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Fruit yield and survival of five commercial strawberry cultivars under field cultivation and salinity stress

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ABSTRACT

Strawberry is one of the most salt-sensitive horticultural crops, and important to the economies of both United States and California, the highest producer country and state, respectively. Thus, the increasing salinity (electrical conductivity) of irrigation water (EC_{iw}) in semiarid areas of the world is a growing concern to strawberry growers. We evaluated five commercial cultivars under the EC_{iw} of 0.7 (control), 1.0, 1.5, and 2.5 dS m^{-1}, under field conditions for 240 days. Increased EC_{iw} increased Cl^- in all tissues, while Na^+ only increased in roots and petioles. Thus, toxic effects of salinity in leaves were attributed to Cl^-, not Na^+. All cultivars maintained sufficient levels of both macro and micronutrients in shoots without competition between Na^+ and K^+, or Ca^{2+} or between Cl^- and NO_3^-. All cultivars had decreased fruit production, even when EC_{iw} increased to 1.0 dS m^{-1}. Although 'Albion' and 'San Andreas' had the least fruit yield at control salinity, 'Albion' was the cultivar with the least mean relative reduction in fruit yield, marketable fruit size, shoot + root biomass, and survival at EC_{iw} = 2.5 dS m^{-1}, and thus the most salt tolerant. Regarding absolute yield, 'Monterey' was the highest fruit producer under salinity. All cultivars maintained fruit total soluble sugars (Brix%) across salinity levels with 'Albion', 'Monterey', and 'Benicia' having the highest values (11–13% Brix) regardless of salinity. 'Albion' and 'San Andreas' were the best at maintaining commercial fruit size under salinity. 'Albion', 'Benicia', and 'Monterey' had higher fruit yields at EC_{iw} = 2.5 dS m^{-1} than 'Ventana' and 'San Andreas' and can enable farmers to produce strawberries with irrigation water EC_{iw} up to 1.5 dS m^{-1}, although with some fruit yield loss. Results indicate that these newer commercial cultivars are more salt-tolerant than cultivars previously tested, and with enough variability in salt tolerance to improve selection for irrigation water salinity with EC_{iw} > 1.0 dS m^{-1}.

1. Introduction

The United States is the largest producer of strawberry in the world with an estimated yield of 1,312,960 metric tons in 2011, which is approximately 30% of all the strawberry produced worldwide (http://faostat.fao.org/site/339/default.aspx). Within the US, California is the major producer, and accounted for over 85% of the fresh and frozen fruits commercialized in 2011 (http://www.californiastrawberries.com/about_strawberries). The crop depends heavily on irrigation in California and other major production regions. The increasing salinization of irrigation waters used by strawberry farmers in southern and central California, and elsewhere, means that growers must either find new water sources or accept significant yield loss and profitability. Alternatively, researchers may identify varieties that can tolerate high salinity levels in irrigation water.

Strawberry is highly sensitive to salinity with a low threshold of 1.0 dS m^{-1} for the electrical conductivity of the soil saturation extract (ECe), after which yield decreases 33% with each increasing ECe unit (Grieve et al., 2012). Salinity tolerance work, previously done under greenhouse conditions, with the *Fragaria ananassa* cultivars Douglas and Toro showed that sodium and sulfate did not cause ion toxicity in strawberries, whereas chloride-based waters (NaCl and KCl) led to leaf scorching after 26 days, or six irrigations, with waters containing 18 mmol L^{-1} (an approximate salinity of EC_{iw} = 1.8 dS m^{-1}) of either salt (Martinez-Barroso and Alvarez, 1997). These authors also determined that leaf Cl^- concentrations of less than 1% and an electrical conductivity of the irrigation water (EC_{iw}) of less than 2.0 dS m^{-1} did not produce toxicity symptoms on the cultivars studied, but that salinities over 5 dS m^{-1}, even with low leaf Cl^- concentrations could cause leaf damage.

Strawberry plants genetically engineered to overproduce osmotin were reported to tolerate salinity close to EC of 20 dS m^{-1} (Husaini and Abdin, 2008). However, no high-osmotin strawberry plants have been released for commercial production so far. Based on the knowledge that

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salinity effects will vary within the same species and among different cultivars, screening of commercial and wild type strawberry cultivars can be a feasible approach to find salinity-tolerant strawberry cultivars and to study the mechanism by which different cultivars can cope with salinity stress. Traditional breeding of strawberries has resulted in varieties with improved fruit yield, size (e.g, 'San Andreas'), appearance (e.g., 'Benicia' and 'Ventana') and sweet taste for fresh fruit in the US and Asian markets (e.g., cv. 'Monterey'), resistance to fungal and bacterial diseases, resilience to transportation, and increased post-harvest shelf life (Capocasa et al., 2008). In 2012, the six most cultivated cultivars bred by the University of California, in decreasing order, were 'Albion', 'San Andreas', Portola, 'Ventana', 'Monterey', and 'Benicia'. Our study involved five commercial strawberry cultivars used in California and elsewhere (the day-neutral cultivars 'Albion', 'Monterey', and 'San Andreas', and short-day cv. 'Benicia', and 'Ventana') and aimed to evaluate the cultivars for salt tolerance based on fruit yield, plant biomass, and plant survival.

2. Materials and methods

2.1. Experiment design

Bare-rooted crowns of five cultivars of strawberry released by the University of California breeding program were freshly dug out and donated by Sierra-Cascade Nursery (Susanville, Calif.) and included the day-neutral cultivars 'Albion' (released 2004), 'Monterey' (released 2008) and 'San Andreas' (released 2008), and short-day (June bearing) cultivars 'Benicia' (released 2010) and 'Ventana' (released 2001). Crown diameters varied among cultivars, but were fairly homogeneous within each cultivar. The plants were at 5 °C for two weeks until planted in a non-fumigated sandy loam soil (Suarez and Grieve, 2009) as a split plot design with salinity as the main plot or block variable, and cultivar as the subplot variable. The experimental site was located at the USDA-ARS, U.S. Salinity Laboratory, Riverside, California (Lat. 33E58′24″N, Long. 117E19′12″W). The area was divided into 12 raised beds (main plot or block) to accommodate four salinity levels (SL) assigned to each of the five cultivars (CV), with three replicates (R). There were 5 subplots (containing five CV each) per bed. Each main plot, or bed, had 12 plants of each cultivar amounting to 60 plants (each bed received a salinity treatment) with a total of 720 plants for the whole experiment (12 beds × 5 CV × 4 SL × 3 R). Each subplot occupied 2.294 m^2 comprising 12 plants of one cultivar (in two rows of six plants), including the space between beds. The spacing between plants in adjacent beds was approximately 1.3 m (including space between beds) and the length of each bed was 9 m (4.2 × 30 feet), evenly divided into 5 subplots longitudinally. There was a trough of 60 cm between salinity treatments within a raised bed to prevent mixing of salinity treatment during drip irrigation. The five cultivars were randomly assigned as subplots into each treatment (plot), according to a random map generated by SAS PLAN procedure. The experimental area was sprinkled with Riverside municipal water (EC_w = 0.6 dS/m) for a week to lixiviate excess salts from soil. Bed soil was homogenized with a rototiller and mounded to prepare new beds (35 cm in height). Then, two soil samples (15 cm deep) were taken per bed and analyzed for salinity at the US Salinity Lab before assigning the treatments, and before adding fertilizer. The planting density was 52,310 plants/ha. Two soil samples per bed were also taken at the termination of the experiment.

The planting was on Oct. 31 and Nov. 1, 2012 with two rows of plants per bed and 6 plants per row for each subplot (12 plants). Two drip lines were installed along the two rows of plants, respectively on each bed. Underneath each drip line, a 12–15 cm deep and 10 cm wide trench was dug and slow-release fertilizer (10-10-10 in N-K-P with micronutrients) was applied at 9.4 g per plant, and subsequently the trench was backfilled with soil.

