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MODELING TRANSPIRATION AND GROWTH OF SALINITY AND DROUGHT STRESSED TOMATOES

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Till Mamma

"Vad du ej klart kan säga vet du ej.
Med tanken ordet föds på mannens läppar.
Det dunkelt sagda är det dunkelt tänkta."
Esaias Tegnér

PREFACE AND ACKNOWLEDGEMENTS

Something that is directly against my nature, not to mention the severe damaging effects it has on my sensitive being, is refraining myself from using too many words when trying to express myself. During the last two years, my verbal celibate has caused an accumulated word surplus of insurmountable amounts. Fearing for my mental well being I see no other solution but to use this section of the thesis as emergency mitigation of the most pressing symptoms. In addition, acknowledgement is of course the part of a thesis most curious human beings like myself would start by reading, and for you I am hereby making sure that you get your vital dose of acknowledgement to keep you going through the coming Christmas. Let the story begin…

First of all I would like to express my gratitude to my main supervisor, Per-Erik. Thank you for all your ideas and solutions to my innumerable problems, and for your remarkable patience with my bad moods. I know that I am stubborn. I am also grateful to my co-supervisor, Uri Shani, for many heated but fruitful discussions and for lots of constructive ideas on parameterisations and text. You made my stay in Israel an unforgettable experience. Thank you!

This thesis would never have been realised without the mental support from my friend and colleague Magnus. Thank you for listening to my constant complaints and for all your invaluable suggestions on how to structure my work and how to proceed, when I most of all just wanted to give in. Answering the question "what am I doing and why?" is not always an easy task. I am also grateful to my colleagues in the Environmental Physics research group for support and ideas. Thank you David for all the help with the sometimes very troublesome CoupModel and for your help with other modelling problems. My gratitude also goes to the rest of the staff at the Dept. of Land and Water Resources Eng. for making it a very nice working environment. Alon Ben-Gal, who I still haven't had the privilege to meet, provided the data used in this thesis. Thank you for letting me use your measurements and for your prompt and constructive replies on the manuscripts. I would also like to thank the whole research team in Israel at the Dept. of Soil and Water Sciences, Hebrew University of Jerusalem for your help and friendship, and especially Eran for your hospitality and generosity.

This thesis is dedicated to my mother. Thank you for always encouraging me, for always believing in me, for always thinking that all I do is a miracle and fantastic (even if not), for always, since I learnt to speak, having listen to me and respected my opinion, for giving up your career to take care of us children and for all the endless and unconditional love you have always given me. Indirectly, it is also a dedication to all other amazing and bright women of the world, especially the ones that I have had the great fortune of meeting and getting to know, you all know who you are. I am very proud of being your friend.

Nevertheless, I am also grateful for having many nice men around me. My warmest gratitude goes to Duncan, Pappa and Karl-Johan, and to all my other male friends for being there for me. I really appreciate you all.

Finally, I am grateful to the Swedish International Development Cooperation Agency (SIDA) for providing the funding for this work.

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ABSTRACT

Irrigation with saline waters is an agricultural practice that is becoming increasingly common as competition for fresh water increases. In this thesis the mechanisms behind salinity and drought stress has been studied using data from field experiments in combination with a modelling tool, the CoupModel. Measurements from field experiments on salinity, boron toxicity and drought stressed tomatoes grown during two climatically different seasons in the Arava desert, Israel, showed a linear relationship between relative growth and evapotranspiration, for all treatments and seasons. Data from the spring was used to concurrently simulate growth and transpiration, hence accounting for feedback mechanisms between the plant and the environment. Salinity stress was modelled as an osmotic effect (reduction of water uptake at high soil salinities, W approach) or a toxicity effect (direct reduction of photosynthesis with soil salinity, G approach). Good agreement between simulated growth and transpiration was achieved with both salinity stress approaches, with two exceptions. When growth and transpiration were simulated with the W approach at different salinity levels, transpiration was underestimated at high stress. The G approach resulted in an underestimation of growth at high water stress under moderate salinity. A direct decrease of photosynthesis leads to a decreasing water-use efficiency with salinity while water-use efficiency remains constant with salinity when the salinity stress is modelled as a reduction in water uptake. Measurements showed decreasing water-use efficiency for the salinity gradient, explaining why the W approach was not applicable. It was not possible to detect any considerable differences between three different approaches for water uptake tested in the study.

Keywords: Water-use efficiency; osmotic effect; ion toxicity; semi-arid.

LIST OF PAPERS

This thesis is based on the following papers that are referred to by their Roman numerals:

I. Ben-Gal, A., Karlberg, L., Jansson, P-E. & Shani, U., *Temporal robustness of linear relationship between production and transpiration*. Plant Soil (PLSO10471). In Press.

II. Karlberg, L., Ben-Gal, A., Jansson, P-E. and Shani, U., *Modelling transpiration and growth in salinity stressed tomatoes with a physically based dynamic model*. Submitted to Ecological Modelling in November 2002.

III. Karlberg, L., Ben-Gal, A., Jansson, P-E. and Shani, U., *Interactions between abiotic and biotic processes in salinity and drought stressed tomatoes*. Accepted for publication in IAHS "Red Book" Conference Proceedings, 2nd IWRM symposium; Stellenbosch, South Africa, January, 2003.

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1. BACKGROUND

1.1 Irrigation and salinisation

About one-third of the world's population live in countries with moderate to high water stress i.e. in areas where the withdrawal of fresh water exceeds 10% of the renewable storage (UNEP, 1999). Constantly increasing populations aggravate the problem of access to fresh water. The worst situation is found in Africa and western Asia. In these regions more than 80% of the fresh water is used in agriculture (UNEP, 1999). Water scarcity is becoming one of the major limiting factors to economic development and welfare in large parts of the semi-arid regions of the world. Unfavourable agricultural premises such as erratic rainfall, high evaporative demand and inherently low fertilised soils, make future population support a matter of strong concern (Falkenmark & Rockström, 1993). Several agricultural practices have been developed in order to alleviate these problems and meet the demands of high production using small amounts of water (e.g. FAO, 1997). For example, different irrigation techniques such as water harvesting and soil mulching (e.g. Hatfield *et al.*, 2001) are commonly used in order to minimise soil evaporation.

