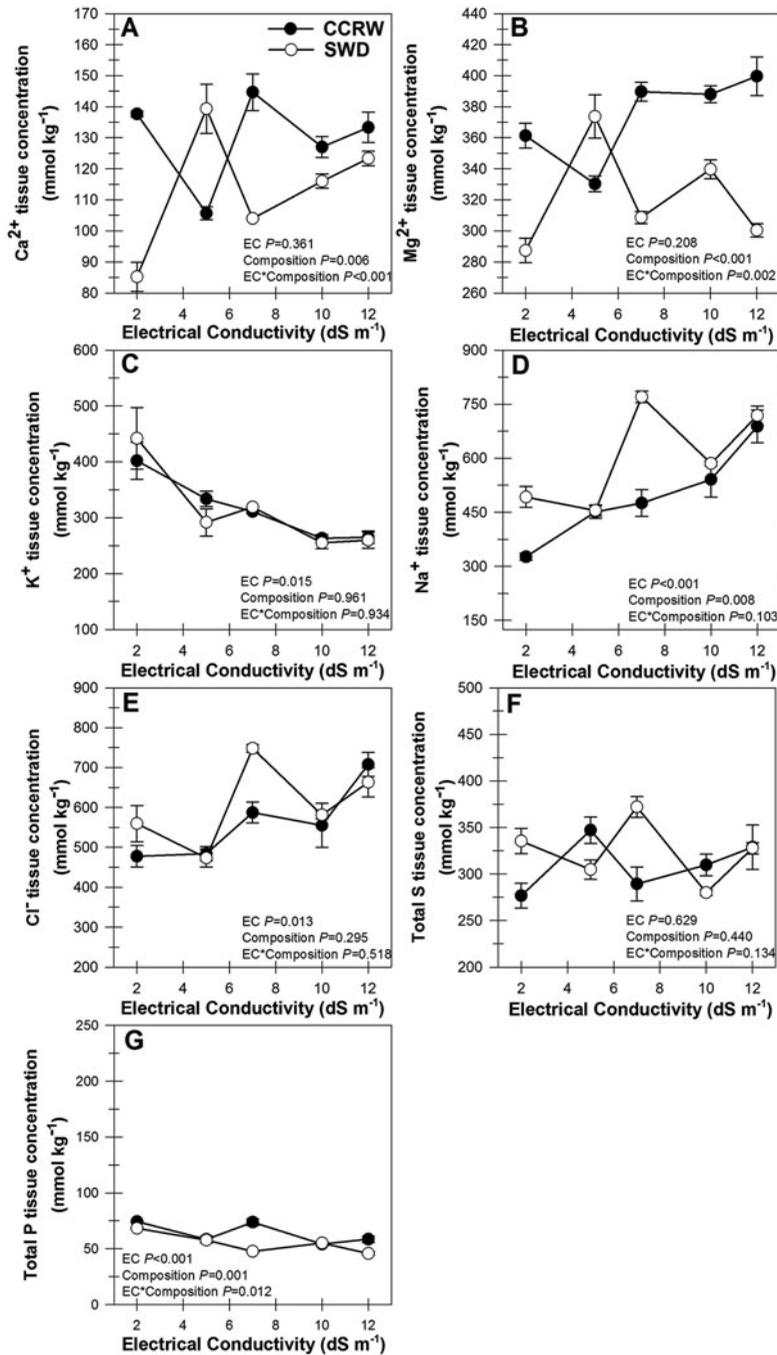


FIGURE 1 Ion concentration in shoots of *lisianthus* 'Pure White' plants irrigated with dilutions of water with the typical composition of sea water dilutions (SWD, open symbols) or concentrations of Colorado River Water (CCRW, closed symbols). Bars represent the standard error of the mean (n = 3).

