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Photosynthetic Response of Potato Plants to Soil Salinity

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Abstract:

In order to determine the potential production, it is important to know the response of crops such as potato (*Solanum Tuberosum L.*) which is one of the important starch crops in human diet under abiotic stress conditions. Salinity is one of the abiotic stress factors for potato limiting crop yield. The aim of this study is to determine the effects of saline water and proline applications on the yield and physiological characteristics of Morfona potato variety grown under cover just for rainfall proof under the Eastern Mediterranean conditions. In the experiment conducted between January-June 2010, foliar applied proline concentrations as much as 10 mM and 20 mM were applied to potato crop irrigated with water having electrical conductivity of 0.19 dS m^{-1} (T_0), 3.54 dS m^{-1}($T_{3.5}$), 7.12 dS m^{-1} (T_7), 9.57 dS m^{-1} (T_{10}) and 12.86 dS m^{-1} (T_{13}). Different levels of saline irrigation water were obtained by adding NaCl into the tap water. Irrigation water requirement, crop water use and water use efficiency were decreased as much as 4.5%-18.9%, 3%-16%, 16.45-19.36%, respectively, as the irrigation water salinity levels increased. The increase in soil salinity caused to decrease in all parameters (total fresh tuber yield, tuber number, tuber dry weight, weight of potato classified as Grade A, biomass and leaf area) except harvest index. Foliar application of proline to diminish the effect of salinity did not affect t significantly the most of the yield parameters. The most affected parameter by salinity was found to be stomatal conductance (Sc) among photosynthesis (Pn), transpiration (Tr) and stomatal conductance (Sc). The values of Pn, Tr and Sc increased in T_7 treatment compared to $T_{3.5}$. Irrigation water salinity affected significantly tuber bulking I and tuber bulking II periods whereas the effect of proline was found to be significant on tuber initiation and tuber bulking II periods ($p<0.01$). Leaf aging was accelerated in treatments where salinity was higher. Towards the harvest stage, it was observed that Pn, Tr and Sc were not affected by salinity, possibly as a result of leaf aging.

Key word: Potato, photosynthesis rate, transpiration rate, stomatal conductance, soil salinity

Patates Bitkisinin Toprak Tuzluluğu’na Fotosentetik Tepkisi

Özet

Patates gibi insan beslenmesinde çok önemli bir yere sahip bitkilerin abiyotik stres koşullarına verdikleri tepkinin belirlenmesi potansiyel üretim miktarının belirlenmesi açısından önemlidir. Tuzluluk, patates yetiştiriciliğinde ürün miktarını kısıtlayan en önemli abiyotik stres parametrelerinden biridir. Tuzlu koşullarda bitkilerin tolerans düzeylerinin artırılmasında tuz- verim ilişkilerinin bilinmesi ve kültürel önlemler ile tuzluluğa dayanımın artırılması öncelikli bir konudur. Bu çalışmada, Türkiye’nin kurak ve yarı kurak iklime sahip Doğu Akdeniz Bölgesinde farklı tuz ve prolin düzeylerinin yağmurdan korunaklı ortamda yetiştirilen Morfona çeşidi patatesin verim ve fizyolojik özelliklerine etkilerinin belirlenmesi amaçlanmıştır. Araştırmada 0.19 dS m^{-1} (T_0), 3.54 dS m^{-1} ($T_{3.5}$), 7.12 dS m^{-1} (T_7), 9.57 dS m^{-1} (T_{10}) ve 12.86 dS m^{-1} (T_{13}) sulama suları ve 10 mM (P_{10}), 20 mM (P_{20}) prolin düzeylerinin etkisi incelenmiştir. Sulama suyu tuzluluğunun oluşturulmasında NaCl tuzu kullanılmıştır. Sulama suyu gereksinimi, bitki su tüketimi ve su kullanma randımanı (WUE) tuzluluğun yüksek olduğu konularda, azalmıştır. Tuzluluk arttıkça sulama suyu gereksinimi 4.5%-18.9%, bitki su tüketimi 3%- 16%, WUE %16.45-19.36 arasında azalmıştır. Toprak tuzluluğundaki artış, hasat indeksi dışında verim parametrelerinin (toplam yumru verimi, yumru sayısı, yumru kuru ağırlığı, Asınıfı yumru büyüklüğü biomass ve yaprak alan indeksi) tamamının azalmasına neden olmuştur. Tuzluluk stresinin azaltılması için yapraktan uygulanan prolinin, çoğu verim parametrelerine etkisi istatistiksel olarak önemli bulunmamıştır. Fotosentez (Pn), transpirasyon (Tr) ve stoma iletkenliği (Sc) parametreleri arasında tuzluluktan en fazla Sc, en az Pn etkilenmiştir. Pn, Tr ve Sc, $T_{3.5}$ uygulaması ile kıyaslandığında T_7 konusunda artmıştır. Bunun nedeninin, patatesin tuzluluğa karşı içsel dayanım mekanizmasını harekete geçirme çabasından kaynaklandığı ve anılan düzeydeki tuzluluğun gaz değişimini teşvik ettiği sonucuna varılmıştır. Yumru gelişiminin farklı dönemlerinde yapılan ölçümlerde tuzluluğun Tuber bulking I ve Tuber bulking II dönemlerine, prolinin Tuber initiation ve Tuber bulking II dönemlerine etkisi istatistiksel olarak önemli bulunmuştur ($p<0.01$). Tuzluluğun yüksek olduğu uygulamalarda yaprak yaşlanmasının hızlandığı belirlenmiştir. Hasat dönemine yaklaştıkça Pn, Tr ve Sc'nin tuz düzeylerinden etkilenmediği bu durumun yaprak yaşlanmasının bir sonucu olduğu değerlendirilmiştir. Hasatta ürün miktarına bitkinin hangi gelişim döneminin etkili olduğu ve bu dönemlerde stresi azaltacak uygulamaların etkilerinin bilinmesi farklı bitkilerde ayrıntılı olarak irdelenmesi gereken bir konudur.

