CROP ECOLOGY, MANAGEMENT & QUALITY

Root-Zone Salinity: I. Selecting a Product–Yield Index and Response Function for Crop Tolerance

H. Steppuhn,* M. Th. van Genuchten, and C. M. Grieve

ABSTRACT

Six empirical functions were compared for describing the product yields of agricultural crops grown while subject to increasing levels of root-zone salinity. The four nonlinear functions fit the test data from a spring wheat (Triticum aestivum L., cv. Biggar) experiment conducted in Canada's Salt Tolerance Testing Facility closer than the two linear functions. Although each of the four nonlinear declining functions could reasonably describe the data, the modified compounddiscount equation recorded the lowest root mean square error and the highest R^2 value. Additional response data using the nonlinear discount function obtained from 33 separate trials averaged 11% closer in statistical fit and 45% lower in statistical error than the best linear function. The discount function $\{Y_r = 1/(1 + [(C/C_{50})^{\exp(sC_{50})}]\}$ follows a sigmoidal form and relates relative yield (Y_r) to a measure of root-zone salinity (C) such as the solute concentration with an electrical conductivity of an equivalent saturated soil paste extract (EC_e). This function features two parameters, the salinity level producing 50% of the nonsaline crop yield (C_{50}) and the absolute value of the general decline in relative yield with salinity at and near C₅₀, the steepness constant (s). These parameters combine to form a singlevalue, salinity-tolerance index (ST-Index) consisting of the 50% reduction in crop yield (C₅₀) plus the tendency to maintain some product yield as the crop is subjected to increasing salinity levels approaching C_{50} , i.e., ST-Index = $C_{50} + s(C_{50})$. The ST-Index for the Biggar wheat registered 6.44. Approximations for C_{50} and s can be derived from the threshold salinity (C_i) and declining slope (b) parameters of the threshold-slope linear response function $[Y_r = 1 - b(C - C_t)]$. Procedures for converting C_t to C_{50} and b to s offer linkages between these linear and nonlinear response function parameters, and are further explored in this paper's companion. The resulting ST-Index-values equal 6.56, 9.43, and 5.67 for sample field (corn, Zea mays L.), forage (alfalfa, Medicago sativa L. and falcata L.), and vegetable (radish, Raphanus sativus L.) crops, respectively.

LABORATORY AND FIELD TESTS to identify decreases in crop yield in response to increasing root-zone salinity have been conducted for many years and are listed by Francois and Maas (1978, 1985) and Ulery et al. (1998), among others. The inherent ability of crop plants to withstand the effects of elevated solute concentrations in their root-zone solutions and still produce a

Published in Crop Sci. 45:209–220 (2005). © Crop Science Society of America

677 S. Segoe Rd., Madison, WI 53711 USA

measurable agricultural product defines the magnitude of crop tolerance or resistance to salinity. Salinity generally slows the rate of crop growth, resulting in plants with smaller leaves, shorter stature, and reduced economic yield (Shannon et al., 1994). The degree to which growth is curtailed by salinity differs with crop species and variety (Shannon and Grieve, 1999).

In this study, we briefly review the factors that affect the response of crops to root-zone salinity, summarize and evaluate a number of models that have or could be used for the crop salt tolerance response function, and propose a Salinity Tolerance Index that provides a relative ranking of crops according to their tolerance to rootzone salinity.

CROP YIELD RESPONSE TO SALINITY

Avers and Westcot (1985) define a salinity problem as a condition where the salts in solution within the crop root zone accumulate in concentrations which decrease crop yield. Although all dissolved solids and gasses contribute ions to the total concentration, these authors, writing for FAO, list the most common excess constituents as calcium, magnesium, sodium, carbonate, bicarbonate, chloride, sulfate, nitrate, ammonium, phosphate, potassium, boron, and various trace elements. Solutes in aqueous solutions decrease osmotic potential, which affects plant water uptake (Wadleigh and Ayers, 1945; Munns and Termaat, 1986; Jacoby, 1999; Katerji et al., 1997). Osmotic effects contribute to reduced growth rate, changes in leaf color, and developmental characteristics, such as root/shoot ratio and maturity rate. In addition, ion toxicities or nutritional deficiencies may arise as a result of the excessive presence of specific ions and/or a competition among specific cations or anions (Bernstein, 1974; Torres-Bernal et al., 1974; Shannon and Grieve, 1999). Ionic effects are often manifested by leaf and meristem damage or as symptoms typical of nutritional disorders. For example, Na or Cl ions may accumulate in plant leaf tissue and cause necrotic tips and/or margins (Bernstein et al., 1956; 1969). Salinity-induced nutritional deficiencies present symptoms generally similar to those that occur in the absence of salinity. Often cited is the presence of sulfate and large Na/Ca ratios in root-zone solutions which were thought to lead to symptoms of calcium deficiency (Maas and Hoffman, 1977; Janzen and Chang, 1987, 1988). More commonly,

H. Steppuhn, Semiarid Prairie Agricultural Research Centre, Agriculture and Agri-Food Canada, Box 1030, Swift Current, SK, Canada S9H 3X2; M.Th. van Genuchten, Soil Physics/Pesticide Unit, George E. Brown, Jr. Salinity Laboratory, Agricultural Research Service, U.S. Department of Agriculture, Riverside, CA; C.M. Grieve, Plant Sciences Group, George E. Brown, Jr. Salinity Laboratory, Agricultural Research Service, U.S. Department of Agriculture, Riverside, CA. Received 8 Sep. 2003. *Corresponding author (SteppuhnH@agr.gc.a).

Abbreviations: EC_e , electrical conductivity of saturated soil paste extract; EC_i , electrical conductivity of the irrigated water; EC_s , electrical conductivity of test solution; FAO, Food and Agriculture Organization, United Nations; ST-Index, salinity tolerance index.

nutritional effects tend to work in conjunction with specific ion toxicity but vary in their degree of manifestation in different crops (Curtin et al., 1993; Grattan and Grieve, 1999).

Salinity is commonly measured in units of electrical conductivity at 25°C and an electrode spacing of 10 mm. Representative soil samples are obtained from the root zone to which deionized water is added to derive saturatedpaste extracts following standard procedures (Rhoades, 1982). The electrical conductivity (EC_e) of these extracts provides a consistent, repeatable, and widely accepted salinity standard (U.S. Salinity Laboratory Staff, 1954). An advantage of using EC_e as a salinity measure is that it relates to saturated field soil water conditions. Other measures of root-zone salinity include solute concentration (C_s) and osmotic potential (Ψ_o) of the soil extracts. For many soil extracts,

$$EC_e \approx 640 \ (C_s)$$
 [1]

nd
$$\Psi_{\rm o} \approx -36.47 \; ({\rm EC_e})$$
 [2]

where EC_e, C_s, and Ψ_0 are respectively expressed in decisiemens per meter (dS/m), parts per million (ppm), and kilopascals (kPa) (U.S. Salinity Laboratory Staff, 1954). Experience has also shown that the electrolyte concentration resulting from the saturated soil-paste-extract procedure equals approximately one-half that of the soil pore water at field capacity (Ayers and Westcot, 1985).

а

The relative effects of specific ions in root-zone solutions compared with decreased osmotic potential resulting from elevated solute concentrations has been debated at length. Palmer (1937) noted that adding Na_2SO_4 to potted soils was more injurious to cereals than adding MgSO₄, but less than when NaCl was added. Magistad et al. (1943) found little, if any, significant differences in the yields of garden beets, wax beans, or carrots when the chloride and sulfate salt concentrations were converted to osmotic pressures and compared. The United States Salinity Laboratory Staff (1954) agreed with Magistad et al. (1943) but with the corollary that deviations from direct osmotic-yield relationships were caused by specific-ion effects.

One of the concerns with salinity-tolerance response functions relates to anion dominance of the test solutions, i.e., between chloride and sulfate ion concentrations. Warne et al. (1990) measured better growth for Chenopodium rubrum L. plants subjected to Cl solutions as compared with plants grown in SO₄-dominated systems. In contrast, Boursier and Läuchli (1990), Wu and Huang (1991), Mor and Manchanda (1992), and Curtin et al. (1993), respectively, observed that, at moderate sulfate salinity, crop growth of sorghum [Sorghum bicolor (L.) Moench], tall fescue (Festuca arundinacea Schreber), table pea (Pisum sativum L.), and Kochia sco*paria* (L.) Schrad. was generally less limiting than under comparable chloride salinity. More recently, Grieve and Suarez (1997) and Grieve et al. (1999, 2001b) demonstrated the feasibility of applying sulfate-based irrigation water to Portulaca oleracea L. (a halophyte), wheat, and nine leafy vegetable crops and still realize satisfactory yields. Maas (1990) cited the work of Bernstein (1962) in suggesting that upward salt-tolerance adjustments of 1 to 3 dS/m are appropriate where calcium sulfate salinity dominates soil solutions to apply cropyield data obtained at the same EC_e in chloride-dominated response tests.

