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Growth of Avocado Plants Under Saline Conditions

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ABSTRACT. Avocado (*Persea americana* Mill.) is an important multipurpose tree crop. A study was conducted to investigate the growth and gas exchange characteristics of avocado seedlings growing under different salinity levels. Plants were grown in 4.5 liter plastic pots containing soil were subjected to 0 (control), 15, 30, 45 and 60 mM NaCl salinity treatments. Growth, net photosynthetic rate (P_N), stomatal conductance (gs), transpiration rate (E), water use efficiency (WUE) and chlorophyll (chl) concentration decreased in response to increasing salt concentration. Substomatal CO_2 concentration (Ci) and chloride content increased as salt concentration increased. The findings from this study demonstrate that salinity inhibits growth and gas exchange of avocados. doi:10.1300/J492v07n01_06

KEYWORDS. Leaf chlorophyll concentration, net photosynthesis, salinity stress

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INTRODUCTION

Salt stress is one of the major environmental stresses that causes decreases in growth and photosynthesis (Netondo et al., 2004a). Three major hazards associated with salinity are: osmotic stress, ion toxicity, and mineral deficiencies (Reinhardt and Rost, 1995; Hasegawa et al., 2000; Netondo et al., 2004a). Reduction in photosynthesis is directly related to stomatal conductance, though non-stomatal factors are also associated with lower photosynthetic capacity in salt treated plants (Ashraf et al., 2002; Netondo et al., 2004b). Growth and photosynthesis are particularly important under saline conditions since resistance to external salinity is much influenced by plant vigor. The more vigorous the plant growth under non-saline conditions, the greater is its resistance to salt (Flowers et al., 1988). Photosynthetic performance in plants is usually enhanced by additional environmental factors such as high light irradiance, water availability and soil fertility (Jimenez et al., 1997; Hofshi, 1998).

Avocado (*Persea americana* Mill.) is a salt sensitive tree crop (Hofshi, 1995; Hofshi, 1998; Mickelbart and Arpaia, 2002) and is often grown in areas with relatively low rainfall and saline soils (Branson and Gustafson, 1972). Growth rates of avocado trees on avocado rootstocks have been shown to be reduced during an active growth flush under salinity stress (Mickelbart and Arpaia, 2002). Previous work by Mickelbart and Arpaia (2002) has indicated that sensitivity to salinity among avocado cultivars was reflected in different growth reductions and leaf necrosis. Schaffer and Whiley (2003) have indicated that stomatal conductance is a more reliable early indicator of stress in avocado than measurements of leaf water content, leaf water potential or growth variables. There is little information available on the possible interaction between salinity and PAR on photosynthetic activity, stomatal behavior and water use efficiency of avocado rootstocks. Also, there are no reports in the literature on the effects of long-term exposure to increased atmospheric CO_2 on photosynthesis under saline conditions. The current interest in the utilization of saline soils necessitates knowledge of gas exchange characteristics for this fruit tree under salinity stress, which is a suitable candidate for incorporation into agroforestry systems.

Our objective was to evaluate the influence of salinity stress on growth, net photosynthetic rate (P_N), stomatal conductance (gs), transpiration rate (E) and water use efficiency (WUE) and total chlorophyll concentration in young avocado plants as part of study to determine the

combined effects of salinity and low PAR irradiance. Data obtained may explain physiological mechanisms by which salinity affects growth and development in avocado and may help improve the management of avocado productivity in saline environments and in agroforestry systems.

MATERIALS AND METHODS

Plant Material and Growth Conditions

Three-month-old avocado plants (*Persea americana* Mill.) were raised inside a naturally illuminated greenhouse which had a temperature min/max of 20/41°C and a relative humidity min/max of 50%/95% during the experiment. The CO_2 concentration in the greenhouse was not controlled. The plants were selected on the basis of uniformity of size and transplanted in 4.5 liter plastic pots filled with local soil classified as acrisol (FAO, 1965). The exposed soil had been covered with aluminium foil to prevent growth of algae. The mineral fertilizer used was 20 g of diammonium phosphate (DAP) per pot at planting. Plants were separated into five lots of 4 plants each; with one lot as control (0 mM NaCl) with the other four being subjected to different salinity treatments of 15, 30, 45 and 60 mM NaCl. The saline treatments were administered in a step-wise fashion, adding daily increments of 300 ml of 15 mM saline water until the desired concentration was reached. The application rate of saline solution was adequate to ensure more than 30% drainage of applied solution through perforations at the bottom of the pots. The pots were arranged in a completely randomized design on a bench. Weeds were controlled by hand pulling, while recommended pesticides were used to control pests.

