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Assessing the effect of solar radiation on plant salt tolerance as defined by the static and dynamic indices

F. N. Dalton[1,4], A. Maggio[2] & G. Piccinni[3]
[1]*USDA-ARS U. S. Salinity Laboratory, 450 W. Big Springs Road, Riverside, CA 92507, USA.* [2]*ENEA – Ente Per le Nuove Tecnologie, l'Energia e l'Ambiente, Centro Ricerche Trisaia, S.S. Jonica Km 419+500, 75026 Rotondella (MT), Italy.* [3]*Texas A&M University, Agricultural Research Center, 1619 Garner Field Road, Uvalde, TX 78801-6205, USA.* [4]*Corresponding author**

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Abstract

Any interaction between plant salt tolerance and environment is critical to crop breeders, geneticists, molecular biologists, soil-water-crop modelers and all researchers interested in 'global change'. A common criterion used for plant salt tolerance is a threshold value of root zone salinity, a static index that delimits the onset of yield reduction. According to this criterion, it was discovered that tomato salt tolerance decreases significantly with reduced solar radiation. In contrast, the threshold values of a new index based on the dynamic processes of salt accumulation relative to growth, are invariant to solar radiation. The variability and stability of the respective indices provides new insights for accessing physical and biochemical processes governing plant response in saline environments.

Abbreviations: SSI – salinity stress index; PAR – photosynthetic active radiation; FS – full sun; C – cloudy; CS – cloudy with shade

Introduction

Plant growth and crop productivity can be severely reduced by low temperature, drought and salinity stress (Boyer, 1982). For the near future, and with respect to salinity, water resources can be managed to optimize yield by maintaining salt stress at acceptable levels depending on the crop, soil type and quality of irrigation water. For the long term, plant scientists may identify specific cellular mechanisms, which account for yield reduction and then attempt to use natural selection or bioengineering to increase plant salt tolerance. Both of these approaches require functional definitions of plant salt tolerance that set analytic criteria for their respective objectives. Ultimately, salt tolerance must be determined by observing whole plant response in saline environments. Whole plant salt tolerance has traditionally been defined in terms of plant response functions obtained by correlating yield with root zone salinity. This is done by using a piece-wise linear regression (threshold-slope model) of experimental data relating yields to root zone salinity (Maas and Hoffman, 1977; Van Genuchten and Hoffman, 1984). Accordingly, yields remain constant with increasing root zone salinity until a critical threshold value is reached. Thereafter, yields are reduced at a crop specific rate proportional to increases in root zone salinity. The threshold values of root zone salinity are measured in terms of salt concentration, osmotic potential or electrical conductivity of the soil water, and are used to rank salt tolerance among species and cultivars. The root zone salinity threshold value is a static index. This concept of plant salt tolerance has been adopted for a wide variety of applications and provides the basis for model simulations that predict yield according to measured or simulated values of root zone salinity (Bresler, 1972; Cardon and Letey, 1992; Grant, 1995; Majeed et al., 1994; Simunek et

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* FAX No: +1909 342 4963. E-mail: fdalton@ussl.ars.usda.gov

al., 1996; Van Shilfgaarde et al., 1974). The use of plant response functions based on root zone salinity is also proposed as a basis for genetic improvement of plant salt tolerance (Subbarao and Johansen, 1994).

The alleged effects of environment on plant salt tolerance have been observed and discussed (Hasegawa et al., 2000; Hoffman and Jobes, 1978; Hoffman et al., 1971; Lunt et al., 1960; Meiri et al., 1982; Niemann and Poulson, 1971), but because plant growth can be affected by sub-optimal climatic conditions in addition to variable salt stress in the root zone, plant response functions obtained under different environmental conditions may obscure the true measure of salt tolerance. A dynamic salinity stress index, SSI, was formulated in an attempt to separate environmental from salt-sensitive biochemical processes affecting the plant response. The analytic formulation of the SSI has been defined in terms of the time-integrated flux over the growing period, from root zone to shoot, of the dominant salinizing anion (chloride) relative to shoot biomass (Dalton et al., 1997, 2000). This analytic definition, when integrated over the growing period, results in an expression which can be determined experimentally with relative ease;

$$\mathrm{SSI} = \frac{\text{accumulated shoot chloride}}{\text{total shoot biomass}} \tag{1}$$