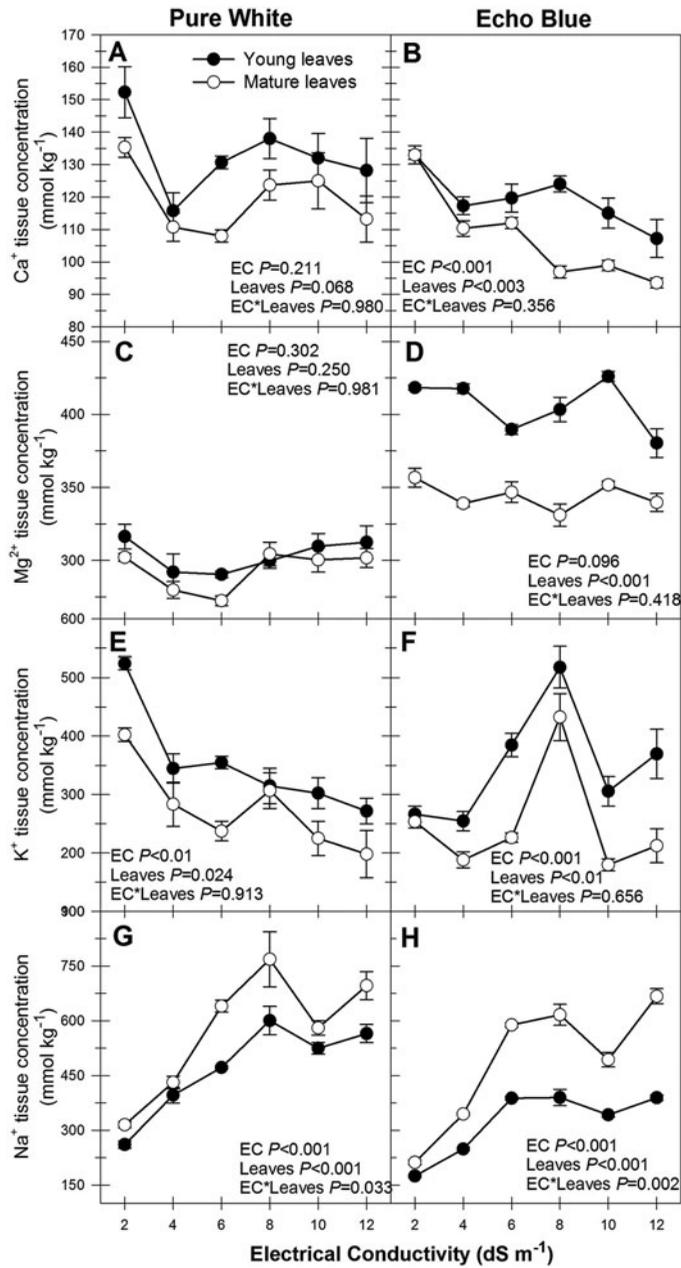


FIGURE 2 Calcium, magnesium, potassium, and sodium concentration in young (closed symbols) and mature (open symbols) leaves of lisianthus ‘Echo Blue’ and ‘Pure White’ plants irrigated with dilutions of water with the typical composition of concentrations of Colorado River water. Bars represent the standard error of the mean ($n = 3$).

accumulation in young leaves is in contrast to reports by Maggio et al. (2007) that indicate that mature leaves of tomato plants exposed to high salinity contained higher Ca^{2+} concentration than younger leaves, which was attributed to Ca^{2+} accumulation in the thicker cell walls of older leaves and other storage structures. Since Ca^{2+} is not readily remobilized from older to younger leaves due to its limited mobility in phloem, the higher concentration detected in the younger leaves is probably explained by a) the maintenance of the transpiration stream for Ca^{2+} transport under saline conditions, or b) the higher availability of Ca^{2+} in CCRW of increasing EC (Tables 1 and 2). The last hypothesis is supported by the numerous reports indicating the beneficial effects of supplemental Ca^{2+} in the tolerance to salinity in species such as tomato (Lopez and Satti, 1996) and strawberry (Khayyat et al., 2011). The ameliorating effects of Ca^{2+} have been associated with an increase in the activity of enzymes of the antioxidant system, as demonstrated in *Cakile maritima* (Ben Amor et al., 2010) and a lower production of active oxygen species.