Anahtar Kelimeler: Patates, fotosentez hızı, transpirasyon hızı, stoma iletkenliği, tuzluluk

Introduction

Drought problems in arid and semi-arid regions are forcing to use marginal quality waters (brackish, reclaimed, drainage and waste water) in irrigation. Many countries over the world are planning to use those waters in their long-term development plans (Chartzoulakis, 2005). About 17% of the global cultivated area is irrigated and more than 30% of the agricultural production comes out of this area. (Hillel, 2000). Taking into consideration that global salt affected soils are 830 million ha, it is obvious that saline water-yield relations should be investigated in more detailed studies (Martinez-Beltran and Manzur, 2005).

The studies (Bruns and Caesar, 1990; Levy and G.C.C. Tai, 2013; Qadir et al., 2010) conducted using saline water shows that saline water is changing soil physical and chemical properties as a result of accumulated salt content, hinders water uptake, decreases infiltration rate and aeration rate of soils. (Ayers and Westcot, 1985). The increase of salt content in soil also causes hormonal changes (Munns, 2002), decay in carbohydrate metabolism (Gao et al., 1998), decrease in certain enzyme activities and (Munns, 1993) close up stomata and decrease transpiration rate and yield (Ben Asher et al., 2006).

The crops having active role in human nutrition should be in priority when saline water-yield relation is evaluated. Potato crop is the fourth crop after wheat, rice and maize in terms of production area (CIP, 2007). While the acreage of potato growing area, tuber yield, and yield efficiency in 2010 in the world was 18.6 million hectare, 324.4 million ton, and 1.744 ton per decare, respectively, the same data for Turkey was 140665 ha, 4548090 ton, and 3.233 ton per decare (FAO. 2010). Potato is known as salt sensitive crop. (Maas and Hoffman, 1977). Especially early development stage is the most vulnerable stage for potato crop in terms of salinity (Nadler and Heuer, 1995). Plant height, leaf area and fresh weight accumulation were decreasing depending on increased salinity. (Heuer and Nadler, 1995). Physiologically, potato crop is more sensitive to salinity early in the tuber formation (Bruns and Caesar 1990). Fidalgo et al. (2004) reported that transpiration rate, leaf stomatal conductance, and relative water content of Desire potato variety are decreasing as a result of salt stress. Vos and Groenwold (1989), stated that canopy stomatal conductance reacts earlier than photosynthesis to soil water deficit resulting a decrease in CO_2 concentration in plant leaves. The authors also determined a curvilinear relation between net photosynthesis rate and stomatal conductance.

Crops are accumulating proline as a first physiological reaction when they are exposed to stress factors such as salinity and draught. Increase of proline concentration in the vacuole inside the cell is a measure of how long the crop is under stress and how the crop is tolerant to that stress factor. Researches indicate that proline is occurred during protein decay resulting and is synthesized inside the cell. It is reported that proline has significant function in stabilizing osmotic effects by balancing of ion concentrations such as Na, K, Mg and Ca, in strengthening the cell wall and in other enzymatic actions (Iba, 2002). It is stated that higher salt concentration (NaCl) in the root zone causes to accumulate Na on the leaves resulting in chlorosis by exchanging magnesium on the chlorophyll molecules with Na. Similarly, as a result of higher Na concentration, proline which is a stress protein is produced and accumulated in the cells (Avcıoğlu et al., 2003).

Researches regarding proline are mostly concentrated on how crops synthesize proline and the amount of concentration of synthesized amino acid. The research regarding combined effects of salt stress and foliar applied proline are lacking. Therefore, in this study, the effects of different level of salt stress and proline concentration on gas exchange parameters are examined.

Material and Method

Plant and soil description

The experiment was carried out between January-June 2010 in a greenhouse (300 m^2) located in the research area of department of field crops, Mustafa Kemal University, Hatay, Turkey. The greenhouse used in the experiment is located at a latitude of 36º 19′ north, a longitude of 36º 11′ east and an altitude of 28 m. The climate of the region is typically Mediterranean, i.e. mild and rainy in winter, dry and hot in summer. Potato variety called Marfona which is moderately tolerant to salt (Khrais, 1998) and grown extensively in Turkey was used in the study. The crops were grown in plastic containers filled with the mixture of sand and loamy soil at a ratio of 1:1 (v:v). The diameter and height of the containers were 26 cm and 42 cm, respectively. Containers were filled with soil-sand mixture such that each of them weighted 18 kg on an electronic scale. The bulk density, weight base field capacity and wilting point are 1.38 g cm^{-3}, 25% and 12%, respectively. The chemical properties of soil are given in Table 1. One tuber is planted in each container.

