

# Productivity and Mineral Nutrition of *Limonium* Species Irrigated with Saline Wastewaters

C. M. Grieve<sup>1</sup> and J.A. Poss

U.S. Department of Agriculture, Agricultural Research Service, George E. Brown, Jr., Salinity Laboratory, 450 West Big Springs Road, Riverside, CA 92507

S.R. Grattan

Department of Land Air and Water Resources, University of California, One Shields Avenue, Davis, CA 95616

P.J. Shouse

U.S. Department of Agriculture, Agricultural Research Service, George E. Brown, Jr., Salinity Laboratory, 450 West Big Springs Road, Riverside, CA 92507

J.H. Lieth

Department of Land Air and Water Resources, University of California, One Shields Avenue, Davis, CA 95616

L. Zeng

U.S. Department of Agriculture, Agricultural Research Service, Crop Genetics and Production Research, 141 Experiment Station Road, Stoneville, MS 38776

Additional index words. cut flowers, drainage water reuse, ion selectivity, salinity, sand cultures, statice, stem length

**Abstract.** To explore the possibility that saline wastewaters may be used to grow commercially acceptable floriculture crops, a study was initiated to determine the effects of salinity on two statice cultivars. *Limonium perezii* (Stapf) F. T. Hubb. 'Blue Seas' and *L. sinuatum* (L.) Mill. 'American Beauty' were grown in greenhouse sand cultures irrigated with waters prepared to simulate saline drainage waters typically present in the western San Joaquin Valley (SJV) of California. Seven salinity treatments were imposed on 3-week-old seedlings. Electrical conductivities of the irrigation waters (EC) were 2.5 (control), 7, 11, 15, 20, 25, and 30 dS·m<sup>-1</sup>. Vegetative shoots were sampled for biomass production and ion analysis ten weeks after application of stress. Flower stem numbers, length, and weight were determined at harvest. Stem length of *L. perezii* was significantly reduced when irrigation water salinity exceeded a threshold of 2.5 dS·m<sup>-1</sup>. Salt tolerance threshold based on stem length for *L. sinuatum* was 7 dS·m<sup>-1</sup>. The species exhibited significant differences in shoot-ion relations which appear to be related to differences in salt tolerance. Sodium, K<sup>+</sup>, Mg<sup>2+</sup>, and total-P were more strongly accumulated in the leaves of *L. sinuatum* than *L. perezii*. Both species accumulated K<sup>+</sup> in preference to Na<sup>+</sup>, but selectivity for K<sup>+</sup> over Na<sup>+</sup> was significantly higher in *L. sinuatum* than in the more salt-sensitive *L. perezii*. Chloride concentration in *L. sinuatum* leaves increased significantly as salinity increased, whereas the 20-fold increase in substrate-Cl had no effect on leaf-Cl in *L. perezii*. Both *Limonium* species completed their life cycles at salt concentrations exceeding 30 dS·m<sup>-1</sup>, a character associated with halophytic plants. Maximum growth of each species, however, occurred under relatively low salt stress, and steadily declined as external salinity increased. Based on this crop productivity response, *L. perezii* should be rated as sensitive and *L. sinuatum* as moderately tolerant.

As water quality and quantity becomes limited in many parts of the world, new options are sought to make more efficient use of wastewaters in arid and semi-arid climates. Agriculture is the main user of our water sup-

plies, therefore, strong interests and incentives have been promoted to increase the efficiency of water management through reuse options. Reuse of wastewaters would conserve greater amounts of high quality water and, at the same time, may provide a valuable resource for the production of selected floriculture crops. Because many of these high value crops are salt sensitive, growers have traditionally used good quality waters for irrigation. However, demands on high quality water supplies have increased through competition between urban and agricultural users. Growers, in many instances, must eventually rely more on low quality water resources. It becomes impor-

tant, therefore, to identify floral species that will produce a commercially acceptable crop when irrigated with brackish wastewaters. This strategy, together with typical management practices that avoid excessive salinity stress in the root media, will provide the grower with an economically and environmentally sound wastewater reuse options.

Several commercially important floral and ornamental crops possess some degree of salt tolerance. Growers have exploited this variability to expand profitable cut flower industries in regions where reliable sources of high quality water are limited. Successes in breeding and selection techniques, coupled with improved methods of cultivation, have led to expansion of cut flower industries in these areas (Pasternak and Nerd, 1996). Salinity sometimes offers benefits in the production of certain floral species. Positive effects include the induction of earlier flowering, increase in the number of blooming flowers per inflorescence, and reduction of peduncle length to prevent stem collapse or drooping of the inflorescence (Shillo et al., 2002).

Many wild annual statice (*Limonium* sp.) are highly salt-tolerant halophytes native to saline habitats (Woodell and Mooney, 1970). In a compilation of salt-tolerant plants of the world, Aronson (1989) lists 52 *Limonium* species, 5 of which (including *L. perezii* and *L. sinuatum*) are known to complete their life cycles under hypersaline conditions, i.e., 56 dS·m<sup>-1</sup>. Some of the cultivated species and varieties of *Limonium* have retained the biochemical and physiological mechanisms and characters necessary to meet the challenges posed by moderately saline environments (Aларon et al., 1999; Hanson et al., 1994; Morales et al., 2001). For example, irrigation water salinity up to an electrical conductivity (EC) of 11.5 dS·m<sup>-1</sup> had little or no effect on the number, height, or weight of flowering stems of hybrid Japanese *Limonium*. In this study, cultivars 'Emily Tall' and 'Emily Pink' were grown under nonsaline conditions (EC = 1.8 dS·m<sup>-1</sup>) for 7 months before the imposition of the salt treatments (Shillo et al., 2002).

