HortScience 43(6):1888–1891. 2008.

Sodium Chloride Effects on Growth, Morphology, and Physiology of Chrysanthemum (*Chrysanthemum ×morifolium*)

M. Kate Lee and Marc W. van Iersel[1]

Department of Horticulture, University of Georgia, 1111 Miller Plant Science Building, Athens, GA 30602

Additional index words. salinity, NaCl, stomatal conductance, *Chrysanthemum ×morifolium*, growth retardant

Abstract. **As a result of the decreasing availability of high-quality irrigation water, salinity tolerance of greenhouse crops is of increasing importance. Saline irrigation water can have many negative effects on plants, but also has the potential to act as a growth regulator because of its ability to reduce plant height. To determine the effects of NaCl in the irrigation water on the growth, physiology, and nutrient uptake of chrysanthemums (*Chrysanthemum ×morifolium* Ramat.), plants were watered with solutions with different NaCl concentrations (0, 1, 3, 6, or 9 g·L^{-1}). Plants receiving 9 g·L^{-1} NaCl had a 76% reduction in shoot dry weight, a 90% reduction in stomatal conductance (g_S), and a 4-day delay in flowering compared with control plants. Chrysanthemums receiving 1 g·L^{-1} NaCl had a 4-cm reduction in height with only a small reduction in shoot dry weight. Stomatal conductance and transpiration were reduced by more than 60% by NaCl concentrations of 1 g·L^{-1} as compared with control plants. The combination of a small reduction in dry weight and a large decrease in transpiration resulted in increased water use efficiency when plants received 1 g·L^{-1} NaCl. Concentrations of 3 g·L^{-1} NaCl or higher resulted in poor-quality plants either as a result of wilting of the leaves (3 g·L^{-1}) or severely stunted plants (6 and 9 g·L^{-1}). Our findings indicate that chrysanthemums can be grown successfully with 1 g·L^{-1} NaCl in the irrigation water without negative impacts on plant quality. This has important implications for the greenhouse industry as the availability of nonsaline water decreases. Saline water may be more readily available and can have the added benefit of reduced plant height, which is an important quality characteristic for floriculture crops.**

Salinity tolerance of greenhouse plants is of increasing importance as a result of the decreasing availability of high-quality irrigation water. In coastal areas, the availability of high-quality irrigation water is threatened as a result of saltwater intrusion into the groundwater. Saltwater intrusion into groundwater is a leading cause of the contamination of irrigation water and can be defined as "the movement of saline water into freshwater aquifers and most often is caused by groundwater pumping from coastal wells" (Barlow, 2005). This occurs along the Georgia coastline and is a problem throughout the coastal parts of the United States as well as other parts of the world.

The role of Na$^+$ in plants is not fully understood. Some species, especially halophytes and some plants with the CAM- or C4-photosynthetic pathway, grow better in the presence of Na$^+$. Whether Na$^+$ is an essential micronutrient for higher plants in general is unclear (Marschner, 1995). The function of Cl$^-$ is better understood; Cl$^-$ is a component of the water-splitting system of photosystem II and involved in the stomatal regulation of many species and is therefore an essential micronutrient. Because chloride can be supplied by the soil, irrigation water, rain, fertilizer, or air pollution, deficiencies are not generally a problem. Toxicity of Cl$^-$ is a much more common concern (Marschner, 1995).