In plants of 'Pure White' irrigated with SWD, shoot Ca^{2+} concentration significantly increased as EC rose to $5 \text{ dS} \cdot \text{m}^{-1}$ (Figure 1A); contrastingly, in plants irrigated with CCRW there was a significant Ca^{2+} decrease in shoots (Figure 1A) and leaves (Figure 2A and 2B) when EC rose from 2 to 4 or $5 \text{ dS} \cdot \text{m}^{-1}$. This may be due to a dilution-concentration effect, since maximum shoot growth was detected in the control plants irrigated with SWD water and in the $5 \text{ dS} \cdot \text{m}^{-1}$ plants irrigated with CCRW (Valdez-Aguilar et al., 2013). At higher EC, Ca^{2+} tissue concentration was totally or partially restored in 'Pure White' irrigated with CCRW (Figures 1A and 2A). Alternatively, the restoration of Ca^{2+} tissue concentration may have been due to a concentration effect caused by plant growth inhibition since external Ca^{2+} activity decreased at high EC, making nutrient uptake more difficult. The fact that plants were able to grow at higher EC despite the increasing salinity and high alkalinity of water may be explained by the excess Ca^{2+} in the nutrient solution used to mimic CCRW. Higher Ca^{2+} concentrations in the external solution allowed acceptable internal concentrations of the nutrient, alleviating the growth of plants under such stressful conditions.

Magnesium

In experiment 1, Mg^{2+} concentration in shoots of 'Pure White' (Figure 1B) exhibited a response similar to that of Ca^{2+} (Figure 1A) when irrigated with either SWD or CCRW. In experiment 1 (Figure 1B) and 2 (Figures 2C and 2D), increasing EC had no significant effects on Mg^{2+} accumulation in either water type or lisianthus cultivar. Salinity is reported to induce contrasting results as to internal Mg^{2+} concentration; *Celosia argentea*, for example, exhibited increased leaf Mg^{2+} (Carter et al., 2005b) whereas Mg^{2+}

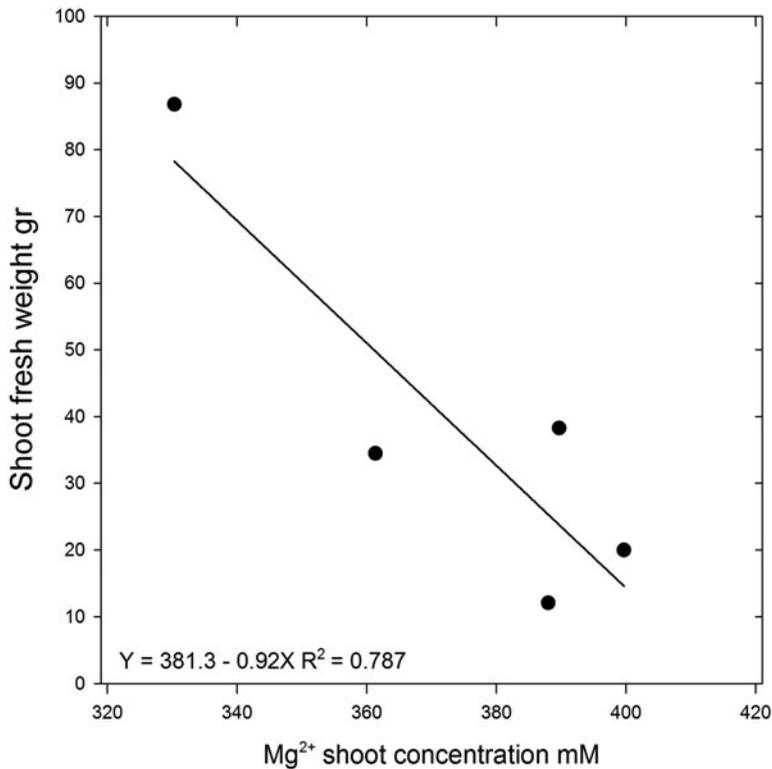


FIGURE 3 Correlation of magnesium shoot concentration and shoot fresh weight of lisianthus 'Pure White' plants irrigated with concentrations of Colorado River water.