Table 1
Electrical conductivity of irrigation water (EC_{iw}), osmotic potential, composition of irrigation waters (in dS m^{-1}), and initial soil EC_e. Concentrations of calcium (Ca^{2+}), Na^+, and Cl^- of irrigation waters used to apply salt treatments are also presented. Ratio of Na^+:Ca^{2+} was = 1:1 in mmol$_c$ L^{-1}.

EC_{iw} (dS m^{-1})	Osmotic potential (MPa)	Ca^{2+}	Na^+ (mmol$_c$ L^{-1})	Cl^-	Initial soil EC_e (dS m^{-1})
0.7	−0.029	2.6	2.6	1.2	0.32
1.0	−0.038	4.5	4.5	5.0	0.45
1.5	−0.057	6.8	6.8	9.6	0.68
2.5	−0.093	11.4	11.4	18.8	1.14

Note: The Ca^{2+}, Na^+, and Cl^- concentrations in Riverside municipal water (tap) water were taken into consideration when preparing the solutions to achieve the target EC values. EC_e = Electrical conductivity measured in the extract of the saturated soil paste.

2.2. Salt treatment

Salt treatment composition to achieve target electrical conductivity of irrigation water (EC_{iw}) was constructed using ExtractChem model (Suarez and Taber, 2012) to have four salinity levels, measured as electrical conductivity (EC), and with a ratio of Na^+:Ca^{2+} = 1:1 in mmol$_c$ L^{-1} balanced by Cl^- (Table 1), and applied through the irrigation waters. The water used to prepare saline treatments was Riverside municipal water of EC_w = 0.6 dS m^{-1} and pH = 7.5. This water was analyzed at the US Salinity Lab and contained in average (in mmol$_c$ L^{-1}): 0.45 NO_3-, traces of PO_4^{3-}, 0.1 K^+, 3.2 Ca^{2+}, 0.8 Mg^{2+}, 1.2 SO_4^{2-}, 1.8 Na^+, 0.9 Cl^-, 3.5 HCO_3^-. NaCl and $CaCl_2$ were used as the salinizing salts. Irrigation waters were stored in 1400-L, covered plastic tanks. Plants were irrigated once daily at mid-day during the winter and twice daily, at mid-day and mid-afternoon during the growth period after winter. This system provided roughly irrigation water amounts of 0.24, then 0.48 cm daily. Salt treatment was initiated on Nov. 29, 2012, approximately one month after planting.

2.3. Sampling of fruits, plants, and soil

Fruits that developed more than 75% red color were harvested at each sampling time, immediately brought to the laboratory and weighed for fresh weight. Fruits weighing 10 g or less are of no commercial value and were not considered for fruit production, but were recorded to quantify marketable fruit size percentage of cultivars under salinity.

At the end of the experiment, live plants were collected and separated into leaves, petioles, and roots. These were dried separately and ground to approximately 1 mm particle size and used for the determination of macro and micronutrients, sodium, and chloride, with methodology described elsewhere (Dias et al., 2016). Runners were not analyzed, only the plant parts bearing fruits.

Two soil samples were collected from each of the 12 plots before and after the experiment. After the experiment, samples were taken in the bed to a depth of 15 cm underneath where plants and drippers were located. Samples were dried in the laboratory and saturation pastes were prepared, and solutions extracted and analyzed to determine the electrical composition of the saturated soil paste (EC_e) and major inorganic ions.

2.4. Fruit sugars

Fruit sugar content was measured using a portable Refractometer, MA871 (Milwankee, Romania) as total soluble sugars (Brix %). Freshly harvested fruits were cut into halves, placed in a garlic press lined with two layers of cheese cloth, and squeezed into a test tube. Two samples of 100 μL were measured from six fruits per cultivar and averaged for each of the three replicates of the five sub-plots, with n = 3.

2.5. Data analysis

Significant differences ($P \leq 0.05$) were determined for all plants, such as survival, shoot and root dry weight loss, tissue macro and micronutrients, fruit number per plant, fruit yield, Brix%, and seasonal fruit yield across salinity treatments using the split-plot ANOVA model in SAS GLM procedure (version 9.3, SAS Institute, Cary, N.C.). The Bonferroni multi-comparison method in the GLM procedure was also used to analyze the significant differences ($P \leq 0.05$) among salinities, or among cultivars or tissue types. The plant and fruit growth parameters in response to salinity for any given cultivar were further analyzed using a salt-tolerance model described by van Genuchten (1987, unpublished report) equation:

$$Y/Y_o = 1/\ [1 + (EC/EC_{50})^{\gamma}] \qquad (1)$$

where, EC is the salinity of the irrigation water referred in the text as EC_{iw}, Y is biomass yield, Y_o is the biomass yield at the control EC_{iw}, and EC_{50} is the value of EC_{iw} at which there is a 50% yield reduction, and γ is an empirical constant generally set to 3.0. The EC_{50} values were found by fitting the equation with the observed biomass data at the different salinities using TableCurve 2D version 5.0 (SYSTAT, 2002), and further analyzed using Bonferroni multi-comparison method in the SAS- GLM procedure to test the salt tolerance difference among cultivars. Initial soil saturation extract salinity values are presented in Table 1. As expected, these values are approximately half the value of the irrigation waters, indicating that the soil salinities are equilibrated with the irrigation water.

3. Results and discussion

3.1. Soil salinity

After the experiment, the mean soil salinity levels (EC_e) in the treatment plots were 3.35 (± 0.44) 3.75 (± 0.47), 4.9 (± 0.76) and 6.45 (± 0.78) for the plots irrigated with water of EC 0.7, 1.0, 1.5 and 2.5 dS m^{-1}, respectively. The measured soil EC reflects the salt added by the irrigation water, the dissolved fertilizer, and the concentration of salts resulting from plant water uptake. Based on our addition of 10 g of fertilizer per plant and irrigation of 83.4 L water per plant over the course of the experiment, we calculated that the slow release fertilizer added an additional 0.1 dS m^{-1} of salinity to that of the irrigation water. We used these values, the EC of the irrigation water (EC_{iw}), the measured EC_e, and the following equation to obtain leaching fractions (LF).

$LF = EC_{iw}/\ (5(EC_e) - EC_{iw})$ (Rhoades, 1974)

The calculated leaching fractions for EC_{iw} of 0.7, 1.0, 1.5 and 2.5 dS m^{-1} irrigation water treatments were 0.044, 0.065, 0.072, and 0.09, respectively. Since all plants received the same volumes of water, the increased leaching fraction with increasing salinity is attributed to decreased water consumption by the plants with increasing salinity. These leaching fractions reflect efficient irrigation practices, but are likely less than usual commercial practice.

3.2. Sodium, chloride, and nutrients

Salinity did not affect Na^+ concentration in leaves of any cultivar (Table 2). However, salinity increased Na^+ concentration in both roots (94%) and petioles (183%). As salinity increased from control ($EC_{iw} = 0.7$ dS m^{-1}) to the highest salinity level ($EC_{iw} = 2.5$ dS m^{-1}), Na^+ concentration increased, depending on the cultivar, from 113 to 292% in petioles and from 72 to 142% in roots. Salinity also increased Cl^- concentrations significantly in all tissues analyzed, on average among cultivars, 318% in petioles, 170% in roots, and in 122% in leaves (Table 2), comparing highest salinity level with control. This

Table 2
Macronutrients (N and K), sodium (Na) and chloride (Cl) in leaves, petioles, and roots of five strawberry cultivars irrigated with waters of four electrical conductivities (EC_{iw}). Data are means, n = 3 (subplot, 4 plants per subplot).

