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GROWTH, YIELD, AND ION RELATIONS OF STRAWBERRY IN RESPONSE TO IRRIGATION WITH CHLORIDE-DOMINATED WATERS

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□ *Strawberry is listed as the most salt sensitive fruit crop in comprehensive salt tolerance data bases. Recently, concerns have arisen regarding declining quality of irrigation waters available to coastal strawberry growers in southern and central California. Over time, the waters have become more saline, with increasing sodium (Na^+) and chloride (Cl^-). Due to the apparent extreme Cl^- sensitivity of strawberry, the rising Cl^- levels in the irrigation waters are of particular importance. In order to establish the specific ion causing yield reduction in strawberry, cultivars 'Ventana' and 'Camarosa' were grown in twenty-four outdoor sand tanks at the ARS-USDA U. S. Salinity Laboratory in Riverside, CA and irrigated with waters containing a complete nutrient solution plus Cl^- salts of calcium (Ca^{2+}), magnesium (Mg^{2+}), Na^+, and potassium (K^+). Six salinity treatments were imposed with electric conductivities (EC) = 0.835, 1.05, 1.28, 1.48, 1.71, and 2.24 dS m^{-1}, and were replicated four times. Fresh and dry weights of 'Camarosa' shoots and roots were significantly higher than those of 'Ventana' at all salinity levels. Marketable yield of 'Camarosa' fruit decreased from 770 to 360 g/plant as salinity increased and was lower at all salinity levels than the yield from the less vigorous 'Ventana' plants. 'Ventana' berry yield decreased from 925 to 705 g/plant as salinity increased from 0.835 to 2.24 dS m^{-1}. Relative yield of 'Camarosa' decreased 43% for each unit increase in salinity once irrigation water salinity exceeded 0.80 dS m^{-1}. Relative 'Ventana' yield was unaffected by irrigation water salinity up to 1.71 dS m^{-1}, and thereafter, for each additional unit increase in salinity, yield was reduced 61%. Both cultivars appeared to possess an exclusion mechanism whereby Na^+ was sequestered in the roots, and Na^+ transport to blade, petiole and fruit tissues was limited. Chloride content of the plant organs increased as salinity increased to 2.24 dS m^{-1} and substrate Cl increased from 0.1 to13 $mmol_c L^{-1}$. Chloride was highest in the roots, followed by the leaves, petioles and fruit. Based on plant ion relations and relative fruit yield, we determined that, over the range of salinity levels studied, specific ion toxicity exists with respect to Cl^-, rather than to Na^+ ions, and, further, that the salt tolerance threshold is lower for 'Camarosa' than for 'Ventana'.*

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INTRODUCTION

Strawberry (*Fragaria* × *ananassa* Duch.) follows the typical two-phase response to salinity stress, exhibiting growth suppression long before the leaves show any signs of salt injury (Brown and Voth, 1955; Ehlig and Bernstein, 1958). Growth suppression is typically a nonspecific salt response, depending more on osmotic stress created by the total concentration of soluble salts than on the level of specific solutes (Hoffman, 1981). The osmotic effects are rapid, starting immediately after the salt accumulation in the root zone exceeds some threshold level. At that point, subtle changes occur due to water loss from leaf cells and reduction of cellular volumes. Within hours, however, the plant adjusts osmotically, cell volumes and turgor are restored, but irreversible damage has already been done. Cell elongation and cell division are reduced and as a result, shoot growth decreases, leaves expand and emerge more slowly, and fewer lateral branches form (Munns and Tester, 2008). Another effect of plant response to salinity is ion specific and occurs much later than the osmotic phase. As salt concentrations reach toxic levels in the older leaves, they die. If the older leaves die prematurely, the photosynthetic capacity of the plant is reduced, decreasing the supply of photoassimilates required by the young leaves, slowing their growth rate. For many plants, the ionic phase has less impact on plant growth than the osmotic phase at low and moderate salinities (Munns and Tester, 2008). However, for crops, such as strawberry, which lack the ability to control uptake and transport of specific toxic ions, the ionic phase dominates.

The specific ion causing toxicity in salt-stressed strawberry is controversial, although the response may be cultivar-dependent. Some investigators suggest that leaf injury is primarily caused by levels of chloride (Cl^-) well beyond that required for optimum growth (Martinez Barroso and Alvarez, 1997; Keutgen and Pawelzik, 2009). Ulrich et al. (1980) reported that the Cl^- requirement was extremely low and that Cl^- sufficiency in strawberry leaves ranged between 0.07 and 0.04% of dry matter. Injury occurred when leaf Cl^- exceeded 1%, but the presence of sodium (Na^+) in the tissues did not notably intensify the damage (Martinez Barroso and Alvarez, 1997). Some strawberry cultivars inhibited translocation of Cl^- to the leaves by storing it in the roots and crowns, but this mechanism appeared to be relatively weak (Saied et al., 2005). Chloride toxicity symptoms, characterized by necrosis of the blade margins followed by progressive scorch towards the base, became evident in strawberry cultivars 'Lassen' and 'Shasta' when Cl^- levels in the soil saturation extract exceeded 8 and 5 mM, respectively (Ehlig and Bernstein, 1958; Bernstein, 1980). Waters containing in excess of 5 mM Cl^- are

not recommended for irrigation of California strawberries (Schrader and Welch, 1990).

Leaf injury in strawberry may occur when leaf-Na exceeds 0.10% (43 mmol kg^{-1}) (Ulrich et al., 1980). Selected strawberry cultivars were heavily damaged by high external Na^+ concentrations (Ehlig and Bernstein, 1958), whereas some varieties have the ability to exclude Na^+ from leaf tissues when stressed at relatively low salinity levels (Saied et al., 2005; Keutgen and Pawelzik, 2009). Excessive concentrations of Na^+ or Cl^- in the external solution of many plants may affect nutrient ion activities that result in extreme ratios of Na^+/ calcium (Ca^{2+}), Na^+/ potassium (K^+), Ca^{2+}/ magnesium (Mg^{2+}), and Cl^-/ nitrate (NO_3^-) causing ion imbalances and altering essential nutrient requirements within the plants (Grattan and Grieve, 1999).

