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ECOPHYSIOLOGICAL RESPONSES OF *Solanum lycopersicum* L. cv RIO GRANDE TO IRRIGATION AND SALINITY REGIMES IN SCREENHOUSE

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ABSTRACT

Increasing population, a rapidly changing climate and declining arable land necessitates knowledge on performance of high valued crops under predicted abiotic stress conditions. Water and salinity stress will dominate future crop production environments. We investigated the effect of three irrigation levels comprising a deficit and an excess irrigation scenario, and four salinity levels of 0, 4, 8 and 12 ppt in a 3x4 factorial design, on the growth, yield and ecophysiological attributes of tomato in screenhouse. Measurements were taken till maturity and data subjected to GLM ANOVA, Spearman Rank Correlation and Factor analyses. Increasing salinity from 0 to 8 ppt significantly decreased the mean number of leaves from 56.02 to 50.64, and leaf area from 1008 to 874 cm^2. Senescence was more at higher salinity. For all salinity levels, transpiration rate per plant were higher for higher irrigation water volumes. Over time, plants irrigated with 4.5 L of water per week transpired more water across all salinity levels with the highest (0.19 L) observed at 8 ppt. Increased irrigation resulted in a higher transpiration rate. Salinity increase from 0 to 12 ppt significantly increased succulence from 2.08 to 5.23, while SMF decreased significantly from 0.8 to 0.55. An increase in irrigation resulted in a mean decrease in WUE from 5.27 to 1.61gl^{-1} and a mean decrease in TUE from 516.2 to 148.05gl^{-1}, while transpiration rate increased for the same irrigation intervals. Therefore tomato is more susceptible to salinity than water stress, and its output will reduce under future saline soil conditions.

Keywords: Deficit irrigation; salt stress; transpiration rate; transpiration use efficiency; water use efficiency.

INTRODUCTION

Global population has continued to increase especially in Africa [1,2], and with it the need for increased production of nutritive high value crops [3,4] to feed the increasing population. The pathways for increased food production are mainly threefold, namely through increase in the area under production, or increased inputs and hence cultivation intensity in the areas currently under cultivation, or through advances in agricultural production technologies. Each of these options has its advantages and negative consequences. Of these options, the most applicable in the developing world is through increase in the area under cultivation. In consequence, increase in food production here is constrained by two main challenges. Firstly, deforestation of land, with the attendant consequences of land degradation and climate change, and

secondly, limitation in the size of available arable land, which compels farmers to increasingly cultivate in fringe zones and during the offseason.

Several authors (Tinker et al. [5]; Chagnon & Bras [6]; Pires & Costa [7]) have shown that deforestation is a major contributor to anthropogenic climate change, contributing to increase in greenhouse gases, altering regional precipitation patterns and rates as well as temperature changes. These changes result in three major forms of water stress. Increased precipitation could lead to water logging or submergence stress while a decrease would result in drought stress [8]. Therefore in irrigated systems, knowledge of threshold for irrigation is essential for both water economy and physiological reasons. Secondly, cultivation of crops in fringe lands that are typically unfertile, is mainly possible through fertilizer application and irrigation, both of which have the potential to increase or cause secondary salinization of the soil. Excess nitrogen in the soil from fertilization with nitrogen-based fertilizers is nitrified, leading to secondary salinization [9], likewise irrigation with low quality water which is often the most affordable or available to farmers in developing countries, also leads to secondary salinization [10]. In consequence, salinity and water stress are seen as the greatest abiotic stressors affecting crop production [11].

The responses of plants to these abiotic stressors differ from species to species because they are genetically coded (Hirayama & Shinozaki [12]; Haak et al. [13]). Therefore thresholds of abiotic factors that result in stress vary from plant to plant. Once the threshold is met, stress occurs. Most plants are sensitive to abiotic stress, and in response display a suite of stress survival responses that often depend on the stressor. In response to waterlogging or submergence, tolerant plants develop aerenchyma and barriers to radial oxygen loss, accumulate ethylene and initiate fermentation for generation of ATP with high consumption of carbohydrates and up-regulation of tolerant genes, as well as restricted metabolism to reduce growth [14]. Responses of plants to drought stress on the other hand are tailored to conserve water, and include reduced leaf area, stomatal closure or increased stomatal resistance, increased root:shoot ratios, overall reduction in growth and reproduction [15]. In response to salinity stress, tolerant plants resort to salt secretion through salt glands and ion compartmentalization and translocation to vacuoles [16]. Common responses to both water stress (waterlogging, flooding and drought) and salinity stress are up-regulation or de novo synthesis of compatible osmolytes like proline, glycinebetaine, polyamines, polyols etc. that function in stabilizing membranes, protecting DNA and in osmoregulation and hence counterbalancing or cancelling the negative effects of high concentrations of reactive oxygen species and membrane lipid peroxidation [16,17]. Except in extremophiles, there is ultimately a reduction in growth, reproduction and yield because the response mechanisms to abiotic stress necessitate either a reduction in photosynthesis rates due to stomatal control and water and nutrient uptake limitation, or a shift of photosynthesis from growth processes to synthesis of biomolecules required for stress response [18].

The extent to which these response pathways are rallied depends on the plant's ability to up-regulate the necessary genes. In consequence, to ensure stability in production of high value crops in a future where increased water stress and secondary salinity of soils is forecast, it is

essential to understand the thresholds to growth and reproduction in the respective plants of interest, under these stressors. *Solanum lycopersicum* L. is a high value horticultural crop across the world. In Cameroon, it is grown in areas with cool temperate-like climate, and in these areas, suitable arable land is already limited. Increasingly there is off-season production which requires irrigation and fertilization with concomitant risk of water stress and secondary salinization. The aim of this research was to evaluate the responses of this crop to different salinity and irrigation regimes in screenhouse, in view of future-proofing its production in an era where these conditions would be more prevalent.