EC_{iw} (dS m^{-1})	N	K (g kg^{-1})	Na	Cl
'Albion'	Leaves			
0.7	α 19.2 a A	β 26.5 b A	β 1.1 a A	α 6.0 b A
1.0	α 18.1 a A	β 27.3 ab A	γ 1.0 a A	α 7.2 b A
1.5	α 20.3 a A	α 28.2 ab A	γ 1.1 a A	α 10.4 a A
2.5	α 19.6 a AB	α 34.3 a A	β 1.4 a A	α 11.1 a A
'Benicia'				
0.7	α 20.5 a A	α 30.0 ab A	β 1.2 a A	α 4.6 c A
1.0	α 19.9 a A	α 33.1 ab A	γ 1.1 a A	α 6.7 b A
1.5	α 18.7 a A	β 29.0 b A	γ 1.0 a A	α 8.9 ab A
2.5	α 19.1 a A	α 35.9 a A	γ 1.2 a A	α 10.3 a A
'Monterey'				
0.7	α 20.0 ab A	α 24.4 a A	β 1.1 a A	α 6.7 d A
1.0	α 18.8 b A	β 25.2 a A	γ 1.2 a A	α 9.5 c A
1.5	α 19.6 ab A	β 26.7 a A	β 1.4 a A	α 11.9 b A
2.5	α 21.4 a A	α 30.4 a A	β 1.6 a A	αβ 11.8 a A
'San Andreas'				
0.7	α 18.3 a A	α 30.0 a A	γ 1.0 a A	α 6.8 b A
1.0	α 18.2 a A	α 30.4 a A	γ 1.0 a A	α 7.7 b A
1.5	α 19.4 a A	β 29.7 a A	β 1.0 a A	α 11.8 a A
2.5	α 21.0 a A	β 34.3 a A	β 1.5 a A	αβ 14.4 a A
'Ventana'				
0.69	α 17.9 a A	α 28.4 b A	β 1.1 a A	α 5.4 b A
1.01	α 18.9 a A	β 31.2 ab A	γ 1.1 a A	α 7.0 ab A
1.5	α 19.6 a A	α 31.7 ab A	γ 1.0 a A	α 9.0 ab A
2.5	α 19.9 a A	β 36.7 a A	β 1.2 a A	α 12.1 a A
'Albion'	Petioles			
0.7	γ 7.3 a A	α 41.8 a A	β 1.5 b A	β 3.5 b A
1.0	γ 6.5 a A	α 42.0 a A	β 1.8 ab A	β 3.8 b A
1.5	γ 7.1 a A	α 43.5 a A	β 2.1 ab A	α 10.8 a A
2.5	β 7.9 a A	α 50.1 a AB	α 3.2 a A	α 11.0 a A
'Benicia'				
0.7	γ 6.6 a A	α 41.4 b A	β 1.3 b A	α 3.2 c A
1.0	β 7.8 a A	α 44.3 ab A	β 2.1 a A	β 4.6 bc A
1.5	γ 7.2 a A	α 49.5 ab A	β 2.5 a A	α 9.3 ab A
2.5	γ 8.1 a A	α 54.4 a AB	β 3.2 a A	α 15.9 a A
'Monterey'				
0.69	β 7.2 a A	α 38.7 a A	β 1.3 c A	α 4.1 c A
1.01	β 7.7 a A	α 39.8 a A	β 2.0 bc A	β 5.1 c A
1.5	γ 6.7 a A	α 44.4 a A	αβ 3.0 ab A	α 12.2 b A
2.5	β 8.1 a A	α 45.2 a A	α 5.1 a A	α 19.6 a A
'San Andreas'				
0.7	β 6.7 a A	α 44.5 b A	β 1.4 b A	αβ 5.3 b A
1.0	γ 6.9 a A	α 45.1 ab A	β 2.2 ab A	α 6.3 b A
1.5	β 7.8 a A	α 48.4 ab A	α 2.9 ab A	α 13.7 a A
2.5	β 7.5 a A	α 53.3 a A	α 4.8 a A	αβ 21.8 a A
'Ventana'				
0.7	γ 6.8 ab A	α 43.5 a A	β 1.4 a A	α 4.2 b A
1.0	γ 6.4 b A	α 46.8 a A	β 2.0 a A	α 6.7 b A
1.5	γ 7.4 ab A	α 48.4 a A	β 1.9 a A	α 9.4 a A
2.5	γ 8.3 a A	α 58.8 a A	αβ 3.1 a A	α 17.2 a A
'Albion'	Roots			
0.7	β 9.3 a A	β 10.0 a A	α 3.6 b A	β 3.3 b A
1	β 9.5 a A	γ 7.2 a AB	α 4.4 ab A	β 3.8 b A
1.5	β 8.8 a B	β 7.3 a A	α 4.4 ab AB	β 5.2 ab A
2.5	β 10.4 a AB	β 10.5 a AB	α 6.2 a A	α 8.1 a B
'Benicia'				
0.7	β 10.2 a A	β 14.7 a A	α 3.0 c A	α 4.3 c A
1	β 9.5 a A	β 9.5 a A	α 4.5 ab A	β 5.0 bc A
1.5	β 10.5 a A	γ 12.2 a A	α 4.1 b B	α 7.3 b A
2.5	β 10.6 a AB	β 19.9 a A	α 5.5 a A	α 12.8 a AB
'Monterey'				
0.7	β 8.0 a A	γ 9.8 a A	α 3.9 b A	α 4.5 b A
1.0	β 8.1 a A	γ 4.6 b B	α 5.2 ab A	β 5.1 b A
1.5	β 8.4 aAB	γ 6.8 ab A	α 6.0 a A	α 9.4 Ab A
2.5	β 8.1a AB	β 6.1 ab B	α 6.4 a A	β 10.9 a AB
'San Andreas'				
0.7	β 8.5 a A	β 8.0 a A	α 3.0 c A	β 3.6 c A
1.0	β 9.1 a A	β 6.3 a AB	α 3.6 bc A	β 4.7 bc A
1.5	β 8.9 a B	γ 7.6 a A	α 4.6 ab AB	β 7.3 ab A
2.5	β 9.0 a AB	γ 7.6 a B	α 6.0 a A	β 10.4 a AB

(*continued on next page*)

Table 2 (*continued*)

EC_{iw} (dS m^{-1})	N	K	Na	Cl
	(g kg^{-1})			
‘Ventana’				
0.7	β 9.5 a A	β 13.4 ab A	α 3.1 b A	α 5.2 b A
1.0	β 10.0 a A	γ 9.8 b A	α 4.0 ab A	α 5.0 b A
1.5	β 10.4 a A	β 11.9 ab A	α 4.4 ab AB	α 9.0 ab A
2.5	β 11.8 a A	γ 19.6 a A	α 6.0 a A	α 14.3 a A

Lower case letters show significant ($P \leq 0.05$) difference among salinity treatments, within a cultivar and tissue type. Capital letters indicate significant ($P \leq 0.05$) difference among cultivars within the same tissue type at the same salinity level. Greek letters indicate significant ($P \leq 0.05$) difference among tissues within the same salinity and the same cultivar.

Fig. 1. Progression of chloride damage in strawberry leaves. Chloride, extruded with water by guttation, progressively leads to necrosis of mature leaves, moving inwards. Lower picture shows mature leaves of *Fragaria ananassa* cv. ‘Monterey’ under irrigation treatment of $EC_{iw} = 1.5$ dS m^{-1} (S3) on 4-11-2013. Young leaves in the center did not yet show symptoms.

indicates Cl^-, not Na^+, is the toxic ion resulting in tissue necrosis observed in leaves (Fig. 1).

There was no overall effect of salinity, within cultivar or tissue type, for the concentration of N, P, and S but, in some cultivars, K increased between control and $EC_{iw} = 2.5$ dS cm^{-1} in leaves (‘Albion’ and ‘Ventana’) and petioles (‘San Andreas’), while in roots it remained unchanged, decreased significantly for ‘Monterey’ or increased (although not significantly) for ‘Ventana’ (Table 2). Our results show that K^+ increased, although not always significantly, or remained constant in petioles and leaves of most strawberry cultivars, while Na^+ remained constant in leaves, but increased in petioles and roots indicating that there was no evidence of competition between Na^+ and K^+ in strawberry leaves or petioles. However, although K^+ concentration remained constant in petioles and leaves of ‘Monterey’, K^+ decreased by 38% in ‘Monterey’ roots. Similar levels of root potassium were also reported elsewhere (Keutgen and Pawelzik, 2009) when strawberry was cultivated under salinity. The levels of Ca^{2+} in all tissues tended to increase (although not significantly) while Mg^+ remained unaltered. Considering the fact that Ca^{2+} increased with salinity of irrigation water (Table 1), significant increases in Ca^{2+} were only seen in the petioles of ‘Albion’, ‘Monterey’, and petioles and roots of ‘San Andreas’ (Table 3). Our results partially agree with those of others who cited an increase in leaf Ca^{2+} with increased salinity (Sun et al., 2015). Many plant studies report an increase in tissue Na^+ and Cl^- with salinity, but studies with *Helianthus tuberosus* indicated that its leaves have mechanisms to avoid Na^+ accumulation under salinity (Dias et al., 2016) as did all the

Table 3
Macronutrients in leaves, petioles, and roots of five strawberry cultivars irrigated with waters of four electrical conductivities (EC_{iw}). Data are means, n = 3 (subplot, 4 plants per subplot).