Irrigation of agricultural land is an ancient agricultural practise. The Old World Mesopotamian civilisation was built upon a prospering agriculture that was supplied with water from the Euphrates and Tigris. The Nile Valley is yet another recent example of an area dependent on irrigation water. In the scope of global population increase and future food production, irrigation of areas where water is the limiting factor for crop production is a matter of high interest. However there are two major undesirable environmental effects of irrigation, which are believed to have caused the destruction of the glorious Mesopotamian civilisation (Tanji, 1990). When irrigation water is allowed to infiltrate in the soil, the ground water table starts to rise and may, in time, bring the zone of saturation close to the surface - a phenomenon called water logging. The other side effect is salinisation and is the focus of this study.

In areas where the climate is hot and dry e.g. the Sahel region, irrigated lands are subject to substantial water losses through evapotranspiration. Salts contained in precipitation and irrigation water remain in the soil and increase in concentration when the water evaporates from the soil or when the plants take up water for transpiration. If the salt is not leached from the soil, the salt concentration increases constantly. This process is called secondary salinisation. As the salt concentration increases in the soil, crop yield decreases subsequently (see below). If the salinisation process is allowed to continue, the land eventually has to be abandoned. To avoid salinisation, excess irrigation water has to be applied to the field in order to leach the salt from the root zone. The leaching water can cause damage to ecosystems downstream the irrigated field.

1.2 Irrigation with saline waters

As competition for fresh water increase, water of better quality is used primarily for household purposes, whereas water of lower quality e.g. saline or polluted water, is used for agricultural purposes, such as supplementary irrigation (Khroda, 1996). One challenge for the future will be to maintain or even increase crop production with less water that may often be of poor quality, e.g. saline waters. Irrigation with saline waters is successfully practiced today in many countries such as Israel, Italy and the US (Rhoades *et al.*, 1992). The basic principle behind a sustainable agricultural system (in terms of long term crop yield) based on the irrigation with saline waters, is that the salt concentration in the soil has to be kept at relatively constant levels, below a threshold value specific for each crop species (Maas & Hoffman, 1977). To some extent this is a self-regulatory process by the plant (Shani & Dudley, 2001). When the soil salinity increases, the plant responds by decreasing water uptake. Thus more water is available for leaching of salts from the soil, removing more salt from the root zone. These feedback interactions by the plant and the soil salinity lead to a relatively constant soil salinity at some specific level if soil evaporation can be avoided.

Hence, evaporation from the soil leads to ion accumulation in the root zone independent of plant behaviour. When irrigating with saline waters, it is therefore desirable to try and eliminate soil evaporation. By applying saline water with appropriate irrigation management techniques, soil evaporation can be minimised, and consequently a long-term sustainable agricultural system can be established (Rhoades *et al.*, 1992). One such irrigation technique is drip-irrigation, which has been successfully used in combination with saline waters (e.g. Shalhevet, 1994). The use of saline water drip-irrigation could be more widespread if the technique was to be significantly simplified, since many small-scale farmers, particularly in the semi-arid regions, rely on simple low-cost techniques. Experiments are needed to test this plausible irrigation management technique.

Therefore, to limit the detrimental effects of salinity on plant growth, i.e. to avoid salinisation, careful management is needed. Numerous variables, such as soil type, potential evaporation, precipitation and crop type, affect the decision of irrigation management strategy. Consequently, efficient irrigation management with saline waters is a complex issue, especially in combination with drought and nutrient stress. Field tests have been carried out at several localities, including many soils and climates (Shalhevet, 1994), but this procedure is both time-consuming and expensive. As a complement to field studies, mathematical models can be used as tools for transferring knowledge between localities and for planning, as well as for studying the underlying processes of the agricultural system.

1.3 Mechanisms behind salinity and drought stress in plants

Several attempts have been made to understand the mechanisms behind plant growth under drought and salinity stress. Drought stress results in growth reductions due to decreased CO_2-uptake when the plant closes its stomata in order to retain water (Stewart *et al.*, 1977). Feddes *et al.*, (1978) describe the water stress factor on plant growth as a function of the soil matric potential. In 1964, Bernstein showed how growth and yield decreases with increasing soil salinity. Growth reductions caused by soil salinity is commonly ascribed either to an osmotic effect or to ion toxicity (Bresler *et al.*, 1982). When water-soluble molecules accumulate in the root zone, the osmotic potential decreases, leading to reduced water uptake and subsequently reduced growth above the crop tolerance level of soil salinity (Maas & Hoffman, 1977; Maas 1986). By adjusting its internal osmotic potential by compartmentation of either synthesised organic solutes in the cytoplasm or of non-organic ions in the vacuole, plants can maintain, or partly maintain, water uptake (Greenway & Munns 1980, Greenway & Munns, 1983; Läuchli & Epstein, 1990; Jacoby, 1994). Compartmentation of ions in the vacuole is also a means of removal of toxic ions from the cytoplasm, where they adversely interfere with plant cell function (Greenway & Munns 1980; Läuchli & Epstein, 1990; Jacoby, 1994). Plants can also avoid ion toxicity by active exclusion of toxic ions from the tissues.

2. OBJECTIVES

An understanding of the governing processes of saline water irrigated agricultural systems is important for creating crop growth models for predictions of growth under saline conditions in combination with different management techniques and environmental conditions. This thesis covers the first part of a larger project with the overall goal of developing such a crop growth model. Hence, the objective of this thesis is to study physical processes behind salt stress on crop growth in semi-arid regions. More specifically, the following objectives can be listed:

1. To increase the understanding of the mechanisms behind salt and water stress on crop growth (papers I, II, III).
2. To refine an existing mechanistic model on soil-plant-atmosphere relations to enable long-term evaluations of irrigation management with saline water under different environmental conditions (papers II, III).

The second phase of the study, which is not dealt with in this thesis, will address the issues of management techniques under various climatic conditions.

3. HYPOTHESES

1. Salinity stress on plant growth cannot fully be explained by an osmotic effect similar to drought stress.
2. A simple empirical model for water uptake by roots gives similar results as a more detailed and mechanistic model when tested on field data.

4. THEORY

4.1 Plant growth and transpiration under drought and salinity stress

Many studies have shown a linear relationship between transpiration and biomass i.e. constant water use efficiency, here defined as production of dry weight biomass per unit of transpired water (deWit, 1958; Childs & Hanks, 1975; Letey & Dinar, 1986; Bresler, 1987; Katerji *et al.*, 1998a). This relationship is used in many models to estimate plant growth from transpiration (Hanks, 1974; Letey *et al.*, 1985; Letey & Dinar, 1986; Pang & Letey, 1998), and can be expressed in relative terms as:

$$\frac{P_a}{P_p} = \frac{E_{ta}}{E_{tp}} \qquad (1)$$

where P is net photosynthesis and E_t is transpiration. a and p denote actual and potential respectively. The equation can be rewritten by substituting the ratio between potential photosynthesis and potential transpiration with ε_W:

$$P_a = \varepsilon_w \cdot E_{ta} \qquad (2)$$

ε_W is a measure of the water use efficiency, WUE, of the system.