Saline irrigation water can have many negative effects on greenhouse crops. When overhead irrigation water has high salinity, the salt may precipitate on the leaves as the water evaporates. This in turn can result in foliar uptake and phytotoxicity (Bailey et al., 1999). The irrigation water may also cause salt to accumulate in the substrate, which may lead to salt uptake by the plants. Salt injury occurs when too much NaCl accumulates in the substrate. When excessive concentrations of NaCl are present in the soil, water uptake may be inhibited (Shalhevet and Bernstein, 1968), causing a physiological drought stress. High levels of NaCl in the root environment decreased the flower and stem quality of gerbera daisies (*Gerbera jamesonii* Bolus ex Hooker f.) (De Kreij and van Os, 1989) and roses (*Rosa ×hybrida*) (De Kreij and van den Berg, 1990). Plant height of greenhouse bell peppers (*Capsicum annuum* L.) decreased by as much as 49% and total leaf area by 82% with NaCl concentrations above 50 mmol·L^{-1} (2.92 g·L^{-1}) (Chartzoulakis and Klapaki, 2000). Vegetative growth of greenhouse eggplants (*Solanum melongena* L.) (shoot length, leaf area, and dry weight) was reduced at NaCl concentrations greater than 10 mmol·L^{-1} (0.58 g·L^{-1}) and salt injury symptoms such as chlorosis, burning of leaf margins, and necrosis occurred at concentrations greater than 50 mmol·L^{-1} (2.92 g·L^{-1}) NaCl. Yield of eggplants was reduced 88% at NaCl concentrations greater than 150 mmol·L^{-1} (8.76 g·L^{-1}) (Chartzoulakis and Loupassaki, 1997). Little research exists on NaCl tolerance of chrysanthemums. *Chrysanthemum indicum* 'Nanjing' showed a decrease in chlorophyll levels at NaCl concentrations greater than 100 mmol·L^{-1} (5.84 g·L^{-1}) and *Chrysanthemum chanetii* chlorophyll levels decreased at 150 mmol·L^{-1} (8.76 g·L^{-1}) (Chen et al., 2003a).

Although NaCl has been shown to decrease yield, it also can decrease plant height (Chartzoulakis and Klapaki, 2000). Therefore, NaCl may have the potential benefit of acting as a growth retardant for floricultural crops in which height control is an important quality issue. It is imperative to better understand the effects of NaCl on crops because high levels of NaCl will ultimately decrease yield (Childs and Hanks, 1975). A better understanding of NaCl effects on plant growth, morphology, and physiology can help to improve cultivation with saline water and perhaps lead to the use of saline water as a growth retardant.

The objective of this study was to quantify the effect of saline irrigation water on chrysanthemums under greenhouse conditions and to determine which NaCl concentrations result in marketable plants. We hypothesized that plant growth is inhibited with increasing concentrations of NaCl and that the physiological drought stress caused by NaCl will reduce stomatal conductance (g_S) and transpiration.

Materials and Methods

Plant materials and treatments. The experiment was carried out in a glass-covered greenhouse at the University of Georgia, Athens, GA. On 14 Sept. 2007, 40 rooted, 8-cm tall chrysanthemum 'Yellow blush' cuttings were planted in 15-cm diameter pots filled with soilless substrate (60% peat:40% perlite; Fafard 2P; Fafard, Agawam, MA). The chrysanthemums were watered-in at planting with regular tap water. Five grams of a 14N–6.02P–11.62K slow-release fertilizer (Osmocote 14-14-14; The Scotts Co., Marysville, OH) were applied to the top of

---

Received for publication 8 May 2008. Accepted for publication 10 June 2008.

We thank Brett Herlocker, Craig Truitt, Dustin Perdue, and JongYun Kim for their help with data collection; Yoder Brothers for donation of the plant material; Conrad Fafard Inc. for donation of the growing medium; and Doug Sturtz and Jonathan Frantz (USDA-ARS Application Technology Research Unit, Toledo, OH) for the tissue analyses.

[1] To whom reprint requests should be addressed; e-mail mvanier@uga.edu

the substrate 3 d after planting. After the initial watering with tap water, plants were watered with solutions containing 0, 1, 3, 6, or 9 $g \cdot L^{-1}$ NaCl. The solution with 0 $g \cdot L^{-1}$ NaCl was tap water with an electrical conductivity (EC) of 0.12 $dS \cdot m^{-1}$. The 1, 3, 6, and 9 $g \cdot L^{-1}$ NaCl solutions had EC values of 2.00, 5.67, 11.30, and 16.90 $dS \cdot m^{-1}$, respectively. All treatments were watered with 250 mL of the appropriate concentration of NaCl solution on an as-needed basis. If one plant in a treatment needed watering, each plant in that treatment was watered. None of the applied water leached from the pots.