EC_{iw} (dS m^{-1})	Ca	Mg	P	S
		(g kg^{-1})		
‘Albion’	Leaves			
0.7	α 21.5 a AB	α 4.9 a A	α 2.4 a A	α 1.5 a A
1.0	α 20.9 a A	α 4.5 ab A	α 2.2 a AB	α 1.4 a AB
1.5	α 23.3 a A	α 4.3 ab AB	α 2.4 a A	α 1.4 a A
2.5	α 22.0 a AB	α 3.6 b AB	α 2.1 a A	α 1.4 a A
‘Benicia’				
0.7	α 13.9 a C	α 4.1 a A	α 2.3 a A	α 1.6 a A
1.0	α 14.7 a B	α 3.5 a A	α 2.3 a AB	α 1.5 a A
1.5	α 16.8 a B	α 4.0 a AB	α 2.0 a A	α 1.6 a A
2.5	α 16.2 a C	α 3.0 a B	α 2.2 a A	α 1.4 a A
‘Monterey’				
0.7	α 25.3 a A	α 5.1 a A	α 1.9 a A	α 1.6 a A
1.0	α 23.7 a A	α 4.8 a A	α 1.8 a B	α 1.4 a A
1.5	α 25.6 a A	α 4.9 a A	α 1.8 a A	α 1.6 a A
2.5	α 24.6 a A	α 4.3 a A	α 1.7 a A	α 1.5 a A
‘San Andreas’				
0.7	α 18.3 a ABC	α 4.6 a A	α 2.6 a A	β 1.4 a A
1.0	α 18.7 a AB	α 4.1 a A	α 2.5 ab A	α 1.4 a A
1.5	α 20.2 a AB	α 4.6 a AB	α 2.1 bc A	α 1.4 a A
2.5	α 20.3 a B	α 4.0 a A	α 1.9 c A	α 1.5 a A
‘Ventana’				
0.7	α 16.3 a BC	α 4.0 a A	α 2.1 a AB	α 1.5 a A
1.0	α 14.3 a B	α 3.6 a A	α 1.9 a B	α 1.5 a A
1.5	α 16.9 a B	α 3.5 a B	α 1.8 a A	α 1.5 a A
2.5	α 19.2 a BC	α 3.5 a AB	α 2.2 a A	α 1.5 a A
‘Albion’	Petioles			
0.7	β 12.3 b A	β 2.9 a AB	α 2.5 a AB	β 0.63 a A
1.0	β 13.3 ab A	β 3.1 a A	α 2.5 a A	β 0.63 a A
1.5	β 15.5 ab AB	β 2.9 a A	α 2.5 a A	β 0.67 a A
2.5	β 15.8 a A	αβ 3.0 a AB	α 2.2 a A	β 0.69 a A
‘Benicia’				
0.7	β 8.6 a C	β 2.3 a AB	αβ 1.9 a AB	β 0.65 a A
1.0	β 9.8 a BC	α 2.4 a A	α 2.3 a AB	β 0.65 a A
1.5	β 9.7 a B	β 2.8 a A	α 2.1 a ABC	β 0.76 a A
2.5	β 10.5 a B	α 2.2 a B	α 2.1 a A	β 0.76 a A
‘Monterey’				
0.7	β 12.2 c A	β 3.1 a AB	α 1.8 a B	β 0.61 a A
1.0	β 12.4 bc AB	β 3.0 a A	α 2.1 a B	β 0.62 a A
1.5	β 14.3 ab A	α 3.4 a A	α 1.9 a BC	β 0.66 a A
2.5	β 16.4 a A	β 3.4 a A	α 1.6 a A	γ 0.70 a A
‘San Andreas’				
0.7	β 11.4 b AB	αβ 3.3 a A	α 2.6 a A	β 0.64 a A
1.0	β 12.4 ab AB	αβ 3.3 a A	α 2.7 a A	β 0.68 a A
1.5	β 13.6 ab A	β 3.6 a A	α 2.4 a AB	β 0.73 a A
2.5	β 15.3 a A	α 3.5 a A	α 2.0 a A	β 0.71 a A
‘Ventana’				
0.7	β 9.3 a BC	β 2.1 a B	α 1.9 a AB	β 0.70 a A
1.0	β 9.5 a C	β 2.3 a A	α 1.6 a B	β 0.67 a A
1.5	β 10.1 a B	α 2.6 a A	αβ 1.6 a C	β 0.72 a A
2.5	β 12.4 a AB	α 2.9 a AB	α 1.8 a A	β 0.77 a A
‘Albion’	Roots			
0.7	β 12.6 a A	β 2.5 a A	β 1.7 a A	α 1.5 a AB
1.0	β 13.0 a A	γ 2.2 a A	β 1.4 a A	α 1.5 a A
1.5	β 11.2 a AB	γ 2.3 a A	β 1.3 a A	α 1.4 a A
2.5	β 14.7 a ABC	β 2.0 a A	α 1.5 a A	α 1.3 a A
‘Benicia’				
0.7	β 10.0 a A	β 2.5 a A	β 1.4 a A	α 1.7 a A
1.0	β 10.7 a A	α 2.2 a A	β 1.2 a A	α 1.4 b A
1.5	β 10.1 a AB	β 2.4 a A	β 1.1 a A	α 1.4 b A
2.5	αβ 12.6 a BC	α 2.6 a A	α 1.4 a AB	α 1.3 b A
‘Monterey’				
0.7	β 12.3 a A	β 2.6 a A	α 1.4 a A	α 1.3 a B
1.0	β 12.9 a A	γ 2.1 a A	β 1.1 ab A	α 1.2 a B
1.5	β 13.8 a AB	β 2.4 a A	β 0.9 ab A	α 1.2 a A
2.5	β 17.5 a AB	β 2.0 a A	β 0.7 b B	β 1.1 a A
‘San Andreas’				
0.7	β 13.0 b A	β 2.7 a A	β 1.3 a A	β 1.7 a A
1.0	β 12.8 b A	β 2.5 a A	β 1.2 a A	α 1.5 ab A
1.5	β 14.7 ab A	β 2.5 a A	β 1.0 a A	α 1.4 ab A
2.5	αβ 18.2 a A	β 2.2 a A	β 0.9 a AB	α 1.3 b A

(*continued on next page*)

Table 3 (*continued*)

EC_{iw} (dS m^{-1})	Ca	Mg	P	S
		(g kg^{-1})		
'Ventana'				
0.7	β 9.3 a A	αβ 2.5 a A	α 1.4 a A	α 1.5 a AB
1.0	β 10.0 a A	β 2.2 a A	β 1.0 a A	α 1.4 a A
1.5	β 9.3 a B	α 2.6 a A	β 0.9 a A	α 1.4 a A
2.5	β 12.3 a C	α 2.8 a A	β 1.1 a AB	α 1.4 a A

Lower case letters show significant ($P \leq 0.05$) difference among salinity treatments, within a cultivar and a tissue type. Capital letters indicate significant ($P \leq 0.05$) difference among cultivars within the same tissue type at the same salinity level. Greek letters indicate significant ($P \leq 0.05$) difference among tissues within the same salinity and the same cultivar.

strawberry cultivars tested here. It is most common to see Cl^- levels increase with salinity in all organs, and salt-tolerance of a species seems to be a matter of tissue tolerance to Cl^- toxicity.