Alternatively photosynthesis can also be estimated as a function of adsorbed global radiation, $R_{s,pl}$:

$$P = \varepsilon_L \cdot R_{s,pl} \qquad (3)$$

where ε_L is the radiation use efficiency (RUE). In this RUE function, drought stress is accounted for by including a reduction function for transpiration, $f(E_{ta}/E_{tp})$ i.e. the ratio between actual and potential transpiration:

$$P = \varepsilon_L \cdot f\left(E_{ta}/E_{tp}\right) \cdot R_{s,pl} \qquad (4)$$

When a soil dries out, the plant eventually responds by closing its stomata to save water and prevent desiccation. Consequently, water uptake and transpiration decrease. The closing of stomata also leads to a reduced CO_2 intake and therefore a lowering of photosynthesis and growth. Assuming that the reduced water loss through stomata is proportionate to the decreased CO_2 intake, WUE (i.e. net photosynthesis per transpired unit) remains constant even under drought stress. Equation (4) is based upon this assumption.

Since the mechanisms behind salt stress are not fully understood, it is unclear whether reductions of transpiration under salinity stress are the cause or the result of a reduction of growth (Shalhevet, 1994). If osmoregulation or ion toxicity leading to increased metabolism (or decreased assimilation) is causing the growth reduction, lower transpiration is a secondary effect of the relatively smaller plant. On the other hand, when a lower osmotic potential in the soil leads to decreased water uptake, the reduction of transpiration is the cause of the reduced growth. In other words the salinity stress is a form of drought stress. This latter approach is the traditional way of estimating yield in crop growth models (Hanks, 1974; Childs & Hanks, 1975; Shani & Hanks, 1993). In these models it is of vital importance to determine the plant water uptake under salinity stress. Cardon and Letey (1992) compared two types of approaches for water uptake under salinity stress. In type I, water uptake is calculated as a function of the hydraulic conductivity and the gradient in pressure head between the soil (i.e. matric plus osmotic potential) and the plant (Nimah & Hanks, 1973; Childs & Hanks, 1975). Alternatively, water uptake can be calculated by an S-shaped stress function, similar to the empirical functions of Maas and Hoffman (1977), which relates relative water uptake to the average salt concentration in the root zone (van Genuchten, 1987) with the use of a soil salinity stress function (van Genuchten, 1983; van Genuchten & Hoffman, 1984; van Genuchten & Gupta, 1993). Cardon and Letey (1992) found that the latter formulation agreed better with measured data.

The soil salinity reduction function that van Genuchten (1987) used is mathematically described as:

$$f\left(\pi(z)\right)=\frac{1}{\left(1+\left(\frac{\pi(z)}{\pi_c}\right)^{p_\pi}\right)} \tag{5}$$

where z is soil depth, $\pi(z)$ is the soil salinity, π_c is the soil salinity level which results in a 50% reduction in growth and p_π is a growth reduction shape coefficient. In the RUE function, the salinity stress reduction factor, $f(\pi)$, can be used to account for salinity stress in two ways. Following the traditional line, $f(\pi)$ can be incorporated in the calculation of plant water uptake, thus resulting in decreased transpiration, E_{ta}, at higher soil salinities. This approach will further be referred to as the water (W) approach. Alternatively, assuming the salinity stress is due to increased metabolism (or decreased photosynthesis), $f(\pi)$ is used to decrease photosynthesis directly by including this function into the growth equation:

$$P=\varepsilon_L\cdot f\left(\pi\right)\cdot f\left(E_{ta}/E_{tp}\right)\cdot R_{s,pl} \tag{6}$$

This approach in which growth is affected directly by salinity is termed the growth (G) approach. Hence, the more traditional W approach and the newly developed G approach, constitute tools with which salinity stress as a reduction in transpiration or an increase in plant metabolism can be studied.

4.2 Plant water uptake functions

There are several alternative ways of expressing plant water uptake. Many approaches focus primarily either on meteorological, soil or plant characteristics. A comparison between the three approaches tested in this study is given in Table 1. No explicit account is taken for the plant water storage in the first two models, so therefore actual transpiration is set equal to water uptake.

Table 1. Description of different water uptake functions.

	Focus of approach	Properties	No of parameters
A. Pressure head	Soil	Empirical parameters	4
B. Steady-state SPAC	Plant	Resistance in plant and soil.	7
C. Dynamic SPAC	Plant	Resistance in plant and soil. Plant water storage	9

A. In the first approach the calculation of actual transpiration, E_{ta}^*, is based on potential transpiration, E_{tp}, and a multiplicative response function for soil pressure head, $f(\psi)$:

$$E_{ta}^* = E_{tp} \int_{z_r}^{0} f(\psi(z)) r(z) dz \qquad (7)$$

where z_r is root depth, $f(\psi)$ is a response function for soil moisture content and $r(z)$ is relative root distribution.

B. In the second approach transpiration is driven by differences in water potential between the plant and the soil. Against these driving forces there are resistances in the plant, $r_{p,i}(\Delta z)$, and in the soil, $r_{s,i}(\Delta z)$:

$$E_{ta}^* = \sum_{i=1}^{n_r} \min \left(\frac{\psi(\Delta z) - \psi_{\min} - (H_p + z)}{r_{p,i}(\Delta z) + r_{s,i}(\Delta z)}, \; E_{tp} \cdot r_i(\Delta z) \right) \qquad (8)$$

where n_r is the number of layers with roots, ψ_{min} is the lowest possible water potential of the plant and H_p is plant height.

C. In the third approach plant water storage is explicitly accounted for. Changes in plant water storage, S_p, are calculated as:

$$\frac{\Delta S_p}{\Delta t} = E_{ta} - q_{upt} \qquad (9)$$

The water uptake, q_{upt}, is calculated with eq.(8) substituting ψ_{min} with a leaf water potential, ψ_l. Transpiration is instead calculated as a function of potential transpiration and the leaf water potential, ψ_l:

$$E_{ta} = f(\psi_l) E_{tp} \qquad (10)$$

5. METHOD: MODELLING TOOL - THE COUPMODEL

In order to test the W and the G approaches, a physically based modelling tool was needed. Such models on the flows of water, energy and nutrients through the soil-plant-atmosphere system have been developed and in this project we used and further developed the CoupModel (Jansson & Karlberg, 2001). The CoupModel is a coupling between a physically based model for heat and water flows in the unsaturated zone, the SOIL model (Jansson, 1998), and a model for nitrogen and carbon flows, the SOIL-N model (Eckersten *et al.*, 1998). The reason for choosing this model was that feedback interactions between the plant and its environment could be accounted for (see description below). There are a few models developed for irrigated agricultural systems that include soil salinity, but these models generally do not include detailed descriptions of meteorological processes (Letey & Dinar, 1986). The relatively strong emphasis on those processes in the CoupModel was another reason for choosing this model.

