Salinity Tolerance of Three Commonly Planted *Narcissus* Cultivars

Maren E. Veatch-Blohm¹, Douglas Sawch, Nicole Elia, and Dominic Pinciotti

Biology Department, Loyola University Maryland, 4501 N. Charles Street, Baltimore, MD 21210

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Abstract. Salinity is a problem for crop production worldwide and may be particularly problematic for ornamental plants because it has the potential to degrade visual quality. Daffodils [*Narcissus* sp. (L.) Amaryllidaceae] are a popular bulb plant, in demand for both landscapes and cut flowers. In this study, we examined how salinities ranging from 0 to 300 mM NaCl affected growth, flower production, and leaf physiology of three of the most popular cultivars of daffodil ('Dutch Master', 'Ice Follies', and 'Tete-a-Tete'). Salinity reduced growth rate and biomass production at salinities greater than or equal to 100 mM NaCl with the greatest reductions in the highest salinity treatments (200 and 300 mM NaCl). Despite reductions in biomass, there was no significant chlorosis of the leaves. Flower quantity was unaffected by salinity in 'Dutch Master' and 'Ice Follies', but anthesis was delayed and flower duration was reduced by 40% to 70% at salinities of 150 mM NaCl and above. Anthesis and flower duration in 'Tete-a-Tete' were unaffected by salinity, but the number of flowers produced was negatively affected (reductions of 50% or more) by salinities of 150 mM NaCl and above. Sodium concentration in the leaves and bulbs increased 53% to 400% compared with the 0 mM NaCl control with lower accumulation in the bulbs than in the shoots. Sodium accumulation occurred at or above 50 mM NaCl in 'Tete-a-Tete', but at salinities greater than 150 mM NaCl in 'Dutch Master' and only in the 300-mM NaCl treatment in 'Ice Follies'. Despite the Na⁺ accumulation in the leaves, the plants in most of the salinity treatments were able to maintain a K⁺:Na⁺ ratio above 1 (except in 'Tete-a-Tete' at salinities 150 mM NaCl or greater), which may have helped the daffodils tolerate the negative affects of Na⁺ and maintain good visual quality. 'Dutch Master', 'Tete-a-Tete', and 'Ice Follies' can be considered highly salt-tolerant because they maintain visual quality (leaf greenness, flower production, and flower duration) at soil NaCl-induced electrical conductivities greater than 6 dS·m⁻¹.

Salinity is a major obstacle for crop production throughout the world. At least one-third of agricultural land is salinized and the amount impacted by salinization is expected to increase (Carter et al., 2005; Cassaniti et al., 2009; Munns and Tester, 2008; Shibli et al., 2007). As high-quality water is diverted for human consumption, agricultural and horticultural production may have to rely on brackish, saline, or reclaimed water that has electrical conductivities (ECs) that may be suboptimal for plant growth (Cassaniti et al., 2013; Kirzhner et al., 2008; Marcum, 2006; Niu and Cabrera, 2010; Safi et al., 2007; Shillo et al., 2002). Soils are considered saline when they have an EC of 4 dS·m⁻¹ or higher (Chinnusamy et al., 2005; Javid et al., 2011), which can be particularly problematic if the increased EC is the result of NaCl (Cassaniti et al., 2013). Soil salinities of 50 mM NaCl (≈6 dS·m⁻¹) are considered moderately saline, whereas

salinities greater than or equal to 150 mM NaCl (≈18 dS·m⁻¹) are considered highly saline (Cassaniti et al., 2013). Most ornamental plants are glycophytes that are typically damaged at irrigation salinities less than 4 dS·m⁻¹ (Flowers and Colmer, 2008; Grattan and Grieve, 1999; Greenway and Munns, 1980).

Salinity can reduce growth and visual quality of plants through physiological drought, ion toxicity, and nutrient deficiency (Green et al., 2008; Gupta et al., 1995; Halperin et al., 1997; Shannon and Grieve, 1999; Shibli et al., 2007). Because visual quality is particularly crucial to the value of ornamental plants, it is important to understand salinity's impact not only on growth, but also on visual quality (Carter and Grieve, 2008; Francois and Clark, 1978; Niu and Cabrera, 2010; Shillo et al., 2002; Sonneveld et al., 1999; Zollinger et al., 2007). In landscapes that are already affected by salinity, it is important to have plants that maintain visual quality even if there are reductions in growth (Cassaniti et al., 2012; Niu and Rodriguez, 2006; Safi et al., 2007; Villarino and Mattson, 2011; Wahome et al., 2000).