*Limonium* is an economically valuable cut and dried flower crop. Nationwide in 1998, 234 floriculture operations produced 3.7 × 10<sup>6</sup> bunches of statice with a value of \$4.3 × 10<sup>6</sup> (Census of Horticultural Specialties, 1998). The goal of this study was to grow two species [*L. perezii* (Stapf) F. T. Hubb. and *L. sinuatum* (L.) Mill.] of this commercially important crop in greenhouse sand tanks irrigated with saline-sodic waters and to compare the performance of these species based on growth, yield potential, and mineral ion uptake.

## Materials and Methods

Seeds of *L. perezii* (Stapf) F. T. Hubb. 'Blue Seas' and *L. sinuatum* L. Mill. 'American Beauty' were sown in vermiculite-filled trays on 25 Jan. (*L. perezii*) and 16 Mar. 2001 (*L. sinuatum*). Time to maturity of *L. sinuatum* (110 to 120 d) is considerably shorter than that of *L. perezii* (180 to 200 d), therefore planting dates were staggered to assure that the plants

Received for publication 8 Sept. 2004. Accepted for publication 5 Dec. 2004. The authors are indebted to Phyllis Nash for statistical analysis and to Donald A. Layfield for mineral ion analysis. This research was supported in part by a CAL-FED grant, administered by the California Department of Water Resources, Project Manager, Debra Gonzalez. Seed for the study were purchased from Johnny's Selected Seed, Albion, Me.

<sup>1</sup>Corresponding author.



Table 1. Composition of salinizing salts in solutions prepared to simulate drainage waters commonly present in the San Joaquin Valley.

EC <sub>1</sub> (dS·m <sup>-1</sup> )	Salinizing salt (mol·m <sup>-3</sup> )				
	Ca <sup>2+</sup>	Mg <sup>2+</sup>	Na <sup>+</sup>	SO <sub>4</sub> <sup>2-</sup>	Cl <sup>-</sup>
2.5	2.5	1.5	13.8	7.0	7.0
7.0	7.8	5.5	50.9	29.5	24.7
11.0	10.1	9.8	87.0	42.0	42.2
15.0	13.0	13.9	123	58.2	59.6
20.0	13.4	20.1	178	79.0	86.3
25.0	13.8	27.9	247	104	111
30.0	14.0	33.6	298	124	144

flowered at about the same time. In total, 15 seedlings of *L. perezii* were transplanted into each of 21 greenhouse sand tanks in Riverside, Calif., on 8 Feb. and 15 seedlings *L. sinuatum* were transplanted into each of a second set of 21 tanks on 26 Mar. 2001. The tanks (1.2 × 0.6 × 0.5 m deep) contained washed sand having an average bulk density of 1.7 Mg·m<sup>-3</sup>. The sand had a volumetric water content at saturation of 0.34 and 0.1 m<sup>3</sup>·m<sup>-3</sup> after drainage had nearly ceased. Other water dynamics of this river sand are given in Wang(2002). Plants were irrigated three times daily with a nutrient solution consisting of (in mol·m<sup>-3</sup>): 2.5 Ca<sup>2+</sup>, 1.5 Mg<sup>2+</sup>, 13.8 Na<sup>+</sup>, 3.0 K<sup>+</sup>, 7.0 SO<sub>4</sub><sup>2-</sup>, 7.0 Cl<sup>-</sup>, 3.0 NO<sub>3</sub><sup>-</sup>, 0.17 KH<sub>2</sub>PO<sub>4</sub>, 0.050 Fe as sodium ferric diethylenetriamine pentaacetate (NaFeDTPA), 0.023 H<sub>3</sub>BO<sub>3</sub>, 0.005 MnSO<sub>4</sub>, 0.0004 ZnSO<sub>4</sub>, 0.0002 CuSO<sub>4</sub>, and 0.0001 H<sub>2</sub>MoO<sub>4</sub> made up with Riverside municipal water. This solution, with an electrical conductivity (EC<sub>1</sub>) of 2.5 dS·m<sup>-1</sup>, served as the control treatment. Daily irrigations were of 15-min duration, which allowed the sand to become completely saturated, after which the solution drained into 765-L reservoirs located in a basement below the sand tanks, for reuse in the next irrigation. Water lost by evapotranspiration was replenished automatically each day to maintain constant electrical conductivities in the solutions.

Seven salinity treatments were imposed with sulfate-dominated irrigation waters designed to simulate saline wastewaters commonly present in the San Joaquin Valley of California and from predictions based on appropriate simulations of what the long-term compositions of the water would be upon further concentrations by plant-water extraction and evapotranspiration (Suarez and Simunek, 1997). Concentrations of the salinizing salts are shown in Table 1. Salinization was initiated 15

Feb. in the solutions irrigating *L. perezii* and on 7 Apr. for those irrigating *L. sinuatum*. Electrical conductivities of the saline treatments were increased to the desired levels by incremental additions of the salts over a 2-week period to avoid osmotic shock to the seedlings. Targeted EC<sub>1</sub> values of the solutions were 2.5, 7, 11, 15, 20, 25, and 30 dS·m<sup>-1</sup>.