where the salt accumulation is measured without regard to partitioning. Dynamic plant response functions are constructed by correlating yield, not with root zone salinity, but rather with a measure of the dynamic process of salt accumulation in the shoot. The theoretical aspects of the salt accumulation component of the dynamic salinity stress index are based on phenomenological equations describing the coupled transport of water and salt into the xylem tissue of a root system and have been used to investigate water and salt transport relations in plant roots (Dalton et al., 1975; Dalton and Gardner, 1978; Gardner, 1990; Joly, 1989; Maggio and Joly, 1995; Shalhevet et al., 1976). There are many factors, in addition to root zone salinity, that determine the total accumulation of salt (N*) in the shoot. The accumulation process is transpiration-driven by hydraulic and osmotic gradients acting between xylem tissue solution and root zone water. It depends not only on root zone salinity but also on plant water use, the effective surface area of the root across which transfer takes place, the ion exclusion properties of roots, hydraulic conductance, osmotic diffusion coefficient and a temperature-dependent metabolic ion uptake term. The total chloride accumulation over the growing period can be calculated from first principles (if the cumulative water use and the root surface area development rate are known) and has been analytically simulated by Dalton et al. (2000) as:

$$\mathrm{N}^* = cC_1 \sum_{j=t_\mathrm{i}}^{j=t_\mathrm{f}} e^{d(j-1)} [\frac{\alpha_1 J_v(j) + \beta_1}{\gamma_1 J_v(j) + \delta_1}] J_v(j), \tag{2}$$

where the sum is taken from the initial time of salinization, t_i, to the final day of salinization, t_f . The coefficients c and d define a time-dependent exponential increase in root surface area, C_1 is a root zone salinity boundary condition, J_v is a time-dependent transpiration flux, α_1, β_1, γ_1, and δ_1 are salt exclusion and temperature-dependent biophysical transport coefficients of the root (Dalton et al., 2000). With this equation, the SSI becomes a quantified manifestation of the effects of all variables in the SPAC (Soil-Plant-Air-Continuum) that simultaneously affect shoot growth and salt accumulation. At harvest, the value of this index is readily determined by two simple measurements: Total shoot chloride and biomass. The advantage of this definition is that the salt flux, and consequently the SSI, can now be interpreted in terms of transpiration-dependent ion uptake models that take into account root surface area, water use and temperature-dependent biophysical transport properties of the root.

Dynamic plant response functions also conform to piece-wise linear threshold-slope models similar to the static plant response functions. Previous experiments with tomato (*Lycopersicon esculentum* Mill.) showed that an increase in root zone temperature from 18 °C to 25 °C almost doubled the threshold value of root zone salinity from about 33 to 64 mM Cl. In contrast, the threshold value of a dynamic salinity stress index, expressed as mmol Cl per gram dry weight, was found to be invariant to root temperature (Dalton et al., 1997). These findings show that when growth rate is modulated by root temperature, the fundamental gauge identifying onset of yield reduction was a critical value of SSI, an intrinsic property of the shoot, and not root-zone salinity.

The SSI was simulated in terms of a temperature-dependent physical-mathematical model describing the simultaneous transport of water and salt into the shoot of a transpiring plant, Equation (2), and compared with experimentally determined SSI's at root temperatures of 18 °C and 25 °C and respective root-zone chloride concentrations of 33 and 64 mM. Root surface area development rates and cumulative water use were measured as input parameters for the model. Experiment and model simulation showed good agreement at 18 and 25 °C. The shoot chloride simulations for two environments with different growth potentials demonstrate that the salt accumulation process is controlled by the transpiration flux, the development rate and biophysical transport properties of the root. To test the concept of an environmentally invariant SSI threshold further, it was imperative that experiments be performed where the potential growth was modulated by some variable climatic condition that would affect growth by distinctly different physiological mechanisms than root temperature. The objectives of this study were to assess the effects of different photon flux densities on the static and dynamic stress indices for salt tolerance. Because water use and transpiration flux are ultimately governed by the root/shoot ratio, the salinity dependence of the root/shoot ratio was also determined.

