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Impact of potassium sulfate salinity on growth and development of cranberry plants subjected to overhead and subirrigation

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1 **Impact of potassium sulfate salinity on growth and development of**
2 **cranberry plants subjected to overhead and subirrigation**

3 M-E. Samson, J. Fortin, S. Pepin, J. Caron

4 Département des Sols et de Génie Agroalimentaire, Université Laval, Québec, Québec G1V 0A6, Canada

5 **ABSTRACT.** New recommendations in cranberry production suggest reducing overhead
6 irrigation and the use of subirrigation as an alternative irrigation method, two strategies suspected
7 to increase the risk of salt build-up in soil. Since very little is known about cranberry tolerance to
8 salinity, this study was conducted to determine if deficit irrigation and subirrigation could cause
9 salinity issues and affect plant yield. In a greenhouse, cranberry plants were submitted to eight
10 different treatments combination from two irrigation methods (overhead irrigation and
11 subirrigation) and four salinity levels created by increasing amounts of applied K₂SO₄ (125
12 (control), 2 500, 5 000 and 7 500 kg K₂O ha⁻¹). Irrigation methods showed no significant
13 difference in measured EC_{ss} (electrical conductivity of soil solution). Meanwhile, growth and
14 yield parameters decreased significantly with soil salinity in both irrigation treatments and an
15 average EC_{ss} of 3.2 dS m⁻¹ during flowering caused a 22% drop in relative photosynthetic rate and
16 a 56% decrease in yield when compared to control. Cranberry seems to be salt sensitive and
17 further work should investigate EC_{ss} levels under different field and irrigation practices, to make
18 sure that it does not reach critical levels.

19 **Key words:** *Vaccinium macrocarpon*, salinization, osmotic stress, pressure volume curves,
20 photosynthesis, yield.

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Abbreviations: EC_{ss}, electrical conductivity of soil solution; TLP, xylem water potential at turgor loss point; EU, experimental unit.

Each year, 70% of worldwide water withdrawals are used for agricultural purposes (Burton, 2010). Of the 287 million irrigated hectares worldwide (Burton, 2010), about one third sees its productivity limited by salinity problems (Bohn et al., 2001). It is now recognized that the refinement of irrigation methods is a key element to ensure the protection of global water resources. In cranberry production, large volumes of water are used both for irrigation and crop management. The majority of cranberry growers use overhead sprinkler irrigation to supply water to their crop and also as a frost and heat stress protection method. In order to optimize yield and water productivity in cranberry crops, recent studies have suggested using real-time automated sprinkler irrigation based on soil matric potential with a threshold between -7 and -8 kPa (Bonin, 2009; Pelletier et al., 2013; Caron et al., 2016). However, cranberry fields have a particular bed configuration (a 30-50 cm sand layer covering an impermeable layer, with drain tiles laying on it and the whole field surrounded by berms), adapted to the fact that water table is raised at the end of the season to harvest the crop and to provoke the formation of a protective ice layer over winter. Such a unique configuration does offer the possibility to subirrigate the crop with much more efficiency than with overhead irrigation and this practice is increasing in popularity. As a result, a recent study also recommended the use of deficit subirrigation in cranberry production by maintaining the water table at a depth of 60 cm under the root zone, which corresponds to a -5 to -6 kPa matric potential at the root zone level in their study (Pelletier et al. 2015a). When compared to current irrigation strategies, these new recommendations generally represent a decrease in soil water content (Pelletier et al., 2013), with a potential risk of salinity increase.

Indeed, subirrigation leads to upward water flux that may lead to accumulation of salts in the root zone (Rouphael et al. 2005; Incorcci et al. 2006) and thus may result in an electrical conductivity

