BARD

FINAL REPORT

PROJECT NO. US-3065-98

**Modeling Plant Response to Deficit Irrigation with
Saline Water: Separating the Effects of Water and Salt
Stress in the Root Uptake Function**

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2003

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Cover Page**

Date of Submission of the report: March 20, 2003

BARD Project Number: US-3065-98R

Project Title: Modeling Plant Response to Deficit Irrigation with Saline Water: Separating the Effects of Water and Salt Stress in the Root Uptake Function

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Keywords *not* appearing in the title and in order of importance. Matric Potential, Osmotic Potential, Yield, Chloride, Water Uptake, Hydrochemical Model

Abbreviations commonly used in the report, in alphabetical order:

Budget: IS: \$148,000

US: \$122,000

Total: \$270,000

Signature
Principal Investigator

Signature
Authorizing Official, Principal Institution

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Publication Summary (numbers)

	Joint IS/US authorship	US Authors only	Israeli Authors only	Total
Refereed (published, in press, accepted)	2		1	3
Submitted, in review, in preparation	1		2	3
Invited review papers	1			1
Book chapters				
Books				
Master theses				
Ph.D. theses	1			1
Abstracts	1			1
Not refereed (proceedings, reports, etc.)				

Postdoctoral Training: List the names and social security/identity numbers of all postdocs who received more than 50% of their funding by the grant.

Clinton Williams

Cooperation Summary (numbers)

	From US to Israel	From Israel to US	Together, elsewhere	Total
Short Visits & Meetings	1	3	2	6
Longer Visits (Sabbaticals)				

Description of Cooperation:

Patent Summary (numbers)

	Israeli inventor (s) only	US inventor (s) only	Joint IS/US inventors	Total
Submitted				
Issued (allowed)				
Licensed				

Abstract

Standard salinity management theory, derived from blending thermodynamic and semi-empirical considerations leads to an erroneous perception regarding compensative interaction among salinity stress factors. The current approach treats matric and osmotic components of soil water potential separately and then combines their effects to compute overall response. With deficit water a severe yield decrease is expected under high salinity, yet little or no reduction is predicted for excess irrigation, irrespective of salinity level. Similarly, considerations of competition between chloride and nitrate ions have lead to compensation hypothesis and to application of excess nitrate under saline conditions. The premise of compensative interaction of growth factors behind present practices (that an increase in water application alleviates salinity stress) may result in collateral environmental damage. Over-irrigation resulting in salinization and elevated ground water threatens productivity on a global scale. Other repercussions include excessive application of nitrate to compensate for salinity, unwillingness to practice deficit irrigation with saline water, and under-utilization of marginal water.

The objectives for the project were as follows:

- 1) To develop a database for model parameterization and validation by studying yield and transpiration response to water availability, excessive salinity and salt composition.
- 2) To modify the root sink terms of an existing mechanism-based model(s) of water flow, transpiration, crop yield, salt transport, and salt chemistry.
- 3) To develop conceptual and quantitative models of ion uptake that considers the soil solution concentration and composition.
- 4) To develop a conceptual and quantitative models of effects of NaCl and boron accumulation on yield and transpiration.
- 5) To add a user interface to the water flow, transpiration, crop yield, salt transport, chemistry model to make it easy for others to use.

We conducted experiments in field plots and lysimeters to study biomass production and transpiration of corn (*Zea mays* cv. Jubilee), melon (*Cucumis melo subsp. melo* cv. Galia), tomato (*Lycopersicon esculentum* Mill. cv. 5656), onion (*Allium cepa* L. cv. HA 944), and date palms (*Phoenix Dactylifera* L. cv. Medjool) under salinity combined with water or with nitrate (growth promoters) or with boron (growth inhibitor). All factors ranged from levels not limiting to plant function to severe inhibition. For cases of combined salinity with water stress, or excess boron, we observed neither additive nor compensative effects on plant yield and transpiration. In fact, yield and transpiration at each combination of the various factors were primarily controlled by one of them, the *most limiting factor* to plant activity. We proposed a crop production model of the form $y_r = \min\{g_i(x_i)\}$, where $y_r = y_i \cdot y_m^{-1}$ is relative yield, y_m is the maximum yield obtained in each experiment, x_i is an environmental factor, g_i is a piecewise-linear response function, y_i is yield of a particular treatment. We selected a piecewise-linear approach because it highlights the irrigation level where the response to one factor ceases and a second factor begins. The production functions generate response “envelopes” containing possible yields with diagonal lines represent response to x_i alone and the lines parallel to the X-axis represent response to salinity alone. A multiplicative model was also derived approximating the limiting behaviour for incorporation in a hydrochemical model. The multiplicative model was selected because the response function was required to be continuous. The hydrochemical model was a better predictor of field-measured water content and salt profiles than models based on an additive and compensative model of crop response to salinity and water stress.

Achievements

Significance of Main Scientific Achievements or Innovations

Standard salinity management theory, derived from blending thermodynamic and semi-empirical considerations leads to an erroneous perception regarding compensative interaction among salinity stress factors. With deficit irrigation a severe yield decrease is expected under high salinity, yet little or no reduction is predicted for excess irrigation, irrespective of salinity level. Similarly, considerations of competition between chloride and nitrate ions have lead to compensation hypothesis and to application of excess nitrate under saline conditions. The premise behind present practices, that an increase in water application alleviates salinity stress, may result in environmental damage. Today, 1.4 million hectares of irrigated land in California have a water table within 1.5 meters of the surface and 1.7 million hectares are saline or sodic. The Australian National Land and Water Resources Audit has identified about 8.8 million hectares in Western Australia are at high risk of developing shallow saline water tables by the year 2050. Other repercussions include excessive application of nitrate to compensate for salinity, unwillingness to practice deficit irrigation with saline water, and under-utilization of marginal water.

Figure 1. Experimental (symbols) and computed (lines - assuming a dominant factor model) results for yield response to combined salinity and other environmental factors. A) Melon and corn response to increasing water application at two salinities. Insert shows application of compensative model. B) Response of tomatoes and date palms to B at increasing salinity levels. C) Response of corn and onion to N at various salinity levels.

We conducted experiments in field plots and lysimeters to study biomass production and transpiration of corn (*Zea mays* cv. Jubilee), melon (*Cucumis melo subsp. melo* cv. Galia), tomato (*Lycopersicon esculentum* Mill. cv. 5656), onion (*Allium cepa* L. cv. HA 944), and date

palms (*Phoenix Dactylifera* L. cv. Medjool) under salinity combined with water or with nitrate (growth promoters) or with boron (growth inhibitor). All factors ranged from levels not limiting to plant function to severe inhibition. Details of the experimental designs and protocols are given in the appendix. For cases of combined salinity with water stress, or excess boron, we observed neither additive nor compensative effects on plant yield and transpiration. In fact, yield and transpiration at each combination of the various factors were primarily controlled by one of them, the *most limiting factor* to plant activity (Fig. 1).

The response model (Fig. 1) follows the concept of the Liebig-Sprengel law:

$y_r = \min\{g_i(x_i)\}$, where $y_r = y_i \cdot y_m^{-1}$ is relative yield, y_m is the maximum yield obtained in each experiment, x_i is an environmental factor, g_i is a piecewise-linear response function, y_i is yield of a particular treatment. We selected a piecewise-linear approach because it highlights the irrigation level where response to irrigation ceases. The parameterization method generates response “envelopes” containing possible yields. The diagonal lines represent response to x_i alone and the lines parallel to the X-axis represent response to salinity alone.

The window in Fig. 1A depicts a compensative response model to water and salinity:

$y_r = 1 - \sum f_i(x_i)$ The compensative approach deviates from measured data: first, the model predicts a salinity response at low irrigation levels whereas measured data fall on the water response curve with no compounding salinity effect; and second, prediction of a continuous increase in yield with water addition in contrast to the data that attain a maximum yield determined by salinity level. The data show neither additive nor compensative effects of the two factors. Results for salinity-boron and salinity-nitrate experiments showed similar behavior. Where yield was limited by one factor, there was no yield response over a significant variation in the other factor.

The environmental ramifications of misuse of present practices can be illustrated by a simple calculation. The compensative curve in Fig. 1A indicates that melons require 1.1 meters of 9 dS m⁻¹ water are required to achieve maximum yield (the intersection of compensative curve and X-axis parallel) whereas the data show that maximum yield is achieved with application of 0.6 meters (intersection of the parallel and diagonal). Thus, producers managing according to the compensative model would increase water application by 0.5 meters and salt loading by 20,000 kg ha⁻¹ over the amount of water (and salt) required to achieve the maximum yield. Other

environmental and resource management repercussions of changing the salinity management paradigm from a compensative to a limiting factor response are also significant. Irrigation water may both be saline and contain B; however, management should consider only the limiting constituent freeing managers to use water of limited quality which would reduce the quantity of drainage water. Similarly, Fig. 1C suggests that additional nitrate does not compensate for salinity. Counter to practice, lower levels of nitrogen are required where saline water limits production; excess nitrates simply contaminate the environment.

Details of Cooperation

The PI's Dudley and Shani met twice each year to analyze data and formulate quantitative models of the observed crop responses. Both the piece-wise linear crop response model and the algorithm coded into the hydrochemical model were formulated during the meetings of the PI's. The most significant publications, the field data paper describing melon, corn and alfalfa response to water and salt stress, the computer modeling paper and the paper submitted to *Science* were joint efforts of the US and Israel. The synergism between the PI's created insights into the meaning of the data that led to new models that seriously challenge the existing view of plant response to environmental factors in combination with salinity. Collaboration was significantly enhanced in the final year of the project by having Dr. Shani's Ph.D. student, Alon Ben-Gal, post-doc with Dr. Dudley. The exchange of a student facilitated development of the "limiting concept" model and writing of the summary manuscript. Moreover, Dr. Ben-Gal's participation in the two laboratories provided new avenues for future collaboration.

List of Publications

- Shani U and Dudley M 2001 Field studies of crop response to drought and salt stress. *Soil Sci. Soc. Am. J.* 65:1522-1528.
- Ben-Gal A. and Shani U. 2002. Yield, transpiration and growth of tomatoes under combined excess boron and salinity stress. *Plant and Soil* 247: 211-221.
- Dudley, L. M., U. Shani, C. Williams, A. Ben-Gal. 2001. Modeling crop response to water, salt and specific ion toxicity. *International Union Soil Sci., Sustained Management of Irrigated Land for Salinity and Toxic Element Control*. Riverside, CA, June 25-27, 2001.

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A manuscript summarizing the significant conceptual findings of the project has been submitted to the journal *Science* as a Brevia contribution (one page article) and is the first section of this report. Following the *Science* submission, accomplishments are presented by objective.

Research activities addressed all five of the project objectives. Field lysimeters and greenhouse studies initiated in Israel and the United States, respectively, were directed toward fulfilling objectives 1, 3 and 4 and preprints and reprints of manuscripts summarizing this work are attached. A manuscript summarizing our progress under objective 2 has been submitted to the journal *Vadose Zone*; the manuscript has been returned for revision with provisional acceptance for publication. The manuscript is included in this report. Objective 5 has been accomplished and the model will be released through the Utah Agricultural Experiment Station as a report. This report is presented in paper format so each section contains a bibliography and figure and table number begin at one.

Environmental implications of changing the paradigm for salinity management

Salinity management theory, derived from thermodynamic and semi-empirical considerations (1,2) causes erroneous perception regarding additive compensative interaction among salinity stress factors. Application of this paradigm results in increased water application designed to compensate for salinity stress and is responsible, at least in part, for environmental damage such as salinization and elevation of water tables. Thirty percent of the conterminous United States has moderate to severe potential for developing salinity problems (3). Other repercussions are excessive application of nitrate to compensate for salinity, unwillingness to practice deficit irrigation with saline water, and under-utilization of marginal water. As increasing demands on water resources necessitate greater irrigation efficiency and/or use of marginal quality water, continued application of the current theory is likely to exacerbate contamination of water and soil resources with salts and their associated compounds (borate, nitrate, selenate, arsenate, etc.).

Strategies for use of marginal water in an environmentally responsible manner require quantitative understanding of system response at the field scale. Integration from sub-cellular mechanisms involving specific ions to whole-plant level response is not yet achievable. Moreover, application of sub-cellular plant response to a single environmental factor like salinity involves several concurrent operational mechanisms including osmotic effects, specific-ion interferences to plant physiology, and, through feedback mechanisms, changes in soil matrix

potential and hydraulic conductivity. Consequently, whole-plant/field-scale response approaches are applied.

