WATER TRANSPORT AND SALT LOADING: A UNIFIED CONCEPT OF PLANT RESPONSE TO SALINITY

F. N. Dalton and J. A. Poss
USDA–ARS U.S. Salinity Laboratory
Riverside, CA , U.S.A.

Abstract

A transpiration activated quantity called the salinity stress index (SSI) is introduced and defined in terms of the xylem solute flux, J_S, and the shoot volume production rate, V_S.

$$SSI = \int Js(t)dt / \int Vs(t)dt.$$

The ion flux, J_S, can be experimentally measured or analytically simulated in terms of the osmotic potential of the soil solution, water and ion transport coefficients of the root, the volume flux of water into the root and active root surface area. The shoot volume production term, V_S, is assumed an intrinsic property of the plant and was estimated experimentally with fresh weight measurements. This dynamic variable is integrated over the period of observation and is correlated to crop yield reduction in a saline environment. The effect of root temperature on growth response, and ion accumulation by tomato (*Lycopersicon esculentum* Mill.) grown under various levels of salinity stress is analyzed and interpreted according to this conceptual model.

1. Introduction

The effect of salt on crop yield is traditionally studied by correlating some measure of salinity in the root zone (e.g., chloride level, osmotic potential, bulk soil or pore water electrical conductivity) with yield. It is often observed that yield is reduced uniformly with decreasing osmotic potential of the nutrient solution. Therefore, excluding the effects of specific ion toxicity or nutrient deficiencies, plants appear to respond more to the colligative properties of the soil water than to its chemical composition (Bernstein, 1961) In this sense it can be said that the common or unifying index of root zone salinity to which plants respond is the osmotic component of the total water potential. This concept has provided the basis for much research in attempting to understand salinity–yield interactions. In addition to understanding the physiological effects of salinity, it has been vitally important to simply characterize the effect salinity has on yield reduction for a particular agronomic species or cultivar. In this regard, extensive work has been carried out to determine the relative growth response of many agronomic crops to various levels of salinity (Maas and Hoffman, 1977, Maas, 1986). Nevertheless, there does not exist a common or unified index for salt tolerance which is capable of intrinsically responding to the different environmental conditions that exist in the crop canopy or root zone.(e.g. water content, soil temperature, net radiation, air temperature, relative humidity...). The complexity of plant development under salinity stress would seem to discourage any attempt at constructing such a simple index. However, using the analytic method of systems analysis, it may be possible to develop a unified and dynamic plant stress index for saline environments that is composed of parameters dependent on other environmental conditions than just root zone salinity. This means that specific mechanisms of salt injury to plants are not specified. Rather the index is simply shown to correlate with yield reduction. Predicting plant response to salinity in any environment is then achieved with system parameters that define the index.

In this paper, a dynamic salinity stress index is defined and compared to the static stress index (e.g. root zone salinity) as they correlate with yield reduction at various root temperatures. This dynamic index is a measure of the rate of accumulation of salt in the shoot relative to the rate at which the shoot grows and is ultimately controlled by the soil–plant–air continuum, the biophysical transport properties of the root (Dalton et al., 1975), and plant geometry.

2. Theoretical development

The transport of salt from the soil solution to plant shoot via the root system is common to all higher plants transpiring in a saline environment. The effective concentration in the shoot resulting from this salt loading depends not only on how fast salts are transported to the shoot but on the rate of shoot volume development. Thus, a salinity stress index (SSI) is introduced and defined in terms of a transpiration activated salt loading term, Js, and the shoot volume production rate, V_S.

$$SSI = \frac{\int J_S(t)dt}{\int V_S(t)dt}. \qquad [1]$$

The salt loading term, J_S is the xylem ion flux into the shoot and is composed of a convective, diffusive, and metabolic component. It can be experimentally measured or analytically described in terms of the osmotic potential of the soil solution, water and ion transport coefficients of the root, metabolic ion uptake rate, active root surface area and the volume flux of the water (Dalton et al., 1975). The shoot volume production rate, V_S is assumed to be an intrinsic property of the plant and in this report the shoot volume is estimated by fresh weight measurements.