was not substantially affected by saline irrigation in *Limonium perezii* (Carter et al., 2005a). In our study, the effect of EC on leaf Mg²⁺ concentration in 'Echo Blue' was also marginal, but there was a marked preference for partitioning Mg²⁺ to the younger leaves (Figure 2D).

Carvajal et al. (1999) reported that growth and fruit production of tomato was inhibited under highly saline conditions as Mg²⁺ increased in the external solution. 'Pure White' plants irrigated with CCRW exhibited similar response since high shoot Mg²⁺ concentration (experiment 1) was negatively associated with a reduction in shoot fresh weight (Figure 3). In 'Echo Blue', the highest shoot fresh weight was obtained by plants with internal concentrations of Ca²⁺ above the average provided internal Mg²⁺ concentrations were below the average (Figure 4A), suggesting that a potential Mg²⁺ toxicity may be accountable for the decrease in plant growth.

The fact that the production of a low shoot fresh weight was associated with low salinity (Valdez-Aguilar et al., 2013) suggests an apparent beneficial effect of salinity on plant growth. However, the reduced growth of plants even at low salinity may be due to the excess Mg²⁺ and low Ca²⁺ accumulation in plants irrigated with such water type. The increased Mg²⁺

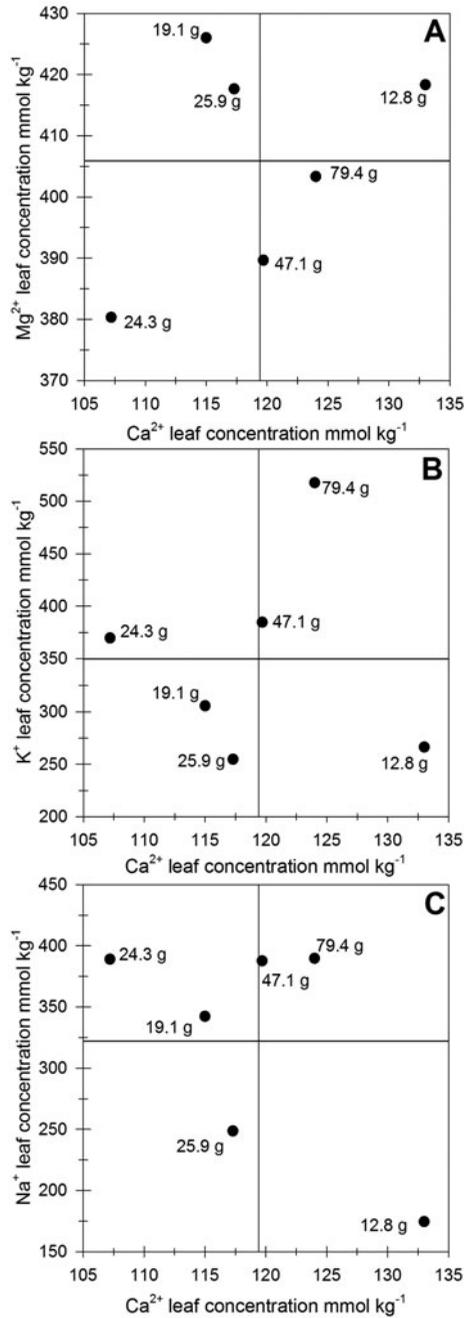


FIGURE 4 Relationship of calcium concentration with A) magnesium, B) potassium, and C) sodium concentration in young leaves of 'Echo Blue' plants irrigated with concentrations of Colorado River water. Lines represent the respective ion concentration averaged across the salinity treatments described in Table 2. The numbers correspond to the average shoot fresh weight for each salinity treatment.