Many studies of crop salt tolerance have been conducted with NaCl as the sole salinizing salt with the results focusing on Na^+ uptake, transport and selectivity processes rather than on Cl^- relations (Kepenek and Koyuncia, 2002; Kaya et al., 2002b; 2002c; Yilmaz et al., 2009). Teakle and Tyerman (2010) point out that the heavy emphasis on Na^+ in reviews on salt tolerance is a reflection of the significant number of experimental papers that only measure Na^+ (and usually other cations), but not Cl^- in salt-stressed tissues. As a result, the importance of Cl^- toxicity in the response of strawberry and other salt sensitive crops, is often not addressed.

The objective of this study was to evaluate the effect of irrigation with saline waters containing Cl^- salts of Ca^{2+}, Mg^{2+}, Na^+ and K^+ on growth, fruit yield and ion relations of strawberry cultivars 'Ventana' and 'Camarosa' grown in outdoor sand cultures.

MATERIALS AND METHODS

The experiment was conducted at the USDA-ARS U. S. Salinity Laboratory, Riverside, CA in outdoor sand tanks. The tanks, each 82 cm long × 202 cm wide × 84 cm deep, were filled with coarse sand having an average bulk density of 1.4 Mg m^{-3}. At saturation, the sand had an average volumetric water content of 0.34 m^3 m^{-3}. Sand in the tanks was fumigated with methyl bromide (TriCal, Inc., Corona, CA, USA) on 27 October 2007. Tanks were irrigated on 5 Nov with a nutrient solution consisting of 1.7 mM calcium nitrate [$Ca(NO_3)_2$], 2.0 mM potassium nitrate (KNO_3), 0.50 mM magnesium sulfate ($MgSO_4$), 0.1 mM potassium chloride (KCl), 0.17 monopotassium phosphate (KH_2PO_4), 50 μM Fe as sodium ferric diethylenetriamine pentaacetate, 23 μM boric acid (H_3BO_3), 5 μM manganese sulfate ($MnSO_4$), 0.4 μM zinc sulfate ($ZnSO_4$), 0.2 μM copper sulfate ($CuSO_4$) and 0.1 μM molybdic acid (H_3MoO_4) added to deionized water. The electrical conductivity (ECiw) of this solution was 0.835 dS m^{-1}. Irrigation waters were pumped from 1750-L reservoirs in an underground basement to the tanks

TABLE 1 Composition of salinizing salts in waters used to irrigate strawberry cultivars 'Camarosa' and 'Ventana' grown in outdoor sand tanks

	($mmol_c L^{-1}$)				
Electrical Conductivity(dSm^{-1})	Ca	Mg	Na	K	Cl
0.85	3.4	2.0	0	2.1	0.1
1.05	3.4	2.0	2.0	2.1	2.1
1.28	3.8	2.0	3.8	2.1	4.3
1.48	4.5	2.4	4.5	2.3	6.7
1.71	5.2	2.6	5.2	2.6	8.2
2.24	6.8	3.4	6.8	3.4	13.0

and returned by gravity through a subsurface drainage system to maintain a uniform and constant profile of salinity.

Rooted vegetative runner plants of strawberry cultivars 'Camarosa' and 'Ventana', were supplied by Sierra-Cascade Nursery, Susanville, CA. On 6 November 2007, uniform-sized plants were selected and planted in the tanks. Each tank contained one row of each cultivar. Rows were 77 inches (195 cm) long, spaced 9.8 inches (25 cm) apart with 8 plants per row. Planting density was equivalent to 39,000 total plants per acre (96,000 plants per ha). Sand in each tank was covered with black plastic mulch.

Chloride salts of Ca^{2+}, Mg^{2+}, Na^{+}, and K^{+} were added to the base nutrient solution in the reservoirs on 15 November 2007. Plants were furrow-irrigated with treatment solutions once a day for the first 6 weeks of the growth cycle, and then twice daily until the end of the experiment. Each irrigation continued for ~2 min. The pH of the irrigation waters was not controlled and ranged between 7.5 and 8.2 over the course of the experiment.

The experiment consisted of six salinity treatments (EC = 0.835, 1.05, 1.28, 1.48, 1.71, and 2.24 dS m^{-1}), four replications, and two strawberry cultivars. Salinizing ion compositions are shown in Table 1. Solution ion compositions were calculated using the Extract Chem model (Suarez and Taber, 2007) from the chemical routines in UNSATCHEM (Suarez and Simunek, 1997). Calculations, accounting for maximum evapotranspiration, soil water-holding capacity and intervals between irrigations, indicated that the salinity of the irrigation water was generally equivalent to that of the sand water. Previous studies (Wang, 2002) demonstrated that the EC of this sand is approximately 2.2 times the EC of the saturated soil extract (EC_e) The EC_e is the salinity parameter used to characterize salt tolerance in most studies (Ayers and Westcot, 1985). Therefore, the salinity treatments (EC_{iw}) for this experiment were estimated as 0.3, 0.48, 0.58, 0.67, 0.78 and 1.02 dS m^{-1}, expressed as EC_e.

Solutions were " analyzed for mineral ion content three times during the experiment by inductively coupled plasma optical emission spectrometry (ICPOES) to confirm that target ion concentrations of Ca, Mg, Na, K, sulfur

(S), phosphorus (P) and the micronutrients were maintained. Chloride was determined by coulometric-amperometric titration.

Mature fruit from each cultivar was harvested twice weekly at the 'full-ripe' stage (Strand, 2008), counted, weighed, and graded for marketability. Fruit weighing less than 10 g was rated as unmarketable. Fresh weight of individual berries was determined by dividing the total fresh weight of the marketable berries harvested from each cultivar and each tank by the total number of marketable berries per tank and cultivar. Relative berry yield curves were generated from non-linear fits of threshold (the maximum irrigation water salinity which did not reduce yield below that obtained under nonsaline conditions) and slope (the percentage of expected yield reduction per unit increase in salinity above the threshold value) with the maximum yield fixed at 100% for each cultivar independently (Maas and Hoffman, 1977; van Genuchten and Hoffman, 1984).

