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Implications of physiological integration of stolon interconnected plants for salinity management in soilless strawberry production

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ABSTRACT

Salinity can be a greater problem in shallow soilless media than in field soils because of the small root zone volume that commonly occurs in such systems. Clonal integration (the capability of reciprocal resource translocation among interconnected plantlets through their shared stolon) can alleviate salinity injury in strawberry (*Fragaria x ananassa* 'Albion'). Here we report the effect of clonal integration on leaf area, shoot and root dry biomass, net CO_2 assimilation rate (A_N), stomatal conductance (g_s), intercellular CO_2 (ci), transpiration (E), and instantaneous water use efficiency (WUE). Interconnected mother-daughter pairs of strawberry plants were grown in stirred solution culture under greenhouse conditions. Combinations with independent salinity levels on the mother and daughter side were imposed in a 4 × 3 complete randomized factorial design. Salinity levels of 1, 3, 6 and 9 dS m^{-1} were established by adding calcium chloride ($CaCl_2$) and sodium chloride (NaCl) as needed to a 1 dS/m nutrient solution. Interconnected daughter plants grew in 0.2 $CaSO_4$, or the 1 dS m^{-1} nutrient solution, or the same solution supplied to the mother plant. Values of all measured attributes decreased with salinity, with the exception of C_i, which increased at the highest salinity combination of mother and daughter plants. In contrasting salinity conditions, clonal integration ameliorated salt stress in mother plants through water transfer from daughter to mother plants. Interclonal resource translocation was mainly driven by the contrast in stress intensity between mother and daughter plants.

1. Introduction

Salinity can be a greater problem in shallow soilless media than in field soils because of the small root zone volume and large substrate water-holding capacity that commonly occur in such systems. Salt concentrations can increase rapidly in small root volumes, and the extraction of a significant fraction of the soil moisture can result in extremely high salt concentrations.

In open systems, mitigation of salinity typically is achieved by frequent leaching of salts out of the system, resulting in lower water use efficiency and potential water quality problems due to the presence of fertilizers and pesticides in the leachate. These water quality problems have led many countries to impose restrictions on irrigation discharge from agricultural fields (Voogt and Sonneveld, 1997).

Soilless field production introduces the possibility to reduce leaching losses and water pollution by employing a closed system in which irrigation water containing fertilizers is recirculated. However, crop yields and quality may be reduced in recirculating systems because of increasing salt concentrations, especially where irrigation water quality is poor. Thus, recirculating systems may be effective only where water quality is high (Voogt and Van Os, 2012).

Strawberry is sensitive to salinity (Maas and Hoffman, 1977; Martinez Barroso and Alvarez, 1997; Saied et al., 2003). Its growth is impaired when the osmotic potential in the root environment is lower than −0.2 MPa (Ondrasek et al., 2006). Salinity has diverse effects on strawberry (Martinez Barroso and Alvarez, 1997) where Na^+ and Cl^- are the ions most commonly reported to cause these effects (Khan et al., 2000a,b; Mansour, 2000). Keutgen and Pawelzik (2007) reported that osmotic effect caused a reduction in fruit yield up to 46% when strawberry 'Elsanta' was treated with 80 mM NaCl. Kaya et al. (2002a,b) observed a reduction in chlorophyll content and plant growth in cultivars 'Oso Grande' and 'Camarosa' when grown at NaCl salinity of

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35 mM. They attributed the negative effects observed to high leaf Na, and they suggested that the low leaf Ca and N they observed was due to ion interactions, precipitation, and increased ionic strength. Pirlak and Esitken (2004) reported decreased number of crowns and leaves, lower foliar concentrations of N, P and K, and increased foliar Na and Cl when 'Fern' and 'Camarosa' strawberries were grown at an EC of 7.5 dS m^{-1} that was elevated by addition of NaCl. NaCl salinity may change nutritional status and ion balance, causing disorders due to lack of nutrient availability, competitive uptake, transport, and partitioning of nutrients within the plant (Grattan and Grieve, 1999). Turhan and Eris (2009) observed an increase in leaf proline content in cultivars 'Camarosa' and 'Chandler' that had been treated with 34 mM NaCl, which they regarded as indicator of salt damage. Saied et al. (2003) reported reduced photosynthetic capacity of 'Elsanta' strawberry when treated with 60 mM NaCl. Khayyat et al. (2009) reported a negative effect of 35 mM NaCl on 'Selva' strawberry that resulted in a reduced shoot to root ratio. Strawberry leaf injury (necrosis, scorching) and low productivity have been attributed to high EC in the soil solution and accumulation of Na or Cl in leaves (Carter, 1982; Hoffman, 1981; Turhan and Eris, 2009; Ulrich et al., 1980).