Narcissus sp. (L.) Amaryllidaceae (daffodils), along with seven other genera, account for 90% of the world bulb production

(Benschop et al., 2010). They are an important bulb crop in Israel, The Netherlands, the United Kingdom, and the United States (Benschop et al., 2010; Carder and Grant, 2002; ERS, 1995; Hanks, 2002). Daffodils are in demand as landscape plants and cut flowers (Benschop et al., 2010; Hanks, 2002; Steininger, 2010). Daffodils are forced to provide cut flowers and potted plants during the winter as well as during their typical growing season (Anderson and van der Hoeven, 1998; Cantor and Gheorghita, 2011). In the United Kingdom, daffodils are the eighth most popular cut flower and rank sixth in overall sales of cut flowers (Hanks, 2002).

Daffodils are some of the earliest plants to emerge and flower in the spring. They are often planted adjacent to roads or walkways that have been treated with deicing salts during the winter (mainly applied as NaCl). Salt deposition occurs from 5 to 40 m from the road (Blomqvist and Johansson, 1999) with the majority of deposition occurring within the first 5 m of the road (Appleton et al., 2009; Bryson and Barker, 2002). Not only may daffodils experience salt exposure as they emerge, but also during the chilling period required for floral initiation. Deicing salts have been shown to have adverse effects on landscape plants such as leaf scorch, plant dieback, reduced growth and turgor, and nutrient imbalances, which may adversely affect plants as they begin to grow through damage resulting from salt spray or during active growth as salts are taken up by the plant (Berkheimer and Hanson, 2006; Cunningham et al., 2008; Green et al., 2008).

'Tete-a-Tete', 'Dutch Master', and 'Ice Follies' are early to midseason cultivars that are consistently ranked in the top five daffodil cultivars based on sales and production of bulbs (Benschop et al., 2010; Hanks, 2002). Our previous research showed that moderate salinity (up to 50 mM NaCl) did not have an effect on growth or flower production of these three cultivars regardless of when salinity exposure began (Veatch-Blohm et al., 2013). In this study we wanted to determine levels of salinity these three cultivars could tolerate while maintaining visual quality.

Materials and Methods

Daffodil cultivars. The three following cultivars were used throughout the study: 'Dutch Master' (*Narcissus* sp.) from Division I (Trumpet Daffodils), 'Ice Follies' (*Narcissus* sp.) from Division II (Large Cupped Daffodils), and 'Tete-a-Tete' (*Narcissus* sp.) from Division XIII (Miscellaneous Daffodils). We chose these three varieties because they are some of the most popular cultivars of daffodils grown (Benschop et al., 2010; Hanks, 2002) and have similar flowering times, which were typically within 10 to 20 d after removal from cold induction (Veatch-Blohm et al., 2013).

Growth conditions. The bulbs were planted in October each year (2010–12) with

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¹To whom reprint requests should be addressed; e-mail mblohm@loyola.edu.

the tip of the bulb at the soil line in 8-inch pots in Sunshine Potting Mix #1. The potted bulbs were then placed in a cold room at 4 °C for 13 weeks. The plants were irrigated by hand every ≈ 21 d during the cold induction period. All nutrient solutions contained 0.6 g·L⁻¹ 20N–8.6P–16.7K (Peter's 20-20-20; Scotts, Allentown, PA). All bulbs not assigned to the 0 mM NaCl control were initially irrigated with the 50 mM NaCl solution. At each subsequent irrigation, the plants were irrigated with the next highest salinity until the target salinity treatment was reached (i.e., 100, 150, 200, 300 mM NaCl). Salinity was ramped up in a stepwise fashion because we assumed that exposure to deicing salts throughout the winter would build up salinity in a gradual fashion.

After 88 d of cold exposure, the pots were transferred to the greenhouse without supplemental lighting and the experiments set up as a randomized complete block. The pilot experiment was planted to obtain baseline data for the range of salinities that daffodils could tolerate. During the initial pilot experiment (Jan. to Feb. 2011) only 'Dutch Master' was used, and the plants were exposed to salinities ranging from 0 to 200 mM NaCl (0, 50, 75, 100, 150, 200 mM NaCl). The pilot experiment was set up as a randomized complete block with four blocks (n = 4 for each cultivar under each salinity). The next two runs of the experiment (Jan. to Feb. 2012 and 2013) included all three cultivars and included salinities ranging from 0 to 300 mM NaCl (0, 50, 100, 150, 200, 300 mM NaCl). In 2012 the experiment was set up as a randomized complete block with five blocks (n = 5 for each cultivar under each salinity). In 2013 the experiment was set up as a randomized complete block with six blocks (n = 6 for each cultivar under each salinity).