The thermodynamic approach (1,2) treats matric and osmotic components of soil water potential separately and adds their effects when computing overall response, predicting an additional yield decrease under high salinity and deficit water and no yield reduction with excess irrigation, regardless of salinity. Considerations of competition between chlorides and nitrates have lead to compensation theory and to excess nitrate fertilization under saline conditions (4). In the cases of water and salinity (5), and salinity and boron (6) we observed neither additive nor compensative effects on plant yield and transpiration. In fact, only the factor most limiting to plant activity controlled yield and transpiration (Fig. 1). Herein, for the various salinity effects in combination with other environmental factors, we extend the concept of single-factor limitation to plant activity and discuss the environmental implications.

In field plots and lysimeters, we studied biomass production and transpiration of corn (*Zea mays* cv. Jubilee), melon (*Cucumis melo subsp. melo* cv. Galia), tomato (*Lycopersicon esculentum* Mill. cv. 5656), onion (*Allium cepa* L. cv. HA 944), and date palms (*Phoenix Dactylifera* L. cv. Medjool) under conditions of salinity combined with water levels or nitrate (growth promoters) or with boron (growth inhibitor). All factors ranged from levels not limiting to plant function to severe inhibition. Details of the experimental designs and protocols are given in Shani and Dudley (5), Ben-Gal and Shani (6) and Shenker et. al. (7).

The response model (Fig. 1) follows the concept of the Liebig-Sprengel law (8):

$y_r = \min\{g_i(x_i)\}$, where $y_r = y_i \cdot y_m^{-1}$, y_m is the maximum yield obtained in each experiment, x_i is an environmental factor and g_i is a piecewise-linear response function. We selected a piecewise-linear approach because it plainly shows the irrigation level where response to irrigation ceases. The parameterization method (5) generates response “envelopes” containing all possible yields. The diagonal lines represent response to x_i alone and the lines parallel to the X-axis represent response to salinity alone.

Figure 1. Experimental (symbols) and computed data assuming a dominant factor model (lines) for yield response to combined salinity and other environmental factors. A) Melon and corn response to increasing water application at two salinities. Insert shows application of additive model. B) Response of tomatoes and date palms to B at increasing salinity levels. C) Response of corn and onion to N at increasing salinity levels.

The window in Fig. 1A depicts an additive response model to water and salinity: $y_r = 1 - \sum f_i(x_i)$. The additive model differs from the measured data in two respects. First, the model predicts a salinity effect at low water levels whereas measured data fall on the water response curve with no additional salinity effect. Second, the modelled curves increase continuously with added water in contrast to the data that reach a maximum level that is a function of salinity. The data show neither additive nor compensative effects of the two factors. Environmental consequences are exposed by simple calculation. For melons irrigated with 0.5 meter of 9 dS m^{-1} , the additive model increases salt loading by $20,000 \text{ kg ha}^{-1}$ over the amount indicated by data. Results for salinity-boron and salinity-nitrate experiments showed similar behavior. Where yield was limited by one factor there was no response in terms of production over a significant variation in the other factor. Differences between crop tolerances to the various growth/stress factors are evident as well; see e.g., dates and tomato for boron (Fig 1B).

Environmental and resource management repercussions of changing the salinity management paradigm from an additive to a limiting factor response are significant. For example, Figure 1B shows that when irrigating with 2.0 dS m^{-1} , yield of date palms decreased with increasing B, but with 12 dS/m B did not affect yield. The converse is also true; at B levels found to limit yield, salinity had no influence. Irrigation water may both be saline and contain B; however, management should consider only the limiting constituent. Similarly, Fig. 1C suggests that additional nitrate does not compensate for salinity. Counter to practice, lower levels are required where saline water limits production; excess nitrates simply contaminate the environment.

- 1 Bresler, E. 1987. Application of conceptual model to irrigation water requirement and salt tolerance of crops. *Soil Sci. Soc. Am. J.* 51:788-793.
- 2 Letey, J. and A. Dinar. 1986. Simulated crop-production functions for several crops when irrigated with saline waters.. *Hilgardia* 54:1-32.
- 3 Tanji, K.K. 1990. The nature and extent of agricultural salinity problems. IN: K. K. Tanji (ed.) *Agricultural Salinity Assessment and Management*. ASCE No. 71. New York.

- 4 Kafkafi U. 1984. Plant nutrition under saline conditions. In Soil Salinity under Irrigation. I. Shainberg and J. Shalhevet Eds. Springer Verlag, Berlin, 349 p.
- 5 Shani U and Dudley M 2001 Field studies of crop response to drought and salt stress. Soil Sci. Soc. Am. J. 65:1522-1528.
- 6 Ben-Gal A. and Shani U. 2002. Yield, transpiration and growth of tomatoes under combined excess boron and salinity stress. Plant and Soil 247: 211-221.
- 7 Shenker M., Ben-Gal A., and Shani U., (2003)
- 8 van der Ploeg RR 1999 On the origin of the theory of mineral nutrition of plants and the law of the minimum Soil Sci. Soc. Am. J. 63:1055-1062.

Objective 1

A reprint of the manuscript "Field studies of crop response to drought and salt stress" is attached. The manuscript provides a more detailed description of the "envelope" response model outlined above.

Objective 2

The following is a manuscript has been submitted to the journal *Vadose Zone* and describes our results under objective 2.

Plant Response to Drought and Salt Stress: Reformulation of the Root-sink Term

L. M. Dudley¹ and U. Shani²

ABSTRACT

Because transpiration is often the largest component of the water budget in arid systems, the efficacy of computer simulation models as predictors of water and salt movement is predicated on their ability to predict transpiration. The objective of this study was to improve the root-sink term for water extraction and thus, improve predictions of transpiration. The root-sink terms often use either a transpiration apportioning, empirical function for the plant response to

the soil matrix and osmotic potential, or a potential-flow function. Three root-sink terms, a transpiration apportioning (TA) formulation, a potential-flow (PF) formulation and a combination of the two (PFTA) (a transpiration apportioning function for computing water uptake in response to salinity and a potential-flow function for computing water uptake in response to water availability) were coded into a simulation model and model predictions were compared to field-collected data. When predicted and measured relative yields ($\text{yield}/\text{yield}_{\text{max}}$) were compared the PF produced the poorest agreement with data ($y = 0.8741x + 0.0251$), the TA gave better agreement ($y = 0.9283x + 0.0476$) and PFTA provided the best agreement ($y = 0.9909x + 0.0430$). The plant and plant-soil based formulation predicted the salinity profile at the end of the field experiment under conditions of high salinity (EC irrigation water = 6.0 dS/m) and irrigation equal to potential evaporation. The plant-soil formulation was the better predictor under the same salinity condition with irrigation at 40 percent of potential evaporation. The simulated evolution of the water content and salinity profile over time was also examined.

INTRODUCTION

Competition for finite water resources will necessitate water conservation and in some cases, the use of waters of marginal quality for irrigation. Conserving water by minimizing or foregoing leaching during an irrigation season, or even over several irrigation seasons causes salt to accumulate within the root zone. Naturally, salinization of the root zone is exacerbated when waters of marginal quality are used. Moreover, some degree of deficit in irrigation, relative to potential evaporation, is required to minimize leaching. The effects of the combined stresses of deficit irrigation and salt accumulation on crop production are site specific and depend on the integration of factors such as plant variety, irrigation frequency, physical soil and chemical properties, climate, and irrigation water chemistry.

Hydrochemical models that simulate the interplay among the previously enumerated factors provide an attractive alternative to the laborious process of field-testing irrigation management schemes for optimizing water use for plant production and for protection of water and soil resources (Huston et al., 1990). Transpiration is often the dominant component of the water budget in arid and semi-arid environments and as such, has a major effect on water flow and contaminant transport under both natural and agricultural settings. Estimates of water uptake

are important to predictions of crop response, impacts of irrigated agriculture on ground and surface water quality and to extension of models to non-agricultural settings. In a review of hydrochemical modeling of physical, chemical and biological processes within the vadose zone, Huston et al. (1990) commented that plant response functions have received much less attention than other components of most hydrochemical models.

Mechanism-based, vadose-zone hydrochemical models developed for use in irrigated systems such as LEACHC (Huston and Wagenet, 1992), SOWACH (Dudley and Hanks, 1991), V-H (Cardon and Letey, 1992b) and UNSATCHEM (Simunek and Suarez, 1996) use a macroscopic approach to modeling water uptake by roots wherein a root-sink term is added to the Richard's Equation (Zhang and Elliot, 1996). According to Mmolawa and Or (2000), the macroscopic approach has the advantage of requiring simpler flow geometry and avoids problems in the microscopic formulation of scaling the simulated uptake by individual roots to root systems (see Aura, 1996 as an example of the microscopic approach). Of the models listed above, LEACHC and SOWACH use a formulation categorized as a potential-flow theory by Zhang and Elliot (1996) and V-H and UNSATCHEM uses a transpiration apportioning formulation (Zhang and Elliot, 1996). Some relative merits of the two approaches, as specifically used in the hydrochemical models listed above, were discussed by Cardon and Letey (1992a). In LEACHC and SOWACH the root-sink term is computed from the product of the soil hydraulic conductivity and the difference between the water potential in the root and the soil (Childs and Hanks, 1975). An underlying assumption of this formulation of the root-sink term is an equal and additive effect of matric and osmotic potentials on water availability as shown by the equation (Childs and Hanks, 1975)

$$S(z,t) = \frac{K(\theta) RDF(z)}{\Delta z \Delta x} [H_{root} + R_r * z - h(z,t) - \pi(z,t)] \quad [1]$$

where $S(z,t)$ is the extraction rate of water at soil depth z and time t , $RDF(z)$ is the fraction of roots at z , $K(\theta)$ is the bulk-soil hydraulic conductivity, Δx and Δz are the distance from the root to where water is extracted, H_{root} is the root water head bounded by minimum value, H_{min} (e.g.

-1500 m, (Nimah and Hanks, 1973) or -900 m (Bresler, 1987)), R_r is a root resistance term, $h(z,t)$ is the matric head, and $\pi(z,t)$ is the osmotic head.

For apportioning transpiration in response to matric and osmotic potentials within the root zone, van Genuchten (1987) proposed an S-shaped function with an initial plateau and a decreasing section that approximates the Maas-Hoffman response curve (Maas and Hoffman, 1977). The root-sink term for water uptake as a function of the matric and osmotic potentials as used in the V-H model is written

$$S(z,t) = \frac{S_{\max} \cdot RDF(z)}{1 + \left(\frac{ah(z,t)}{h_{50}} + \frac{\pi(z,t)}{\pi_{50}} \right)^p} \quad [2]$$

where $S_{\max}$ is the potential transpiration, a is a constant that accounts for a difference in plant response to osmotic and matric head, π_{50} is the osmotic head that causes a 50 percent yield loss, h_{50} is the matric potential that causes a 50 percent yield loss, and p is a constant that is usually taken as 3. UNSATCHEM uses the van Genuchten equation but separates matric and osmotic response functions as discussed below.

The two formulations of the root-sink term differ in the way water is extracted from a specific depth increment (node) and the way water is extracted from the entire soil profile. Cardon and Letey (1992a) were approximately correct in stating that Eq. [1] operates as a step function within each node. More precisely, the water extraction rate may change very quickly as the soil water potential approaches H_{min} and the hydraulic conductivity decreases. Moreover, water uptake from a node may be prohibited by low values of the matric potential, low values of the osmotic potential, or a combination of the two. Thus, the model may predict a response to relatively low salinity levels as the soil matric potential nears H_{min} . The empirical plant-based root-sink term, on the other hand, permits differentiation in the sensitivity to matric and osmotic stress through the constant a . Even though the relative effects of matric and osmotic stresses are added, the effects are independent and a crop response is not predicted until the osmotic head falls on the decreasing portion of the curve.

The extraction of water over the entire profile should also be considered in comparing the two root-sink terms. The process for obtaining the values for H_{root} in the potential-flow

formulation causes water to be taken from nodes having water potential values greater than H_{root} in order to meet potential transpiration. This simulates the plant's ability to differentially take water from the root zone according to the distribution of water, salinity and roots. For the transpiration apportioning formulation, values of the soil matric or osmotic potential that fall on the decreasing portion of the response function curve, at any node, decrease the amount of water extracted irrespective of the availability of water at other nodes. With respect to water extraction over the root zone, the potential-flow formulation better represents the behavior of the plant. Differential extraction of water within the root domain may prove to be important in the simulation of water-limited systems including non-agricultural environments.

As applied in the models SOWACH, LEACHC and V-H, both the potential-flow and transpiration-apportioning formulations assume that the effects of salt and water stress are additive. In a study of water and salt stress, Shani and Dudley (2001) found the effect of salinity on yield appeared to decrease when water availability was limited. When irrigation was nearly equal to or greater than potential evaporation, crop yield was a function of the salinity level, but at ratios of irrigation to pan evaporation less than 0.7, salinity had a negligible effect on yield. This led Shani and Dudley (2001) to hypothesize that the effects of water and salt are not equal or additive. Since both formulations assume additive matric and osmotic effects on plant transpiration and yield, neither formulation properly represents plant response to combined matric and osmotic stress over a broad range of values. Further, Shani and Dudley, (2001) suggested that at low irrigation levels, transpiration, and hence yield, might have been moisture flux limited. In this respect, the Darcy-based formulation represents the plant-soil relationship better than the crop-based formulation.

