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Spinach biomass yield and physiological response to interactive salinity and water stress

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ABSTRACT

Critical shortages of fresh water throughout arid regions are forcing growers to decide among the following options, applying insufficient fresh water, causing water stress, applying saline water causing salt stress or applying some combination minimizing saline water application, causing combined water and salt stress. A comprehensive approach to manage drought and salinity is to evaluate the impact of water stress and salt stress individually and then examine their interactions on plant production. To analyze salinity and water stress responses and their interaction together on spinach growth, an experiment was conducted from April 1 to May 21, 2013, using 6 different irrigation waters at electrical conductivity (EC): 0.85, 4, 7, 9, 12, 15 dS m^{-1}. Soil moisture was recorded by sensors and stress treatments had the following soil water matric pressure control (−45 kPa), −200 to −300 kPa, and −400 to −500 kPa. We evaluated three replicates per treatment for yield, vegetative parameters, ion composition, and physiological parameters. The results showed that the spinach yield response to salt and water stress was very different. Spinach yield initially increased with salinity and subsequently decreased only when the irrigation water was EC 9 dS m^{-1} and above (osmotic pressure of −310 kPa). In contrast, yield decreased at the first water stress level (−230 kPa) relative to control. The additional presence of salinity stress decreased the relative yield response due to water stress. Similarly under water stress the relative yield response to increasing salinity was reduced. Although no model provided good prediction of stress response, the best predictive model (relative error) was one that considered the response to multiple stresses as the product of the response to the individual stresses.

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1. Introduction

Drought and salinity are the two major abiotic stresses dramatically limiting crop growth and productivity worldwide and the area affected by these two stresses is still increasing (Wang et al., 2003). The optimal approach to counter drought and salinity stress is development of tolerant crop varieties. Thus, it is important to understand the mechanisms of drought and salinity tolerance in plants, both to develop new varieties and to develop management practices to minimize the adverse effects. Drought is considered the primary destructive, crop yield-limiting factor, and detailed knowledge of its impact on plant growth regulation is crucial (Avramova et al., 2015). The adverse impact on crop production may increase as climate change is predicted to increase the frequency and severity of crop water stress, causing significant yield loss (Trenberth et al., 2014; Obidiegwu et al., 2015; Zhan et al., 2015). Salinity, another important abiotic stress limiting crop production is also increasing in extent worldwide at an estimated rate of 1.5 million ha per year (Eynard et al., 2006) and is estimated to affect 23% of cultivated lands (Tanji and Wallender, 2012).

Drought, salinity, extreme temperatures and oxidative stress are often interconnected, and may induce similar cellular damage. For example, drought and/or salinity are considered to be manifested primarily as osmotic stress, resulting in the disruption of homeostasis and ion distribution in the cell (Serrano et al., 1999; Zhu, 2001). The apparent similarity of the effects of salinity and drought has raised the question as to whether the same change in the plant water status caused either by salinity or by drought leads to the same yield reduction (Katerji et al., 2004).

Several studies have separately evaluated the effects of salinity stress and drought stress expressed as osmotic and matric potential (De Pascale et al., 2007; Xu and Leskovar, 2015). A few studies have evaluated the interaction of salinity and water application as related to yield (Shani and Dudley, 2001; Shani et al., 2007), interac-

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tions of salinity and leaf water potential (Katerji et al., 2009; Katerji et al., 2011), consecutive salinity and non-saline (PEG) osmotic treatments as a proxy for water (matric) stress (Nagy and Galiba, 1995). However, there is very little information on plant response where the matric stress was measured and controlled. Ahmed et al. (2013), examined salt and water stress interactions by withholding irrigation, allowing the water content to decrease to a soil moisture content of 4% where it remained for 10 more days. Previous studies thus either made periodic irrigations to saturate the soil and then delayed subsequent irrigation, applied less quantities of water to induce drought without measuring matric potential or induced drought at the end of the experiment. In these instances matric potentials were either unknown or fluctuated widely during the experiments.

Our objective in this study was to determine and then compare the separate and interactive effects of water and salinity stress, conducting experiments under defined and essentially constant matric and osmotic stress over almost the entire life cycle of the plant (after seedling establishment). We also tested the hypothesis that the effect of combined stress on yield can be represented by multiplying the response to the individual stresses.

2. Materials and methods

The experiment was conducted outdoors with spinach (*Spinacia oleracea* L., cv. Racoon) during the interval between 1 April-21 May 2013 at Riverside, Calif., (lat.33E58′24′, long. 117E58′12′). Seeds were sown directly in sand culture tanks, 10 cm apart and 40 cm between rows. We planted three rows per tank in the outside large tanks at 1 April. The seedlings were later thinned to 25 plants per row. Sand culture tanks ($1.5 \times 3 \times 2$ m deep) were filled with sand mixed with 10% peat moss (at volume basis) with an average bulk density of 1.38 g cm^{-3}. Peat moss was added to increase the water holding capacity of the sand. The sand mix had an average volumetric water content of 0.30 m^3 m^{-3}.

