Greenhouse Rose Yield and Ion Accumulation Responses to Salt Stress as Modulated by Rootstock Selection

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Abstract. Greenhouse rose (*Rosa* × spp. L.) production is facing the use of poor-quality irrigation waters and regulatory pressures to recycle runoff and drainage effluents. Two experiments (were conducted to evaluate the yield and quality and ion accumulation responses of roses grafted on various rootstocks to increasing salinity stress. In Expt. 1, the scion 'Bridal White' grafted on 'Manetti', *R. odorata* (Andr.), 'Natal Briar', and 'Dr. Huey' were irrigated over four flowering cycles with complete nutrient solutions supplemented with NaCl at 0, 5, and 30 mM. In Expt. 2, plants of 'Red France' on 'Manetti' and 'Natal Briar' were irrigated over six flowering cycles with complete nutrient solutions supplemented with NaCl + CaCl₂ (2:1 M ratio) at 0, 1.5, 3, 6, 12, and 24 mM. Salt concentration increases significantly and negatively affected the biomass, cut flower production, and foliage quality of the roses in both experiments, but the responses were modulated by rootstock selection. 'Manetti' plants in general sustained better absolute and relative biomass and flower yields, accumulated less Na⁺ and Cl⁻ in its tissues, and showed less toxicity symptoms with increasing salinity than the others. 'Natal Briar' also had similar absolute productivity responses as 'Manetti' but were afflicted by a significantly different mineral nutrient profile, including higher accumulations and toxicities with Na⁺ and Cl⁻ that led to lower foliage visual ratings. Conversely, the relative yields of plants on 'Dr. Huey' and *R. odorata* were similarly reduced by increasing salinity, but the former had lower Na⁺ and Cl⁻ concentrations in its tissues and better visual scores than the latter, which fared as the worst. A combined analysis of the results suggests that on a productivity basis (biomass and flower yields), greenhouse roses could withstand overall maximum electrical conductivities (i.e., osmotic effects) of applied fertigation solutions of 3.0 ± 0.5 dS·m⁻¹. On the other hand, and considering the aesthetic responses (visual scores) of on-plant and harvested foliage (cut flower shoots), greenhouse rose tolerance to applied Na⁺ and Cl⁻ concentrations (ion-specific effects) could range up to 10 ± 2 mM.

The production of greenhouse roses for cut flowers is primarily based on hybrid tea cultivars budded or grafted on clonally or seed-propagated rootstocks (Cabrera, 2002; de Hoog, 2001; de Vries, 2003; Hanan and Grueber, 1987). Rootstock use has been based on the observation that plant performance and flower productivity in grafted plants is higher than in plants growing on

their own roots (Cabrera, 2002; Hanan and Grueber, 1987). Up until 2 decades ago, *Rosa* 'Manetti' (syn. *R. noisettiana* 'Manetti') and *R. odorata* (Andr.) (syn. *R. indica* L. 'Major', *R. chinensis* 'Major'), and to a lesser extent *R. 'Dr. Huey'*, were among the most widely used rootstocks by the greenhouse rose industry in North and South America (de Vries, 2003; Hanan and Grueber, 1987). During the decade of 1990, however, the introduction of the South African *R. 'Natal Briar'*, of unknown lineage, has practically and completely pushed aside 'Manetti' as the rootstock of choice thanks to its induced vigor (to scion) and ease of propagation and grafting (de Vries, 2003).

Roses have historically been reported to be sensitive to salinity with appreciable yield losses observed when the electrical conductivity (EC) in saturated soil/media paste extracts (EC_e) exceeds 3 dS·m⁻¹ (Bernstein et al., 1972; Davidson, 1969). Such EC levels are easily reached in greenhouse rose production because the crop is irrigated with nutrient solutions (fertigation) that commonly range between 1.5 and 2 dS·m⁻¹ (Cabrera, 2003; White, 1987). Depending on irrigation frequency and volume, the EC in the root zone,

however, can reach undesirable high values as a result of plant water uptake and soil/media evaporation (de Hoog, 2001). In recent years, dwindling availability of good-quality irrigation water and environmental pressures are forcing growers to use poor-quality waters and recycle/reuse leached and runoff solutions (Baas and van den Berg, 1999; Bernstein et al., 2006; de Hoog, 2001; Raviv et al., 1998), all of which contribute to higher salt stress levels. Besides the overall EC (i.e., osmotic effect) of a nutrient solution, roses have also been reported to be sensitive to toxicity (i.e., ion-specific effects) by relatively low sodium (Na⁺) and chloride (Cl⁻) concentrations in the range of 2 to 4 mM (Hughes and Hanan, 1978; Yaron et al., 1969). A recent 12-month study in a soilless production system, however, reported that 'Bridal Pink' (on *R. 'Manetti'*) roses tolerated, remarkably well, increasing NaCl concentrations up to 30 mM (Cabrera and Perdomo, 2003). Flower and dry weight yields were not significantly affected by the overall EC (up to 7.0 dS·m⁻¹) and high Cl⁻ concentrations (up to ≈70 mM) recorded in their leachate solutions. This is a noteworthy result considering that the EC and Cl⁻ concentrations exceeded their maximum recommended thresholds (Bernstein et al., 1972; Hughes and Hanan, 1978; Yaron et al., 1969) by two- to threefold and five- to 25-fold, respectively. Based on their results, and comparing their data with the contrasting observations from other rose salinity studies, Cabrera and Perdomo (2003) contended that rootstock selection was a key factor involved in salinity tolerance along with the use of well-drained substrates and moderate to high leaching fractions.

Although ion composition in irrigation waters varies widely across the globe, it is often dominated by the cations Na⁺, Ca²⁺, and Mg²⁺ and the anions Cl⁻, SO₄²⁻, and HCO₃⁻ (Grattan and Grieve, 1999). Waters with very high salinity such as those in oceans and coastal areas are dominated primarily by Na⁺ and Cl⁻, whereas the bulk of the waters outside of these regions often have compositions dominated by other ions. For instance, western U.S. irrigation waters with intermediate salinities up to 2.0 dS·m⁻¹ often have Na⁺/(Na⁺ + Ca²⁺) ratios between 0.1 and 0.7, indicating Ca²⁺ is a major contributor to the total solution EC, strongly suggesting that the composition of saline waters in experimental studies in these regions should reflect these ratios (Grattan and Grieve, 1999). Most salinity studies on horticultural or agronomic crops have typically used NaCl as the sole salinizing agent, ignoring the fundamental distinction between saline and sodic conditions. The use of NaCl as the main or only salinizing salt thus seriously limits the extent to which the results can be interpreted (Grattan and Grieve, 1999) and often is irrelevant in an ecological sense (Greenway and Munns, 1980).

The main objectives of our studies were to evaluate the interactive effects of salinity and rootstock selection in greenhouse rose yield, quality, and ion accumulation responses considering first a NaCl-only salt stress experiment

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followed by a second experiment with a mixed NaCl + CaCl₂ salt stress.