In its most general form, the SSI is a dynamic variable that is evaluated by integration over any arbitrary period of observation. The SSI can be theoretically simulated and experimentally determined. For this investigation the integral is evaluated by measuring the total amount of solute transported to the shoot relative to the shoot volume production. The static and dynamic salinity stress indices are then correlated with yield.

In effect, the SSI is a measure of the salt loading to the shoot relative to the the growth rate of the shoot. As defined, the salinity stress index is a unifying measure of salt stress experienced by higher plants which are transpiring significant amounts of water in a saline environment. As a first approximation we expect that a critical value of the SSI exists below which no yield reduction occurs and above which yield is reduced linearly.

This concept is illustrated in figure 1, where for completeness we acknowledge the complicating and unknown factor of plant age. It is noted that after a critical value of SSI is reached, any further increase in the rate of salt accumulation relative to shoot volume production results in yield reduction.

Since this index depends on a dynamic relationship between growth and transport, it will be important to experimentally determine the variation of threshold values amongst cultivars and species. In this first study, the experimental results from a temperature dependence study of the traditional salt tolerance curves for tomato are used to investigate this concept.

3. Materials and methods

3.1. Experimental set up

A glasshouse experiment was conducted to evaluate the effects of root temperature on the biophysical mechanisms responsible for the growth response of tomato (*Lycopersicon esculentum* Mill.) in continuously aerated saline base nutrient solution (BNS). Tomato seeds

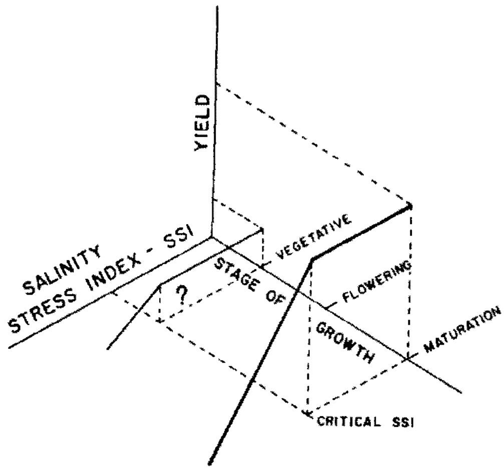

Figure 1 — Schematic diagram of the plant response to the salinity stress index (SSI) based on the classical threshold model.

(cultivar Heinz 1350) were sown in vermiculite in November and kept moist until the eight–day–old seedlings were transplanted into temporary BNS pots at ambient temperature. Twenty–four days after germination, root temperature and salinity treatments were imposed after transplanting one plant to each 10 l crock. The crocks were then immersed in four temperature baths (0.8 m H x 1.3 m L x 0.9 m W) to maintain root temperatures at 15.3 ± 0.4 °C, 20.5 ± 0.2 °C, 25.3 ± 0.8.°C, and 30.0 ± 0.9 °C. Root temperature targets were reached within 24 hours from ambient conditions. Salination was accomplished by adding equal increments of $NaCl:CaCl_2$ (2:1 molar basis) over a five day period to decrease the osmotic potentials (OP) of the BNS to –0.15, –0.25, –0.35, –0.45, and –0.55 MPa (salt was added to the BNS at less than –0.1 MPa per day per treatment to avoid shock) for five of the crocks. Two control crocks (–0.05 MPa) were added to the five salinity treatments for each temperature. Within each temperature bath salinity treatments were positioned to minimize shading effects from larger plants. No replication was possible.

The BNS (in mol m^{-3}) was composed of: 2.5 $Ca(NO_3)_2$, 3.0 KNO_3, 1.5 $MgSO_4$, 1.7 x 10^{-1} KH_2PO_4, 5.0 x 10^{-2} Fe (as sodium ferric diethylenetriamine pentaacetate),2.3 x 10^{-2} H_3BO_3, 4.8 x 10^{-3} $MnSO_4$, 4.0 x 10^{-4} $ZnSO_4$, 2.0 x 10^{-4} $CuSO_4$, 2.0 x 10^{-4} H_2MoO_4. Root bath temperatures were maintained by using a controller–driven alternate/simultaneous heating and refrigeration system. Thermocouples were used in conjunction with a micrologger to monitor root bath temperatures every 30 seconds.