of the soil solution (EC_{ss}) that could damage plant growth. Even if rainfall and harvest flooding can help prevent salt accumulation in cranberry production, water salinity and fertilizer applications can still result in soil salinity problems during the growing season. Indeed, since 2006 in Québec, Canada, cranberry has to be cultivated in a closed system involving water recirculation (MAPAQ, 2010). This could cause deterioration of water quality over time. A high concentration of salts in the root zone can affect plants in many different ways including toxicity, antagonistic effects leading to ion imbalances, metabolic dysfunctions, and osmotic stress limiting water intake which impacts plant turgor and photosynthetic machinery (Hopkins, 2003; Munns, 1993; Hasegawa et al. 2000). Thus, photosynthetic activity and water use efficiency are often measured to determine if a plant is under abiotic stress (Chaves et al. 2009). Yield and yield components such as fruit set and the number of buds were also proven to be useful indicators of cranberry productivity (Eaton and Kyte, 1978; Pelletier et al. 2015b). Leaf necrosis, a reduced vegetative growth or leaf expansion can also be indicators of salt stress (Kozłowski, 1997). Certain plants can adapt to salinity by tolerating or avoiding salts (Kozłowski, 1997). Salt stresses can induce osmotic adjustment in certain plant species, a typical response also observed under drought conditions to allow maintenance of cell turgor and water uptake (Chaves et al. 2009). Solute accumulation in plant tissues and increased tissue elasticity are two biophysical plant strategies to lower the water potential at which turgor loss occurs (Meizner et al. 1990). Pressure-volume curves have been used in numerous studies to quantify plant drought or salinity tolerance by determining the leaf water potential at turgor loss point (TLP) using a plot of leaf water potential against water volume in drying leaves. This parameter is related to cellular composition of the plant and is classically known to be a major indicator of plant osmotic stress where more negative potentials indicate increasing stress (Bartlett et al. 2012).

In blueberry production, saline irrigation water is known to reduce gas exchange and to cause leaf necrosis (Wright et al. 1993). Surprisingly, while it is well established that salt tolerance varies

considerably among species and genotypes (FAO, 1976), very little is known about cranberry tolerance to salinity. One study investigating the effects of de-icing salt runoff in fields constructed near highways showed a 43% decrease in photosynthetic activity when cranberry plants were exposed to recurrent NaCl applications (Jeranyama and DeMoranville, 2009). A preliminary study using a subirrigation system with an average matric potential of -4.2 kPa and an overhead irrigation system with an average matric potential of -3.6 kPa coupled with average EC_{ss} ranging from 0.55 to 10.8 dS m⁻¹ indicated that both irrigation treatments resulted in a linear decrease in photosynthetic rates ($p = 0.0175$), and a decline in total leaf area ($p = 0.0435$) with increasing salinity (Samson, 2016).

In agriculture, water availability to plants is mainly controlled by the matric and osmotic potential of the soil (Lal and Shukla, 2004). With increasing pressure to reduce water use and to use subirrigation in cranberry production, there exists a risk of salinity increase with potential yield damage to the crop. Therefore, coupling low matric potentials that barely meet plant water needs to low osmotic potentials could easily lead to water and/or salt stress and lower yield (Chaves et al. 2009; FAO, 1976), but little information is available on this aspect for cranberry. The objectives of this study were therefore: (i) to assess the impact of two irrigation methods (subirrigation vs overhead irrigation) on soil salinity; and (ii) to determine cranberry tolerance to salinity on plant development.

MATERIAL AND METHODS

Plant material and growth conditions

In November 2013, blocks of undisturbed cranberry plants (*Vaccinium macrocarpon* ‘Stevens’) with soil (25 cm L x 25 cm W x 15 cm H) were collected from a 2-year-old sandy field (90.8% sand, 9% silt and 0.2% clay on a mass basis) in Saint-Louis-de-Blandford, Québec, Canada. The average initial soil pH (1:1 soil:water ratio) was 4.58 and the average soil saturated

extract EC_{ss} was 0.20 dS m^{-1} . Each experimental unit (EU) consisted of a custom-built plastic container (6 mm thick polycarbonate; 25 cm x 25 cm W x 42 cm H) with a 0.5 cm hole drilled at the bottom center and covered with an open mesh fabric (SEFAR Nitex 15 μ m, Depew, NY, USA). A 3.5 cm layer of glass microspheres (Spherglass 2900, Potters Industries, Malvern, PA, USA), another layer of mesh fabric, a 20 cm layer of sand from the same field and a cranberry block were successively added to achieve a 38.5 cm soil height within each container. Plants were vernalized in a 2°C cold room for 3 months. During that period, each EU received 500 mL of rainwater once every 3 weeks. In February 2014, the plants were placed in a greenhouse at 15°C for the first 10 days. Thereafter, temperatures were maintained between 12-16°C at night and 21-26°C during the day with a 60% average air relative humidity. Plants were grown under natural light and from 10% flowering to fruit set, bumblebees were introduced to ensure adequate pollination. The 32 EU (8 treatments, four replicates) were arranged in a randomized complete block design surrounded by guard rows (Figure 1). Treatments were a factorial combination of two irrigation methods (subirrigation and overhead irrigation) and four soil salinity levels obtained with different amounts of K_2SO_4 .