UNSATCHEM computes stress factors for the matric, f_h , and osmotic, f_π , heads separately from equations of the van Genuchten form, written (Simunek and Suarez, 1996)

$$f_h = \frac{1}{\left(\frac{h}{h_{50}}\right)^p} \text{ and } f_\pi = \frac{1}{\left(\frac{\pi}{\pi_{50}}\right)^p} \quad [3]$$

The stress factors are combined in a multiplicative approach to apportion potential water uptake

$$S = f_h f_\pi S_p \quad [4]$$

A multiplicative approach to combining stress factors was first proposed by Baule in 1918 (Paris, 1992) and has been reported to accurately represent yield response to combined plant stresses factors (Wallace, 1990).

Our objective was to reformulate the root-sink term so it better represents the soil-plant system, accounting for differential water uptake by roots and differential response to water and salt stress. So that the results of this study could be readily incorporated in an existing hydrochemical model, elements of the root-sink terms already used in the models were selected as the foundation for the reformulation. The criteria used to evaluate model predictions were agreement between measured and predicted yields and salinity profiles, and the ability of the model to predict a differential response to the matric and osmotic potentials. Predictions of SOWATSAL (Hanks and Cui, 1990) with three different formulations of the root-sink term are compared to data from field studies of crop yields under conditions of salt and moisture stress. The effects of the three root-sink formulations on predictions of salt and water distribution in the profile are also presented.

THEORY

The rational in reformatting the root-sink term is described in the following two paragraphs. As written, Eq. [1] uses the difference in water potential between the soil adjacent to the root (usually taken as 1 cm) and some point across the root membrane, pairing this gradient with the soil hydraulic conductivity. Abdul-Jabbar et al. (1983) found that the greatest resistance to flow changes from the root membrane to the soil at some critical water content which would be a function of soil and plant properties. To be correctly parameterized over the range of water contents that would be encountered under conditions of water stress such as deficit irrigation, Eq. [1] should use the root membrane conductivity and the water potential gradient between the root and the soil adjacent to the root at high water content then switch to the soil hydraulic conductivity and the difference matric potential between the soil adjacent to the root and the bulk soil at some critical water content. Such a formulation would introduce an undesirable level of complexity, particularly in terms of defining a limiting root resistance for a variety of plants. A straightforward solution is to remove the osmotic head from Eq. [1] and use, as a set of parameters for Eq. [1], the soil hydraulic conductivity and the matric head gradient near the root.

Such a parameterization may over-predict water uptake in the upper range of water contents, but accuracy would improve as the soil water content decreases and water stress increases.

Removing the osmotic potential from Eq. [1] permits reintroduction of the osmotic effect in a multiplicative model. Relative to an additive model, the multiplicative approach should better reproduce the “putative increase in salt tolerance under conditions of limited irrigation” reported by Shani and Dudley (2001) in a field study of the response of alfalfa, melons and corn to irrigation and salinity. For example, if limited irrigation results in an f_m value of 0.9 and the salt level results in an f_π value of 0.9 then transpiration would be 81 percent of potential or a decrease of about 10 percent per factor. These relative differences might be observable in field data. If, under the same salinity, the irrigation is severely limited such that f_m is 0.5 then transpiration would be 45 percent of potential and the effect of salinity might not be observable given the variability commonly encountered in field data. If plant response to irrigation and salinity was additive, a 10 percent decrement in transpiration resulting from osmotic stress might be observable over large range of irrigation levels. Thus, the transpiration partitioning approach of Simunek and Suarez (1993) was used as a basis for computing osmotic effects on water uptake.

So that the effects of different formulations of the root-sink terms on model predictions could be fairly compared, three options for the root-sink term were coded into the model SOWATSAL (Hanks and Cui, 1990). The three options for the root-sink term will be referenced as follows: Eq. [1] = **PF** (potential flow), Eq. [2] = **TA** (transpiration apportioning), and **PFTA** (combined potential flow and transpiration apportioning) described below. SOWATSAL is based on one-dimensional, second order, Crank-Nicholson numeric approximations to the Richard's equation (with a root extraction term) and the equation of continuity for transport of a conservative solute. Details regarding the mathematical development of the model are given by Hanks et al., (1969), Nimah and Hanks, (1973), Childs and Hanks, (1975), and Hanks and Cui, (1990) and a field test of the model was reported by Dudley et al., (1981).

For the **PFTA** formulation, the values of H_{root} at each time step and for each node and f_π at each time step were computed through a simple, iterative algorithm. In the algorithm, transpiration was first reduced, if necessary, for osmotic stress and then a potential-flow equation

$$f_\pi^1 = \sum_i \frac{RDF(z,t)}{1 + \left(\frac{\pi(z,t)}{\pi_{en}} \right)^p} \quad [5]$$

computed uptake of water from the root zone. At the first iteration, a stress factor for the effect of salinity, f_π , was computed by weighting the relative effect of salinity on uptake from each node by the fraction of roots within the node:

In turn, potential transpiration, T_p , was reduced by the salinity-scaling factor

$$T_{\max} = T_p \cdot f_\pi \quad [6]$$

where $T_{\max}$ is the maximum transpiration used to compute the root-sink term from the matric head through the potential-flow function,

$$S(z,t) = \frac{K[\theta(z,t)]RDF(z,t)}{\Delta x \Delta z} [H_{root}(t) + R_r * z - h(z,t)] \quad [7a]$$

subject to the constraints

$$T_{\max} \geq \sum_z S(z,t) \text{ and } H_{root} \geq H_{\min} \quad [7b]$$

The value of H_{root} that makes $S(z,t) = T_{\max}$ is obtained by rearranging Eq. [5a] such that,

$$H_{root}(t) = \frac{\sum_z K(z,t)RDF(z,t)[R_r * z - h(z,t)]}{\sum_z K(z,t)RDF(z,t)} \quad [7c]$$

If a value of H_{root} that is less than $H_{\min}$ is computed from Eq. [7c] then H_{root} is set to $H_{\min}$ and water can only be extracted from nodes with matric potentials greater than $H_{\min}$. After the first iteration, the salinity response function was recomputed by weighting to the relative uptake from each node

$$f_\pi^n = \sum_z \left(\frac{1}{1 + \left(\frac{\pi(z,t)}{\pi_{50}} \right)^p} \right) \cdot \frac{S(z,t)}{T_{\max}} \quad [8]$$

A new estimate of T_{max} was obtained from Eq. [6] and the value of $S(z,t)$ was recomputed. The loop, Eqs. [6], [7c] and [8], was executed until a stable value of T_{max} was obtained. During the modeling exercises described below, a limit of 25 iterations was set on the loop, but a stable value of T_{max} was always achieved in less than 25 iterations.

Relative yield (Y_r) at the end of the simulation was assumed to be equal to relative accumulated transpiration (T_r) (Letey and Dinar 1986; Shani and Dudley, 2001):

$$Y_r = \frac{Y}{Y_{max}} = T_r = \frac{\sum_t \sum_z S(z,t)}{\sum_t T_p(t)} \quad [7]$$

where Y is the yield and Y_{max} is the maximum yield.

MATERIALS AND METHODS

The details of the field experiments in which melon yields (*Cucumis melo subsp. melo* cv. Galia) were determined under conditions of variable irrigation and salinity were given by Shani et al. (1987) and Shani and Dudley (2001) and will only be briefly recounted here. The study was conducted at the Arava Research and Development Farm in Yotvata, Israel. The Arava sandy loam soil is a Typic Torrifluent and the chemical and physical properties were reported by Shani et al. (1987). Irrigation water was applied through drippers placed under a polyethylene sheet to eliminate evaporation and seedlings were planted through holes in the cover. The drippers were installed 0.33 m apart to promote one-dimensional water flow (Shani and Dudley, 2001). The treatments were combinations of irrigation levels (expressed as a ratio of irrigation, " I ", to pan evaporation, " E_0 ") and salinity. The melons were irrigated at I/E_0 levels of 0.2, 0.4, 0.7, 1.0, 1.3, and 1.7 with waters that had EC values of 1.2, 3.0, 6.0, and 9.0 dS/m. The EC values correspond to one level below the Mass-Hoffman threshold value (a control) and three levels above the threshold for salt tolerance (Maas, 1990). The melon fruit and canopy were harvested 1.5 m from the plot margins 57 days after planting (DAP). The plots were pre-leached with the 1.2 dS/m water to establish a constant salinity profile and the study was initiated when the root zone was at field capacity ($\theta_v = 0.18$).

With the exception of the crop response parameters, h_{50} , π_{50} and $Hmin$, the same set of model parameters, boundary and initial conditions were used in all simulations. In addition to the initial soil water content and salinity profile, and characteristic curve, a number of parameters relating to water flow and crop development are required. For all simulations the root zone was divided into 12 nodes of 0.05 m. A daily average of the pan-estimated potential evaporation adjusted by a crop coefficient (taken from an extension service recommendation for the region) was used as potential transpiration in specifying surface boundary condition unless irrigation was simulated, in which case, the irrigation rate was the surface boundary condition. The boundary condition at the bottom of the root zone for moisture flow was a constant gradient and for solute transport the bottom boundary condition was constant concentration. The parameters related to crop

cover and root development were: crop cover at maturity = 100 percent, days to full crop cover = 41 DAP, time to mature root development = 41 DAP. Details regarding the model input parameters may be obtained from the users' manual (Hanks and Cui, 1990). The duration of all simulations was 1152 hours.

The three models required estimates of some combination of the crop response function parameters: $Hmin$, π_{50} and h_{50} . Childs and Hanks (1975) suggest a value of -1500 m for $Hmin$, which was taken as an initial estimate. However, comparison of predicted and measured yield indicated that -1500 m provided a poor estimate of the available water and that most of the available water was held at much higher values of the matric potential. An "optimal" value of $Hmin$ was obtained by trial-and-error to fit yield data. The value for π_{50} was estimated by solving the Maas-Hoffman equation with slope = 10 and threshold EC = 2.5 dS/m (Maas, 1990) for $Y_r = 0.5$ and multiplying by -36 (Richards, 1954) to obtain -450 m. As an initial estimate, h_{50} was assumed to be equal to π_{50} (van Genuchten, 1987). Because crops are more sensitive to the matric potential than the osmotic potential (Meiri, 1984), the value of h_{50} was also fine tuned by trial-and-error fitting to the data.

RESULTS AND DISCUSSION

Yield Predictions

When $Hmin$ was -1500 m, **PF** overpredicted yields at the lowest two irrigation levels. Increasing $Hmin$ to -600 m produced the best overall fit to the measured values of Y_r (Fig. [1]), but over predicted the data from the control. Further increasing $Hmin$ to -150 m resulted in better agreement for the control but under prediction of Y_r for the salinity treatments. At EC = 9.0 dS/m, **PF** predicted little growth at any irrigation level. Failure of **PF** to predict Y_r for both the control and salinity treatments over the irrigation levels using a single value of $Hmin$ as a threshold for the responses to both the soil matric and osmotic potential suggests that the assumption of an equal and additive plant response to osmotic and matric potentials may be invalid. The use of a single parameter for estimating the plant response to the two potentials also resulted in hyper-sensitivity of the root-sink term to values of $Hmin$.

The **TA** root-sink term overestimated yield at the lowest irrigation level (Figure [2a]), but the agreement between measured and predicted relative yields were better at the higher irrigation levels for the simulations in which it was assumed the $h_{50} = \pi_{50} = -450$ m. Agreement between predicted and measured relative yield at the higher irrigation levels may be due, at least in part, to the calibration of π_{50} to salt tolerance data. In contrast, the value of h_{50} is estimated without benefit of similar matric potential response data. Increasing h_{50} to -150 m slightly improved the agreement between measured and predicted relative yield at the lowest irrigation level, but caused the model to under predict relative yield at the other irrigation levels (Figure [2b]). Under prediction of Y_r at irrigation levels > 0.2 may result from the inability of the transpiration apportioning formulation of the root-sink term to compensate for nodes with limited water by extracting water from nodes where it is available. If $S < S_{max}$ at any node, then $T < T_p$ for the time step.

Comparing **TA** and **PF**, **PF** was the best predictor of Y_r values at the lowest irrigation treatments and the **TA** was the best predictor at the highest irrigation treatments. This result might be expected because the critical response parameter, H_{min} , was selected based on crop response to water stress and π_{50} (from which h_{50} was initially obtained) was obtained from the melon response to salt stress.

