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Jerusalem artichoke (Helianthus tuberosus, L.) maintains high inulin, tuber yield, and antioxidant capacity under moderately-saline irrigation waters

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ABSTRACT

Information on management strategies and alternative crops adaptable to saline waters is scarce. We investigated the effects of high-salinity water (HSW) blended or sequentially applied with low-salinity water (LSW) on growth, mineral nutrients, and tuber biochemistry of Jerusalem artichoke (*Helianthus tuberosus*, L. cv. 'Stampede'). Plants were irrigated with blended waters of electrical conductivity (EC_w) ranging from 1.2 dS m^{-1} (LSW control) to 12 dS m^{-1} (highest HSW treatment) or with LSW followed by hsw at set intervals (sequential management). Both growth and tuber yield were significantly reduced between LSW control (ECw = 1.2 dS m^{-1}) and 12 dS m^{-1}. An increase in salinity from 1.2 to 6.6 dS m^{-1} reduced shoot biomass by 37%, but tuber yield only by 11% showing that the plant can tolerate soil-water salinity (EC_{sw}) = 6.6 dS m^{-1}, while increasing salinity to 12 dS m^{-1} caused a 67% decrease in shoot and 47% decrease in tuber yield. Shoot biomass was similar for blended and sequential treatments of equivalent salinity. Tuber yield of sequential treatments was similar to control salinity if 75% of irrigations used LSW. 'Stampede' accumulated sodium in roots, but not in shoots. Chloride increased in all organs, mainly in leaves and roots, and high chloride, not sodium, accounted for decreased shoot and tuber biomass. In general, salinity had no effect on the concentrations of minerals, inulin-type fructans and their degree of polymerization, or on tuber antioxidants, but decreased tuber sucrose significantly. Tubers had 50–60% inulin-type fructans and less than 0.02% starch. 'Stampede' is an early cultivar adapted to moderate salinity (EC_w = 6.6 dS m^{-1}) producing, at 5.6 plants m^{-2}, 83 Mg ha^{-1} of tubers (41.5 Mg of inulin ha^{-1}) and, at control salinity, 92 Mg ha^{-1} (46 Mg of inulin ha^{-1}). The crop is a rich source of feedstock for biofuels or for non-caloric, prebiotic, soluble fiber for the food industry.

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1. Introduction

Helianthus tuberosus, L. (Asteraceae), also known as Jerusalem artichoke or sunchoke, is originally from North American being one of the few crops taken from the New World to Europe and Asia. Its tubers were an important source of food for Native Americans. Although the whole plant can be used as animal feed (Seiler and Campbell, 2004), and the tubers as food and feed, it has been mainly studied in the past 10 years as a biomass crop for ethanol production (Gunnarsson et al., 2014; Johansson et al., 2015) yielding 7 to 14 t ha^{-1} of carbohydrates (Denoroy, 1996). Its tubers accumulate inulin-type fructans (polymers of fructose molecules) to at least 50% DW (Danilcenko et al., 2008), 6–12% protein (Cieślik et al., 2011; Seiler, 1990), and amino acids (Danilcenko et al., 2013). Fructans with a short chain length are known as fructooligosaccharides – FOS. Inulin is a natural storage fructan carbohydrate present in over 36,000 plant species, including wheat, onion, bananas, garlic, asparagus, Jerusalem artichoke, and chicory. Because inulin is soluble in water, it is osmotically active. Plants can change the osmotic potential of cells by changing the degree of polymerization of inulin molecules through hydrolysis, without changing the total amount of carbohydrates. This osmotic regulation role helps plants tolerate cold and drought during winter periods (Boeckner et al., 2001). Inulins with both high and low degree of polymerization (DP), the latter referred to as FOS, can be used for biofuel production,

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Abbreviations: lsw, low-salinity water; hsw, high-salinity water; EC_w, electrical conductivity of irrigation water; ROS, reactive oxygen species.

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nutritional purposes such as low caloric soluble dietary fiber (Al-Sheraji et al., 2013), and as prebiotics that stimulate the growth of probiotic gut bacteria, mediate sugar and lipid metabolism (Wada et al., 2005), and stimulate the immune system (Judprasong et al., 2011). Most of the inulin-type FOS commercially available today are extracted from chicory roots, which contain only 20% inulin (Baert and Van Bockstaele, 1993), or are synthesized from sucrose (Niness, 1999; Wada et al., 2005).

The scarcity of fresh water in semiarid regions is the main factor limiting the increase in irrigated cultivated area needed to feed a growing world population. This limited water supply forces many farmers to use non-conventional, or recycled, irrigation water that lowers the yield of agricultural crops and, in the long run, increases salinization of irrigated areas. Examples of recycled waters are brackish groundwater, saline drainage waters, municipal wastewater, and brine resulting from water desalination plants. Currently, feasible replacement of fresh water with saline water requires the selection of salt-tolerant crops with economically-viable yields according to the expected root-zone salinity, adequate drainage, and the application of a suitable irrigation water management strategy that can save fresh water. Salt tolerance is generally defined by the ratio of yield under saline conditions divided by the yield under non-saline conditions (Maas and Hoffman, 1977). Salt-tolerant crops are often lower yielding under non-saline conditions so crop selection must also consider absolute yield under the specific growing conditions. When saline water is abundant, and fresh water limited, the following management strategies can be used to reduce the effects of salinity on plants: saline waters used alone, blended with fresh water, or in sequence with fresh water (Malash et al., 2008; Medeiros et al., 2014; Nangare et al., 2013). The advantages of sequential use over blending has been established for crop rotations where one crop is salt sensitive and the other crop is more tolerant (Murtaza et al., 2006; Rhoades et al., 1989), but has not been tested in Jerusalem artichoke. Due to its reduced costs, saline water blended with fresh water can be a viable alternative to save fresh water while maintaining crop yield. Although this blended-water management strategy can enable crop irrigation at lower costs, it may increase the total salts retained by soils with poor drainage and result in soil and shallow groundwater salinization.