Crops have been tested for salt tolerance in both field and greenhouse experiments in soil and sand cultures. Yaron et al. (1972) studied regression procedures for estimating the yield of field-grown crops in response to soil water content and salinity. Using grapefruit (*Citrus* \times paradisi Macfad.) and peanut (Arachis hypogaea L.) data, they identified many of the difficulties associated with correlating yield with salinity when soil water contents vary. Typically, randomly arrayed field plots or large tanks containing the crops under investigation are separately salinized artificially with an irrigated solution whose solute concentration equates to one of a range of increasing salinities. In the field, within soil, the time required for complete mixing and diffusion of the irrigated test solutions with the initial soil solutions throughout the root zone can require days or weeks or longer as compared to minutes or hours for greenhouse sand cultures. Field tests with soil provide greater opportunity for evapotranspiration or rainfall to concentrate or dilute the in situ, dissolved salts, especially following infrequent applications of saline test solutions. Unless growing conditions carefully duplicate those of the target growing season, greenhouse testing can also cause skewed responses. In addition, soil-based, salt-tolerance testing may have to contend with preferential flow and with spatial and temporal salinity transients in the root zones. Unless irrigated with large leaching fractions, the soil may act as either an ion source or sink. Variations in the actual solute concentration of the solutions acting on the roots of test crops, especially in field trials, can cause considerable variations in the resulting crop yields.

Besides changes in solute concentrations, many other crop-environment interactions may cause variations in salinity-yield relationships, such as those involving temperature, radiation, humidity, atmospheric pollutants, wind, soil water content, and fertility (Shannon et al., 1994). The combination of high temperatures and low humidity may decrease crop salt tolerance, especially if soil water reserves are limited (Bernstein, 1974). Hoffman et al. (1978) observed that pinto bean grown in a cool, humid environment tolerated higher salt levels than those predicted from published data. Drought often combines with salinity adding to the difficulties faced by crop plants (Bresler et al., 1982; Katerji et al., 1992; Feng et al., 2003a, 2003b). Testing for crop salt tolerance involves separating the simultaneous effects of any water deficits from those resulting from the salinity. Root-zone fertility and aeration in the absence or presence of salinity contribute eminently to the productivity of crop plants. Doughty and Stalwick (1940), Lunin et al. (1961a, 1963), Ravikovitch and Porath (1967), Ravikovitch and Yoles (1971), Bernstein (1974), and Peters (1983) are among many who reported salinity-fertility interactions affecting interpretations of salt-tolerance data. If the yield response to increasing root-zone salinity encounters nutrient or oxygen deficits, a threshold limit for maximum productivity typically results (Maas and Hoffman, 1977). Shallow water tables or very frequent irrigation can cause poor soil aeration, and thereby, negatively affect the testing of crops for their tolerance of salinity, as exemplified in tomato and wheat (Aubertin et al., 1968; Aceves-N et al., 1975).

Plant ontogeny or growth stage also affects crop tolerance of salinity. For example, turnip (Brassica rapa L.) is most salt tolerant at germination, but more sensitive as a seedling than at harvest (Francois, 1984). In general, the earlier and longer that crop plants must cope with root-zone salinity, the greater the reduction in vegetative growth (Lunin et al., 1961b, 1962, 1963; Kaddah and Ghowail, 1964; Francois et al., 1994; Katerji et al., 1998). A common practice in testing crop plants for their salinity tolerance is to delay salinization of root zones until after the plants have been established (Maas and Grattan, 1999). Delaying salinization from sowing to establishment causes variation in crop yields (Lunin et al., 1962; Steppuhn et al., 1996). In wheat, delaying salinization beyond emergence increases the number of primordia, the final leaf number, and likely the grain weight (Grieve et al., 2001a). Even the same variety can respond differently depending on the interactions of phenology and the initiation of the root-zone salinity (Shannon and Noble, 1990).

Genetic, physiological, and ecological crop differences combine to determine how a crop will respond to salinity. Wheat, for example, varies in tolerance among many of its varieties, cultivars, and strains (Torres-Bernal and Bingham, 1973; van Hoorn et al., 1993; Steppuhn and Wall, 1997). At the same time, plants grown from larger seeds, at least for two wheat cultivars, tend to show better salinity tolerance than plants from smaller seeds (Grieve and Francois, 1992). Ecologically, crop yields in saline environments vary in their response to plant density. In wheat, widely spaced crop plants tend to show the effects of saline root-zones more than closely spaced plants (L.E. Francois, personal communication; Steppuhn, 1997). The distinction between testing for salt tolerance among agricultural crops rather than among agricultural plants guides the discussion and work presented herein.

Most lists of the relative salinity tolerance among agricultural crops are based on comparisons of parameters in specific salinity–yield functional relationships (van den Berg, 1950; U.S. Salinity Laboratory Staff, 1954; Allison, 1964; Bernstein, 1974; Maas and Hoffman, 1977; Bresler et al., 1982; Maas, 1986; Francois and Maas, 1994; Maas and Grattan, 1999). The parameters in these functions have come to serve as indices for salinity tolerance. The objective of this study was to compare various yield functions to suggest a general response and index, which, though empirical, most closely reflects the general response of agricultural crops to root-zone salinity.

RESPONSE FUNCTIONS

Crops produce a wide array of agricultural commodities and do so with efficiencies measured by crop yield. Yields vary depending on crop species, cultivar, ambient environment, soil fertility, pest damage, and many other factors besides salinity. Yields also vary because the commodities produced from plant crops originate from a diverse array of plant components: leaves, stems, flowers, fruits, seeds, roots, tubers, and other tissues. To compare the tolerance of crops to root-zone salinity, yields are usually standardized and expressed on a relative basis. The usual procedure for converting absolute yield (Y) to relative yield (Y_r) employs a scaling divisor (Y_m) based on the production where salinity has very little or no influence on yield (Maas, 1990). Such a divisor normalizes the data set, and almost always equals the maximum yield resulting from the response test. A Y_r value is determined for each cultivar in each test by

$$Y_{\rm r} = Y/Y_{\rm m}$$
 [3]

Various empirical equations have been applied or suggested for describing Y_r as a function of a variable, which reflects the average root-zone salinity (*C*). Measures used for *C* have included C_s , Ψ_o , EC_e , and EC_i , where EC_i equals the electrical conductivity of the irrigation water.

Simple Linear Function

Early analyses of crop yield responses to salinity commonly followed a simple linear relationship of the form

$$Y_{\rm r} = a - b(C) \tag{4}$$

Researchers restrictively applied a fitted linear function over the range of the salinities tested, or they simply showed the plotted response points without a fitted function (Palmer, 1937; Magistad et al., 1943; Ayers et al., 1943; Wadleigh and Ayers, 1945; Batchelder et al., 1963; Holm, 1983). Rarely, if ever, were the regression coefficients *a* and *b* identified as representing any biophysical characteristics of the response.

Modified Weibull Function

The statistical Weibull cumulative probability distribution exponentially relates one variable to another and increases in value from zero to one as the independent variable ranges from its upper to its lower values (Weibull, 1951). Used as a response function to root-zone salinity, the Weibull distribution has been modified and expressed in terms of the proportionate Y_r yield remaining at any *C* as follows:

$$Y_{\rm r} = \exp[a(C^b)]$$
 [5]

where the regression coefficient a is always negative and defines the intensity of the relationship, and the constant b reflects the shape of the response curve. Neither a nor b specify any distinct biophysical characteristic. The modified Weibull function has served as an analog for the response of crop growth or yield to environmental toxicity and solute excess (Rawlings and Cure, 1985; Taylor et al., 1991; Jalil et al., 1994a, 1994b).

Bi-Exponential Function

van Genuchten (1983) included a more general exponential response function for analyzing crop salt-tolerance data,

$$Y_{\rm r} = \exp[aC - b(C^2)]$$
 [6]

in which the empirical constants *a* and *b* again lack any biophysical identity and can be evaluated by nonlinear regression. van Genuchten and Hoffman (1984), Steppuhn et al. (1996), and Wang et al. (2002) used the biexponential function to describe the yield-responses of perennial ryegrass (*Lolium perenne* L.), wheat, and elephant grass (*Pennisetum purpureum* Schum.), respectively.