Because **PF** produced the best agreement to the control when the H_{min} value was -150 m and **TA** when π_{50} was -450 m, these values were used in executing **PFTA**. These values produced agreement between predicted and measured relative yields over all irrigation levels (Fig. [3]). The agreement between measured and predicted Y_r values was better for **PFTA** than that obtained for **TA** when -450 m was used for h_{50} and π_{50} in **TA** and better than the agreement obtained with **PF** (Fig. [4]). In addition to overall fit, **PFTA** reproduced a decrease in the effect of salinity with decreasing water availability, a trend observed by Shani and Dudley (2001). At approximately $I/E_0 < 0.7$ the response of melon dry matter and fruit yield were independent of the salinity treatment (Shani and Dudley, 2001). Response curves generated by **TA** and **PF**, in which effects of matric and osmotic stress are additive, diverge near the origin in Figs. [1] and [2], counter to the findings of Shani and Dudley (2001). Response curves generated by **PFTA**, with the

multiplicative relationship between osmotic and matric stress, reproduced the coalescence of the data at low irrigation treatments.

Predicted Water Contents and Salt Profiles

While it might be argued that the difference in predictions of relative yield among the models is not large, the three formulations predicted differences in the evolution of the water content profile and marked differences in predicted salt profiles. The two treatments shown in the Figs. [5] through [9], $E_0/I = 1.0 + EC = 6.0$ dS/m and $E/I_0 = 0.4 + EC = 6.0$ dS/m illustrate differences in the response to salinity and to deficit irrigation, respectively. Figure [5a] shows greater values of the water content throughout the profile than Figs. [5b] and [5c] that are similar. The similarity in water content profile through time shown in Figs. [5b] and [5c] was expected at high irrigation levels because the dominant stress is salinity and **TA** and **PFTA** use a similar function to compute salinity response. The difference between the water content profile through time simulated by **PF** and the other two formulations was due to the use of the water potential in computing the threshold for water uptake. The soil water potential was often less than H_{min} preventing any water extraction from node(s) resulting in higher water contents throughout the profile.

The differences in water content are reflected in the salinity profiles (Fig. [6]). Significantly less salt was retained in the **PF**-simulated soil profile (Fig. [6a]) than in the **P** and **PFTA**-simulated profiles (Figs. [6b] and [6c]). More salt was retained in the **PFTA**-simulated profile than in the **P**-simulated profile indicating that more water was taken in the **PFTA** simulation. The **PFTA** formulation predicts greater salt and water stress tolerance than the additive formulation used in **PF** and **TA**. Adding a water stress component to the simulation further emphasizes the differences in the three formulations (Figs. [7] and [8]). Predicted water contents and salt leaching after 600 hours were greatest for the **PF**-simulated profiles. Water contents at the three depth and over time were similar for **TA** and **PFTA** simulations (Figs. [7b] and [7c]), but the salinity profiles were markedly different (Figs. [8b] and [8c]) in that more salt was retained in the upper 0.3 m of the profile in the **PFTA** simulation. This reflects increase water use under conditions of both water and salt stress.

The greatest differences among the simulations were observed in the salt profiles. Thus, predicted salt profiles at the end of the simulation were compared to values measured after harvest. Because **TA** and **PFTA** provided better predictions of yield than **PF**, only the results of **TA** and **PFTA** simulations are shown in Fig. [9]. Both **TA** and **PFTA** produced acceptable predictions of salt profiles when I/E_0 was 1.0 (Fig [9a]). Below 0.2 m when $I/E_0 = 0.4$ (Fig. [9b]), **TA** failed to reproduce the salinity profile indicating that **PFTA** better represents plant response to combined water and salt stress and the plant's ability to adjust uptake according to the distribution of available water, salt and root density.

CONCLUSIONS

Shalhevet and Hsiao (1986) questioned cause and effect in yield response to simultaneously imposed salt and water stress; does salinity decrease transpiration that, in turn, decreases yield, or does salinity decrease yield decreasing transpiration? The **PFTA** model reduces the maximum transpiration, and hence, maximum yield in response to salinity (Eq. [4]). Transpiration is subsequently computed from the values of the matric potential and hydraulic conductivity through the root-zone. In the other formulations (Eqs. [1] and [2]), both the osmotic and matric potentials determine transpiration, in turn, determining Y_r . While not providing a mechanistic answer to the cause and effect question, the results shown in Fig. [4] are suggestive.

Hydrochemical models have been suggested to be efficient tools for evaluating irrigation management schemes that maintain crop yields and minimize deleterious effects of irrigated agriculture on water resources and soil resources. In arid systems, computation of transpiration is critical to prediction of the water budget that, in turn, strongly affects salt transport. The **PFTA** formulation gave significantly different predictions of salt dynamics in the profile and the final salt profile was in better agreement with the measured values than the **TA** formulation. Reformulation of the root-sink term along the lines of **PFTA** appears warranted.

ACKNOWLEDGEMENTS

This research was supported by Research Grant Award No. US-3065-98R from BARD, the United States – Israel Binational Agricultural Research and Development Fund and the Utah Agricultural Experiment Station is gratefully acknowledged.

Figure 1. Measured and predicted yield by the soil-based model using $H_{min} = -600$ m.

Figure 2. Measured and plant-based model predicted relative yield using $h_{50} = \pi_{50} = -450$ m (a) and $h_{50} = -150$ m and $\pi_{50} = -450$ m (b).

Figure 3. Measured and plant-soil based model predicted relative yield using $H_{min} = -150$ m and $\pi_{50} = -450$ m.

Figure 4. Measured and predicted relative yield pairs are compared to a 1:1 line for all treatments. The regression equation for the three models were as follows: soil-based model $y = 0.8741x + 0.0251$, plant-based model $y = 0.9283x + 0.0476$ and plant-soil based model $y = 0.9909x + 0.0430$.

a

b

c

Figure 5. The predicted evolution of the water content at three locations in the profile for the soil-based model (a), the plant-based model (b) and the plant-soil based model (c) for irrigation equal to pan evaporation and an irrigation water salinity of 6.0 dS/m.

a

b

c

Figure 6. The predicted evolution of the salt content (a non-interactive tracer) at three locations in the profile for the soil-based model (a), the plant-based model (b) and the plant-soil based model (c) for irrigation equal to pan evaporation and an irrigation water salinity of 6.0 dS/m.

a

Figure 7. The predicted evolution of the water content at three locations in the profile for the soil-based model (a), the plant-based model (b) and the plant-soil based model (c) for irrigation equal to 40 percent of pan evaporation and an irrigation water salinity of 6.0 dS/m.

a

b

Figure 8. The predicted evolution of the salt content (a non-interactive tracer) at three locations in the profile for the soil-based model (a), the plant-based model (b) and the plant-soil based model (c) for irrigation equal to 40 percent of pan evaporation and an irrigation water salinity of 6.0 dS/m.

Figure 9. A comparison of the predicted and measured salt profile at melon harvest for the 6.0 dS/m salinity treatments with irrigation equal to pan evaporation (a) and 40 percent of pan evaporation (b). The cross symbol for the measured data is positioned at the mean and the width of the cross indicates the standard deviation.

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Objective 3

Studies of uptake and yield response of tomatoes and bean studies to Na, Cl and salinity were conducted in greenhouse lysimeters. The treatments for the studies based on the Maas-Hoffman threshold response to salinity with three SAR levels as shown in Table 1. In addition to the salts for each treatment (CaCl_2 and NaCl) the solution contained 1/8 Hogland's. Greenhouse space limited each experiment to twenty four pots. Each treatment was duplicated and experiments were twice for each crop. Lysimeters were weighed twice each week and solution was added to compensate for transpiration and the weight loss was recorded. The electrical conductivity and Ca, Na, Cl and Hogland's components were measured in a solution sample collected twice each week. Based on the analysis, the concentrations of Ca, Na and Cl were adjusted each week to maintain approximately constant conditions. All seeds were germinated in the nutrient solution and treatments were imposed after germination.

Table 1. Target electrical conductivity for crops grown in hydroponics solutions.

	Crop	
	Tomato	Bean
50% EC [†] Threshold [‡]	1.1	0.5
Threshold EC	2.2	1.0
50% Yield Reduction [‡] EC	7.6	3.6
75% Yield Reduction EC	9.8	4.9

[†]All solutions were made with sodium adsorption ratios of 2, 4, and 8 such that there was a total of 12 different solutions per crop.

[‡]Threshold and yield reduction EC values taken from Mass-Hoffman values.

Beans were harvested about 50 days after imposing treatments and tomatoes were harvested about 60 days after imposing treatments. Wet and dry matter production for roots, shoots, leaves, and in the case of tomatoes, fruit were determined. Plant tissues were digested with $\text{HNO}_3\text{-H}_2\text{O}_2$ for determination of tissue Ca, Mg, Na, K and S by inductively coupled plasma spectrophotometry. Tissue Cl was extracted with hot water

and determined by an ion-selective electrode.

The results failed to show any clear trends with respect to yield and measured quantities such as solution concentrations or thermodynamic activity. Yields were also not related to tissue contents of Na or Cl. Examples data for the tomato experiments are shown in Figures 1 and 2. Solution concentrations are given as time average values computed from an average of the measured concentration at the beginning and end of each addition of solution to the hydroponic containers.

Figure 1. A plot of the relative yield (yield/maximum yield) as a function of the time average EC (a), Na (b) and Cl (c) in hydroponic experiments. The regression line and the regression equation are shown on the figure.

Figure 2. The relative yield (yield/maximum yield) as a function of the tissue Na (a) and Cl (b) in hydroponic experiments. The regression line and the regression equation are shown on the figure.

Plant tissue levels of Na and Cl were poorly correlated with the time average solution concentration of the elements as shown in Figure 3.

Figure 3. Plant tissue contents of Na (a) and Cl(b) as functions of the time average solution concentrations. The regression line and the regression equation are shown on the figure.

One interesting result was obtained from the data. A "reflection coefficient" was

computed from the ratio of product of the measured tissue concentration of each ion and the dry matter, and the product of the time average solution concentration and transpiration. The “reflection coefficient”, R , was a mass ratio:

$$R = \frac{C_s^i * T}{C_p^i * Y} \quad [1]$$

where C is the concentration of ion i in the solution (mg/L), s , or the plant (mg/kg), p , T is total transpiration (L) and Y is the dry matter yield (kg).

The reflection coefficient decreased exponentially with the mass of solute that could have been taken up by the plant by mass flow (Figure 4). This suggests that ion exclusion by the plants was an active process and that exclusion increased exponentially with the amount of ion in the solution and transpiration. Modeling solute uptake requires an adjustable exclusion parameter complicating the situation. Plant response models aimed at irrigation management under conditions of salinity and other environmental stress might be better accomplished by macroscopic approaches such as the one developed under objective 2.

Figure 4. Reflection coefficients for Na (a), Cl (b) and Ca (c) as a function of the amount of solute that would have been take up by mass flow.

Similar calculations were performed for other data sets including the field data

reported under objects 1 and 4 and similar trends were observed. Moreover, the reflection coefficients were linearly correlated with one another. Further data analysis with respect to our reflection coefficient is planned to determine if any generalities may be extracted.

Objective 4

Reprints of the tomato response to boron and salinity manuscript from *Plant and Soil* are attached. A manuscript summarizing studies on boron and water stress has been submitted to *Plant and Soil* and the preprint follows.

WATER USE AND YIELD OF TOMATOES UNDER LIMITED WATER AND EXCESS BORON

Alon Ben-Gal^{*} and Uri Shani

Key words: boron, combined stress, drought, tomato, toxicity, yield response.

Abstract

Boron is essential to growth at low concentrations and limits growth and yield when in excess. Little is known about plant response to excess boron (B) and water stress occurring simultaneously. The influences of B and water supply on tomatoes (*Lycopersicon esculentum* Mill.) were investigated in lysimeters. Water application levels were 30, 60, 100, 130 and 160% of potential evapotranspiration. Boron levels in irrigation water were 0.02, 0.37, and 0.74 mol m⁻³. Conditions of excess boron and of water deficits were found to decrease yield and transpiration of tomatoes. Simultaneous B and drought stresses did not result in a larger effect but rather, one or the other stress-causing factor was found to be dominant in plant response. Both irrigation water quantity and boron concentration influenced water use of the plants in the same manner as they influenced yield. A dominant-stress-factor model following the Liebig-Sprengel law of the minimum was assumed and validated. The model applies the principle that, when a plant is submitted to conditions of stress caused by B in conjunction with water and/or salinity stress, the most severe stress determines yield.

