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Tomato Root and Shoot Responses to Salt Stress Under Different Levels of Phosphorus Nutrition

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ABSTRACT

Crops differ in their ability to grow under saline conditions and their responses are quite variable and not fully understood. This study was conducted to evaluate the root and shoot responses of tomato to salt stress conditions under different levels of phosphorus (P) nutrition. Tomato seedlings (cv Riogrande) were grown in 500 mL glass jars containing Hoagland's solutions which were salinized by four levels of NaCl salt (0, 50, 100, and 150 mM NaCl) and/or enriched with three P levels (0.5, 1, and 2 mM P) making nine combination treatments. Plants were harvested at the vegetative growth stage and data were collected for root and shoot characteristics. The results indicate that increasing salinity stress was accompanied by significant reductions in shoot weight, plant height, number of leaves per plant, and a significant increase in leaf osmotic potential and peroxidase activity regardless of the level of P

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supplied. Both root length and root surface area per plant were decreased significantly under higher salinity conditions at all levels of phosphorus. On the other hand, increasing the phosphorus levels enhanced root growth through increasing both root length and root surface area. This phenomenon was observed at all levels of salinity. It can be concluded that root morphology parameters and peroxidase activity are additional sensitive parameters which are affected by salt stress and, therefore, can be employed as a criteria for monitoring plant response mechanisms to salt stress conditions.

INTRODUCTION

Salinity is considered a significant factor affecting crop production and agricultural sustainability in many regions of the world as it reduces the value and productivity of the affected land. Salinity mainly occurs in arid and semiarid conditions (Ehret and Ho, 1986) where the precipitation is not enough to leach the excess soluble salts from the root zone. Salinity problems can also occur in irrigated agriculture, particularly when poor quality water is used for irrigation (Mitchell et al., 1991; Shibli, 1993).

The scarcity of water resources in most countries of the arid and semiarid regions has led many farmers to use poor quality water for irrigation. Considerable amounts of such marginal water are available and can be successfully used for irrigation under proper management (Mitchell et al., 1991). Crops differ in their ability to grow successfully under saline conditions and to accumulate high concentration of salts in their tissues. Increasing the level of the soluble salts in the soil solution tends to increase its osmotic pressure and/or cause an individual ion toxicity (Greenway, 1973) which leads to decrease in the water and nutrient uptake by plants (Smith et al., 1992).

Growing plants in hydroponic solution with salinizing salts added is an easy technique that rigorously controls the root environment for evaluation of the response of the plants to salinity (Feigin et al., 1987; Smith et al., 1992; Shibli, 1993). With this technique most of the complexities and interferences induced by soil and environmental factors are avoided and better control of the experiment is achieved (Meyer et al., 1989).

The effect of salinity on plant growth has been extensively investigated under different nitrogen regimes (Ahmed et al., 1993; Garg et al., 1993). The mechanisms by which plant growth is reduced under high salinity conditions are not well understood (Evlagon et al., 1992). Salinity can alter nutrient uptake through antagonistic effects with essential nutrients (Shibli, 1993). Nutrient imbalance resulting from both antagonistic and synergistic interaction in saline growth media can also affect nutrient uptake and reduce plant growth (Feigin, 1985; Feigin et al., 1987).

The growth and yield of tomato is significantly reduced by high salinity (Feigin et al., 1987; Shalhevet and Hsiao, 1986; Smith et al., 1992). The response of tomato

to salinity is variable according to lines and cultivars (Shannon et al., 1987). Evlagon et al. (1992) found that the root length was reduced by 54% after 4 days exposure to 0.1 strength Hoagland's solution salinized with 100 mM NaCl, while surface area was reduced by 20% when 100 mM Ca was added to the salinized solution.

The adverse effect of soil salinity on the growth and development of crops can be due to poor soil physical conditions (surface crusting, poor water use efficiency, seed germination or root penetration) and to nutritional imbalance and interference with uptake of essential nutrients or sodium toxicity. Several management practices can be adopted in this regard to minimize the adverse effect of the use of marginal water for irrigation. Phosphorus has been recognized to enhance root growth (Samuel et al., 1993) and it was found that the plant root growth under drought conditions was stimulated by localizing the P fertilizers in the root zone (Mohammed, 1993). This effect on root growth may enhance the performance of crops grown in saline conditions. Salinity also induces biochemical changes in the exposed plants such as the activity of peroxidases as a group of enzymes affected by salt stress (Sancho et al., 1996). So far the relationship between peroxidases and both salinity and P has not been investigated.