Plant Growth Measurements

The data for growth parameters were recorded once every week before and after the commencement of the salinity treatments. Shoot height was measured using a meter rule, from the stem base up to the shoot apex. The number of fully expanded mature leaves per plant on the main stem and branches were counted and recorded. The change in growth of the stem diameter was determined for each plant by measuring the diameter at a height of 10 cm from the stem base using a vernier caliper. All the above measurements were done once every week. At the

end of the experiment the plants were harvested, and their roots and shoot regions were separated. Roots were rinsed in tap water after soaking, then were blotted dry on paper towels and weighed using an electronic weighing balance (Denver Instrument Model XL-3100D). Fresh weight reading for the shoot was taken immediately after harvesting. All the plant samples were then oven-dried at 60°C to constant dry weights, for at least 48 hours, after which time their dry weights were determined. Treatments were continued for 39 days.

Gas Exchange Measurements

An open infrared gas analyzer system in which the CO_2 concentration of in- and out-coming air was measured differentially (CIRAS-1, PP Systems, Stotfield, Hitchin, Herts, UK) was used to measure gas exchange parameters (PN, gs, E and Ci). Gas exchange was determined from an area of 2.5 cm^2 of the fully expanded sun-exposed fifth leaf (from the shoot apex) of plants in each treatment between 0900 and 1230 h. Photosynthetic rates were measured at 26°C to 37°C. The photosynthetically active radiation (PAR) measured at the leaf surface was 120-200 μmol $m^{-2}s^{-1}$. The vapor pressure deficit within the leaf cuvette was maintained throughout these experiments at 0.5-0.7 kpa using this system. The air flow rate through the cuvette was 200 ml min^{-1}. Ten consecutive measurements were taken at 3 seconds intervals. Measurements were made indoors and began on the seventh day after commencement of salt treatment and were done once per week.

Water Use Efficiency

Water use efficiency was calculated using the formula of Ashraf et al. (2002), as follows:

$$\text{Water use efficiency (WUE)} = P_N/E$$

Where,
P_N = net photosynthetic rate
E = transpiration rate

Chlorophyll Concentration

The fourth fully expanded leaves were harvested at the end of the experiment. The chlorophyll concentration was determined in 80% ace-

tone extract on a spectrophotometer (Model Novaspec II, Pharmacia Biotech, Cambridge, England). Absorbency was measured against an 80% acetone blank at 645 nm and 663 nm. The tchl (mg/g) was obtained by summation of the calculated values of chl *a* and chl *b* following the formulae of Arnon (1949).

Leaf Chloride Ion

Finely ground oven dried tissue (0.1 g) was digested overnight with 25 cm^3 of 0.1 M HNO_3 at room temperature according to Sibole et al. (2003). Chloride content was determined from the aqueous extract by titration with silver nitrate. Ion concentrations were calculated on a tissue basis from the dry masses of the same leaf. Twenty-five cm^3 of the aqueous extract was used to titrate with 0.1 M $AgNO_3$.

Statistical Analysis

The data collected were subjected to analysis of variance (ANOVA) using SAS statistical computer package to compare treatment effects of avocado seedlings growth and photosynthetic rate. Treatment differences were evaluated using the least significance difference (LSD) at $P \leq 0.05$. Standard error of difference of means (SED) was given.