Introduction

Until recently it was claimed that the range between concentrations of boron essential for growth and concentrations leading to toxicity is extremely narrow (Eaton, 1944; Gupta et al., 1985). Of late, this classification is questioned (Blamey et al., 1997; Chapman et al., 1997) but nonetheless, boron is essential for all plants at certain low concentrations and becomes toxic for many plants at concentrations which can be found in natural and agricultural situations (El-Motaium et al., 1994; Keren and Bingham, 1985; Maas, 1990; Tsadalis, 1997). Boron is often found in high concentrations in association with agriculture in arid regions where saline soils and saline irrigation water can be prevalent. Municipal and other wastewater effluents used for irrigation are also sources of excess boron in agricultural systems (Tsadilis, 1997).

Yields reportedly are reduced in tomatoes as well as in other plant species as concentrations of boron in plant matter are increased (Eaton, 1944; Francois, 1984). In sensitive crops, toxic responses have been exhibited in field conditions when plant tissue B approaches levels even under $200 \mu\text{g g}^{-1}$ (Gupta et al., 1985). Most studies of B tolerance for crops are based on incidence of B injury and not on decline in yields. Works by Francois (1984) and by Bingham et al. (1985) using sand culture are exceptions to this. Francois' study on the effect of excess B on tomato found a piecewise linear decrease in yield with a threshold level of 0.53 mol m^{-3} B in soil solution and a relative yield reduction of 3.4% with each additional 0.1 mol m^{-3} increase in soil solution B. Francois (1984) found that visual symptoms of B toxicity appeared at soil concentrations lower than the yield threshold values. Bingham et al. (1985) successfully tested the Maas-Hoffman (Maas and Hoffman, 1977) model of salinity tolerance for boron toxicity and found threshold values and relative grain yield decrease in relation to B concentration in nutrient solution for wheat, barley and sorghum. Bingham et al. (1985) did not find an association between salinity tolerance and boron tolerance but did find relationships between increased leaf B concentration and decreased grain yield.

Little research has investigated interactive effects of boron toxicity with water stress. Shani (Shani and Hanks, 1993; Shani et al., 1992) reported that B affects yield but does not significantly reduce transpiration in plants whereas the consequences of drought and salinity are directly seen in reduced transpiration. Shani and Hanks (1993) modeled

boron toxicity, salinity, and drought stress based on independent multiplicative effects but warned that their range of experimental crops and stress factor levels did not provide sufficient data for large generalizations.

Influences of B and salinity on tomatoes were investigated by Ben-Gal and Shani (2002b). Yield and transpiration of tomatoes decreased with excess boron but response to B was inhibited when plants were exposed to simultaneous B and salinity stress. Ben-Gal and Shani present a dominant-stress-factor model based on the Liebig-Sprengel law of the minimum (Black 1993, Browne 1942), applying the principle that when a plant is submitted to conditions of stress caused by B in conjunction with salinity, the more severe stress determines yield. A dominant stress response was also found regarding drought stress and salinity stress for corn, melon and alfalfa (Shani and Dudley 2001).

The dominant factor concept for water, salinity and boron as stress causing factors can be described as follows:

$$Y = \min \begin{cases} f_1(I/T_p) \\ f_2(EC) \\ f_3(B) \end{cases} \quad [1]$$

Where Y is yield, I is irrigation quantity, T_p is potential transpiration, EC is salinity and B is boron concentration in soil solution.

The objective of this study was to investigate response of yield and transpiration of tomatoes to stress caused by combined boron concentrations and water quantities and to evaluate the nature of the response.

Materials and Methods

Experiments were conducted in lysimeters situated at The “Arava” Research Station in the Southern Arava Valley in Israel (29° 53' N, 53° 3' E). Freestanding two hundred liter lysimeters were filled with Arava Sandy Loam soil from the plow horizon of an adjacent agricultural field. Shani et al. (1987) gives detailed properties of the soil. The lysimeters had automatic systems for preparation and delivery of irrigation water and for collection and measurement of drainage water. The lysimeters incorporated highly conductive rockwool drainage apparatus to control water head at the lower soil boundary (lysimeter bottom). A detailed description of the lysimeter system is given in Ben-Gal and Shani (2002a). Effects of excess boron and water supply were investigated over two

seasons representing different climatic evaporation demands (fall and spring). Details of climatic conditions, growth and transpiration response for the two seasons are given by Ben-Gal et al. (2002). The fall growing season, lasting from September 23 to January 06, was characterized by initial days with high temperatures of greater than 40°C and potential evapotranspiration (ET_p) rates of greater than 10 mm day⁻¹ developing into cooler days with high temperatures of around 20°C and ET_p rates of 3-4 mm day⁻¹. The spring growing period, from March 1 until June 10, was at the outset characterized by days with high temperatures of 25°C and ET_p of 4-5 mm increasing over time to daily highs of greater than 40°C and ET_p of 12 mm.

After leaching and allowing the lysimeters to drain to field capacity, tomatoes (*Lycopersicon esculentum* Mill. Cv “5656”, determinate growth) were planted as seedlings and irrigated initially for 4 days using identical water quantities. Two seedlings were planted in each lysimeter and thinned to one plant after ten days. Treatments began four days after planting. Sawdust mulch was applied to the soil surface to reduce evaporative losses to a minimum. Tomatoes were irrigated and fertilizer was applied through the irrigation water at levels used in local commercial cultivation. Tomatoes were irrigated with varied amounts of water with electrical conductivity (EC) of 3 dS·m⁻¹ (local commercial irrigation water) containing boron as boric acid at concentrations of 0.027 mol·m⁻³, 0.37 mol·m⁻³ and 0.74 mol·m⁻³ B. Target irrigation levels included the following fractions of potential transpiration (T_p): 0.3 · T_p (I - 0.3), 0.6 · T_p (I - 0.6), 1.0 · T_p (I - 1.0), 1.3 · T_p (I - 1.3) and 1.6 · T_p (I - 1.6). Control treatments of low B (0.027 mol·m⁻³), low EC (0.5 dS·m⁻¹) and high irrigation level (130%) and lysimeters receiving zero added water after planting were included in each of the two seasons. Daily water balance generated transpiration (T) data for each lysimeter (plant). Transpiration was calculated using: $T = I - Dr + \Delta \theta \cdot Z$, where I is irrigation, Dr is drainage, $\Delta \theta$ is change in soil water determined from tensiometer readings and changes in lysimeter weight, and Z is soil depth. T_p was determined using water balance data from plants in the experiment where 100% corresponded to the maximum T level (T_{max}) found on a daily basis from the lysimeters. A correction for evaporative loss was calculated for lysimeters where plants did not provide full surface coverage. Drainage quantity and EC were measured daily. Drainage water B content, Cl, Na, and Ca concentrations were analyzed weekly. Boron

concentration in the drainage water of the last four weeks was used for assessment of plant response.

Fruit was harvested as it ripened. Plants were harvested and fresh and dry yields were measured for fruit, leaves and stems after 94 days in the spring and 104 days in the fall. Dry plant material was analyzed for B, Cl, Na, Ca and K content. Soil samples were taken from each lysimeter during the eighth week and immediately prior to the end of the experiment. Boron in soil and plant matter extracts and in water samples was determined by the azomethine-H method (Page et al., 1982). Analysis of ions of soluble salts including Na, Ca, Mg, and Cl were accomplished by atomic absorption spectrometry and titration methods (Page et al., 1982). Soil solution B concentration in the actual water content was determined as in Shani et al. (1992) using saturation B concentrations determined in the laboratory and solving:

$$C(\theta) = \frac{((BB^2 - 4AA \cdot CC)^{0.5} - BB)}{2AA}$$

$$AA = \theta \cdot K$$

$$BB = C(\theta_s) \cdot \theta_s \cdot K - S \cdot K + \theta + K \cdot M \cdot \rho_b$$

$$CC = S - C(\theta_s) \cdot \theta_s$$
[2]

$$S = \frac{M \cdot K \cdot C(\theta_s)}{1 + K \cdot C(\theta_s)}$$

where $C(\theta)$ stands for soil solution B, θ ($\text{m}^3 \cdot \text{m}^{-3}$) is volumetric water content and θ_s ($\text{m}^3 \cdot \text{m}^{-3}$) is saturated volumetric water content. M ($\text{mol} \cdot \text{kg}^{-1}$) and K ($\text{L} \cdot \text{mol}^{-1}$) are empirical constants from the Langmuir equation where S is concentration in the adsorbed phase and C concentration in the solution. The B adsorption isotherm for the relevant soil is found in Ben-Gal and Shani (2002b), giving Langmuir constants $M=3.26 \cdot 10^{-3} \text{ mol} \cdot \text{kg}^{-1}$ and $K=0.215 \text{ mol} \cdot \text{kg}^{-1}$.

Linear switching regression models (Ben-Gal and Shani 2002b, Shani and Dudley 2001) have been used to describe the relationship between yield and stress factors. Specific equations for B, EC and normalized I were introduced into Equation 1 as follows:

$$Y_r = \min \begin{cases} \begin{cases} Y_m & ; B \leq B_{cr} \\ Y_m - a(B - B_{cr}) & ; B > B_{cr} \end{cases} \\ \begin{cases} Y_m & ; EC \leq EC_{cr} \\ Y_m - g(EC - EC_{cr}) & ; EC > EC_{cr} \end{cases} \\ \begin{cases} Y_m & ; I/T_p > I_c \\ b \cdot I/T_p & ; I/T_p \leq I_c \end{cases} \end{cases} \quad [3]$$

where EC_{cr} and B_{cr} are salinity and B threshold levels below which B or salinity does not affect yield and I_c is threshold irrigation above which additional water does not increase yield. Estimated maximum relative yield, Y_m , is defined for the case in which neither water, boron nor salinity limit plant growth. a , b and g are slopes of the relevant response curves. The parameters Y_m , b , a , g , EC_{cr} , B_{cr} and I_c are all plant specific. Parameters in Equation 3 were estimated using the Ordinary Least Square model (Quantitative Micro Software 1997). A Wald test (Kennedy 1992, Quantitative Micro Software 1997) was performed for the null hypotheses that Y_r of the various water treatments was equal. The same test was conducted on the parameters a and b . A value of $\alpha = 0.05$ was used for statistical significance. The data sets for parameterization regarding salinity g and EC_{cr} were taken from Ben-Gal and Shani (2002b).

Results and Discussion

While maximum transpiration, and therefore irrigation amounts, in the spring were 1.3-1.4 times greater than in the fall, leaf and stem biomass were nearly equivalent and total biomass in the spring was some 50% of that of the fall due to very low fruit production (Table 1). Obvious reductions in vegetative growth and fruit production occurred when reduced irrigation water content led to water stress. Over both seasons plants provided with approximately 30% of T_p produced some 35% total biomass as compared to unstressed plants. Plants given 60% of T_p produced approximately 55% of potential yield and plants provided 100% of T_p produced around 80% of the highest yields. Maximum yields were found when plants were provided 130 and 160% of T_p . The same relative reduction in yield as a function of water stress was found for leaf, stem and fruit biomass as was found for total biomass. In the fall season, the B-0.027 and B-0.37 treatments had equivalent results and the B-0.74 treatments produced reduced biomass. This reduction for B-0.74 treatments was repeated in the spring for the

treatments receiving greater than I-1.0 water quantities.

No differences in Cl, Ca, K, or Na content in leaves were found between the two seasons (Table 2). Chloride concentration ranged from 5.5 to 16 mmol kg⁻¹, sodium ranged from 0.8 to 2.2 mmol kg⁻¹, Calcium from 5-10 mmol kg⁻¹ and potassium from 1.7–5.1 mmol kg⁻¹ of leaf dry matter. Ca, K Na and Cl content of leaves were not affected by irrigation water quantity or by boron treatment. Boron in leaf matter accumulated to over 100 mmol kg⁻¹ in the spring season; some 1.4 times the concentrations reached in the fall. Boron accumulation in leaves increased as a function of irrigation water boron but was not found to be a function of water quantity. Average leaf boron was 11.1 mmol kg⁻¹ in the lowest boron treatment (B-0.027), 38.1 mmol kg⁻¹ in the B-0.37 treatment and 65.4 mmol kg⁻¹ in the B-0.74 treatment during the fall season and 9.7 mmol kg⁻¹ in B-0.027, 70.4 mmol kg⁻¹ in the B-0.37, and 86.6 mmol kg⁻¹ in the B-0.74 treatment during the spring.

Transpiration by the tomato plants decreased when B concentration increase or water availability decreased exactly as did yield. Linear correlations were found between biomass and total seasonal accumulated transpiration for both the spring and the fall (Table 1) and as reported in Ben-Gal et al. (2002). Total dry biomass (g) was associated as $DM = 3.51 \cdot T + 59.00$ ($r^2 = 0.95$) in the fall and $DM = 1.51 \cdot T - 35.03$ ($r^2 = 0.98$) in the spring. Relationships between relative water use and relative yield as in Figure 1 are often used for yield and water uptake prediction. Linear relationships between water use and yield have been documented previously for various crops and climates under conditions of water deficit (De Wit, 1958; Childs and Hanks, 1975; Letey and Dinar, 1986), conditions of salt stress (Hanks 1974; Bresler and Hoffman, 1986; Bresler, 1987; Shani and Dudley, 2001), and for boron toxicity (Ben-Gal and Shani 2002b).