accumulation may be due to the reportedly increase in cation uptake in plants grown in high alkalinity. Islam et al. (1980) reported a higher Ca^{2+} and Mg^{2+} tissue concentrations in several species when grown in solutions with a pH of 8.5. Similarly, Ylivainio et al. (2004) and Roosta (2011) reported an increase in internal Mg^{2+} concentration in lettuce when alkalinity was high. The previous reports are in agreement with our results since Mg^{2+} in both cultivars was marginally affected by increasing salinity (Figures 2C and 2D) and the experiments were conducted in alkaline conditions since irrigation water pH (pH was 7.8 to 8.4 over the course of the experiments) was not adjusted. According to Marschner (1995), the increase in Mg^{2+} , and other cations, under high alkalinity may be due to a decrease in the efficiency of the H^+ pump at high H^+ concentrations in the external medium, causing a decrease in cation uptake at acid pH, while uptake increases with alkaline pH.

'Echo Blue' showed a negative effect of a high Mg^{2+} uptake compared to the uptake of other cations (Mg^{2+} ratio) (Figure 5). In summary, high Mg^{2+} resulting from high alkalinity of CCRW and/or increasing EC was associated

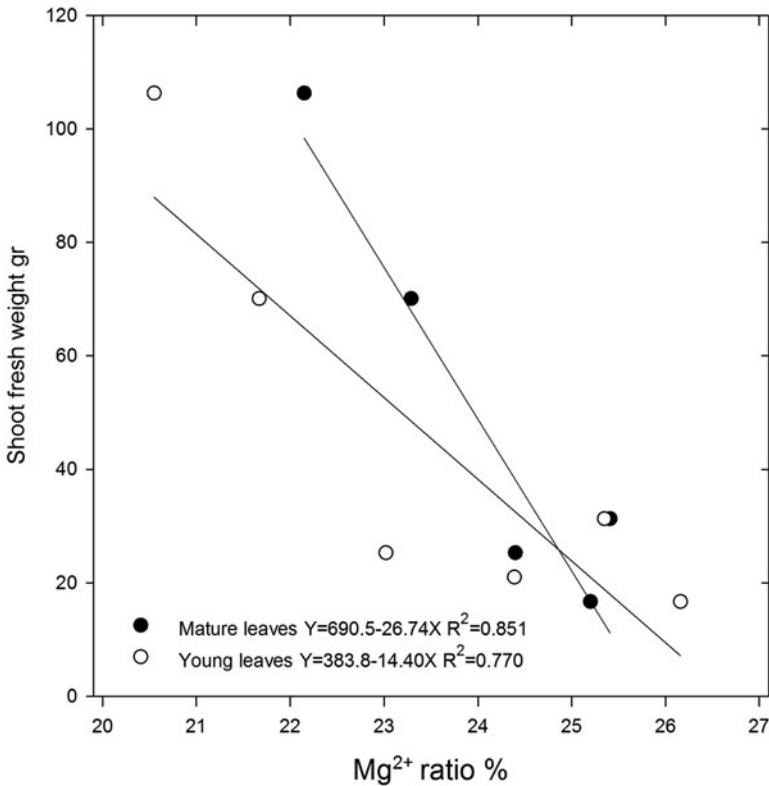


FIGURE 5 Correlation of leaf Mg^{2+} ratio (proportion of magnesium in regards to total cation concentration) and shoot fresh weight of lisianthus 'Echo Blue' plants irrigated with concentrations of Colorado River water.

with growth reductions in 'Pure White', whereas in 'Echo Blue' higher Mg^{2+} combined with low Ca^{2+} under such conditions were detrimental for plant growth.