Fruit subsamples were washed in deionized water. Dry fruit weight measurements were made on 100-g samples of fresh fruit. Final fruit harvest occurred 21 July 2008. At that time, the aboveground biomass of each plant in the sand tanks (8 plants per cultivar per tank) was harvested, stolons and cymose stems were discarded, and the remaining shoot tissues were weighed. Fresh shoot weights of the eight plants were averaged and the mean shoot weight from the four replicates was determined. A composite sample of the youngest, fully-expanded leaves of each plant was obtained, divided into blades and petioles, and washed in deionized water. Roots of all the plants were harvested, rinsed in tap water to remove soil, then washed in deionized water. All tissues were dried in a forced-air oven for 72 hr at 70°C, weighed, and ground in a Wiley mill to pass a 20-mesh screen. Total-S, total-P, Ca, Mg, Na, K, Fe, Mn, Zn and Cu were determined on nitric-perchloric acid digests of the plant tissues by ICPOES. Chloride was determined on nitric-acetic acid extracts by coulometric-amperometric titration.

During the course of the " experiment, daytime air temperatures ranged from 3.1 to 41.8°C (mean = 20.1°C); nighttime temperatures ranged from 2.9 to 35.5 (mean 12.8°C). Relative humidity ranged from 3.1 to 98.3% with a mean of 20.1% during the day and 64.8% during the night. Plants were inspected twice a week for the presence of pests and control measures were taken as necessary.

Statistical analyses for this study were performed by analysis of variance with mean comparisons at the 95% level based on Duncan's Multiple Range Test. SAS release version 8.02 was used (SAS Institute, Cary, NC, USA).

RESULTS

Plant Growth

Vegetative biomass production of 'Camarosa' was significantly higher than that of 'Ventana' at all salinity levels (Figure 1). Fresh weight (FW) of

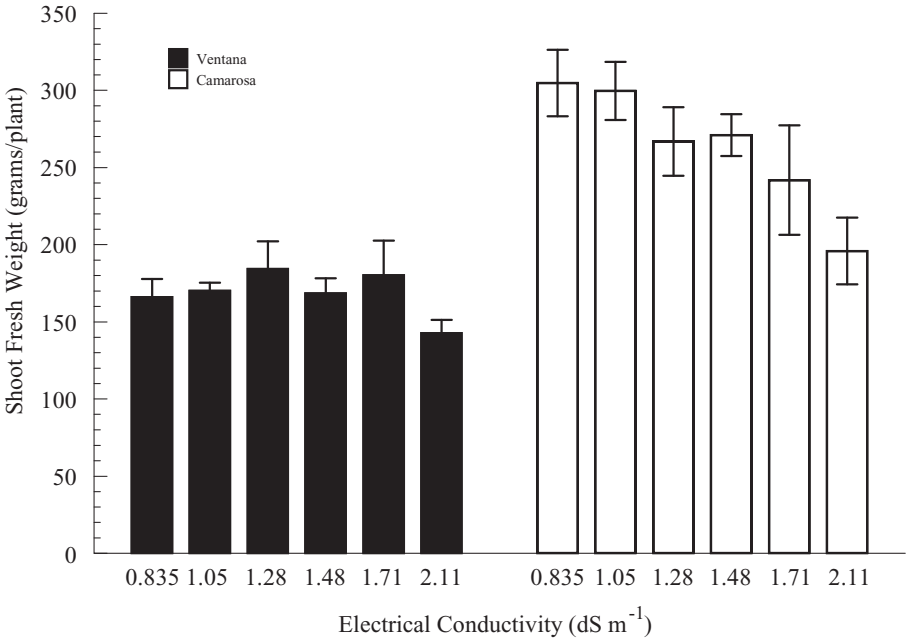

FIGURE 1 Effect of irrigation water salinity on shoot fresh weight of strawberry cultivars, 'Camarosa' (□) and 'Ventana' (■), grown in outdoor sand tanks irrigated with chloride-dominated waters. Values are the means of 8 observations ±s.e.

'Camarosa' shoots decreased from 305 to 195 g/plant as external salinity increased from 0.835 to 2.21 dS m^{-1}, but this reduction was not significant until external EC exceeded 1.71 dS m^{-1} (Figure 1). In contrast, 'Ventana' shoot biomass accumulation was unaffected by the EC of the irrigation waters and averaged 170 g FW/plant across salt treatments. Fresh weight to dry weight (DW) ratios for 'Camarosa' shoots were not affected by salt stress and averaged 2.7 across salinity levels; for 'Ventana', however, FW/DW ratios decreased from 6.8 to 5.0 as salinity increased (data not shown). In common with many plants grown under salt stress (Shannon et al., 1994), 'Ventana' shoot growth was inhibited more by salinity than root growth, and the shoot/root (S/R) ratio decreased from 12.4 to 9.3 as salinity increased. The S/R ratio for 'Camarosa' was unaffected by treatment and averaged 10.1 across salinity treatments (Data not shown). However, when 'Camarosa' was grown under higher levels of salinity than we used in our study, the S/R ratio increased from 10.8 to 12.8 as NaCl concentration in the irrigation waters increased from 0 to 35 $mmol_c L^{-1}$ (Kaya et al., 2001, 2002a, 2002b, 2003).

Fruit Yield

Marketable fruit yield of 'Ventana' was not significantly reduced ($P < 0.05$) from a maximum of 925 g/plant until the EC of the irrigation