Profiles of soil solution B concentration during the spring experiment demonstrate increases of B with increased B in irrigation water (Figure 2). In the case of deficient irrigation quantities (I - 0.3 and I - 0.6), B concentrations of greater than ten times that of the irrigation water were found in the upper 10-20 cm of soil and concentrations three to four times that of the irrigation water were found deeper in the profile. Where sufficient irrigation water was provided ($I \geq 1 \cdot T_{max}$), B concentrations were two to three times those of irrigation water and did not vary substantially with depth. Soil solution B

concentrations found at the bottom of the root zone were also characterized using weekly analysis of leachate water that is presented in Figure 3 for the fall experiment. The choice of spring data for soil B profiles and fall data for temporal drainage B concentration was arbitrary, as both seasons exhibited similar results. Root zone B concentrations were a function of both the irrigation water B concentrations and of relative water application level. Most of the treatments were characterized by rising and then falling B concentrations that peaked at 3 to 6 times their irrigation water concentrations with a peak occurring around the midpoint of the experiment. Irrigation quantities were based on maximum transpiration rates from the entire experiment. As plant biomass and transpiration decreased with excess B or limiting water, leaching fraction increased and soil water B was subsequently diluted.

Yield response to combinations of excess boron and water content is presented in Figure 4. In the graphs, lines represent the “dominant stress” model (Equation 3) and symbols reveal the measured data. The dominant factor is determined by the specific combination of B, salinity and water and by plant sensitivity to all three stress factors. Yield response to B and water (Figure 4) is defined by two line sets. The outer line (solid) depicts yield due to dominant B, and the inner lines (dashed) set the yield when water deficit or salinity is the dominant stress. Equation [3] was simultaneously solved for all water and B levels for a salinity level of $EC = 3 \text{ dS m}^{-1}$. The salinity response, the resulting B_{cr} and maximum yield for each water level, and the B response curve are parameterized in Table 3. Effects of each of the stress causing factors are evident in Figure 4A. Salinity of the irrigation water of $EC=3.0 \text{ dS m}^{-1}$ dictated a maximum relative yield for the experiment of $0.85 \cdot Y_m$. Water restricted plant yield in much of the low water (I-0.3, I-0.6 and I-1.0) treatments where B was not at the highest levels as seen in the parallel dashed lines. Critical boron levels causing yield reduction increased with decreasing relative water application quantity. Boron-salinity interactions were investigated independent of water stress by Ben-Gal and Shani (2002b) in a greenhouse study. The response to B alone (salinity or water was not limiting) curve from the above mentioned work has been added as a dotted line in Figure 4A. The B response from Ben-Gal and Shani (2002b) is similar to that found in this work despite the obvious differences in climatic conditions including a much lower T_p in the greenhouse

experiment (T_p equaled about 100 and 500 liters per plant per season for the greenhouse and spring experiments respectively). The dominant stress type model was found to hold true not only for evaluating total biomass yield as a function of B in soil solution (Figure 4A, Table 3A), but also for economic yield shown as fresh fruit biomass (Figure 4B, Table 3B).

Irrigation water of $3.0 \text{ dS}\cdot\text{m}^{-1}$ (local water) was used for all the B treatments. The higher salinity explains why the measured data of relative yield that are included figure 4 do not reach the potential $Y/Y_{\max}=1$. Maximum yield was obtained in the control treatments utilizing water of EC-0.52, B-0.027 and I-1.3 (Table 1). The response curves seen in Figure 4 appear analogous to response curves found in the literature for a single parameter. The plateau of the lines at low B concentrations preceding linear response (Bingham et al., 1985; Francois 1984) has been attributed to a threshold value similar to that obtained under saline conditions, below which yields are not affected by the stress causing factor (Maas 1990, Mass and Hoffman 1977). The B-salinity-water dominant effect response model presented here exploits response curves with no threshold values. The slope of the boron response curve found in this work was 3.1% yield per $0.1 \text{ mol}\cdot\text{m}^{-3}$ B increase in soil water. This agrees with Francois (1984) who found a similar 3.4% yield decrease per $0.1 \text{ mol}\cdot\text{m}^{-3}$ B increase for tomatoes grown in sand tanks. Francois reported a threshold value of $0.53 \text{ mol}\cdot\text{m}^{-3}$ below which there was no response to changes in soil B. Results from this work suggest the threshold values reported in the literature for crop response to boron may well be artifacts of response to some overlying stress.

Summary

Excess boron in soil water was found to decrease yield and transpiration of tomatoes. This effect was less when plants were exposed to B and water stresses. Both irrigation water quantity and boron concentration influenced water use of the plants in the same manner as they influenced yield. A dominant-stress-factor model based on the Liebig-Sprengel law of the minimum was validated. The model applies the principle that, when a plant is submitted to conditions of stress caused by B in conjunction with limiting water and/or salinity, the more severe stress determines yield. The results of this study have significance in modeling and management of high boron conditions.

Acknowledgement

This research was supported by Research Grant Award No. US-3065-98R from BARD, The United States – Israel Binational Agricultural Research and Development Fund.

Figures

Figure 1. Total relative biomass yield as a function of total relative accumulated transpiration for tomatoes grown over two seasons under varied levels of irrigation water B concentrations and varied irrigation water quantities. Line is linear regression for entire data set with $r^2 = 0.97$.

Figure 2. Profiles of B in soil solution for B and water level treatments determined from soil samples taken during the 8th week and the 13th week of the spring experiment. Horizontal lines show range of B concentrations for each depth.

Figure 3. Soil water B as determined from drainage water samples over the course of the fall experiment for all B and water level treatments.

Figure 4. Relative yields (Y/Y_m) of tomato plants as a function of boron in soil solution for varied soil water conditions. A. Total dry biomass, B. total fresh fruit yield. Symbols are experimental measurements and lines show the dominant factor model. Solid line is common yield response to boron function and broken lines correspond to maximum yields for each particular irrigation quantity level. The dotted line in (A) represents B response adapted from Ben-Gal and Shani's (2002b) greenhouse boron-salinity study.

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Table1. Yield and water use of tomatoes. Each row presents data for a single lysimeter/plant with a unique B concentration - irrigation quantity combination.

	Irrigation		Total		Total Transpiration (L)	Dry Weights		Fruit		Total Dry Biomass (g)
	Water		Irrigation Quantity (L)	Irrigation Treatment (IT_p^{-1})		Leaves (g)	Stems (g)	Fresh (g)	Dry (g)	
	Boron mol m ⁻³	Salinity dS m ⁻¹								
Fall	0.027	3	15.0	0.04	27.4	33.6	23.9	150	34.0	91.4
	0.027	3	120.0	0.29	110.0	131.5	56.9	4840	481.4	669.7
	0.027	3	272.9	0.65	215.7	160.6	62.8	6690	546.9	770.3
	0.027	3	444.4	1.06	299.0	211.4	107.9	10030	754.7	1074.0
	0.027	3	570.8	1.37	383.6	254.5	120.8	12640	1091.9	1467.2
	0.027	3	688.1	1.65	359.5	281.2	111.9	11960	955.6	1348.6
	0.37	3	163.9	0.39	153.9	124.0	39.4	4390	364.2	527.7
	0.37	3	247.6	0.59	192.9	198.5	75.7	8550	606.9	881.1
	0.37	3	377.7	0.90	258.9	238.8	87.9	9150	722.6	1049.3
	0.37	3	527.1	1.26	365.0	324.1	120.1	14640	1015.4	1459.5
	0.37	3	683.0	1.64	381.6	277.7	117.7	12710	948.6	1344.1
	0.74	3	128.5	0.31	100.0	101.5	43.9	2990	207.9	353.3
	0.74	3	245.6	0.59	153.3	134.6	60.8	4860	368.5	563.9
	0.74	3	432.4	1.04	264.2	206.9	79.2	8540	612.5	898.6
	0.74	3	523.5	1.25	277.7	237.2	89.7	10220	697.1	1024.1
	0.74	3	646.5	1.55	313.2	263.5	108.2	10640	697.6	1069.4
	0.027	0.5	598.5	1.43	417.7	308.5	142.3	15262	1147.3	1598.1
Spring	0.027	3	31.0	0.06	43.3	27.3	12.1	0	0.0	39.4
	0.027	3	166.7	0.31	167.9	101.5	60.2	560	58.6	219.4
	0.027	3	321.2	0.60	291.8	174.5	76.4	1810	154.1	403.6
	0.027	3	513.9	0.97	406.4	244.1	101.9	3805	253.1	597.1
	0.027	3	660.3	1.24	411.8	200.4	102.8	4384	265.0	565.9
	0.027	3	774.9	1.46	433.3	304.8	141.9	3990	255.9	700.3
	0.37	3	169.4	0.32	181.4	129.1	41.7	534	52.6	221.8
	0.37	3	320.4	0.60	280.7	164.1	61.8	2040	146.8	371.2
	0.37	3	496.2	0.93	354.6	241.1	90.5	2585	178.7	509.0
	0.37	3	656.2	1.23	486.7	323.1	158.8	4510	248.0	726.8
	0.37	3	807.5	1.52	495.7	285.3	115.4	4979	306.7	705.7
	0.74	3	150.0	0.28	145.4	115.1	49.3	587	48.4	212.9
	0.74	3	318.4	0.60	274.6	174.7	65.2	1770	125.5	363.8
	0.74	3	553.8	1.04	408.5	234.8	86.3	3070	199.4	517.9
	0.74	3	657.1	1.24	426.1	257.6	103.8	3530	221.7	583.1
	0.027	0.5	680.2	1.28	531.5	306.0	145.5	5768	329.0	778.0

1 *Table 2.* Content of selected ions in leaf dry matter of tomato plants.

	Irrigation Water	Cl	Ca	K	Na	B	
	Boron	Relative	mmol kg ⁻¹				
	mol m ⁻³	Quantity					
		I/Tmax					
Fall	0.027	0.04	12.3	8.8	2.4	3.5	9.3
	0.027	0.30	5.4	8.9	4.6	1.0	8.3
	0.027	0.69	12.3	7.7	2.1	1.8	15.7
	0.027	1.13	11.5	7.8	2.7	2.2	11.1
	0.027	1.45	14.9	9.4	1.7	2.2	12.0
	0.027	1.74	11.9	8.0	2.9	2.1	10.2
	0.37	0.42	11.7	8.3	1.9	1.3	38.9
	0.37	0.63	11.7	8.5	3.2	2.2	38.0
	0.37	0.96	16.1	8.0	1.9	2.2	40.7
	0.37	1.34	6.3	7.4	4.5	1.3	34.3
	0.37	1.73	13.1	8.0	2.3	2.2	38.9
	0.74	0.33	5.8	9.9	2.3	1.5	72.2
	0.74	0.62	11.7	8.3	2.3	2.1	69.4
	0.74	1.10	9.3	7.4	3.5	2.0	63.0
	0.74	1.33	9.0	8.0	3.2	2.0	57.4
	0.74	1.64	15.4	8.3	2.3	2.2	64.8
Spring	0.027	0.06	6.2	5.1	5.8	0.8	7.4
	0.027	0.31	12.9	8.3	2.2	1.3	7.4
	0.027	0.60	11.3	7.8	2.7	1.2	14.8
	0.027	0.97	8.9	8.6	3.2	1.1	15.7
	0.027	1.24	7.2	8.6	3.7	1.0	6.5
	0.027	1.46	8.8	8.1	4.2	1.1	6.5
	0.37	0.32	15.4	8.0	2.6	1.7	102.8
	0.37	0.60	13.2	9.5	1.9	1.3	78.7
	0.37	0.93	13.1	9.0	2.7	1.7	65.7
	0.37	1.23	9.6	7.9	3.9	1.0	53.7
	0.37	1.52	8.4	8.6	3.3	0.9	50.9
	0.74	0.28	15.7	8.3	2.3	1.7	101.9
	0.74	0.60	12.3	8.6	2.5	1.3	102.8
	0.74	1.04	9.1	7.2	5.1	1.1	70.4
	0.74	1.24	5.8	7.3	4.9	0.8	71.3

Table 3. Tomato response to salinity, boron and water content levels using dominant factor piecewise linear model for yield response to soil water B. Y_m is maximum relative yield, g is the slope of the overlying salinity response curve. I_{CR} is critical irrigation level for Y_m of water quantity with b being slope of the water response. The parameter a is the slope of the soil water B response curve. Y_I and B_{cr} show calculated relative maximum yields and critical B concentrations for the different water levels. Different letters in the group column represent difference at probability of 0.95 ($\alpha=0.05$).