The plants were irrigated with 300 mL of the appropriate irrigation solution at least two times per week to keep the soil moist during active growth (The American Daffodil Society, 2006). The average leaching fraction was between 15% and 25%. To each nutrient solution, containing 0.6 g·L⁻¹ 20N–8.6P–16.7K, was added the appropriate NaCl concentration. Average EC of each treatment and the soil effluent at the end of each experiment ranged from 0.85 to 57.34 dS·m⁻¹ and is recorded in Table 1. The average high and low temperatures $\pm$ SD in the greenhouse were as follows: 23.8 $\pm$ 6.6 and 16.8 $\pm$ 3.7 °C for 2011, 25.8 $\pm$ 5.9 and 18.6 $\pm$ 4.4 °C for 2012, and 23.7 $\pm$ 6.0 and 16.0 $\pm$ 4.7 °C for 2013.

Plant evaluation. At planting the initial bulb weight was recorded. The mean bulb weight $\pm$ SE was 52.24 $\pm$ 1.67 g for 'Dutch Master', 41.94 $\pm$ 1.01 g for 'Ice Follies', and 29.91 $\pm$ 1.65 g for 'Tete-a-Tete'. Once the plants were transferred to the greenhouse, they were grown for 5 to 6 weeks, until flower senescence of at least 80% of the plants in 2011 and 2012 and 100% of the plants in 2013. The growth of the plants was measured weekly by measuring the length of the

Table 1. Electrical conductivity (EC; dS·m⁻¹) $\pm$ SD of irrigation solution and soil effluent after saline irrigation (0, 50, 100, 150, 200, and 300 mM NaCl) for 88 d preemergence and 35 d post-emergence (n = 3 for each run of the experiment).

Treatment (mM NaCl)	EC (dS·m ⁻¹)	
	Irrigation solution	Soil effluent
0	0.85 $\pm$ 0	2.91 $\pm$ 1.84
50	6.31 $\pm$ 0	15.90 $\pm$ 3.85
100	12.81 $\pm$ 0	25.22 $\pm$ 6.71
150	19.74 $\pm$ 0	38.87 $\pm$ 2.51
200	26.42 $\pm$ 0	43.39 $\pm$ 3.34
300	39.63 $\pm$ 0	57.34 $\pm$ 7.13

Fig. 1. Mean growth (leaf length) $\pm$ SE of three daffodil cultivars exposed to 0 mM ($\blacklozenge$), 50 mM ($\square$), 100 mM ($\triangle$), 150 mM ($\blacksquare$), 200 mM ($\times$), or 300 mM NaCl ($\circ$) irrigation for 88 d preemergence and 35 d post-emergence. (A) 'Ice Follies'; (B) 'Dutch Master'; (C) 'Tete-a-Tete'. Data are means $\pm$ SE of two runs of five and six replications for all three cultivars (n = 11 for each cultivar within each salinity). Salinities within the same cultivar with the same letter are not significantly different according to Tukey's honestly significant difference (HSD) ($P < 0.05$). 'Tete-a-Tete' and 'Ice Follies' grew only 54% to 70% as much as 'Dutch Master' at all salinities except 0 and 100 mM NaCl, where growth was not significantly different among cultivars.

longest leaf from each leaf bundle and adding all the lengths together.

Carbon assimilation rate, transpiration rate, and stomatal conductance (g_s) were measured four times in 2012 (after 12, 18, 24, and 27 d of growth in the greenhouse) and once in 2013 (at 33 d of growth in the greenhouse) within an hour of solar noon. On Days 12 and 18 there were some missing data points; therefore, only the data from Days 24, 27, and 33 are presented. Measurements were collected using an LCI Portable Photosynthesis System (ADC Bioscientific Ltd., Great Amwell, U.K.) using ambient conditions on sunny days on fully expanded leaves that were not shaded by other leaves on the plant. The average photosynthetically active radiation $\pm$ SE was $481.3 \pm 3.3 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$.

The date of anthesis was recorded for each plant. Anthesis was the time when the first flower on the plant was fully open. In 2013, the date when flower senescence began was also recorded. A flower was considered senesced when the petals lost succulence and became translucent. Relative chlorophyll content of intact leaves was recorded for three leaves per plant in 2013 [optical density, chlorophyll concentration index (CCI), CCM-200 plus Chlorophyll Content Meter; Apogee Instruments, Logan, UT].

At harvest, leaf samples were collected at solar noon from the upper third of the leaf for determination of relative water content (RWC) (Bogeat-Triboulet et al., 2007) and leaf osmotic potential (Ψ_s). Leaf Ψ_s was determined using a Wescor Vapro 5220 Vapor Pressure Osmometer (Wescor Inc., Logan, UT). Both above-ground and below-ground biomass were weighed at harvest, rinsed, and then dried at 80 °C for dry biomass determination. A mix of dried samples was taken from both the leaves and bulbs with bulb samples coming from the interior of the bulb only and prepared for atomic absorption through HNO_3 digestion as described in Grusak (1994). The samples were analyzed for Ca^{2+} , Mg^{2+} , K^+ , and Na^+ content using flame atomic absorption spectrometry (Olsen and Ulicny, 2001).