118

119 *Irrigation management*

120 The overhead irrigation setup consisted of a closed system with 4 lines each irrigating a
121 different salinity level treatment. Blocks 2 and 3 were equipped with tensiometers (models T-80
122 and TX-80, Hortau, Lévis, Canada) installed vertically in the center of each EU to a depth of 7.5
123 cm to determine real time matric potential. These tensiometers were also used to automate
124 overhead irrigation using Irrolis wireless control system (Hortau, Lévis, Canada). The irrigation
125 threshold was set to -8 kPa to maintain an average target matric potential of -6 kPa. Rain water was
126 collected from the greenhouse rooftop and used as irrigation water. Each EU under overhead
127 irrigation was equipped with 2 sprayers (model Spray Stake, NetafimTM, Aviv, Israel) calibrated to
128 provide 500 mL of rain water during each irrigation event. Subirrigation treatments were obtained

by simulating the presence of a water table under the container. To achieve this, a plastic tube connected the hole at the bottom of the box to an Erlenmeyer flask filled with rain water. At the beginning of the experiment, water level was slowly raised in the soil container until the soil was saturated. The Erlenmeyer was then slowly lowered until the water level was about 60 cm beneath the root zone, corresponding to a -6 kPa matric potential. A Mariotte bottle connected to the Erlenmeyer ensured that the water table level was maintained despite plant water uptake and evaporation. To remain consistent with field conditions, rainfall events were simulated by applying water with a watering can on each EU. The amount of water applied for each month during growing season was determined based on 25-year averages recorded at the Environment Canada station for Saint-Louis-de-Blandford, Québec, Canada, located near the sampling site. It corresponded to the rainfall received during the months of the normal cranberry growth cycle, that is 96 mm for June, 102 mm for July, 97 mm for August, 107 mm for September, and 94 mm for October. Because the experiment ran from March to July with supplemental lighting under greenhouse conditions, the corresponding water volume for June was applied in March, that of July in April and so on. This amount of water was subdivided into an equal number of applications throughout the month, performed on Monday, Wednesday and Friday of each week. This included the water used for diluting fertilizers and K_2SO_4 treatments. Hence, all EU received exactly the same amount of water through their growth cycles as the average 25-year rainfall through the growing season. As a result of these regular overhead water applications, irrigation was never applied by the overhead irrigation system, as the soil matric potential never reached the -8 kPa irrigation threshold (see Figure 2).

150

151 *Nutrient solution management*

152 Potassium sulfate (K_2SO_4) was selected as salinization agent since it is the most
153 commonly used potassium fertilizer among cranberry producers and therefore, the most likely to
154 accumulate. Based on the results of previous unpublished studies (2013) four salinity treatments

were investigated: 125 (control treatment based on cranberry needs according to the CRAAQ, 2011), 2500, 5000 and 7500 kg K₂O ha⁻¹. The K₂SO₄ equivalents were calculated and these amounts of fertilizer were divided equally in four weekly applications starting at 10% flowering and ending at the end of fruit set to correspond to field application scenario. For each application, fertilizers were diluted in rain water and each EU received 16 mm of the solution associated with its salinity treatment. A solution containing ammonium sulfate [(NH₄)₂SO₄] and monoammonium phosphate [NH₄H₂PO₄] was also applied with the same schedule to provide 40 kg N ha⁻¹ and 60 kg P₂O₅ ha⁻¹, according to the recommendations from the CRAAQ (2011) for Quebec cranberries. The K₂SO₄ applications used here were far above recommended applications but for the control treatment. However, such rates were used to make sure that the reached EC_{ss} levels may be stressful enough for the plant, under conditions of rainfall and irrigation events used throughout the experiment. Such salinity levels were necessary as so far no data existed on values of EC_{ss} possibly reached under subirrigation in presence of rainfall and EC_{ss} levels appear difficult to predict. Hence, high levels were required to make sure that not all solutes would be leached in these very light soils.