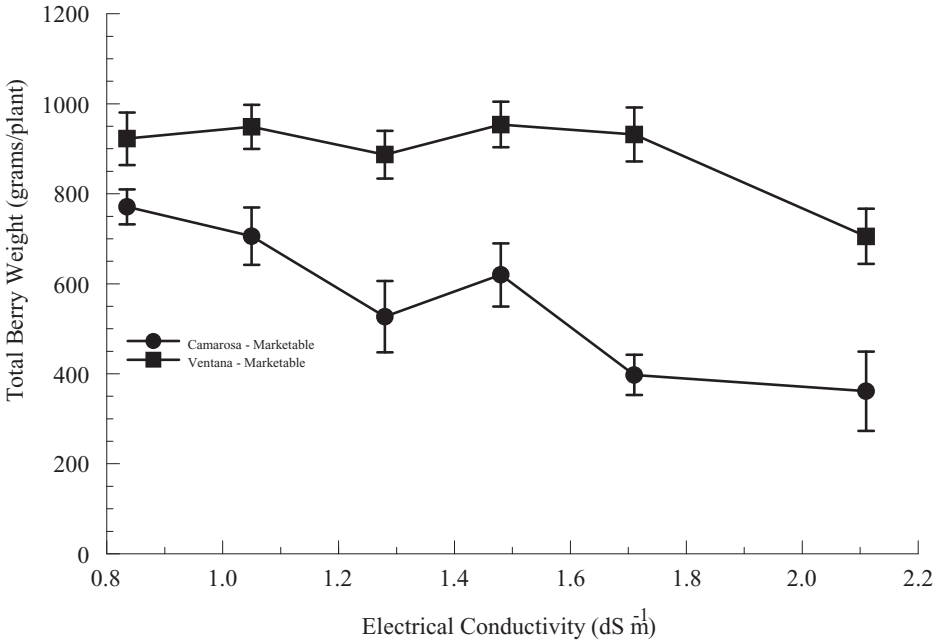

FIGURE 2 Effect of irrigation water salinity on marketable fruit yield of strawberry cultivars 'Camarosa' (●) and 'Ventana' (■) grown in outdoor sand tanks irrigated with chloride-dominated waters. Values are the mean of 4 observations ±s.e.

waters exceeded 1.71 dS m^{-1} and solution Cl^- exceeded 8.2 $mmol_cL^{-1}$ (Figure 2). Fruit yield of 'Camarosa' was lower than that of 'Ventana' at all salinity levels, ranging from 779 to 360 g/plant as salinity increased (Figure 2). 'Camarosa' yield decreased with the first addition of salt above the nonsaline control treatment. Linear regression analysis of relative berry yield for both cultivars is presented in Figure 3. Relative yield of 'Ventana' closely followed the patterns based on absolute yield. The salt tolerance threshold (the maximum irrigation water salinity that did not reduce yield below that obtained under nonsaline conditions) was 1.71 dS m^{-1}, and thereafter, each additional unit of salinity reduced 'Ventana' berry yield 61%. Analysis of relative 'Camarosa' yield showed that for each salinity unit above the non-saline control level (EC = 0.835 dS m^{-1}) berry yield was reduced 80%. Application of these values to field conditions requires knowledge of the soil EC_e, generally calculated from EC_{iw} and leaching fraction.

Cultivar differences in average individual berry weight in the absence of salt stress were not significant (20 g/'Ventana' berry; 19.0 g/'Camarosa' berry). As salinity increased to 2.24 dS m^{-1}, however, the weight of 'Camarosa' berries decreased to 16 g. Weight of 'Ventana' berries was reduced to 18 g when EC of the irrigation water exceeded 1.71 dS m^{-1}, the EC at which yield started to decline. At salinity levels higher than 0.835 dS m^{-1}, 'Ventana' berries were significantly ($P < 0.05$) heavier than 'Camarosa'

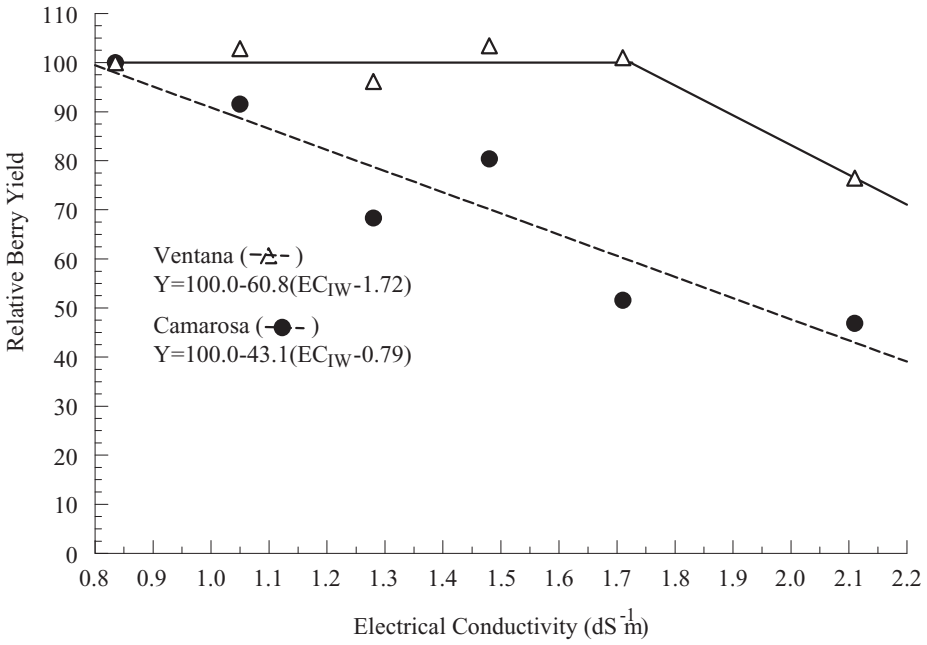

FIGURE 3 Relative berry yield of strawberry cultivars, 'Camarosa' (•) and 'Ventama' (■) as a function of irrigation water salinity.

berries (Figure 4). Although fresh berry weight decreased as salinity increased, berry count was identified as the yield component most affected by salt stress. The number of 'Ventana' berries was significantly higher than the number of 'Camarosa' berries once the EC of the irrigation waters exceeded 1.05 dS m^{-1} (Data not shown). In contrast, Awang et al. (1995a) found that salinity has no effect on fruit number, and overall yield was a function of decreasing fresh weight of individual berries.

Weight of unmarketable berries produced by both 'Camarosa' and 'Ventana' totaled 100 g/plant regardless of salinity level. Based on total berry yield per plant, the cull rate of 'Camarosa' berries increased from 11 to 22% as salinity increased; whereas, over the range of salinities, unmarketable 'Ventana' berries increased from 10 to 12% of the total yield (data not shown). Depending on year and location, the cull rate for 'Camarosa' is reported to range from 10 to 28% (Norton and Larson, 1996). Cull rate for 'Ventana' grown in southern California in 2006–2009 is reported as 21.5% (Larson, 2010).