Tomato shoot and fruit physiological responses to salt stress conditions have been extensively investigated (Cruz et al., 1990; Mitchell et al., 1991; Niedziela et al., 1993). However, information on the effect of salinity on root growth is limited (Snapp and Shennan, 1994). Studying the salinity effect on root growth and senescence in tomato, Snapp and Shennan (1994) stated that conventional observations of root length are not adequate and observing root system architecture should be considered. Root morphology parameters are important criteria of crop growth and responses to water and salt stress conditions. However, these parameters are often not determined due to difficulties associated with their measurements (Shannon et al., 1987). Better methods for measuring root morphology parameters (root length, root surface area root diameter) are needed (Baker, 1989). In this study, edge discrimination analysis using the desktop scanner was used to measure the root morphology (Pan and Bolton, 1991). The objective of this study was to evaluate the root and shoot response of tomato to salt stress condition under different levels of P nutrition.

MATERIALS AND METHODS

Tomato (*Lycopersicon esculentum* Mill. cv Riogrande) seeds were germinated as described by Shibli (1993). Two weeks after germination, seedlings were transferred to 500 mL glass jars containing Hoagland's solutions (Hershey and Merritt, 1986) representing the investigated treatments. Treatments included different P concentrations (0.5, 1, and 2 mM P) and four concentrations of NaCl salt (0, 50, 100, and 150 mM NaCl, which represent 2.4, 8.2, 11.9, and 17.6 dS m^{-1} salinity levels). The pH of the nutrient solution was maintained at 6±0.5 (Knight et al., 1992). Plants were held in place using cotton inserted in aluminum foil caps on

the top of the jars. Jars were painted brown to avoid light penetration to roots. One plant was grown in each jar. The jars were arranged in a randomized complete block design, where the treatments were replicated three times. The whole nutrient solution in the jars was changed every week. Aeration was maintained through an aquarium bubble stone by an oil-less diaphragm pump (Meyer et al., 1989; Shibli, 1993). Plants were grown for 28 days at room temperature (about 23±1°C) in a special chamber with supplementary light (photosynthetic photon flux, PPF=75-100 $\mu mol\ m^{-2}\ s^{-1}$).

Plants were harvested after four weeks and data were collected for shoot length, shoot and root fresh weight. Leaf tissue samples were packed into syringes, quick frozen at -80°C and then thawed at room temperature for 30 minutes. Sap was expressed from these leaf samples by depressing the syringe plunger. Osmotic potential of the sap was measured by loading of 0.1 mL on a vapor pressure osmometer (Wescor 5500, Logan, UT) (Knight et al., 1992). The roots were separated and morphological parameters were measured by edge discrimination analysis using a desktop Scanner (Pan and Bolton, 1991). Soluble and tonically bound Peroxidases were extracted and assayed according to Garraway et al. (1989). Peroxidase activity represented by the rate of tetraguiacol formation was determined as the change in one absorbency unit at 470 nm per min per mg protein using a Pye Unicam SP6-550 UV/VIS spectrophotometer from Philips. A Bio-Rad assay was used to determine protein concentration of the enzyme extract using bovine albumin as a protein standard (Bradford, 1976). Total phosphorus was determined in the dry ash digestion with the ascorbic acid molybdate blue method (John, 1970).

Phosphorus uptake was reported per fresh weight not per dry weight because subsamples from the fresh shoot were immediately taken for osmotic pressure and for peroxidase measurements. The remaining fresh shoot was oven dried, then dry ashed at 550°C.

Statistical analysis was performed as for two factorial randomized complete block design (RCBD) (Steel and Torrie, 1968). The means were separated by the least significant difference (LSD) using MSTATC (Michigan State University, East Lansing, MI).