Daily water use was measured in each crock by measuring replenished distilled water for each crock. BNS pH was maintained between 5.5 and 6.5 Plants were harvested on day 52 and fresh weight of shoots and roots were obtained. Dry weights were obtained by first rinsing all plant shoots and roots with distilled water and then drying the tissue in an oven at 60 °C.

Shoot chloride concentration was determined on dilute acetic and nitric acid extracts by coulometric–amperometric titration (Cotlove, 1963). Total shoot chloride accumulation was determined by multiplying the chloride concentration on a dry weight basis by total shoot dry weight.

3.2. Evaluation of the salinity stress index

The components of the salinity stress index (Eq. 1) can be experimentally determined by measuring the solute concentration in the shoot and estimating the shoot volume by fresh weight measurements. Thus,

$$\int J_S(t)dt = \text{moles of solute in shoot,} \quad [2]$$

and

$$\int V_S(t)dt = \text{volume of shoot.} \quad [3]$$

The SSI is seen to represent an effective solute concentration term in the shoot. For this study, the SSI is calculated relative to the chloride ion for each plant in the experiment and then compared to plant yield.

3.3. Expressing the plant response function

A quantitative estimate of salt tolerance is often determined by a threshold value of salinity below which there is no decrease in yield. The tacit assumption in this model assumes that crop yield will be maximal until the threshold value of root zone salinity is reached. A further increase in salinity results in a linear decrease in yield. This relationship formed by the yield–salinity data set is called the plant response function. This data set is usually analyzed by a subjective hand–fitting process. In this study we used a non–linear least squares inversion method to estimate the critical threshold values for yield in terms of both nutrient solution electrical conductivity and the salinity stress index (van Genuchten and Hoffman, 1984).

4. Results

The vegetative yields of tomato plants grown at four root temperatures are plotted as a function of root zone salinity in figure 2. Best fit lines are drawn through the data according to the classical concepts of salt tolerance. With the exception of the 20° C trial, threshold values increase over the temperature interval 15° C–25° C and decreases over the temperature interval

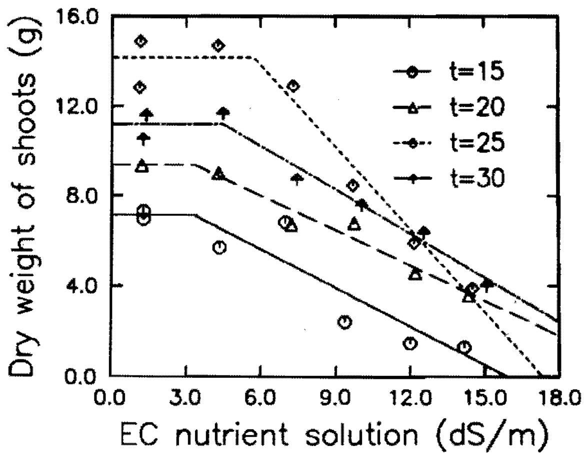

Figure 2 – Dry matter production as a function of the electrical conductivity of the nutrient solution at four root temperatures, (15, 20 25 and 30 ° C)..

25° C–30° C. This observation is even inclusive of the 20° C run if an unrealistically high value of the control yield is excluded from the best fit analysis. From this traditional analysis it can therefore be tentatively concluded that tomato salt tolerance is not a fixed quantity under total genetic control but in fact can increase with increasing root temperature.

In contrast, figure 3 shows yield plotted as a function of the salinity stress index,(SSI), from which there appears to be a common threshold value at each temperature studied. Again, this observation is inclusive of the 20° C data set if the anomalously high control yield data point is omitted in the analysis. These results are even more interesting when it is recognized that the components of the SSI, that is the total salt flux and shoot growth, are significantly different for each temperature studied. Conclusions from this analysis would suggest that, at least for tomato, salt loading of the shoot relative to shoot growth is the critical factor affecting yield and that plant salt tolerance is invariant with root temperature.