MATERIALS AND METHODS

Study Site

This study was carried out in a screenhouse constructed at the Divisional Delegation for Agriculture and Rural Development for Meme, Kumba, Cameroon located at the geographical coordinates 4°38'N 9°27'E and 4.63°N 9.45°E and an elevation of 240 metres (790 ft) above sea level. The site is within Cameroon's Agro-ecological Zone IV with an annual rainfall of 2200 mm and an average annual temperature of 31°C (IRAD, unpublished data).

Experimental Design

A 3 by 4 factorial design was used. There were two factors, namely, salinity and irrigation, with four salinity levels (S_1 = 0ppt, S_2 = 4 ppt, S_3 = 8 ppt and S_4 = 12 ppt) obtained by dilution of seawater with freshwater. There were three irrigation regimes namely I_1 corresponding to 1100 mm, half the mean annual irrigation for Kumba representing a deficit irrigation scenario, for which each pot received 1.5 L of irrigation water per week; I_2 corresponding to 2200 mm per year, the mean annual rainfall for the region, for which plants received 3 L of irrigation water per week; and I_3 corresponding to 3300 mm which is one and a half times the normal irrigation for the region representing an excess irrigation scenario, for which each pot was irrigated with 4.5 L of irrigation water. This gave a total of 12 treatments. The 12 treatments were replicated three times to give a total of 36 experimental units. Within each experimental unit, four plants were grown. The pots were randomized within the screen house for more uniform micro environment across treatments.

Characteristics of Planting Material

The study species was *Solanum lycopersicum* L. commonly known as tomato. The cultivar used was the Rio Grande variety. Seedlings were raised from certified seeds produced by Griffaton, France. Prior to purchase the seeds had been sealed in cans containing 50g tomato seed and treated with THIRANE. The percentage viability was 95% and the seeds germinated with high and uniform vigour.

Soil Collection, Potting and Pre-planting Soil Analysis

Top soil was collected from the top 30 cm in a fallow area within the research site, well mixed and used to fill 36 plastic pots of volume 10 L each with a surface area of 530.9 cm^2. The pots were perforated uniformly using a 6 mm rod, with 10 holes below and 12 holes by the sides at regular intervals. A sample of the soil was collected and sent to the Plant and Soil laboratory of the University of Dschang for pre-planting soil analysis, to determine the suitability of the soil for the experiments. Results of this

analysis are presented in Table 1. The soil was sandy clay, slightly acidic, rich in organic matter, with suitable levels of exchangeable cations (Table 1). We concluded is has suitable characteristics for growth of tomato under controlled conditions.

Agronomic Operations

One hundred and forty four healthy tomato seedlings of similar heights were selected from the nursery and transplanted into the pots with each pot having four plants. Transplanting was done three weeks after germination in the nursery. The plants were irrigated three times a week at regular intervals with freshwater for two weeks until they were fully established. Then the different treatments were applied on the plants. Weeding was done regularly to prevent competition and control pests. Fungicide (Mancozebe and Ridomil Gold) and insecticides (Onex Super) were sprayed twice a week to ensure the plants were free from disease. Spraying of insecticides was regulated during flowering. This was to avoid killing useful insects that could be beneficial for pollination.

Application of Treatments

The treatments commenced two weeks after transplanting. For each salinity level, the three replicates of each treatment were irrigated with the respective volumes of irrigation water as described in Section 2.2. Irrigation water for each week was applied in three split applications. For one replicate of the treatments, the schedule of treatments is shown in Fig. 1.

Data Collection

Collection of data commenced two weeks after transplanting to get the baseline measurements before applying the treatments. The following parameters were measured: height, number of branches, number of leaves, leaf area, rate of transpiration, number of flowers, number of fruits, fruit size, fruit weight, chlorophyll concentration and plant biomass.

Table 1. Characteristics of soils used for the experiment

Soil property	Value	Soil property	Value
Texture	Sandy Clay	**Exchangeable cations (me/100 g)**	
pH (water)		Calcium	1.84
pH (KCl)	4.7	Magnesium	0.88
Organic Matter		Potassium	1.67
Organic carbon (%)	4.24	Sodium	0.34
Organic matter (%)	7.31	Total	4.73
Total nitrogen (g/kg)	0.77	**Exchangeable acidity (me/100g)**	
C/N ratio	55.08	H+ Al (EA)	
		Cation Exchangeable capacity (CEC)	
		Effective CEC	9.12
		S/CECE (%)	42.5
		Available Phosphorous (ppm)	9.5