None of our five cultivars had any significant increase in leaf Na^+ under the field conditions tested for 240 days. Our results disagree from those of others (Keutgen and Pawelzik, 2009) who reported leaf Na^+ to increase 20–30 times with salinity in the cultivars Elsanta and Korona when salinity was 4 dS m^{-1}. However, our results agree with those who reported strawberry to be a Na^+ excluder (Saied et al., 2005), others (Kaya et al., 2002) who reported only 3 to 3.5 fold increase in Na^+ in strawberry leaves of cv. Oso Grande when salinity was increased to 3.5 dS m^{-1}, and with Sun et al. (2015) who studied seven strawberry cultivars under salinities ranging from 1.1 to 4.4 dS m^{-1} and reported Na^+ in shoots to increase only 1.6 ('Albion') to 3.3 fold ('Chandler'). Although the latter did not separate petioles from leaves (Genhua Niu, personal communication), they also reported 'Albion' to be among the three cultivars most tolerant to salinity. Our results also agree with those reported for 'Ventana' and 'Camarosa' in that a 20-fold increase in Na^+ in irrigation water only increased leaf Na^+ of 'Ventana' and 'Camarosa' two and four fold, respectively (Suarez and Grieve, 2009). Our results suggest a mechanism of either exclusion or efflux of Na^+ from leaves, found in the strawberry cultivars tested here. This mechanism is found mostly in halophytes and seagrass (Rubio et al., 2011), but also in terrestrial crops that accumulate Na^+ in roots while maintaining low Na^+ in leaves such as rice, soybean, pumpkin, and sweet pepper (Raul Lopez et al., 1999; Blom-Zandstra et al., 1998). Recirculation of Na^+ in sweet pepper has been attributed to the pith cells, between xylem and phloem (Blom-Zandstra et al., 1998). This process seems to apply to strawberry as well because Na^+ increased significantly in roots (72–142%) and petioles (113–292%), although not in leaves. Our field results contrast with those of others who reported a decrease in leaf K^+ in strawberry cultivars, including 'Albion', 'Benicia', and 'San Andreas' when salinity increased from 1.1 to 4.4 dS m^{-1} in a greenhouse pot experiment (Sun et al., 2015). An efficient retention of K^+ in shoots and roots has been attributed as one of the reasons for the remarkable salt tolerance of *Chenopodium quinoa* (Adolf et al., 2013) and, according to our results, could be also a mechanism available to strawberry plants, although strawberry tissues are not as salt-tolerant as those of some glycophytic plants (e.g., sugar beets, spinach, alfalfa, and Jerusalem artichoke).

Our N concentration data for all organs of strawberry plants do not agree with the results reported by some that the accumulation of salts causes nutrient imbalance in plants, such as accumulation of Cl^- in the soil solution causing decreased absorption of NO_3^- by tomato plants, and decreased N in tissues (Pessarakli and Tucker, 1988). Our data clearly shows that despite an average Cl^- increase of 122% (leaves), 170% (roots), and 318% (petioles), none of these tissues suffered from N deficiency (Table 2). Our data agrees with recent work with alfalfa grown under salinity, or with recycled water, that established that leaf N increased with salinity (Cornacchione and Suarez, 2015; Díaz et al., 2018; Ferreira et al., 2015).

For macronutrients and salts, leaves were significantly higher in N, Ca^{2+}, Mg^+, and Cl^-, but equally high as stems in P, and as roots in S. Stems were the highest in K^+, and roots were the highest in Na^+ (Table 2 and 3). For micronutrients, leaves were the highest in Mn, while roots were the highest in Fe, Cu, and Zn, and the second highest in Mn after leaves (Annex Table 1). Roots had Fe concentrations that were 5–10 times higher than in stems and leaves. Fe and Cu play important roles in the redox chemistry and electron transfer in plant metabolism. Both metals also are found in the superoxide dismutase (SOD) antioxidant enzyme family, where functions and location of the Cu/Zn-dependent enzymes overlap with the Fe-dependent enzyme (Andresen et al., 2018). Higher levels of these micronutrients in roots of strawberry may help the plant maintain ion homeostasis in shoots, neutralize reactive oxygen species produced in cells under high levels of stress, and maintain photosynthetic efficiency, respiration, growth, and fruit production under normal and stress conditions. This is known to be the case at least for Fe (Briat et al., 2015). Proper transport and homeostasis of Cu, Fe, and Zn is also known to be critical for plant growth and development and to maintain proper levels of these nutrients in fruits and seeds that will be consumed by humans (Grotz and Guerinot, 2006).

Within each cultivar, micronutrient concentrations in plant tissue were very similar and not significantly different, but the roots of all cultivars had significantly reduced concentrations of Zn ('Benicia', −36%; 'San Andreas', −38%; 'Ventana', −38.64%; 'Albion', −40%; and 'Monterey', −48.25%) compared to the control, although Zn concentrations in leaves (ranged from 19 to 38 mg kg^{-1}) or petioles (30–58 mg kg^{-1}) remained constant across salinity and cultivars (Annex Table 1). We found no reports of salinity causing a significant decrease in root Zn in strawberries. However, there are reports that Zn supplementation in Zn-deficient soil under salinity has decreased the translocation of both Na^+ and Cl^- to young and old leaves of tomato (*Lycopersicum esculentum*) (Alspalan et al., 1999) and reduced shoot concentration of Na^+, while increasing K^+ concentration in shoots of pepper (*Capsicum annuum*) (Aktas et al., 2006). Our plants all received the same micronutrient basic fertilization, suggesting that Zn was less absorbed by roots as salinity increased (Annex Table 1), perhaps due to a competitive absorption with Na^+, whose average root concentration increased from 64 to 142%, or was translocated to leaves to maintain appropriate Zn levels for enzymatic functions. Micronutrient concentrations in strawberry leaves should have the following range (in mg kg^{-1} dry weight): Fe 60–250, Mn 50–200, Zn 20–50, Cu 6–20 (Hancock, 2008; Lieten, 1997). Thus, our plants had appropriate levels of all micronutrients (including Zn) for growth, development, and fruit yield, and were maintained at sufficient levels by plants even under the highest salinity treatment (Annex Table 1). Our results are contrary to those (Khayyat et al., 2009) who reported increased concentrations of Zn in both roots and shoots under similar salinity, but using only NaCl (3.5 dS m^{-1}). Others reported that Zn remained unchanged or increased in roots of the cultivars Camarosa and 'Ventana', respectively, irrigated with salt-balanced waters of up to 2.24 dS m^{-1} (Suarez and Grieve, 2013). However, our results (Annex Table 1) agree with the latter authors working with "Ventana" and 'Camarosa' in that all micronutrients, except Zn, remained unchanged with salinity increases in all organs of strawberry plants.

Strawberry plants developed a typical necrosis of older leaves (Fig. 1). We believe that this was a result of accumulation of Cl^- in leaf hydathodes (pores involved in guttation) causing progressive necrosis and eventually death of older leaves, while young leaves did not present this symptom. Studies of strawberry leaves, in the absence of salinity, showed that older leaves of field-grown 'Allstar' had the hydathodes of older leaves occluded by epicuticular waxes preventing guttation (Takeda et al., 1991). More recently, hindering of guttation in banana leaves induced by increased osmotic stress caused by KCl resulted in aggravated boron (B) toxicity symptoms and increased B accumulation in leaves (Shapira et al., 2013). These authors quantified B in guttation drops by ICP and verified that the droplets had high B concentration and that the application of 20 mM KCl decreased guttation in 75% compared to control. As high root pressure lead to guttation in banana (Shapira et al., 2013), we infer that guttation in strawberry is also a result of high root pressure. As salinity significantly reduced guttation in banana plants, the same may occur in strawberry plants leading to an imbalance in the transport of minerals from root to leaves.