170

171 *Soil physical and chemical data*

In blocks 2 and 3, tensiometers and lysimeters were installed vertically at a depth of 7.5 cm in the soil corresponding to the middle of the root zone. TDR probes were installed horizontally at the same depth through the middle of the container wall. Soil matric potential was recorded every 5 minutes with tensiometers (T-80 and TX-80, Hortau, Lévis, Québec, Canada) while TDR probes (model CS645, Campbell Scientific, Logan, UT, USA) calibrated with the equation from Topp et al. (1980) recorded soil water content and bulk EC every 30 minutes to a data logger (model CR1000, Campbell Scientific, Logan, Utah, USA). Lysimeters were sampled weekly to determine EC_{ss} using a conductivity probe and a meter (*SymPhony*, VWR inc., Radnor, PA, USA). At the end of the growing season, soil samples were collected at an average depth of 7.5, 20 and 38

181 cm below the soil surface and were used to perform a 1:1 soil saturated extract as described by
182 Rhoades (1996). Extracts from each soil depth were submitted to ion chromatography and flame
183 atomic absorption to determine the concentration of SO_4^{2-} and K^+ . In order to determine water
184 desorption curves and hydraulic conductivities, five soil cores (5.5 cm height by 8.2 cm diameter)
185 were sampled at a 7.5 cm depth after the experiment. The samples were saturated bottom-up over
186 24 hours, then saturated hydraulic conductivity was measured using a vertical constant head soil
187 core method (Reynolds and Elrick, 2002) slightly modified in order to enable automatic
188 measurements. Cores were then equipped with a small tensiometer inserted in the middle/center of
189 each core and these tensiometers were mounted with a differential electronic pressure detector to
190 automatically monitor soil matric potentials on a data logger (model CR1000, Campbell Scientific).
191 These cores were placed on a suction table (Romano et al., 2002) and weighed at each step for
192 desorption (0, -15, -25, -47, -74, and -100 cm) and wetting (-100, -50, -24, and -1 cm) curves.
193 Full saturation (0 cm) was assumed for total porosity measurement after core drying (24 hours at
194 105°C) at the end of the suction table experiment. This dry weight also allowed the calculation of
195 soil bulk density and soil volumetric water content at each step. The values were used to estimate
196 air-filled porosity for each step. This method also allowed the calculation of unsaturated hydraulic
197 conductivities by inverse modeling in HYDRUS-1D (Šimůnek et al., 2005-2008). We used the
198 water desorption and wetting curves as well as continuous soil matric potential measurements at
199 the center node to calibrate the soil-hydraulic van Genuchten-Mualem model (van Genuchten,
200 1980; Mualem, 1976) implemented in HYDRUS. These measurements were done to obtain a
201 general characterization of the material only; no statistical analysis was performed on these
202 parameters.

203

204 *Plant physiological responses*

205 Photosynthesis measurements were performed on each EU using a portable
206 photosynthesis system (LI-6400XT, Li-Cor Biosciences, Lincoln, NE, USA) equipped with a 2x3

opaque chamber and a LED light source (6400-02B LED source, Li-Cor Biosciences). Air flow was set to $400 \mu\text{mol s}^{-1}$, CO_2 concentration in the reference chamber was $400 \mu\text{mol mol}^{-1}$, light intensity was set to $800 \mu\text{mol m}^{-2} \text{s}^{-1}$ and block temperature was maintained at 20°C throughout measurements. At the beginning of the experiment, a runner and a vertical stem (commonly referred to as upright by practitioners) were selected in each EU and were repeatedly measured until the end of the experiment. Gas exchange measurements were carried out between 9 and 12 AM and performed on each stem twice before the beginning of the salinity treatments, twice between each salt application and twice a week after the last salt application. The foliage enclosed in the LI-6400XT chamber was removed at the end of the experiment and the leaves of each stem were digitalized with a flatbed scanner to determine leaf area using the ImageJ software (Schneider et al., 2012). Gas exchange parameters were then corrected for the leaf area in the chamber. To reduce the variability between stems, each measurement was divided by the stem initial rate of photosynthesis (average of the two initial measurements) to obtain the relative photosynthetic rate. Salinity treatments were concluded when the berries were ready to harvest. At this point, pressure volume curve measurements were performed as described by Hinckley and Richter (1980) with a pressure chamber (PMS Instrument Company, Albany, OR, USA) on a selected runner in each EU of the blocks 1, 2 and 4. One block was performed per day. Plant water relation parameters were derived using the C model of Schulte and Hinckley (1985).