KCl = potassium chloride, me = milliequivalent, CEC = cation exchange capacity

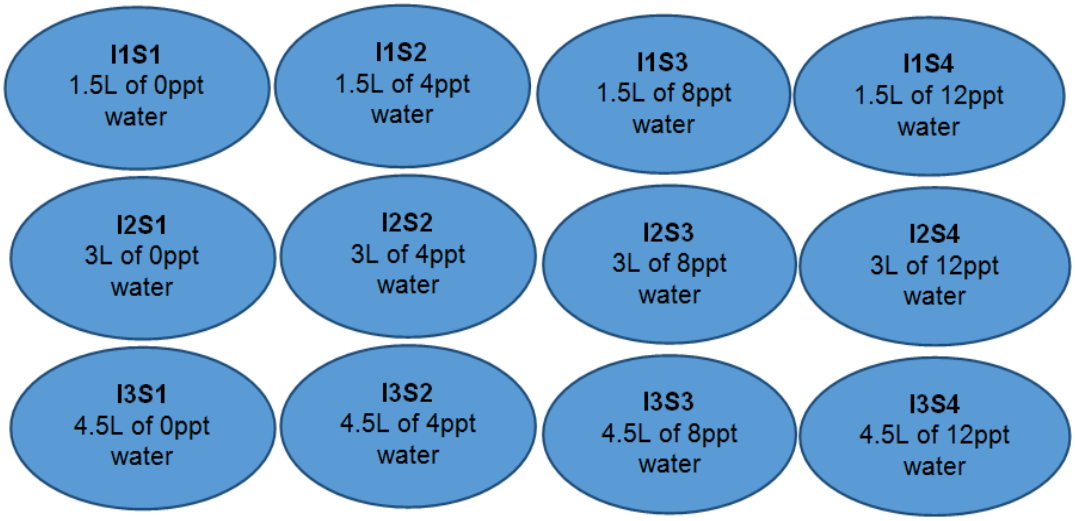

Fig. 1. Treatments applied according to a 3x4 factorial design of 3 irrigation levels (I1 to I3) and 4 salinity levels S1 to S4

Growth parameters

Height of plants, number of leaves, total leaf area and number of branches were measured weekly. Plant height was measured from the base to the crown of the plant using a meter tape graduated in centimetre. The total number of leaves was obtained by counting. Leaf area was measured using the method of tracing on graph paper graduated in mm [19]. The average leaf area of the traced leaves was then multiplied by the total number of leaves on the plant to have the total leaf area available for photosynthesis. The total number of branches were also determined by counting.

Chlorophyll concentration

Uniform leaf discs measuring 1 cm in diameter, were collected from intact leaves still attached, and placed in vials with 10 ml 95% ethanol in the cold room for 24 hours to extract. The absorbances were then read in a Cyanscan Spectrophotometer at 664.1 and 648.8 nm. Chlorophyll concentration was then calculated according to Lichtenthaler et al. (1984) as follows;

$$C_{a+b} = 5.24A_{664.2} + 22.24A_{648.6} \quad (1)$$

Where A = absorbance, C_a = chlorophyll a, C_b = chlorophyll b, C_{a+b} = total chlorophyll

Reproductive parameters (Biomass partitioning, fruit yield and harvest index)

At the start of measurements, an initial sample of 20 plants were harvested and weighed. They were separated into roots and shoots, then oven-dried separately at 60°C for 48 hours and re-weighed to obtain the dry mass, which was then averaged to get the initial dry mass per plant for each fraction. At the end of the experiment, two plants from each treatment were harvested, separated into roots and shoots, weighed separately to obtain the fresh mass, then oven-dried at 60°C for 48 hours and re-

weighted to obtain the dry mass for each fraction. The mass of each fraction was then averaged to obtain the corresponding final dry mass. A sample of fruits were equally weighed fresh, then oven-dried to constant mass at 60°C, then re-weighed to get the dry mass. This was used to establish a regression equation from which dry mass of all subsequent harvest was determined. The final biomass was a combination of root, shoot and fruit dry masses:

$$Biomass\ of\ plant\ (g) = root\ DM(g) + shoot\ DM(g) + fruit\ DM\ (g) \quad (2)$$

Where DM = dry mass

The number of fruits produced in each replicate were counted cumulatively from the beginning to the end of the experiment, and averaged for the number of plants to obtain the number of fruits per plant. The fruits per plant were also weighed fresh to obtain the fruit mass. The harvest index was determined as the ratio of the economic to the biological yield:

$$HI = \frac{Economic\ yield(g)}{Biological\ yield\ (g)}\ that\ is, \frac{Fruit\ fresh\ mass(g)}{Plant\ Biomass(g)} \quad (3)$$

Ecophysiological parameters

WUE

The volume of water used for irrigation was recorded for the duration of the experiment. At the end of the experiment, the biomass was measured as previously explained. The water use efficiency represents the ratio of biomass accumulated per unit volume of irrigation water, according to [20]:

$$WUE = \left(\frac{g}{l}\right) = \frac{Total\ plant\ Biomass}{Total\ volume\ of\ irrigation\ water} \quad (4)$$

Transpired water volume and transpiration rate

To determine the volume of water transpired and the corresponding transpiration rate, the mass difference method was used, where each pot was placed in an intact transparent polythene bag and irrigated with its corresponding irrigation regime. The pots were then completely sealed by tying around the stems of the tomato plants, so that the only possible avenue of water loss would be through transpiration. The pots were weighed using a digital balance to get the initial mass (w1) at 8 am. At 1pm the pots were re-weighed to obtain the final mass (w2). The rate of transpiration was determined as follows:

$$TR\left(\frac{g}{hr}\right) = \frac{w1-w2}{t} \quad (5)$$

Where TR = Transpiration rate, w1 = initial mass of irrigated pot and plant, w2 = final mass of irrigated pot and plant.