The trend of increasing root Ca^{2+} with increasing salinity was not significant for most cultivars, and was similar to the trend in Ca^{2+} concentrations in leaves. Similarly, the fact that there was no significant increase in Ca^{2+} concentration with salinity in petioles of ‘Albion’, ‘Monterey’, and ‘San Andreas’ (Table 3), indicated that root pressure was maintained and so was the transport of minerals. Thus, we believe that guttation in strawberry leaves is a physical mechanism to maintain ion homeostasis and alleviate Cl^- toxicity as reported for sorghum (Nagai et al., 2013). However, Cl^- accumulation in hydathodes may have damaged guttation pores and resulted in visible symptoms of Cl^- leaf edge toxicity pictured in Fig. 1. Guttation in strawberry leaves (and the volume and mineral analysis of the guttation droplets) may be a valuable way to study water and mineral transport in strawberry plants under salinity stress.

3.2.1. Plant dry weight

All cultivars had their total (shoots + roots) plant dry weight (PDW) similarly reduced as salinity increased, mainly between control salinity and 2.5 dS m^{-1} (data not shown). Although percent reductions were not significant for ‘Albion’ (44.2%) and ‘Benicia’ (51.6%), PDW was reduced by 66% for ‘Monterey’, 56% for ‘Ventana’, and 53.6% for ‘San Andreas’. There was no correlation between PDW and fruit yield and, based on control salinity ($EC_{iw} = 0.7$ dS/m), PDW varied with cultivar. Average mean PDW (in g/plant) was 64 for ‘Ventana’), 49.7 for ‘Benicia’, 46.8 for ‘Monterey’, 44 for ‘San Andreas’, and 38.7 for ‘Albion’. Calculated EC_{50} (salinity that reduced 50% of PDW) also was very similar for all cultivars, ranging from (in dS m^{-1}) 1.46 (‘Benicia’ and ‘Monterey’) to 1.7 (‘Ventana’ and ‘San Andreas’), and 1.87 (‘Albion’). It is believed that new tissue production can help plants cope with salinity by diluting salts in shoots. However, ‘Albion’ had the smallest PDW even at control salinity, but still coped well with salinity and was the only cultivar that had 44% biomass reduction, while all other cultivars had reductions in PDW ranging from 51.6 (‘Benicia’) to 66% (‘Monterey’). As we found out that Cl^- was more toxic than Na^+ for strawberries, ‘Albion’ may have coped better with salinity as its Cl^- accumulation was the second lowest in leaves after ‘Monterey’ (85% and 76%, respectively), the lowest in petioles (214% vs. 309–396% for the other cultivars), and the second lowest in roots after ‘San Andreas’ (145% and 129%, respectively) (Table 2). In addition to keeping Cl^- tissue concentration at lower levels, ‘Albion’ may also have higher tissue tolerance to Cl^-, considering the fact that ‘Monterey’ was the second lowest in leaf chloride concentration, but had the greatest loss (66%) in shoot biomass. Also, these increased concentrations of Cl^- in ‘Albion’ shoot and root tissues had no antagonism on the absorption of either Ca^{2+} or Mg^{2+}, as previously reported by others (Saied et al., 2005).

3.2.2. Plant survival

‘Albion’ had the highest survival rate (94%) at the highest salinity of irrigation water (2.5 dS/m), followed by ‘San Andreas’ and ‘Benicia’ (77% and 75%, respectively) and ‘Ventana’ (67%). ‘Monterey’ had the lowest survival (53%) at 2.5 dS m^{-1} (Table 4). Based on the *P* values (5% significance) for the effect of salinity on plant survival, we conclude that ‘Albion’ was the most salt tolerant, with ‘San Andreas’ and ‘Benicia’ second, and ‘Monterey’ as the most susceptible to salinity (Table 4). It is known that a higher uptake of Na^+ impairs the uptake of K^+, Ca^{+2}, and Mg^+, in plants such as in soybeans (Essa, 2002). These authors also reported that the cultivar most tolerant to salinity had smaller concentrations of Na^+ and Cl^- in leaves, higher concentrations of K^+, and a higher K/Na ratio. In contrast, there was no increase in Na^+ in leaves or competition between Na^+ and K^+ in any cultivar in our study. There was an average increase (across cultivars) of over 150% in the concentration of Na^+ in both petioles and roots, but Na^+ has been attributed a very small role (if any) as a toxic ion in strawberries and their tolerance to salinity. In addition, K^+ leaf concentrations tended to increase (although not significantly) in all cultivars. On the other hand, Cl^- has been long indicated as accountable for major ion toxicity in strawberries (Martinez-Barroso and Alvarez, 1997) and its average concentration, across cultivar increased 122% in leaves, 318% in petioles, and 170% in roots. As ‘Albion’ and ‘Monterrey’ were the best and the worst survivor respectively, it is puzzling that they had the lowest increase in Cl^- in leaves and roots. The striking difference was that ‘Albion’ presented a better tissue tolerance to Cl^- than ‘Monterrey’, as indicated by chlorosis of leaf margins (Fig. 2).

Table 4
Plant overall relative survival rate (PSR) 240 days after salinity treatment. Salinity was expressed as irrigation water electrical conductivity (EC_{iw}) in deciSiemens per meter (dS m^{-1}) and *P* values (at 5% significance) express the significance (or not) of salinity on decreased plant survival. Survival at ECiw = 0.7 dS m^{-1} is shown as relative survival of 100%.

Cultivar	EC_{iw} (dS m^{-1})					
	0.7	1.0	1.5	2.5	PSR (%)	*P* values
Survival (%)						
‘Albion’	100	94	94	94	94	0.583^{ns}
‘San Andreas’	100	100	87	76	76	0.085^{ns}
‘Benicia’	100	100	77	75	75	0.038*
‘Ventana’	100	95	80	67	67	0.033*
‘Monterey’	100	97	80	53	53	0.029*

^{ns} = not significant; *significant at $P \leq 0.05$.

Rosa spp. rootstocks, in the same family as strawberries, and as sensitive to salt stress, have been selected for salt tolerance based on their lower accumulation of Cl^- and lower chlorosis rates in their leaves (Cabrera et al., 2009), and due to the plant survival after two months of exposure to NaCl stress (Wahome et al., 2000). Our results agree with the ones reported for *Rosa* spp. by these authors as ‘Albion’ (the most salt tolerant cv.) had the least leaf chlorosis and the highest survival after 240 days under salinity stress under field conditions.

3.3. Fruit production

Fruit number per plant (FPP) and fruit yield per plant (FY) as both cumulative average fruits per plant and mean fruit yield per hectare, and the calculated EC_{50} yield values (EC_{iw} at which there is a 50% decrease in fruit number) are presented in Tables 5 and 6, respectively. Reduction in cumulative number of fruits per plant (FPP) between control salinity ($EC_{iw} = 0.7$ dS m^{-1}) and the highest salinity tested ($EC_{iw} = 2.5$ dS m^{-1}) ranged from 18.7% to 52.3% and was significant for all cultivars, except ‘Monterey’ (35.5%) and ‘Albion’ (18.7%) (Table 5). Reduction in FPP between the control and the treatment with $EC_{iw} = 1.0$ dS m^{-1} for the most affected cultivars ranged from 22.7% in ‘San Andreas’ to 28.6% in ‘Ventana’, while ‘Monterey’ and ‘Albion’ average FPP decreased by only 15.5% and 3%, respectively. This indicates that even a small increase in irrigation water salinity of 0.3 dS m^{-1}, can affect the total yield. Although ‘Albion’ was the least fruit-producing cultivar at control salinity, it was the cultivar least affected by increased salinity and at the highest salinity of $EC_{iw} = 2.5$ dS m^{-1} it had only a non-significant drop of 19% in FPP relative to the control. The resilience of ‘Albion’ to salinity is also indicated by its highest (although not significantly different) EC_{50} value of 3.33 dS m^{-1} (Table 5).

Marketable fruit percent (MFP) decreased significantly with increased salinity for all cultivars, except for ‘San Andreas’ (which decrease was not statistically significant), as shown in Fig. 3. The smallest

Fig. 2. General appearance of plants harvested on July 15, 2013, after 240 days under salinity of EC_{iw} = 2.5 dS m^{-1} (S4), except 'San Andreas' that was pictured from treatment EC_{iw} = 1.5 dS m^{-1} (S3). Chloride damage to hydathodes may have led to impaired guttation and typical leaf-margin death of older leaves.

decreases in MFP at EC_{iw} = 2.5 dS m^{-1} were found for 'Albion' and 'San Andreas', both maintaining above 70% of MFP. 'Albion' was also the cultivar with the least decrease in fruit per plant, as discussed earlier.