Yield and growth parameters

At the end of the experiment, fruit set was calculated in each EU by dividing the number of berries by the total number of flowers for each upright. Berries were also counted and weighed. The buds produced by each EU were also counted and divided by the initial amount of buds in that EU. Each stem was measured and defoliated in order to evaluate plant total leaf area. Leaves were placed on a scanner and each image was analyzed with the imaging program ImageJ (Schneider et al., 2012).

233

234 *Statistical analysis*

235 A factorial ANOVA model was used to compare the effects of irrigation method and
236 salinity levels on yield, fruit set, growth parameters, leaf area, relative amount of buds, TLP,
237 average EC_{ss} and average photosynthetic rate during flowering. The MIXED procedure of SAS
238 (SAS Institute Inc., Cary, USA) was used with blocks as random factor and the statement
239 REPEATED to allow us to model the heterogeneity due to one or another factor. A residual
240 analysis was used to verify the assumptions of normality and homogeneity of the model. A
241 transformation of the data was performed if assumptions were not met. Multiple comparisons
242 were made using the "Protected Fisher's LSD (Least Significant Difference)" method and
243 polynomial contrasts were tested. The same model with repeated measures was used to study the
244 effect over time of irrigation, salinity and the type of stem on photosynthesis measurements. The
245 repeated factor was time and the random factor was block. The mixed procedure of SAS was used
246 with REPEATED statement to allow us to model the correlation among measurements taken on
247 the same EU. Variance-covariance matrix was chosen to minimize the Akaike criterion. The
248 Kenward-Roger method was used to calculate the degrees of freedom. The analysis of the effects
249 of irrigation, salinity and depth on the amount of ions accumulated in different root layers was
250 performed with the same method, using depth as the repeated factor and block as the random
251 factor. A simple regression model was also used to evaluate the effect of EC_{ss} on relative
252 photosynthetic rate. The results of these statistical tests are reported for a significance level of
253 0.05.

254

255 RESULTS AND DISCUSSION

256 *Water dynamic and solute transport*

257 The change of EC_{ss} with time is shown in Figure 3 with a significant interaction between
258 time and salinity treatments ($p < 0.0001$). It was observed that each application of fertilizers

(from April 3rd to April 24th) resulted in an increase in EC_{ss} and salinity treatments were rapidly differentiated. However, irrigation methods did not have a significant influence on EC_{ss} (data not shown). This could be attributed to net water flow. A decrease in EC_{ss} under overhead irrigation as compared to subirrigation was expected because of potentially higher salt accumulation with higher net water movement to the top surface between irrigation or rainfall events under purely subirrigated treatments. However, both irrigation treatments received regular water application to simulate natural rainfall, and the difference in water movement was likely small, as little water had to be added to the Mariotte bottle to maintain constant water potential in this treatment through capillary rise. Indeed, that water supplied to the Mariotte bottle represented between 5 to 10% of the total water applied (see above description). This volume was less likely to create a major difference between the irrigation treatments than if no overhead water had been applied. Moreover, as soil matric potential was higher in overhead irrigation than in subirrigated treatments (mean value of -4.10 kPa and -6.34 kPa, respectively; Figure 3 and 4 and Table 1), it indicates that between water application events, more water had drained down from the subirrigated treatments (volumetric water contents were clearly lower for the subirrigation treatment). This phenomenon could be explained by the fact that the location of free water was lower in the subirrigated treatment than in container with free drainage. Indeed, free water will be located at the top of the surface level in the Mariotte bottle (60 cm below the mid root zone), while in the free drainage container, free water will accumulate at the bottom of the container, that is at 42 cm below the top surface. This lower potential or higher suction in the subirrigated treatment resulted in a slightly higher soil bulk density (Table 1), but the soil air-filled porosity was still sufficient to respond to cranberry needs in both irrigation treatments (Laurent, 2014). Furthermore, despite a lower matric potential and lower volumetric water content in the subirrigated treatment, the non-saturated hydraulic conductivity (Table 1) was adequate for plant daily water uptake (Bonin, 2009).