Statistical analysis. All data were analyzed using the general linear model in the FitModel platform of JMP8 (SAS Institute Inc., 1998–2008). Initial bulb weight was used as a covariate for all analyses. Each model included the following explanatory variables: block, salinity, cultivar, and salinity $\times$ cultivar. When the data analysis combined data from more than one run of the experiment, run was also included as an explanatory variable. To meet the assumptions of normality, all of the growth and nutrient composition data were natural log-transformed. Specific comparisons among groups were conducted using Tukey's honestly significant difference. A P value ≤ 0.05 was considered significant throughout.

Results

Pilot study. Growth rate was significantly affected by salinity with all plants in salinity

treatments 100 mM NaCl or higher growing slower than the control (data not shown). The mean number of flowers produced per plant $\pm$ SE (1.13 ± 0.36) and mean time to anthesis $\pm$ SE (10.60 ± 1.25 d) were unaffected by salinity. Shoot dry weight was reduced only in the 200-mM NaCl treatment, which was reduced by 50% compared with the control (2.62 ± 0.47 g compared with 1.22 ± 0.47 g). Bulb weight was not significantly affected by salinity (data not shown).

Relative water content was reduced only in the 200-mM NaCl treatment ($83.50\% \pm 6.11\%$ in the control compared with $61.25\% \pm 3.86\%$ in the 200-mM NaCl treatment). Shoot Ψ_s was unaffected by salinity with an average $\Psi_s \pm$ SE of -1.04 ± 0.07 MPa. The only cation content that was affected by salinity was Na^+ content in the bulbs with the highest Na^+ accumulation occurring in 200-mM NaCl treatment (data not shown). Because flower production was unaffected by the salinities tested, we extended the range of salinity for the next two runs of the experiment.

Plant growth: 2012 and 2013. Growth over the first 5 weeks, as measured by leaf length, in all three cultivars was significantly affected by salinity, cultivar, and there was a salinity $\times$ cultivar interaction (Fig. 1). To allow time for flower senescence in all plants in 2013, plants were grown for 1 additional week, but growth leveled off in all treatments somewhere between 5 and 6 weeks of treatment; therefore, only the combined data for the first 5 weeks of growth are included. At the majority of the salinities, 'Dutch Master' plants grew more than 'Tete-a-Tete' and 'Ice Follies', which grew only 54% to 70% as

much as 'Dutch Master'. The only exceptions were the 0-mM NaCl control and the 100-mM NaCl treatment, where there were no differences among cultivars. For all 'Dutch Master' and 'Tete-a-Tete' plants, leaf growth did not decrease compared with the control until salinity was above 100 mM NaCl, and in 'Ice Follies', salinity decreased growth starting with the 100-mM NaCl treatment. A growth reduction in all three cultivars of 55% to 71% and 60% to 79% was observed in the 200- and 300-mM NaCl treatments, respectively, compared with the 0-mM NaCl control (Fig. 1). Leaf number was also decreased by salinity, but only in 'Tete-a-Tete' with the greatest reduction in the 300-mM NaCl treatment, which was reduced on average by $\approx 40\%$ compared with the control (Table 2).

Shoot dry weight was significantly affected by salinity and cultivar, but there was no salinity $\times$ cultivar interaction (Fig. 2A). 'Tete-a-Tete' had the lowest biomass production of the three cultivars. Shoot biomass was reduced compared with the 0-mM NaCl control in all salinities 100 mM NaCl or greater. Shoot biomass, combined for all cultivars, in the 200- and 300-mM NaCl treatments was on average 29% and 17% of the control, respectively (Fig. 2A). Shoot biomass was also different between runs of the experiment with all the plants in the 0-mM NaCl treatments in the first run having reduced biomass production compared with Run 2. However, because growth was comparable between the 2 years and the overall trend was decreased biomass production as salinity increased, we presented the combined means for both runs. Bulb dry weight

Table 2. Leaf number, osmotic potential (Ψ_s) and flowering characteristics of three daffodil cultivars exposed to saline irrigation (0, 50, 100, 150, 200, and 300 mM NaCl) for 88 d preemergence and 35 d post-emergence.^a