A) Relative total dry biomass (Figure 4A)

Y_m	g $\frac{Y/Y_m}{EC}$	b $\frac{Y/Y_m}{I}$	I_{CR} I/T_{max}	n $\frac{Y/Y_m}{B}$	I/T_{max}	Y_I Y/Y_m	B_{cr} mol m^{-3}	Group
1.03	-0.074	0.557	1.66	-0.206	.2-.4	0.28	3.08	a
					.5-.7	0.45	2.52	b
					.9-1.1	0.67	1.78	c
					1.2-1.5	0.82	1.22	d
					1.5-1.75	0.82	1.22	d

B) Relative fresh fruit yield (Figure 4B)

Y_m	g	b	I_{CR} I/T_{max}	n	I/T_{max}	Y_I Y/Y_{max}	B_{cr} mol m^{-3}	Group
1.03	-0.095	0.612	1.56	-0.215	.2-.4	0.16	3.93	a
					.5-.7	0.35	3.07	b
					.9-1.1	0.59	1.94	c
					1.2-1.5	0.77	1.12	d
					1.5-1.75	0.77	1.12	d

Figure 1.

Figure 2

Figure 3

Figure 4

Corn response to combined nitrogen and salinity environmental stresses

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ABSTRACT

To define the nature of the combined response curve of corn (*Zea mays* L.) plants to nitrogen and salinity, a lysimeter study was designed to follow water and solute budgets with combinations of the two variables over wide ranges of 0.5-7.5 dS·m⁻¹ and 0-150% of local N-fertilization recommendations (LNFR). Patterns of water-use efficiency, N content, N uptake, and yield indicated the predominance of environmental interactions over Cl-nitrate physiological antagonism. At low salinities, the leaf N content, N uptake, and yield increased with increased N fertilization up to 45% LNFR, nitrogen was efficiently stripped from the percolating water and practically no nitrate was leached. At higher N fertilization the amount of leached N increased linearly with increased N input, and N uptake and yield were independent of N rates, leveling off at increased values for decreased salinities. The Liebig-Sprengel and Mitscherlich-Baule models were evaluated against measured data. Both models summed up to similar values for the system's inherent N, the salinity level corresponding with zero yield, and the predicted yields, which were highly correlated with the experimental data ($R^2 > 0.9$). It is suggested that both models can be used successfully in mechanistic-based plant-soil-solution models to predict yield, water and nutrient needs, and the resulted N leaching.

Key-words: corn; interactions; Liebig-Sprengel model; Mitscherlich-Baule model; nitrogen; response curves; salinity; water-use efficiency.

INTRODUCTION

Understanding yield dependence on growth factors and combinations of factors is indispensable in planning desirable inputs (*e.g.* water and fertilizers) and evaluating the risk of contaminating soil, ground water or down-stream water sources. A case of special agronomic

and environmental interest is the combined effects of N and salinity on plant growth, water and nutrient uptake, and the resultant nitrate and chloride leaching. Nitrate-N, as a crucial macronutrient for crop culture, and Cl, as a micronutrient and a major salinity agent, are known to be antagonistic to each other in the uptake system of plants (Tisdale *et al.* 1993; Marschner 1995; Xu *et al.* 2000; Mengel & Kirkby 2001). The antagonistic relationship is attributed to the negative membrane potential of root cells and the negative charge of both nitrate and chloride, whether by using separate carrier systems (Dhugga, Waines & Leonard 1988) or by competing for the same carrier system, probably operated by co-transport with protons (Pope & Leigh 1990). Such an interaction results in diminished N uptake and decreased plant growth at increased Cl concentrations (Bernal, Bingham & Oertli 1974), and in decreased Cl uptake at increasing nitrate concentrations (Tisdale *et al.* 1993). Nevertheless, Pang & Letey (1998) showed that at a moderate irrigation rate, N uptake by corn plants and their relative yield (actual yield as a proportion of the maximum yield) can be accurately predicted by a combined plant-N-salinity-water response model (ENVIRO-GRO), in which no interaction in the uptake system between the N status of the plant and salinity is assumed. By running the model, they showed that secondary interactions, such as salinity-derived diminished water use, which lead to increased nitrate leaching from the root zone, control the response curve.

Several types of response curves can serve to explain plant behavior under combined stresses. The Liebig-Sprengel model, as postulated in several publications during the first half of the 19th century by Justus von Liebig and Carl Sprengel (hereafter the LS model), suggests that at any given time a single growth factor, the most limiting one, determines yield, and that the yield response to this single factor is of a linear nature. Because many factors are involved in plant growth, the LS approach results in a stepwise “constant returns” response curve (Black 1993; Van der Ploeg, Boehm & Kirkham 1999). In 1909 Mitscherlich proposed the concept of diminishing plant response (Black 1993). The biological basis of this plant response might be ascribed to saturation of the root-carrier-mediated uptake system. An assembly of “Mitscherlich-type” growing factors that simultaneously affect plant growth and do not interact with each other was proposed by Baule in 1918 to act additively (Stewart 1932). The combined Mitscherlich-Baule approach is denoted MB hereafter. Other types of combined response curves prevail in

cases of synergistic or antagonistic interactions between the tested growth factors, as described in detail by Black (1993) and Lark (1997).

Each of the discussed response models may lead to different conclusions regarding the needed fertilizer input, rate of irrigation, and risk of nutrient leaching to the environment. Thus, the combined MB-type response model implies that if five growing factors, out of the 35 mentioned by Wallace (1990), are in mild shortage, each at 90% of its optimal level, and one growing factor is at 80% of its optimal level, 0.47 of the maximum yield (Y_{max}) is expected ($Y = Y_{max} \times 0.9^5 \times 0.8$). In contrast, the LS model would predict 0.8 of the maximum yield for this case. Similarly, if antagonism versus no interactions between N nutrition, salinity, and irrigation is assumed, different fertilizer and water consumptions are expected. Thus, higher nitrate will be needed at increasing Cl concentrations if antagonism is assumed, while if no interaction rules the response curve and salinity is a LS-type limiting factor, increased nitrate input will not increase yield. This study sets out to address this controversy and to improve mechanistic-based soil-plant-water computer simulation models to better predict the combined effects of water, N nutrition, and salinity on yield and solute uptake and loss. The objectives of the study were to evaluate the relationships between N fertilization and water salinity, and to measure the yield response of corn plants to the combined effects of these factors over a wide range of N and salinity levels.

MATERIALS AND METHODS

Plant-response studies were conducted on corn receiving an array of N and salt concentrations in the irrigation water. Experiments were conducted in lysimeters situated at the “Arava” Research Station in the Southern Arava Valley in Israel. Twenty-three freestanding lysimeters with 100-L capacity were filled with Arava sandy loam soil and situated in a greenhouse. Detailed soil properties can be found in Shani *et al.* (1987). The lysimeter arrangement provided automatic preparation and delivery of irrigation solution and automatic collection and measurement of drainage-water volume and electric conductivity (EC). Two replicates were conducted, the whole experiment being run twice, consecutively. The collective effect of salinity and N was investigated by combining four salinity levels with six N levels in the irrigation water. Salinity (before fertilizer addition) was brought to EC of 0.5, 2.5, 5, and 7.5 dS·m⁻¹ by adding 2:1 molar concentrations of NaCl and CaCl₂. N-fertilization rates were set as

percentage of the local recommended commercial level (Table 1), and varied with plant age. The percentages were 0, 15, 45, 70, 100, and 150. All combinations of salinity levels with N levels were added to the irrigation water. N was added to the irrigation water as ammonium-nitrate. The soil was brought to equilibrium with the irrigation water N by prolonged leaching before corn was seeded. Corn (*Zea mays* L., cv. Jubilee) was seeded in the lysimeters and irrigated initially for 4 days using water of $EC = 0.5 \text{ dS}\cdot\text{m}^{-1}$. Salinity treatments were begun 4 days after germination. Experiments were started with four plants per lysimeter and were thinned to two plants after 20 days. Phosphorus and potassium were applied as commercial phosphoric acid and KCl fertilizers through the irrigation water at the local recommended levels for commercial cultivation (Table 1).

Each lysimeter incorporated a 50-cm highly conductive rockwool drain to ensure negative matric potential and proper soil aeration at the lysimeter bottom. A detailed description of the lysimeter system is given in Ben-Gal & Shani (2002). Water draining through the lysimeters was analysed daily for EC and weekly for NO_3 and Cl during the growing season. A continuous water and salt balance was recorded for each lysimeter and the water uptake was evaluated from the running water balance. Daily water balance generated evapotranspiration data for each lysimeter. Calculations for evapotranspiration (ET) used the equation

$ET = I - Dr + \Delta \theta \cdot Z$ where I is irrigation, Dr is drainage (ET , I , and Dr given as mm day^{-1}), $\Delta \theta$ is the change in volumetric soil water content, and Z is the lysimeter depth (mm). The irrigation rate was set to 130% of the highest daily evapotranspiration measured from the lysimeters in the experiment to ensure leaching. The lysimeters were circulated on a carousel in a greenhouse to ensure uniform climatic conditions. Plants were harvested 60 days after germination at the stage of silking, washed with deionised water, oven-dried at 65°C , and analysed for total N.

Differences of shoot dry-matter yield (Y), relative dry matter (Y_r , where $Y_r = Y/Y_{max}$, Y_{max} being the greatest yield measured for all treatments), leaf N content, and evapotranspiration between the two successive trials were tested by ANOVA (JMP 4 software, SAS Institute Inc., Cary, NC, USA) at $\alpha = 0.05$. The two trials were found not to differ from each other; hence their results were presented and further analysed together.

Two approaches for plant response to growth or stress factor were examined and fitted to the experimental data: the LS model (Equation 1) and the MB model (Equation 2). The LS model for the case of salinity and N is defined as:

$$Y_r = \frac{Y}{Y_{\max}} = \min \begin{cases} Y_m & ; EC < EC_{cr} \\ Y_m - b \cdot (EC - EC_{cr}) & ; EC \geq EC_{cr} \\ n \cdot N_0 + n \cdot N_F & ; N < N_{cr} \\ Y_m & ; N \geq N_{cr} \end{cases} \quad [1]$$

where b is the slope of the Y_r response to salinity and EC_{cr} is the salinity threshold for yield reduction; n is the slope of the Y_r response to N where salinity is negligible, N_{cr} is the N threshold for plant response, N_F is the N added to the soil as fertilizer, and N_0 is the inherent N in the soil-plant system, *i.e.* N that affected plant growth and was not added as a fertilizer (might have originated from initial soil mineral N, mineralized organic soil N during the growth period, fixed N, seed N, etc.). The actual effective N in the soil, N , is the sum of N_F and N_0 . The estimated maximum relative yield, Y_m , is defined for the case in which N and salinity do not limit plant growth. The parameters b , n , EC_{cr} , and N_{cr} are plant-specific.

The MB model for the salinity and N factors is described by:

$$Y_r = Y_m \cdot (1 - e^{-C_N N}) \cdot (1 - e^{C_{EC} (EC - EC_m)}) \quad [2]$$

$$Y_m = 1 - e^{-C_{EC} EC_m}$$

$$N = N_F + N_0$$

where EC_m is the EC at which Y_r equals zero, C_N is the MB efficiency factor for nitrogen, and C_{EC} is the MB susceptibility factor for salinity.

Parameters of the LS and MB models for salinity or N alone were fitted to data reflecting situations in which only one of the factors predominate yield using the Ordinary Least Square model (Quantitative Micro Software 1997). Thus, parameters were fitted simultaneously for N, using experimental data of the lowest salinity only, and for EC, using experimental data of the 100% and 150% N treatments. The combined experimental effect of the two factors at all tested

levels was evaluated against the two models (equations 1 and 2) by a Wald test (Kennedy 1992; Quantitative Micro Software 1997) under the null hypotheses that parameters describing the same property (e.g. slope, intercept) of the various salinity and N treatments were equal.

RESULTS AND DISCUSSION

Yield (total shoot dry matter) as a function of n level in the irrigation water for the various salinity levels is presented in Fig. 1. Yield response to n at low salinity is convex to the origin, increasing at low N and levels off above N level of 45%. Salinity affected yield at high N levels (45% and above), but did not affect yield in the lower N range.