Because of this difference in soil matric potential (larger hydraulic gradient for the subirrigation treatment) between free water position and the top surface, it is therefore expected that more water will be drained from the subirrigation treatment if rainfall dominates the net water movement. Despite compelling evidence from other crop systems that subirrigation causes a salt build-up in the root zone when compared to drip irrigation (Rouphael et al. 2005; Incorreci et al. 2006), the higher matric potential gradient in the subirrigated treatments most likely caused K_2SO_4 to drain rapidly out of the system and could have counteracted the effects of the upward water flux on the EC_{ss} . Soil saturated extracts at 3 different depths at the end of the experiment showed an overall higher amount of ions (K^+ and SO_4^{4-}) in the overhead irrigation treatments ($p = 0.0108$). However, a greater proportion of ions accumulated in the root zone (0 to 7.5 cm) in subirrigated treatments when compared to overhead irrigation treatments ($p = 0.0050$) (data not shown), consistent with an upward flow to the surface. Nevertheless, this lack of difference between treatments was unexpected and cannot be assumed representative of field conditions. This limits the reach of the study with respect to the effect of field irrigation methods and should be interpreted cautiously.

Plant physiological responses to salinity

Early plant responses to water and salt stresses are mostly identical (Munns, 2002). Usually, after an initial decrease in photosynthetic rate, these stresses often induce an osmotic adjustment to maintain cell turgor and plant water uptake (Chaves et al., 2009). A net accumulation of solutes in the symplast and the reduction of plant tissue elasticity are two salt tolerant plant strategies that allow the maintenance of a water potential gradient between the plant and the soil despite drought or saline soil solution (Meinzer et al. 1990). In response to lower soil water potential, plants tend to lower their TLP in order to maintain hydraulic and stomatal conductance, gas exchange and growth (Bartlett et al. 2012). Our leaf water potential data suggest that cranberry plants adjusted their TLP in response to osmotic stress during this experiment.

While the irrigation methods had no significant influence on this parameter, salinity treatments had a linear effect on TLP ($p = 0.0373$; Fig. 5), with plant osmotic responses levelling off at around $5\,000\text{ kg K}_2\text{O ha}^{-1}$. This corroborates results obtained in wheat where the application of increasing amounts of K_2SO_4 on plants under salt stress showed a linear effect on plant osmotic potential (Yagmur et al. 2007). Moreover, Rasico et al. (2001) reported that a higher K^+ concentration in plant tissues was associated with improved tissue hydration. In wheat, osmotic adjustment caused by K^+ accumulation also seemed to level off at a certain stage (Yagmur et al. 2007), which is consistent with our results.

Photosynthesis and cell growth are known to be the first processes to be affected by salinity (Munns et al. 2006) and by water stress (Chaves, 1991). In this study, the EC_{ss} during flowering increased linearly with salinity treatments ($p < 0.0001$; Fig. 6) while the relative photosynthetic rates decreased linearly over the same period ($p < 0.0001$; Fig. 6). In addition, relative photosynthetic rates were lower in subirrigated treatments than in overhead irrigation treatments ($p = 0.0497$) (data not shown). This could be attributed to the difference in matric potential between the two irrigation methods. The lower matric potential in subirrigated treatments coupled with a low osmotic potential could have been more deleterious to the plants, matric potential being additive to osmotic potential in imposing plant water stress. Based on results presented in Figure 6, an average EC_{ss} of 3.2 dS m^{-1} during flowering (corresponding to the $2\,500\text{ kg K}_2\text{O ha}^{-1}$ treatment) induced a significant drop of about 22% in photosynthetic activity. Interestingly, uprights and runners had the same response to the treatments. Our findings are consistent with those of Jeranyama and Demoranville (2009) where cranberry plants exposed to chronic applications of NaCl solution (164 mg L^{-1}) showed a 43% decrease in net CO_2 assimilation rate when compared to control treatment. As expected when examining the data, there was a linear relationship between EC_{ss} and relative photosynthetic rates with an R^2 of 0.57 and 0.73 for overhead irrigation and subirrigation respectively (Fig. 7a). Relative yield also showed a rapid