TUE

Transpiration use efficiency measures the efficiency of water conservation relative to biological production and was determined by:

$$\mathrm{TUE}\left(\frac{\mathrm{g}}{\mathrm{L}}\right) = \frac{\text{total plants biomass}}{\text{total amount of water lost by transpiration}} \quad (6)$$

RGR

The relative growth rate was calculated according to Tabot and Adams [21];

$$RGR = \frac{\ln w2 - lnw1}{t2-t1} \quad (7)$$

Where RGR = relative growth rate, ln = natural logarithm and t2-t1 = duration of measurement

Succulence

Succulence was measured as the ratio of the moisture content to the dry mass:

$$Succulence = \frac{Fm\,(g) - Dm(g)}{Dm(g)} \quad (8)$$

Where Fm = fresh mass of shoot, Dm = dry mass of shoot

SMF

The shoot mass fraction was calculated as a ratio of the mass of the shoot to the total plant biomass

$$SMF = \frac{Shoot\ mass\ (g)}{Total\ plant\ biomass\ (g)} \quad (9)$$

Root: Shoot ratio

The Root shoot ratio was determined as the fraction of the root dry mass to shoot dry mass:

$$Root{:}\,shoot\ ratio = \frac{root\ dry\ mass\ (g)}{Shoot\ dry\ mass\ (g)} \quad (10)$$

Data Analysis

Data were tested for normality and homogeneous variance. They were then subjected to GLM ANOVA with interactions, in tandem with Tukey HSD test at α = .05. Growth Data that were not normally distributed were Cox-Box transformed using the natural log function during analysis. Spearman rank correlation was done to determine data covariance and the relationship between parameters. Factor analysis based on data correlation was done to identify the spatial relationships and contribution of the different factors to the observed variability in the data. All analyses were done in the Minitab Version 17 statistical package (Minitab Inc., PA, USA) and where necessary, significance was determined at the 95% level (α = .05).

RESULTS

Effects of Salinity and Irrigation on Growth Responses of Tomato

Table 2 shows analysis of variance results of the main and interaction effects on growth parameters of tomato. All growth variables measured varied significantly over time ($p<0.0001$). Salinity levels significantly influenced number of leaves and leaf area of tomato. Irrigation levels did not significantly affect any growth variables. The interaction between salinity and irrigation levels had a significant effect on all the growth parameters ($p< .05$) (Table 2).

Table 2. Analysis of variance results on the growth responses of tomato to salinity and irrigation in screenhouse

Factor	Height (cm)	No. of leaves	Total LA (cm^2)
Salinity (S)	0.100	**0.014**	**0.022**
Irrigation (I)	0.539	0.493	0.227
Time (T)	**0.000**	**0.000**	**0.000**
S * I	**0.028**	**0.012**	**0.001**
S * T	0.180	0.345	0.714
I * T	0.789	0.623	0.833
S * I * T	0.999	0.997	0.999

Values represent p values, showing levels of significance. P-values less than 0.05 indicate that the treatment has a significant effect on the response. LA = leaf area

Increasing salinity levels from 0 to 8 ppt significantly decreased the mean number of leaves from 56.02 to 50.64, while leaf area decreased from 1008 cm^2 to 874 cm^2 as salinity increased from 0 ppt to 12 ppt (Table 3). An increase in the irrigation levels from 1.5L to 4.5L per pot per week (data not shown) had no significant influence on all the growth parameters of tomato measured in the screen house. Generally, height ranged from 41.72 cm to 44.36 cm, and leaf area ranged from 14.49 cm^2 to 15.48 cm^2. The mean number of leaves ranged from 51.36 to 57.37 (Table 3).

Over time, all growth parameters increased as expected, irrespective of salinity or irrigation treatment. The interaction between salinity and irrigation (data not shown) had a decreasing effect on the number of leaves of tomato. The highest number of leaves (55) was recorded in plants irrigated with freshwater (0ppt) per week while the lowest number of leaves (37) was observed in plants irrigated with 4.5L of 8 ppt saline water per week. The interaction between salinity and irrigation levels decreased the leaf area of tomato with increased salinity. Plants with the highest leaf area (820 cm^2) were observed under the 0 ppt salinity at irrigation level of 3L per week while those with the lowest (440 cm^2) were irrigated with 4.5L of 12 ppt saline water per week.

Transpiration Responses of Tomato to Salinity and Irrigation in Screenhouse

Analysis of variance results of the main and interaction effects on transpired water and transpiration rate showed that all transpiration variables measured varied significantly over time ($p = 0.000$). Salinity ($p<0.05$) and Irrigation ($p = 0.000$) had significant influence on both transpired water and transpiration rate, which are covariates. Increasing salinity levels from 0 ppt to 8 ppt increased the water transpired from 0.09 to 0.14 L per plant over a five hour period and the rate of transpiration from 0.02 to 0.04 L per hour per plant respectively. As irrigation level increased from 1.5L to 4.5L per plant per week, the mean transpired water (0.06L to 0.19L) and transpiration rate (TR) (0.02 to 0.03L/hr) also increased. For all salinity and irrigation treatments over time transpired water volume and transpiration rate decreased (Table 4).

For all salinity levels, the volume of water transpired and the transpiration rate per plant were higher for higher irrigation water volumes. Transpired water volume and transpiration rate (covariates) increased with increase in salinity. Over time, plants irrigated with 4.5 L of water per week transpired more water across all salinity levels with the highest (0.19 L) observed at 8 ppt. Plants treated with 1.5 L of water per week transpired the least (0.05L) across all salinity levels. This pattern was similar for transpiration rate, where plants that received more irrigation water had a higher transpiration rate compared to those that received less irrigation water (Fig. 2).

Chlorophyll Responses of Tomato to Salinity and Irrigation

Chlorophyll a+b concentrations and chlorophyll a/b ratio did not vary significantly with both increase in salinity and irrigation ($p>0.05$). Generally, chlo a+b concentration ranged from 7.89 µg L^{-1} to 8.04 µg L^{-1} and chlo a/b ratio was 0.34 µg L^{-1}. Over time, chlorophyll concentrations decreased significantly irrespective of salinity or irrigation regime.