	Leaf number	Ψ_s (MPa)	Flower number	Days to anthesis	Flower duration (d)
Ice Follies					
0	6.00 e ^y	-1.12 a	1.00 e	24.00 cd	12.50 a
50	5.55 e	-1.12 a	1.09 e	23.67 bcd	11.67 abc
100	6.45 e	-1.16 a	1.18 e	27.67 a-d	8.83 de
150	6.20 e	-1.17 a	1.09 e	27.17 abc	9.67 cde
200	5.73 e	-1.14 a	0.91 e	31.00 ab	6.33 fg
300	5.27 e	-1.23 a	0.73 e	35.33 a	3.33 h
Dutch Master					
0	7.91 de	-1.15 a	1.45 de	23.50 cd	12.33 ab
50	10.18 cde	-1.26 a	1.45 de	24.50 bcd	12.17 abc
100	8.70 cde	-1.27 a	1.36 de	25.80 cd	10.20 b-e
150	9.45 cde	-1.48 a	1.73 de	27.17 bcd	8.67 def
200	7.91 de	-1.84 b	1.45 de	26.67 bcd	8.67 def
300	8.55 cde	-1.48 a	1.18 e	32.17 ab	4.67 fg
Tete-a-Tete					
0	17.00 ab	-1.21 a	5.09 a	11.17 f	9.83 a-e
50	19.18 a	-1.55 a	4.82 ab	13.17 f	10.33 a-d
100	17.82 ab	-1.35 a	4.00 abc	14.50 f	9.17 cde
150	13.45 abc	-1.89 b	3.10 bcd	13.67 f	9.00 cde
200	12.00 bcd	-1.81 b	1.91 cde	15.17 ef	7.83 ef
300	9.64 cde	-2.23 b	1.36 de	13.83 f	9.17 cde
Salinity (S)	**	***	***	***	***
Cultivar (C)	***	***	***	***	NS
S $\times$ C	*	NS	***	**	***

^aLeaf number, flower number, days to anthesis, and Ψ_s were recorded in both 2012 and 2013 ($n = 11$ for each salinity within each cultivar). Flower duration (time from anthesis to flower senescence) was recorded only in 2013 ($n = 6$ for each salinity within each cultivar).

^yValues within a column with the same letter are not significantly different according to Tukey's honestly significant difference ($P < 0.05$).

NS, ***, **, * Nonsignificant or significant at $P \leq 0.001$, 0.01, or 0.05, respectively.

Fig. 2. Mean $\pm$ SE (A) shoot dry weight and (B) bulb dry weight of three daffodil cultivars irrigated by 0, 50, 100, 150, 200, or 300 mM NaCl for 88 d preemergence and 35 d post-emergence. Cultivar abbreviations are as follows 'Ice Follies' (IF), 'Dutch Master' (DM), and 'Tete-a-Tete' (TT). Salinities with the same letter are not significantly different according to Tukey's honestly significant difference (HSD) ($P < 0.05$). Data are means of two runs of five and six replications for all three cultivars ($n = 11$ for each cultivar within each salinity).

Table 3. Ratios of shoot to bulb biomass, shoot and bulb K^+ and Na^+ content (% DW), and $K^+:Na^+$ ratio in three daffodil cultivars exposed to saline irrigation (0, 50, 100, 150, 200, and 300 mM NaCl) for 88 d preemergence and 35 d post-emergence.^z

	Shoot:bulb	Shoot			Bulb		
		K ⁺	Na ⁺	K ⁺ :Na ⁺	K ⁺	Na ⁺	K ⁺ :Na ⁺
Ice Follies							
0	0.36 a ^y	4.38	2.03 cd	2.13 a	0.74	1.82 d	0.41
50	0.33 a	2.91	1.86 d	1.59 a–d	0.75	1.93 cd	0.39
100	0.23 b	3.46	2.14 cd	1.59 a–d	0.72	2.45 a–d	0.32
150	0.24 b	3.84	2.37 bcd	1.60 a–d	0.86	2.19 bcd	0.41
200	0.13 c	2.14	2.33 cd	0.84 b–e	1.08	2.79 a–d	0.36
300	0.09 d	3.43	3.50 abc	1.07 b–e	0.89	2.53 a–d	0.37
Dutch Master							
0	0.39 a	3.45	1.94 cd	1.81 abc	0.82	1.98 cd	0.42
50	0.30 a	2.70	1.94 cd	1.44 a–e	0.78	2.09 bcd	0.38
100	0.21 b	3.29	2.16 cd	1.57 a–e	0.94	2.52 a–d	0.38
150	0.19 b	3.80	2.29 bcd	1.63 a–d	0.92	3.03 abc	0.31
200	0.13 c	4.34	3.33 bcd	1.51 a–e	1.06	2.37 a–d	0.43
300	0.09 d	4.03	2.86 bcd	1.60 a–e	0.84	2.24 bcd	0.36
Tete-a-Tete							
0	0.73 a	3.89	2.18 cd	1.62 ab	1.08	2.11 bcd	0.53
50	0.44 a	4.38	3.24 bcd	1.37 a–e	1.11	2.29 a–d	0.50
100	0.30 b	2.96	3.30 bcd	1.04 b–e	1.81	2.87 a–d	0.60
150	0.31 b	2.81	4.11 ab	0.74 cde	1.38	2.88 a–d	0.46
200	0.14 c	3.90	8.76 a	0.61 de	1.46	3.26 ab	0.45
300	0.09 d	2.82	7.40 a	0.46 e	1.35	3.36 a	0.40
Salinity (S)	***	NS	***	***	NS	***	NS
Cultivar (C)	NS	NS	***	***	***	***	***
S × C	NS	NS	**	*	NS	NS	NS

^zData are means $\pm$ SE of two runs of five and six replications for all three cultivars ($n = 11$ for each cultivar within each salinity).