Strawberry generates runners (stolons) during normal plant growth and development. Adventitious roots usually develop at the second node, leading to growth of a new plant. This evolutionary adaptation allows the "mother" plant to propagate itself asexually, creating a clonal "daughter" plant that can survive independently if the runner degenerates or is severed. Although runners and daughter plants usually are removed during commercial strawberry production, the connected mother and daughter plants provide an opportunity to explore an alternative approach to salinity management. Clonal integration, the capability of reciprocal resource translocation among interconnected plantlets, may influence their performance in adverse conditions. For example, wild strawberry plants can survive lethal shade or drought stress if connected through clonal integration to a plant growing in a mild environment (Alpert and Mooney, 1986). Interconnected mother and daughter strawberry plants exchanged nitrogen and carbon when exposed to soil N heterogeneity (Friedman and Alpert, 1991). In goldenrod (*Solidago altissima*), transport of water and nutrients through runners is bidirectional, but translocation of other substances may be prevented by physical or physiological isolation (Abrahamson et al., 1991). These findings raise the intriguing possibility that clonal integration could result in sharing of water and nutrients between mother and daughter plants and mitigation of salinity effects if only one of the pair is exposed to elevated salt concentrations. Saied (2004) reported that 'Korona' and 'Elsanta' strawberries exclude Na from the plant and inhibit Cl translocation to leaves by storing it in crowns and roots. Thus, it may be possible to exploit genetic variation among strawberry cultivars to limit these effects of NaCl by using interconnected plants that are able to adapt to stressful conditions and share resources (Alpert and Mooney, 1986).

The purpose of this study was to investigate the physiological integration of mother and daughter plants connected by their own stolon under greenhouse conditions. Our hypothesis was that clonal integration in strawberry could alleviate salt stress in mother plants exposed to high salinity if the daughter plant is exposed to low salinity.

2. Material and methods

The experiment was conducted in a greenhouse at the Environmental Horticulture research facilities at the University of California, Davis, CA. Frigo 'Albion' strawberry bare-root plants were graded by crown diameter, and root systems with similar volumes were trimmed to 10 cm in length. Plants were grown in a continuously stirred and aerated deep-water culture system that consisted of square plastic containers that were 19 cm on a side and 22 cm deep. The nutrient solution (Table 1) was continuously circulated between pairs of containers for homogeneous salinity levels through blue plastic tubing

Table 1
Nutrient solution composition for 'Albion' strawberry plants grown in a stirred solution culture. The final solution EC was between 0.9–1 dS m^{-1}.

Cations		Anions	
Nutrient	Concentration mg L^{-1}	Nutrient	Concentration mg L^{-1}
K	58.5	NO_3-N	63
Ca	80	P	15.48
Mg	18.2	S	32.64
Fe	2.8	B	0.6
Mn	0.4	Mo	0.03
Zn	0.2		
Cu	0.1		

(1.27 cm diameter) to allow continuous recirculation and equal concentrations and solution volumes in each pot. Independent comparable pots for heterogeneous salinity levels were filled with the same nutrient solution. Air was bubbled continuously into each pot by dual diaphragm air pumps (General hydroponics-USA, Sebastopol, CA). Dissolved oxygen was measured with sensors (CS511 Sensorex, Campbell Scientific Inc., North Logan, UT) placed in the nutrient solution. The average dissolved oxygen concentration was 8.35 mg L^{-1} and minimum and maximum values were 6.74 and 9.96 mg L^{-1}, respectively.

Plants were grown for 10 weeks in nutrient solution and each plant was allowed to produce a single runner. The second node of the connected runner was rooted in a separate container to form a clonal system consisting of the two rooted plants united by a stolon, but otherwise isolated from each other in solution culture. The older plant was referred to as the mother and the younger as the daughter (Fig. 1). The mother plants used in experiment were in vegetative phase with an age of five months established after the transplant.

After daughters were well rooted (10 weeks), salinity treatments were imposed in a 4 by 3 factorial design with four replicates per treatment (Table 2), where factor A were the salinity levels for the mother plant (EC = 1, 3, 6 and 9 dS m^{-1}); while the factor B were the salinity levels of the daughter plants (EC = 0.2, 1 and ISO dS m^{-1}), where isotonic (ISO) are the treatments in which the mother-daughter pairs were cultivated at the same level of salinity. Control treatment was the interaction of mother plant subjected to EC of 1 dS m^{-1} and the daughter plant to EC of 0.2 dS m^{-1}. Each mother-daughter pair formed an experimental unit. We refer to these using a convention for indicating the solution electrical conductivities of the mother-daughter pairs; for example, M6/D0.2 refers to the pair in which the mother plant is growing in the 6 dS m^{-1} solution and the daughter in the 0.2 dS/m solution.

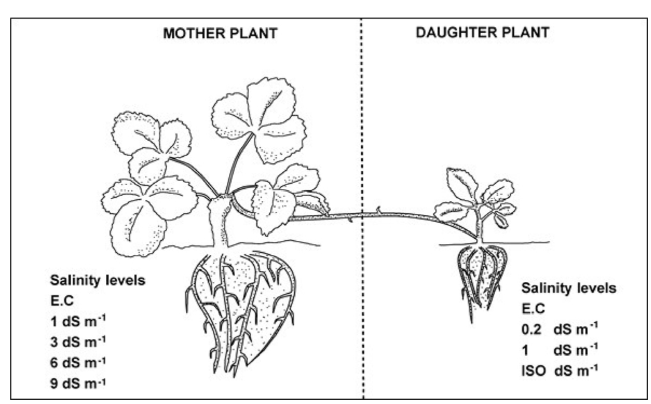

Fig. 1. Design of factorial experiment 4 × 3, where the mother plant presented 4 different C.E and daughter plant different levels of salinity. The evaluated plant was the mother plant, where Iso indicates comparable salinity in both mother and daughter plant.