Table 3. Growth responses of tomato to different levels of salinity in screen house

Salinity	Height (cm)	No. of leaves	Total LA (cm^2)
0	41.9a	**56.02a**	**1008a**
4	44.57a	55.72ab	983ab
8	41.78a	**50.64b**	883ab
12	42.82a	54.76ab	**874b**

Values represent means. Means separated through GLM ANOVA with Tukey HSD test at α = 0.05. Means with the same letter within the column are not significantly different

Table 4. Transpiration responses of tomato to different levels of salinity in screen house

Salinity (ppt)	Transpired water (L/plant)	TR (L/hr/plant)
0	**0.09b**	**0.02b**
4	0.11ab	0.03ab
8	**0.14a**	**0.04a**
12	**0.136ab**	**0.03ab**
Irrigation (L/pot)		
1.5	**0.06a**	**0.02a**
3	**0.11b**	**0.03b**
4.5	**0.19c**	**0.03b**

Values represent means. Means separated through GLM ANOVA with Tukey HSD test at α = 0.05. Means with the same letter within the column are not significantly different. TR = Transpiration rate.

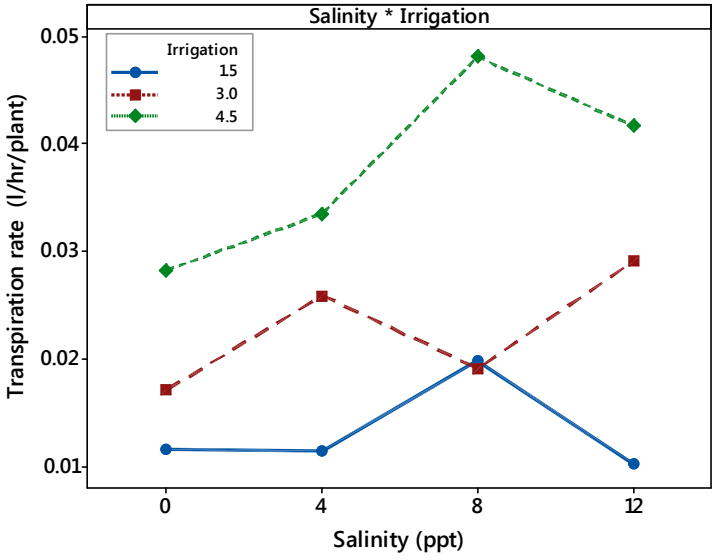

Fig. 2. Effect of the interaction of salinity and irrigation on transpiration rate of tomato over time for different irrigation treatments

Relationship between Growth, Transpiration and Chlorophyll Parameters with Treatments

There was a significant positive correlation of all growth parameters with time ($p = 0.000$), but not with salinity or irrigation ($p>0.05$). There were no correlations between salinity and growth, chlorophyll and transpiration variables ($p>0.05$). Increase in irrigation volume significantly increased transpired water volume and transpiration rate ($\rho = 0.570$, $p<0.0001$). Transpiration rate ($\rho = -0.176$, $p = .020$) and chlorophyll a+b concentration ($\rho = -0.528$, $p<0.0001$) had a negative correlation with time. Factor analysis of the correlation matrix (Fig. 3) shows that the first two factors explain 65.3% of the observed variation in the response variables, with the growth and chlorophyll parameters highly time-dependent, the transpiration variables highly irrigation-dependent, and no clear salinity effect.

Effects of Salinity and Irrigation on Reproductive Parameters of Tomato in Screen House

Analysis of variance results of main and interaction effects on reproductive parameters show that salinity had a significant effect on the harvest index, number of fruits ($p<0.0001$) and fruit mass ($p<0.001$). The levels of irrigation did not have a significant effect on reproductive parameters and the different biomass fractions ($p>0.05$). Increase in salinity from 0 ppt to 12 ppt increased the mean number of fruits per plant from 0.86 to 5.44 and HI from 0.26 to 1.84 (Table 5). This fruit yield is extremely low compared to the norm, and it was observed that the fruits were typically very small, and ripened prematurely, which signifies stimulation of senescence. Fruit mass increased as salinity increased but the rest of the biomass fractions were statistically similar across treatments (Table 5), and these high salinity-treated plants also died off faster. Irrigation did not significantly influence any of the yield and biomass variables measured.

Factor analysis of the correlation matrix (Fig. 4) shows a close positive association between salinity and yield parameters, with strong positive correlations between salinity and number of fruits ($\rho =0.697$, $p <0.0001$), fruits fresh mass ($\rho =0.628$, $p <0.0001$), fruits dry mass ($\rho =0.638$, $p <0.0001$) and harvest index ($\rho =0.692$, $p <0.0001$). There were no clear associations between irrigation and any of the yield and biomass parameters assessed. Overall, the parameters assessed account for 70.3% of the observed variation in the data.

Effects of Salinity and Irrigation on Ecophysiological Parameters of Tomato in Screen House

Of all the ecophysiological parameters measured, salinity had a significant effect on succulence and SMF (Table 6). Irrigation had a significant effect on WUE, transpired water volume, TR and TUE ($p<0.0001$). Interaction between salinity and irrigation had no significant effect on all ecophysiological parameters (Table 6).

An increase in salinity from 0 to 12 ppt significantly increased succulence from 2.08 to 5.23, while SMF decreased significantly from 0.8 to 0.55 for the same salinity range. An increase in irrigation level from 1.5L to 4.5L resulted in a mean decrease in WUE from 5.27 g L^{-1} to 1.61 g L^{-1} and a mean decrease in TUE from 516.2 to 148.05 g L^{-1}, while transpired water volume and transpiration rate increased for the same irrigation intervals (Table 7).