RESULTS AND DISCUSSION

Complete death was observed on plant grown at the highest salinity level (150 mM NaCl), so these jars were excluded from analysis. Increasing salinity stress was accompanied by significant reductions in growth regardless of the level of P supplied (Figure 1). All variables studied except root morphology parameters were significantly affected by the P levels and the interaction effect between P and NaCl levels only at the 0.1 level but not at the 0.05 level of significance. Therefore, root morphology parameters were presented in a two way table to show the interaction effect of P and NaCl levels, while remaining variables are presented in a bar graphs to show the main effect of NaCl levels. The number of leaves per plant and plant

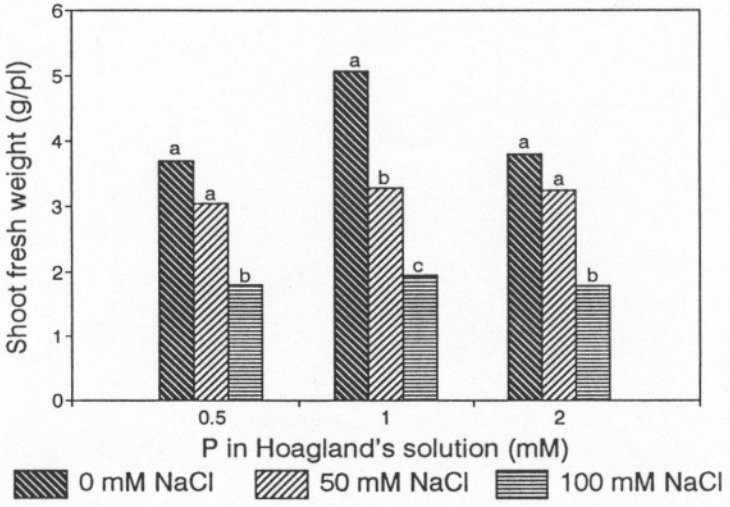

FIGURE 1. Shoot fresh weight of tomato as affected by P and NaCl levels in the Hoagland's solution.

height followed a similar pattern with a significantly maximum value in the control at 2 mM P (Figure 2). These results with salt stress are in general agreement with those of Shannon et al. (1987) but observed on other tomato genotypes. Unlike the present results, Smith et al. (1992) found no consistent change in shoot length in 'Micro-Tom' tomato with increased salinity stress; they attributed that to the highly compacted growth habit of that genotype. Tal and Shannon (1983) reported that salinity stress reduces elongation rate of the main stem in tomato. Cruz et al. (1990) reported that shoot length is one of the most reliable response indicators for a wide range of tomato genotypes under salinity stress. Significant reductions in fresh and dry weight of tomato shoots were reported in response to salinity stress (Bolarin et al., 1991, 1993). According to Cruz et al. (1990), the effect of salinity on plants was expressed as reduced shoot dry weight because vegetative growth in the most widely used index in studies on salt tolerance in tomato. In addition, slower growth due to slower leaf expansion rates of sugar beet and cotton was reported by Shalhevet and Hsiao (1986).

Root morphology parameters were affected by the interaction effect of concentration of phosphorus and salt in the Hoagland's solution (Table 1). Both root length and root surface area per plant were decreased significantly under higher salinity conditions at all levels of phosphorus (Table 1). Compared to the