Potassium

Numerous studies have shown that K^+ tissue concentration declines with increasing salinity due to its lower activity in saline solutions that result from ion competition (Grattan and Grieve, 1999). In the present studies, 'Pure White' exhibited a significant decrease in K^+ concentration when irrigated with increasing EC of either SWD or CCRW waters (Figures 1C and 2E), suggesting that the composition of irrigation water had no influence in the decreasing K^+ accumulation of this cultivar.

Lisianthus 'Pure White' shoots grew best when the plants were irrigated with highly saline CCRW ($EC = 5$ to $8 \text{ dS} \cdot \text{m}^{-1}$) (Valdez-Aguilar et al., 2013) in spite of the decrease in K^+ tissue concentration (Figures 1C and 2C), a critical nutrient and osmobalancer for salinity tolerance (Grattan and Grieve, 1999). Nonetheless, 'Echo Blue' responded in a different manner compared to 'Pure White' (Figure 2F). Potassium concentration in leaves of 'Echo Blue' increased as CCRW salinity increased to $8 \text{ dS} \cdot \text{m}^{-1}$, and then significantly decreased as salinity continued to rise. In 'Pure White' irrigated with SWD, a decrease in K^+ was negatively correlated with shoot fresh weigh ($r = 0.989^{***}$). Tolerance to salinity has been correlated with the capacity of plants to maintain acceptable levels of K^+ (Blumwald, 2000).

In 'Echo Blue', above average tissue concentrations of K^+ and Ca^{2+} were associated with the largest shoot fresh weight (Figure 4B), suggesting that 'Echo Blue', within certain levels, may have some mechanisms to maintain or enhance K^+ acquisition in spite of its reduced activity in saline solutions. The high internal K^+ concentration may have been related to the increase in Ca^{2+} , which is reported to maintain plasma membrane stability when it is supplemented under saline conditions (Grattan and Greive, 1999), and thus may have sustained K^+ acquisition and/or transport. The maintenance of adequate K^+ is essential for plant survival under high salinity because it makes a major contribution as an osmoticum in the stele, a prerequisite for water balance in the roots (Marschner, 1995).

The young leaves of 'Pure White' (Figure 2E) and 'Echo Blue' (Figure 2F) had significantly higher K^+ concentration compared to the mature leaves. In the $6 \text{ dS} \cdot \text{m}^{-1}$ treatment, K^+ concentration in 'Echo Blue' was 79% higher in the younger leaves, indicating that this cultivar has the capacity to mobilize K^+ in the internal tissues, in addition to the higher accumulation of K^+ , at high salinity levels. The increased K^+ concentration in 'Echo Blue' when EC was 6 or $8 \text{ dS} \cdot \text{m}^{-1}$, could have caused an increase in the water potential of xylem sap, facilitating the transport of Ca^{2+} to the younger leaves.

Calcium and K^+ relations may also have been responsible for improved plant performance under increasing salinity, since Ca^{2+} leaf concentration was significantly correlated with K^+ (in young leaves: $r = +0.633^{***}$; in mature leaves: $r = +0.642^{**}$), suggesting that 'Pure White' may have a strong dependency on Ca^{2+} for K^+ uptake, as suggested by Cachorro et al. (1994), and on K^+ for Ca^{2+} mobilization.

Sodium

Tissue Na^+ significantly increased in both cultivars with increasing EC, regardless of the ionic composition of irrigation water (Figures 1D, 2G, and 2H). Water composition, however, significantly affected Na^+ accumulation (Figure 1D) as SWD caused higher tissue Na^+ concentrations than CCRW, an effect probably related to the higher Na^+ levels characteristic of this type of water (Table 1).