Mineral Ion Accumulation and Partitioning

Calcium concentrations were highest in the leaves of both cultivars and progressively less in the roots, petioles and fruit (Tables 2 and 3). As external-Ca increased from 3.4 to 6.8 $mmol_cL^{-1}$, fruit-Ca content exhibited small

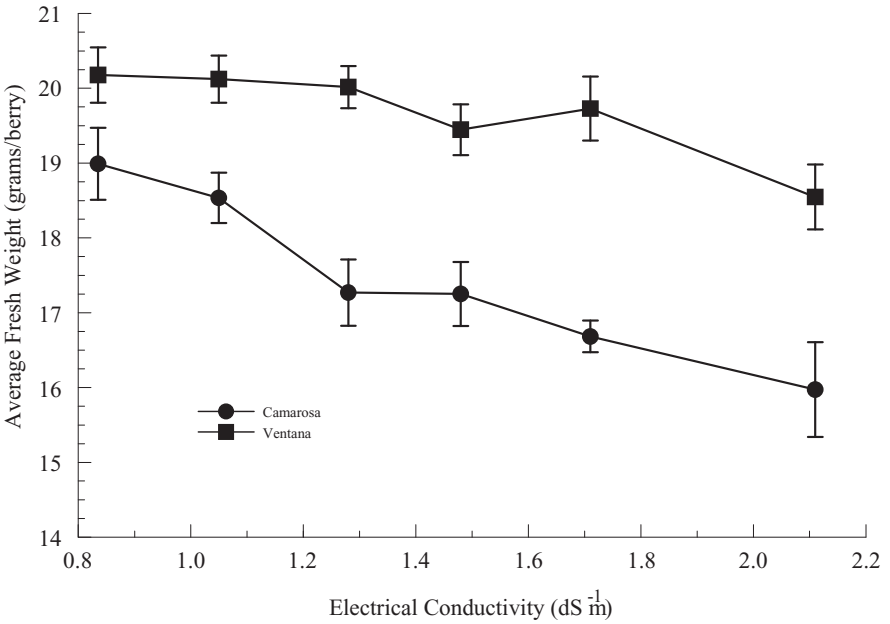

FIGURE 4 Effect of irrigation water salinity on individual fruit weight of strawberry cultivars, 'Camarosa' (●) and 'Ventana' (■), grown in outdoor sand tanks.

increases that were statistically, but perhaps not biologically, significant. Averaged across salinity levels, Ca^{2+} was 51 and 46 mmol kg^{-1} for 'Camarosa' and 'Ventana' fruit, respectively. Calcium increased in leaves of both cultivars, but this response was not statistically significant. Differences in petiole-Ca in response to increasing salinity also were small, but the increase in 'Ventana' petioles was statistically significant as salinity increased from 0.835 to 1.05 dS m^{-1}. Calcium content in 'Ventana' roots was not affected by salinity; however, Ca^{2+} in 'Camarosa' roots increased significantly from 255 to 335 mmol kg^{-1} over the range of salinity treatments.

Salinity caused only slight changes in Mg^{2+} content in the fruit of both cultivars; averaged across salinity levels, fruit-Mg was 78 and 61 mmol kg^{-1} for 'Camarosa' and 'Ventana', respectively, as the Mg^{2+} content of the irrigation water increased from 3.4 to 6.8 $mmol_c L^{-1}$ (Table 1). Magnesium content in 'Ventana' leaves, petioles and roots and in 'Camarosa' roots was unaffected by increasing salinity. However, Mg^{2+} increased significantly in 'Camarosa' leaves (150 to 189 mmol kg^{-1}) and petioles (95 to 133 mmol kg^{-1}) as salinity increased from 0.835 to 2.24 dS m^{-1} (Tables 2 and 3).

As salinity increased and external-Na increased from 0 to 6.8 $mmol_c L^{-1}$, Na^+ levels were low in fruit, leaves and petioles of both cultivars, ranging between 18 and 37 mmol kg^{-1} in those organs and across salinity levels. Sodium in the roots of both cultivars increased significantly as salinity increased (Tables 2 and 3). At each salinity level, root-Na was higher in 'Camarosa'

TABLE 2 Effects of increasing electrical conductivity (EC) of Cl-dominated irrigation waters on mineral macro-ion composition in fruit, blades, petioles and roots of strawberry cultivar 'Camarosa' 2007–2008

	mmoles kg^{-1} dry weight						
EC (dS m^{-1})	Ca	Mg	Na	K	P	S	Cl
Fruit							
0.85	46b†	76b	23bc	472a	98a	39b	7.6d
1.05	46b	77ab	28bc	448a	87a	40b	18cd
1.28	45b	72b	25bc	466a	83ab	38b	26bc
1.48	65a	93a	30ab	543a	98a	47a	33b
1.71	51b	78ab	22c	510a	85ab	39b	39b
2.24	52b	71b	36a	455a	65b	35b	90a
Blades							
0.85	354a	150a	21b	555a	90a	50a	68c
1.05	393a	162ab	19b	545a	68b	46ab	107c
1.28	446a	169ab	25a	549a	82ab	47ab	162b
1.48	458a	175ab	29a	552a	76ab	44b	178b
1.71	457a	185ab	21b	515a	80ab	46ab	207ab
2.24	484a	189a	23ab	495a	66b	49a	233a
Petioles							
0.85	237a	95b	20b	723a	70a	18ab	20d
1.05	268a	123ab	24ab	721a	52ab	18ab	41cd
1.28	264a	120ab	30ab	781a	64ab	17b	77bc
1.48	269a	123ab	33ab	764a	62ab	17ab	85b
1.71	260a	123ab	29ab	767a	71a	18ab	102b
2.24	246a	133a	36a	790a	63ab	21a	151a
Roots							
0.85	255b	147a	118c	341a	80a	96a	147b
1.05	282ab	136ab	201b	278ab	69ab	84a	204ab
1.28	295ab	117b	191b	242ab	67ab	84a	162b
1.48	307ab	111b	233ab	201b	68ab	88a	174b
1.71	314ab	127ab	268a	240ab	75ab	87a	283a
2.24	335a	135ab	198b	196b	63b	74a	274a

† Within columns and plant organs, means followed by a different letter are significantly different at the 0.05 probability level according to Tukey's studentized range test. Values are the means of four observations.

than in 'Ventana', but this effect was not significant (data not shown), thus the yield differences related to salinity are not explained by Na^+ accumulation.