Experimental design and applications

The experiment was designed statistically according to splitted split plot with three replications such that each treatment had 15 pots. NaCl was used as a salt source to obtain the desired electrical conductivity level by adding into the tap water. The chemical properties of water are given in Table 1. The pH of proline (Sigma P5607) was 6.3.

Potato crop was irrigated with water having electrical conductivities (EC_w) of 0.20 (T0, tap water, control), 3.50 (T3.5), 7.00 (T7), 10 (T10) and 13 dS/m (T13) and proline foliar applied having concentration of 0 (P_0), 10 (P_{10}) and 20 (P_{20}) mM. Proline applications were formed as main plots and saline water applications as sub-plot. The saline water was prepared such that Na/(Na+Ca) ratio is between 0.1 and 0.7 for low to moderate salinity as suggested by Grattan and Grive (1999).

Table 1. Chemical properties of soil and water used in the experiment.

	Treat.	EC	pH	Na^+	K^+	$Ca+Mg^{++}$	HCO_3^-	CO_3^-	Cl^-	SO_4^-	SAR
Irrig. Water (EC_w)	T_0	0.19	7.6	1.55	0.13	1.35	1.23	-	1.78	0.02	1.89
	$T_{3.5}$	3.54	7.5	27.11	0.75	12.14	3.87	-	27.13	9.00	11.00
	T_7	7.12	7.6	55.6	1.23	13.55	5.36	-	56.88	8.14	21.36
	T_{10}	9.57	7.6	91.24	1	13.55	3.57	-	97.61	4.61	35.05
	T_{13}	12.86	7.6	118.24	1.22	14.2	4.3	-	123.94	5.42	44.37
Soil (EC_e)		0.186	7.40	1.10	0.09	1.14	1.31	0.15	0.85	0.02	1.46

*unit of anion and cation is me/L, electrical conductivity (EC) is dS m^{-1}

Plant cultivation

One tuber is planted at 10 cm dept in each container on 15 January 2010. Pre-shooting was done on tubers and tubers containing one shoot were chosen to plant so that variation as a result of shooting was diminished. After emergence, each pot was fertilized weekly using solution containing as much as 120 mg N, 120 mg P, 170 mg K and 20 mg Mg (Schittenhelm et al., 2004).

Irrigation treatments and scheduling

The amount of irrigation water was determined adding water in to one pot used for observation until it is at field capacity. The same amount water (liter) was also added in to other pots. Irrigation interval was 7 days. 20% leaching water was also applied to the plots except control plot (T_0). Leaching water was collected at the bottom of the pots and their ECd values were determined. The HH-2 moisture meter (Delta T, WET sensor, **W**ater, **E**lectrical Conductivity, **T**emperature) was used to measure soil water content (cm^3/cm^3), soil salinity (dS/m) and soil temperature (°C). Drainage and irrigation water salinity was measured by EC meter (Orion 3 Star, USA). Calibtated values for soil salinty is y= 0.0127*x + 0.91, (r2=0.96**), and for volumetric soil water content y=0.9442x+0.0295 (r^2 = 0.88**).

Evapotranspiration (Et) and water use efficiency (WUE)

Evapotranspiration was determined using 3 pots by the equation given below (Eq 1).

ET= (soil water at harvest-initial soil water) + (total I)-(total Dp) (1)

where ET: Evapotranspiration (L), I: amount of applied water to bring the pots to field capacity (L), Dp: total drained water (L). Irrigation water use efficiency and water use efficiency was computed by the equation given below (Howell et al., 1994).

$$IWUE = Y/ I \quad (2)$$

$$WUE_{Et} = Y/ ET \quad (3)$$

where; IWUE; Irrigation water use efficiency, (kg m^{-2}

mm^{-1}) for unit area, WUE_{Et}: water use efficiency, (kg m^{-2} mm^{-1}) for unit area, I: applied water (mm), ET: Seasonal evapotranspiration (mm), Y: Yield (kg).

Measurement of yield, dry matter, tuber quality vegetative growth

Tuber yield per plant (kg m^{-2}) and number of tuber (tuber m^{-2}) were determined to examine the different applications. Also, all the vegetative parts per plant was determined at 70 °C. Harvest index was computed as the ratio of dry tuber yield to biomass. Tuber diameter more than 45 mm was graded as Grade A. leaf area was determined in three pots by leaf area meter (LI-COR 3100C, USA).

Gas Ex**change**

The effect of saline irrigation water, soil salinity, and proline concentration on stomatal conductivity (mmol m^{-2} sn^{-1}), transpiration and photosynthesis rate (µmol m^{-2} sn^{-1}) were measured in three crops in each treatment. Photosynthesis (µmol/m^2/s) and transpiration rate (µmol/m^2/s) were measured by portable photosynthesis device (LCA-4), stomatal conductance (mmol/m^2/s) was measured by leaf porometer (model SC-1, LPS0881) between 11:00-14:00 on six young leaves on dates of 20 April, 5 May, 15 May and 20 May (Table 2). Average values of PAR (photosynthetic active radiation), $CO2_{ref}$ and C_i (CO_2 assimilated by plant) were measured as 839.03, 383.09 and 158.18, respectively, (Table 2).