Materials and methods

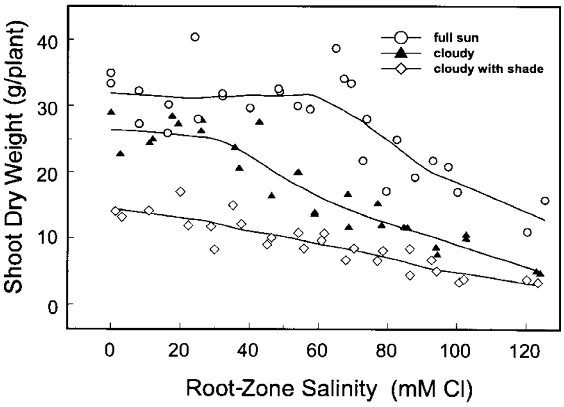

Figure 1. Plant response functions for tomato obtained by non-parametric regression of dry weight yield as a function of chloride concentration in the root zone and at three levels of solar radiation.

Table 1. The effects of growth modulation, by solar radiation and root temperature, on estimates of threshold values (± SE) of root zone salinity and SSI, by piece-wise parametric analysis

Growth modulation		Threshold value	
Solar radiation μmol m^{-2} s^{-1}	Root temperature °C	Root zone mM Cl$^-$	Dynamic SSI mmol Cl$^-$/g dry wt.
Full sun PAR > 1500[a]	25	64±7	1.19±0.10
Cloudy PAR ≈ 601	25	30±7	1.10±0.10
Cloudy with shade PAR ≈ 406	25	28±9[b]	0.97±0.18
Full sun PAR > 1500[a]	18	33±6	1.10±0.08

[a] From Dalton et al. (1997, 2000).

[b] A small or nonexistent root zone salinity threshold value is indicated by non-parametric analysis (solid line, Figure 1).

Glasshouse experiments were carried out at the US Salinity Laboratory, Riverside CA, using tomato (*Lycopersicon esculentum,* cultivar Heinz 1350) grown in hydroponic culture (Dalton et al., 1997). Plant response functions were obtained relative to root zone salinity (static index) and the dynamic SSI, at 14 levels of salinity and three levels of solar radiation, replicated twice. Sixteen days after germination, salinization was accomplished by adding equal increments of NaCl:CaCl$_2$(2:1 molar basis) over a 5-day period to decrease the osmotic potentials of the Basic Nutrient Solution (Dalton et al., 1997) to approximately 0, 0.03, 0.067, 0.10, 0.13, 0.167, 0.20, 0.23, 0.267, 0.30, 0.33, 0.367, 0.40 and 0.50 MPa. Full sun (FS) condition was obtained in July–August, with the average Photosynthetic Active Radiation (PAR) between 11:00 h and 14:00 h exceeding 1500 μmol m^{-2} s^{-1}, and average daytime temperature of 27 °C. Cloudy (C) and cloudy with shade (CS) conditions were obtained in February-March with average PARs of 601 and 406 μmol m^{-2} s^{-1}, respectively, and average day time temperature of 25.7 °C. Specifically, the CS treatment was obtained using a 30% cut-off screen placed 1 m above the canopy. Plants were harvested at beginning of flowering (approximately 40 days after germination). Plant response functions were obtained by non-parametric least squares regression. Chloride determinations were made in dilute acetic acid and nitric acid extracts of leaves and stems by coulometric-amperometric titration (Cotlove, 1963). The SSI was then calculated as mmol chloride/g shoot dry weight (Dalton et al., 1997). Considering that experiments from two different periods of the year have been analyzed together, the comparison has to be intended between different total environments, where the solar radiation is the most critical variable.

Results and discussion

Effect of solar radiation on root zone salinity threshold

Plant response functions for tomato at three levels of solar radiation are shown in Figure 1. These plant re-

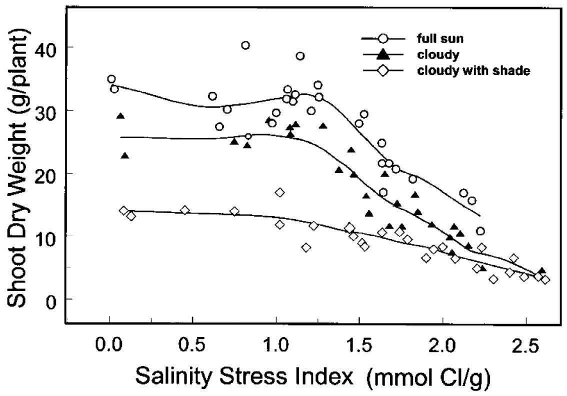

Figure 2. Plant response functions for tomato obtained by non-parametric regression of dry weight yield as a function of the dynamic salinity stress index, SSI, at three levels of solar radiation.