Temperature, relative humidity, and daily light integral (DLI) (cumulative photosynthetic photon flux per day) in the greenhouse were monitored with a data logger (HOBO U12-012; Onset, Bourne, MA) and light sensor (Q-SUN; Apogee Instruments, Logan, UT) from 20 Oct. until harvest on 13 Nov. Minimum and maximum temperature averaged 15.3 ± 3.4 °C and 31.1 ± 3.6 °C, minimum and maximum relative humidity averaged 27% ± 14% and 70% ± 8%, and DLI averaged 8.8 ± 2.5 $mol \cdot m^{-2}$ (mean ± SD).

Measurements. Throughout the experiment, we kept track of the total amount of water applied to each plant, which allowed for the determination of water use efficiency (WUE; calculated as shoot dry weight divided by total amount of water applied). The time until flowering was determined by looking for the first sight of color of an unfolding flower. Using a porometer (LI-1600; LI-COR, Lincoln, NE), g_S and transpiration were measured on one fully expanded leaf near the top of the plant during week 7 of the experiment. The plant height (from the substrate to the tip of the plant), chlorophyll content of the leaves (SPAD meter; Minolta, Tokyo), and bulk EC of the substrate (Field-Scout EC probe; Spectrum Technologies, Plainfield, IL) were measured during week 8. Bulk substrate EC was measured by inserting the EC probe directly into the substrate to a depth of ≈5 cm. The data thus represent the combined EC of the solid components, the pore solution, and the gaseous phase in the substrate (see Scoggins and van Iersel, 2006 for a more detailed discussion of the difference between bulk substrate EC and solution EC).

The plants were harvested after 60 d (13 Nov. 2007) and the leaf area of the uppermost fully expanded leaf of each plant was measured (LI-3100; LI-COR). The shoot dry weight was measured after the plants had been cut at the substrate surface and oven-dried at 80 °C for 3 d. A sample of the shoot tissue of each plant was then sent to the USDA-ARS Application Technology Research Unit in Toledo, OH, for nutrient analysis.

Experimental design and statistical analysis. The chrysanthemums were arranged in a randomized complete block with five NaCl treatments in eight blocks. The NaCl effects on time until flowering were analyzed using analysis of variance with mean separation according to Tukey's honestly significant difference ($P = 0.05$). All other statistics were performed using linear and nonlinear regression analysis with the NaCl concentration of the irrigation water as the independent variable.

Results and Discussion

The results of our experiment provide clear evidence that NaCl in the irrigation water accumulates in both the plants and substrate and inhibits plant growth. At the end of the experiment, substrate EC increased with increasing NaCl concentrations from a bulk substrate EC of 0.17 $dS \cdot m^{-1}$ in the treatment without NaCl to 15.2 $dS \cdot m^{-1}$ in the 9 $g \cdot L^{-1}$ NaCl treatment (Fig. 1) indicating salt buildup in the substrate. The absence of leaching in this study may have aggravated the salt buildup in the substrate.

Treatments with 0, 1, 3, and 6 $g \cdot L^{-1}$ NaCl flowered after 46 d, whereas treatments receiving 9 $g \cdot L^{-1}$ NaCl flowered after 50 d, a 4-d delay (Fig. 2). Increasing amounts of NaCl applied to field-grown annual pursh seepweed [*Suaeda calceoliformis* (Hook.) Moq.] (Williams and Ungar, 1972) and to Dixie iris (*Iris hexagona* Walter) (Van Zandt and Mopper, 2002) also resulted in a delay of flowering. NaCl can reduce flower yield and quality of cut roses; the severity of this reduction, however, is root stock-dependent (Cabrera, 2003).