Table 2. Change of gas parameters depending on tuber growth and development.

Date		PAR	$CO2_{ref}$	Ci
20 Apr.	Tuber initation: 45. Days after planting	890.91	388.20	132.85
05 May	Tuber bulking 1: 60. Days after planting	1027.46	378.31	115.70
15 May	Tuber bulking II: 70. Days after planting	830.61	378.21	149.44
20 May	Tuber maturation initation: 75. Days after planting	613.46	390.88	234.73

Statistical analysis

The data were analyzed statistically by using SPSS 18.0 and the means were compared using Tukey test (Bek and Efe 1988).

Results and Discussion

Soil moisture content and soil salinity

Soil salinity (EC_e) is increased depending on irrigation water salinity (EC_w) (Table 3). A linear relation based on the records obtained during the research was established between irrigation water salinity and average soil salinity and drainage water salinity (EC_d) (EC_e=1.1 EC_w+1.45. r^2=0.87* and EC_d=1.38 EC_w+4.88 r^2=0.99**). The amount water applied in T_0, $T_{3.5}$, T_7, T_{10} and T_{13} treatments are 23.3, 22.3, 21.3, 20.9, 18.9 L, respectively. Although soil water content was uniformly distributed in the beginning of the experiment it increased in treatments irrigated with saline water (Fig. 1-2). This might be a result of ion concentration kept by soil particles and higher hydration radius of the ions such as NaCl (Frenkel et al., 1978). This is also called physiological drought which causes to decrease in leaf area, transpiration ratio and stomatal conductance (Romero-Aranda, 2001). Irrigation water requirement, available water, water use and water use efficiency were decreased in treatments where salinity was higher (Table 3). Irrigation water decreased as much as 3%, 4.5%, 9.4%, 14% and 18.9% in $T_{3.5}$, T_7, T_{10}, and T_{13}, respectively, compared to T_0 treatment. Demirel and Ödemiş (2013), also reported a decrease in water use compared to tap water as much as 60% (EC_w =12 dS m^{-1}) and 37% (EC_w= 3 dS m^{-1}) for potato irrigation. Irrigation water use efficiency (IWUE) and water use efficiency (WUE) decreased on treatments where salinity levels were higher (Table 3). In the study, IWUE and WUE were determined to decrease as much as %5.83-%6.88 in $T_{3.5}$ and %16.45-19.36 in T_7, respectively, compared to T_0 treatment. The decrease in T_{10} and T_{13} treatments were about the same (IWUE, on the average, 34.50%, WUE, on the average 37.17%). Ghamarnia et al., (2012) reported that WUE values of Coriander plant at 2, 4 and 6 dS m^{-1} salinity levels were determined as 8.7-19.12, 46-75.7 and 53.83-86.21 g m^2 mm^{-1}

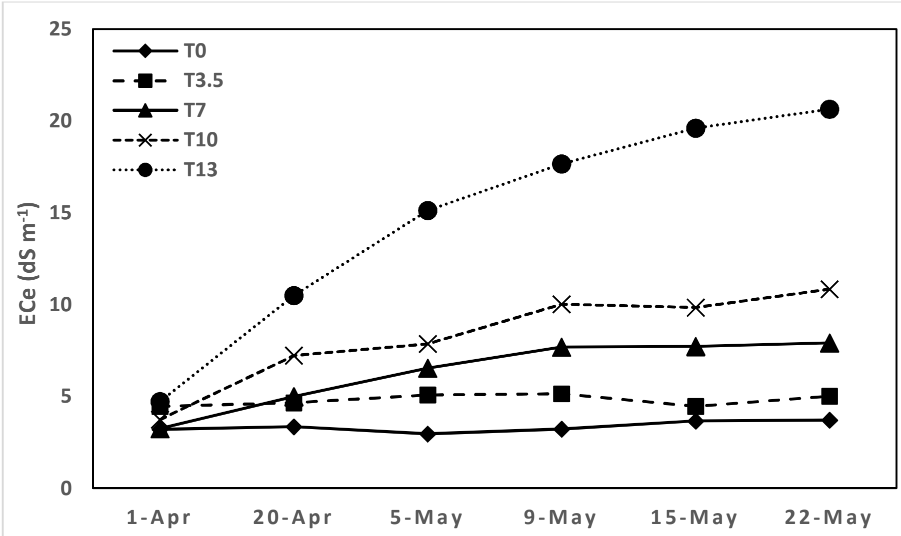

Figure 1. Temporal change of soil salinity.