RESULTS

Plant Growth

There were no significant ($P = 0.05$) differences in shoot height growth between salinity treatments (Table 1a). Salinity significantly increased stem diameter in the first few days after initiation of salt treatments. Salt treated seedlings had significantly ($P \leq 0.05$) fewer number of leaves than control plants. Growth at high salinity resulted in large reductions in fresh and dry weight production of both shoots and roots (Table 1b). The reduction in shoot dry weight was attributed to lower leaf number and development of smaller leaves with increased salinity of the growth medium.

Chlorophyll and Leaf Chloride Ion Content

Total chlorophyll content was higher in the control than in salt treated plants (Table 2). Chlorophyll content decreased at higher salinities. The

TABLE 1a. Analysis of growth parameters for 39 days (D) of saline water irrigation.

Parameter	Treatment NaCl (mM)	D7	D12	D16	D19	D23	D25	D32	D40
Shoot height (cm)	0	38.925a[z]	41.700a	44.750a	47.125a	50.025a	52.875a	54.700a	56.550a
	15	44.425a	48.175a	53.750a	53.300a	55.800a	57.675a	58.475a	59.825a
	30	46.250a	48.500a	51.175a	52.800a	54.700a	56.650a	57.000a	57.700a
	45	43.675a	47.350a	49.500a	51.325a	52.325a	53.850a	53.725a	54.350a
	60	38.500a	40.850a	42.775a	44.675a	45.275a	46.050a	46.350a	46.300a
	LSD	11.811	13.597	14.262	15.147	15.704	15.356	15.333	15.227
Leaf number per plant	0	20.250ab	22.00ab	29.500ab	31.500ab	34.500bc	39.500b	42.750ab	44.750bc
	15	22.500ab	25.500a	33.500a	35.000a	41.250ab	44.750ab	48.500ab	51.000ab
	30	23.750a	25.750a	32.500a	35.250a	46.750a	51.000a	52.500a	55.000a
	45	19.750ab	22.000ab	29.500ab	31.500ab	34.500bc	36.750b	35.000cd	36.750c
	60	18.000b	20.000b	23.250b	24.750b	27.000c	26.750c	26.750d	25.750d
	LSD	4.8455	4.673	8.9504	8.6868	8.4467	8.2092	8.5791	8.4918
Stem diameter (mm)	0	6.8750a	7.3500a	7.7250a	7.7250a	8.0750a	8.3750a	8.5500a	9.1500a
	15	6.9500a	7.4500a	7.8000a	8.0250a	8.1750a	8.3000a	8.4750ab	8.8750ab
	30	7.2750a	7.5500a	8.0500a	7.9250a	8.0750a	8.0750a	8.3000ab	8.3250abc
	45	6.5000a	6.8750a	7.3500a	7.4500a	7.4500a	7.4750a	7.4000ab	7.4000bc
	60	6.4250a	6.7250a	7.0250a	7.000a	7.000a	7.0750a	7.0750b	6.9750c
	LSD	1.5334	1.5189	1.3529	1.6177	1.458	1.4283	1.4543	1.5142

[z] Letters show significant differences at $P \leq 0.05$ with t test.

TABLE 1b. Analysis of growth parameters after 39 days of saline water irrigation

	Parameters			
Treatment				
NaCl (mM)	Root fresh weight (g)	Root dry weight (g)	Shoot fresh weight (g)	Shoot dry weight (g)
0	59.425a	19.425a	89.88a	31.025a
15	31.500b	9.425b	82.00a	26.825ab
30	23.875b	5.450b	81.33ab	20.450bc
45	25.075b	5.950b	51.35bc	16.650c
60	21.750b	4.800 b	42.00c	13.850c
LSD	20.44	6.6741	30.092	10.113

[z]Letters show significant differences at $P \leq 0.05$ with t test.