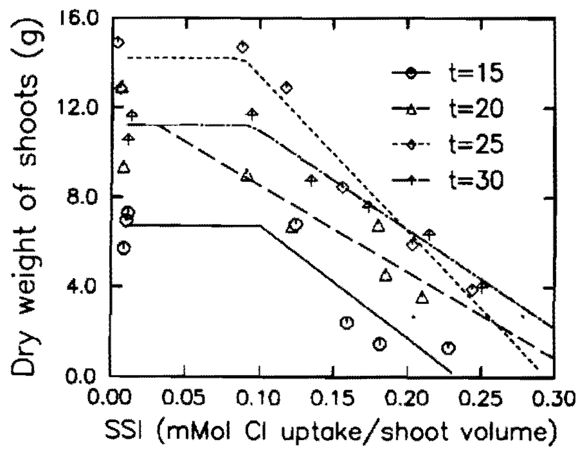

Figure 3 – Dry matter production as a function of the salinity stress index (SSI) at four root temperatures, (15,20,25 and 30 °C).

5. Discussion

Water management practices for maximizing crop yields in saline environments are based primarily on controlling root zone salinity below some crop dependent threshold value. These practices require a large data base of correlations between root zone salinity and yield for agronomic crops. Unfortunately, these correlations are independent of any other parameters in the soil–plant–air continuum. The theoretical and experimental work reported in this research is motivated by the need to develop a simple, yet dynamic, salinity stress index for plants that responds to forces responsible for water and ion transport in the plant and is not limited solely to root zone salinity. The concepts of plant salt tolerance are scrutinized by analyzing quantitative estimates of salt tolerance obtained from temperature dependent studies of the plant response function. Classical plant salt tolerance experiments are analyzed from both the point of view of root zone salinity and the dynamic salinity stress index (SSI). When the experimental data is analyzed in terms of root zone salinity threshold values, it can be concluded that salt tolerance is not a fixed value but can vary with other environmental temperature. From the classical standpoint these findings show that salt tolerance is controlled not only by the intrinsic genetic properties of the plant but also by some as yet to be determined temperature dependent biophysical/chemical processes in the plant.

When the experimental data are analyzed in terms of the SSI, it is concluded that threshold values of the SSI also exists (in similarity with threshold values of root zone salinity), but that they appear to be independent of temperature. This observation is all the more significant when we note the large variation in the factors making up the components of the SSI, namely, the total salt load to the shoot and the total shoot volume production. We also note the variation in total water use and root/ shoot yield. This data is shown in table 1 where $[Cl^-]$ represents the chloride concentration per unit shoot dry weight. The total solute load to the

Table 1 – Solute concentration in shoot, $[Cl^-]$, total plant water use, TWU, fresh weight of tomato shoots, and dry weight of tomato shoots and roots at six levels of salinity, OP, and four root temperatures.

OP	Root Temperature	$[Cl^-]$	TWU	Dry Weight Shoots	Dry Weight Roots	Fresh Weight Shoots
MPa	^{0}C	mol g^{-1}	ml	g	g	g
–0.05	15	0.12	4322	7.15	1.17	82.9
–0.05	20	0.09	6090	11.20	2.31	151.0
–0.05	25	0.06	6796	13.90	3.06	180.0
–0.05	30	0.17	4306	11.10	2.81	158.0
–0.15	15	0.11	4279	5.75	1.30	71.6
–0.15	20	1.31	4796	9.06	1.71	130.0
–0.15	25	1.33	7030	14.80	2.50	224.0
–0.15	30	1.46	3892	11.70	2.70	180.0
–0.25	15	1.69	2489	6.86	1.52	93.2
–0.25	20	1.99	4972	6.76	1.50	110.0
–0.25	25	1.72	5929	13.00	2.73	189.0
–0.25	30	2.17	2486	8.77	2.11	141.0
–0.35	15	1.60	2475	2.47	0.27	24.8
–0.35	20	2.05	3668	6.82	1.25	77.8
–0.35	25	2.04	3742	8.50	1.80	111.1
–0.35	30	2.58	2296	7.62	1.93	113.7
–0.45	15	1.79	799	1.53	0.24	15.1
–0.45	20	2.38	1981	4.61	1.26	59.2
–0.45	25	2.83	1642	5.93	1.50	83.0
–0.45	30	3.06	938	6.39	1.90	91.0
–0.55	15	2.75	1343	1.36	0.42	16.4
–0.55	20	2.58	1047	3.68	1.15	45.1
–0.55	25	3.15	1850	3.94	1.40	50.7
–0.55	30	3.51	658	4.05	1.54	56.7