Stomatal conductance and transpiration decreased with increasing rates of NaCl. Seven weeks into the experiment, the control plants had a g_S of 174 $mmol \cdot m^{-2} \cdot s^{-1}$ and a transpiration rate of 3.77 $mmol \cdot m^{-2} \cdot s^{-1}$ (Fig. 3). Even at NaCl concentrations of only 1 $g \cdot L^{-1}$, transpiration and g_S were reduced by more than 60% as compared with control plants. Treatments receiving 3 to 9 $g \cdot L^{-1}$ NaCl had a g_S of ≈10 $mmol \cdot m^{-2} \cdot s^{-1}$ and a transpiration rate of 0.3 $mmol \cdot m^{-2} \cdot s^{-1}$, reductions of over 90% compared with the control. Similarly, transpiration rates of Chinese white poplar (*Populus tomentosa* Carrière) (Chen et al., 2003b), cotton (*Gossypium hirsutum* L.), bean (*Phaseolus vulgaris* L.) (Brugnoli and Lauteri, 1991), and tomato (*Solanum lycopersicum* L.) (Romero-Aranda et al., 2001) were reduced with increasing salinity.

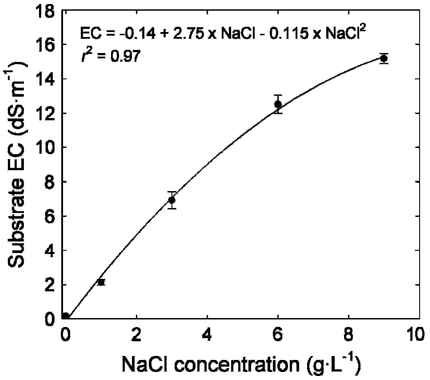

Fig. 1. The substrate electrical conductivity (EC) as affected by the NaCl concentration of the irrigation water. Data points are the mean ± SE (n = 8). The curve represents a significant quadratic effect ($P < 0.0001$).

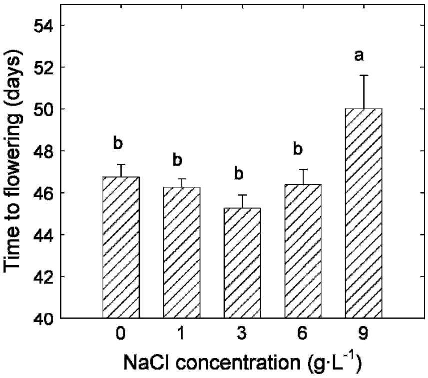

Fig. 2. The effect of the NaCl concentration of the irrigation water on the time until flowering of chrysanthemum. Bars are the mean ± SE (n = 8). Mean separation by Tukey's honestly significant difference ($P = 0.05$).

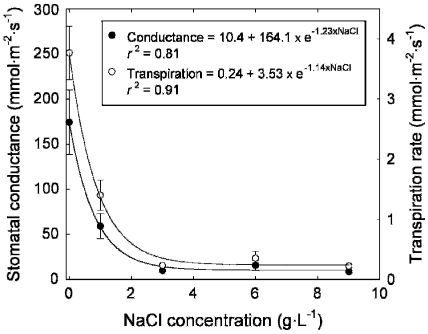

Fig. 3. The stomatal conductance and transpiration of chrysanthemum leaves as affected by the NaCl concentrations of the irrigation water. Data points are the mean ± SE (n = 8). Curves show significant effects ($P < 0.0001$).

During the sixth week of the experiment, leaf wilting became notable in the 3 $g \cdot L^{-1}$ NaCl treatment and remained so for the rest of the experiment. There was no sign of wilting in any of the other treatments. Although wilting is consistent with salt-induced physiological drought stress, it is surprising that wilting was observed in the 3 $g \cdot L^{-1}$ treatment, but not in treatments with concentrations greater than 3 $g \cdot L^{-1}$.