Modified Gompertz Function

According to Lapp and Skoropad (1976) actuaries for many years used a form of an equation proposed by Gompertz (1825) to predict human mortality. In various forms, the same equation has been applied in botany to model germination (Tipton, 1984), emergence (Gan et al., 1992), and growth (Baker et al., 1975). Steppuhn et al. (1998) compared the emergence of two Russian wild ryegrass cultivars from saline seedbeds with the Gompertz function. In the following form, it can also serve as a crop-yield salinity response function:

$$Y_{\rm r} = 1 - \exp[a \exp(bC)]$$
[7]

where empirical constants a and b are always negative, lack any biophysical identity, and can be evaluated by nonlinear regression.

Three-Piece Linear (Threshold-Slope) Function

After reviewing the yield responses measured in a large number of root-zone salinity experiments conducted worldwide, Maas and Hoffman (1977) introduced a two-piece linear model for the response of agricultural crops to increasing salinity. This resulted in their now classic threshold-slope concept. In its most general form, this model can be written as a three-piece response function (van Genuchten, 1983):

$$\begin{array}{ll} Y_{\rm r} = 1 & 0 < C < C_{\rm t} \\ Y_{\rm r} = 1 - b(C - C_{\rm t}) & C_{\rm t} < C < C_{\rm 0} \\ Y_{\rm r} = 0 & C > C_{\rm 0} \end{array}$$

where *b* is the absolute value of the declining slope in $Y_{\rm r}$ with C; C_t is the maximum value of salinity without a yield reduction (the threshold C); C_0 is the lowest value of C, where $Y_r = 0$. The empirical constants, b and $C_{\rm t}$, are usually evaluated by regression and/or visual inspection. Maas and Hoffman (1977) introduced their model as a two-piece expedient, ignoring the third segment, the yield response beyond C_0 . They also defined the "threshold salinity" C_t and the "slope" b, as characteristics that are uniquely specific to each crop, but gave no biophysical reasons for the existence of these characteristics. Maas and Hoffman (1977) also manually fitted the threshold-slope function to data for some 60 crops using experimental salt-tolerance field data reported in the literature. They included reports from experiments in which crops were grown while subjected to two or more levels of salinity plus a nonsaline control. For 25 yr, their threshold-slope values have served as first approximations of crop salinity tolerance. The value of their work is that it demonstrated the use of mathematical response functions and associated parameters to evaluate and compare the salinity tolerance of crops. Feinerman and Yaron (1982) extended the thresholdslope response function to include the effects of soil moisture with all other factors assumed constant.

Modified Discount Function

The compound discount equation can be modified into a sigmoidal-shaped response function,

$$Y_{\rm r} = 1/[1 + (C/C_{50})^{\exp(sC_{50})}]$$
[9]

where C_{50} defines *C* at $Y_r = 0.5$, and s represents the response curve steepness. The steepness parameter equals the average absolute value of the slope (dY_r/dC) of the equation through C_{50} and its steepest segments on either side of C_{50} , evaluated in our study from $Y_r = 0.3$ to 0.7. The argument sC_{50} of the exponent in Eq. [9] contributes to a symmetrical concave-convex yield response with the inflection point at C_{50} and is analogous to the product bC_t of the threshold-slope model (Eq. [8]). Both *s* and *b* indicate unit decreases in relative product yield with unit increases in root-zone salinity. As in the threshold-slope function, the modified discount function features parameters (*s* and C_{50}) with identifiable biophysical characteristics.

van Genuchten (1983) was the first to apply a form of the modified discount function to yield data of agricultural crops growing subjected to increasing rootzone salinity; he used the empirical constant p as the exponent instead of $\exp(sC_{50})$:

$$Y_{\rm r} = 1/[1 + (C/C_{50})^p]$$
[10]

In this form of the discount equation, p is a shape parameter without biophysical identity, which has been evaluated from 1 through 9 (van Genuchten and Gupta, 1993). In all reported applications of this form of the function, the value of p has always exceeded 1.0 (van Genuchten and Hoffman, 1984; van Genuchten and Gupta, 1993; Steppuhn, 1993; Steppuhn et al., 1996). This is related to the property of Eq. [10] that its slope at zero salinity (C = 0) is zero for p values greater than 1, finite $(-1/C_{50})$ when p = 1, and $-\infty$ when p < 1, the latter case being unrealistic from a practical view.

SALINITY TOLERANCE INDEX

Before 1977, the concept of using an index to rate the salinity tolerance of agricultural crops was consistently followed (Ayers et al., 1951; U.S. Salinity Laboratory Staff, 1954; Brown and Hayward, 1956). The practice was to simply use C_{50} , derived directly from experimental data, as the index. The introduction of the threshold-slope function to assess the yield response of agricultural crops to increasing levels of root-zone salinity provided two functional parameters (*b* and C_t) with which to index relative salt tolerance (Maas and Hoffman, 1977). These parameters served as dual indices resulting in various lists of the relative salinity tolerance among agricultural crops (Maas and Hoffman, 1977; Bresler et

al., 1982; Maas, 1986; Francois and Maas, 1999; Maas and Grattan, 1999).

As briefly reviewed in this study, many factors influence the yield of agricultural crops besides the response to increasing root-zone salinity. With a myriad of influences acting on the yield relationship, a single-value index of crop tolerance to root-zone salinity would seem sufficient for comparing the salinity tolerance of agricultural crops. If C_{50} were enhanced by a term, which dictates the shape of the yield response for salinity levels approaching C_{50} , such as the argument of the exponent in Eq. [9], a comprehensive, single-value, Salinity Tolerance Index or ST-Index results:

$$\text{ST-Index} = C_{50} (1 + s)$$
 [11]

where C_{50} and *s* can be computed as regression constants, or approximated by a visual inspection of the response data. The shape of the function for salinity levels greater than C_{50} is not included in this index.

MATERIALS AND METHODS

The crop-yield response data selected for comparing the functional effects to root-zone salinity on crops were obtained from Canada's Salt Tolerance Testing Laboratory (Steppuhn and Wall, 1999). A spring-seeded wheat cultivar, Biggar, was tested for salinity tolerance in an environmentally controlled greenhouse (Steppuhn and Wall, 1997). Biggar produces flour with medium protein, medium gluten, and medium kernel hardness for world trade (DePauw et al., 1991).

The Biggar wheat crop was grown in plastic tanks (0.85-m diam., 1.0 m deep cylinders) containing washed silica sand (99.8% pure) having an average bulk density of 1.5 Mg m⁻³. At saturation, the sand has a mean volumetric water content of 31.3%. In this test, the tanks were flushed four times daily with a modified Hoagland nutrient solution consisting of 2.0 mM Ca(NO₃)₂, 2.5 mM KNO₃, 0.17 mM KH₂PO₄, 1.0 mM MgSO₄, 0.05 m*M* chelated Fe, 0.5 m*M* NH₄NO₃, 0.05 m*M* KCl, 0.023 mM H₃BO₄, plus trace elements including Mn, Zn, Cu, Si, and Mo. Solutions were salinized by adding NaCl and CaCl₂ (1:1 by mass) resulting in pH values of 7.5 to 7.9. Each irrigation continued for five minutes until the sand was completely saturated after which the solutions drained into 612-L reservoirs for the next irrigation. Water lost by evapotranspiration was replenished weekly or more frequently when the volume of the solution in the supply reservoir decreased by 3% or more. The electrical conductivity of each solution was checked initially, weekly, and at harvest.

Eleven treatment solutions were prepared with solution electrical conductivities targeted at 2, 3, 4, 6, 8, 10, 12, 16, 20, 24, and 28 dS m⁻¹. The relative variability in grain yield which likely would occur in association with each conductivity was estimated from previous experiments. These estimates divided by an error tolerance squared and multiplied by an appropriate t-table value squared indicated the treatment replication necessary to maintain accuracy of the planned statistical regressions. The tank arrangement followed a randomized block design with respect to cultivars, but was modified slightly to eliminate any bias caused by taller plants blocking solar radiation associated with low sun angles. Forty-five Biggar wheat seeds were sown per tank on 3 Feb. 1993, 40 mm deep into the sand separated by 80 mm within rows spaced 150 mm apart. After emergence, populations were thinned to 35 plants per tank.