Materials and Methods

General crop culture and management.

For both experiments, the rose plants were grown in 20-L plastic containers filled with a sphagnum peat:pine bark:sand medium (3:1:1 v/v). The medium was amended with 3.0 and 0.6 kg·m⁻³ of dolomitic limestone (Carl Pool Products, Gladewater, TX) and the micronutrient fertilizer Micromax™ (The Scotts Co., Marysville, OH), respectively. The containers were placed, three abreast and spaced at 30-cm centers, on gravel beds lined with a black polyethylene weed barrier inside a research glasshouse at the Texas A&M AgriLife Research and Extension Center in Dallas, TX. Border plants were used in adjacent beds and on the front and back ends of each experimental bed. The greenhouse temperature control equipment was thermostatically set to produce target day and night temperatures of 25 and 18 °C, respectively. Environmental variables (temperature, relative humidity, and photosynthetically active radiation) were monitored with sensors placed at canopy height and data recorded with a data logger-based weather station (Campbell Scientific, Logan, UT).

The plants were fertigated, with their respective experimental treatments, by pumping the nutrient solutions from 160-L containers with submersible pumps (Model 2E-38N; Little Giant Pump Co., Oklahoma City, OK) through 1.3-cm polyethylene irrigation lines and 3.2-mm spaghetti tubing that fed individual (one per pot) calibrated spray stakes (Spot Spitter®; Roberts Irrigation Products, San Marcos, CA). All solutions in both experiments were prepared in tap water having a pH of 7.4, EC of 0.49 dS·m⁻¹, and Na⁺, Ca²⁺ and Cl⁻ concentrations of 1.7, 1.1, and 1.5 mM, respectively. Irrigation (average frequency of two to three times a week) was based on the rate of evapotranspiration (ET) measured gravimetrically from selected plants from each treatment. The volume of solution applied to each treatment was adjusted at every irrigation event to meet ET and produce a target leaching fraction of 25%. The plant-available water fraction in the substrate was empirically calculated in advance and care was taken to irrigate when no more than half of it had been depleted, thus minimizing the potential contribution of low moisture content to osmotic stress. Soil solution samples (Rhizon SMS samplers) or leachate samples from selected treatments were collected regularly (1 to 2 weeks) and analyzed for pH (Accumet® AP63 pH/mV/Ion Meter; Fisher Scientific, Pittsburgh, PA), EC (VWR Conductivity Meter Model 2052; VWR International, Inc., Irving, TX), and Cl concentrations (Digital Chloridometer Model 4425000; Labconco Co., Kansas City, MO).

Plants were managed following conventional pruning practices (Langhans, 1987) to produce synchronized flowering flushes that allowed the majority of the flower shoots to

reach a harvestable stage within 1 week of each other. Relative leaf chlorophyll levels were evaluated in fresh leaves of cut flower shoots using a SPAD-502 Chlorophyll Meter (Minolta Camera Co., Ltd., Osaka, Japan). After stem length determination, harvested flower shoots were put in paper bags and oven-dried at 70 °C until constant weight. The dry weights were recorded along with the number of flowers per plant. Dried leaf tissues previously selected from the middle portion of harvested flower shoots were ground to pass a 40-mesh screen used for full tissues analyses. Whole plants from each treatment were destructively harvested at the end of each experiment, separated into leaves, stems, and roots, and oven-dried to constant weight at 70 °C. Tissues from these organs were later analyzed for mineral content.

Expt. 1. Uniform and well-developed rose plants of the cultivar Bridal White grafted on the rootstocks ‘Manetti’, *R. odorata*, ‘Natal Briar’, and ‘Dr. Huey’ (grafting made by Jackson & Perkins Roses, Somis, CA) were transplanted on 29 Sept. 2000. The plants were grown for 1 year under standard environmental conditions (as mentioned previously) and fertigated with a complete nutrient solution based on the water-soluble fertilizer Scotts Peter® Excel® 15-5-15 (15N-2.2P-12.5K; The Scotts Co.). This base nutrient solution was adjusted to provide a nitrogen concentration (78% as NO₃⁻) of 10 mM providing the following nutrient concentrations (also in mM): 0.66 phosphorus (as H₂PO₄⁻), 2.97 potassium, 1.16 calcium, 0.77 magnesium, 0.014 manganese, 0.013 iron, 0.013 boron, 0.007 zinc, 0.001 copper, and 0.0007 molybdenum. From 28 Dec. 2001 until 7 June 2002, the base nutrient fertilizer solution was salinized with NaCl at concentrations of 0, 15, and 30 mM (final ECs, including fertilizer and water EC, of 1.66, 3.16, and 4.66 dS·m⁻¹, respectively) with their pH adjusted to 6.0 with 4 M H₂SO₄. A total of four flower harvests were done over the 27-week experimental period. A salt burn rating evaluation was taken after the third harvest by two different evaluators using a scale from 0 to 5 (0 = 0%, 1 = 20%, 2 = 40%, 3 = 60%, 4 = 80%, and 5 = 100% of foliage presenting salt burn damage). Dried and ground leaf tissues from harvested flower shoots were analyzed for mineral content (determined by inductively coupled plasma spectroscopy in HCl dissolutions of dry-ashed samples) by the Agricultural Analytical Services Laboratory, Pennsylvania State University (University Park, PA). Tissues of three whole plants of each rootstock were destructively harvested at the end of the experiment, dried, ground, and analyzed for chloride (Digital Chloridometer Model 4425000; Labconco Co.) and sodium (Atomic Absorption Spectrometer AA240FS; Varian, Inc., Perth, Australia) concentrations. The experiment was analyzed as a randomized complete block design with a factorial treatment structure, four rootstocks × three NaCl levels, that used five replications (plants) per treatment combination. Data were analyzed by GLM, regres-

sion, and correlation procedures using SAS® 9.1 for Windows (SAS Institute Inc., Cary, NC). In instances in which the effect of salinity stress was sought without the intrusion of growth differences inherent to rootstock selection, dry weight yield data were first normalized (converted) into a relative scale (0 to 100). This was accomplished by identifying the plant with the highest dry mass within each rootstock (across all salt treatments) and assigning it a value of 100, which was then used to calculate the relative value for the rest of the plants within that cultivar; the data were then subjected to arcsine transformation before statistical analyses. This approach was based on the classical evaluation of relative yield responses of field (agronomic and horticultural) crops to increasing salinity conditions (Maas, 1990).