Chlorophyll content was decreased to 29.2 SPAD units in the 9 $g \cdot L^{-1}$ NaCl treatment as compared with an average of 42.3 SPAD units in the other treatments (Fig. 4). These findings are consistent with an earlier report on two other *Chrysanthemum* species (Chen et al., 2003a) and the finding that NaCl reduces leaf photosynthesis and chlorophyll content at NaCl concentrations above 70 mM (4.1 $g \cdot L^{-1}$) (Montesano and van Iersel, 2007).

Plant height and the area of the uppermost fully expanded leaf were both significantly decreased by increasing concentrations of NaCl. At the end of the experiment, plant height ranged from 31.9 cm in the control to

14.2 cm in the 9 g·L^{-1} NaCl treatment (Fig. 5). Leaf area similarly decreased with increasing concentrations of NaCl, from 25.4 cm^2 in the control to 15.4 cm^2 in the 9 g·L^{-1} NaCl treatment (Fig. 5). Plant height was more sensitive to NaCl than leaf area. The reduction in height was 6.1%, whereas leaf area decreased by 4.8% with every 1 g·L^{-1} NaCl increase in the irrigation water. Plant height and leaf elongation of tomato also decrease with increasing NaCl in the nutrient solution (Al-Karaki, 2000; Montesano and van Iersel, 2007). Salinity not only decreases the area of individual leaves, but also the total leaf area of plants. For example, growth and leaf area development of cotton, bean, and tomato were strongly inhibited by salinity (Brugnoli and Lauteri, 1991; Romero-Aranda et al., 2001). Excessive amounts of salt in plants can become toxic in older leaves, causing premature senescence and a reduction in total photosynthetic leaf area (Munns, 2002). Such reductions in leaf area are likely to decrease whole plant photosynthesis and thus growth.

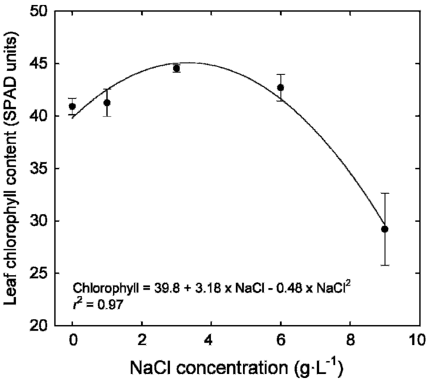

Fig. 4. The leaf chlorophyll content of chrysanthemums as affected by the NaCl concentration of the irrigation water. Data points are the mean ± SE (n = 8). The curve represents a significant quadratic effect (P = 0.0007).

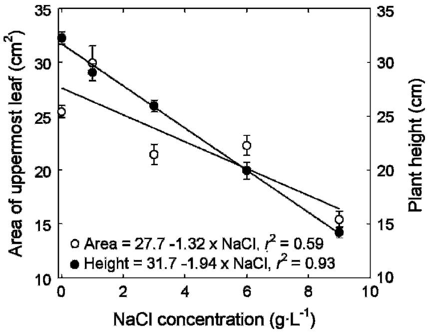

Fig. 5. The effect of NaCl concentration of the irrigation water on the final plant height and area of the uppermost fully expanded leaf of chrysanthemums. Data points are the mean ± SE (n = 8). There are significant correlations between the NaCl concentration and both plant height and leaf area (P < 0.0001).

There was indeed a strong inverse correlation between NaCl concentration and shoot dry weight, which decreased from 8.2 g in the treatment without NaCl to 2 g for plants receiving 9 g·L^{-1} NaCl (Fig. 6). Root and shoot dry weight of tomato plants also decreased as the NaCl concentration increased (Al-Karaki, 2000; Caines and Shennan, 1999; Montesano and van Iersel, 2007; Romero-Aranda et al., 2001).