The procedure for adding salts to the irrigated solutions

in this test approximated that practiced by the U.S. Salinity Laboratory (L.E. Francois, E.V. Maas, and C.M. Grieve, personal communications). Salts were added gradually, with the first third on Day 13 after seeding (plants emerging), the second third on Day 18 (plants showing two leaves), and the final third on Day 22 (three leaves showing). Daylengths were adjusted during the growing period with 475 W sodium lamps positioned 1.5 m above the sand surfaces to mimic a typical field seeding date of 1 May at latitude 50°N. Mean temperatures equaled 24°C daytime and 18°C nighttime. The maximum daily ambient air temperature ranged from 22 to 26°C and the minimum between 16 and 19°C.

The response of the wheat crop to the salinity treatments at harvest was determined by weighing the oven-dried grain yield. Yield measurements were averaged and related to EC_e derived from the electrical conductivities of the test solutions (EC_i) by the conventional relationship followed by the U.S. Salinity Laboratory (Maas, 1990),

$$EC_e \approx 0.5 EC_i$$
 [12]

This equation assumes that the solutions fill the soil pores to field capacity and has been substantiated by Janzen and Chang (1988) and Kohut and Dudas (1994).

The optimal value of Y_m is determined by substituting Y/Y_m (Eq. [3]) for Y_r for each of the response functions tested and estimating Y_m by linear or nonlinear least-squares regression with the data set (van Genuchten, 1983). To ensure a common initial basis for comparing the six response functions with the Biggar wheat data, Y_m was set equal to the yield of the first data pair, 307.0 g m⁻², obtained in the absence of root-zone salinity. With Y_m determined, and Y_r (Y/Y_m) computed, the different response functions were fitted to the EC_e-data to test each model obtaining the associated root mean square error, coefficient of determination, and parameter estimates. Least-square fits were performed by the maximum neighborhood method of Marquardt (1963), which is based on an optimum interpolation between the Taylor series method and the method of steepest descent (Bates and Watts, 1988; SAS, 1995).

In addition to the Biggar wheat data, the absolute or relative yields found within 33 other studies from crops grown in increasingly saline rooting media were assessed. R^2 values and root mean square errors (RMS errors) associated with applications of the threshold-slope and modified discount equations to these additional data sets were computed and compared.

RESULTS AND DISCUSSION

The decline in crop yield for Biggar wheat in response to increasing root-zone salinity corresponds similarly to the declines reported for spring-sown wheats in field salinity trials conducted by Holm (1983) and McKenzie (1988) during comparable daylengths and temperatures. Grain yields produced from the wheat grown under low salinity levels at first deviated only slightly from the nonsaline production (Table 1). As salinity increased, its incremental effect on yield increased to a maximum about midway or two-thirds into the response relationship. Thereafter, increasing salinity had a decreasingly reduced influence on yield. Any one of the functional plots resulting from the six test equations applied to the Biggar wheat test data could serve as an empirical analog of the relationship (Fig. 1–6). The three-piece linear function was determined by selecting the first three data pairs as points within the upper horizontal segment of

Table 1. Average absolute (Y) and relative (Y_r) spring wheat grain yields (cv. Biggar) in response to irrigation with salinized solutions.

Target EC _i †	Actual EC _i	EC _e †	Y	Yr	
	g m ⁻²				
2‡	1.96	0.98	307.0	1.0	
3	3.11	1.55	306.9	0.999	
4	4.20	2.10	282.9	0.921	
6	6.24	3.12	234.9	0.765	
8	8.12	4.06	225.4	0.734	
10	10.60	5.30	170.0	0.554	
12	12.08	6.04	111.0	0.362	
16	16.34	8.17	82.6	0.269	
20	19.94	9.97	64.5	0.210	
24	24.20	12.10	19.9	0.065	
28	27.60	13.80	15.0	0.049	

 \dagger EC, electrical conductivity of the average irrigated test solution; EC, approximate equivalent electrical conductivity of saturated soil-paste extract.

* Nutrients (1 dS m⁻¹) plus background salinity of the hydroponic test water (1 dS m⁻¹), considered nonsaline.



the function. Other data-pair selections would have given different results.

The R^2 values from regression analyses using the six functions ranked from a low of 0.941 for the simple linear to a high of 0.988 for the modified discount relationship (Table 2). RMS errors ranged from a low of 0.0433 for the discount equation to a high of 0.0940 for the simple linear relationship. On the basis of the statistics in Table 2, the modified discount function is slightly better than the other nonlinear functions and considerably better than the linear models. In addition, the discount-based function features empirically derived parameters which represent the biophysical characteristics of mid-yield salinity (C_{50}) and generalize unit decline in yield with salinity (s). These discount parameters respectively dictate the position of the functional curve and the general steepness of the decline along the increasing scale of root-zone salinity. Only the thresholdslope model also features constants which identify biophysical parameters, threshold salinity (C_t) , and linear decline in yield with salinity (b).

Additional R^2 and RMS error values, calculated for



Fig. 2. Modified Weibull response function, $Y_r = \exp[a(C^b)]$, applied to the Biggar spring wheat data.



Fig. 3. Bi-exponential response function, $Y_r = \exp[aC - b(C^2)]$, applied to the Biggar spring wheat data.

33 other data sets (17 different crops) further demonstrate the greater utility of the modified discount function compared to the threshold-slope function (Table 3). Thirty-two out of 33 R^2 values and 30 out of 33 RMS errors favor the discount equation. Arithmetic averages from the 33 comparisons for the threshold-slope linear model R^2 and RMS error equal 0.815 and 0.1276, respectively. For the discount nonlinear model, the averages equal 0.904 and 0.0705, respectively. The modified-discount response function represents an improvement to the linear relationship, decreasing the average error by 45% and increasing the model-fit by an 11% average.

The literature offers no theoretical rationale for the existence of a C_1 . Taylor et al. (1991) even argue against it, stating, "There is no a priori reason to expect the relationship between yield and exposure to a metal ion to be discontinuous." It is true that plant species have evolved various salt-tolerance mechanisms to cope with saline root zones (Yeo and Flowers, 1984). Acceptance



Fig. 4. Modified Gompertz response function, $Y_r = 1 - \exp[a \exp(bC)]$, applied to the Biggar spring wheat data.



Fig. 5. Three-piece linear (threshold slope) response function; $Y_r = 1.0$, $Y_r = 1 - b(C - C_t)$, $Y_r = 0.0$, applied to the Biggar spring-wheat data.

of the threshold concept in crop-yield response requires acceptance of the thermodynamic premise that plants with such mechanisms develop and operate at a constant growth capacity regardless of the magnitude of the rootzone salt concentration (Soo, 1962). That is, the biological energy utilized to grow and operate salt-tolerance mechanisms up to C_t is constant and unrelated to crop yield. A continuous, though small and increasing, cropyield decline at pre- C_t salinity levels would seem to support more plausible thermodynamic logic.



Fig. 6. Modified discount response function, $Y_r = 1/[1 + (C/C_{50})^{\exp(sC_{50})}]$, applied to the Biggar spring wheat data.

Relating Y_r to C/C_{50} by the modified discount function (Eq. [9]), wherein s, the steepness component, is fixed in values from 0.001 through 0.22 and $C_{50} = 10 \text{ dS m}^{-1}$, results in an array of response curves with a common point at $C/C_{50} = 1.0$ (Fig. 7). The change in Y_r with a unit change in C/C_{50} for different values of s is not linear. Figure 8 shows changes in relative yield as a function of relative salinity for four unit changes in parameter s. The plots in Fig. 8 indicate that a maximum change of 15% in Y_r is associated with a C/C_{50} value near 0.35 as s varies from 0.001 to 0.069. This maximum change in Y_r decreases with increases in s and with shifts to higher C/C_{50} values. If s is constant, an increasing value of C_{50} results in relative crop yields (Y_r) which differ depending on the value of C. Three plots of the differences in Y_r for three changes in C plotted with increasing C_{50} and s = 0.11 reveal that percentage differences in relative yield do not exceed 11% of a unit difference in root-zone salinity and that percentages decrease as C increases (Fig. 9).

Acceptance of the continuous, discount response function for crop yield with increasing root-zone salinity also accepts the threshold-slope function as an approximation. This implies that the parameters of the two functions are related and can be derived from relationships based on each other. For example, if C_t and b are known for any crop, it should be possible to estimate C_{50} and s from them. Various methods for deriving C_{50} and s from C_t and b are explored, and the best procedures for the conversions are selected in the companion

Table 2. Parameters and statistical results from regression analyses of six functions relating relative Biggar wheat yields (Y_r) to rootzone salinity $(C = EC_e)$.