Expt. 2. Bare-rooted rose plants of the cultivar Red France, budded on the rootstocks ‘Manetti’ and ‘Natal Briar’, were transplanted on 16 Jan. 2004 and fertigated with nutrient solution made with Scotts Peter® Excel® 15-5-15 (15N-2.2P-12.5K; The Scotts Co.) adjusted to deliver 10 mM of nitrogen. On 16 Mar., the plants received a hard pinch and began to be fertigated with a modified half-strength No. 2 Hoagland formulation (Hoagland and Arnon, 1950; first solution on Table 1). Starting on 23 Apr., this nutrient solution was salinized with six concentrations (0 to 24 mM) of a NaCl + CaCl₂ (1:1 equivalent ratio, 2:1 M ratio) salt mixture (Table 1). The 38-week experimental period, which ended on 14 Jan. 2005, yielded a total of six harvest events. A salt burn rating evaluation was taken between Harvests 3 and 4 by two different evaluators using a scale from 0 to 5 (0 = 0%, 1 = 20%, 2 = 40%, 3 = 60%, 4 = 80%, and 5 = 100% of foliage presenting salt burn damage). Dried and ground leaf tissue samples from flower shoots were sent to the Louisiana State University AgCenter Soil Testing and Plant Analysis Laboratory (Baton Rouge, LA) for nutrient content determinations. Nitrogen was measured in a Leco CN analyzer (LECO Corp., St. Joseph, MI) and the rest of the elements by inductively coupled plasma spectroscopy in HNO₃-H₂O₂ tissue digests. Tissues from leaves in flower shoots and whole-plant harvests were also analyzed for Cl content with a Digital Chloridometer (Model 4425000; Labconco Co.) and for sodium content by flame emission spectroscopy (Atomic Absorption Spectrometer AA240FS; Varian, Inc.). The experimental design was a randomized complete block design with a factorial (two × six) arrangement of rootstock by salt mixture concentrations for a total of 12 treatments with seven replications each (one plant as single replication). Quantitative data were analyzed like in the previous study, whereas categorical data (salt burn ratings) were analyzed by χ^2 procedures using SAS® 9.1 for Windows (SAS Institute).

Results

Expt. 1. Rootstock selection (RS) and NaCl salt concentration (SC) had no interactive

effects on soil solution EC, but did have separate main effects. Across SC, the 'Manetti' plants averaged the highest soil solution EC values ($5.23 \text{ dS}\cdot\text{m}^{-1}$) followed closely by 'Natal Briar' ($4.78 \text{ dS}\cdot\text{m}^{-1}$) and more distantly by *R. odorata* and 'Dr. Huey' (4.34 and $4.10 \text{ dS}\cdot\text{m}^{-1}$, respectively). Across RS, the EC in soil solution throughout the experiment averaged 2.23 , 4.89 , and $6.72 \text{ dS}\cdot\text{m}^{-1}$ for the 0 , 15 , and 30 mM NaCl levels, respectively. Soil solution pH values were unaffected by RS or SC, averaging 7.32 ± 0.22 over the entire experimental period.

No interactive effects were found between RS and SC for any of the cut flower yield and quality variables (sum of four harvests) and dry weights of organs in whole plants harvested at the end of the experiment (Table 2). The RS main effect was significant for flower productivity (dry weight and number of flower stems) with 'Dr. Huey' being the less productive rootstock. Although RS did not have an effect on average flower shoot length, foliage greenness expressed as chlorophyll index was significantly higher in plants

grafted on 'Manetti' and *R. odorata*. Rootstock selection also affected the dry weights of roots in the final, whole-plant harvest with 'Natal Briar' and 'Manetti' having the highest and lowest values, respectively, an observation that very significantly affected the shoot-to-root (S:R) ratios in these plants with 'Manetti' producing the highest and 'Natal Briar' the lowest in comparison with the other RS (Table 2). 'Dr. Huey' plants recorded the lowest stem dry weights in the final, whole-plant harvest. Compared with the nonsalinized controls, i.e., 0 mM NaCl, increases in SC significantly and negatively affected most flower productivity, quality, and plant biomass variables, except chlorophyll index and final root dry weights (Table 2).

Although these results indicate that on an absolute dry weight basis, all RS responded equally and negatively to the 15 and 30 mM NaCl treatments, this response is differential among RS when the yield data are expressed in relative terms (Fig. 1). The reduction of relative dry weights in 'Manetti' plants between 0 and 15 mM NaCl was minimal (and

nonsignificant) compared with the downward slope in the other cultivars, particularly 'Natal Briar'. Conversely, although the drop in relative yields was similar for 'Manetti', *R. odorata*, and 'Dr. Huey' in the 15 to 30 mM NaCl range, the yield in 'Natal Briar' plants remained unchanged (Fig. 1).

By the second flowering, flush visual symptoms of salt injury in old foliage started to become noticeable in the NaCl salinized plants, albeit the severity of the salt burn was differentially expressed across RS (Table 2). A qualitative evaluation of plant quality after flower Harvest 3 [145 d after treatment (DAT)] showed that the foliage of plants on 'Manetti' and 'Dr. Huey' had the lowest salt burn ratings compared with those on *R. odorata* and 'Natal Briar'. Salt burn symptoms included the typical scorching and necrosis around leaf margins, extending to the whole laminae over time and leading ultimately to leaf drop. Salt damage symptoms were observed in the foliage of some of the cut flower shoots from Harvest 4 and primarily on plants receiving the highest salt concentration (30 mM NaCl).

There were no interactive RS $\times$ SC effects for any of the essential leaf macro- and micronutrient concentrations in harvested cut flowers (data not shown). The RS main effect was significant for all nutrients with 'Natal Briar' having the most distinctive nutrient profile by the fourth flower harvest (170 DAT) with the highest leaf concentrations of magnesium (Mg, 0.38 versus 0.30% for other RS) and boron (B, 147 versus $82 \text{ mg}\cdot\text{kg}^{-1}$ for other RS) and the lowest of potassium (K, 2.18% versus 2.35% for other RS) and iron (Fe, 58 versus $68 \text{ mg}\cdot\text{kg}^{-1}$ for other RS). Across all RS, increases in the applied NaCl salt concentration significantly

Table 1. Ion composition, electrical conductivity (EC), and Na/Na + Ca ratio of the nutrient solutions used to irrigate 'Red France' rose plants grafted on 'Manetti' and 'Natal Briar' (Expt. 2).

Treatment NaCl-CaCl ₂ (mM)	Ion concn (mM)										EC (dS·m ⁻¹) ^z	Na ⁺ (Na ⁺ + Ca ²⁺) ^y
	Mg ²⁺	K ⁺	Ca ²⁺	NH ₄ ⁺	Na ⁺	NO ₃ ⁻	H ₂ PO ₄ ⁻	SO ₄ ²⁻	Cl ⁻			
0.0	1	3	2	1.5	0	8	0.5	1	0	1.65		0.24
1.5	1	3	2.5	1.5	1	8	0.5	1	2	1.85		0.30
3.0	1	3	3	1.5	2	8	0.5	1	4	2.05		0.34
6.0	1	3	4	1.5	4	8	0.5	1	8	2.45		0.39
12.0	1	3	6	1.5	8	8	0.5	1	16	3.25		0.44
24.0	1	3	10	1.5	16	8	0.5	1	32	4.85		0.48

^zEC, calculated as the sum of cations or anions (in mEq·L⁻¹) divided by 10. Includes EC of tap water ($0.6 \text{ dS}\cdot\text{m}^{-1}$) used to prepare the salinized nutrient solutions.