Shoot tissue in the 9 g·L^{-1} NaCl treatment contained almost 100 mg·g^{-1} Na$^+$ (Table 1), whereas plant tissue in the control had Na$^+$ concentrations of only 1 mg·g^{-1}. Increasing Na$^+$ uptake has been reported to interfere with uptake of K$^+$ (Al-Karaki, 2000; Montesano and van Iersel, 2007; Serrano and Rodriquez-Navarro, 2001). However, we found the lowest K$^+$ concentrations in the control treatment and the highest K$^+$ concentrations with 6 g·L^{-1} NaCl.

Tissue N concentrations were lowest with 9 g·L^{-1} NaCl, which is consistent with NaCl-induced leaf senescence (Munns, 2002). Tissue phosphorus concentrations decreased, whereas calcium and sulfur concentrations increased with increasing NaCl concentrations. For many other nutrients, there was a quadratic relationship between tissue and NaCl concentrations, often indicating an increase in tissue concentrations as the NaCl increased from 0 to 3 or 6 g·L^{-1} and then a decrease in tissue concentrations as NaCl increased to 9 g·L^{-1} (Table 1). The increase in tissue concentrations as the NaCl increased to 3 and 6 g·L^{-1} may have been the result of a dilution effect. The higher dry weight of the control plants may have diluted the nutrients in the tissue of these plants, resulting in lower nutrient concentrations.

Because each treatment received water on an as-needed basis and there was no leaching, we were able to determine the total amount of water used. The control plants received 5.5 L/plant, and the 9 g·L^{-1} NaCl treatment received only 2.5 L/plant. This resulted in a WUE of 1.5 g·L^{-1} in the control, a slightly higher WUE with 1 and 3 g·L^{-1} NaCl, and a reduction in WUE at higher NaCl concentrations down to a WUE of 0.8 g·L^{-1} in the 9 g·L^{-1} NaCl treatment (Fig. 7). The increase in WUE at NaCl concentrations of 1 and 3 g·L^{-1} is consistent with our finding that g_S and transpiration were greatly reduced at these NaCl concentrations, whereas shoot dry weight was reduced much less. Previous reports on the impact of salinity on WUE are mixed; Al-Karaki (2000) reported that increasing NaCl concentrations in the nutrient solution reduced WUE, whereas Montesano and van Iersel (2007) found that increasing salinity increased WUE of tomatoes. Our results suggest that NaCl effects on WUE are concentration-dependent because we found the highest WUE at NaCl concentrations of 1 and 3 g·L^{-1}, whereas higher NaCl concentrations reduced WUE.

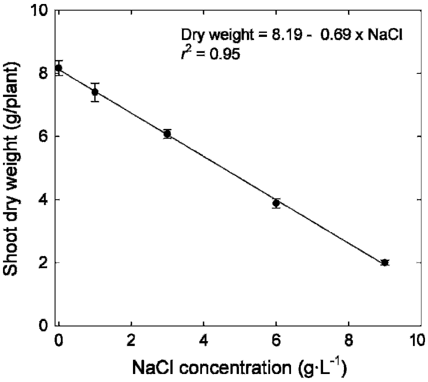

Fig. 6. The correlation between the NaCl concentration of the irrigation water and the dry weight of the chrysanthemum shoots. The line represents a significant linear effect (P < 0.0001). Data points are the mean ± SE (n = 8).

Our findings differ from the general recommendations regarding water quality for greenhouse production by Bailey et al. (1999), who suggest an upper limit of 69 mg·L^{-1} for Na$^+$ and 71 mg·L^{-1} for Cl$^-$ for the container production of plants, which is a concentration much lower than the 1 g·L^{-1} NaCl that resulted in satisfactory growth and quality in this study. It is important to note that we applied the water directly to the substrate. Applying irrigation water overhead will apply the NaCl to the foliage as well as the substrate and may lead to foliar toxicity symptoms (Bailey et al., 1999). Furthermore, ornamental species differ in their tolerance to salinity (Niu and Rodriguez, 2006), so 1 g·L^{-1} of NaCl may not be suitable for other species.