Six different irrigation waters (mixed salt composition) at EC; 0.85 (control), 4, 7, 9, 12, 15 dS m^{-1} were used in the experiment (Table 1). Each plot was irrigated with solutions prepared in individual reservoirs (1.5 m diameter × 2.2 m deep) having a volume of 4500 L. Irrigation solutions were pumped from the reservoirs to the tanks and then returned to the reservoirs through a subsurface drainage system at the bottom of each tank, maintaining a uniform and constant salinity profile. Initial irrigations consisted of nutrient solution made up in Riverside California U.S.A. tap water with nutrients added as (in mM): 2.5 Ca $(NO_3)_2$, 3.0 KNO_3, 0.17 KH_2PO_4, 1.5 $MgSO_4$, 0.05 Fe as sodium ferric diethylenetriamine pentaacetate (NaFe-EDTA), 0.023 H_3BO_3, 0.005 $MnSO_4$, 0.0004 $ZnSO_4$, 0.0002 $CuSO_4$, and 0.0001 H_3MoO_4. This solution served as the base nutrient solution. The base nutrient solution without added salts served as a non-saline control (<1.0 dS m^{-1}) in all experiments. As the water from each of the sand tanks drained back into its own irrigation reservoir we were able to measure water use in each tank by measuring water volumes in the irrigation reservoirs.

Final electrical conductivities of the saline irrigation waters (EC_{iw}) of 4, 7, 9, 12, 15 dS m^{-1} were achieved by adding $CaCl_2$, $MgCl_2$, $NaCl_2$, Na_2SO_4 and base nutrients to tap water (Table 1). For calculation of the treatment salt concentrations we used the EXTRACT CHEM model (Suarez and Taber, 2012) that predicts the EC and osmotic pressure of input solution compositions. Salinization was initiated after the first pair of true leaves was fully expanded on all the plants. Salts were added in 4 equal increments over a period of 4 days to avoid osmotic shock to the seedlings.

Measurements of the water content (θ) of the substrate were accomplished using calibrated ($\ln(\theta) = -6.99 + 16\,V - 9.9V2$, $R^2 = 0.91$) dielectric soil moisture sensors (ECH_2O-10 probes, Decagon, Pullman, WA, USA[1]) inserted at 10 cm depth. A total of 16 ECH_2O moisture sensors were used in the study. The ECH_2O moisture sensors were connected to a multiplexer (AM25T, Campbell Sci., Logan, UT, USA), which in turn was connected to a data logger (CR10X, Campbell Sci.) to record the sensor output. The water retention curve was determined using the pressure plate method (Klute, 1986). The measured water contents from the sensors were then converted to matric potential using the water retention curve. Drought treatments were designed with soil water matric pressure targets of D1 (−200 to −300 kPa), treatment D2 (−400 to −500 kPa) and control D0 (no water stress, >−45 kPa).

Plant photosynthetic rate (Pn), stomatal conductance (g_s), transpiration rate (T_r) and concentration of intercellular CO_2 (C_i), were measured on the third fully expanded upper leaves along the right abaxial side of the leaf lamina between 10:00-11:00 am one week before harvest using a portable Li-Cor 6400 Photosynthesis System. The measurement conditions were leaf chamber PAR (photosynthetically active radiation), 1100 μmol m^{-2} s^{-1}; leaf to air vapor deficit pressure, 1.7–2.6 kPa, leaf temperature 20–22 °C and chamber CO_2 concentration 400 μmol mol^{-1}. The leaf greenness of the spinach plants was determined by a portable chlorophyll meter (SPAD-502; Konica Minolta Sensing, Inc., Japan) at the time of the gas exchange measurements and given as leaf chlorophyll values. SPAD measurements were made on the youngest, fully expanded leaves, then averaged (Khan et al., 2003).[1]

We measured the fresh weight of the above ground parts of all plants (three rows) for each replication (three). A plant from each of three rows and for each replication (9 plants per treatment) was also measured for root length, root weight, shoot height, number of leaves, and leaf area. We measured the water consumption from each of the reservoirs below the tank and combined these data with the fresh weight yield to obtain the water use efficiency (WUE). WUE (g mm^{-1}) was calculated by dividing the total plant fresh weight (g) by the actual evapotranspiration (ETa in mm) as described by De Pascale et al. (2011). ETa of spinach grown in tanks was calculated using a water balance equation where

$$ET_a = \Delta V/A \quad (1)$$

and ETa is the actual evapotranspiration (mm), ΔV is the water consumed by the crop (mm^3) and A is the area of the experimental tank (mm^2). The ΔV is calculated from,

$$\Delta V = V_i - V_f \pm \Delta S - D \quad (2)$$

where V_i, and V_f and are the initial and final volumes (mm^3) in the reservoir system, respectively, D is the water volume discharged out of the system and ΔS is the change in sand tank moisture content (mm^3). Since we have a closed system (tank plus reservoir) with no discharge, D is zero. The experimental design was a randomized complete block design with three replications for yield, vegetative parameters, ion composition, and physiological parameters. All of the data obtained from the measurements were evaluated statistically by analysis of variance to compare the effects of drought levels and irrigation waters using SPSS package software (SPSS, 2004). The differences among the means were compared using the Duncan multiple tests. General Linear Model analysis was performed to determine the relationship between selected parameters.

In order to evaluate the abiotic stress models with an additional data set, we included data from a preliminary experiment conducted during December 2012- March 2013. The general details of the salt tolerance aspect of the experiment are provided in Ors and

[1] Mention of trade names or commercial products in this publication is solely for the purpose of providing specific information and does not imply recommendation or endorsement by the U.S. Department of Agriculture.

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