Table 5. Effects of salinity and irrigation on yield parameters and biomass partitioning of tomato in screen house

Salinity	No. of fruits	HI	Fruit FM (g)	Fruits DM(g)	Shoot DM (g)	Root DM (g)	Biomass
0	**0.86b**	0.26b	**10b**	**1.29b**	21.57a	4.43a	27.29a
4	1.75b	0.65b	**21.88ab**	5ab	23.88a	5.13a	34a
8	2.89b	**0.72b**	**26.11ab**	5ab	22.78a	5.22a	33a
12	**5.44a**	**1.84a**	**55.6a**	**9.11a**	17a	3.89a	30a
Irrigation							
1.5	2.7a	0.94a	33a	6.2a	21.6a	3.8a	31.6a
3	3.5a	0.84a	27.92a	4.92a	22.75a	5.333a	33a
4.5	2.36a	0.96a	28.6a	5a	19.18a	4.727a	28.91a

Values represent means. Means separated through GLM ANOVA with Tukey HSD test at α = 0.05. Means with the same letter within the column are not significantly different.

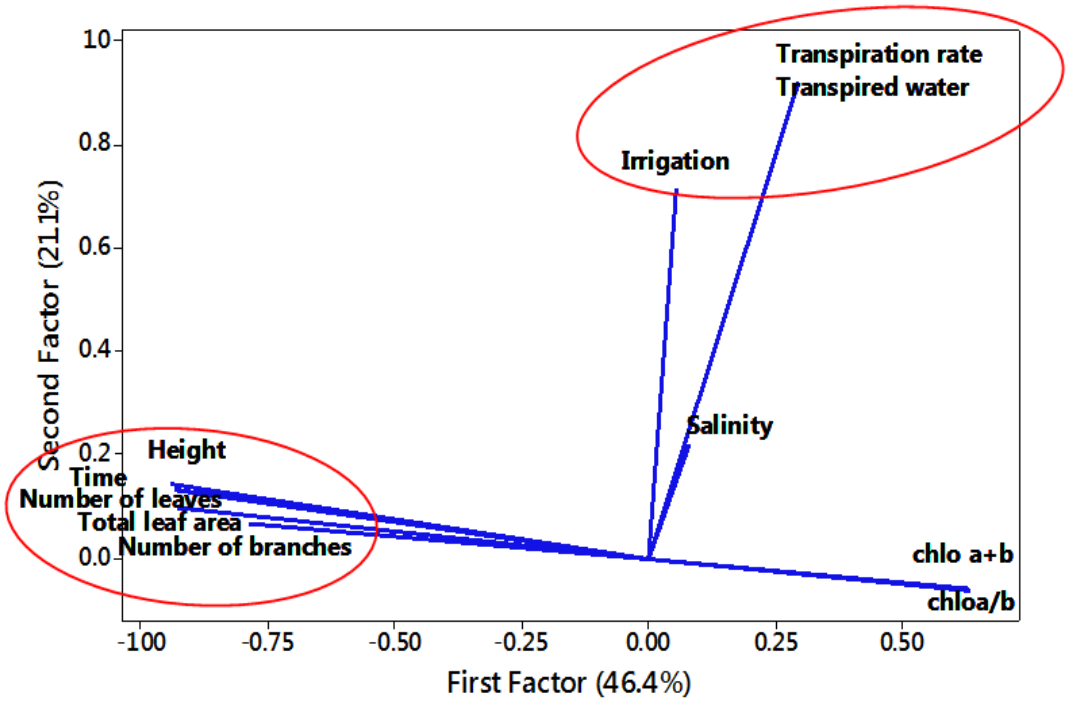

Fig. 3. Factor analysis of the correlation matrix showing association of growth, transpiration and chlorophyll parameters with treatments

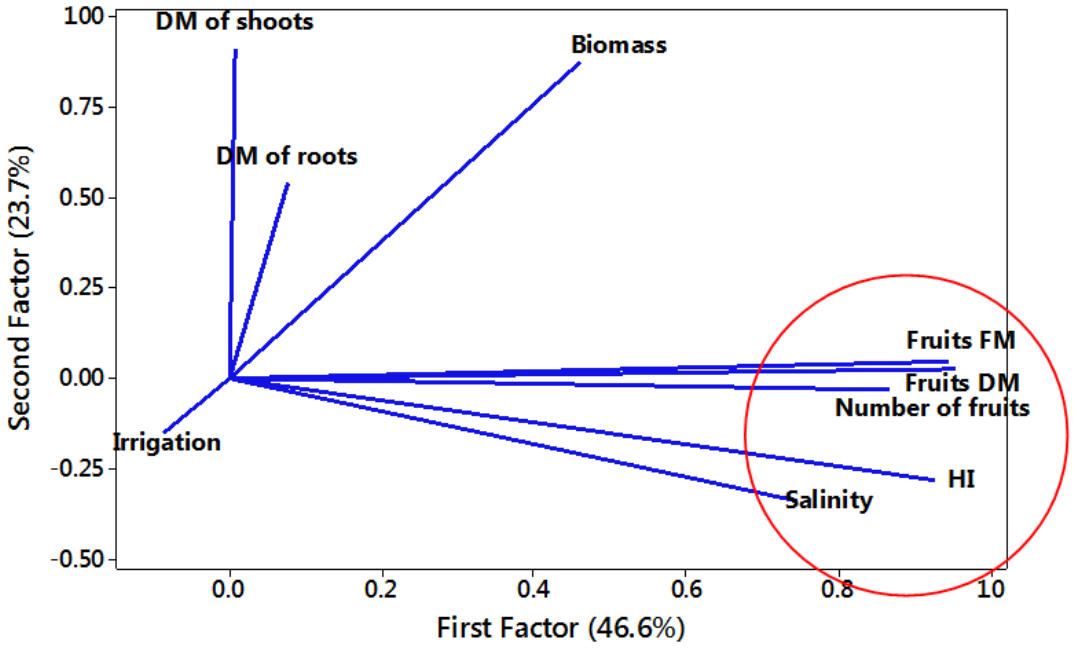

Fig. 4. Factor analysis of the correlation matrix showing association of yield parameters with treatments