As mentioned above, there were also other reasons for choosing a modelling tool to study the processes behind salinity stress. One advantage with models is that a large, complex and interacting system, such as the soil-plant-atmosphere-continuum, can be understood as an integrated system and at the same time at a very detailed scale. The models also allow us to transfer and test the applicability of empirical data between different sites. Thirdly modelling is cheap compared to field experiments, and can be used as predictive tools for management techniques under various environmental conditions. A vast number of experiments on crop tolerance of salinity and effects on yield etc have been carried out mainly in laboratories but also in the field (Maas & Hoffman, 1977; Shalhevet, 1994). The data collected from these experiments may be studied and efficiently incorporated into operational tools by use of models.

5.1 Feedback mechanisms between the plant and its environment

There are several ways that a plant affects its environment. For example, by intercepting light and precipitation the plant alters both the hydrological and the temperature conditions of the soil surface. Often these alterations result in changes that in turn affect plant growth. These feedback interactions are important in the ecosystems and are incorporated in the CoupModel in several ways. Figure 1. gives an example on some of the important feedback links between the plant and its environment.

When the plant is stressed by drought or soil salinity, the relatively smaller plant affects its environment differently than a non-stressed large plant. For example, the stressed plant develops a small leaf area and consequently intercepts only a little amount of radiation. This leads to more radiation reaching the soil and thus to a higher soil evaporation, which in turn will affect water uptake and growth.

5.2 Adapting the model to the field experiments

Field experiments were carried out to create a database for testing the processes behind salinity and drought stress. These experiments are described in detail below, but important for the modelling was that the studied species, in this case tomato plants were grown in lysimeters standing in a row in a field. Thus, the conditions differ from a natural ecosystem in some aspects that had to be taken into account in the modelling process. At the early stages of plant development, the canopy of the tomato covered only parts of the soil, but as the plant grew bigger its branches stretched out of the sides of the pot. Unlike plants growing next to each other in a field, these plants could also intercept radiation from two sides where neighbours did not shelter them. Thus, in relation to the soil area, the plant could intercept a large amount of radiation. In the CoupModel, the area of the soil in the pot is considered a unit area. Consequently the canopy coverage reached above 100% when the intercepted radiation exceeded the amount of radiation a plant with full canopy coverage of the soil and with homogenous identical neighbours would have intercepted under the same climatic conditions. This value was not measured in the experiments but was estimated by the following function:

$$f_{cc} = p_{c\max}\left(1 - e^{-p_{ck}A_l}\right) \qquad (11)$$

p_{cmax} is the maximum surface coverage and p_{ck} determines the rate at which the plant reaches its maximum surface coverage. These two parameters were obtained by calibrating the simulated transpiration to match the observed.

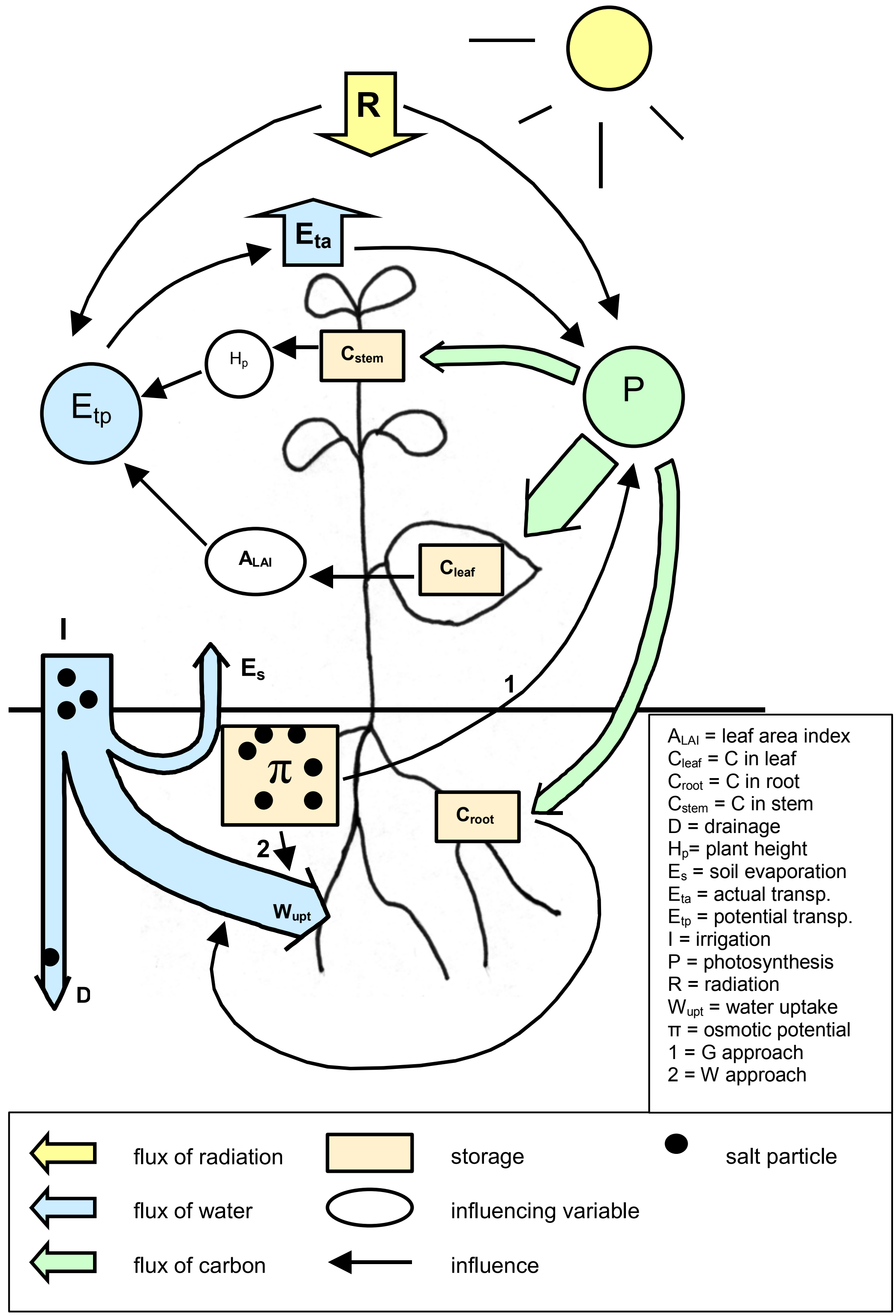

Figure 1. Feedback interactions between the plant and its environment.