The yield-evapotranspiration relationship is crucial for predicting N uptake, since N is transported from soil to the uptake sites mainly by mass transport (Barber 1995). Linear relationships between water use and yield have been documented for various crops and climates under conditions of water deficit (deWit 1958; Childs & Hanks 1975; Letey & Dinar 1986) and salt stress (Hanks 1974; Bresler & Hoffman 1986; Bresler 1987; Shani and Dudley 2001). In this experiment, the evapotranspiration by the corn plants responded to the stress factor similarly to yield and a linear correlation was found between biomass and ET (Fig. 2). The slope represents the water-use efficiency (WUE) of the plants. Small variations in WUE between salinity treatments are not significant and the combined WUE for all salinity levels was 4.46 g DW L^{-1} ($R^2 = 0.89$). However, when biomass is examined as a function of ET for the various N levels, two WUE values are obtained: at zero N_F $WUE = 2.17$ ($R^2 = 0.83$), while for all higher N levels WUE is 4.37 ($R^2 = 0.93$). It is evident that at moderate N deficiency, N stress reduces plant growth and consequently transpiration is reduced keeping the WUE unchanged. Severe N stress, however, results not only in diminished plant growth, but also disrupts regulation of transpiration, probably by damaging the structural or functional components of the transpiration water-flux regulation system.

Adequate N content in plant tissues is a prerequisite for optimal biomass production. This relation is clearly shown to hold true for the two lowest salinity levels tested in this experiment, by the dependence of shoot dry weight on leaf N content (Fig. 3). At the highest salinity level, however, the yield did not respond to increased leaf N content, indicating the existence of another factors controlling plant growth. The direct factor might be salinity *per se* (i.e. osmotic effect) or Cl toxicity, as discussed by Xu *et al.* (2000). Up to 2.9% N content in the leaves

showed no saturation of yield for the two lowest salinity levels. However, no further increase in leaf N content was obtained by increasing N concentration in the irrigation water (Fig. 4). The N concentration in the leaves of plants grown at all the tested salinity levels responded similarly to N-fertilization level (Fig. 4). In the lower range, with severe N deficiency, as indicated by the low (1 to 1.6%) N content in the leaves, increased N in the irrigation water resulted in increased leaf N content. Leaf N content increased with increased N level in the irrigation water up to 2.1% at 45% of the recommended N-fertilization rate. Above this fertilization rate, the N concentration in the leaves levelled off at the adequate N content of 2.1 to 2.9%. This concentration is in the low part of the adequate range as given by Reuter & Robinson (1986) (2.25-3.50%) and Martin-Prével & Gautier (1984) (2.76-3.50%) for the ear leaf of corn plants, but it is well within the 2 to 4% range given by Mengel & Kirkby (2001) as the normal N concentration in all plant material, and as evident from the relationship between yield and N content in the leaves in this study. These results suggest that the local commercial recommendations for N fertilization (Table 1) are in large excess over plant demand.

Total N uptake in the lower N-fertilization range was identical for all salinity levels and increased with increased N-fertilization rate, while at N fertilization $\geq 45\%$ of the recommended rate, the total N uptake reached plateau levels at decreasing values for each increase in salinity (Fig. 5). Evidently, if Cl had controlled N uptake through physiological antagonism, N uptake would be suppressed at the lower N fertilization, while at the higher N rates not much effect of the antagonism would be expected. Thus, the data presented here demonstrate predominance of environmental over physiological interactions between N nutrition and salinity, and the diminished N uptake at the higher salinity levels resulted from salinity-derived inhibited plant growth rather than from Cl-nitrate physiological antagonism. This conclusion corresponds with the results of Khan, Silberbush & Lips (1994) who reported similar effects of $\text{NO}_3\text{-N}$ versus $\text{NH}_4\text{-N}$ fertilization on amelioration of NaCl-salinity-derived plant-growth inhibition.

The loss of nitrate with surplus water that drains from the lysimeters, as represented by $\text{NO}_3\text{-N}$ concentration in the drainage water collected in the last week of the experiment (Fig. 6) and on other dates (data not shown), was negligible at low fertilizer-N rates; however from as low as 45% of the recommended rates, it was linearly correlated to the applied N rates. Thus, as a plant encounters deficient N nutrition, it effectively strips dissolved N from the percolating

water, and as water leaves the root zone practically no N is left. When N was supplied at 45% or more of the recommended rates, N level did not limit N uptake and the surplus remained in the percolating water. Although N in the drainage in this range was linearly correlated with the N content in the irrigation water, the surplus did not affect yield. The yield relation to the drained N is shown in Fig. 7. Two distinct phenomena are evident: (i) any yield increase due to higher N level in the irrigation water results in total consumption of the added N, and consequently, zero N is detected in the drainage water; (ii) there is no response to excess N, all of it is present in the leachate, and the plant responds only to salinity.

The parameters of the LS and MB models of relative yield response to salinity and N are summarized in Table 2. These parameters were substituted into Equations 1 and 2 for the LS and MB models, respectively, to calculate the combined plant response to salinity and N. Measured data (symbols) and calculated curves (lines) of plant response to salinity at N_F levels of 0, 15, and 100% are presented in Fig. 8(a,b) for the two approaches. It should be noted that the parameters of the two models were fitted only to the non-interactive treatments, *i.e.* varied salinity at N_F levels of 100 and 150%, and varied N at a salinity level of $0.5 \text{ dS}\cdot\text{m}^{-1}$. Nevertheless, good agreement between measured and calculated data for both models persisted for the treatments in which combined salinity and N stresses were applied. No difference was found in the estimation of N_0 between the LS and MB models: both estimated higher N_0 for the first trial relative to the consecutive one. Similar values of about $9 \text{ dS}\cdot\text{m}^{-1}$ were estimated by the two models for the salinity level corresponding with zero yield. The validity of the LS and MB models was verified by comparing the calculated relative yields according to the two models with the parameters presented in Table 2, to the experimental relative yields for all combinations of salinity and N treatments (Fig. 9). The slopes of the linear regression of the two models vs. experimental data (0.950 for the MB model, $R^2 = 0.906$, and 0.94 for the LS model, $R^2 = 0.956$) did not differ from each other or from the 1:1 slope at $\alpha \leq 0.05$.

The LS curves in Fig. 8a present two line sets applying the principle that when a plant is submitted to conditions of stress caused by limiting N in conjunction with salinity, the more severe stress determines yield. The outer line depicts yield due to salinity, and the inner lines describe the yield when N level is the dominant stress. The dominant factor is determined by the specific combination of N and salinity and by the plant's sensitivity to both stress factors. The

LS responsiveness to salinity, 0.11 Y_r decrease per $\text{dS}\cdot\text{m}^{-1}$, is similar to the value of 0.12 corn yield decrease per $\text{dS}\cdot\text{m}^{-1}$ of saturated soil extract, as given by Maas & Hofmann (1977). However, while these authors postulated $1.7 \text{ dS}\cdot\text{m}^{-1}$ as the threshold value for corn plants, our results indicate that the actual threshold is dependent on the N level; thus, when N does not limit plant growth, the apparent EC threshold is as low as $0.5 \text{ dS}\cdot\text{m}^{-1}$, whereas when N is limiting plant growth, the apparent threshold may increase to high values such as $4 \text{ dS}\cdot\text{m}^{-1}$ at a 20% N-fertilization rate and even higher as N rate decreases. Similarly, the threshold for N depends on salinity. Assuming the irrigation water is of known salinity, determined by the available water source, the conditional threshold level of nitrogen, N'_{cr} , at $EC > EC_{cr}$, as determined by the model, is given by $N'_{cr} = 35.3 - 3.7 \cdot EC$, where N'_{cr} and EC units are as above. An application of N higher than N'_{cr} will result in increased N leaching, but not increased yield. This obviously indicates, once again, that the local commercial recommendations for N fertilization are in excess of plant demand.

The MB model, as stated by Mitscherlich and defined in Equation 2, applies the assumption that the parameter C for each growth factor is constant. This assumption has been questioned by many researchers (Stewart 1932; Black 1993). The analysis, presented in Figures 8 (for three N levels) and 9 (for all the experimental data), support Mitscherlich's conclusion regarding the consistency of the C parameters, and good agreement between measured and calculated data prevails when a single C value for each of the factors is used for the combined effect of salinity and N, as suggested by Baule (Stewart 1932) and Wallace (1990).

SUMMARY

The plant-soil-water system is extremely complex and many interactions prevail among its components. Nevertheless, the plant's overall combined response to wide ranges of salinity and N fertilization is shown in this study to be well described by both LS and MB simplistic models, even though they are based on different assumptions. The LS model assumes no interaction between the various growth factors - at each level only one factor affects yield. In contrast, the MB model is defined to address simultaneous effects and interactions and to correspond to physiological plant responses. Our study demonstrates that while conceptual disagreement exists between the two models, both sum up with similar predicted yields, and it is suggested that both can be used successfully in mechanistic-based plant-soil-solution computer-

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simulation models to predict yield and the related evapotranspiration, water and nutrient needs of the crop, and the resultant nitrate leaching below root depth in response to wide ranges of salinity and N-fertilization rates. Moreover, we propose that the two models should not be regarded as contradictory. Separation in time and space can bridge the gap between the two models. Thus, at certain combinations of salinity and N, salinity might be a LS-type limiting factor at times of high evapotranspiration, at the end of the interval between irrigation cycles, or at the edge of the wetted zone of a point irrigation source, such as a dripper. The N might become a LS limiting factor during and soon after plants are irrigated, and for roots located in the centre of the irrigated zone. Such a situation would prevent the sharp curve fracture predicted by the LS model and could result in a MB-like response curve. Nevertheless, valuable information can be culled from each of the models once the parameters are experimentally determined. Thus, in addition to yield prediction, the MB model can be used, as suggested by Mitscherlich, to estimate the intrinsic soil nutrient content, and the LS model is useful for determining the threshold of N fertilization at any known salinity level.

The effect of each of the factors was shown to vary as the level of the other factor changes; however, the mode of interaction was not physiological antagonism. Hence, we suggest that the effect of N-fertilizer on N uptake, plant growth, and the resultant evapotranspiration and nitrate loss over the tested salinity range is controlled by an assembly of environmental factors, such as water availability and uptake or plant reaction to other growth factors, and the dominant interactions are environmental rather than physiological. While dominance of physiological antagonism between Cl and N would suggest increasing N fertilization at increased salinity to compensate for the competition between Cl and nitrate uptake, the dominance of environmental interactions and the resultant response curves suggest lower demand for N at increased salinity.

ACKNOWLEDGEMENT

This research was supported by Research Grant Award No. US-3065-98R from BARD, The United States – Israel Binational Agricultural Research and Development Fund.

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Table 1. Local commercial recommendation for N, P, K-fertilization of corn plants, serving as the basis for N-fertilization levels in the experiment

Growth stage	Seeding to germination	Tillering	Tasselling	Silking
N [†]	60-80	100-120	80	80
P [†]	7-10	15	20	10
K [†]	40-60	80	40	40

[†] g nutrient (N, P, or K) m⁻³ irrigation water

Table 2. Best fit parameters for the LS and MB models, as calculated for EC using experimental data with N levels of 100 and 150%, and for N using experimental data with salinity of 0.5 dS·m⁻¹

Parameter	Value	Units
<u>LS model</u>		
Salinity threshold (EC_{cr})	0.5	dS·m ⁻¹
Nitrogen threshold (N_{cr})	33.5	% of recommended level
EC at which Y equals zero (EC_m)	9.56	dS·m ⁻¹
Inherent nitrogen (N_0)	3.2 ^(†) , 6.6 ^(‡)	% of recommended level
Responsiveness to salinity above EC_{cr}	0.11	Y_r decrease per dS·m ⁻¹
Responsiveness to N below N_{cr}	0.029	Y_r increase per % N increase
<u>MB model</u>		
Efficiency factor for N (C_N)	0.044	% of recommended level ⁻¹
Susceptibility factor for salinity (C_{EC})	0.34	m·dS ⁻¹
EC at which Y equals zero (EC_m)	8.4	dS·m ⁻¹
Inherent nitrogen (N_0)	3.4 ⁽¹⁾ , 8.5 ⁽²⁾	% of recommended level

(†) - first trial; (‡) - second trial

FIGURES

Figure 1. Dry matter yield as a function of N level (% of the local recommended level) for the various salinity levels. Error bars represent $\pm$ standard error. No error bar represents an average of two plants in a single lysimeter.

Figure 2. Evapotranspiration-yield relationships for all plants at various N levels.

Figure 3. Yield (dry weight) in relation to leaf N content at different salinity levels.

Figure 4. Leaf N content in relation to N fertilization at different salinity levels.

Figure 5. Nitrogen uptake in relation to N fertilization at different salinity levels.

Figure 6. Nitrogen in drainage water associated with N-fertilization rates.

Figure 7. Yield as a function of nitrogen in leachate at different salinity levels.

Figure 8. Relative yield in relation to salinity at 0, 15, and 100% N_F levels for the LS (a) and MB (b) models. Measured data are presented by symbols and models are presented by lines.

Figure 9. Comparison of measured and calculated relative yields according to LS (diamonds) and MB (squares). Lines represent linear regression.

Fig. 1

Fig. 2

Fig. 3

Fig. 4

Fig. 5

Fig. 6

Fig. 7

Fig. 8

Fig. 9