Salt tolerance differs among species and among cultivars of the same species. Also, in the same cultivar, tolerance may vary according to the plant phenological stage (del Amor et al., 1999). Jerusalem artichoke (*Helianthus tuberosus*, L.) is reported to be both a salt and drought-tolerant species that can adapt and grow in soils that are both saline and alkaline (Newton et al., 1991) and unsuitable for staple agricultural crops. The crop grows well in the pH range of 5.8–7.0, but growth is favored by slightly alkaline pH (Cosgrove et al., 2016). During two years of field trials in Spain, plants of the cultivar Nahodka that had 50% and 75% of their optimal water supply restricted during the first stage of growth, decreased their tuber yield by only 0–13% (Conde et al., 1991). However, most salinity research on Jerusalem artichoke has focused on short-term salt stress and most cultivars used were neither well characterized nor available commercially (Chen et al., 2011). Newton et al. (1991) assessed the salt tolerance of irrigated Jerusalem artichoke for its shoot and tuber biomass in both greenhouse and field trials. Salinity of irrigation water ranged from 0.7 to 12 dS m^{-1} in the greenhouse trial and from 0.2 to 10 dS m^{-1} in the field trial. Based on dry matter yield of tubers of greenhouse-grown plants and of shoots of greenhouse-grown and field-grown plants, their unidentified cultivar was classified as 'moderately sensitive' to salinity, according to Maas and Hoffman (Maas and Hoffman, 1977).

In the past decade, accumulated evidence suggests that abiotic stresses, including salinity, are associated with plant built-up of reactive oxygen species (ROS) that can induce stressed plants to increase enzymatic and non-enzymatic metabolites in an attempt to counteract excessive ROS and adapt to stress (Di Baccio et al., 2004). These authors showed that Jerusalem artichoke irrigated with 10% seawater ($EC_W = 6.4$ dS m^{-1}) significantly increased levels of ascorbate and glutathione in roots, and glutathione reductase in leaves and roots, while the levels of ascorbate reductase remained unchanged by salinity in both leaves and roots. Xue et al. (2008) reported that salt-stressed (150 $mmol_c$ L-1 NaCl – about 15 dS m^{-1}) reduced the activity of superoxide dismutase, peroxidase, and catalase. Malondialdehyde has also been described as an indicator of membrane damage caused by lipid peroxidation and used to differentiate salt-tolerant from salt-sensitive species (Chen et al., 2011). However, there is no published information on the effects of salinity stress on the concentration of sucrose and inulins, accumulation/decrease of non-enzymatic antioxidants (e.g. flavonoids and phenolics), and on the complete mineral nutrient status of Jerusalem artichoke shoots and tubers.

Our first objective was to relate salinity of irrigation waters to plant growth, shoot and tuber biomass accumulation, tuber inulin concentration, degree of inulin polymerization, fructose, sucrose, and glucose as sources of carbon for biofuels. Second, we aimed to identify salinity effect on the uptake of Na^+ and Cl^-, macro and micronutrients, and tuber antioxidant capacity. The third objective was to evaluate the use of high-salinity water (hsw) blended with low-salinity (tap) water (lsw) *vs*. sequential use of lsw followed by hsw.

2. Material and methods

The experiment was conducted at the U.S. Salinity Laboratory (USDA-ARS), Riverside, CA (Lat. 33.9°58′24″ N, Long. 117°19′12″ E and Alt. 311 m). The average maximum and minimum temperatures during the growing season (April 29 to July 18, 2014) were 29.8 and 15 °C, respectively. There was no rainfall during the period over which the experiment was conducted. Day lengths for the growing season changed from 13 h 29 min (April 29, planting) to 14 h 9 min (July 18, shoot biomass harvest), then to 12 h 46 min (September 4, tuber harvest) according to http://www.calendar-365.com/calendar/2014/April.html

2.1. Plant material and growth conditions

Whole tubers of Jerusalem artichoke (*Helianthus tuberosus,* L., cv. 'Stampede'), obtained from a commercial farm (Potato Garden, Austin, CO, USA), were homogenized for size and planted on April 29, 2014 in large (3.0 m long × 1.5 m wide × 2.0 m deep) outdoor tanks, part of an outdoor lysimeter system, filled with loamy sand and equipped with an automated irrigation system. This system enables complete recycling of the irrigation waters while maintaining stable root-zone salinity (Fig. 1). The system is contained to prevent environmental contamination while maintaining thermal and drainage properties similar to the ones found in sandy soils (Wang, 2002). The irrigated experimental plot had 24 tanks, each connected to irrigation reservoirs (3605 L) through ½ HP pumps that circulate the water inside reservoirs and irrigate the tanks in the corresponding outdoor sand tank (Fig. 1). Irrigation was done twice a week with treatment waters (nutrient/salt solutions) completely saturating and leaching the sand culture medium. In each tank, the nutrient/salt solution returned to the reservoir, after irrigation, through a subsurface drainage system at the bottom of the tanks, thus maintaining an relatively uniform and constant salinity in the root zone.

In each tank, tubers were planted 5-in. deep in two rows spaced 0.6 m apart, and 0.3 m apart within the rows. The loamy sand in the tanks was mixed with 10% peat moss (v/v) resulting in an average bulk density of 1380 kg m^{-3} and an average volumetric water + air