quadratic drop with increasing EC (Fig. 7b). When relative yields were compared to guidelines provided by Maas (1993), cranberry clearly appears as a sensitive crop, as the yield drop occurred below 9 dS m⁻¹. This is consistent with data for many other small berries (Maas, 1993). Even if K₂SO₄ is not generally known as the most deleterious salinization agent and is often used to alleviate salinity stress induced by NaCl (Yagmur et al. 2007; Ebrahimi et al. 2012), this high level may explain the damaging effects observed in this study. The presence of other ions in irrigation water could cause a different effect on cranberry plants and should also be investigated.

Photosynthetic rates were also affected by time and salt applications (Fig. 8). While the effect of salts appeared soon after the first application in the 7 500 kg ha⁻¹ treatment, it took all four applications to differentiate completely the three other salinity treatments. This is likely due to the ability of a plant to adapt to a salt and/or a water stress depending, among other things, on how quickly the stress is imposed (Chaves et al. 2009). Similarly, a technical report from the University of Massachusetts Transportation Center (DeMoranville, 2005) demonstrated that the frequency and intensity of salt applications influenced cranberry responses to stress. Chronic exposure seemed to be the most damaging for cranberry when compared to acute or intermittent salt applications coupled with regular flushing. Even though flushing also occurred in our experiment due to rainfall simulation, the control treatment was the only one to show a photosynthetic rate greater than its initial value throughout the experiment (Fig. 8). At the end of the experiment, a significant difference of 33% in relative photosynthetic rate was observed between the control and the 2 500 kg ha⁻¹ dose while the highest salinity level caused a 100% decline when compared to the control.

Plant growth

Salinity stress is known to affect leaf expansion (Munns and Tester, 2008) and to cause leaf necrosis (DeMoranville, 2005; Wright et al., 1993) among different species. Cranberry plants

363 exposed to increasing amounts of salts presented a linear decrease in their total leaf area ($p <$
364 0.0001; Fig. 9). Visual observations suggest that this was mainly the result of leaf necrosis and
365 death. No significant difference was observed between the number of uprights and their lengths
366 whereas salinity treatments decreased runner growth. Indeed, the number of runners and their
367 average length were linearly reduced with increasing salinity ($p < 0.0001$ and 0.0053) and
368 irrigation type ($p = 0.0052$) with fewer runners in subirrigated plants. DeMoranville (2005)
369 observed an increase of runner dry weight with chronic application of NaCl on cranberry plants.
370 Since the amount of salts applied corresponded approximately to the 5000 kg ha^{-1} dose, it seems
371 that the nature of the ions used or the limited water availability in our study caused the damage
372 observed on runner growth. In addition to the effects on plant growth, subirrigation had a
373 significant deleterious effect on fruit set ($p = 0.0177$) which is consistent with our photosynthesis
374 results. In both irrigation treatments, fruit set values varied between 14 and 41% for the control
375 salt treatment which is fairly low. Indeed, values obtained from cranberry fields varied between
376 40 and 70% (Pelletier, 2015b). At the beginning of flowering, bumble bees were too numerous in
377 the greenhouse and caused damage to a few flowers before their density was adjusted. Moreover,
378 light intensity in the greenhouse was limited by thermal screens used to control temperature.
379 Typical photosynthetic photon flux density values during a sunny day in the greenhouse were
380 between 200 and $700 \mu\text{mol m}^{-2} \text{ s}^{-1}$ while field data recorded by our team ranged from 900 to 1600
381 $\mu\text{mol m}^{-2} \text{ s}^{-1}$ for the same day period. Both light intensity and bumblebees could have affected
382 fruit set. This parameter also decreased rapidly with increasing salinity following a quadratic
383 curve ($p = 0.0089$; Fig. 9) and yield decreased in the same way ($p = 0.0336$; Fig. 9). A significant
384 difference of 56% in yield was observed between the control and the 2500 kg ha^{-1} treatment.
385 Since the relative amount of buds also decreased with salinity ($p = 0.0022$; Fig. 9), subsequent
386 year yield could also be affected by previous year salt stress considering that the number of buds
387 formed at the end of a growing season is known to be a major yield component of the subsequent
388 year production (Eaton and Kyte, 1978; Pelletier et al. 2015b).