In the calculation of the plant radiation interception the degree of surface canopy cover, f_{cc}, is multiplied by the total global incoming radiation per unit soil area in order to obtain the fraction of the radiation that could be retrieved by the plant. The plant interception of global radiation, R_{is}, is calculated according to Beer's law:

$$R_{s,pl} = \left(1 - e^{-k_{rn}\frac{A_{LAI}}{f_{cc}}}\right) \cdot f_{cc}\left(1 - a_{pl}\right) R_{is} \quad (12)$$

where k_{rn} is the extinction coefficient and a_{pl} is the plant albedo.

6. Material: Field experiments on tomato grown under saline, boron toxicity and drought stress in the Arava desert

Two tomato varieties, (*Lycopersicon esculentum* Mill. Cv "*Daniella*" and *Lycopersicon esculentum* Mill. Cv "*5656*"), were grown under salinity, boron and hydrological gradients in lysimeters (diameter approx. 60 cm, volume 225 dm^3) in the field at the Arava Experiment Station, Southern Arava Valley in Israel (29° 53´ N, 53° 3´E), in the autumn of 1997 and spring of 1998. The *Daniella* variety grew more upright, because it was trellised and pruned, whereas *5656* was allowed to grow freely. *5656* is an open field terminating variety, where most of the fruit ripens together and the plant ceases to grow vegetatively, stops flowering and dies, whereas *Daniella* is a non-terminating variety used in greenhouses, and thus continues to grow vegetatively and reproductively as long as you let it. To minimise soil evaporation, the soil in the lysimeters was covered with sawdust mulch.

Different treatments were applied to the tomatoes to create different forms of plant stress. By adding water corresponding to 30–130% (and also 160% for *5656*) of measured actual transpiration in non-stressed tomatoes, a water availability gradient was created in order to study drought stress. Across the water availability gradient the irrigation water salinity was held constant at EC = 3 dS m^{-1}. The tomatoes were also irrigated with saline water that ranged from EC = 1–11 dS m^{-1}, with a constant irrigation amount of 130% of measured actual transpiration in non-stressed tomatoes. Boron stress in combination with drought was achieved by adding boron at concentrations between 0–8 mg L^{-1} for the same drought gradient as described above.

Electrical conductivity, EC, estimates the amount of total dissolved salts or the total amount of dissolved ions in the water, and is the reciprocal to electrical resistance. The SI unit for measuring resistivity is Ohm m, and thus the unit for electrical conductivity was originally μmhos cm^{-1} (i.e. ohm spelled backwards). Micro Siemens per centimetre (1 μS cm^{-1} = 1 μmho cm^{-1}) is the SI unit for measuring electrical conductivity, or for convenience, dS m^{-1} (1 000 dS m^{-1} = 1 μS cm^{-1}). The range of salinities used in the field experiments, i.e. 1–11 dS m^{-1}, corresponds to 585–6640 mg NaCl L^{-1} or 300–3300 cm water.

7. Analysing measurements from the field experiments

7.1 Results

The field experiments confirmed the linear relationship between relative transpiration and relative growth (I). In Figure 2 results from the autumn and the spring experiments on both varieties under salt, drought and boron stress are merged for the *5656* variety.

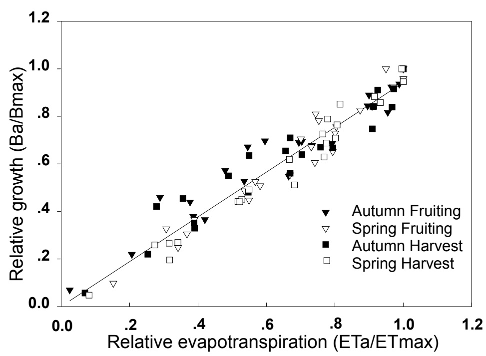

Figure 2. Relative growth (B_a/B_{max}) as a function of relative evapotranspiration (ET_a/ET_{max}) for tomatoes during spring and autumn growing seasons. Symbols differentiate two sampling periods as well as spring and autumn experimental seasons (redrawn from I).

A closer look at these data reveals that actual growth per actual transpiration, i.e. WUE, at each growth stage seems to be relatively constant in the spring experiment, while it increases for each growth stage during the autumn experiment (Fig. 3). The linear relationship between transpiration and growth is not clear for the first vegetative growth, but this might be a result of high soil evaporation in relation to transpiration when the plant is still small.

The apparent difference in the behaviour of WUE development with plant age between the spring and the autumn experiment might be due to differences in climate between the two seasons (I). For example, radiation and temperature influence potential transpiration and photosynthesis, which in turn affects water uptake and growth.

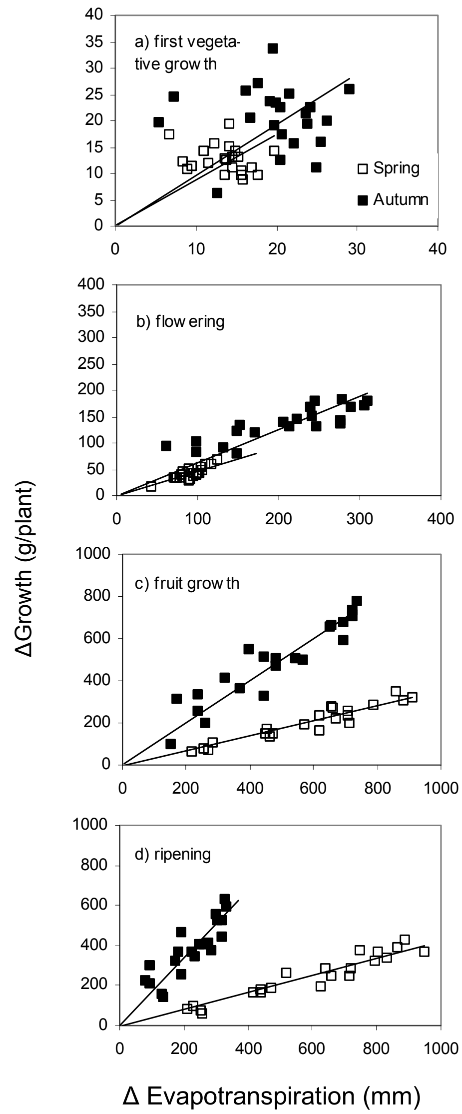

Figure 3. Change in accumulated biomass as a function of the change in accumulated evapotranspiration for four distinct plant developmental stages. Variations in ET and B levels were caused by differences in B concentrations, salinity and water content. The slope of the graph is a measure of the WUE of the system. All graphs were plotted with a 1:1 relationship between the x and the y-axis, to allow for comparisons of WUE between different plant development stages (redrawn from I).