As fruit number per plant (FPP) does not account for differences in total fruit weight, we also evaluated the tolerance of each cultivar to salinity based on total fresh fruit yield (FY) in megagrams per hectare (Mg ha^{-1}). All cultivars, except 'Albion', had significant decreases in FY between control and the highest salinity level, and ranged from 54 to 62.6%. 'Albion's 38.2% FY reduction was not statistically significant (Table 6). Again, 'Albion' was able to tolerate irrigation water salinity of up to 2.5 dS m^{-1}. Albion was the cultivar with the highest EC_{50}, significantly higher than that for Ventana and San Andreas (Table 6).

The reductions in all the measured plant dry weight and fruit yield parameters were adequately described by the salt–tolerance model of Eq. (1) with significance at $P \leq 0.05$) except that 'Albion' plant dwt showed a marginal significance with a P value of 0.08 (Table 6). Using the EC_{50} values and FY to evaluate salinity tolerance, 'Albion' was the most salt tolerant, 'San Andreas' and 'Ventana' were the least salt tolerant, and 'Benicia' and 'Monterey' were intermediate (Table 6). Thus, according to fruit yield per hectare, 'Albion' was the most salt-tolerant cultivar, and 'Ventana' the most salt-sensitive among the five tested strawberry cultivars.

Since most salt tolerance data is reported as EC_e rather than EC_{iw}, we measured EC_e and also calculated the EC_e values from the water budget and irrigation water salinity. We measured a water application of 42.0 cm of water over the interval between planting and final harvest. The local CIMIS ET_0 for the period was 88.76 cm. Using the weekly strawberry crop coefficients (Cahn and Farrara, 2012) for a 52 inch bed width in combination with the local CIMIS data, we calculated a potential crop ET of 35.8 cm, thus a leaching fraction of 0.15. Using the conversion factor of 1.6 previously developed (Ayers and Westcot, 1985), this EC_{iw} and leaching fraction correspond to calculated EC_e values of 1.12, 1.60, 2.4, and 4 dS m^{-1} for irrigation waters of 0.6, 1.0, 1.5 and 2.5 dS m^{-1}, respectively. The measured average soil EC_e samples at the end of the experiment were higher than the calculation based on strawberry coefficients and water applications discussed above, thus suggesting less than 0.15 leaching (estimated leaching fractions of 0.044, 0.065, 0.072 and 0.090 for irrigation waters of 0.7, 1.0, 1.5 and 2.5 dS m^{-1}, respectively).

The EC_{e50} for strawberry has been reported as 2.23 (Steppuhn et al., 2005), and Grieve et al. (2012) reported that strawberry plants would have an expected FY reduction of 33% for every unit increase in EC_e above the threshold EC_e of 1.0 dS m − 1; thus, an EC_e of 2.5 dS m^{-1} at

Table 5

Mean yield [n = 3, ± 1SE (standard error)] in number of fruits per plant (FPP) and reduction in FPP (%), relative to control, for five commercial strawberry cultivars after 240 days under four salinity levels, expressed as EC_{iw}. Capital letters in the same row (within cultivar) show statistical difference among salinity treatments compared to control. There were no differences for cultivars within salinity treatments or within EC_{50} (EC_{iw} at which there is a 50% decrease in fruit number).

Cultivar	EC_{iw} (dS m^{-1})					
	0.7	1.0	1.5	2.5	Reduction in FPP(%)	EC_{50} (dS m^{-1})
Mean yield (FPP)						
'Benicia'	50.5 ± 6.3^{A}	37.7 ± 2.6^{AB}	36.5 ± 2.7^{AB}	27.5 ± 3.6^{B}	44	2.40 ± 0.23
'Ventana'	48.5 ± 3.7^{A}	35.0 ± 2.6^{AB}	31.0 ± 3.8^{AB}	27.1 ± 6.3^{B}	45	1.95 ± 0.30
'Monterey'	45.4 ± 3.2^{A}	37.6 ± 3.4^{A}	37.7 ± 2.4^{A}	29.7 ± 3.9^{A}	36^{ns}	2.62 ± 0.34
'San Andreas'	44.0 ± 1.8^{A}	34.8 ± 1.0^{AB}	30.8 ± 2.5^{B}	21.3 ± 2.0^{C}	52	2.16 ± 0.15
'Albion'	31.8 ± 0.2^{A}	31.4 ± 2.5^{A}	30.4 ± 2.7^{A}	25.5 ± 3.8^{A}	19^{ns}	3.33 ± 0.12

Table 6
Total mean [n = 3, ± 1SE (standard error)] fresh fruit yield (FY) in megagrams per hectare (Mg ha^{-1}), relative to control, for five commercial strawberry cultivars (CV) at four salinity (EC_{iw}) levels. Capital letters in the same row (within each CV) show statistical difference among salinity treatments. There were no differences within salinity treatments. Small letters in the last column show statistical difference for EC_{50} = (EC_{iw} at which there is a 50% decrease in fruit yield).

Cultivar	EC_{iw} (dS m^{-1})					
	0.7	1.0	1.5	2.5	Reduction (%)	EC_{50} (dS m^{-1})
Mean FY (Mg ha^{-1})						
'Monterey'	45.2 ± 4.6^{A}	32.6 ± 3.5^{AB}	29.3 ± 1.5^{AB}	18.5 ± 3.0^{B}	59.0	1.90 ± 0.1^{ab}
'Ventana'	44.4 ± 2.4^{A}	30.2 ± 1.3^{B}	24.0 ± 2.1^{BC}	16.6 ± 3.4^{C}	62.6	1.68 ± 0.1^{b}
'Benicia'	41.9 ± 4.2^{A}	33.1 ± 1.6^{AB}	28.4 ± 0.6^{BC}	19.3 ± 2.5^{C}	54.0	2.09 ± 0.1^{ab}
'San Andreas'	39.1 ± 2.6^{A}	29.5 ± 2.1^{AB}	24.2 ± 1.8^{BC}	15.3 ± 1.2^{C}	61.0	1.84 ± 0.1^{b}
'Albion'	29.6 ± 0.3^{A}	25.9 ± 2.8^{A}	23.6 ± 2.5^{A}	18.3 ± 3.0^{A}	38.2^{ns}	2.82 ± 0.4^{a}

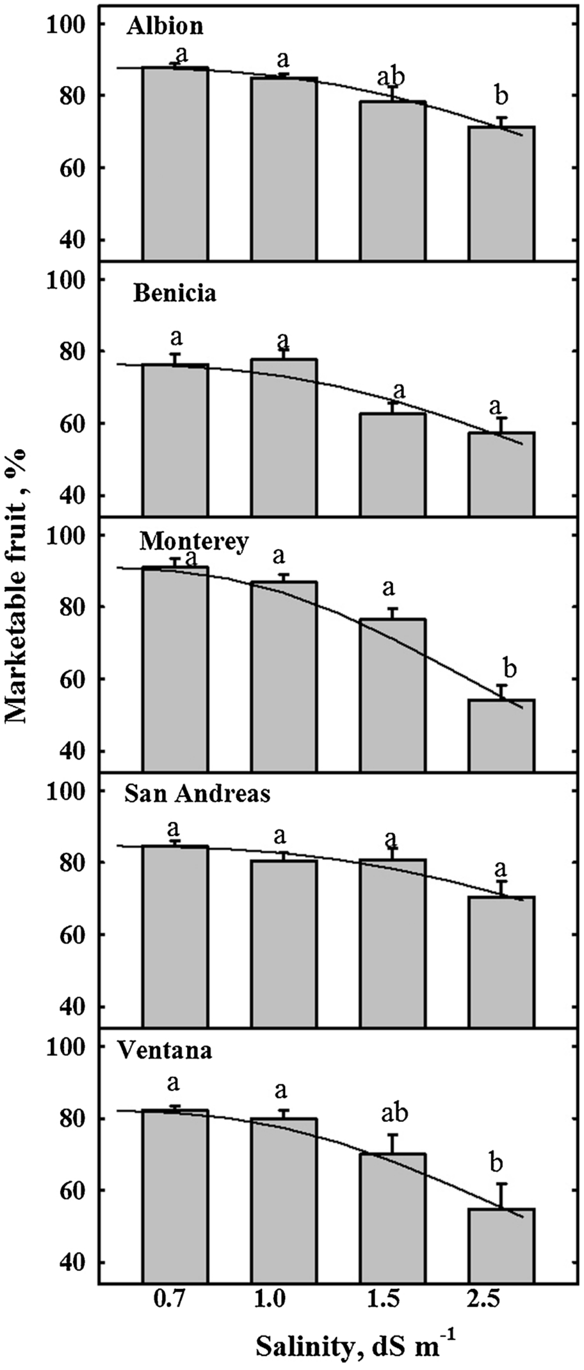

Fig. 3. Change in the percentage of marketable fruits of five commercial cultivars of strawberry under saline irrigation for 240 days.