Sodium tended to accumulate more in the mature leaves of both lisianthus cultivars (Figures 2G and 2H). The difference in Na^+ concentration between young and mature leaves was more accentuated in 'Echo Blue', suggesting a capacity to exclude Na^+ from the actively growing organs of the shoot apex of this cultivar. Maggio et al. (2007) reported similar results in tomato when EC of water was $< 6 \text{ dS} \cdot \text{m}^{-1}$; however, the authors reported that at higher EC there was no Na^+ preference for accumulation in mature or young leaves. The correlation between Na^+ and Ca^{2+} concentration in 'Echo Blue' in the mature leaves was negative ($r = -0.770^{***}$) but not in the young leaves ($r = -0.199^{\text{NS}}$), thus, a higher Na^+ concentration was associated with a lower Ca^{2+} concentration in the older leaves, suggesting that the restricted Na^+ translocation could have allowed for more Ca^{2+} transport to the young leaves since Na^+ is known to displace Ca^{2+} from extracellular binding sites (Cramer et al., 1985).

Sodium concentrations of 300 and $400 \text{ mmol} \cdot \text{kg}^{-1}$ have been reported to be high enough to cause 38% and 63% decrease in dry weight of maize and bean plants, respectively (Marschner, 1995). In our studies, both 'Pure White' and 'Echo Blue' exhibited the best growth with internal concentrations much higher than those reported in maize and bean, suggesting that lisianthus cultivars can tolerate higher concentrations of Na^+ compared to other species. The tolerance exhibited by 'Echo Blue' may be due to Na^+ retention in the mature leaves, since maximum Na^+ in the young leaves was around $375 \text{ mmol} \cdot \text{kg}^{-1}$, compared to $600 \text{ mmol} \cdot \text{kg}^{-1}$ in the mature leaves. The limited transport of Na^+ to the young leaves may have allowed for the increase in K^+ concentration at higher EC (Figure 2F) since competition between both ions decreased.

Sodium concentration in leaves of 'Pure White' was higher than in 'Echo Blue' but Na^+ exclusion was less marked (Figure 2G). The increasing Na^+ concentration in 'Pure White' was associated with decreasing K^+ in the