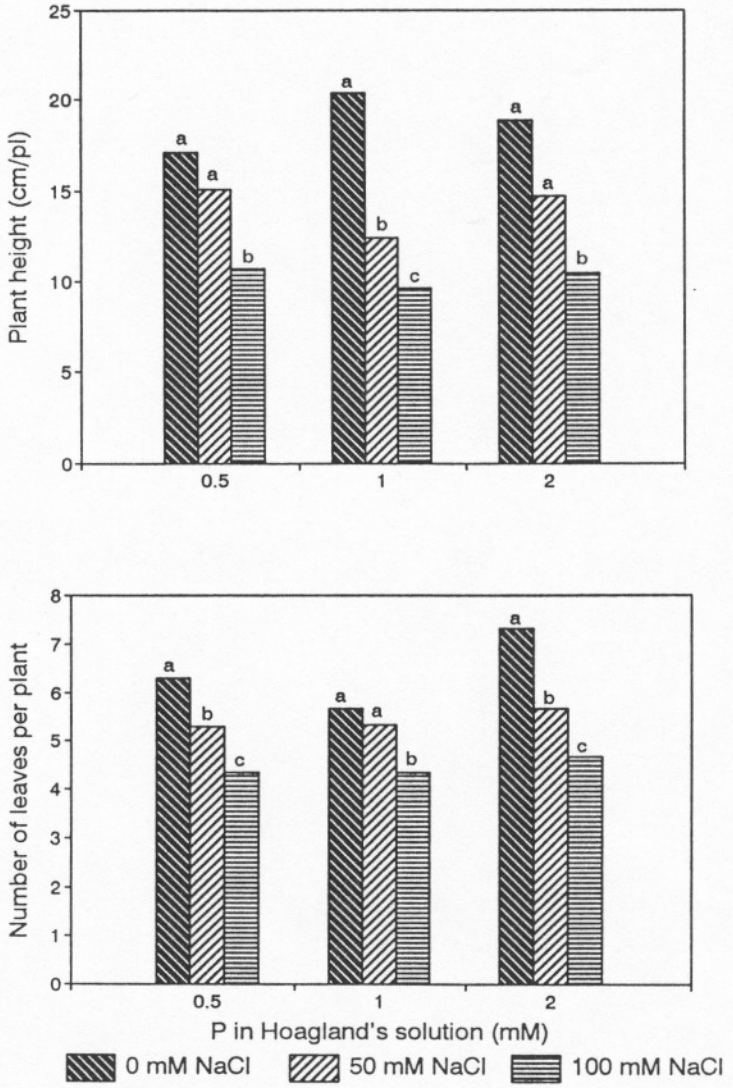

FIGURE 2. Plant height and number of leaves per plant as affected by P and NaCl levels in the Hoagland's solution.

TABLE 1. Root morphology parameters as affected by the interaction effect of phosphorus and salt levels in the Hoagland's solution.

Salt level (mM NaCl)	Root length (cm plant^{-1})			Root surface area (cm^2 plant^{-1})		
	P level (mM P)			P level (mM P)		
	0.5	1	2	0.5	1	2
0	409.4b*	559.8a	511.5a	29.2bc	44.7a	41.4a
50	353.9c	408.9b	267.9d	26.9c	32.3b	18.4d
100	207.1de	251.1d	195.3e	10.5de	16.4d	14.7de

lowest salt level (0 mM NaCl) the highest salt level (100 mM NaCl) decreased the root length by 49%, 55%, and 62% at the 0.5, 1, and 2 mM P levels of phosphorus, respectively. Compared to the 0 mM NaCl the 100 mM NaCl level decreased the root surface area by 64%, 63% and 64% at the 0.5, 1, and 2 mM P levels of phosphorus, respectively. However, the adverse effect of salinity on roots was not as obvious at the 50 mM NaCl level as it was at the highest salinity level. Roots have been reported to be less sensitive to salinity than leaves (Rendig and Taylor, 1989), however, root morphology parameters were negatively affected by the highest level of salinity in this study. Investigating the adverse effect of salinity on root growth, other researchers found various types of responses. It was reported by

TABLE 2. Phosphorus concentration and content in plant tissue as affected by the interaction effect of phosphorus and salt levels in the Hoagland's solution.

Salt level (mM NaCl)	P concentration (mg g^{-1})			P content (mg fresh-plant^{-1})		
	P level (mM P)			P level (mM P)		
	0.5	1	2	0.5	1	2
0	5.1d*	6.5c	8.6ab	18.8cd	33.2a	32.7a
50	6.8c	8.1b	9.6a	20.4c	26.7b	30.7a
100	6.9c	7.2c	9.3a	12.4e	14.4de	16.7cde