50% yield reduction. Using the water budget data, the calculated EC_{e50} of our experiment corresponds to 3.04, 2.72, 3.36, and 4.48 dS m^{-1} for 'Monterey', 'Ventana', 'San Andreas', and 'Albion', respectively, and 5.42, 5.05, 5.74 and 7.0 dS m^{-1} using our measured EC_e data. The salt tolerance of these newer varieties was thus much higher than reported for older varieties. While 'Monterey' was not the most salt tolerant, it was the highest producer up until EC_{iw} = 2.5 dS m^{-1}. A study evaluating 12 commercial strawberry cultivars from 2007 to 2010, without salinity, reported that 'Albion' was among the five with the largest fruits, the three with the most firm fruits, and the three with the highest concentrations of vitamin C (followed by 'Nancy' and "Ventana"), but was the second lower fruit producer in g/plot (Masny and Żurawicz, 2010). These authors also reported that 'Albion' had no infection from powdery mildew in the three years of trial in Poland. Regarding fruit production, our study confirms the low fruit productivity of 'Albion' under non-saline conditions, but it had the highest EC_{iw50} (2.82), which indicates that it was the cultivar requiring the highest salinity to reduce fruit production by 50% (Table 6).

Evaluating the cultivar response over the duration of the experiment, 'Albion' had the lowest plant mortality (6%), while 'Monterey' had the highest (47%) at EC_{iw} = 2.5 dS m^{-1}. Changes in plant survival caused by salinity were noticeable in 'Albion' and 'San Andreas' only after 205 and 190 days, respectively, while the other cultivars started showing changes 160–170 days after treatment initiation in Riverside, not a commercial strawberry production area. This indicates that these cultivars would do even better in cooler production areas of Southern California, such as Santa Maria and Oxnard (towards the coast). Regarding the number of fruits per plant, 'Albion' showed the least difference between control irrigation and EC_{iw} = 2.5 dS m^{-1}, followed by 'Monterey'. Regarding grams of fruit per plant, 'Albion' was also the cultivar that showed the least difference between control and EC_{iw} = 2.5 dS m^{-1}. 'Ventana' was the cultivar that showed the most striking differences for plant mortality, fruits per plant, and grams of fruit per plant between control irrigation and irrigation water with EC_{iw} = 2.5 dS m^{-1} (Annex Fig. 1).

3.4. Fruit sugar concentration

Fruits harvested on May 24, 2013 were used to measure total soluble sugars (Brix%) within one hour from harvest. There was no significant effect ($P > 0.05$) of irrigation water salinity on fruit Brix% for any of the five cultivars. Also, there was no significant difference ($P > 0.05$) of cultivar at each salinity level (data not shown). However, when data for Brix% was pooled for each cultivar across all salinity levels, the cultivars ranked as follows (from the sweetest to the least sweet) with the following significance letters: 'Albion' (a), 'Monterey' = 'Benicia' (ab), and 'San Andreas' = 'Ventana' (b) as shown in Fig. 4. A recent study evaluated several fruit characteristics of 'Albion' cultivated under greenhouse, with controlled temperatures ranging from 10 to 30 °C, and at six stages of fruit maturity (Ornelas-Paz et al., 2013). Interestingly, these authors reported the highest total soluble solids

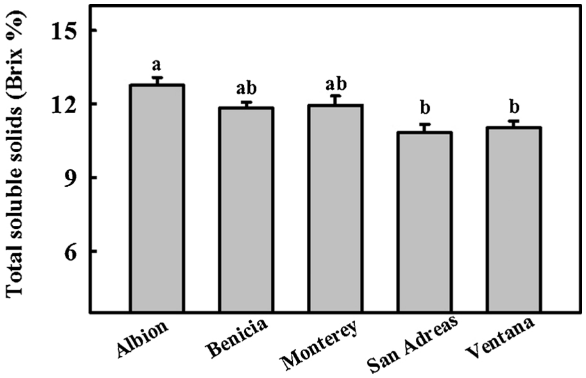

Fig. 4. Total soluble sugars (Brix%) of freshly harvested strawberries, pooled across salinity treatments (n = 12).

(Brix%) of 'Albion' to be 9%, while our fruits had Brix% ranging from 11 to 13%, the highest being achieved for 'Albion'. This difference in Brix% could be attributed to our fruits being from outdoor plants, which endured temperature extremes of 14–15 centigrade at night and 28–35 °C during the day. Although other authors (Keutgen and Pawelzik, 2007) reported a significant decrease in total soluble sugars (Brix%) for 'Elsanta', but not for 'Korona', with both 40 and 80 mM NaCl, our extended salinity experiment had no detriment on the total soluble sugars of any of the cultivars tested, even under elevated Na^+ (11.4 $mmol_c$ L^{-1}) and Cl^- (18.8 $mmol_c$ L^{-1}). To the best of our knowledge, this is the first report on total soluble sugars of these cultivars under saline conditions.

4. Conclusions

Our field data clearly illustrate that there is sufficient variability among commercial strawberry cultivars to consider salt tolerance as a criterion when selecting varieties to be grown with irrigation water above EC_{iw} 0.7 dS m^{-1}. However, selection for salt tolerance alone is not sufficient because the criteria of commercial interest to growers include also optimal yield and early production. 'Albion' had the least reduction in fruit yield, commercial fruit size, and in plant survival when comparing control irrigation water (EC_{iw} = 0.7 dS m^{-1}) to EC_{iw} = 2.5 dS m^{-1}. However, 'Monterey' and 'Benicia' had similar absolute fruit yields as 'Albion' at the highest salinity. Considering that both 'Monterey' and 'Benicia' outproduced 'Albion' at 1.5 dS m^{-1}, these cultivars would be preferred under moderate salinity. All cultivars were able to limit Na^+ accumulation in leaves despite increased salinity, but Cl^- accumulated in every organ. The damage seen in older leaves may be due to the Cl^- damage to leaf hydathodes (modified pores), caused by the exudation of water and chloride through guttation on leaf margins. Once these hydathodes, connected to the vascular system, are damaged by Cl^- the leaf may lose its only way to extrude toxic Cl^-. 'Albion' was the cultivar that accumulated the least amount of Cl^- in both roots and petioles, having the highest plant survival, and being the cultivar with the highest total soluble sugars. The data on survival, fruit production, and soil salinity at the end of the experiment suggest that these relatively-new varieties are much more salt tolerant than older varieties reported in the literature. In terms of breeding new varieties for salt tolerance, the features presented by 'Albion' are noteworthy and make 'Albion' a valuable germplasm for breeders looking to develop cultivars with higher salt tolerance, while enhancing or maintaining fruit taste.

Disclaimer

The authors declare no conflict of interest. The mention of proprietary brands and names is solely for the convenience of the reader and does not imply endorsement by the authors or the USDA versus similar products. The USDA is an equal-opportunity employer.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.scienta.2018.07.016.

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