TABLE 2. Analysis of means of chlorophyll concentration and chloride content after 39 days of saline water treatment

Treatment NaCl (mM)	Chl a mg/g fresh leaf weight	Chl b mg/g fresh leaf weight	Total chl mg/g fresh leaf weight	Chloride content mg/g leaf dry matter
0	0.015725 a	0.0057750a	0.021500 a	0.0003000c
15	0.009925 b	0.0035250 b	0.013450 b	0.0030325 d
30	0.009100 b	0.0030500 b	0.012150 b	0.0047300 c
45	0.009075 b	0.0030500 b	0.012125 b	0.0098025 b
60	0.007075 b	0.0026000 b	0.009675 b	0.0192025 a
LSD	0.004	0.0012	0.005	0.0008

[z] Letters show significant differences at $P \leq 0.05$ with t test.

differences between these and more saline conditions were significant at $P \leq 0.05$). However, chlorophyll *a* content was higher in the leaf than Chl *b*. An increase in the Chl *a*:*b* ratio occurred in plants receiving salt concentrations from 15-45 mM NaCl (Figure 1) while those receiving the higher salt concentration of 60 mM NaCl experienced a marked decrease. Total chloride content of leaves increased significantly ($P \leq 0.05$) with external salinity in the growth medium (Table 2). Tip burn symptoms due to chloride (Mickelbart and Arpaia, 2002) were visible on mature leaves of avocado plants exposed to high levels of NaCl salinity (30, 45 and 60 mM).

Gas Exchange

Salinity stimulated P_N in the first few days of salt application for the plants receiving low salt concentrations (Table 3). Net photosynthetic rate of salinised plants was 63.6 to 93.3% of the control plants after 39

FIGURE 1. The effect of saline water irrigation on Chl*a*:Chl*b* ratio of avocado seedlings after 39 days. Each value is the mean of four replications ± SE

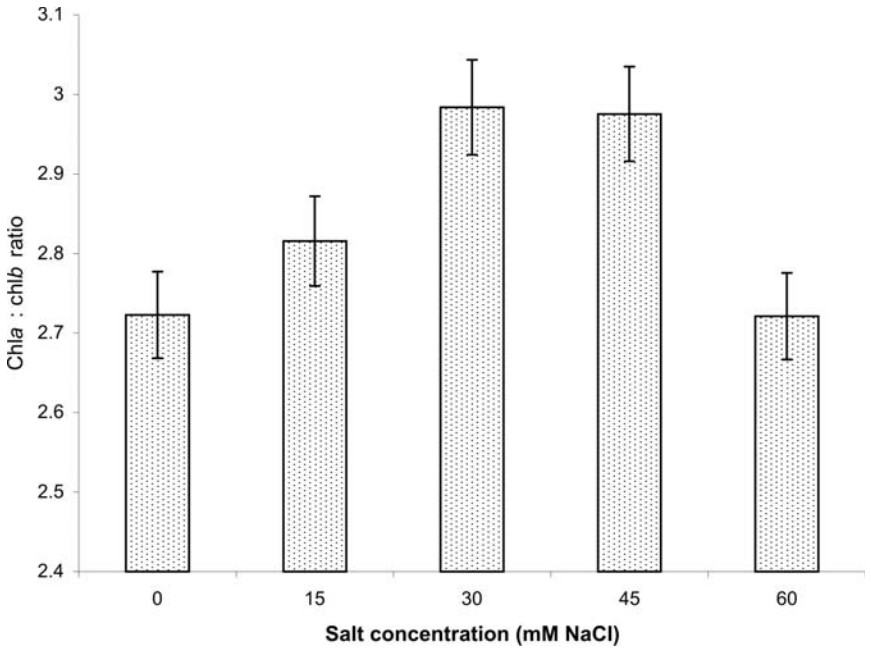


TABLE 3. Analysis of means of net photosynthetic rate and related parameters for 39 days (D) of saline water irrigation