^yCalculation with concentrations in mg·L⁻¹. Tap water Na⁺ and Ca²⁺ concentrations (1.7 and 1.1 mM , respectively) were also used in calculation.

Table 2. Effect of rootstock selection and NaCl (salt) concentration on biomass, flower yields, and quality parameters of *Rosa* 'Bridal White' (Expt. 1).^z

Component	Flower harvests (all four flushes)					Final harvest of whole plants					
	Dry wt. (g/plant)	Flowers (no./plant)	Shoot length (cm)	SPAD index	Salt burn index ^v	Roots (g/plant)	Stems (g/plant)	Leaves (g/plant)	Top (g/plant)	Total (g/plant)	Shoot-to-root ratio
Rootstock ^y											
<i>R. Manetti</i>	83.6 a	24.6 a	32.6 a	47.1 a	0.67 ± 0.26	13.4 c	65.2 a	27.5 a	92.7 a	106.1 a	7.1 a
<i>R. odorata</i>	77.6 ab	23.3 a	33.0 a	46.0 ab	1.71 ± 0.53	16.8 b	59.3 ab	22.3 a	81.6 a	98.4 a	5.1 b
<i>R. Natal Briar</i>	84.7 a	22.6 ab	33.8 a	45.4 b	1.33 ± 0.26	24.7 a	67.2 a	21.7 a	88.9 a	113.6 a	3.6 c
<i>R. Dr. Huey</i>	67.3 b	20.1 b	32.6 a	45.5 b	0.68 ± 0.21	18.1 b	55.7 b	26.0 a	81.7 a	99.8 a	4.6 b
Salt (NaCl) conc.											
0 mM	95.8	26.8	34.2	45.7	0.19 ± 0.07	18.3	67.4	26.1	93.5	111.8	5.6
15 mM	78.5	22.8	33.0	46.4	0.92 ± 0.14	17.6	63.8	26.8	90.6	108.2	5.6
30 mM	60.5	18.5	31.8	46.0	2.20 ± 0.32	18.9	54.4	20.1	74.5	93.4	4.1
ANOVA ^x											
Rootstock (RS)	*	*	NS	*	—	***	*	NS	NS	NS	***
Salt conc. (SC)	***	***	***	NS	—	NS	**	**	**	*	***
RS $\times$ SC	NS	NS	NS	NS	—	NS	NS	NS	NS	NS	***
Best fit for SC ^w	L^{***}	L^{***}	L^{***}	—	—	—	L^{**}	Q^*	L^{**}	Q^*	Q^*
R^2	0.404	0.398	0.251	—	—	—	0.260	0.219	0.301	0.239	0.167
Parameter estimates											
Intercept	95.93	26.84	34.22	—	—	—	68.37	26.15	93.55	111.84	5.62
B_1	-1.177	-0.278	-0.082	—	—	—	-0.044	0.285	0.240	0.132	0.049
B_2	—	—	—	—	—	—	—	-0.016	-0.029	-0.025	-0.003

^zThe plants were subjected to the salinity treatments over four flushes of flowering (27 weeks).

^yMean separation of rootstock main effect by Duncan's least significant difference (0.05). Mean values having similar letters are not significantly different from each other.

^xAnalysis of variance (main effects: RS, SC, and interaction RS*SC). NS = not significantly different; *, **, and *** indicate significance at $P \leq 0.05$, ≤ 0.01 , and ≤ 0.001 , respectively. The qualitative data of salt burn index were not analyzed by ANOVA procedures.

^wRegression analysis for the salt concentration main effect. L and Q denote linear and quadratic fits, respectively. NS = not significantly different; *, **, and *** indicate significance at $P \leq 0.05$, ≤ 0.01 , and ≤ 0.001 , respectively.

^vRatings taken in between Harvests 3 and 4. Data for RS and SC are means $\pm$ SE of 12 and 20 plants, respectively.

Fig. 1. Relative cumulative harvested flower dry weight yields in 'Bridal White' roses grafted on four rootstocks as affected by incrementing NaCl salinity over a 27-week experimental period (Expt. 1). Data are means $\pm$ SE of five plants.

decreased leaf calcium (Ca, 1.99% to 1.69%) and Fe (72 to 57 mg·kg⁻¹) and increased manganese (Mn, 128 to 191 mg·kg⁻¹), B (87 to 117 mg·kg⁻¹) and zinc (Zn, 37 to 45 mg·kg⁻¹).

The salinizing Na⁺ and Cl⁻ ions were the only ones showing significant interactive RS $\times$ SC effects (Fig. 2). Tissue Cl⁻ concentrations increased with NaCl additions, but differentially across organs and RS with lower concentrations observed in roots and stems (ranging from 1,170 to 6,490 mg·kg⁻¹) compared with old leaves and leaves on harvested flower shoots (2,246 to 25,576 mg·kg⁻¹; Fig. 2A–D). Interestingly, and across all SC, the rootstocks 'Manetti' and 'Dr. Huey' had higher Cl⁻ concentrations in their roots (Fig. 2D) compared with 'R. odorata' and 'Natal Briar' (grand averages of 5,081 versus 3,341 mg·kg⁻¹), but the opposite occurred in the leaves of harvested flower shoots (Fig. 2A) and in the old leaves (Fig. 2B) at the end of the experiment (grand averages of 8,658 versus 11,290 mg·kg⁻¹ and 12,574 versus 16,130 mg·kg⁻¹, respectively). Regarding Na⁺, its overall accumulation across all RS decreased from the roots toward the leaves in the 0- and 15-mm NaCl treatments, but the opposite was observed at the 30-mm treatment (Fig. 2E–H). On the other hand, across all SC, the RS had significant differences in Na⁺ accumulation patterns with 'Manetti' and 'Dr. Huey' having the lowest concentrations in leaves from harvested flower shoots (Fig. 2E) and old leaves (Fig. 2F) at the end of the experiment (grand averages of 106 and 826 mg·kg⁻¹, respectively) compared with those in 'R. odorata' and 'Natal Briar' (grand averages of 3236 and 3959 mg·kg⁻¹, respectively). Compared with leaves, the average Na⁺ concentrations

in the roots (Fig. 2H) of 'Manetti' and 'Dr. Huey' were higher (average of 2890 mg·kg⁻¹) than those observed in 'R. odorata' and 'Natal Briar' (average of 1651 mg·kg⁻¹).

The relationships between plant relative dry weight yields (Fig. 1) and salt burn indices (Table 2) with leaf Cl⁻ and Na⁺ concentrations (Fig. 2) were evaluated with simple correlation analyses. Regarding relative dry weight yields, the only significant associations were found in *R. odorata*, which correlated negatively with both leaf Cl⁻ ($r = -0.89$; $P \leq 0.001$) and leaf Na⁺ ($r = -0.86$; $P \leq 0.001$). Leaf salt burn ratings were significantly, and positively, correlated with leaf Cl⁻ concentrations in all rootstocks: 'Dr. Huey' $r = 0.59$, 'Manetti' $r = 0.69$, 'Natal Briar' $r = 0.79$, and *R. odorata* $r = 0.93$ (all at $P \leq 0.01$). Significant correlations between salt burn and leaf Na⁺ were only found in the *R. odorata* plants ($r = 0.94$; $P \leq 0.001$).