Table 6. Analysis of variance results on the effects of salinity and irrigation on ecophysiological parameters of tomato in screen house

Factor	WUE (g/l)	TW (l)	TR (l/hr)	TUE (g/l)	RGR	S (l/g)	SMF	R:S ratio
Salinity (S)	0.823	0.456	0.456	0.891	0.565	**0.037**	**0.000**	0.913
Irrigation (I)	**0.000**	**0.000**	**0.000**	**0.000**	0.723	0.371	0.868	0.392
S * I	0.942	0.396	0.396	0.232	0.746	0.821	0.109	0.108

Values represent p values, showing levels of significance. P-values less than 0.05 indicate that the treatment has a significant effect on the response. WUE = water use efficiency, TW = transpired water volume, TR = transpiration rate, TUE = Transpiration use efficiency, RGR = Relative growth rate, S = succulence, SMF = shoot mass fraction, R:S = Root shoot ratio

Correlation and Factor Analysis

Results of correlation analysis show that there was a significant positive association between salinity and shoot succulence (ρ = 0.534, p = 0.001), and a negative correlation with shoot mass fraction (ρ = -0.635, p <0.0001). Irrigation associated closely with transpired water volume (ρ = 0.769, p <0.0001) and transpiration rate (ρ = 0.769, p <0.0001) with which it had positive correlations, and with TUE (ρ = -0.650, p <0.0001) and WUE (ρ = -0.851, p <0.0001) with which it had strong negative correlations. These variables explain 67.2% of the total variation in the data (Fig. 5).

Table 7. Effects of salinity on ecophysiological parameters of tomato in a screen house

Factor	WUE (g/l)	TW (l)	TR (l/hr)	TUE (g/l)	RGR	S (l/g)	SMF	R:S ratio
0	2.74a	0.10a	0.03a	351.9a	0.48a	**2.08a**	**0.80a**	0.21a
4	3.16a	0.15a	0.04a	280.8a	0.51a	3.25ab	0.71a	0.23a
8	3.35a	0.156a	0.04a	345a	0.50a	3.64ab	0.70a	0.24a
12	3.19a	0.14a	0.03a	311.2a	0.49a	**5.13b**	**0.55b**	0.26a
Irrigation								
1.5	**5.27a**	0.075a	0.02a	**516.2a**	0.50a	4.39a	0.69a	0.19a
3	**2.75b**	**0.12a**	**0.03a**	**319b**	0.50a	3.24a	0.69a	0.25a
4.5	1.61b	**0.20b**	**0.05b**	148.05b	0.49a	3.35a	0.67a	0.26a

Values represent means. Means separated through GLM ANOVA with Tukey HSD test at α = 0.05. Means with the same letter within the column are not significantly different. WUE = water use efficiency, TW = transpired water volume, TR = transpiration rate, TUE = Transpiration use efficiency, RGR = Relative growth rate, S = succulence, SMF = shoot mass fraction, R:S = Root shoot ratio

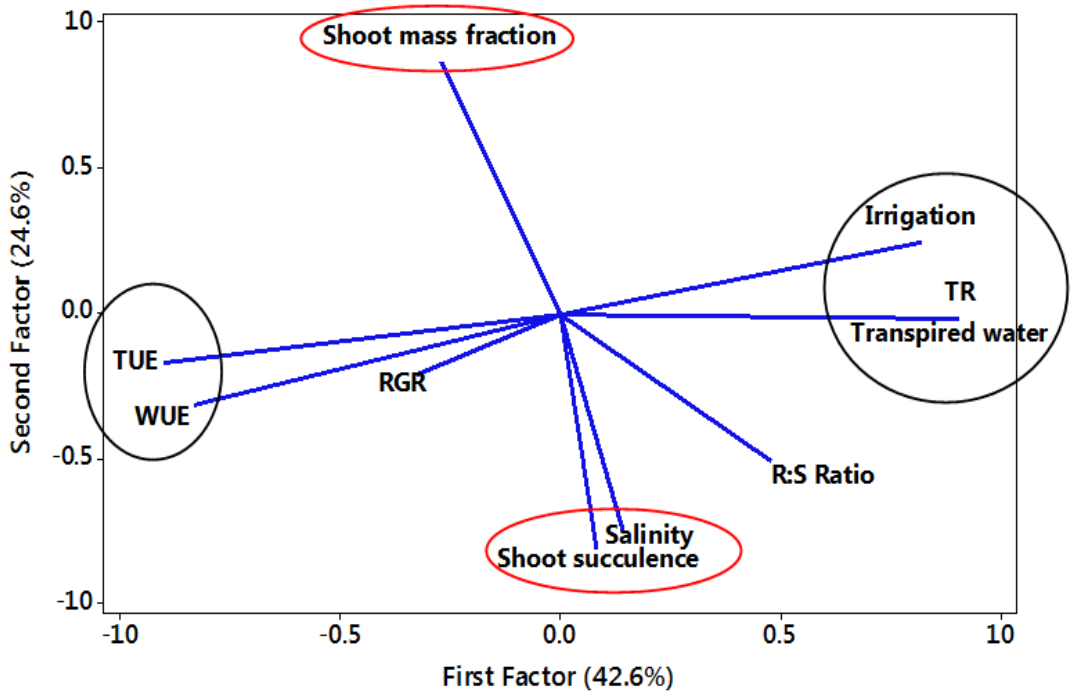

Fig. 5. Factor analysis of the correlation matrix for association of yield parameters with salinity and irrigation. TUE = transpiration use efficiency; WUE = water use efficiency; RGR = relative growth rate; R:S = root shoot; FM = fresh mass; DM = dry mass; HI = harvest index

DISCUSSION

Crop ecophysiological studies are essential as they enable us project or predict crop production under some future environmental conditions. Such predicted conditions include increased variability in irrigation water volume and increased salinization of arable lands, or irrigation with saline water. This research aimed at determining the responses of *S. lycopersicum* to these future conditions.