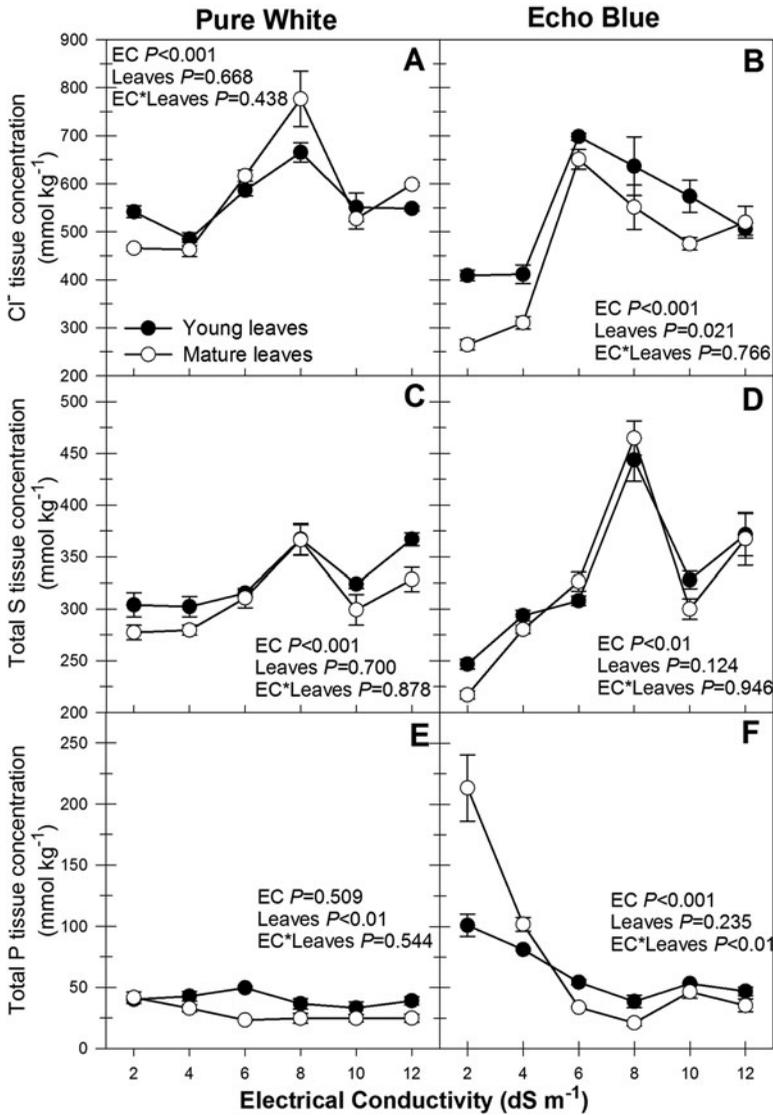


FIGURE 6 Chloride, total sulfur, and total phosphorus concentration in young (closed symbols) and mature (open symbols) leaves of lisianthus 'Echo Blue' and 'Pure White' plants irrigated with dilutions of water with the typical composition of concentrations of Colorado River water. Bars represent the standard error of the mean ($n = 3$).

young ($r = -0.855^{***}$) and mature leaves ($r = -0.526^*$), however, optimum growth in this cultivar occurred when Na^+ concentration was highest and there was a decrease in K^+ , possibly due to partial substitution of K^+ by Na^+ and/or accumulation of excess Na^+ in the vacuole or other plant parts. In contrast, high concentrations of Na^+ had little effect in 'Echo Blue' leaves provided high concentrations of Ca^{2+} were also present (Figure 4C).

Chloride, Total-S, and Total-P

Chloride (Figures 1E and 6A) tissue concentration in 'Pure White' exhibited a trend similar to that of Na^+ (Figures 1D and 2G) while in 'Echo Blue' (Figure 6B) was similar to that of K^+ (Figure 2E). Total-S in 'Pure White' and 'Echo Blue' exhibited similar trend when irrigated with CCRW (Figures 1F, 6C, and 6D). Total-P concentration in shoots of 'Pure White' decreased significantly with increasing salinity of CCRW and SWD irrigation waters (Figure 1G), but plants irrigated with SWD were slightly, but significantly, more affected. In experiment 2, total-P concentration did not show a regular pattern (Figures 6E and 6F). The reduction of total-P tissue concentration with increasing salinity may be due to the reduced activity of P due to the high ionic strength of the solution and the formation of calcium-phosphate minerals of low solubility (Grattan and Grieve, 1999).

CONCLUSIONS

Growth of lisianthus was affected by the ionic composition of irrigation water and increasing salinity. The best growth of 'Pure White' irrigated with CCRW at higher salinities (5 or 8 dS m^{-1}) demonstrates that this cultivar can tolerate the higher osmotic potential associated to high EC. The tolerance, however, depended on ionic composition of water, as the best plant growth occurred when this cultivar was irrigated with SWD at 2 $\text{dS} \cdot \text{m}^{-1}$. This observation demonstrates that 'Pure White' is sensitive to specific ion toxicity (Na^+ and Cl^-). The lower predominance of Na^+ and Cl^- , as well as the higher Ca^{2+} availability in CCRW, were associated to increased growth provided Mg^{2+} was not at toxic levels in plant tissues.

'Echo Blue' showed different adaptive responses to high salinity. Compared to 'Pure White', 'Echo Blue' retained more Na^+ in the mature leaves, thereby decreasing its accumulation up to toxic levels in the developing organs. In addition, retention of Na^+ in mature leaves was associated with a marginal reduction of Ca^{2+} concentration in the young leaves. 'Echo Blue' also showed a higher capacity for maintaining K^+ accumulation, an effect probably associated with the lower Na^+ accumulation.

The reduced growth of 'Pure White' and 'Echo Blue' when irrigated with CCRW of low salinity was associated to the accumulation of toxic levels of Mg^{2+} , which may have due to the alkalinity of irrigation water.

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