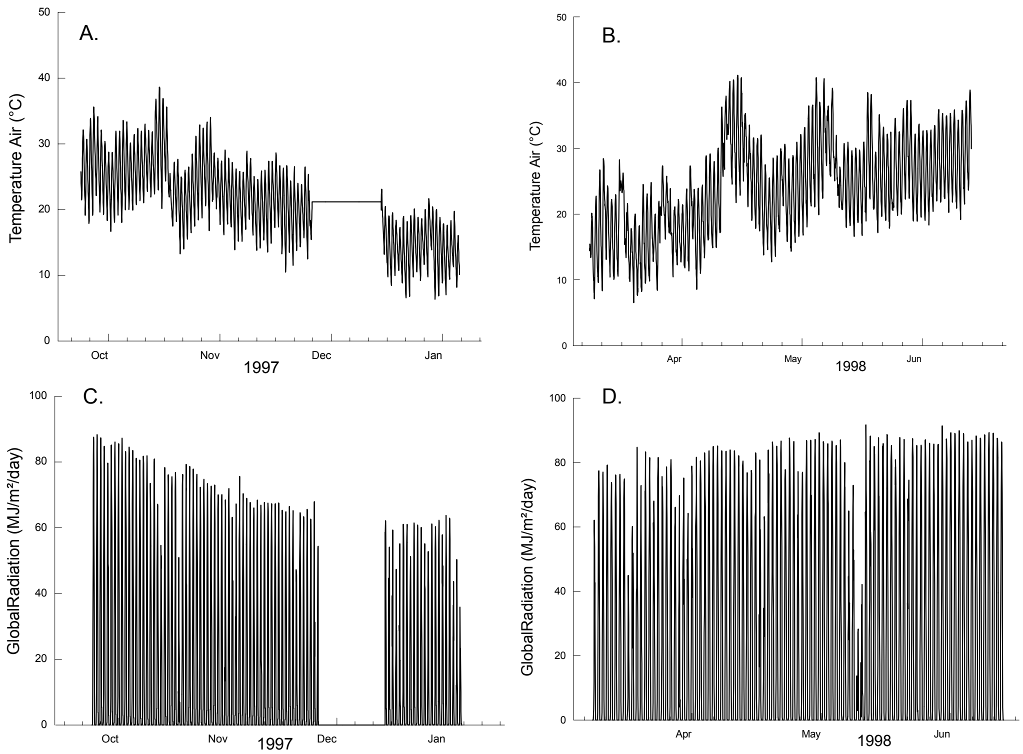

Figure 4. Hourly values on air temperature for A.) autumn and B.) spring experiments and global radiation for C.) autumn and D.) spring experiments.

Climatic data on global radiation and air temperature presented in Figure 4 show higher temperature and radiation levels for the spring period compared to the autumn. According to a study on tomatoes by Bolanos and Hsiao (1991), temperature stress occurs above 35 °C. Therefore, high temperatures might have caused damage to the spring tomatoes during several consecutive days in mid April. During the spring the tomatoes might also be saturated with radiation during parts of the day, assuming a global radiation saturation level of approximately 80 MJ m^{-2} day^{-1} (Bolanos & Hsiao, 1991).

7.2 Discussion

Comparing the ratio between normalised growth and transpiration, i.e. normalised WUE, for stressed (left hand side of graph) and non-stressed plants (right hand side of graph) reveals a different pattern for the spring and the autumn experiment (Fig. 3). While stressed plants seem to have a higher WUE than the non-stressed plants in the autumn experiment, they have a relatively low WUE during the spring. WUE could be influenced by several factors (Table 2).

1. Taleisnik (1987) showed that respiration increases in salinity stressed tomatoes. This finding indicates that the salinity stress is caused by or partly caused by increased energy expenditure. Osmotic adjustment, which is an energy consumptive process, has been shown to maintain turgor potential in tomatoes under moderately saline conditions (Katerji *et al.*, 1998b). If salinity stress is due to ion toxicity, either by increased respiration or by a direct decrease in photosynthesis, a smaller amount of assimilates will be allocated to plant growth per transpired unit of water, thus leading to a lower WUE in

comparison with non-stressed plants. A reduced WUE with increasing salinity stress was shown in several studies (Chaudhuri & Choudhuri, 1998; Khan *et al.*, 1998; Aldesuquy & Ibrahim, 2001; Hester et al. 2001). The same mechanism is likely to cause lower WUE at high boron levels.

2. If salinity stress is a result of decreased osmotic potential in the soil, the mechanism behind the plant stress reaction is similar to that of drought stress. Under conditions of water stress the plant responds by closing of stomata. Since photosynthesis is less strongly affected by stomatal conductance than transpiration (e.g. Gijzen, 1995), WUE is expected to increase under conditions of water stress. Several studies have shown an increasing WUE at high drought (Amede *et al.*, 1999; Liang *et al.*, 2002) and salinity stress (Brugnoli & Björkman, 1992; Marcelis & van Hooijdonk, 1999). However, one recent study showed decreased WUE during drought (Reichstein *et al.*, 2002).
3. Further, the size of the plant might also affect WUE (Marler & Mickelbart, 1998). Photosynthesis and transpiration is lower inside the canopy than on the canopy surface. WUE inside the canopy can therefore be higher or lower than on the canopy surface, depending on relative decrease in photosynthesis and transpiration with distance from the surface. A difference in WUE between surface and interior leaves would result in different WUE between large and small plants, since the ratio between the surface area and the entire plant volume varies with plant size. deSoyza *et al.* (1996) showed that WUE was higher for large desert shrubs than for small. However, assuming that a later plant development stage represents a larger plant size, no such size effect was discovered in the measurements in this study when comparing different growth stages (Fig. 3). An additional complication in this specific experiment is the high global radiation levels in the spring tomatoes, which therefore might be saturated with radiation during parts of the day. At radiation saturation, transpiration rate can be expected to be relatively high in comparison to the rate of photosynthesis, resulting in lower WUE at the canopy surface.
4. There are a number of other additional factors that also are of importance for WUE under salinity stress that have not been dealt with so far. For example, Marcelis and van Hooijdonk (1999) showed that the specific leaf area decreases with increasing salinity. The effect of a lower specific leaf area on WUE is difficult to estimate, since both photosynthesis and transpiration are likely to be affected.