Table 1. The effect of NaCl concentrations in the irrigation water on the mineral composition of chrysanthemum

NaCl concn	N	P	K	Ca	Mg	S	Na	B	Cu	Fe	Mn	Mo	Si	Zn
(g·L^{-1})	mg·g^{-1}							µg·g^{-1}						
0	27.9	7.19	37.1	8.6	4.28	2.35	1.0	15.3	6.77	60	131	1.10	220	27.8
1	28.3	5.95	37.6	9.7	5.23	2.51	13.8	13.5	6.42	68	157	1.22	230	32.0
3	30.1	6.11	44.7	9.9	4.34	2.38	18.7	15.4	6.83	75	191	1.50	225	35.9
6	31.9	5.96	49.2	10.5	4.63	2.82	42.6	16.4	6.98	98	194	1.62	224	41.3
9	25.9	4.93	44.6	11.2	5.81	2.75	98.0	15.3	5.95	73	140	1.06	207	34.8
Significance	Q***	L***	Q***	L***	Q*	L***	Q***	NS	Q**	NS	Q***	Q*	NS	Q***
R^2	0.51	0.53	0.62	0.48	0.45	0.50	0.90	—	0.51	—	0.64	0.24	—	0.74

$^{NS, *, **, ***}$Nonsignificant or significant linear (L) or quadratic (Q) effects at P > 0.05, P > 0.01, and P > 0.001, respectively.

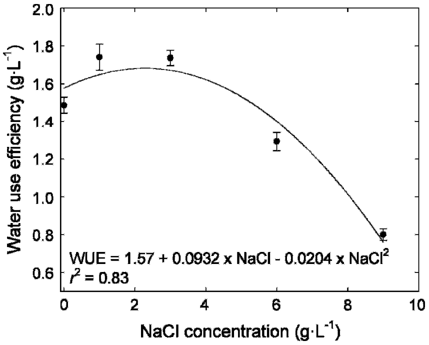

Fig. 7. The effect of the NaCl concentration of the irrigation water on the water use efficiency (WUE) of chrysanthemum. Data points are the mean ± SE (n = 8). The curve indicates a significant quadratic effect ($P < 0.0001$).

Conclusions

The results of this experiment are relevant to the floriculture industry as high-quality irrigation water becomes less available. Application of 1 g·L^{-1} NaCl resulted in only a small reduction in plant dry weight while reducing plant height by 4 cm and increasing WUE. The reduction in plant height may reduce the need for plant growth regulator applications, which would result in financial savings, whereas the increase in WUE could result in water savings. Concentrations of NaCl higher than 1 g·L^{-1} stunted growth in a manner that decreased marketability. Plants remained wilted during the end of the production period when irrigated with 3 g·L^{-1} NaCl and were severely stunted at even higher concentrations. Our findings indicate that growers may be able to use slightly saline water (at least up to 1 g·L^{-1} NaCl) for the greenhouse production of chrysanthemum without detrimental effects on plant growth.

Literature Cited

Al-Karaki, G.N. 2000. Growth, water use efficiency, and sodium and potassium acquisition by tomato cultivars grown under salt stress. J. Plant Nutr. 23:1–8.

Bailey, D., T. Bilderback, and D. Bir. 1999. Water considerations for container production of plants. HIL 557. North Carolina Cooperative Extension Service, Raleigh, NC.

Barlow, P. 2005. Ground water in freshwater-saltwater environments of the Atlantic coast. US Geological Survey. Circ. 1262. 20 Apr. 2008. <http://pubs.usgs.gov/circ/2003/circ1262/>.