Expt. 2. Leaching fractions were similar between RS and among SC levels averaging 25.1% $\pm$ 2.6%. There were no differences between rootstocks for leachate EC and Cl⁻ concentration, and these two variables were highly correlated ($r = 0.96$, $P < 0.0001$) and positively affected by increasing salt levels. Leachate EC and Cl⁻ concentration throughout the experiment averaged 3.0, 3.6, 6.4, and 7.2 dS·m⁻¹ and 177, 463, 1473, and 1960 mg·L⁻¹ for the 0, 3, 12, and 24 mM NaCl+CaCl₂ levels, respectively.

In this experiment, no interactive effects were found between RS and the SC used in this experiment, NaCl + CaCl₂, for any of the cut flower yield and quality variables (over six harvests) and dry weights of organs in whole plants harvested at the end of the experiment. Across all SC, the 'Manetti' plants produced significantly more harvested

biomass (142 g versus 119 g), cut flowers (39 versus 35), had longer stems (38 cm versus 36 cm), and higher biomass weights on all of their organs (old leaves, roots, and stems; averages of 87 g versus 61 g for whole plants) than those in 'Natal Briar'.

Across both RS, increases in SC significantly and negatively affected most flower productivity, quality, and plant biomass variables, except chlorophyll index and final S:R ratio (data not shown). These responses were best fit by linear models for harvested dry biomass ($R^2 = 0.34$, $P \leq 0.001$) and flower shoots per plant ($R^2 = 0.38$, $P \leq 0.001$) and quadratic models for flower shoot length ($R^2 = 0.11$, $P \leq 0.05$) and leaf chlorophyll index ($R^2 = 0.34$, $P \leq 0.001$). With respect to total harvested flower dry weight, it should be noted that there were no discernible differences for the 0 to 6 mM NaCl + CaCl₂ concentration range, averaging 145.2 g per plant across these salt treatments, whereas the 12- and 24-mm treatments reduced dry weights by 19.3% (117.2 g per plant) and 43.4% (82.1 g per plant), respectively. Similar responses were observed for the dry weights of organs/whole plants harvested at the end of the experiment (data not shown).

Salt injury, expressed as bronzing and scorching of leaf edges, started to become evident on the lower leaves of harvested flowering shoots of both rootstocks by the fourth harvest event (144 DAT). This response was, however, differentially expressed in both RS observed only at the highest 24 mM NaCl + CaCl₂ in 'Manetti', whereas 'Natal Briar' harvested shoots presented the symptoms from 3- to 24-mm concentrations. By the fifth harvest (at 192 DAT), flowering shoots of 'Manetti' plants subjected to the two highest SC had salt burn damage on the lower leaves whereas 'Natal Briar' plants at the 24-mm treatment did not produce any flowering shoots and the rest of the newest foliage was small and slow to develop. The extent of salt injury on the older foliage (structural foliage nonharvested in flowering shoots) of the plants was also different between rootstocks across salt concentration levels ($P < 0.0001$). The foliage of 'Manetti' plants was less affected by salinity because 83.3% of these plants presented salt damage on only 0% to 20% of the foliage, whereas 47.7% of the 'Natal Briar' plants had salt burn damage on 41% to 100% of their foliage.

There were no interactive RS $\times$ SC effects for any of the mineral elements, including Cl⁻ and Na⁺, in leaves of the harvested cut flowers (data not shown). By the fifth flower shoot harvest (192 DAT), the RS main effect was significant only for five elements with 'Natal Briar' having the lowest leaf concentrations of K (2.16% versus 2.40%) and Fe (48 versus 53 mg·kg⁻¹) and the highest Mg (0.23% versus 0.18%), chlorine (Cl, 11,980 versus 9,060 mg·kg⁻¹), and B (83 versus 37 mg·kg⁻¹) compared with 'Manetti'. Across both RS, increases in the applied NaCl + CaCl₂ salt mixtures significantly increased leaf Ca (1.61% to 1.78%), K (2.17% to 2.54%), and Cl (3,944 to 23,773 mg·kg⁻¹)

Fig. 2. Chloride (A–D) and sodium (E–H) concentrations in tissues of ‘Bridal White’ roses grafted on four rootstocks and subjected to incrementing NaCl salinity (Expt. 1). Data are means of five (Leaves H4) or three plants (rest of tissues). Notice the differential concentration scale used on the leaf tissues compared with the one used for stems and roots. H4 = flower Harvest 4; WP = whole plant (at end of 27-week experiment); Man = ‘Manetti’, Odo = *R. odorata*; NBr = ‘Natal Briar’; DrH = ‘Dr. Huey’.

and decreased Mg (0.23% to 0.18%). Interestingly, both rootstocks showed similar leaf sodium concentrations across all salt treatments, averaging 46 mg·kg⁻¹.

In the organs of whole plants harvested at the end of the 38-week experimental period, there were differential interactive RS × SC effects for the accumulation of Cl⁻ (stems and roots) and Na⁺ (leaves and stems) (Fig. 3). In general terms, across both RS and SC, tissue Cl⁻ concentrations increased from roots to leaves and in relation to NaCl + CaCl₂ additions (Fig. 3A–C), but with differentially higher concentrations observed in the roots and stems of ‘Manetti’ plants (3,714 to 6,332 mg·kg⁻¹ and 3,158 to 18,681 mg·kg⁻¹, respectively) compared with ‘Natal Briar’ (1,885 to 5,388 mg·kg⁻¹ and 3,440 to 12,735 mg·kg⁻¹, respectively). There were no RS effects for leaf Cl⁻ accumulation, increasing asymptotically (8,020 to 27,446 mg·kg⁻¹) with NaCl + CaCl₂ additions (Fig. 3A), except for the lack of data for the 24-mm treatment resulting from nearly complete defoliation. Regarding Na⁺, there was an overall reduction in its accumulation, across all RS and SC, from the roots (grand average of 3768 mg·kg⁻¹; Fig. 3F) toward the leaves (grand average of mg·kg⁻¹; Fig. 3D). Although there were no RS effects in the roots, Na⁺ concentrations increased with NaCl + CaCl₂ addi-

tions up to 12 mM and then decreased at 24 mM (Fig. 3F). For stem Na⁺ concentration, there was a differential RS effect increasing with salt stress up to 6 mM but then dropping at the higher salt applications (Fig. 3E). Sodium concentrations in the old leaves increased with salt applications but were higher in ‘Natal Briar’ compared with ‘Manetti’ (Fig. 3D). As mentioned, as a result of severe defoliation, there was not enough tissue to measure leaf Na⁺ at the 24-mm salt treatment.