The pH was not controlled and ranged from 7.7 to 8.2. Irrigation waters were analyzed by inductively coupled plasma optical emission spectrometry (ICPOES) to confirm that target ion concentrations were maintained. Chloride in the solutions was determined by coulometric-amperometric titration. The experiment was a randomized block design with seven salinities, two *Limonium* species, and three replications.

Temperature, radiation, and humidity were measured and recorded at hourly intervals at a point slightly above the plant canopy. During growth of *L. perezii* (8 Feb. to 1 Aug. 2001), daytime air temperatures in the greenhouse ranged from 12.2 to 36.0 °C (mean 28.5 °C); nighttime temperatures were 11.1 to 31.7 °C (mean 22.9 °C). During the growth of *L. sinuatum* (26 Mar. to 1 Aug. 2001), daytime air temperatures ranged from 20.0 to 36.6 °C (mean 29.0 °C). Daily relative humidity was the same for both periods and ranged from 42% to 48% (mean 45%).

Ten weeks after application of salt stress (24 Apr. for *L. perezii* and 8 May 2001 for *L. sinuatum*) the seedlings were still in the vegetative stage. Aboveground biomass of five plants from each tank was harvested at this time which also served to thin the plants to ten per tank. Samples were weighed, washed with deionized water, dried in a forced air oven for 1 week at 70 °C, reweighed, then ground in a Wiley mill to pass a 60-mesh screen. Total S,

total P, Ca<sup>2+</sup>, Mg<sup>2+</sup>, Na<sup>+</sup> and K<sup>+</sup> were determined on nitric-perchloric acid digests of the plant tissues by ICPOES. Chloride was determined on nitric-acetic acid extracts by coulometric-amperometric titration.

Flower stalks of both species were harvested on 28 June, 16 July, and 1 Aug. 2001. Height and weight of stems plus inflorescence were measured.

Ion selectivity coefficients were calculated from the ratio of specific ions in the plant divided by the ratio of those ions in the medium (Flowers and Yeo, 1988). Statistical analyses were performed by analysis of variance with mean comparisons at the 95% level based on Tukey's studentized range test. SAS release version 6.12 was used (SAS Institute, Inc., 1997).

## Results and Discussion

**Growth and yield potential.** Ten weeks after application of salinity, all seedlings survived at all treatment levels and none showed visible signs of ion toxicity or nutrient deficiency disorders. Growth of *L. perezii* rosettes was reduced by 50% as irrigation water salinity rose from 2.5 to 7 and 11 dS·m<sup>-1</sup>, and was further reduced to 25% of the controls as salinity increased to 30 dS·m<sup>-1</sup> (Table 2). *Limonium sinuatum* plants were much more vigorous than *L. perezii*. Weights of *L. sinuatum* shoots at the same developmental stage were two to 3-fold greater than *L. perezii*. Reduction of shoot dry matter production of *L. sinuatum* by salinity was not significant until the EC of the irrigation waters exceeded 15 dS·m<sup>-1</sup>.

The *Limonium* species also differed in productivity based on length, fresh weight, and numbers of flowering stems (Table 2). Under nonsaline conditions, total stem count over the harvest season for *L. sinuatum* was 284, twice that of *L. perezii* (140). Stem count per *L. perezii* plant significantly decreased from 15 to 2 as salinity increased from 2.5 to 30 dS·m<sup>-1</sup>. In contrast, salinity had little effect on the number of stems produced by *L. sinuatum*. Stem numbers of *L. sinuatum* harvested from all salinity treatments in this greenhouse study exceeded seasonal stem number per *L. sinuatum* plant harvested from field trials (Armitage, 1993; Starman et al., 1995; Whipker and Hammer, 1994).

Table 2. Effect of saline-sodic irrigation waters on vegetative growth, stem length, stem fresh weight and stem numbers per plant produced by two statice species grown in greenhouse sand tanks.

Salinity (EC) (dS·m <sup>-1</sup> )	<i>Limonium perezii</i>				<i>Limonium sinuatum</i>			
	Shoot <sup>a</sup> dry wt (g)	Stems <sup>b</sup> / plant (no.)	Stem Length (cm)	Stem fresh wt (g)	Shoot dry wt (g)	Stems/ Plant (no.)	Stem Length (cm)	Stem fresh wt (g)
2.5	1.6 a <sup>x</sup>	15 a	62 a	24 a	3.2 a	32 a	72 a	25 a
7	0.82 b	9 b	41 bc	11 bc	3.2 a	36 a	58 b	17 b
11	0.83 b	9 b	48 b	14 b	2.3 ab	32 a	55 b	14 bc
15	0.59 b	5 bc	31 cd	7 cd	2.7 ab	32 a	50 bc	13 bc
20	0.41 b	4 bc	26 d	5 d	1.4 b	30 a	42 cd	10 cd
25	0.40 b	2 c	23 d	4 d	1.5 b	27 a	37 de	7 d
30	0.38 b	2 c	23 d	4 d	1.2 b	25 a	30 e	5 d

<sup>a</sup>Shoots harvested 10 weeks after the application of salinity. Values are the means of three replications.

<sup>b</sup>Stems harvested on 28 June, 16 July, and 1 Aug 2001. Values are the combined means of three replications.

<sup>x</sup>Within columns, means followed by a different letter are significantly different at the 0.05 probability level according to Tukey's studentized range test. Values are the means of three replications.