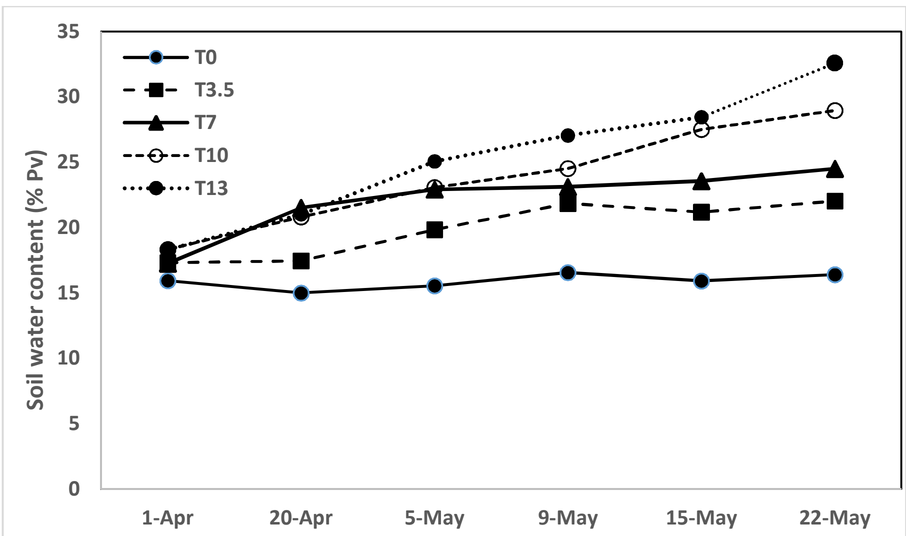

Figure 2. Temporal change of volumetric soil water content.

Table 3. Effects of irrigation water salinity on soil salinity, gas transport and water use efficiency (Et=I-Dp±ΔS)

Treat.	EC_e	EC_d	I	Dp	ΔS	Et	Pn	Tr	Sc	IWUE	WUE
T_0	3.23	4.97	440	88	82.3	434.3	6.95	1.83	72.61	13.60	13.79
$T_{3.5}$	4.98	9.29	421	84	84.9	421.9	6.53	1.67	62.53	12.87	12.84
T_7	7.69	15.20	402	80	89.3	411.3	7.11	1.78	69.95	11.38	11.12
T_{10}	9.60	19.25	394	75	91.2	410.2	5.14	1.45	53.11	8.98	8.64
T_{13}	18.21	21.62	357	70	76.8	363.8	3.89	1.27	43.56	8.86	8.69

I: ırrigation water (mm). Et: evapotranspiration (mm) ECw. ECe and ECd: electrical conductivity of irrigation water. soil extract. and drain water (dS m-1). Pn: photosynthesis (μmol m^{-2} s^{-1}). Tr: Transpiration (μmol m^{-2} s^{-1}). Sc: Stomalatal Conductance (mmol m^{-2} s^{-1}). WUE irrigation water use efficiency (kg m^{-2} mm^{-1}) and WUE water use efficiency (kg m^{-2} mm^{-1}).

Effects of salinity, proline and photosynthesis on yield

Increase in soil salinity caused to decrease all the parameter except harvest index (Table 4). An increase as much as 1 dS m^{-1} in soil salinity decreased TTY about 3.09% (*p<0.05),* T_{num} about 0.76% (*p>0.05*), HI about 0.85% (*p<0.01*), Grade A about 5 potatoes (*p>0.05*), Tdw about 2.65 % (*p<0.01*), biomass about %2.11 (*p<0.01*) and leaf area about %2.61 (*p<0.01*). Studies conducted to search saline water – yield interactions in potatos showed also that yield and yield parameters are decreasing. (Katerji et al., 1998; Paliwal and Yadav, 1980; Patel et al., 2001). Van Hoorn et al., (1993), reported that yield decreased about 37% in soil salinity of 5.9 dS m^{-1} compared to soil salinity of 0.8 dS m^{-1}. Similarly, saline irrigation water (6.2 dS m^{-1}) decreased leaf area index and canopy functions. (Bustan et al., 2004). Slowing leaf and tuber growth, leaf burn, limited root water uptake, decrease in tuber yield and tuber browning are major symptoms of salt stess (Elkhatib et al., 2004).

Proline is one of the organic molecules accumulated in crops when they exposed to abiotic stresses such as drought and salinity (Nanjo et al. 1999). Under osmotic stress conditions, proline take a role as a conservator of major molecules and even stress sign by osmotically regulating medium (Hasegawa et al. 2000). Foliar applied proline did not affect yield parameters positively as expected (Table 4). However, there are some studies reporting that NaCl in irrigation water is promoting proline accumulation (Lin et al. 2002, Yoshiba, et al. 1995, Choudhary et al., 2005), in salt tolerant potato varieties (Rahnama and Ebrahimzadeh, 2004) and rice (Widodo et al., 2009). Rahnama and Ebrahimzadeh (2004) stated that no correlation exists between proline accumulation and salt tolerance. Although proline seems to be accumulated on many of the plants for different stress factors, it depends on the stress tolerance of plants, the timing of the stress as well the strength of the stress.

In the study, a statistically significant linear relation between average values of photosynthesis measured at different times and harvest and biomass, leaf area was found. But, no statistically significant relation was obtained for TTY, T_{num}, HI and Grade A (Fig. 3).