Like in the previous experiment, simple correlation analyses were used to evaluate the relationships between plant dry weight yields and salt burn indices with leaf Cl⁻ and Na⁺ concentrations (Fig. 3). In both rootstocks, leaf Cl⁻ concentration had negative correlations with dry weight and number of flowering shoots harvested per plant ($r = -0.65$ and -0.55 in ‘Manetti’, respectively; and $r = -0.36$ and -0.36 in ‘Natal Briar’, respectively; $P < 0.0001$ for both RS and variables). Leaf chlorophyll index was negatively associated with leaf Cl⁻ in ‘Natal Briar’ plants only ($r = -0.23$; $P = 0.0016$). Although no association between leaf Na⁺ and flower productivity and quality variables were found in ‘Manetti’ plants, negative correlations were observed in ‘Natal Briar’ plants, being $r = -0.49$, -0.45 , and -0.54 (all at $P \leq 0.001$) for flowering

shoot dry weight, number, and leaf chlorophyll index, respectively.

Discussion

Analyses of soil solutions and leachates collected from both experiments reflected the definitive and differential effect of the salt treatments on root zone EC and Cl⁻ concentrations, which surpassed the maximum recommended values for roses, 3 dS·m⁻¹ and 4 mM, respectively (Bernstein et al., 1972; Cabrera, 2003; Davidson, 1969; Hughes and Hanan, 1978; Yaron et al., 1969) at even the lowest applied salt concentrations. These soil solution parameters were, however, differentially modulated by RS, particularly in the first experiment with NaCl, which served as a first indicator of their relative salt uptake.

Although data from both experiments showed a lack of interactions between RS and SC, each main factor had significant effects on flower yield and foliage quality (salt burn index). In Expt. 1, and across salt treatments, flower productivity was lowest in ‘Dr. Huey’. This was not surprising because its primary use has been as a landscape rose rootstock (Hanan and Grueber, 1987), whereas the rest of the RS, all purposely selected for use in cut flower production (de Vries, 2003; Hanan and Grueber, 1987),

Fig. 3. Chloride (A–C) and sodium (D–F) concentrations in tissues of ‘Red France’ roses grafted on two rootstocks and subjected to increasing NaCl–CaCl₂ salinity (Expt. 2). These tissues are from whole plants harvested at the end of the experiment. Symbols represent mean $\pm$ SE of three (B, C, D, E) or six (A, F) plants. *, **, *** denote significance at $P \leq 0.05$, $P \leq 0.01$, and $P \leq 0.001$, respectively. Data in E could not be fitted adequately with polynomial models and thus a segmented linear regression approach was used. The linear equations fitted to the stem sodium concentrations up to the “peak” 6 mM NaCl–CaCl₂ level in ‘Manetti’ and ‘Natal Briar’ rootstocks are, respectively, $\text{Na} = 413 + 848X$ ($R^2 = 0.79$, $P \leq 0.001$) and $\text{Na} = 2457 + 322X$ ($R^2 = 0.32$, $P \leq 0.01$).

showed no differences among themselves. A noteworthy observation is that flower productivity in these greenhouse RS was equally sustained despite significant differences in the allocation of plant biomass across organs, in particular that between ‘Manetti’ and ‘Natal Briar’ plants with the highest and lowest S:R ratios, respectively (Table 2). As previously pointed in a report in nonstressed rose plants, these contrasting plant biomass allocations illustrate both the physiological efficiency (in ‘Manetti’) and the scion vigor/yield induction (in ‘Natal Briar’) that can be derived from a given rootstock selection (Cabrera, 2002). Interestingly, and across SC treatments, the longer experimental period in Expt. 2 (with NaCl + CaCl₂ as the salinizing source) showed significantly higher yields in ‘Manetti’ than in ‘Natal Briar’ plants, a response attributed to differences in their relative salinity tolerance influenced by differential ion uptake and accumulation, as discussed subsequently.

In both experiments, increases in SC reduced flower productivity, plant biomass, and foliage quality (salt burn index) in all rootstocks. Although analyses of absolute harvested yield data did not distinguish differences in salinity stress between RS, analyses of relative biomass yield response to

salt stress in the first experiment showed differential behaviors (Fig. 1). ‘Manetti’ plants exposed to 15 mM NaCl (total applied EC of 3.2 dS·m⁻¹) were not significantly different from the nonsalinized controls (total applied EC of 1.7 dS·m⁻¹) in Expt. 1, whereas the rest of the RS showed significant reductions in harvested flower biomass. On the other hand, increasing NaCl concentration to 30 mM (total applied EC of 4.7 dS·m⁻¹) caused reductions in the relative yields of ‘Manetti’ plants, but not in ‘Natal Briar’ plants, compared with the 15-mM salt treatment. In Expt. 2, both ‘Manetti’ and ‘Natal Briar’ showed no differential response to NaCl + CaCl₂ applications up to 6 mM (total applied EC of 2.5 dS·m⁻¹), albeit ‘Manetti’ had greater yields. These responses observed by ‘Manetti’ plants is confirmed by a previous study (Cabrera and Perdomo, 2003), which actually showed increases in flower and biomass yields in plants grafted in this RS that were exposed to NaCl levels up to 10 mM (total applied EC of 2.3 dS·m⁻¹) over a similar period of time (four flowering cycles). In fact, increasing NaCl levels to 15 and 30 mM (total applied EC of 2.8 and 4.3 dS·m⁻¹, respectively) for an additional four flowering cycles did not produce significant reductions in flower and biomass yields, albeit it negatively

affected flower shoot quality at the 30-mM salt level.

It appears that the vigorous nature of ‘Natal Briar’, imparted on scions growing on it by yielding more and longer flowers than other common greenhouse rose rootstocks (de Hoog, 2001; de Vries, 2003; Safi, 2005), is not observed under even moderate salt stress levels. Other abiotic stresses like poor air-filled porosity (i.e., poor soil aeration) have been shown to significantly affect the root and shoot growth of ‘Natal Briar’-grafted plants (Evans et al., 2009), which contrasts the historically proven yielding performance of ‘Manetti’-grafted plants in heavy (clay)-textured and shallow field soils (Hanan and Grueber, 1987). The rootstock *R. odorata* (also known as *R. indica* ‘Major’), once very popular in North America (Hanan and Grueber, 1987), still much-esteemed and highly used in the cut rose industry in the Mediterranean area (de Vries, 2003; Raviv et al., 1993), lagged significantly in biomass response to salinity stress compared with ‘Manetti’ and ‘Natal Briar’ (Table 2). This observation is supported by data from Wahome et al. (2000), who observed the worst growth and eventual death of this rootstock compared with the rootstock *R. rubiginosa* and the scion ‘Kardinal’ when irrigated

with NaCl concentrations of 10 to 30 mM. Similarly, Niu et al. (2008) reported that *R. odorata* was not as salt-tolerant as the garden rose rootstock *R. ×fortuniana* Lindl., showing sharper reductions in fresh biomass weights when irrigated with salinized nutrient solutions with EC of 1.6 to 9.0 dS·m⁻¹ (87% of salinization provided by NaCl).