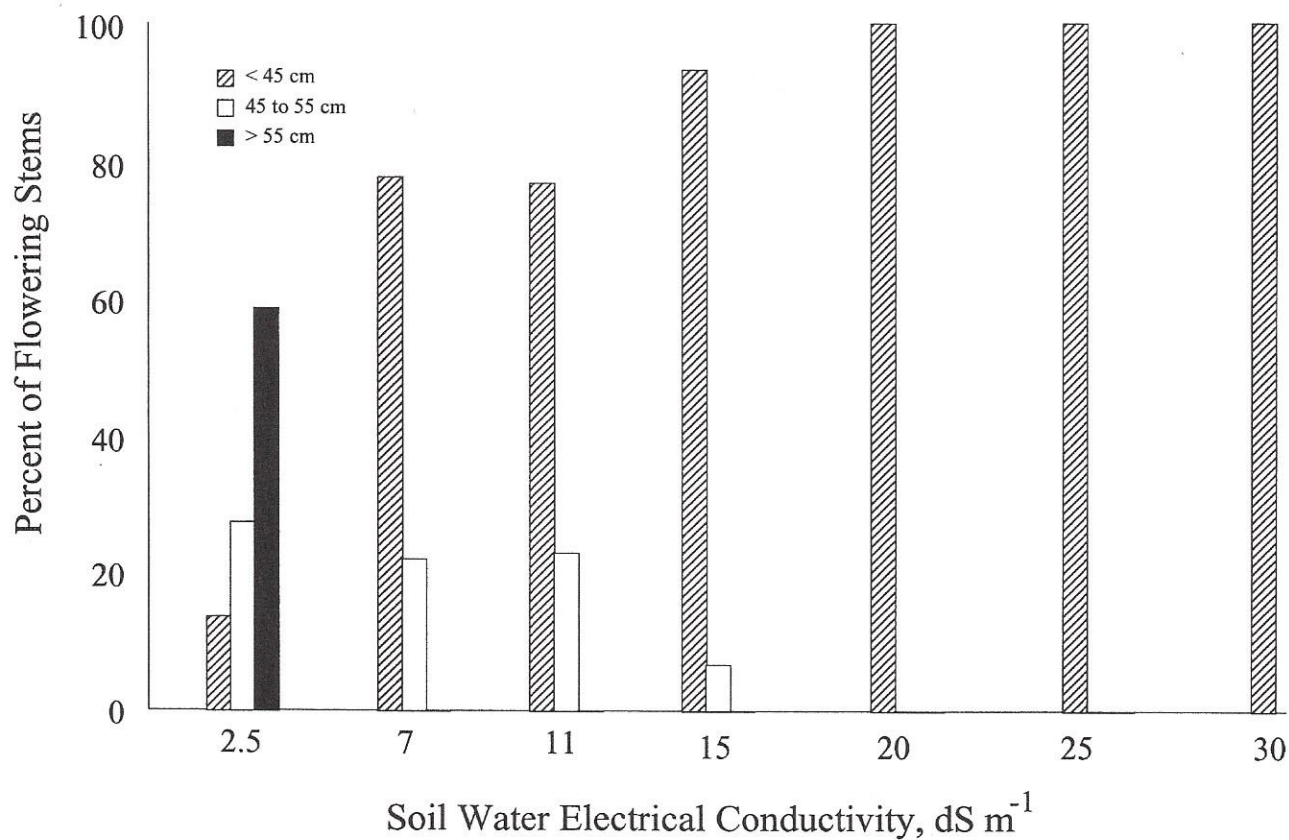


Fig. 1. Flowering stem length distribution of *Limonium perezii* as a function of irrigation water salinity.