CONCLUSION

For both overhead and subirrigation treatments combined, a 22% drop in relative photosynthetic rate and a 56% decrease in yield were observed for an average EC_{ss} during flowering of 3.2 dS m^{-1} . With EC_{ss} ranging from 0.41 to 9.1 dS m^{-1} , growth parameters showed a linear response while productivity parameters had an early quadratic response to salinity levels, suggesting a pronounced sensitivity to salinity. Our data clearly suggest that cranberry can be salt sensitive. Despite this irrigation treatment comparison, very little is known about the actual EC_{ss} that can be induced by deficit subirrigation under field conditions in cranberry production and the type of ions that are most likely to be encountered in irrigation water. Future studies should investigate the effects of subirrigation on soil salinity under field conditions to determine the nature and amount of ions that can accumulate in the root layer over a growing season. Additionally, since our data suggested a linear negative response of photosynthesis to increasing amounts of K_2SO_4 , further research should investigate the relationship between EC_{ss} and yield within the 0 to 3.2 dS m^{-1} range with higher accuracy. *In situ* salinity monitoring should be recommended to prevent EC_{ss} from reaching levels that can impair plant growth and productivity in cranberry production.

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Figure 1. Experimental design consisting of four blocks each containing 8 treatments where "o" stands for overhead irrigation, "s" stands for subirrigation and 125, 2500, 5000 and 7500 are K₂O kg ha⁻¹ levels.

Figure 2. Average soil matric potential (8 replicates) recorded by tensiometers for aspersion and subirrigation treatments throughout the experiment.

Figure 3. Mean values of electrical conductivity of soil solution combining irrigation treatments and replicates. Salinity treatments were applied on April 1st, 8th, 10th and 22nd 2014. Measurements were taken with suction lysimeters and a conductivity meter two days after the treatment for each application. For each day, standard errors are presented and treatments with a different letter are significantly different with a 0.05 confidence level.

Figure 2. Water retention curves obtained with tensiometers and TDR probes compared to laboratory retention curves for aspersion and subirrigation treatments.

Figure 3. Average xylem water potential at turgor loss (n=3) as a function of salinity treatments. Data from the two irrigation treatments were pooled because there was no significant difference between overhead irrigation and subirrigation. Standard error bars show that no significant difference was observed between means but the linear contrast was significant at a 0.05 confidence level.

Only

Figure 4. Average EC of soil solution and average relative photosynthetic rates during flowering as a function of salinity treatments. Different letters along the same line indicates that the average is significantly different.

Figure 5a. Correlation between the average EC_{ss} and the average relative photosynthesis rates for overhead irrigation and subirrigation

Figure 6b. Relationship between the average EC_{ss} and the average relative yield rates for overhead irrigation and subirrigation combined. Salt sensitivity zones proposed by Maas (1993) are reported on the figure.

Figure 7. Changes in relative photosynthetic rates of cranberry plants exposed to four salinity treatments over time. Treatments were applied on April 1st, 8th, 15th and 22nd. For each time sampling date, means featuring with a different letter are significantly different. Standard error bars are shown for each mean.

Figure 8. Growth and yield parameters as a function of salinity treatments. Mean values with standard error bars for both irrigation treatments combined.

Table 1. Basic soil characteristics

Parameter	Aspersation	Subirrigation
Average soil matric potential (- k Pa)	4.1	6.34
Bulk density (g cm ⁻³)	1.41	1.47
Porosity (cm ³ cm ⁻³)	0.47	0.39
Air-filled porosity at average matric potenial (cm ³ cm ⁻³)	0.17 to 0.37	0.19 to 0.29
Average water content (cm ³ cm ⁻³)	0.25	0.14
Unsaturated hydraulic conductivity at average matric potential (mm h ⁻¹)	3.21	2.76

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