All the essential leaf macro- and micro-nutrient concentrations in leaves of harvested cut flowers in both experiments were within the sufficiency ranges reported in the rose nutrition literature (Cabrera, 2002, 2003; White, 1987) and were unaffected by interactive RS × SC effects, but there were significant main effects. Among rootstocks, 'Natal Briar' displayed the most distinctive nutrient profile in comparison with the rest, including the highest concentrations of Mg and B and the lowest concentrations of K and Fe. These results are mirrored by those from a previous comparative rose rootstock study under nonsaline growing conditions (Cabrera, 2002) and highlight the propensity of 'Natal Briar'-grafted plants to develop nutrient disorders when fertilization programs are not carefully monitored and adjusted. Plants grafted on 'Natal Briar' also displayed the lowest average chlorophyll index readings (Table 2; Cabrera, 2002), which coupled with significantly lower leaf Fe concentrations and anecdotal references from rose growers about chlorosis problems in plants growing in this rootstock (K.W. Zary, Jackson & Perkins Roses, Medford, OR, and J.C. Gonzalez, Grupo Chía, Bogotá, Colombia, personal communication), suggest it has a lower iron use efficiency. Studies on the Fe-reducing ability and Fe use efficiency in rose rootstocks are limited (McDonald and Reed, 1989) but suggest that they vary significantly among *Rosa* species and hybrids and should allow for the identification of rootstocks adapted to alkalinizing substrates or growing environments, including closed hydroponic systems in which Fe concentrations can significantly change within 2 d leading to rapid development of deficiencies (Lykas et al., 2001).

Regarding the effect of salinity increases on essential macro- and micronutrient concentrations in rose leaf tissues, salt source had a major differential influence across all RS with NaCl applications (Expt. 1) increasing leaf Mn, B, and Zn and reducing Ca²⁺ and Fe concentrations compared with NaCl + CaCl₂ applications (Expt. 2), which increased leaf Ca²⁺ and K and reduced Mg concentrations. Overall, these results agree with those reported in the literature on salinity–mineral nutrient relations in horticultural crops, in particular with the observations that Na⁺-dominated salinity (like in Expt. 1) reduces Ca²⁺ availability and transport and increases tissue Zn concentrations (Grattan and Grieve, 1999). Conversely, when Ca²⁺ is a dominant or codominant cation in the salinity stress (like in Expt. 2), it increases Ca²⁺ uptake and accumulation in tissues, which in turn often and competitively suppresses the uptake of Mg (Grattan and Grieve, 1999; Marschner, 1995). Furthermore, the presence of adequate

Ca²⁺ in a saline environment influences the K⁺/Na⁺ selectivity by shifting the uptake ratio in favor of K⁺ at the expense of Na⁺ (Grattan and Grieve, 1999) as it was observed in the rose leaf tissues in Expt. 2.

Increasing salinity stress significantly influenced the uptake and accumulation of both Cl⁻ and Na⁺ in rose tissues modulated by both rootstocks and salt source. Because Cl⁻ was the dominant anion in both experiments, its accumulation in tissues increased with salt additions, albeit differentially across plant organs and rootstock selections (Figs. 2 and 3). In the first experiment (NaCl stress), tissue Cl⁻ concentrations increased from roots to leaves, but with the plants grafted on 'Manetti' and 'Dr. Huey' having significantly higher concentrations in the roots and less in the leaves compared with 'Natal Briar' and *R. odorata*. Similar contrasting results were recorded for 'Manetti' and 'Natal Briar'-grafted plants when exposed to the NaCl + CaCl₂ salt stress in Expt. 2, confirming the differential uptake and partitioning of Cl⁻ inherent to each rootstock. Other studies have also reported similar results, highlighting the propensity of *R. odorata* (also known as *R. chinensis* 'Major') and 'Natal Briar' to accumulate more Cl⁻ in their tissues, particularly in their leaves or leaves of their scions compared with other rootstocks growing under both under saline and nonsaline conditions (Cabrera, 2002; Niu et al., 2008; Wahome et al., 2001). The presence of high Ca²⁺ concentrations in the substrate have been reported to suppress the transport of Cl⁻ to the leaves of *Citrus* species (Bañuls et al., 1991), which might help explain the lack of interactive RS × SC effects for rose leaf Cl⁻ concentrations when exposed to a NaCl + CaCl₂ salt mixture (Expt. 2). Nevertheless, 'Manetti'-grafted plants had lower average leaf Cl⁻ concentrations than those on 'Natal Briar' alluding to their inherent differential abilities to accumulate Cl⁻ in their leaves, as expressed also in Expt. 1 and in another study without salt stress (Cabrera, 2002).

The literature indicates that plant species with relatively low salt tolerance are typical Na⁺ excluders and capable at low and moderate salinity levels of restricting its transport to the leaves and thus minimizing its toxicity (Greenway and Munns, 1980; Marschner, 1995). Although this remark holds true in the low to moderately salt-sensitive roses (Cabrera, 2002, 2003), the contention that rootstock selection plays a major differential role (Cabrera and Perdomo, 2003) was also confirmed in the present studies. Across SC, plants grafted on 'Manetti' and 'Dr. Huey' had a significantly higher leaf Na⁺ exclusion ability compared with *R. odorata* and 'Natal Briar' by compartmentalizing more Na⁺ to their roots and stems (Figs. 2E–H and 3D–F). A mass balance analyses conducted on whole plants harvested at the end of Expt. 1 (data not shown) showed that plants grafted on 'Manetti' and 'Dr. Huey' partitioned significantly more Na⁺ to the roots and less to the leaves (average of 23.4% and 11.0% of total plant Na⁺ mass allocated to roots and

leaves, respectively) compared with 'Natal Briar' and *R. odorata* (average of 12.5% and 25.0% of total plant Na⁺ mass allocated to roots and leaves, respectively). Other salinity and mineral nutrition studies have also reported that *R. 'Manetti'*, *R. rubiginosa*, and *R. ×fortuniana* were better at excluding Na⁺ from their leaves than *R. 'Natal Briar'*, *R. chinensis* 'Major' (also known as *R. odorata*), *R. multiflora*, and *R. canina* 'Inermis' (Cabrera, 2002; Fernández Falcón et al., 1986; Niu et al., 2008; Sadasivaiah and Holley, 1973; Wahome et al., 2001).