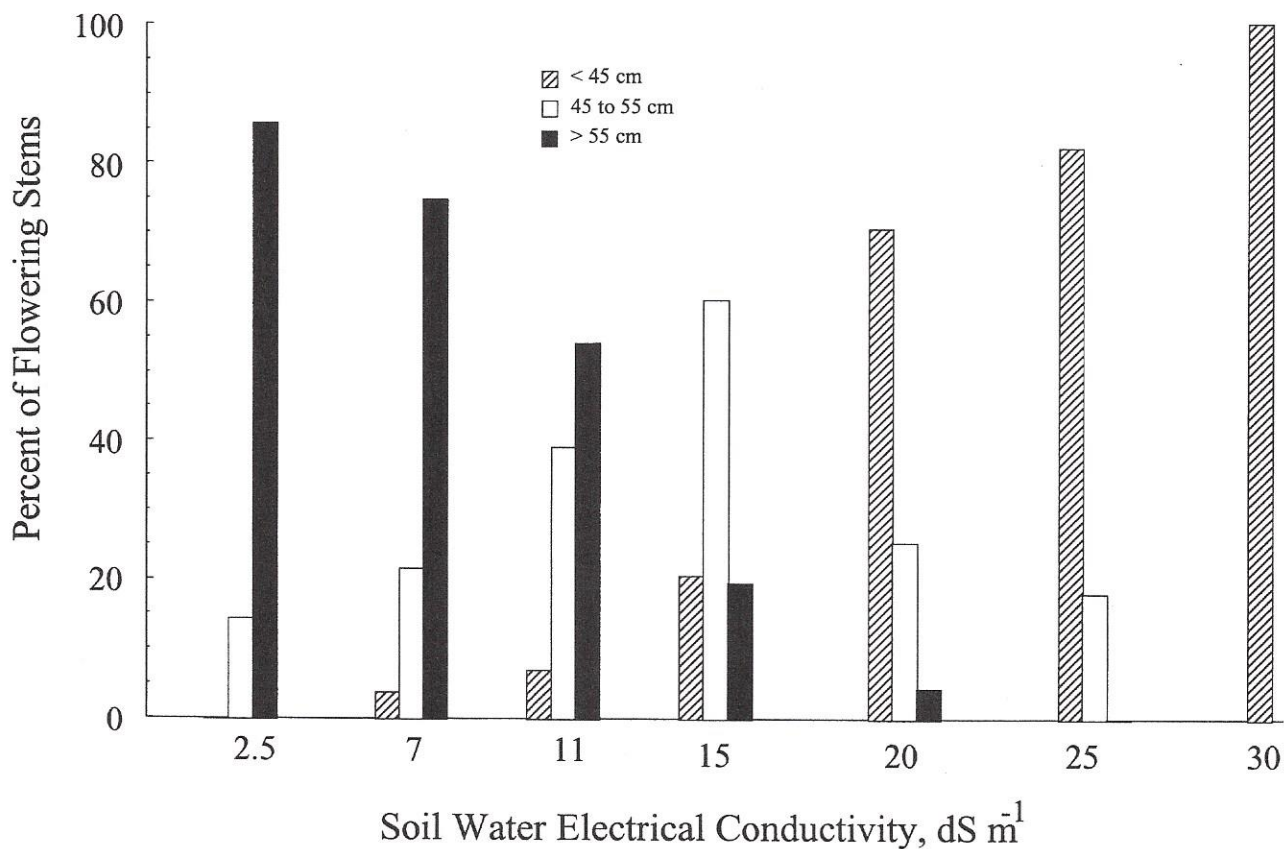


Fig. 2. Flowering stem length distribution of *Limonium sinuatum* as a function of irrigation water salinity.



Stem length of both species decreased about 60% as salinity increased from 2.5 to 30 dS·m<sup>-1</sup> (Table 2). At all salinity levels, *L. perezii* produced shorter and lighter stems than *L. sinuatum*. Stem length distribution as a function of salinity shows that once irrigation water salinity exceeded 2.5 dS·m<sup>-1</sup>, most *L. perezii* stems were 45 cm or less (Fig. 1), whereas 80% of *L. sinuatum* stems produced in the 15 dS·m<sup>-1</sup> treatment were 45 cm or more (Fig. 2). Height of static cultivars grown under ideal conditions generally ranges from 61 to 76 cm (Armitage, 1993). Based on this quality criterion, *L. perezii* produced commercially acceptable stems only under nonsaline conditions, whereas marketable stems of *L. sinuatum* were produced by plants irrigated with both 2.5 and 7 dS·m<sup>-1</sup> waters. Other horticulturists suggest that the commercial standard for static stem length is 41 cm (Barr, 1992; Starman et al., 1995). Accordingly, *L. sinuatum* and *L. perezii* would produce marketable stems if soil water salinities were as high as 20 and 15 dS·m<sup>-1</sup>, respectively. Therefore, under field conditions, *L. sinuatum* could be safely irrigated with saline waters of 6.7 dS·m<sup>-1</sup>, respectively, assuming the EC of the soil water is about twice the EC of the saturated soil paste EC<sub>s</sub> and a continuous leaching fraction of 15% to 20% is achieved (Ayers and Westcot, 1985).

The effect of salinity on stem fresh weight was also pronounced (Table 2). Reduction of *L. sinuatum* stem weight was not significant until irrigation water EC exceeded 7 dS·m<sup>-1</sup>. In contrast, weight of dS·m<sup>-1</sup> stems from the 7 dS·m<sup>-1</sup> treatment was reduced by about 50%.

Average stem fresh weight of our greenhouse-grown *L. sinuatum*, 'American Beauty', was about 40% heavier than reported for the same cultivar from a field trial (Whipker and Hammer, 1994).

Both *Limonium* species were able to complete their life cycles at salt concentrations exceeding 350 mM (30 dS·m<sup>-1</sup>), clearly a halophytic trait typical of the genus (Alarcon et al., 1999; Aronson, 1989; Pasternak and Nerd, 1996). Growth response to salinity, however, more closely resembled that of glycophytic than halophytic plants. Maximum growth occurred at low salinity and decreased steadily as salt stress increased. In combination, these characters describe a class of halophytic plants (Flowers et al., 1986) termed miohalophytes (Salisbury, 1995). This nomenclature is undoubtedly useful in ecophysiological studies. However, neither cultivar examined in this study possessed a high degree of salt tolerance as understood by horticulturists and agronomists whose research focuses on crop yield response to salinity (Maas and Grattan, 1999). Evaluation of the marketable yield of *Limonium* suggests that *L. perezii* should be rated as salt sensitive; *L. sinuatum* as moderately tolerant. Reduction in stem length should not, however, be the limiting factor in species selection for other horticultural applications. For example, 'American Beauty' and 'Blue Seas' have great value as bedding or landscape plants in problem areas. Under severe salt stress, both static cultivars produced acceptable, healthy plants with attractive foliage and colorful inflorescences on sturdy, albeit short, stems.