Function	Equation	R^2	RMSE	Paramete	Parameter values		
				———— (units or	(units omitted) —		
Simple Linear	$Y_{\rm r}=a-b(C)$	0.941	0.09398	a = 1.0350	b = 0.0811		
Weibull	$Y_r = \exp[a(C^b)]$	0.984	0.05058	a = -0.0289	b = 1.8226		
Bi-Exponential	$Y_r = \exp[aC - b(C^2)]$	0.982	0.05310	a = -0.0092	b = 0.0193		
Gompertz	$Y_r = 1 - \exp[a \exp(bC)]$	0.985	0.04839	a = -5.0256	b = -0.3515		
Threshold-Slope	$\dot{Y_r} = 1 - b(\dot{C} - \dot{C}_1)$	0.966	0.07715	$C_{\rm t} = 1.5730$	b = 0.1306		
Discount	$\dot{Y}_{\rm r} = 1/[1 + (C/C_{50})^{\exp(sC_{50})}]$	0.988	0.04328	$C_{50} = 5.442$	<i>s</i> = 0.1838		

Table 3. Resulting	coefficient	-of-determinati	on (<i>R</i> ²) ar	nd root-mean-so	uare-error (RMSE) v	alues deriv	ed from t	hreshold-slope	and
modified-discou	nt response	functions for p	roduct vie	lds with increasi	ing root-zone	e salinity in	n tested ag	ricultural o	crops.	

	ECe		Response function				
Test crop	(dS m ⁻¹)	Threshold-slope		Discount		
Cultivar	Min-Max	N	R^2	RMSE	R^2	RMSE	Data source
Alfalfa (Medicago sativa L.; M. falcata L.)							
Beaver	0.7-14	8	0.930	0.1187	0.972	0.0746	Steppuhn et al., 1999
Rangelander	0.7 - 14	8	0.866	0.1629	0.997	0.0233	Steppuhn et al., 1999
Calif. common	2-18	4	0.957	0.0626	0.964	0.0577	Brown and Hayward, 1956
Barley (Hordeum vulgare L.)	- 10	-	0000	0.0020		000077	Dio vii uliu Iluj vuluj 1900
Ronanza	0 75-19	15	0 867	0 1136	0.972	0.0522	÷STTL 1990
Bonanza	0.75-18	12	0.007	0.1150	0.968	0.0685	Stennuhn 1003
Bridge	0.75 10	15	0.044	0.1033	0.900	0.0005	STTI 1000
Dridge	0.75-19	13	0.944	0.07.30	0.973	0.0304	Still, 1990 Stonnubn, 1002
bridge	0.75-18	12	0.955	0.0988	0.958	0.0908	Steppunn, 1995
Harrington	0.75-19	15	0.832	0.0990	0.951	0.0538	STIL, 1990
Harrington	0.5-16	7	0.944	0.0992	0.976	0.0650	Steppuhn et al., 2004
Canola (Brassica napus L.)							
Hyola 401‡	0.5-16	7	0.911	0.1418	0.955	0.1010	Steppuhn et al., 2002
Hyola 401§	0.75 - 14	7	0.946	0.0950	0.950	0.0921	Steppuhn et al., 2002
InVigor2573§	0.75-14	7	0.894	0.1462	0.988	0.0497	Steppuhn et al., 2002
Quantum [‡]	0.5-16	7	0.946	0.1023	0.938	0.1096	Steppuhn et al., 2002
Carrot (Daucus carota L.)							
Early French	0.625 - 7.5	12	0.795	0.1669	0.978	0.0546	Magistad et al., 1943; Osawa, 1965
Foxtail, meadow (Alopecurus pratensis L.)							
unknown	1-14.5	8	0.958	0.0718	0.997	0.0188	Brown and Bernstein, 1953
Harding-grass (Phalaris tuberosa I)	1 1.40	0	0.000	0.0710	0.))//	0.0100	brown and beinstein, 1965
Stonontoro	08 13 7	6	0 805	0.0882	0.070	0.0472	Brown and Bornstoin 1053
Dro foll (Secolo corogle L.)	0.0-13.7	0	0.075	0.0002	0.970	0.0472	brown and bernstein, 1955
Rye, fail (Secure cereare L.)	59 150	6	0 527	0 1652	0 604	0 1 4 4 9	Example of al 1000
	5.6-15.9	0	0.527	0.1055	0.004	0.1448	Francois et al., 1989
Kyegrass, perennial (Lolium perenne L.)					· ·		
unknown	1-13.7	8	0.742	0.1408	0.774	0.1293	Brown and Bernstein, 1953
Sorghum [Sorghum bicolor (L.) Moench]							
NK-265	3-12.4	12	0.905	0.1202	0.972	0.0670	Francois et al., 1984
Sugarbeet (Beta vulgaris L.)							
unknown	0.95-10.3	7	0.615	0.1018	0.665	0.1030	Bower et al., 1954
Tomato [Lycopersicon lycopersicum (L.) Karsten]							
unknown	1-14	6	0.808	0.1646	0.982	0.0499	Osawa, 1965
Turnip (Brassica rapa L.)							,
Purple-ton	0.9-8.3	4	0.989	0.0360	0.998	0.0139	Francois, 1984
Wheat durum (<i>Triticum turgidum</i> L. var. <i>durum</i> Desf.)	015 010	-	0.000	0.00000	00550	000103	1 10000, 1901
Kylo	1_0	10	0 781	0 180	0.965	0.040	Stannuhn at al. 1006
Whoat spring (Triticum agetivum I)	1-)	10	0.701	0.100	0.705	0.040	Steppuni et al., 1990
Noopowo	1 14	12	0 775	0 100	0.052	0.040	Stonnubn of al. 1006
neepawa Di	1-14	12	0.775	0.100	0.955	0.040	Steppunn et al., 1990
Biggar	1-14	12	0.692	0.170	0.934	0.000	Steppunn et al., 1996
Katepwa	1-14	10	0.754	0.200	0.890	0.100	Steppuhn et al., 1996
Fielder	1-14	10	0.717	0.230	0.730	0.260	Steppuhn et al., 1996
Wheatgrass, green (<i>Elymus hoffmannii</i> Jensen & Asay)							
Saltlander§	0.75-25	8	0.824	0.1798	0.961	0.0849	Steppuhn and Asay, 2004
Saltlander‡	0.75 - 24	9	0.799	0.1988	0.985	0.0546	Steppuhn and Asay, 2004
Wheatgrass (Elymus hoffmannii Jensen & Asay)							•·
NewHy	0.75 - 24	9	0.700	0.1880	0.985	0.0414	Steppuhn and Asay, 2004
Wheatgrass, tall [=Thinopyron ponticum (Podn.)							EE CONTRACTOR
Lin & Wang]							
Orbits	0 75_25	8	0.012	0 1163	0 070	0.0677	Stennuhn and Acay 2004
Orbitt	0.75 24	0	0.912	0.1105	0.970	0.0547	Stonnubn and Asov 2004
01001+	0.75-24	,	0.010	0.1077	0.717	0.0302	Steppulli and Asay, 2004

† STTL, unpublished data, Canada's Salinity Tolerance Testing Lab.

‡ Predominately chloride salts.

§ Predominately sulfate salts.

paper (Steppuhn et al., 2005). Converted values for the discount parameters determined in the companion paper serve as comparisons and are shown in this paper as examples for a field, forage, and vegetable crop (Table 4).

As briefly reviewed in this study, many factors influence the yield of agricultural crops besides exposure to increasing root-zone salinity. Consequently, the singlevalue, Salinity Tolerance Index would seem more appropriate for comparing agricultural crops than any of the dual parameters of any of the response functions. The index is based on the nonlinear parameters of C_{50} and s (Eq. [11]). The ST-Index identifies a salinity value equal to the 50% reduction in crop yield from that of the nonsaline yield plus a measure of the tendency to maintain some product yield as the crop is subjected to salinity levels less than but approaching C_{50} :

$$ST-Index = C_{50} + s(C_{50})$$
[13]

The ST-Index for the Biggar wheat test data equals 6.44, which ranks it less tolerant of salinity than alfalfa, more tolerant than radish, and about equal to that of field corn (Table 4). The three ST-Index values in Table 4 reflect rankings based on the ambient conditions of the response tests for the three representative crops and a conversion of linear to nonlinear functional parameters using the procedures detailed in the companion paper (Steppuhn et al., 2005).