Potassium was more strongly accumulated in the petioles, followed by leaves, fruit and roots of both cultivars. The increase in external-K from 2.1 to 3.4 $mmol_c L^{-1}$ caused only minor and non-significant effects on K-content in 'Camarosa' fruit, blades and petioles. 'Camarosa' root-K, however, decreased from 341 to 196 mmol kg^{-1} as salinity increased. The effects of salinity on K accumulation in 'Ventana' organs were inconsistent (Tables 2 and 3).

The phosphorus status of strawberry is most accurately assessed by determining P-content of the petioles. Petiole-P concentrations higher than 700 ppm (23 mmol kg^{-1}) indicate that P nutrition is adequate for strawberry (Ulrich et al., 1980). Total-P was higher in 'Camarosa' petioles than in

TABLE 3 Effects of increasing electrical conductivity (EC) of Cl-dominated irrigation waters on mineral macro-ion composition in fruit, blades, petioles and roots of strawberry cultivar 'Ventana', 2007–2008

	mmoles kg^{-1} dry weight						
EC (dS m^{-1})	Ca	Mg	Na	K	P	S	Cl
Fruit							
0.85	45ab	58a	18b	454a	74a	37b	7.6d
1.05	48a	64a	22ab	474a	77a	40a	16cd
1.28	42b	58a	23ab	474a	81a	38ab	22bc
1.48	45ab	58a	22ab	463a	79a	38ab	28bc
1.71	47ab	63a	23ab	479a	81a	40a	34b
2.24	49a	62a	25a	504a	73a	40a	68a
Blades							
0.85	387a	131a	19b	548b	72ab	53a	69e
1.05	434a	135a	23ab	621a	61ab	46a	120d
1.28	416a	133a	25ab	620a	76a	51a	149dc
1.48	428a	1310a	25ab	591ab	66ab	47a	180bc
1.71	413a	137a	26a	625a	71ab	51a	208ab
2.24	428a	135a	23ab	575ab	58b	49a	235a
Petioles							
0.85	230b	87b	21c	816ab	51a	19a	22d
1.05	263a	103ab	25bc	851a	42a	18ab	45cd
1.28	260a	105ab	31ab	840ab	44a	17b	69c
1.48	265a	114a	37a	772b	40a	18ab	94b
1.71	263a	111a	32ab	773b	47a	18ab	113b
2.24	255a	103ab	29b	884a	41a	18ab	151a
Roots							
0.85	270a	138ab	96d	398a	57a	76ab	130d
1.05	286a	140ab	172c	388ab	59a	81ab	187cd
1.28	287a	119b	183bc	257c	62a	82ab	163d
1.48	282a	130ab	222ab	299bc	59a	77ab	236bc
1.71	284a	130ab	234a	348abc	63a	87a	293b
2.24	269a	150a	188bc	350abc	57a	70ab	387a

† Within columns and plant organs, means followed by a different letter are significantly different at the 0.05 probability level according to Tukey's studentized range test. Values are the means of four observations.

'Ventana' petioles in all salinity treatments and this response was statistically significant when salinity increased to 1.05 dS m^{-1}. Across salinity levels, total-P averaged 65 mmol kg^{-1} and 44 mmol kg^{-1} in 'Camarosa' and 'Ventana' petioles, respectively (Tables 2 and 3).

Total sulfur was highest in the roots, with decreasing concentrations in blades, fruit and petioles of both cultivars. External-SO_4 concentration was constant (2 $mmol_c L^{-1}$) across treatments and increasing salinity had little effect on total-S accumulation in the strawberry organs (Tables 2 and 3).

Chloride was also highest in roots, with decreasing concentrations in blades, petioles and fruit of both cultivars. Chloride content in the organs increased significantly as salinity increased. Chloride was higher in 'Ventana' blades than 'Camarosa' blades at each salinity level, but this effect was not significant (Tables 2 and 3). Slight to moderate chlorotic and necrotic areas

were observed on blade margins of both 'Camarosa' and 'Ventana' plants when blade-Cl exceeded 180 mmol kg^{-1}, a value similar to that given for Cl-toxicity injury in strawberry leaves (Ulrich et al., 1980).

Foliar, petiole, and root analyses are standard methods for assessing the micronutrient status of plants. The critical ranges for optimum nutrition in California strawberries have not been determined (Strand, 2008). However, the lower limit for adequate strawberry micronutrient leaf content was established by Ulrich et al. (1980). Micronutrient concentrations in strawberry blades, compiled from American surveys, give the following sufficiency ranges (in mg kg^{-1} dry weight): Fe 60–250, Mn 50–200, Zn 20–50, Cu 6–20 (Hancock, 2008).

Iron was accumulated most strongly in the roots and, across salinity levels, averaged 1975 mg Fe kg^{-1} in roots of both cultivars. Analytical values indicated that blade-Fe of both cultivars was within the recommended range which suggests that the relatively high substrate pH levels attained in this experiment did not reduce Fe availability to the leaf tissues. Blade-Fe in 'Camarosa' plants was not affected until substrate salinity exceeded 1.71 dS m^{-1} and then increased about 2-fold. 'Camarosa' fruit-Fe decreased significantly from 75 to 21 mg kg^{-1} as salinity increased. Salinity had no effect on petiole-Fe which averaged 52 mg kg^{-1} across salinity levels. Iron decreased in 'Ventana' blades as salinity increased, but iron accumulation in fruit and petiole tissue was not affected by treatment (Table 4). Retention of high concentrations of Fe in root tissues and patterns of partitioning to the aboveground organs has also been observed in the same cultivars irrigated with waters of comparable composition and salinity levels under field conditions (D. L. Suarez, unpublished).