*Shoot-ion concentrations and interactions.* The species showed unique differences in mineral ion concentration patterns in response to increasing sodium sulfate dominated-salinity (Table 3). Sodium in both species rose significantly as substrate Na increased. *Limonium sinuatum* was the stronger Na<sup>+</sup> accumulator at higher salinity levels. Shoot Ca, in contrast, decreased about 40% as salinity increased, although Ca<sup>2+</sup> concentration in the substrate rose from 2.5 to 14 mol·m<sup>-3</sup>. Reduction in shoot-Ca may have resulted from high external ratios of Na<sup>+</sup>/Ca<sup>2+</sup> which limited Ca<sup>2+</sup> availability to the plant (Suarez and Grievé, 1988). The Na<sup>+</sup>/Ca<sup>2+</sup> ratios in *L. perezii* shoots generally reflected the ratios in the irrigation waters, i.e., ranging from about 5 in the control treatment to about 20 as salinity increased to 30 dS·m<sup>-1</sup>. The Na<sup>+</sup>/Ca<sup>2+</sup> range in *L. sinuatum* shoots was somewhat wider (e.g., 5 to about 29).

Patterns of shoot Mg differed between the static species (Table 3). Magnesium concentration in *L. sinuatum* grown under control conditions was nearly twice as high as that in *L. perezii*, which may indicate a significant species difference in Mg<sup>2+</sup> requirement. As salinity increased from 2.5 to 30 dS·m<sup>-1</sup> and external Mg<sup>2+</sup> increased from 1.5 to 34 mol·m<sup>-3</sup>, Mg<sup>2+</sup> in *L. perezii* shoots significantly increased, whereas *L. sinuatum* shoot Mg decreased.

The K<sup>+</sup> requirement under control conditions also appeared to be higher for *L. sinuatum* than for *L. perezii*. Potassium in shoots of both species decreased significantly as salinity increased (Table 3). Potassium strongly competes with Mg<sup>2+</sup> for plant uptake. Plants with

Table 3. Effect of increasing salinity on shoot-ion concentrations in two *Limonium* species. Values are the means of three replications.

EC (dS·m <sup>-1</sup> )	Ion concn (mmol·kg <sup>-1</sup> dry wt)						
	Ca <sup>2+</sup>	Mg <sup>2+</sup>	Na <sup>+</sup>	K <sup>+</sup>	Total P	Total S	Cl <sup>-</sup>
<i>L. perezii</i> 'Blue Seas'							
2.5	152 a <sup>c</sup>	347 b	781 d	1017 a	103 a	334 d	907 a
7	101 b	411 ab	1132 cd	741 b	83 ab	418 cd	995 a
11	98 b	417 ab	1251 bc	687 bc	85 ab	483 cd	1044 a
15	97 b	389 ab	1404 abc	575 bcd	72 bc	562 bc	943 a
20	101 b	452 ab	1707 a	474 d	56 c	756 a	974 a
25	82 b	444 ab	1653 ab	511 cd	78 b	670 ab	1074 a
30	91 b	479 a	1722 a	481 cd	76 bc	788 a	1019 a
<i>L. sinuatum</i> 'American Beauty'							
2.5	147 a	671 a	659 e	1496 a	213 bc	401 e	983 c
7	92 b	634 ab	1095 d	1320 ab	165 c	430 de	1151 c
11	94 b	530 b	1760 bc	1231 bc	249 b	558 bc	1506 b
15	108 b	592 ab	1692 c	1175 bcd	198 bc	497 cde	1927 a
20	81 b	529 b	1834 bc	1277 b	326 a	549 bcd	1872 a
25	77 b	518 b	2054 b	1085 cd	200 bc	660 ab	1727 ab
3	85 b	522 b	2445 a	1047 d	165 c	772 a	1961 a

<sup>a</sup>Within columns and species, means followed by a different letter are significantly different at the 0.05 probability level according to Tukey's studentized range test. Values are the means of three replications.

Table 4. Potassium-sodium ratios and selectivity coefficients for *Limonium perezii* and *L. sinuatum* grown in greenhouse sand cultures and irrigated with saline-sodic wastewaters.

EC (dS·m <sup>-1</sup> )	<i>L. perezii</i>				<i>L. sinuatum</i>			
	K <sup>+</sup> /Na <sup>+</sup>	S <sub>K,Na</sub>	K <sup>+</sup> /Mg <sup>2+</sup>	S <sub>K,Mg</sub>	K <sup>+</sup> /Na <sup>+</sup>	S <sub>K,Na</sub>	K <sup>+</sup> /Mg <sup>2+</sup>	S <sub>K,Mg</sub>
2.5	1.3 a <sup>c</sup>	6.0 c	3.0 a	1.5 c	2.3 a	11 c	2.2 a	1.1 d
7	0.66 b	11 bc	1.8 b	3.3 c	1.2 b	21 b	2.1 a	3.0 d
11	0.55 bc	16 b	1.7 bc	5.4 b	0.70 c	20 b	2.3 a	7.6 c
15	0.42 bc	17 b	1.5 bc	6.8 b	0.70 c	28 b	2.0 a	9.2 c
20	0.28 d	16 b	1.1 bc	7.1 b	0.70 c	42 a	2.4 a	16 b
25	0.31 c	26 a	1.1 bc	11 a	0.53 c	44 a	2.1 a	20 a
30	0.28 c	28 a	1.0 c	11 a	0.43 c	43 a	2.0 a	23 a

<sup>a</sup>Within columns, means followed by a different letter are significantly different at the 0.05 probability level according to Tukey's studentized range test. Values are the means of three replications.



high  $K^+$  content generally require high  $Mg^{2+}$  in order to prevent  $K$ -induced  $Mg^{2+}$  deficiency (Marschner, 1995). Potassium-magnesium relations in *Limonium* provide an example of the interaction. The ratio of  $K^+/Mg^{2+}$  in *L. perezii* shoots decreased significantly from 3 to 1 as salinity increased, but the ratio in *L. sinuatum* was 2.2 regardless of salinity level. Foliar analysis of *L. sinuatum* grown under nonsaline field conditions gave an identical  $K^+/Mg^{2+}$  ratio (about 2.2) (Armitage, 1993).