Fig. 7. Relative crop yield from the modified discount function, $\mathbf{Y}_r = 1/[1+(C/C_{50})^{\exp(sC_{50})}]$, with relative root-zone salinity for $C_{50} = 10$ dS m⁻¹ and a wide range of values for *s*.



Fig. 8. Change in relative crop yield $(\triangle Y_r)$ as a function of relative root-zone salinity (C/C₅₀) for four unit changes in parameter (s) using the modified discount function.

CONCLUSIONS

Relative crop yield has evolved as the primary indicator of agricultural crop tolerance or resistance to rootzone salinity. Experimental data to evaluate the relative tolerance of crops to salinity require yield response functions which account for the high degree of variability associated with testing for crop yields and include responses from factors other than salinity. With an aim to compare various yield functions to suggest a general empirical response and index which most closely reflect the general agricultural crop response to root-zone salinity, this study has led to the following conclusions.

1. A comparative salinity tolerance index (ST-Index), based on the nonlinear (modified-discount) regression parameters of C_{50} (the salinity level associated with a 50% yield of the relative nonsaline, crop production) and *s* (the absolute steepness of the general relative yield decline with salinity), can

Table 4. Nonlinear discount parameters and the Salinity Tolerance Index (STI) derived from linear threshold-slope parameters by the conversion methods detailed in the companion paper (Steppuhn et al., 2005).

Crop	Linear	•	Ň		
	b†	C_{t} ‡	$\overline{C_{50}}$ §	s¶	STI
	$(dS m^{-1})^{-1}$	— dS m ⁻¹ —		$(dS m^{-1})^{-1}$	
Corn	0.120	1.70	5.54	0.183	6.56
Alfalfa	0.073	2.00	8.49	0.111	9.43
Radish	0.130	1.20	4.73	0.198	5.67

 $\dagger b$, Absolute value of the linear regression slope parameter.

 $\ddagger C_i$, "Threshold" salinity parameter.

§ C_{50} , Salinity where crop yield equals 50% of the nonsaline yield. If s, Absolute value of the nonlinear steepness parameter



Fig. 9. Differences in relative crop yield (Y_t) derived from the modified discount function with increasing C_{s0} -salinity and constant *s* (s = 0.11) for three sets of changes in root-zone salinity (*C*) from 1 to 10, 5 to 15, and 10 to 20 dS m⁻¹.

serve to rate agricultural crop tolerance to rootzone salinity [ST-Index = $C_{50} + s(C_{50})$].

- 2. Of the six response functions applied to data from the spring-wheat cultivar Biggar, the modified-discount, sigmoidal-shape response function $\{Y_r = 1/[1 + (C/C_{50})^{\exp(sC_{50})}]\}$ gave the lowest root mean square error and the highest R^2 value.
- 3. The modified-discount, nonlinear relationship compared to the threshold-slope linear model for product yield-salinity response data in 33 separate trials (17 crops) averaged 11% closer in statistical fit and 45% lower in statistical error.
- 4. From sensitivity analyses, a maximum change of 15% or less in relative yield resulted from a 100% change in *s* or C_{50} of the modified discount function.
- The availability of nonlinear regression software makes it unnecessary to approximate nonlinear sigmoidal response parameters with parameters derived from linear functions.
- 6. Various procedures for converting the linear parameters of threshold salinity (C_t) and slope (b) into the nonlinear parameters of the salinity at 50% yield reduction (C_{50}) and the central unit decline in relative yield with salinity (s) are explored for a large array of agricultural crops in the companion paper (Steppuhn et al., 2005).

ACKNOWLEDGMENTS

With thanks, the authors acknowledge the valuable contributions of Mr. K.G. Wall, Mr. K.W. Deobald, Dr. Y.W. Jame, Dr. S. Yang-Steppuhn, and staff members of the George E. Brown, Jr. Salinity Laboratory and the Semiarid Prairie Agricultural Research Centre to this research.

REFERENCES

- Aceves-N., E., L.H. Stolzy, and G.R. Mehuys. 1975. Combined effects of low oxygen and salinity on germination of a semi-dwarf Mexican wheat. Agron. J. 67:530–532.
- Allison, L.E. 1964. Salinity in relation to irrigation. Adv. Agron. 16: 139–180.
- Aubertin, G.M., R.W. Rickman, and J. Letey. 1968. Differential saltoxygen levels influence plant growth. Agron. J. 60:345–349.
- Ayers, A.D., C.H. Wadleigh, and L. Bernstein. 1951. Salt tolerance of six varieties of lettuce. Proc. Am. Soc. Hortic. Sci. 57:237–242.
- Ayers, A.D., C.H. Wadleigh, and O.C. Magistad. 1943. The interrelationships of salt concentration and soil moisture content with the growth of beans. J. Am. Soc. Agron. 35:796–810.
- Ayers, R.S., and D.W. Westcot. 1985. Water quality for agriculture. FAO Irrigation and Drainage Paper 29 (Revision 1), Food and Agriculture Organization of the United Nations, Rome.
- Baker, C.H., R.D. Horrocks, and C.E. Goering. 1975. Use of the Gompertz function for predicting corn leaf area. Trans. ASAE 18(2):332–336, 330.
- Batchelder, A.R., J. Lunin, and M.H. Gallatin. 1963. Saline irrigation of several vegetable crops at various growth stages. II. Effect on cation composition of crops and soils. Agron. J. 5:111–114.
- Bates, D.M., and D.G. Watts. 1988. Nonlinear regression analysis & its applications. John Wiley & Sons, New York.
- Bernstein, L. 1962. Salt-affected soils and plants. p. 139–174. In Problems of the arid zones. Proc. UNESCO Symp., Paris, France.
- Bernstein, L. 1974. Crop growth and salinity. Chap. 3, p. 39–54. In J. van Schilfgaarde (ed.) Drainage for agriculture. Agron. Monogr. 17. ASA, Madison, WI.
- Bernstein, L., J.W. Brown, and H.E. Hayward. 1956. The influence of root stock on growth and salt accumulation in stone-fruit trees and almonds. Proc. Am. Soc. Hortic. Sci. 68:86–95.
- Bernstein, L., C.F. Ehlig, and R.A. Clark. 1969. Effect of grape root stocks on chloride accumulation in leaves. J. Am. Soc. Hortic. Sci. 94(6):584–590.
- Bower, C.A., C.D. Moodie, P. Orth, and F.B. Gschwend. 1954. Correlation of sugar beet yields with chemical properties of a salinealkali soil. Soil Sci. 77(6):443–451.
- Boursier, P., and A. Läuchli. 1990. Growth responses and mineral nutrient relations of salt-stressed sorghum. Crop Sci. 30:1226–1233.
- Bresler, E., B.L. McNeal, and D.L. Carter. 1982. Saline and sodic soils, principles-dynamics-modeling. Springer-Verlag, Berlin.
- Brown, J.W., and L. Bernstein. 1953. Salt tolerance of grasses. Effects of variation in concentrations of sodium, calcium, sulfate, and chloride. Report to Collaborators. U.S. Salinity Lab., Riverside, CA.
- Brown, J.W., and H.E. Hayward. 1956. Salt tolerance of alfalfa varieties. Agron. J. 48:18–21.
- Curtin, D., H. Steppuhn, and F. Selles. 1993. Plant responses to sulfate and chloride salinity: Growth and ionic relations. Soil Sci. Soc. Am. J. 57:1304–1310.
- DePauw, R.M., K.R. Preston, T.F. Townley-Smith, E.A. Hurd, G.E. McCrystal, and C.W.B. Lendrum. 1991. Biggar red spring wheat. Can. J. Plant Sci. 71(2):519–522.
- Doughty, J.L., and A.E. Stalwick. 1940. The effect of alkali salts on plant growth. Sci. Agric. 20(5):272–276.
- Feinerman, E., and D. Yaron. 1982. Linear crop response functions to soil salinity with a threshold salinity level. Water Resour. Res. 18(1):101–106.
- Feng, G.L., A. Meri, and J. Letey. 2003a. Evaluation of a model for irrigation management under saline conditions: I. Effects on plant growth. Soil Sci. Soc. Am. J. 67:71–76.
- Feng, G.L., A. Meri, and J. Letey. 2003b. Evaluation of a model for irrigation management under saline conditions: II. Salt distribution and rooting pattern effects. Soil Sci. Soc. Am. J. 67:77–80.