Brugnoli, E. and M. Lauteri. 1991. Effects of salinity on stomatal conductance, photosynthetic capacity, and carbon isotope discrimination of salt-tolerant (*Gossypium hirsutum* L.) and salt-sensitive (*Phaseolus vulgaris* L.) C3 non-halophytes. Plant Physiol. 95:628–635.

Cabrera, R.I. 2003. Demarcating salinity tolerance in greenhouse rose production. Acta Hort. 609:51–57.

Caines, A.M. and C. Shennan. 1999. Interactive effects of Ca^{2+} and NaCl salinity on the growth of two tomato genotypes differing in Ca^{2+} use efficiency. Plant Physiol. Biochem. 37:569–576.

Chartzoulakis, K. and G. Klapaki. 2000. Response of two greenhouse pepper hybrids to NaCl salinity during different growth stages. Sci. Hort. 86:247–260.

Chartzoulakis, K. and M.H. Loupassaki. 1997. Effects of NaCl salinity on germination, growth, gas exchange and yield of greenhouse eggplant. Agr. Water Mgt. 32:215–225.

Chen, F., S. Chen, W. Guo, and S. Ji. 2003a. Salt tolerance identification of three species of chrysanthemums. Acta Hort. 618:299–305.

Chen, S., J. Li, S. Wang, E. Fritz, A. Hütterman, and A. Altman. 2003b. Effects of NaCl on shoot growth, transpiration, ion compartmentation, and transport in regenerated plants of *Populus euphratica* and *Populus tomentosa*. Can. J. For. Res. 33:967–975.

Childs, S.W. and R.J. Hanks. 1975. Model of soil salinity effects on crop growth. Soil Sci. Soc. Amer. Proc. 39:617–622.

De Kreij, C. and T.J.M. van den Berg. 1990. Nutrient uptake, production and quality of *Rosa hybrida* in rockwool as affected by electrical conductivity of the plant nutrient solution, p. 519–523. In: Van Beusichem, M.L. (ed.). Plant nutrition—Physiology and applications. Kluwer Academic Publishers, Dordrecht, The Netherlands.

De Kreij, C. and P.C. van Os. 1989. Production and quality of *Gerbera* in rockwool as affected by electrical conductivity of the nutrient solution. Proc. 7th Intl. Congr. Soilless Culture. p. 255–264.

Marschner, H. 1995. Mineral nutrition of higher plants. Academic Press, New York, NY.

Montesano, F. and M.W. van Iersel. 2007. Calcium can prevent toxic effects of Na^{+} on tomato leaf photosynthesis but does not restore growth. J. Amer. Soc. Hort. Sci. 132:310–318.

Munns, R. 2002. Comparative physiology of salt and water stress. Plant Cell Environ. 25:239–250.

Niu, G. and D.S. Rodriguez. 2006. Relative salt tolerance of selected herbaceous perennials and groundcovers. Sci. Hort. 110:352–358.

Romero-Aranda, R., T. Soria, and J. Cuartero. 2001. Tomato plant–water uptake and plant–water relationships under saline growth conditions. Plant Sci. 160:265–272.

Scoggins, H.L. and M.W. van Iersel. 2006. *In situ* probes for measurement of EC of soilless substrates: Effects of temperature and substrate moisture content. HortScience 41:210–214.

Serrano, R. and A. Rodriquez-Navarro. 2001. Ion homeostasis during salt stress in plants. Curr. Opin. Cell Biol. 13:399–404.

Shalhevet, J. and L. Bernstein. 1968. Effects of vertically heterogeneous soil salinity on plant growth and water uptake. Soil Sci. 106:85–93.

Van Zandt, P.A. and S. Mopper. 2002. Delayed and carryover effects of salinity on flowering in *Iris hexagona* (Iridaceae). Amer. J. Bot. 89:1847–1851.

Williams, M.D. and I.A. Ungar. 1972. The effects of environmental parameters on the germination, growth, and development of *Suaeda Depressa* (Pursh). Wats. Amer. J. Bot. 59: 912–918.