^yValues within the same column with the same letter were not significantly different according to Tukey's honestly significant difference at $P \leq 0.05$.

NS, ***, **, * Nonsignificant or significant at $P \leq 0.001$, 0.01, or 0.05, respectively.

was significantly affected by salinity and cultivar, but there was no salinity $\times$ cultivar interaction (Fig. 2B). Although there was no interaction, in 'Dutch Master' and 'Ice Follies', which had greater bulb weights than 'Tete-a-Tete', exposure to 200 and 300 mM NaCl increased bulb dry weight compared with the control, whereas it did not in 'Tete-a-Tete'. Shoot-to-bulb ratio was only affected by salinity with the shoot-to-bulb ratio decreasing in the same fashion observed previously for shoot dry weight (Table 3).

Flower number was significantly affected by both salinity and cultivar with a significant interaction (Table 2). 'Ice Follies' and 'Dutch Master' typically sent up only a single flower and this did not change as salinity increased. In contrast, 'Tete-a-Tete' plants' flower number was reduced as salinity increased with the greatest reduction in the 300-mM NaCl treatment, which was reduced by 75% compared with the 0-mM NaCl control. Despite the deleterious effect of salinity on flower number of 'Tete-a-Tete', it had no effect on how quickly the plants flowered or how long the flowers lasted before senescence (Table 2). However, in 'Ice Follies' and 'Dutch Master' there was a 10- to 11-d increase in the time it took for the plants in the 300-mM NaCl treatment to flower compared with the 0-mM NaCl control, and the flowers only lasted 26% and 38% as long as those in the control for 'Ice Follies' and 'Dutch Master', respectively (Table 2). Only the plants in the 50-mM NaCl treatment had flowers that consistently lasted as long as the flowers in the control plants for these two cultivars (Table 2).

Leaf parameters. Leaf RWC was unaffected by salinity or cultivar and had an average $\pm$ SE of $73.83\% \pm 0.91\%$. Leaf Ψ_s was reduced by salinity and was different among cultivars (Table 2). Although there was no significant cultivar $\times$ salinity interaction, there appeared to be the strongest response to salinity in 'Tete-a-Tete', where Ψ_s was 0.68, 0.60, and 1.02 MPa lower than the control in the 150-, 200-, and 300-mM NaCl treatments, respectively (Table 2). In 2013 only we measured the relative chlorophyll concentration of the leaves in all treatments. There were no differences among salinity treatments, but there were differences among cultivars with 'Ice Follies' (77.24 ± 2.00 CCI units) having a higher relative chlorophyll concentration than both 'Dutch Master' (67.77 ± 3.50 CCI units) and 'Tete-a-Tete' (34.74 ± 2.30 CCI units).

Carbon assimilation rate was not reduced by salinity until 27 d in the greenhouse, which was 115 d after the onset of salinity treatment. At this time, carbon assimilation rate was reduced only in the 200- and 300-mM NaCl treatments (Table 4). Within the next 7 d, carbon assimilation rate increased in the 0-mM NaCl control, whereas carbon assimilation rate in all the salinity treatments was reduced by 66% to 93% compared with the control. Transpiration rate was also not reduced by salinity until 27 d in the greenhouse. On Day 33 transpiration rate was reduced compared with the control by $\approx 50\%$ in the

Table 4. Mean carbon assimilation rate (A), transpiration rate (E), and stomatal conductance (gs) of three daffodil cultivars ('Ice Follies', 'Dutch Master', and 'Tete-a-Tete') exposed to saline irrigation (0, 50, 100, 150, 200, and 300 mM NaCl) for 88 d preemergence and 35 d post-emergence.^a

Salinity	Days of salinity treatment		
	112 ^b	115	121
A ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)			
0	2.51	5.78 a [*]	6.76 a
50	3.05	6.29 a	2.98 b
100	3.59	3.42 ab	1.65 b
150	2.52	5.53 a	0.48 b
200	1.26	1.14 bc	0.90 b
300	1.13	-0.23 c	1.23 b
E ($\text{mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)			
0	0.77	1.12 a	0.74 a
50	0.36	0.77 ab	0.45 ab
100	0.48	0.63 bc	0.16 b
150	0.27	0.53 bc	0.11 b
200	0.14	0.28 c	0.07 b
300	0.05	0.34 c	0.04 b
gs ($\text{mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)			
0	40.00	38.00 a	38.75 a
50	14.00	28.30 ab	21.42 ab
100	25.00	28.00 ab	6.67 ab
150	13.30	15.00 bc	4.28 ab
200	20.00	15.00 bc	1.67 b
300	10.00	5.00 c	6.67 b
Salinity (S)	NS	**	**
Cultivar (C)	NS	*	*
S $\times$ C	NS	NS	NS

^aMeasurements were taken on Days 24, 27, and 33 in the greenhouse, which correspond to 112, 115, and 121 d of salinity treatment, respectively. Data are means of one run of three replications of each cultivar in each salinity (n = 9 for each salinity).