Species preference for  $K^+$  over  $Mg^{2+}$  did not differ at low levels of salinity. Thereafter,  $K^+:Mg^{2+}$  selectivity increased as salinity increased and was significantly higher in *L. sinuatum* than in *L. perezii* at all other levels of salinity (Table 4).

The ratio of  $K^+/Na^+$  in the shoots decreased as the ratio in the external solution decreased (Table 4). Many researchers suggest that the  $K^+/Na^+$  ratio in the tissues of glycophytes should be maintained above 1 to supply the  $K^+$  necessary for normal functioning of metabolic processes (Ashraf, 1994; Maathuis and Amtmann, 1999). According to this criterion, the  $K^+/Na^+$  ratios for *L. perezii* and *L. sinuatum* are lower than recommended in most treatments (Table 4). Potassium was, however, preferentially acquired and transported against a strong concentration gradient of  $Na^+$ , a process necessary for plant survival under saline conditions (Marschner, 1995). Both species exhibited a decided preference for  $K^+$  over  $Na^+$  and selectivity coefficients ( $S_{K, Na}$ ) increased with increasing salinity (Table 4). The comparatively higher salt tolerance of *L. sinuatum* relative to *L. perezii* may be the result of more effective  $K^+-Na^+$  selectivity.

Phosphorus appears to be required in higher concentrations by *L. sinuatum* than by *L. perezii*. Total P was 2-fold higher in shoots of *L. sinuatum* than in *L. perezii* at all salinity levels. Phosphorus concentration in shoots of *L. perezii* decreased significantly as salinity increased, but this effect was not consistent in *L. sinuatum* shoots. The concentration of total P in nonsaline leaf tissue of *L. sinuatum* (213  $mmol \cdot kg^{-1}$ ) was identical to the value reported for the species grown under field conditions (Armitage, 1993).

Total S was strongly accumulated in shoots of both species as salinity increased and external  $SO_4$  rose from 7 to 124  $mol \cdot m^{-3}$ . Shoot S concentrations in the *Limonium* species equaled or exceeded those found in well-known active S accumulators such as cruciferous vegetables grown under irrigation with saline-sodic waters of the same ionic composition (Grieve et al., 2001). In response to a 23  $dS \cdot m^{-1}$  treatment, total-S in tatsoi (*Brassica rapa* L.), mustard greens (*B. juncea* L.), and kale (*B. oleracea* L.) was 396, 371, and 515  $mmol \cdot kg^{-1}$  dry weight, respectively. Irrigation with saline waters (20  $dS \cdot m^{-1}$ ) of the same composition resulted in 756  $mmol$  total S in *L. perezii* and 540  $mmol$  total S/kg in *L. sinuatum*.

Another striking species difference in ion relations was in shoot Cl concentrations in

10-week-old seedlings. Generally, plant Cl increases proportionally with increases in external Cl. However, as salinity increased and external Cl rose from 7 to 144  $mol \cdot m^{-3}$ ,  $Cl^-$  in *L. sinuatum* shoots doubled, but the effect of the 20-fold increase in substrate Cl was not significant for *L. perezii*. Various other species also exhibit a similar response whereby large increases in substrate Cl do not result in significant increases in plant Cl. The effect has been observed when certain plants are grown under irrigation with sodium-sulfate dominated waters, e.g., the saline drainage effluents present in the SJV which typically contain equimolar ratios of  $Cl^-$  to  $SO_4^{2-}$ . For example, 14-fold increases in external-Cl resulted in significant increases in  $Cl^-$  concentration in aboveground biomass of pac choi (*B. rapa* L.), kale, and spinach (*Spinacia oleracea* L.), but shoot Cl content of endive (*Cichorium endivia* L.), radicchio (*C. intybus* L.) and swiss chard (*Beta vulgaris* L.) was not significantly affected (Grieve et al., 2001). These response may illustrate a competitive inhibition of  $Cl^-$  uptake and/or transport by  $SO_4^{2-}$ . White and Broadley (2001) point out that under saline conditions, anion channels in the plasma membrane facilitate  $Cl^-$  uptake. The channels are also permeable to other physiological anions ( $NO_3^-$ ,  $SO_4^{2-}$ ) which may limit  $Cl^-$  transport to the shoot. Inhibition of shoot- $Cl^-$  accumulation by this process, however, did not appear to confer salt tolerance. *Limonium sinuatum*, the more salt tolerant of the two species, was an active  $Cl^-$  accumulator whereas the salt sensitive *L. perezii* tended to restrict  $Cl^-$  concentration in the shoots.

The overall conclusions of this study are 1) the ability of a plant to survive and complete its life cycle under highly saline conditions does not necessarily confer a high level of salt tolerance based on yield; 2) quality of the marketable product indicates that *L. perezii* is salt sensitive, whereas *L. sinuatum* is moderately tolerant; 3) high selectivity of  $K^+$  over  $Na^+$  may have contributed to enhanced tolerance of *L. sinuatum*; and 4) the differential response in shoot Cl accumulation from substrates containing high levels of  $SO_4^{2-}$  and  $Cl^-$  warrants further investigation.