Table 2. Processes affecting WUE.

Process / characteristic	**Relevant plant stress type**	**Mechanism**	**WUE**
Ion toxicity	Salinity and boron	Increased respiration / decreased photosynthesis	low
Water deficiency	Salinity and drought	Closing of stomata, which results in lower H_2O loss while maintaining photosynthesis	high
Plant size	All	Unclear importance of ratio between surface area to canopy volume, and the relative decrease in transpiration and growth with distance from canopy surface.	?
Additional factors	All	E.g. decreasing specific leaf area with increasing salinity.	?

Consequently there are several mechanisms that can affect WUE. Stronger mechanisms could mask some mechanisms that have a less pronounced effect, and distinguishing between an actual stress effect and a pure size effect is a difficult task.

8. Applying the CoupModel on measurements from the spring experiment

8.1 Results

The CoupModel was applied on measurements from the spring experiment, excluding the tomatoes grown under boron stress, using the RUE function (II, III). The G approach showed a good agreement between measured and simulated daily transpiration, both for various salinity and drought stress levels (ME = ±2 mm day^{-1}) when using the same parameter values for all treatments (Fig. 5) (III). This figure can be compared with a daily mean transpiration rate of 6–20 mm day^{-1}.Simulated above ground biomass also correlated well with measurements for the salinity gradient (ME = ±1 gC day^{-1}), but underestimated growth at high stress levels under combined salinity and drought stress (ME = -3–1 gC day^{-1}). Using the same parameterisation the simulations were run with the W approach. In this case simulated and measured biomass correlated well (ME = 0–2 gC day^{-1}). Transpiration under combined salinity and drought stress also showed a good agreement with measurements (ME = -2–0 mm day^{-1}) whereas the simulations underestimated transpiration at high salinities (ME = -4–1 mm day^{-1}).

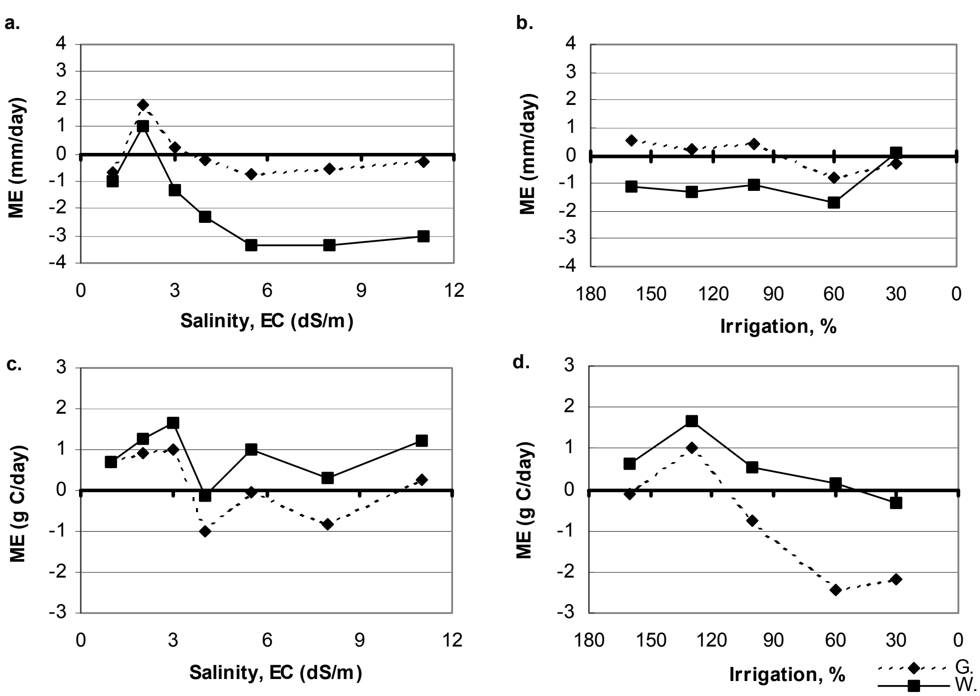

Figure 5. Mean error (ME) of simulated daily transpiration along a) the salinity gradient, b) the drought gradient, and above ground biomass along c) the salinity gradient and d) the drought gradient. Symbols represent the G and W approaches respectively (III).

Table 3. Description of modelling accuracy for three water uptake functions.

Normalised Root Mean Square Error, NRMSE (-), of daily transpiration for different treatments (STDEV within parenthesis)			
Treatment	**A.**	**B.**	**C.**
Drought, (n=9)	0.38 (0.05)	0.38 (0.05)	0.38 (0.05)
Salinity, (n=14)	0.44 (0.14)	0.44 (0.14)	0.44 (0.14)
All, (n=21)	0.42 (0.12)	0.42 (0.12)	0.42 (0.12)
Mean Error, ME (mm day^{-1}), of daily transpiration for different treatments (STDEV within parenthesis)			
Treatment	**A.**	**B.**	**C.**
Drought, (n=9)	0.17 (0.95)	0.19 (0.95)	0.08 (0.88)
Salinity, (n=14)	0.36 (1.54)	0.39 (1.56)	0.29 (1.59)
All, (n=21)	0.24 (1.38)	0.26 (1.40)	0.17 (1.40)
Mean Error, ME (gC day^{-1}), of daily growth for different treatments (STDEV within parenthesis)			
Treatment	**A.**	**B.**	**C.**
Drought, (n=9)	-0.85 (1.50)	-0.88 (1.55)	-1.13 (1.61)
Salinity, (n=14)	0.21 (1.12)	0.21 (1.09)	0.14 (1.21)
All, (n=21)	-0.37 (1.37)	-0.39 (1.38)	-0.53 (1.52)

A comparison of the three different functions A, B and C for water uptake showed no considerable difference in accuracy between the various functions (Table 3) (II). The result is very similar for function A. and B., while C. has got a slightly better accuracy for transpiration and a slightly lower accuracy for growth, in comparison with the other two functions

8.2 Discussion

The explanation to the difference between the two approaches is given if WUE is studied (Fig. 6) (II, III). In the G approach the direct effect of salinity on growth leads to decreasing WUE with salinity, treating the salinity stress as an increased metabolism or a decreased gross photosynthesis due to ion toxicity, ion compartmentalisation or osmoregulation. In the W approach, WUE is not affected by salinity stress, since salinity is only reducing plant water uptake and hence transpiration. The RUE function does not take into account a disproportionate decrease in transpiration and photosynthesis due to the closing of stomata as a response to water stress, and therefore WUE does not increase with increasing salinity in the W approach. Since measured WUE decreased with increasing salinity in the spring experiment (Fig. 6), the G approach shows a better correlation with measurements for the salinity gradient than the W approach. The underestimation of transpiration in the W approach indicates that the tomatoes grown under high salinity stress seem to be transpiring more than predicted if the stress had only been due to a decrease in the soil osmotic potential leading to a lower water uptake and transpiration.