Growth Responses of *S. lycopersicum* to Salinity and Irrigation Regimes

Increase in salinity to 12 ppt suppressed all growth variables, while variation in irrigation water from half the norm (deficit irrigation) to one and an half times the current mean annual precipitation (excess irrigation) had no significant impact on growth variables. Reduction in growth parameters under salinity stress is the norm in most plants and has been widely reported in the literature for example Tabot et al. [22] on potato, Al-zubaidi [23] on eggplant and Zhang et al. [24] on tomato produced in hydroponics systems. This reduction in growth as salinity increased in irrigation water and soil can be explained by three main processes. Firstly, salinity limits nutrient uptake from the soil by fixing nitrates especially, which are necessary for most metabolic and biosynthetic processes in plants [25]. This restricts protein synthesis, and hence structural molecules required for growth cannot be built [26]. Secondly, salinity restricts water uptake, and in consequence stomatal control could kick in, restricting the rate of photosynthesis, since CO_2 does not readily diffuse in under closed stomatal conditions. Thirdly, there could be diversion of photosynthate from growth, to synthesis of biomolecules required for stress response, such as proline and glycinebetaine, which function in osmotic adjustment, stabilization of membranes and protection of enzymes [11]. The fact that growth parameters were not significantly influenced by irrigation levels suggests that even at half the current mean annual precipitation (1100mm) available soil water is sufficient for *S. lycopersicum* plants to grow well, but results show that salinity is the dominant stressor because interaction between salinity and irrigation decreased growth parameters.

Yield and Related Parameters

In most plants, salinity stress would decrease yields because of restriction of nutrient uptake, photosynthesis and biosynthesis of molecules necessary for stress tolerance [27]. Contrary to expectation, increasing salinity resulted in increased fruit numbers, fruit mass and harvest index while biomass was not statistically different across treatments. This suggests that salinity stress rather stimulated yield of the crops; however, closer evaluation revealed that fruit mass and fruit sizes were far less than what would obtain in well irrigated non-saline conditions and plants irrigated with water of higher salinity died rapidly after producing these premature fruits, suggesting rather that this was a strategy of rapid maturity and early senescence in the saline treatments, rather than a positive stimulation of yield. Deficit irrigation typically reduces crop yield [28]. Contrary to expectation, reducing irrigation to the equivalent of half the current annual precipitation rate had no significant effect on yield of tomato, likewise increasing to one and a half the mean annual precipitation. This suggests that tomato would do well over a wide range of precipitation (and hence irrigation) scenarios, and that the imposed treatments had not reached a

threshold necessary to influence yields. This holds promise for better water rationing in irrigated tomato production systems, in the context of decreasing water availability.

Transpiration and Water Balance

Increasing salinity and irrigation volume both increased transpiration rate, which decreased over time irrespective of salinity. Determinants of transpiration rate include stomatal conductance, the level of tugor of plant cells, availability of soil water and ability of plants to take up water from the soil, as well as environmental parameters like temperature and relative humidity. Soil salinity makes water uptake difficult and hence stomatal conductance is supposed to drop as stomata close to restrict the amount of water loss by plants. This decrease has been reported for wheat cultivars [29,30] and in the solanaceous hot pepper [31]. However, we found that as salinity increased, the rate of transpiration increased, which suggests the need to keep stomata open and hence photosynthesis to survive the stress.

Increase in irrigation volume significantly increased transpiration rate implying when water is low in the soil, the plants effectively engage stomatal control of transpiration and hence the rate of transpiration reduces in deficit irrigation scenarios [32]. This is the expected trend, and shows that under deficit irrigation, plants control water loss, but this would also have an impact on photosynthesis, as gaseous exchange is reduced concurrently with increased stomatal resistance. Water availability is therefore proportional to water loss in transpiration, and this explains why in the current study, increasing irrigation volume reduced both the transpiration use efficiency and the water use efficiency of the plants. One strategy to survive internal water scarcity as a result of salinity or drought stress is succulence, that is, the ratio of the moisture content of the plant to the dry mass. In the current study, salinity increased succulence and decreased shoot mass fraction of the plants, suggesting that tomato has the ability to accumulate water to an extent relative to dry mass, under salinity stress. A reduction in shoot mass fraction suggests that there is re-allocation of photosynthate to root architecture, and this is an adaptation to enhance water uptake and nutrient foraging ability of the plants.

CONCLUSION

In a future where salinity and water stress are predicted to increase in crop production systems, these results are significant and show that increasing salinization will suppress growth and stimulate early senescence in tomato, consequently reducing its production. On the other hand, deficit irrigation would be possible as the plant does well over a broad range of water-available conditions.

AUTHORS' CONTRIBUTIONS

Authors PTT and MPM conceived the research, and produced the experimental plan. Authors BCN, AJA and NCK implemented the research and collected field data. Author PTT analysed the data. All authors contributed in the writing and approval of the manuscript.

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COMPETING INTERESTS

Authors have declared that no competing interests exist.

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