sponse functions are obtained by the application of a nonparametric regression analysis to the biomass-root zone salinity data. This analysis, provided by Axum (Axum TriMetrix, 444 NE Ravenna Blvd., Suite 210 Seattle, WA)[1] is a locally weighted least squares technique that gives a smooth curve with a scatter plot of the associated data. Unlike the linear piece-wise model, this analysis can reveal a more realistic plant response function because there are no *a-priori* assumptions as to its expected behavior (Cleveland, 1993). The obvious plateaus and break points for the high and medium radiation experiments, as shown by the non-parametric analysis, closely approximates the piece-wise linear model, with its associated breakpoint, proposed by Hoffman and Van Genuchten (1984). The linear piece-wise model gives threshold values of 64±7 and 30±7 mM Cl for these experiments (Table 1). The non-parametric analysis for the low radiation experiment shows a very small plateau, if any, and yield immediately declines at a constant rate with increasing root-zone salinity. The linear piece-wise analysis, with its forced breakpoint, yields a threshold value of 28±9. These results support the postulate that as the environmental growth potential decreases the root-zone salinity threshold value also decreases, and are similar to those previously obtained with respect to the effects of root temperature (Dalton and Poss, 1989; Dalton et al., 1997, 2000) and atmospheric CO$_2$ concentrations (Dalton et al., submitted)

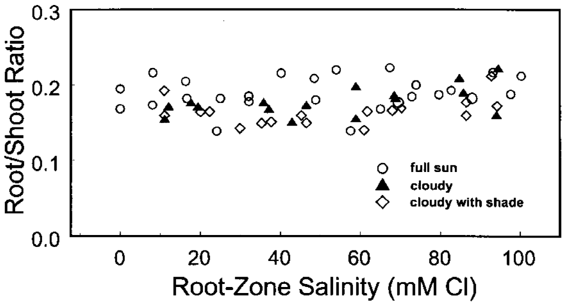

Figure 3. Root–shoot ratios on a dry weight basis for tomato as a function of root-zone chloride concentration at three levels of solar radiation.

Effect of solar radiation on the dynamic index threshold

Plant response functions based on the SSI exhibit distinct plateaus and threshold values for each radiation level (Figure 2). However, in dramatic contrast to the variability of the threshold values based on root-zone salinity, the threshold values of the dynamic index remain constant. Again, the solid curves are obtained by the least squares non-parametric analysis. The invariance of the SSI threshold value for three different radiation loads is further evidence that the plant responds primarily to its internal salt status rather than the osmotic potential of the root-zone nutrient solution. It is an impressive observation that when growth potential is moderated by distinctly different physiological mechanisms, either root zone temperature or photon flux density, the threshold value of the dynamic salinity stress index remains relatively constant (Table 1). This is a strong indication that the basic physiological mechanisms of plant salt tolerance are unaffected by these different environments. What is affected is the delicate balance between the rate of salt accumulation in the shoot relative to the growth rate of the shoot. Flowers and Yeo (1986) and Bressan et al. (1990) suggested that plants response to salinity depends on their ability to accommodate salt influx with growth, also. This balance has been analytically quantified by the dynamic index, SSI, and supports the postulate that environments with suboptimal conditions for growth inherently have a reduced threshold root-zone salinity (Dalton et al., 1997, 2000). The reduction in root-zone salinity threshold value might not be due to reduced efficiency of some biochemical mechanism in the shoot but rather is a manifestation of physical processes governing salt accumulation relative to growth.

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[1] Names and products are mentioned for the benefit of the reader and do not imply endorsement or preferential treatment by the USDA.

Root–shoot ratio

The relation between root and shoot growth emphasizes the dynamic rather than static interdependence of their functional relationships (Baker et al., 1991; Dalton, 1996; Klepper, 1991). Root-shoot ratios were independent of root-zone salinity for the three levels of solar radiation investigated (Figure 3). The mean and confidence limits of the root/shoot ratios for full sun, cloudy and cloudy with shade environments were 0.19±0.01, 0.17±0.01 and 0.16±0.01, respectively, and they are not statistically different at the 95% confidence limit. It is a reasonable assumption that plant response in saline environments is a form of optimum autoregulation and that the root/shoot ratio is a state of homeostasis (Klepper, 1991), which is independent of root-zone salinity. Because the SSI threshold is independent of solar radiation and root-zone temperature, it follows from the definition of the SSI that the plant can tolerate a higher root-zone salinity by reducing the rate of salt accumulation relative to its growth rate. Thus, manipulating root/shoot ratios through natural selection or bioengineering might represent an important new strategy to improve plant response in saline environments.