Table 4. Average values and variance analysis results for soil salinity (ECe) and proline (mM) applications

	Treatment	TTY	T_{num}	HI	Grade A	T_{dw}	Bıomass	LA
Salinity	T_0	1.511 e	46.72	35.66	0.935 e	219.37 d	619.95 d	1.43 d
	$T_{3.5}$	1.367 d	47.83	35.57	0.842 d	200.42 cd	565.71 c	1.23 c
	T_7	1.154 c	49.37	34.27	0.480 c	186.77 c	547.89 c	1.22 c
	T_{10}	0.894 b	45.66	34.13	0.322 b	166.77 c	487.41 b	1.04 b
	T_{13}	0.798 a	42.17	31.24	0.233 a	129.31 a	414.55 a	0.82 a
*Slope of relative yield decrease depend on ECe		-3.10	-0.76	-0.85	-4.98	-2.65	-2.11	-2.61
Proline	P_0	1.148	51.48 b	31.58 a	0.596 b	37.58	564.43 c	1.29 b
	P_{10}	1.137	40.71 a	34.31 b	112.19 a	0.534	526.10 b	1.07 a
	P_{20}	1.149	40.81ab	36.64 b	116.87 ab	0.557	490.71 a	1.08 a
Variation source								
ECe		***	***	Ns	***	***	***	***
P		ns	***	*	**	ns	***	***
ECe * P		***	***	Ns	***	ns	***	***

ECe; electrical conductivity of soil saturation extract (dS m^{-1}), P: proline (mM). TTY: total tuber yield (kg m^{-2}), T_{num}: number of tubers in the pot (number m^{-2}), HI: harvested ındex (%), Grade A: first class tuber weight (kg m^{-2}), Tdw: Tuber dry weight (gr m^{-2}), LA: leaf area ındex. *% yield decrease for unit ECe (1 dS m^{-1}) increase.

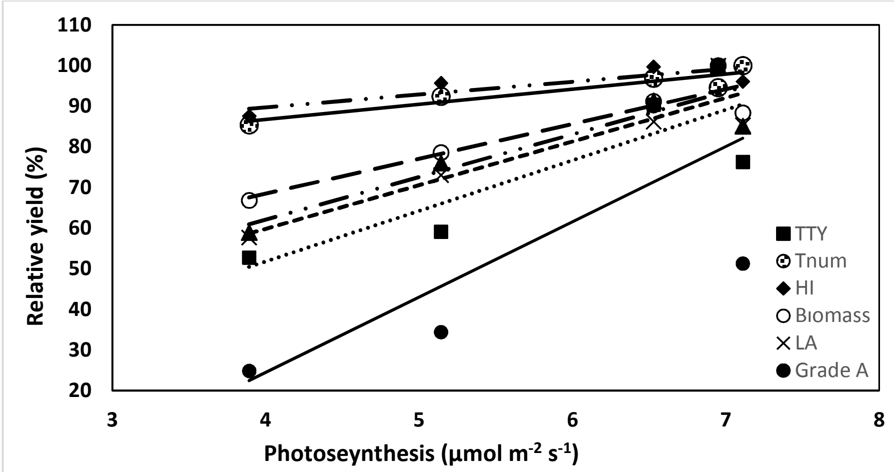

Figure 3. Rates of change in crop variables as a function of photosynthesis. TTY= 12.44 Pn+2.03, r^2=0.73 ($p>0.05$); Tnum= 3.72 Pn+71.87 r^2=0.87 ($p<0.05$); HI= 3.15 Pn+77.18 r^2=0.74 ($p>0.05$); Biomass =8.59 Pn+34.115 r^2=0.87 ($p<0.05$); LA =10.732 Pn+16.923 r^2=0.87 ($p<0.05$); Grade A= 18.53 Pn–49.65 r^2=0.58 ($p>0.05$). Tdw= 10.492 Pn+20.137 r^2 = 0.84 ($p<0.05$). Each point represents average of 15 measurements.

It seem that photosynthesis rate is more related to vegetative growth. The size of the leaves where photosynthesis is realized affects total photosynthesis capacity of the plant. Dwelle et al., (1981), stated that photosynthetic capacity (photosynthesis rate x leaf area) has a good correlation with tuber yield. The reason that the relation between photosynthesis and harvest data is not significant might be low values of first and last photosynthesis measurements. These measurement were differentiated too much from the average because of low leaf area in the first growth stage old leaves towards the harvest. Because of the reasons just stated, the correlation between photosynthesis and yield at Tuber bulking I and II stage was found to be statistically significant at *p<0.001* (Table 5). Except yield, the same is valid also for T_{dw}, Grade A when leaf area is at maximum.

Table 5. Effects of photosynthesis measured at different stages on yield parameters at harvest.

	Photosynthesis (µmol m^{-2} s^{-1})			
	Tub. Initation	Tub. Bulking I	Tub. Bulking II	Tub. Maturation Ini.
TTY (kg m^{-2})	Pn= 8.21 TTY + 2.01 r^2 = 0.45	Pn= 7.40 TTY - 0.03 r^2= 0.99**	Pn=5.00 TTY-1.75 r^2= 0.99**	Pn=-0.43 TTY+4.31 r^2= 0.13
Tnum	Pn=1.34 Tnum-51.05 r^2= 0.98**	Pn=0.51 Tnum -15.10 r^2= 0.37	Pn=0.36Tnum-12.95 r^2= 0.42	Pn= 0.059Tnum + 1.08 r^2= 0.19
Tdw (kg m^{-2})	Pn = 0.081 Tdw-3.25 r^2= 0.58	Pn= 0.06 Tdw - 2.51 r^2= 0.85**	Pn= 0.042 Tdw-3.68 r^2= 0.93**	Pn= -0.002Tdw+ 4.23 r^2= 0.05
HI	Pn= 1.546 HI – 41.416 r^2= 0.56	Pn= 1.014 HI - 26.23 r^2= 0.64	Pn= 0.736 HI- 21.19 r^2= 0.75	Pn= -0.015 HI+4.34 r^2= 0.006
Grade A (kg m^{-2})	Pn= 6.76 A+7.61 r^2= 0.33	Pn= 6.97 A+ 4.52 r^2= 0.92**	Pn=4.72 A x+1.32 r^2= 0.94**	Pn = -0.503x + 4.09 r^2= 0.19
Bıomass. (Kg m^{-2})	Pn= 0.036x-7.520 r^2= 0.59	Pn= 0.027x-5.85 r^2= 0.89*	Pn=0.0188x-5.93 r^2= 0.95**	Pn= -0.001x+4.39 r^2= 0.06
LA (m^2 m^{-2})	Pn= 12.35 LA-2.77 r^2= 0.57	Pn= 9.32 LA - 2.27 r^2= 0.87**	Pn= 6.47 LA-3.45 r^2= 0.93**	Pn=-0.403 LA+4.27 r^2= 0.06