Parameter	Treatment NaCl (mM)	D7	D12	D16	D19	D23	D25	D32	D40
Net photosynthetic rate, (µmol $m^{-2}s^{-1}$)	0	3.75.a[z]	4.975a	5.000a	2.775 a	4.6000a	3.1500a	6.525a	4.175a
	15	3.325ab	5.1500a	5.100a	2.4250b	4.3750a	3.0750ab	4.975ab	4.375a
	30	3.050b	4.775ab	3.4750b	1.7500c	4.6250a	2.7750b	3.800bc	3.850a
	45	3.45ab	4.425bc	2.525b	1.8500c	3.9000b	2.7750b	2.575bc	3.850a
	60	3.550a	4.075c	2.825b	1.700c	3.5500b	2.2500c	1.925c	2.350b
	LSD	0.4769	0.5125	0.9618	0.3431	0.4688	0.3702	2.4067	0.9347
Stomatal conductance (mmol m^{-2} s^{-1})	0	19.7500a	20.00ab	10.500a	17.250a	21.7500a	14.7500a	10.2500a	12.750a
	15	17.25c	19.500ab	11.750a	14.250b	21.500b	12.7500b	8.2500ab	14.000a
	30	16.5000c	20.750a	10.000a	11.750c	18.5000b	13.0000b	10.0000a	10.250b
	45	17.7500c	18.00ab	9.750a	11.500c	17.7500b	13.000ab	9.7500a	10.250b
	60	19.0000a	16.500b	11.00a	11.500c	14.0000c	12.0000b	7.5000b	8.250b
	LSD	1.5342	3.6077	2.5355	2.2895	2.0718	1.5724	2.0813	2.4842
Sub-stomatal CO_2 concentration (ppm)	0	172.75c	93.50b	159.25b	290.50c	74.06c	263.25c	77.5c	224.0b
	15	250.00ab	111.25b	126.50b	384.25b	150.25b	352.00bc	355.5bc	189.5b
	30	276.50a	97.25b	379.50a	544.25b	146.50b	351.50bc	483.8bc	265.5b
	45	219Bc	97.25b	519.00a	532.50a	170.50b	372.75b	728.8ab	367.0b
	60	199.25bc	194.25a	445.0a	552.75a	261.50a	516.25a	1004.8a	834.0a
	LSD	53.148	63.168	168.17	88.432	47.806	104.03	463.8	410.52
Transpiration rate (mmol m^{-2} s^{-1})	0	1.25250a	0.92250a	0.70000a	0.98500a	0.99250ab	0.68500bc	0.63250ab	0.58000ab
	15	1.05000cd	0.88250a	0.77500a	0.87500ab	0.95500b	0.60750c	0.53000b	0.67750a
	30	1.01500d	0.91000a	0.66750a	0.78750b	1.04750ab	0.72500ab	0.7100a	0.48000bc
	45	1.13500bc	0.82250ab	0.66500a	0.77500b	1.06750a	0.77500a	0.69500a	0.47500bc
	60	1.18250ab	0.76000b	0.71500a	0.76250b	0.81250c	0.68750bc	0.59250ab	0.42500c
	LSD	0.0868	0.1492	0.1834	0.1501	0.101	0.0835	0.1341	0.1083

[z] Letters show significant differences at $P \leq 0.05$ with t test.

days. Salinity treatment had significant effect on P_N ($P \leq 0.05$) after 39 days of salt application. At 60 mM NaCl, the plants were slightly more affected than at all other salinity levels. There were fluctuations in P_N almost every week, which may be associated with the growth behavior of avocado plants, since there are periods when the plants tend to have high percentage of young leaves. It is also possible that the observed fluctuations in P_N were due to slight fluctuations in temperature because P_N in avocado are significantly affected by temperature variations. Generally, gs of salinised plants significantly ($P \leq 0.05$) decreased throughout the experimental period in contrast to control plants (Table 3). The gs values after 39 days of salt application ranged from about 65.6 to 78.5% of values from control plants. It is possible that the fluctuations in gs observed from time to time were due to increased vapor pressure deficit, which is known to increase with increased temperature. Transpiration rate (E) decreased in response to increasing salt concentration of the growth medium (Table 3). From 15 to 60 mM NaCl, the decreases in E were 94.1, 93.9, 95.1 and 87.9 percentages of control plants, respectively, after 39 days. Significant ($P \leq 0.05$) differences in E between control and salinity treatments were evident in all the days of measurement except on day 16. Stomatal limitation of water loss may account for these observations. Salinity stress of the growth medium (Table 3) caused significant ($P \leq 0.05$) increase in Ci. The increases in Ci were 141.7, 187.8, 222.0 and 295.8% of control plants values, from 15 mM to 60 mM NaCl, respectively, after 39 days of salt application.