- Francois, L.E. 1984. Salinity effects on germination, growth, and yield of turnips. HortScience 19:82–84.
- Francois, L.E., and E.V. Maas. (ed.) 1978. Plant responses to salinity: An indexed bibliography. U.S. Dep. Agric.-SEA (Science and Education Admin.) Agric. Reviews and Manuals, ARM-W-6. U.S. Gov. Print. Office, Washington, DC.
- Francois, L.E., and E.V. Maas. (ed.) 1985. Plant responses to salinity: A supplement to an indexed bibliography. U.S. Dep. Agric., ARS-24. U.S. Gov. Print. Office, Washington, DC.
- Francois, L.E., and E.V. Maas. 1994. Crop response and management of salt-affected soils. Chap. 7, p. 149–181. In M. Pessarakli (ed.) Handbook of plant and crop stress. Marcel Dekker, Inc. New York.
- Francois, L.E., and E.V. Maas. 1999. Crop response and management of salt-affected soils. Chap. 8, p. 169–201. In M. Pessarakli (ed.) Handbook of plant and crop stress, Second ed. Marcel Dekker, Inc. New York.
- Francois, L.E., T.J. Donovan, K. Lorenz, and E.V. Maas. 1989. Salinity effects on rye grain yield, quality, vegetative growth, and emergence. Agron. J. 81:707–712.
- Francois, L.E., T.J. Donovan, and E.V. Maas. 1984. Salinity effects on seed yield, growth, and germination of grain sorghum. Agron. J. 76:741–744.
- Francois, L.E., C.M. Grieve, E.V. Maas, and S.M. Lesch. 1994. Time of salt stress affects growth and yield components of irrigated wheat. Agron. J. 86:100–107.
- Gan, Y., E.H. Stobbe, and J. Moes. 1992. Relative date of wheat seedling emergence and its impact on grain yield. Crop Sci. 32:1275– 1281.
- Gompertz, B. 1825. On the nature of the function expressive of the law of human mortality and on a new mode of determining the value of life contingencies. R. Soc. London Phil. Trans. 36:513–585.
- Grattan, S.R., and C.M. Grieve. 1999. Mineral nutrient acquisition and response by plants grown in saline environments. Chap. 9, p. 203–229. *In* M. Pessarakli (ed.) Handbook of plant and crop stress, Second ed. Marcel Dekker, Inc., New York.
- Grieve, C.M., and L.E. Francois. 1992. The importance of initial seed size in wheat plant response to salinity. Plant Soil 147:197–205.
- Grieve, C.M., and D.L. Suarez. 1997. Purslane (*Portulaca oleracea* L.): A halophytic crop for drainage reuse systems. Plant Soil 192:277–283.
- Grieve, C.M., L.E. Francois, and J.A. Poss. 2001a. Effect of salt stress during early seedling growth on phenology and yield of spring wheat. Cereal Res. Commun. 29(1–2):167–174.
- Grieve, C.M., M.C. Shannon, and J.A. Poss. 2001b. Mineral nutrition of leafy vegetable crops irrigated with saline drainage water. J. Veg. Crop Prod. 7(1):37–47.
- Grieve, C.M., D.L. Suarez, and M.C. Shannon. 1999. Effect of saline irrigation water composition on selenium accumulation by wheat. J. Plant Nutr. 22(9):1443–1450.
- Hoffman, G.J., J.A. Jobes, Z., Hanscom, and E.V. Maas. 1978. Timing of environmental stress affects growth, water relations and salt tolerance of pinto bean. Trans. ASAE 21(4):713–718 and 722.
- Holm, H.M. 1983. Soil salinity, a study in crop tolerances and cropping practices. Sask. Agriculture, Plant Industries Branch, Publ. 25M/ 3/83.
- Jacoby, B. 1999. Mechanisms involved in salt tolerance of plants. Chap. 5, p. 97–123. In M. Pessarakli (ed.) Handbook of plant and crop stress, Second ed. Marcel Dekker, Inc. New York.
- Jalil, A., F. Selles, and J.M. Clarke. 1994a. Growth and cadmium accumulation in two durum wheat cultivars. Commun. Soil Sci. Plant Anal. 25(15 and 16):2597–2611.
- Jalil, A., F. Selles, and J.M. Clarke. 1994b. Effect of cadmium on growth and uptake of cadmium and other elements by durum wheat. J. Plant Nutr. 17(11):1839–1858.
- Janzen, H.H., and C. Chang. 1987. Cation nutrition of barley as influenced by soil solution composition in a saline soil. Can. J. Soil Sci. 67:619–629.
- Janzen, H.H., and C. Chang. 1988. Cation concentration in the saturation extract and soil solution extract of soil salinized with various sulfate salts. Commun. Soil Sci. Plant Anal. 19(4):405–430.
- Kaddah, M.T., and S.I. Ghowail. 1964. Salinity effects on the growth of corn at different stages of development. Agron. J. 56:214–217.
- Katerji, N., J.W. van Hoorn, A. Hamdy, N. Bouzid, S. El-Sayed, and M. Mastrorilli. 1992. Effects of salinity on water stress, growth and yield of broad beans. Agric. Water Manage. 21(1+2):107–117.

- Katerji, N., J.W. van Hoorn, A. Hamdy, and M. Mastrorilli. 1998. Response of tomatoes, a crop of indeterminate growth, to soil salinity. Agric. Water Manage. 38(1):59–68.
- Katerji, N., J.W. van Hoorn, A. Hamdy, M. Mastrorilli, and E. Mou Karzel. 1997. Osmotic adjustment of sugar beets in response to soil salinity and its influence on stomatal conductance, growth and yield. Agric. Water Manage. 34(1):57–69.
- Kohut, C.K., and M.J. Dudas. 1994. Comparison of immiscibly displaced soil solutions and saturated paste extracts from saline soils. Can. J. Soil Sci. 74(4):409–419.
- Lapp, M.S., and W.P. Skoropad. 1976. A mathematical model of conidial germination and appressorial formation for *Colletotrichum* graminiocola. Can. J. Bot. 54(19):2239–2242.
- Lunin, J., M.H. Gallatin, and A.R. Batchelder. 1961a. Effect of saline water on growth and chemical composition of beans: II. Influence of soil acidity. Proc. Soil Sci. Soc. Am. 55:372–376.
- Lunin, J., M.H. Gallatin, and A.R. Batchelder. 1961b. Effect of stage of growth at time of salinization on the growth and chemical composition of beans: I. Total salinization accomplished in one irrigation. Soil Sci. J. 91(3):194–202.
- Lunin, J., M.H. Gallatin, and A.R. Batchelder. 1962. Effect of stage of growth at time of salinization on the growth and chemical composition of beans: II. Salinization in one irrigation compared with gradual salinization. Soil Sci. J. 92(3):194–201.
- Lunin, J., M.H. Gallatin, and A.R. Batchelder. 1963. Saline irrigation of several vegetable crops at various growth stages. I. Effect on yields. Agron. J. 55:107–110.
- Maas, E.V. 1986. Salt Tolerance of Plants. Appl. Agric. Res. 1(1): 12–26.
- Maas, E.V. 1990. Crop salt tolerance. Chap. 13, p. 262–304. In K.K. Tanji (ed.) Agricultural salinity assessment and management. Am. Soc. Civil Engineers Manual on Engineering Practice 71. Am. Soc. Civil Engineers, New York.
- Maas, E.V., and S.R. Grattan. 1999. Crop yields as affected by salinity. Chap. 3, p. 55–108. *In* R.W. Skaggs and J. van Schilfgaarde (ed.) Agricultural drainage. Agron. Monogr. 38, ASA, Madison, WI.
- Maas, E.V., and G.J. Hoffman. 1977. Crop salt tolerance–current assessment. J. Irrigation and Drainage Div., Am. Soc. Civil Eng. 103(IR2):115–134.
- Magistad, O.C., A.D. Ayers, C.H. Wadleigh, and H.G. Gauch. 1943. Effect of salt concentration, kind of salt, and climate on plant growth in sand cultures. Plant Physiol. 18:151–166.
- Marquardt, D.W. 1963. An algorithm for least-squares estimation of nonlinear parameters. J. Soc. Industrial Appl. Math. 11:431–441.
- McKenzie, R.C. 1988. Tolerance of plants to soil salinity. Soil and Water Program, 1987. Alberta Special Crops and Horticultural Research Centre Pamphlet 88–10. Brooks, AB.
- Mor, R.P., and H.R. Manchanda. 1992. Influence of phosphorus on the tolerance of table pea to chloride and sulfate salinity in a sandy soil. Arid Land Res. Rehab. 6(1):41–52.
- Munns, R., and A. Termaat. 1986. Whole-plant responses to salinity. Aust. J. Plant Physiol. 13:143–160.
- Osawa, T. 1965. Studies on the salt tolerance of vegetable crops with special reference to mineral nutrition. Bull. Univ. Osaka Prefect. Ser. B 16:13–57.
- Palmer, A.E. 1937. Kind, position and toxicity of alkali salts in certain Alberta irrigated soils. Sci. Agric. 18(3):132–140.
- Peters, J.R. 1983. The effect of phosphate fertilizer on the salt tolerance of barley grown on summerfallow land. Can. J. Soil Sci. 63(2): 327–337.
- Ravikovitch, S., and A. Porath. 1967. The effect of nutrients on the salt tolerance of crops. Plant Soil 26(1):49–71.
- Ravikovitch, S., and D. Yoles. 1971. The influence of phosphorus and nitrogen on millet and clover growing in soils affected by salinity.I. Plant development. Plant Soil 35(3):555–567.
- Rawlings, J.O., and W.W. Cure. 1985. The Weibull function as a dose–response model to describe ozone effects on crop yields. Crop Sci. 25:807–814.
- Rhoades, J.D. 1982. Soluble salts. Chap. 10, p. 167–179. *In* Methods of soil analysis, Part 2, Chemical and microbiological properties. 2nd ed. Agron. Monogr. 9, ASA and SSSA, Madison, WI.
- SAS. 1995. JMP (Version 3.2.1). Statistical Discovery Software. SAS Institute, Inc., Cary, NC.