^bData from Days 112 and 115 were collected in 2012. Data from Day 121 were collected in 2013.

^{*}Means with the same letter for each parameter on the same day are not significantly different according to Tukey's honestly significant difference ($P < 0.05$).

NS, ***, **, * Nonsignificant or significant at $P \leq 0.001$, 0.01, or 0.05, respectively.

50-mM NaCl treatment, whereas the transpiration rate was reduced by 79% to 95% in the remaining salinity treatments with no differences among those treatments (Table 4). Stomatal conductance followed the same trend as carbon assimilation and transpiration rate with a decline starting at 27 d in the greenhouse (Table 4). Stomatal conductance was reduced 83% to 96% compared with the control in all salinity treatments except the 50-mM NaCl treatment (Table 4).

Plant ion content. Shoot Ca^{2+} and Mg^{2+} were unaffected by salinity, but shoot Ca^{2+} was affected by cultivar, which was highest in 'Tete-a-Tete' and lowest in 'Ice Follies'. The mean percent shoot dry weight $\pm$ SE for Ca^{2+} was $0.31\% \pm 0.02\%$ and for Mg^{2+} was $0.16\% \pm 0.008\%$. Shoot K^{+} content was unaffected by salinity or cultivar (Table 3). On the other hand, shoot Na^{+} content was significantly affected by salinity and cultivar with a salinity $\times$ cultivar interaction (Table 3). For all three cultivars, Na^{+} accumulation in the shoot increased with increasing salinity; this increase was most dramatic in 'Tete-a-Tete'. Na^{+} accumulation in the 200- and 300-mM NaCl treatments of 'Tete-a-

Tete' was almost four times greater than Na^{+} accumulation in the 0-mM NaCl control and was more than twice as much as that accumulated in the 300-mM NaCl treatment in 'Ice Follies' and 'Dutch Master' (Table 3). Shoot $\text{K}^{+}:\text{Na}^{+}$ ratio was decreased by salinity, but only in 'Ice Follies' and 'Tete-a-Tete' (Table 3).

Bulb Ca^{2+} and Mg^{2+} content were only different among cultivars with the highest content in 'Dutch Master' and lowest in 'Ice Follies'. The mean percent bulb dry weight $\pm$ SE for Ca^{2+} was $0.24\% \pm 0.02\%$ and for Mg^{2+} was $0.08\% \pm 0.003\%$. Bulb K^{+} was not significantly affected by salinity but was affected by cultivar with the highest K^{+} content in 'Tete-a-Tete' (Table 3). Bulb Na^{+} content was different among salinities and cultivars, but there was no interaction (Table 3). Bulb Na^{+} content was increased compared with the 0-mM NaCl control in all salinity treatments 100 mM NaCl or greater. Bulb $\text{K}^{+}:\text{Na}^{+}$ ratio was only affected by cultivar but not salinity with the highest ratio in 'Tete-a-Tete' (Table 3).

Discussion

Ornamental plants are considered highly tolerant to salinity when they can grow in soils with an EC greater than 6 dS·m⁻¹ without significant damage or reductions in visual quality and moderately tolerant with growth reductions of between 25% and 50% (Cassaniti et al., 2012; Niu et al., 2007; Niu and Rodriguez, 2006). Multiple parameters in our study indicate that these three cultivars would be considered tolerant up to and including irrigation water with a NaCl imposed EC of 12 dS·m⁻¹, which led to a soil effluent EC of ≈ 25 dS·m⁻¹. This soil effluent EC is much higher than the 4-dS·m⁻¹ threshold in the soil that is used to indicate salinity tolerance in vegetable crops (Shannon and Grieve, 1999).