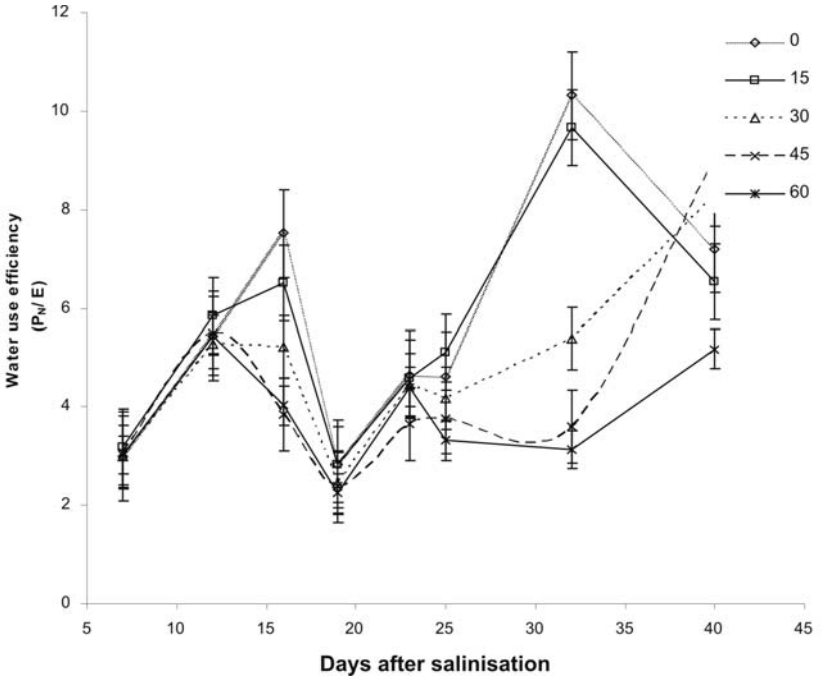
Water Use Efficiency (WUE)

Generally water use efficiency of salt treated plants was lower than that of control plants, but the differences among treatments were not statistically significant ($P \geq 0.05$) between day 7 and day 12 (Figure 2). However, further application of saline water resulted in increased water use efficiency at higher salt concentration levels compared to control plants. Probably this is a consequence of minimizing water loss at the expense of carbon acquisition, which may be an adaptive mechanism to water stress due to salinity stress.

DISCUSSION

Salinity had a significant influence on the growth pattern of the avocado seedlings. The pattern of growth performance in height and dry

FIGURE 2. Effects of saline water irrigation on water use efficiency of avocado seedlings. Each point represents the mean of four replications ± SE.



weight indicate that growth parameters were decreased by saline irrigation. Salinity reduced shoot and root growth (Table 1a and 1b) of especially plants receiving water of highest salinity. A reduction in growth caused by increasing salinity is a well known phenomenon, but the growth of some plants may be stimulated by sodium chloride (Soussi et al., 1998). An increase in shoot height and stem diameter growth observed from the study, but not detectable at 60 mM NaCl, may suggest increased cell growth and increased cell number due to osmotic adjustment. In most cases, salinity stress reduces root growth (Reinhardt and Rost, 1995; Musyimi, 2005), although mild stress can increase extension as a result of osmotic adjustment process which maintains root growth during periods of salt stress. There was a short term stimulation of PN and growth during the first days of saline water irrigation (Table 1a and 3), except for 60 mM treatment. This stimulation was also evident in the results for stem diameter growth. According to Soussi et al.