According to the sufficiency range given above, Mn would be rated as deficient in blades of both 'Camarosa' and 'Ventana'. While the Mn status of both cultivars may be below normal, the blades showed no netted, clear-dotted veining symptoms which are characteristic of Mn deficiency (Ulrich et al., 1980). The range for adequate Mn nutrition may be wider than that reported by Hancock (2008). Ulrich et al. (1980) determined blade-Mn less than 25 mg kg^{-1} indicated deficiency. Manganese was higher in roots than in the above ground organs (Table 4).

Zinc was also higher in roots than in above-ground organs of both cultivars. Root-Zn increased as salinity increased, but this response was significantly only for 'Ventana'. Blade-Zn was not affected by salinity treatment. Averaged across salinity levels, blade-Zn was 35 and 32 for 'Camarosa' and 'Ventana', respectively, well within the sufficiency range as given by Ulrich et al. (1980) and Hancock (2008) (Table 4).

Blade-Cu values were also below the normal range (Hancock, 2008), but higher than the concentration (3 mg kg^{-1}) determined by Ulrich et al. (1980) for Cu deficiency (Table 4). Characteristic symptoms of Cu

TABLE 4 Effects of increasing electrical conductivity (EC) of Cl-dominated irrigation waters on mineral micronutrient composition in fruit, blades, petioles and roots of strawberry cultivar 'Camarosa'and 'Ventana', 2007–2008

	mg kg^{-1} dry weight							
EC (dS m^{-1})	Fe	Mn	Zn	Cu	Fe	Mn	Zn	Cu
Fruit	Camarosa				Ventana			
0.85	75a	23a	27a	1.4a	29a	30a	24a	1.3a
1.05	62ab	35a	28a	1.9a	36a	11a	26a	1.5a
1.28	49abc	14a	25a	1.0a	60a	12a	23a	1.4a
1.48	33bc	17a	28a	1.4a	51a	30a	23a	1.5a
1.71	35bc	18a	26a	1.2a	35a	19a	24a	1.7a
2.24	21c	14a	25a	1.1a	41a	15a	26a	1.8a
Blades								
0.85	131b	15a	30a	4.2a	249ab	20ab	31a	4.8a
1.05	136b	20a	35a	5.2a	263a	21ab	32a	5.2a
1.28	138b	27a	34a	4.0a	138b	41ab	30a	5.0a
1.48	154b	66a	37a	4.5a	164ab	16b	34a	4.5a
1.71	147b	27a	36a	4.5a	146ab	48a	33a	4.7a
2.24	288a	44a	37a	4.3a	147ab	28ab	32a	4.8a
Petioles								
0.85	37a	18a	25a	2.6a	39a	9.3a	24a	2.5a
1.05	48a	20a	31a	2.7a	36a	8.2a	26a	2.2a
1.28	39a	18a	31a	2.2a	41a	17a	28a	2.3a
1.48	53a	24a	29a	2.6a	55a	6.7a	29a	2.5a
1.71	79a	39a	27a	2.3a	37a	11a	27a	1.9a
2.24	57a	15a	31a	2.5a	38a	12a	28a	2.3a
Roots								
0.85	1480a	84ab	77a	11a	1935a	82a	89b	13a
1.05	1817a	84ab	89a	16a	2035a	67a	113ab	16a
1.28	2337a	88a	91a	14a	1846a	86a	86b	14a
1.48	1861a	65ab	84a	14a	1863a	63a	101b	16a
1.71	2080a	55b	89a	14a	2295a	106a	107b	15a
2.24	2294a	62ab	103a	15a	1865a	96a	139a	15a

† Within columns and plant organs, means followed by a different letter are significantly different at the 0.05 probability level according to Tukey's studentized range test. Values are the means of four observations.

deficiency, i.e. bleaching, green-veining, and pronounced green leaf margins (Ulrich et al., 1980) were not observed in this study.

DISCUSSION

Fruit production in numerous species is influenced by the competition between vegetative and reproductive growth. Vegetative growth of strawberry beyond some critical point is detrimental to fruit yield, and, conversely, reproductive development and fruiting are known to be antagonistic to vegetative growth (Ehlig and Bernstein, 1958; Awang et al., 1993; Pérez de

Camacaro et al., 2002). Conditions that favor vegetative growth invariably reduce flowering and fruit yield (Ehlig and Bernstein, 1958; Voth et al., 1967). Awang et al. (1995b) conducted a comparative study to determine growth and yield of large, mid-sized, and small strawberry plants of the same cultivar, and found that, under control conditions as well as under salt stress, plants with more foliage produced lower fruit yields than smaller plants with fewer leaves. These investigators speculated that, during the early reproductive stage of the larger plants, vegetative structures represented such exceptionally strong sinks that competition for assimilates would be high, thereby reducing the intensity of floral initiation and differentiation, and ultimately, berry yield. For the smaller plants, competition for assimilate by the vegetative organs appeared to be relatively weak, thus allowing inflorescence and fruit initiation to proceed unimpeded. Results of our study with strawberry cultivars 'Camarosa' and 'Ventana' support this conclusion. 'Camarosa' produced luxurious foliage, and yet, fruit yield was low compared to that produced by the noticeably smaller 'Ventana' plants (Figures 1, 2 and 3).

Among the most common effects of soil salinity on plants is growth inhibition which may have a number of causes, but is often correlated with high internal Na^+ concentration that can result in a wide range of metabolic and osmotic problems for plants. Metabolic disorders occur due to the ability of Na^+ to compete with K^+ for entry into plant cells and for binding sites essential to cellular function. Plant survival under saline conditions requires a highly selective K^+ uptake system in order to provide sufficient K^+ resources for the maintenance of adequate K^+ nutrition and for lowering the osmotic potential in root cells, a pre-requisite for controlling solute transport and water balance (Shabala and Cuin, 2007; Zhang et al., 2010). Sodium toxicity, the primary cause of ion-specific damage to many glycophytes, is often associated with Ca^{2+} deficiency in salt-stressed plants. Calcium plays an essential role in processes that preserve the structural and functional integrity of plant membranes, stabilize cell wall structures, regulate ion transport and selectivity of Na^+ and K^+, control ion-exchange behavior and cell wall enzyme activities (Grattan and Grieve, 1999). Calcium, however, is readily displaced by Na^+ from its binding sites on proteins, cell membranes and cell walls. The negative effects of Na^+ usually are alleviated by addition of Ca^{2+} to the external solution (Tester and Davenport, 2003). Higher plants have evolved various adaptive mechanisms in order to avoid the adverse effects of Na^+, including regulation of Na^+ entry into root epidermal and cortical cells and subsequent control of Na^+ loading to the xylem and transport to the shoot, particularly to the leaf blades (Shannon 1997; Zhang et al., 2010). The exclusion mechanism functions efficiently in most glycophytes at low and moderate salinities, but fails at higher salinities whereupon Na^+ is readily transported to the aerial parts of the plant. In our study, Na^+ was excluded from the aboveground tissues in both strawberry cultivars (Tables 2 and 3). The maximum salinity level, however, was low (2.2 dS m^{-1})