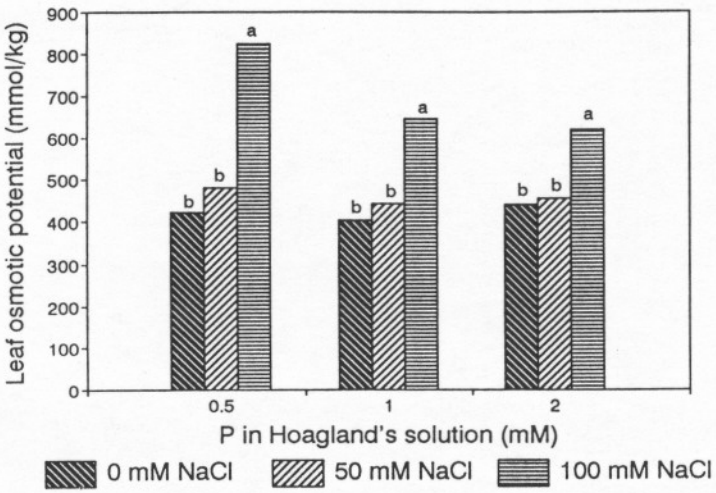

FIGURE 3. Leaf osmotic potential as affected by P and NaCl levels in the Hoagland's solution.

Munns and Termaat (1986) that roots of barley, bermudagrass and sorghum were enhanced under low and moderate salinity, however root growth under high salinity was not reported. On the other hand, Leo (1964) reported that high salinity decreases elongation rates of roots and found that tomato root tips subjected to .1% NaCl solution elongated at 26% of the elongation rate observed in the control nutrient solution. In addition, elongation rates of cotton radicles were also decreased as total water potentials were modified by NaCl solution. Anderson (1984) and Preece (1995) reported that rooting of microshoots was decreased with increasing salt and Anderson observed that rooting increased from 19% on full strength medium to 77% on 1/4-strength medium.

Increasing the phosphorus levels tended to enhance root growth through increasing both root growth and root surface area. This phenomenon was observed at all levels of salinity. Compared to the lowest P level (0.5 mM P) the second highest P level (1 mM P) increased the root length by 37%, 15%, and 21% at the 0, 50, and 100 mM NaCl levels, respectively. Compared to the 0.5 mM P the 1 mM P increased the root surface area by 53%, 20%, and 56% at the 0, 50, and 100 mM NaCl levels, respectively. Root enhancement by P has been observed under field soil conditions by other researchers (Mohammed, 1993; Pan and Hopkins, 1991). The highest P level (2 mM P) increased the root length and root surface area of the control plants, but not as much as the 1 mM P did. However, when NaCl were supplied the highest P level either decreased or had no significant effect on both