#### Literature Cited

- Alarcon, J. J., M. A. Morales, A. Torrecillas, and M. J. Sánchez-Blanco. 1999. Growth, water relations and accumulation of organic and inorganic solutes in the halophyte *Limonium latifolium* cv. Avignon and its interspecific hybrid *Limonium caspia* × *Limonium latifolium* cv. Beltlaard during salt stress. *J. Plant Physiol.* 154:795–801.
- Armitage, A.M. 1993. Speciality cut flowers, 372 p. Varsity Press/Timber Press, Portland, Ore.
- Aronson, J.A. 1989. HALOPH. A data base of salt tolerant plants of the world. Office of Arid Lands Studies, Univ. Arizona, Tucson.
- Ashraf, M. 1994. Breeding for salinity tolerance in plants. *Crit. Rev. Plant Sci.* 13:17–42.
- Ayers, R.S. and D.W. Westcot. 1985. Water quality for agriculture. FAO Irr. Drainage Paper 29 Rev. 1.
- Barc, C. 1992. The kindest cuts of all: How to evaluate

- new crops. *Greenhouse Mgr.* 11:82–84.
- Census of Horticultural Specialties. 1998. Cut flowers sold by state, p. 167–181. [97/horticulture/horticulture.htm](http://horticulture/horticulture.htm).
- Flowers, T.J., M.A. Hajibagheri, and N.J.W. Clipson. 1986. Halophytes. *Quart. Rev. Biol.* 61:313–337.
- Flowers, T.J. and A.R. Yeo. 1988. Ion relations of salt tolerance, p. 392–416. Chapter 10. In: D.A. Baker and J.L. Hall (eds.), *Solute transport in plant cells and tissues*. John Wiley & Sons, New York.
- Grieve, C.M., M.C. Shannon, and J.A. Poss. 2001. Mineral nutrition of leafy vegetable crops irrigated with saline drainage water. *J. Veg. Crop Prod.* 7:37–47.
- Hanson, A.D., B. Rathinasabopathi, J. Rivoal, M. Burnet, M.O. Sillon and D.A. Gage. 1994. Osmoprotective compounds in the Plumbaginaceae: A natural experiment in metabolic engineering of stress tolerance. *Proc. Natl. Acad. Sci. USA* 91:306–310.
- Maas, E.V. and S.R. Grattan. 1999. Crop yields as affected by salinity, p. 55–108. In: R.W. Skaggs and J. van Schilfgaarde (eds.), *Agricultural drainage*. Amer. Soc. Agron. Monogr. 38.
- Maathuis, F.J.M. and A. Amtmann. 1999.  $K^+$  nutrition and  $Na^+$  toxicity: The basis of cellular  $K^+/Na^+$  nutrition. *Ann. Bot.* 84:123–133.
- Marschner, H. 1995. *Mineral nutrition of higher plants*. Academic Press, New York.
- Morales, M.A., E. Olmos, A. Torrecillas, M.J. Sánchez-Blanco, and J.J. Alarcón. 2001. Differences in water relations, leaf ion accumulation and excretion rates between cultivated and wild species of *Limonium* sp. grown in conditions of saline stress. *Flora* 196:345–352.
- Pasternak, D. and A. Nerd. 1996. Research and utilization of halophytes in Israel, p. 325–348. In: R. Choukr-Allah, C.V. Malcolm, and A. Hamdy (eds.), *Halophytes and biosaline agriculture*. Marcel Dekker, New York.
- Salisbury, F.B. 1995. Units, symbols, and terminology for plant physiology, Utah State Univ., Logan.
- SAS Institute, Inc. 1997. SAS/STAT software: Changes and enhancements through release 6.12. SAS Inst., Cary, N.C.
- Shillo, R., M. Ding, D. Pasternak, and M. Zaccat. 2002. Cultivation of cut flower and bulb species with saline water. *Sci. Hort.* 92:41–54.
- Starman, T.W., T.A. Cerny, and A.J. MacKenzie. 1995. Productivity and profitability of some field-grown specialty cut flowers. *HortScience* 30:1217–1220.
- Suarez, D.L. and C. M. Grieve. 1988. Predicting cation ratios in corn from saline solution composition. *J. Expt. Bot.* 39:605–612.
- Suarez, D. L. and J. Simunek. 1997. UNSATCHEM: Unsaturated water and solute transport model with equilibrium and kinetic chemistry. *Soil Sci. Soc. Amer. J.* 61:1633–1646.
- Wang, D. 2002. Dynamics of soil water and temperatures in above ground sand cultures used for screening plant salt tolerance. *Soil Sci. Soc. Amer. J.* 66:1484–1491.
- Whipker, B.E. and P.A. Hammer. 1994. Growth and yield characteristics of field-grown *Limonium sinuatum* (L.) *HortScience* 29:638–640.
- White, P.J. and M.R. Broadley. 2001. Chloride in soils and its uptake and movement within the plant: A review. *Ann. Bot.* 88:967–988.
- Woodell, S.R.J. and H.A. Mooney. 1970. The effect of seawater on carbon dioxide exchange by the halophyte *Limonium californicum* (Boiss.) Heller. *Ann. Bot.* 34:117–121.