Implications of an environmentally-dependent index for plant salt tolerance

Root-zone salinity threshold values for tomato, the common measure of plant salt tolerance were significantly increased with increasing levels of solar radiation. Unfortunately, such environmentally-induced variations in root-zone salinity threshold values will prohibit their general use in global crop models that predict yield or irrigation management in terms of root-zone salinity alone. Possibly even more important to crop breeders, geneticists and molecular biologists is whether or not the observed changes in threshold values of root zone salinity actually indicate a change in some physiological mechanisms affecting ‘salt tolerance.’ We discovered that, not only were the SSI threshold values invariant to solar radiation and root temperature, but the SSI thresholds tended to the same value (Figure 2, Table 1). These results imply that the critical salt-sensitive biochemical mechanisms affecting plant salt tolerance are unaffected by either solar radiation or root temperature and that variations in threshold values of root-zone salinity are not to be interpreted as changes in plant salt tolerance. The invariance of SSI threshold values is also evidence that the plant’s response to salinity is primarily due to its internal salt status rather than the osmotic potential or salt concentration of the root-zone solution. Taken together, the common SSI thresholds for variable solar radiation and root temperature are remarkable when we recall that growth has been modulated by distinctly different physiological mechanisms. Changes in root-zone salinity threshold values are explained on the basis of the definition of the dynamic index and its nearly constant threshold value. That is, for those conditions where the potential for growth was higher (e.g. higher solar radiation or root temperature), the induced increase in the growth rate was greater than the associated increase in the rate of salt accumulation in the shoot. Under these circumstances, the value of SSI will tend to decrease, see Equation (1). Then, to reach the threshold SSI at the higher growth rate, it is necessary to increase the chloride flux to the shoot commensurate with the induced increase in shoot growth. This condition can be met, in part, by increasing the chloride concentration, C_1, in the root zone, thereby increasing the threshold value of root-zone salinity. It follows from Equation (2) that the chloride accumulation will increase with increasing root-zone chloride concentration C_1. The solute flux is also influenced by the transpiration flux, J_v. Shoot chloride accumulation was successfully simulated for tomato, over a 54-day growing period, at two root temperatures and two root-zone chloride concentrations by using Equation (2) (Dalton et al., 2000). Salt accumulation in the shoot and therefore SSI, could be explained by a physical interaction between the transpiration rate, temperature-dependent ion and water transport properties of the root, and root surface area development rates. Root-zone salinity is just one of many physical parameters that determine salt accumulation in the shoot and resultant reduction in growth, whereas the SSI threshold value is a more comprehensive measure of plant salt tolerance. In addition, the SSI analysis provides new insights on the location of the critical mechanisms for salt tolerance in plants. Serrano and Gaxiola (1994) pointed out that there is no clear consensus as to the location, shoot or root, of the biochemical mechanisms responsible for salt tolerance. The data in this and previous reports (Dalton et al., 1997; 2000) demonstrate the SSI threshold, a shoot property, to be a critical value below which the plant can produce optimally in a variety of environments each with different root-zone salinity threshold values.

Conclusions

Identifying an index for plant salt tolerance, which is mathematically defined and generates satisfactory results in simulation approaches, can be extremely useful in defining strategies to improve plant response in saline environments. Any manipulation of metabolic pathways that increase the threshold SSI would constitute an improvement in plant salt tolerance. It should be recognized, however, that morphological changes related to root surface area and leaf area index can impact the functional relation between root and shoot defined by water use, ion accumulation and growth, and thereby affect threshold root-zone salinities without changing threshold SSI's. Even though a constant SSI threshold indicates no intrinsic change in plant salt tolerance, there are still opportunities for optimizing yield through irrigation management. It follows from both the solar radiation and root temperature data that when growth potential is increased due to more favourable climatic conditions, the root-zone salinity threshold value is also increased. These insights provide new and useful strategies for irrigation management. It is now conceivable to use irrigation water of moderate salinity more efficiently for warm soil conditions and high solar radiation, while better quality irrigation water might be saved for cool soil temperatures and cloudy days.

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