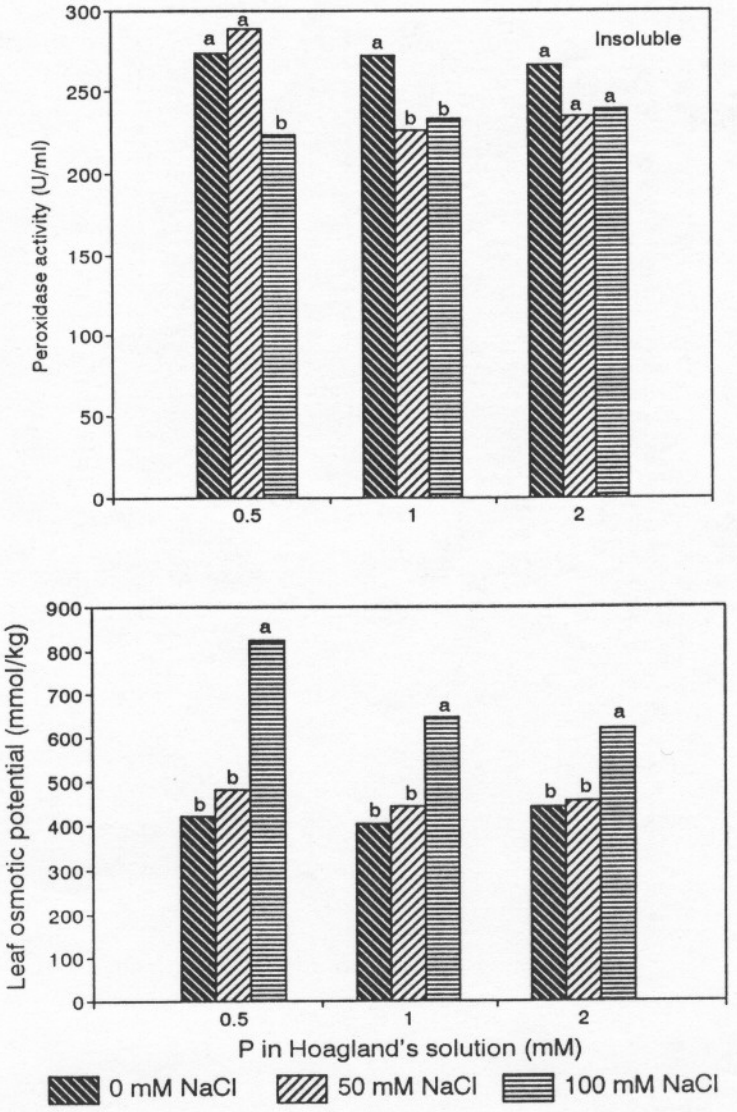

FIGURE 4. Soluble and tonically bound (insoluble) peroxidases in plant tissue as affected by P and NaCl levels in the Hoagland's solution.

root parameters. Under high phosphorus availability, increasing the salinity imposed by Cl^- salts has been found to increase the P uptake up to toxic levels due to enhanced rates of phosphorus uptake by the roots and of translocation to the shoot (Roberts et al., 1984). This may negatively affect the shoot and root growth due to phosphorus toxicity or nutrient imbalance. Root diameter was not significantly affected by the treatments and therefore data are not presented. Root fresh and dry weight were reported to decrease in response to increased induced salinity stress in other tomato genotypes (Shibli et al., 1997). Root systems have been considered as the basic system to counteract salinity stress (Smith et al., 1992).

Phosphorus concentration was affected by the interaction effect of both P and NaCl levels in the nutrient solution (Table 2). Shoot P concentration increased with the increase in the P level in the solution at all levels of salinity. Compared to the non salinized nutrient solution the P concentration was increased by salinization similarly with both levels of NaCl at all levels of P. This agrees with the observations of enhanced P uptake under highly saline conditions. Phosphorus uptake by the plant has a trend different from that of P concentration mainly due to the differences in the fresh weights of the shoots. The uptake increased with increasing P levels in the nutrient solution at all levels of salinity. However, the uptake decreased with increasing salinity levels at all levels of P regardless of the increase in the P concentration by higher levels of salinity. This can be largely attributed to the greater weight of the non-salinized plants.

Leaf osmotic potential was increased significantly with increased salinity stress up to 100 mM NaCl regardless of P level (Figure 3). However, the maximum leaf osmotic potential tended to be reached at the lowest P level (0.5 mM P). Leaf osmotic potential was reported to decrease (more negative) with the increased salinity stress in 'Micro-Tom' tomato (Smith et al., 1992).

Soluble peroxidase activity was maximum at 50 mM NaCl salinity stress at 0.5 mM P and showed a variable response to increasing salinity, while tonically bound (insoluble) activity mostly decreased with increased salinity stress (Figure 4). There was a tendency of increasing the soluble enzyme and of decreasing the tonically bound enzyme with the increase in the salinity levels at all levels of P, although this was not a clear cut response. Peroxidases have been shown to play a big role in plant responses to stress conditions (Sherf and Kolattuudy, 1993). Adapted tomato cells were reported to grow in the presence of 15 g l^{-1} NaCl and increased peroxidase activity was reported in response to salt stress (Sancho et al., 1996). It was also reported that lignin peroxidase activity is higher under low P conditions (Haapala and Linko, 1993). The results of this study indicate higher activity of soluble peroxidase only when plants are growing at the 50 mM NaCl salinity level (Figure 4). Since peroxidase isozyme are involved in the cell wall structure and expansion (Fry, 1986; Brett and Waldron, 1990) it could be considered a key factor in cell response and adaptation to salt stress (Sancho et al., 1996;

Cortelazzo et al., 1996). The results suggest that peroxidase activity could also be considered with other parameters in studying the salt adaptation process and screening crops for salt tolerance.

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