Under combined drought and salinity stress, measured WUE was more or less constant with increasing stress. Even though the irrigation water salinity was kept constant, soil salinity increases with decreasing irrigation water amounts due to less leaching of salts. Consequently, there is a corresponding salinity gradient to the drought gradient. Therefore simulated WUE with the G approach decreased with increasing drought stress, whereas in the W approach, WUE was constant, thus correlating better with measurements than the G approach. The underestimation of growth in the G approach at high drought stress indicates an overestimation of the soil salinity stress on plant growth under combined drought and salinity stress. Other studies have shown that under combined salinity and drought stress, only the most limiting factor will determine growth (Russo & Bakker, 1987; Shani & Dudley, 2001). Thus, by removing the salinity stress effect in the simulation of the combined salinity and drought stress gradient, the correlation between measured and simulated values might increase for the G approach.

As have been discussed previously, the decreased WUE under salinity stress conditions could be related directly to salinity stress or be an indirect effect of decreased plant size at high levels of stress. For the combined drought and salinity gradient no such size effect could be seen since WUE was constant over the whole gradient. It is possible that a decreased WUE with drought, due to small size in combination with radiation saturation, was masked by an increased WUE with drought due to the partial closing of stomata.

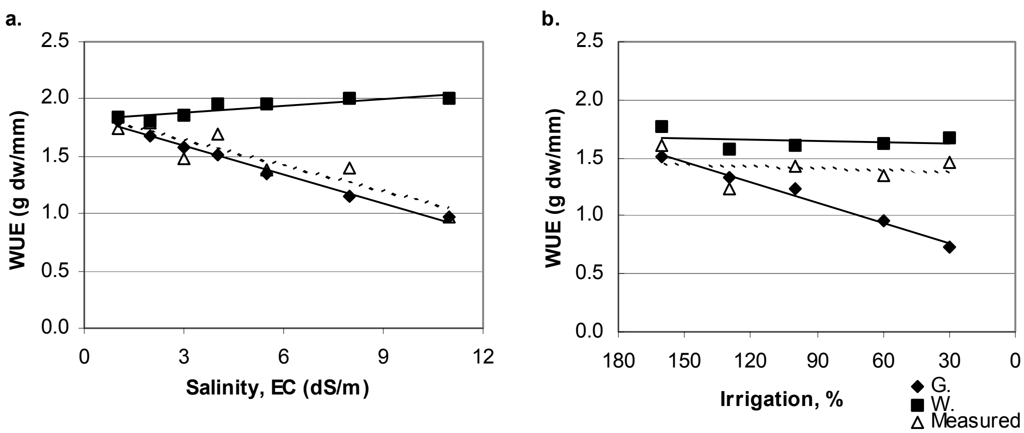

Figure 6. Simulated (solid line) and measured (dotted line) WUE over a) the salinity gradient and b) the drought gradient. Symbols differentiate the G and W approaches and the measurements (III).

9. CONCLUDING REMARKS

Measurements on transpiration and growth from a field experiment on tomatoes grown under boron toxicity, salinity and drought stress for two seasons, showed a linear relationship between relative growth and relative evapotranspiration. WUE varied between different seasons, which is probably explained by climatic differences. The CoupModel was successful in simulating growth and transpiration under salinity and drought stress for the spring season, using a radiation use efficiency function to simulate growth. Salinity stress was simulated in two ways; by a direct reduction of photosynthesis (G approach) and by a decreased water uptake with subsequent growth reductions (W approach). The G approach was more successful in simulating the salinity gradient, while the W approach showed better correlation with measurements under combined salinity and drought stress. Thus, the first hypothesis could not be falsified. The result could be explained by comparing simulated and measured WUE. Independent data for the second season, autumn, will be used to validate these findings, for which the CoupModel might need further development to include adjustments for radiation saturation and temperature stress. No considerable differences in accuracy were shown for the three functions for water uptake tested in the study, and therefore the second hypothesis could not be falsified.

10. Future work

The second phase of the overall project is intended to focus on different low-cost irrigation management techniques with saline waters, by applying the model on data from new field experiments with tomatoes irrigated with saline water. Field experiments will be carried out on station during the dry season in the semi-arid northern South Africa. The objectives are to study the long-term sustainability and yield of a system that minimises soil evaporation, namely drip irrigation, compared to a conventional irrigation system, furrow irrigation, and to identify and understand important physical processes in the systems. Environmental conditions typical for semi-arid Africa, such as a high potential evapotranspiration, constitute a frame for irrigation with saline waters that have to be tested in field experiments. The study will test the following hypotheses:

- Drip-irrigation of tomatoes with saline waters is economically feasible as well as ecologically sustainable in semi-arid Africa.
- A feedback mechanism between soil salinity and plant water uptake creates a steady-state salinity in the soil. By minimising soil evaporation, this steady-state concentration is not disrupted and thus enables long-term sustainability of the system.

By combining measured data with the model, the model will be used for predictions of long-term sustainability and yield of other treatments and at other locations e.g. the length of salt water to fresh water application, and the timing of the salt water application, the irrigation amount, allowing for different leaching amounts, soil type, fertilisation, planting density and mulching.

11. Contributions

- Paper I: The initiative to the field measurements came from Uri Shani and the fieldwork was carried out by Alon Ben-Gal. Alon Ben-Gal also wrote the manuscript. All authors are responsible for results and discussion.
- Paper II: The initiative to the field measurements came from Uri Shani and the fieldwork was carried out by Alon-Ben Gal. Louise Karlberg made the parameterisation and simulations, and wrote the manuscript. The initiative to the modelling came from Per-Erik Jansson. All authors are responsible for results and discussions.
- Paper III: As paper II.

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