shoot is then the product of [Cl^-] and shoot dry weight. As noted previously the shoot volume is estimated from fresh weight measurements. Analysis of salt tolerance in terms of the SSI indicate that the genetic and environmental forces affecting plant salt tolerance for tomato can be separated. Since a common threshold value of the SSI is obtained over the temperature interval studied, the possibility exists that the SSI is a unifying index in that it is invariant to environment and between some cultivars and species. This point is under current investigation.

It is an expectation that analytic expressions for the components making up the SSI can be used for predicting plant response to salinity in any environment. The xylem ion flux, J_S, controlling salt loading to the shoot has been previously described (Dalton et al.,1975) in terms of the ion and water flux across the root surface. It is composed of a diffusive component, ($\omega\Delta\pi$), a convective component, $(1-\sigma)CJ_S$ and a metabolic active term, k, where ω, σ, and k are the osmotic permeability, reflection coefficient and active transport parameters respectively. $\Delta\pi$ is the osmotic potential difference between the soil solution and xylem solution, C is the molar concentration of the soil solution and Jv is the transpiration flux. The molar flux can be given in terms of the nutrient solution osmotic potential and the root transport coefficients as:

$$J_S = (1-S)\pi J_V/nRT \qquad [4]$$

where the selectivity coefficient S is given by,

$$S = \frac{\sigma - nRTk/\pi_1 J_V}{1 - nRT\omega/J_V} \qquad [5]$$

For monovalent salts, n = 1 and R and T are the universal gas constant and temperature respectively. Equation 4 and 5 show that the molar ion flux depends heavily on transpiration and the biophysical transport properties of the root. Among these properties, the metabolic component of the ion flux, k, is important to both the salt loading process and water use (Dalton and Gardner, 1978). This salt loading concept of plant response to salinity provides an analytical link to yield, not only in terms of root zone salinity but also to: 1) bio-physical transport properties of the root, 2) soil-plant-air continuum variables affecting transpiration and 3) plant geometry as it pertains to root and shoot surface areas across which ion and water transport occur.

Future research should take into account that salt tolerance is a dynamic property depending on many more variables than root zone salinity. With this generalized approach, yield reduction is explicitly related not only to the root zone salinity, but to environmental conditions of the shoot and genetically controlled geometric and physical properties of the root.

References

Bernstein, L. 1961. Osmotic adjustment to plants to saline media. I, Steady State. Amer. J. Bot. 48:909–918.

Cotlove, E., 1963. Determination of true chloride content of biological fluids and tissues. Analysis by simple nonisotopic methods. Anal. Chem. 35:101.

Dalton, F. N. and Gardner, W. R., 1978. Temperature dependence of water uptake by plants. Agron J. 20: 404–406.

Dalton, F. N, Raats, P. A. C., and Gardner, W. R., 1975. Simultaneous uptake of water and solutes by plant roots. Agron. J. 67:334–339

Maas, E. V. 1986. Salt tolerance of plants. Appl. Agric. Res. 1:12.

Maas, E. V. and Hoffman, G. J., 1977. Crop salt tolerance–current assessment. J. Irrig. and Drainage Div., ASCE 103(IR2):115–134.

van Genuchten, M.Th., Hoffman G. J. (1984) Analysis of crop salt tolerance data. In: Shainberg I., Shalhavet, J (eds). Soil salinity under irrigation. Springer, Berlin Heidelberg New York. Ecological Studies Vol. 51: 258.