- Shannon, M.C., and C.M. Grieve. 1999. Tolerance of vegetable crops to salinity. Sci. Hortic. 78(1/4):5–38.
- Shannon, M.C., and C.L. Noble. 1990. Genetic approaches for developing economic salt-tolerant crops. Chap. 8, p. 161–185. *In* K.K. Tanji (ed.) Agricultural salinity assessment and management. Am. Soc. Civil Engineers Manual on Engineering Practice 71. Am. Soc. Civil Engineers, New York.
- Shannon, M.C., C.M. Grieve, and L.E. Francois. 1994. p. 199–244. In R.E. Wilkinson (ed.) Whole-plant response to salinity. Marcel Dekker, New York.
- Soo, S.L. 1962. Analytical thermodynamics. Prentice Hall, Inc., Englewood Cliffs, NJ.
- Steppuhn, H. 1993. Crop tolerances and solution parameters for modelling soil salinization. Final Report to the Research Component of the National Soil Conservation Program, Ottawa, ON.
- Steppuhn, H. 1997. Increasing plant density in spring wheat to ameliorate the effects of salinity on grain yield. Trans. ASAE 40(6):1599– 1606.
- Steppuhn, H., and K.A. Asay. 2004. Emergence, height growth, and yield of tall, NewHy, and green wheatgrass forages grown in increasingly saline root zones. Can. J. Plant Sci. (in press).
- Steppuhn, H., and K.G. Wall. 1997. Grain yields from spring-sown Canadian wheats grown in saline rooting media. Can. J. Plant Sci. 77(1):63–68.
- Steppuhn, H., and K.G. Wall. 1999. Canada's salt tolerance testing laboratory. Can. Agric. Eng. 41(3):185–189.
- Steppuhn, H., M.Th. van Genuchten, and C.M. Grieve. 2005. Rootzone salinity: II. Indices for tolerance in agricultural crops. Crop Sci. 45:221–232.
- Steppuhn, H., K.G. Wall, and B. Nybo. 1999. Improving alfalfa salinity tolerance. Wheatland Conservation Area, Assoc., Canadian Agric. & Agri-Food Matching Investment Initiative Program, Final Report, 25p.
- Steppuhn, H., K.G. Wall, and J.C. Payne. 2002. Salt tolerance evaluation of canola crops. Southern Applied Res. Assoc., Canadian Agric. & Agri-Food Matching Investment Initiative Program, Final Report, 30p.
- Steppuhn, H., K. Wall, V. Rasiah, and Y.W. Jame. 1996. Response functions for grain yield from spring-sown wheats grown in saline rooting media. Can. Agric. Eng. 38(4):249–256.
- Steppuhn, H., H. Wang, and Y. Gan. 1998. Evaluating Russian wild ryegrass emergence from saline seedbeds using the Gompertz function. Can. Agric. Eng. 40(4):241–247.
- Taylor, G.J., K.J. Stadt, and M.R.T. Dale. 1991. Modelling the phytotoxicity of aluminum, cadmium, copper, manganese, nickel, and zinc using the Weibull frequency distribution. Can. J. Bot. 69(2): 359–367.
- Tipton, J.L. 1984. Evaluation of three growth curve models for germination data analysis. J. Am. Soc. Hortic. 109(4):451–454.
- Torres-Bernal, C., and F.T. Bingham. 1973. Salt tolerance of Mexican wheat: I. Effect of NO₃ and NaCl on mineral nutrition, growth, and grain production of four wheats. Soil Sci. Soc. Am. Proc. 37: 711–715.
- Torres-Bernal, C., F.T. Bingham, and J. Oertli. 1974. Salt tolerance of Mexican wheat: II. Relation to variable sodium chloride and length of growing season. Soil Sci. Soc. Am. Proc. 38:777–780.
- Ulery, A.L., J.A. Teed, M.Th. van Genuchten, and M.C. Shannon. 1998. SALTDATA: A data base of plant yield response to salinity. Agron. J. 90:556–562.
- U.S. Salinity Laboratory Staff. 1954. Diagnosis and improvement of saline and alkali soils. U.S. Dep. Agri. Handbook 60. U.S. Gov. Printing Office, Washington, DC.
- van den Berg, C. 1950. The influence of salt in the soil on the yield of agricultural crops. Fourth International Cong., Soil Sci. Trans. 1:411–413.
- van Genuchten, M.Th. 1983. Analyzing crop salt tolerance data: Model description and user's manual. UDSA, ARS, U.S. Salinity Lab. Research Report No. 120. U.S. Gov. Printing Office, Washington, DC.
- van Genuchten, M.Th., and S.K. Gupta. 1993. A reassessment of the crop tolerance response function. J. Indian Soc. Soil Sci. 41(4):730– 737.
- van Genuchten, M.Th., and G.J. Hoffman. 1984. Analysis of crop salt tolerance data. p. 258–271. *In* I. Shainberg and J. Shalhevet (ed.)

Soil salinity under irrigation–Process and management. Ecological Studies 51. Springer-Verlag, New York.

- Van Hoorn, J.W., N. Katerji, A. Hamdy, and M. Mastrorilli. 1993. Effect of salinity on water stress, growth and yield of wheat and potatoes. Agric. Water Manag. 23(3):247–265.
- Wadleigh, C.H., and A.D. Ayers. 1945. Growth and biochemical composition of bean plants as conditioned by soil moisture tension and salt concentration. Plant Physiol. 20:106–132.
- Wang, D., J.A. Poss, T.J. Donovan, M.C. Shannon, and S.M. Lesch. 2002. Biophysical properties and biomass production of elephant grass under saline conditions. J. Arid Environ. 52(4):447–456.
- Warne, P., R.D. Guy, L. Rollins, and D.M. Reid. 1990. The effects of sodium sulphate and sodium chloride on growth, morphology,

photosynthesis, and water use efficiency of *Chenopodium rubrum*. Can. J. Bot. 68(5):999–1006.

- Weibull, W. 1951. A statistical distribution function of wide application. J. Appl. Mech. 18:293–297.
- Wu, L., and Z.-Z. Huang. 1991. Chloride and sulfate salinity effects on selenium accumulations by tall fescue. Crop Sci. 31:114–119.
- Yaron, D., H. Bielorai, J. Shalhevet, and Y. Gavish. 1972. Estimation procedures for response functions of crops to soil water content and salinity. Water Resour. Res. 8(2):291–300.
 Yeo, A.R., and T.J. Flowers. 1984. Mechanisms of salinity resistance
- Yeo, A.R., and T.J. Flowers. 1984. Mechanisms of salinity resistance in rice and their role in physiological criteria in plant breeding. Chap. 8, p. 151–187. *In* R.C. Staples and G.H. Toennissen (ed.) Salinity Tolerance in Plants, Strategies for Crop Improvement. John Wiley & Sons, New York.