as was the maximum external Na^+ concentration (6.8 $mmol_cL^{-1}$). Preliminary results from a related study where irrigation waters contained chloride salts of Ca^{2+}, Mg^{2+}, N**a**$^+$ and K^+, however, indicated that the Na^+ exclusion mechanism for 'Ventana' was still functional at 3.8 dS m^{-1} (external Na^+ = 9 $mmol_cL^{-1}$) and in 'Camarosa' at 5.8 dS m^{-1} ($Na^+ = 13.4$ $mmol_cL^{-1}$) (D. L. Suarez, unpublished). Other investigators have also demonstrated that Na^+ is effectively excluded from leaf tissue, and have concluded that Na^+ plays only a minor role in growth and yield reduction of salt-stressed strawberry (Ehlig and Bernstein, 1958; Larson, 1994; Martinez Barroso and Alvarez, 1997; Saied et al., 2005.)

Chloride, the most prevalent anion in saline soils, is a plant-essential micronutrient that controls enzyme activities in the cytoplasm, functions as a co-factor in photosynthesis, acts as a counter anion to stabilize membrane potential, and contributes to turgor and pH regulation (Marschner, 1995; Xu et al., 2000; White and Broadley, 2001). Many glycophytes are able to control Na^+ transport better than Cl^-, and it is Cl^-, rather than Na^+, that accumulates to toxic levels in shoot tissues and is most harmful to the plant (Zhang et al., 2010). For these plants, Cl^- uptake appears to be the key to their salt sensitivity, and yet the general research focus continues to be on the role of Na^+ in salt tolerance, while mechanisms of Cl^- transport are less well understood than those of cation transport (Teakle and Tyerman, 2010). Regulation of Cl^- uptake in the strawberry cultivars we studied was weak, although more Cl^- tended to be retained in the root tissues than was translocated to the aboveground organs where it was partitioned most strongly to the leaves, then to the petioles and fruit (Tables 2 and 3).

Analysis of variance indicated that fruit yield of both 'Camarosa' and 'Ventana' was not significantly affected by substrate-Na, whereas the concentration of Cl^- in the irrigation waters had a strong, negative influence on fruit yield ($P < 0.0002$). The correlation between leaf-Na and fruit yield was not significant for either cultivar. Leaf-Cl content was strongly correlated with the reduction in 'Camarosa' yield ($P < 0.003$), but not with 'Ventana' yield ($P < 0.065$). The lack of a response by 'Ventana' is not surprising since there was yield loss only at the highest EC treatment.

Numerous procedures have been used to evaluate the effect of saline irrigation waters on growth and yield of strawberry. Studies have been conducted in soilless cultures: hydroponics (Yildiz et al., 2008), pumice (Yilmaz and Kina, 2008; Yilmaz et al., 2009), quartz sand (Saied et al., 2005; Keutgen and Pawelzik, 2009), perlite (Turhan and Eris, 2005; 2007; 2009); peat and perlite (Pirlak and Eşitken, 2004); rockwool (Awang et al., 1995b), and coir (D'Anna et al., 2003). Sodium chloride was the sole salinizing salt used in all these studies, a practice which may depress nutrient-ion activities in the substrate (Suarez and Grieve, 1988) that may cause nutritional disorders within the plant that reduce growth and yield (Grattan and Grieve, 1999).

The inherent nutritional problems that may arise from the use of soilless substrates irrigated with NaCl-dominated waters for strawberry salt tolerance evaluations is acknowledged by many investigators who use this sole-salt system. As a consequence, much of their research has been directed towards improving adverse mineral ion interactions in the external solution that reduce the availability of essential plant nutrients or by correcting the cation ion imbalances that occur in foliar or floral organs. Foliar application of NO_3-salts of Ca^{2+}, Mg^{2+} and K^+ (Kaya et al., 2001, 2002a,, 2003; Khayyat et al., 2009; Yildirim et al., 2009) and KH_2PO_4 (Kaya et al., 2001) were effective in partially alleviating the effects of NaCl stress on strawberry growth. The possible contribution of anion (either NO_3^- or PO_4^{3-}) towards ameliorating the effects of NaCl salinity was not addressed in any of the reports cited.

External cation ratios used in the present experiment were balanced in order provide optimal plant nutrition and to reduce ion interactions that might otherwise lead to nutrient deficiencies causing growth reductions and yield losses (Table 1). Any potentially adverse effects of Na^+ on the Ca^{2+} and/or K^+ status of the plants, for example, may have been mitigated by relatively high Ca^{2+}/Na^+ and K^+/Na^+ ratios present in the substrate. In this regard, both strawberry cultivars 'Camarosa' and 'Ventana' exhibited a mechanism whereby Na^+ was retained in root tissues and Na^+ transport to above-ground organs was limited.

In summary, this study demonstrated there is a delicate physiological balance between vegetative and reproductive growth of strawberry cultivars 'Camarosa' and 'Ventana'. Although similar-sized runner plants of the cultivars were transplanted, the vigorous shoot and root growth of 'Camarosa' did not translate into high berry yield. Fruit yield of the smaller 'Ventana' plants was significantly higher than 'Camarosa' at all salinity levels. Over the range of salinity levels studied, both cultivars exhibited an efficient exclusion mechanism which severely limited Na^+ translocation to the shoot. Chloride uptake and partitioning to the aboveground tissues, however, was not as closely regulated, and reduction in fruit yield was highly correlated with increases in leaf-Cl.

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