TTY: total tuber yield (kg m^{-2}), T_{num}: number of tubers in the pot (number m^{-2}), HI: harvested ındex (%), Grade A: first class tuber weight (kg m^{-2}), Tdw: Tuber dry weight (gr m^{-2}), LA: leaf area ındex. *% yield decrease for unit ECe (1 dS m^{-1}) increase.

Changes in photosynthetic parameters depending on salt and proline and their relations

Photosynthesis (Pn), transpiration (Tr) and stomatal conductance (Sc) were decreased depending on salinity (Fig. 4-5). Sc was the most affected parameter whereas Pn was the least. An increase of 1 dS m^{-1} in salinity caused to decrease as much as 0.21 µmol m^{-2} s^{-1} in Pn, 1.85 µmol m^{-2} s^{-1} in Sc and 0.037 µmol m^{-2} s^{-1} in Tr. The decrease in T_{13} compared to non-saline treatment was %56, %69, and %60 in Pn, Tr, and Sc. It is reported that salinity decreased stomatal conductance (Clough and Sim, 1989) and photosynthesis rate (Nielsen and Orcutt, 1996). Stomatal conductance is controlled by root water potential together with an increase in ABA concentration in xylem sap (Tardieu et al., 1991).

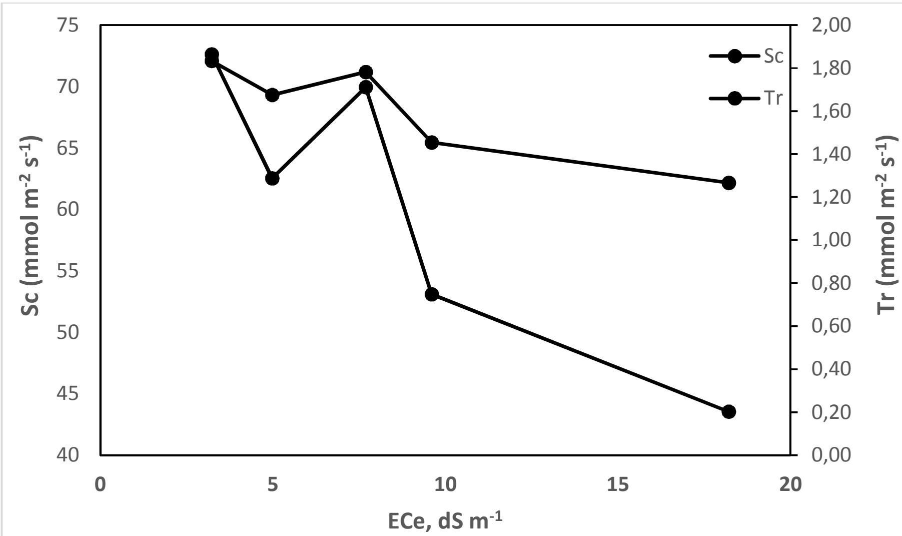

Figure 4. Changes of transpiration and stomatal conductance depending on soil salinity. (each point represetns average of 36 reading made on 4 different time (20 Apr., 5 May, 15 May, 20 May). Sc=-1.846x+76.48 r^2 = 0.80. $p<0.05$). Tr= -0.037x+1.926 r^2 = 0.83 $p<0.05$).

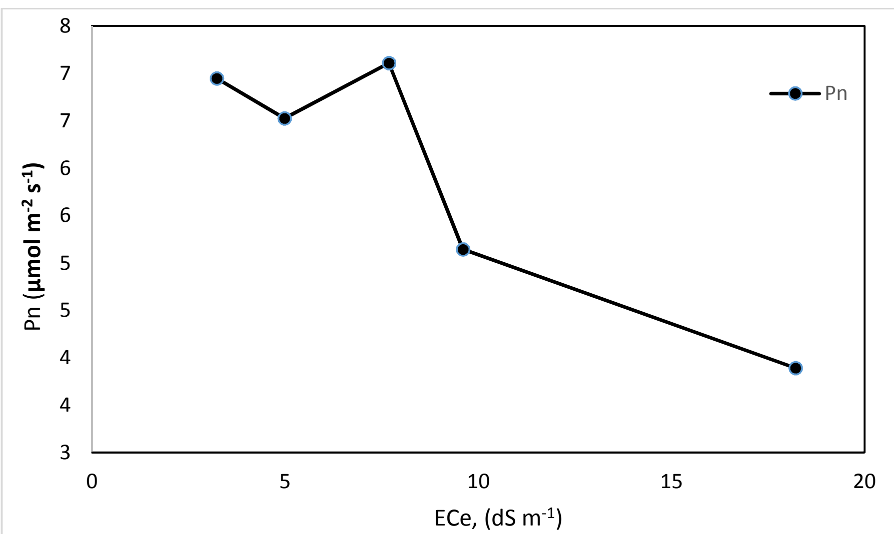

Figure 5. Changes of photosynthesis depending on soil salinity. (each point represents average of 36 reading made on 4 different time (20 Apr., 5 May, 15 May, 20 May)). Pn=-0.213x+7.79 r^2 = 0.82. $p<0.05$).