(1998), this observation may be attributed to increased activity of phosphoenolpyruvate carboxylase (PEPC). The stimulation may also be linked to improved water use efficiency through reduced water loss (Figure 2). Increased leaf death and defoliation evidenced during the study may account for the few number of leaves (Table 1a) and hence reduced P_N. Salinity toxicity showed up as interveinal leaf burn, scorch and dead tissue along the outside edges of leaves. The decline in net photosynthesis with increasing salinity was associated with similar reductions in gs in salt treated plants; so that there were only small changes in Ci of control plants than of salt treated plants (Table 3). Closure of the stomata could reduce Ci and CO_2 assimilation rate (Ashraf et al., 2002; Netondo et al., 2004b), but in the present study closure of the stomata had only minimal contribution to reduction in internal CO_2 concentration of salt treated plants; suggesting a presence of a non-stomatal factor being involved in reduction in PN (Hand et al., 1982; Bradford, 1983a; Sharp and Boyer, 1986; Rao et al., 1987; Belkhodja et al., 1999).

The results indicate that chloride may play an important role in the inhibition of chloroplasts reactions by inhibiting the synthesis of rubisco (ribulose-1,5-biphosphate carboxylase/oxygenase) and chlorophyll or accelerate chlorophyll degradation (Soussi et al., 1998; Ashraf et al., 2002). The results indicated that chl *a* was higher than chl *b* showing that salinity induced a marked decrease in chl *b*. Reduction of chl *b* may suggest structural damage of the photosystem II reaction centers; and would explain the high Ci in salt treated avocado plants (Table 3). Earlier findings by Lutts et al. (1996) have indicated that chl *b* is associated with PS antenna. Losses in chloroplast activity include decreases in electron transport and photo-phosphorylation, and are associated with changes in conformation of the thylakoids and of the coupling factor (ATP synthetase, a sub unit of the thylakoids), and decreased substrate binding by the coupling factor (Bradford, 1983; Rao et al., 1987). Several researchers have reported that non-stomatal factors may be the limiting factors in decreases of photosynthetic activity under salinity stress (Richardson and McCree, 1985; Bar et al., 1996; Soussi et al., 1998; Ashraf et al., 2002) and include inhibition of electron transport (Robertson et al., 1985; Soussi et al., 1998; Sibole et al., 2003; Netondo et al., 2004b). High external salt concentrations could affect thylakoid membranes by disrupting lipid bilayer or lipid protein associations and impair electron transport activity (Netondo et al., 2004b). According to Farquhar and Sharkey (1982), the greater inhibition of net photosynthesis at high Ci than low, would suggest that salinity stress affects ribulose bisphosphate (RUBP) regeneration. Reduction in chlorophyll may

partly account for the reduction in photosynthetic rate of avocado seedlings.

Water use efficiency is an important aspect in tolerance to salinity stress (Flowers et al., 1988; Gorrham et al., 1985). Initially plants exhibited reductions in WUE with increasing NaCl levels and later only plants at higher salinity levels increased their WUE (Figure 2). The observed results may be due to reduced water loss in salt treated plants compared to controls caused by a rapid decrease in water potential in the growth medium (Hand et al., 1982; Richardson and McCree, 1985; Munns, 2002). Higher salinity resulted in lower transpiration rates (Table 3), indicating that salinity caused a reduction in water loss per unit leaf area. This effect of salinity on transpiration has been reported in other plant species (Gorrham et al., 1985; Marler and Zozer, 1996; Ashraf et al., 2002). Other researchers have observed limited carbon supply due to increased incidence of necrotic margins on the leaves of salinity stressed plants (Oster and Arpaia, 1992; Cramer et al., 1994; Mickelbart and Arpaia, 2002), which would reduce the transpiration rate because of the reduced leaf area. An increase in WUE means that there was a greater reduction in the transpiration rate than in the net photosynthesis per single leaf.

CONCLUSIONS

This study presents evidence showing that high growth inhibition of avocado seedlings at high salinity may be related to high leaf chloride content. The results show not only that salinity reduces growth and photosynthetic capacity of avocado plants, but also the combined effects of salinity and low PAR irradiance may contribute to reduced photosynthetic rate. Further studies are needed to determine the parameters related to chlorophyll fluorescence and gaseous exchange of the individual leaves to bring complementary information on the nature of constraints acting on photosynthetic processes. The study has shown clearly that this Kenyan avocado rootstock (var. Puebla) is sensitive to substrate salinity and hence cannot be depended upon in reclaiming saline problematic soils.

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