Maintaining a relatively high $\text{K}^{+}:\text{Na}^{+}$ ratio in plant tissues is a mark of salinity tolerance (Cassaniti et al., 2012; Shirazi et al., 2005; Zhu, 2007). For all three daffodil cultivars in this study, the K^{+} content, as percent of dry weight, was unaffected by salinity. Therefore, although Na^{+} uptake increased as the NaCl content in the solution increased, the plants, particularly in 'Dutch Master' and 'Ice Follies', were able to maintain shoot $\text{K}^{+}:\text{Na}^{+}$ ratios above 1 at all salinities, whereas the 'Tete-a-Tete' plants were able to maintain ratios greater than 1 through 100 mM NaCl. High K^{+} levels are important in salinity tolerance because K^{+} plays a crucial role in cellular function, including protein synthesis and enzyme activation (Grattan and Grieve, 1999; Shirazi et al., 2005; Zhu, 2007). However, K^{+} demand may increase as the exposure to salinity increases as has been observed in other species (Grattan and Grieve, 1999); therefore, if growers noticed a decrease in plant quality under saline irrigation, K^{+} supplementation in irrigation water may improve salinity tolerance.

One important aspect in maintaining visual quality is plant growth. Although these

cultivars did have significant reductions in growth, this was not until 100 mM NaCl with reductions of 23% to 35% compared with the control; therefore, these cultivars would be rated as moderately tolerant to tolerant to salinity compared with other ornamental plants (Cassaniti et al., 2012). Compact plants are often more suitable for landscapes (Cameron et al., 2004; Kjellgren et al., 2000; Niu and Rodriguez, 2007); therefore, these growth reductions might even increase the visual impact of the plants in either landscapes or as potted plants. Another measure of plant visual quality is leaf production because plants with reduced leaf number show gaps in the vegetation of the landscape. The only cultivar where leaf number was reduced was in 'Tete-a-Tete' at salinities greater than or equal to 150 mM NaCl; reductions were 30% to 37% in the 150- and 200-mM NaCl treatments and 50% in the 300-mM NaCl treatment. On the other hand, leaf number was maintained at all salinities in both 'Dutch Master' and 'Ice Follies'. The leaves of most plants also maintained pigmentation without chlorosis or loss of chlorophyll, which is another key to maintaining visual quality and therefore suitability for landscapes or as potted plants (Niu et al., 2007).

Differences in photosynthesis did not become apparent until 27 d after the plants were transferred to the greenhouse. This is consistent with what we observed in our previous study when daffodils were exposed to only moderate salinity (Veatch-Blohm et al., 2013). The biggest differences in overall growth were in 'Tete-a-Tete', which had the smallest bulb weight. The bulb may be fueling the bulk of plant growth during the first few weeks in the greenhouse as has been observed in 'Star Gazer' lilies where the bulb supports plant growth until there are enough leaves to support the plant mainly through photosynthesis (Chang and Miller, 2003). Cultivars with a smaller initial bulb such as 'Tete-a-Tete' may have a stronger or more rapid response to salinity, because its bulb resources are depleted more quickly. In our study, growth was highest in 'Dutch Master', which had the greatest initial bulb size (52.24 ± 1.67 g), next highest in 'Ice Follies', which had the next greatest bulb size (41.94 ± 1.01 g), and lowest in 'Tete-a-Tete', which had the smallest average bulb size (29.91 ± 1.65 g).

Also key to ornamental suitability in landscapes is flower quality, timely initiation of flowering, flower number, and flower duration (Carter and Grieve, 2008; Villarino and Mattson, 2011). Flower number was not reduced by salinity in 'Dutch Master' or 'Ice Follies', but flower duration was only 33% to 66% and 25% to 75% the flower duration in the 0-mM NaCl control for salinities above 100 mM NaCl in 'Dutch Master' and 'Ice Follies', respectively. This corresponded to increased time to anthesis at these higher salinities. On the other hand, 'Tete-a-Tete' flowers lasted an average of 8 d in all salinity treatments, but the number of flowers produced per plant was reduced by 40% or more compared with the control in salinities 150 mM

NaCl or greater. Flower quality may also be positively affected by the maintenance of RWC in all three cultivars. For example, high leaf RWC after harvest has been used as a way to screen for longer vase life in roses (Fanourakis et al., 2012). In *Campanula medium*, high RWC under drought conditions corresponded with increased flower, bud initiation and flower formation and decreased floral bud abortion (Mao et al., 2014).

In addition to being three of the most popular daffodil cultivars, 'Tete-a-Tete', 'Dutch Master', and 'Ice Follies' demonstrate salinity tolerance, which further increases their desirability for cut flower production and landscapes. Interspersing irrigation with high-quality water or a higher leaching fraction may even enable these daffodil cultivars to tolerate short-term exposure to even higher salinities, which would be particularly useful for commercial growers. Based on maintenance of foliage quality, flower production, and flower duration for all three cultivars, we recommend that they can be grown in pots for cut flower production without substantial loss of visual quality with irrigation water with an NaCl induced EC of up to 12.81 dS·m⁻¹. Although we did not test how salinity affects bulb viability in the next season, the salinity tolerance displayed by the plants under controlled conditions indicate that these three cultivars may be good candidates for growth in salinized landscapes.

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