The increasing soil solution concentrations of Ca²⁺ that accompanied the increasing NaCl + CaCl₂ salt stress in Expt. 2 (Table 1) moderated the differential accumulation of Na⁺ in leaf tissues of harvested flower shoots from 'Manetti' and 'Natal Briar' (Fig. 3D–E). Despite a longer experimental period compared with Expt. 1, leaf Na⁺ in leaves of shoots from the fifth flower harvest in Expt. 2 (192 DAT) averaged 46 mg·kg⁻¹ in both RS and even across all NaCl + CaCl₂ levels (0 to 24 mM), albeit there were differences in the accumulation of Na⁺ in the old leaves and stems of the plants at the end of the experiment (Fig. 3D–E). Conversely, when exposed to the single salinizing salt (NaCl) in Expt. 1 (0 to 30 mM), 'Manetti' and 'Natal Briar' plants had average Na⁺ concentrations of 882 and 2988 mg·kg⁻¹, respectively, in leaves of shoots from the fourth flower harvest (170 DAT). These results highlight the observation that high Ca²⁺ concentrations in the substrate could help minimize the uptake of Na⁺ from soil solution, its transport to, and/or severity of Na⁺ toxicity in the leaves of plants (Bañuls et al., 1991; Grattan and Grieve, 1999; Marschner, 1995). We are currently studying whether there are any verifiable ameliorative effects of supplemental Ca²⁺ additions to rose plants grafted on various rootstocks when exposed to moderate salinity stress.

The quality of plant foliage was assessed toward the end of each experiment by means of a salt burn index, which expectedly showed higher salt injury in older foliage with increases in salinity stress but differentially across rootstocks (Table 2). The typical salinity-induced leaf marginal chlorosis, scorching, and necrosis extending to the whole laminae over time and ultimate leaf drop observed, particularly in crop species with low to moderate salt tolerance, are most commonly associated with the toxic accumulation of Cl⁻ and much less the result of Na⁺ (Marschner, 1995). Correlation analyses in both experiments indeed showed that salt burn indices and leaf chlorophyll indices correlated more significantly (positively and negatively, respectively) with rose leaf Cl⁻ concentrations than with Na⁺ concentrations. This closer association of foliar damage with Cl⁻ accumulation is also supported by similar findings in the rose cultivar Bridal Pink budded on 'Manetti' exposed to NaCl (Cabrera and Perdomo, 2003) and 'Grenoble' budded on 'Dr. Huey' exposed to NaCl, Na₂SO₄, CaCl₂, or NaCl + CaCl₂ (Bernstein

et al., 1972). The accumulation of both leaf Na^+ and Cl^- in rose leaves was negatively correlated with harvested dry weight yields of plants grafted on *R. odorata* in Expt. 1 and 'Natal Briar' in Expt. 2 and on this latter experiment, 'Manetti' plants showed their only negative yield correlation with leaf Cl^- concentration.

Considering altogether the overall data on relative biomass yields, foliage quality, and leaf tissue Na^+ and Cl^- concentrations from both experiments, and comparison with other rose salinity studies, it is inferred that the response of rose scions subjected to increasing salinity will be likely limited first by osmotic stress before toxicity effects are observed when grafted on the 'Manetti' rootstock (Cabrera and Perdomo, 2003). Plants on 'Dr. Huey' were similarly tolerant of ion toxicity effects, but their productivity was more affected by the osmotic component of increasing salinity (Bernstein et al., 1972). Although having similar dry weights and flower yields and responses to plants grafted on 'Manetti', the distinctive nutrient status and Na^+ and Cl^- accumulations observed in plants grafted on 'Natal Briar' suggest this rootstock is likely to be more challenged by ion toxicity and nutrient imbalances (Cabrera, 2002) before it is significantly affected by the osmotic effects of increasing salt stress. The rootstock *R. odorata* was overall significantly and negatively affected by both the osmotic and ion toxicity effects of increasing salinity, agreeing with similar results from other studies (Niu et al., 2008; Wahome et al., 2001).

Conclusions

In comparison with other plants and crops, roses have been generally characterized for having a low to moderate tolerance to salinity (Bernstein et al., 1972; Cabrera and Perdomo, 2003; Davidson, 1969; Maas, 1990; White, 1987). Results from the present experiments and other studies (Cabrera and Perdomo, 2003; Niu et al., 2008; Wahome et al., 2001) point, however, to the significant modulating effect of rootstock selection on the productivity and quality of roses exposed to salinity.

A combined analysis of the results from all these studies confirm that on a productivity basis (biomass and flower yield), roses could withstand overall maximum salinities (osmotic effects) of applied fertigation solutions of $3.0 \pm 0.5 \text{ dS m}^{-1}$ (equivalent to $\text{EC}_e \approx 4.5 \pm 0.7 \text{ dS m}^{-1}$), which indeed fall within the sensitive division in the normative classification of crop salinity tolerance (Maas, 1990). On the other hand, and considering the aesthetic responses (i.e., salt burn damage) of on-plant and harvested foliage (flower shoots), greenhouse rose tolerance to applied Na^+ and Cl^- concentrations (ion-specific effects) could range up to $10 \pm 2 \text{ mM}$, which surpasses the older recommended threshold of 2 to 4 mM (Fernández Falcón et al., 1986; Hughes and Hanan, 1978; Yaron et al., 1969). This difference is primarily attributed to the use of well-drained soilless media and intensive irrigation practices (high frequen-

cies and leaching) in current production systems for greenhouse roses (Cabrera, 2003; Cabrera and Perdomo, 2003; de Hoog, 2001). It should be clarified that continuous exposure to these overall EC and Na^+ and Cl^- thresholds for periods exceeding more than four to six flowering cycles could eventually result in worse rose growth, yield, and quality responses, eventually leading to plant death (Cabrera and Perdomo, 2003).

The results from the present studies show 'Manetti' as the most salt-tolerant rootstock for greenhouse rose production, attesting to its widely and favored use in North and South America over most of the 20th century, particularly under challenging soil-based growing systems (Cabrera, 2002; de Vries, 2003; Hanan and Grueber, 1987). Its relatively recent and almost complete displacement by 'Natal Briar' in soilless and hydroponic-based rose production systems (de Vries, 2003) questions the practical application of this change when considering the osmotic and ionic challenges being presented by the increasing use of poor-quality irrigation waters and the regulatory pressures to recycle/recirculate greenhouse effluents (Baas and van den Berg, 1999; Bernstein et al., 2006; de Hoog, 2001; Raviv et al., 1998).

Lastly, the results from these experiments highlight the critical importance of carefully considering the chemical composition of the irrigation solutions in experimental salinity studies aimed at generating ecologically and practically relevant results and recommendations (Grattan and Grieve, 1999; Greenway and Munns, 1980). The $\text{Na}^+ / (\text{Na}^+ + \text{Ca}^{2+})$ ratios of the salinized solutions in Expt. 1, at 0.81 and 0.91 for 15 and 30 mM NaCl, respectively, would be representative of those in irrigation waters in coastal areas, whereas the 0.27 to 0.44 ratios in the solutions from Expt. 2 (Table 1) would be more representative of typical inland irrigation waters (Grattan and Grieve, 1999). The differential supply of Na^+ , Cl^- , and Ca^{2+} indeed led to a differential accumulation in plant tissues in these studies and interacted with the modulating effect of the rootstocks. Experiments are underway to evaluate the effect of accompanying counterions, in different proportions, on the yield and quality responses of greenhouse roses subjected to either Na^+ or Cl^- -dominated salinities.

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