Increase in proline concentrations also increased Tr and Sc values but the increament was not statistically significant ($p>0.05$). Tr increased %37.6 in P_{10} (from 1.25 mmol m^2 sn^{-1} in P_0 to 1.72 mmol m^2 sn^{-1} in P_{10} and %6.98 in P_{20} (1.84 mmol m^2 sn^{-1}) comparing to P_0 treatment. Sc increased from 45.87 mmol m^2 sn^{-1} in P_0 to 54.62 mmol m^2 sn^{-1} in P_{10} and to 80.67 mmol m^2 sn^{-1} in P_{20}. However, Pn was unstable with increasing proline. Pn was 5.80 µmol m^{-2} s^{-1} in P_0 , and 6.20 µmol m^{-2} s^{-1} in P_{10} and finaly 5.78 µmol m^{-2} s^{-1} in P_{20} (Table 6).

In the beginning of the tuber development, all of the gas parameter were affected by proline concentration *(p<0.01)*. Sc and Pn were affected on the same period (15 May) by proline increament. Towards the end of tuber development, proline was effectivve only on Tr.

Generally, proline was effective on early development period and inhibited salt effect on gas transport parameters. Towards the end of tuber development, both salinity and proline was not effective.

Table 6. Change in gas transport parameters during four tuber development periods depending on salinity and proline (y=ax+b, n=5)

Treat.		Photosynthesis (µmol m-2 s-1)	Transpiration (mmol m-2 s-1)	Stomatal Conductance (mmol m-2 s-1)
Salinity (ECe. dS m^{-1})	Tub. Ini.	Pn = -0.507 ECe + 15.75 r^2 = 0.43	Tr = -0.076 ECe + 3.41 r^2 = 0.31	Sc = -4.053 ECe + 142.27 r^2 = 0.28
	Tub. Bulk I	Pn= -0.399 ECe + 12.25 r^2 = 0.93**	Tr = -0.0761 ECe + 2.56 r^2 = 0.97**	Sc = -3.341 ECe + 95.84 r^2 = 0.93**
	Tub. Bulk II	Pn = -0.252 ECe + 6.615 r^2 = 0.97**	Tr = -0.0582 ECe + 1.78 r^2 = 0.96**	Sc = -2.462 ECe + 57.35 r^2 = 0.93**
	Tub. Mat. Ini.	Pn = 0.018 ECe + 3.617 r^2 = 0.09	Tr = 0.023 ECe + 1.37 r^2 = 0.54	Sc = 1.222 ECe + 69.59 r^2 = 0.49
Proline (mM)	Tub. Ini.	Pn = 1.723 Pr + 7.96 r^2 = 0.99**	Tr = 0.880 Pr + 1.00 r^2 = 0.99**	Sc = 43.333 Pr + 20.89 r^2 = 0.98**
	Tub. Bulk I	Pn = -0.684 Pr + 9.81 r^2 = 0.76	Tr = -0.024 Pr + 1.88 r^2 = 0.01	Sc = -2.835 Pr + 69.56 r^2 = 0.27
	Tub. Bulk II	Pn = -0.490 Pr + 4.96 r^2 = 0.99**	Tr = -0.021 Pr + 1.21 r^2 = 0.03	Sc = -5.00 Pr + 41.55 r^2 = 0.85*
	Tub. Mat. Ini.	Pn = -0.421 Pr + 4.65 r^2 = 0.24	Tr = 0.60 Pr + 0.42 r^2 = 0.98**	Sc = 51.00 Pr - 19.22 r^2 = 0.71

TTY: total tuber yield (kg m^{-2}), T_{num}: number of tubers in the pot (number m^{-2}), HI: harvested ındex (%), Grade A: first class tuber weight (kg m^{-2}), Tdw: Tuber dry weight (gr m^{-2}), LA: leaf area ındex. *% yield decrease for unit ECe (1 dS m^{-1}) increase

Proline effects on Pn, Tr, and Sc were unstable especially in Tuber bulking I and Tuber maturation initial as a result of leaf aging most probably.Towards the end of the experiment, reduction in development, especially in the higher salinity treatments, was observed clearly. Similar results were also reported by Downton (1977).

Conclusion

In this study, the effects of salt stress was tried to diminish by foliar application of proline. The effect of proline on Pn, Tr and Sc was mostly pronounced when vegetative development was at maximum whereas salt effect was observed at tuber bulking I and II stages. The most affected parameter by salinity was found to be stomatal conductance (Sc). The values of Pn, Tr and Sc increased in T_7 treatment compared to $T_{3.5}$.

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