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A modified version of ceres-maize model for predicting crop response to salinity stress

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Abstract

A new saline stress index was developed for CERES-Maize, a computer model of maize growth and development, in order to simulate crop response to irrigation with saline water in Mediterranean conditions. Changes from the original model consisted in modifying the estimation of the stress coefficient, which was defined as a function of predawn leaf water potential.

The study was carried out at the Mediterranean Agronomic Institute of Bari using a set-up of 30 drainage lysimeters. Linear regression between mean simulated and measured data showed that the model performed well for final grain yield though it tended to underestimate (~ 8%) above-ground biomass and maximum LAI. The largest evapotranspiration over-estimations were found early in the growing season immediately after each irrigation event. However, the prediction of seasonal evapotranspiration was generally reasonably good.

Keywords: CERES-Maize model; Maize; Saline stress; Simulation; Water stress;

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1.0 Introduction

Irrigation in arid and semiarid areas may increase salt content in the soil and may lead to a deterioration in crop productivity. In the past, irrigation with fresh water was used to satisfy crop water requirements and leach salts out from the root zone (Rhoades, 1984). Currently, the decrease in amount and quality of irrigation water forces growers to revise their irrigation practices. Economic and environmental aspects compel researchers to estimate the risk of pollution.

Considering possible combinations of management practices and environmental conditions and their impact on soil and crop productivity becomes a very complex problem. Fortunately, nowadays we have reasonably accurate methods at our disposal to predict the influence of different climatic and soil conditions and water management on crop response. Mathematical models can integrate all these interactions and are suited to be used in irrigation scheduling or soil water management even in saline conditions.

Available models vary greatly, from very simple to sophisticated, from crop specific to general, and from primarily crop based to soil based. They can be divided into two main groups: seasonal and transient models (Hoffman *et al*., 1990). The first ones are essentially based on an equation that relates yield to the amount of applied water or to the evapotranspiration over the growing season. The models employ very simple methods of accounting for water and solute movement in the soil profile. The main advantage of this approach is its simplicity; its major disadvantage consists in its limited portability.

Transient soil-based models generally use sophisticated numerical solutions of water and solute movement and can predict soil profile conditions in detail. However, the plant roots in the soil are treated as a simple sink and plant growth dynamics are often not considered.

As to transient plant-based models, they describe crop performance quite accurately, under both no-stress and stress conditions, provided a proper calibration. However, they generally do not include salinity effect on the plants.

To predict crop responses to various combinations of irrigation water quality, soil profile and meteorological conditions, we used CERES-Maize, which is a crop specific model simulating crop growth and development (Ritchie, 1985). It requires three types of input information about climate, soil and crop and treats quite accurately of processes considered to be the most influential in determining yields, such as onthogenesis, morphogenesis, growth, senescence, biomass accumulation and carbon partitioning.

However, the original model has two weak points which have made it unsuitable for simulating maize performance in a Mediterranean environment. First, although if it deals with temperature, water and nitrogen stresses, it does not consider any growth and development under saline conditions. Second, CERES models have been evaluated mostly in not water-limited conditions (Hodges *et al.,* 1987; Ritchie and Otter, 1985; Plantureux *et al.,* 1991), but have not yet been extensively tested in areas with a high evaporation demand such as southern Italy.

The aim of this experiment was then to modify the original CERES-Maize model in order to predict the effects of salts on the crop. This included:

modifications in the subroutine POTEV for potential evapotranspiration estimation;

- modifications in the subroutine WATUP concerning the definition of the salinity\water stress coefficients;
- calibration of the most relevant input parameters to adapt the model to the particular experimental conditions (meteorology, soil and plant);
- evaluation of model performance by a comparison of various model outputs (actual evapotranspiration, above-ground biomass, LAI and yield) with experimental data.

Table 1

Soil physical properties

Soil	Particle size in % of mineral parts			$CaCO_3$ in %	% water (v/V)		Dry bulk density (kg/dm^3)
	< 2 µm (clay)	2-50 µm (silt)	>50 µm (sand)		pF2.0	pF4.2	
A	19.0	49.0	32.0	25	36.2	20.4	1.45
B	47.0	37.0	16.0	5	42.0	24.0	1.20

2.0 Experimental design

The study on a crop of maize (*Zea mays*, cv. Hybrid Asgrow 88) was carried out at the Mediterranean Agronomic Institute of Bari (southern Italy). The experimental set-up consisted of 30 drainage lysimeters filled with two types of soil (soil A and B), the principal characteristics are reported in table 1 of. Each group of 15 lysimeters of the same kind of soil was irrigated with water of three different qualities: local fresh water containing 3.7 meq l^{-1} of Chloride (EC = 0.9 dS m^{-1}) as a control (A0 and B0) and two kinds of saline water of 15 meq l^{-1} of Chloride (EC = 2.3 dS m^{-1}, A15 and B15) and 30 meq l^{-1} of Chloride (EC = 3.6 dS m^{-1}, A30 and B30). Thus each of six treatments differing in combinations of soil type $\times$ water quality was replicated in five lysimeters. At the bottom of each lysimeter a pipe serving as drainage outlet connected the lysimeter to a drainage reservoir. Details of this experimental design were described elsewhere (Katerji *et al.,* 1992; van Hoorn *et al.,* 1993; Katerji *et al.,* 1996).

2.1. Measurement of predawn leaf water potential (ψ_b)

Leaf water potential was measured at dawn before sunrise in the upper part of the canopy. Five leaves per treatment were taken from the five replicates, and the water potential was measured with a pressure chamber (Scholander *et al.,* 1965).

2.2. Measurement of evapotranspiration and soil water content

Cumulative evapotranspiration, in mm, was calculated over a period between two successive irrigation events, when drainage stopped, by applying the soil water balance equation:

$$ET = P + I - D \pm \Delta W \quad (1)$$

here P is precipitation, I irrigation, D drainage, and ΔW the difference in water storage of the soil profile, all expressed in mm. In our case, P and ΔW are equal to zero.

Soil water content at the time prior to each irrigation was estimated by subtracting the cumulative evapotranspiration between two successive irrigation events from maximum soil water capacity (the soil supposed at field capacity after each irrigation and at the end of drainage). The value so obtained in mm was then converted in volumetric content.

2.3. Plant and meteorological measurements

Dates of the main phenological events were recorded when attained by 50% of the plants (Doorenbos and Kassam, 1979). The recorded development stages included: sowing, emergence, six-leaf stage, beginning of flowering, beginning of ear formation and harvest.

Leaf area and dry biomass accumulation were determined at each phenological stage, by sampling five plants per treatment, first measuring leaf area (cm^2 $plant^{-1}$) with the "LAH - Licor 1300" apparatus and then dry biomass (g $plant^{-1}$) by oven drying at 75°C for 48 hours. The yield was evaluated as oven-dry weight of the grain at the harvest date.

Daily maximum and minimum temperature and solar radiation, required as input into the CERES model, were measured at the agrometeorological station of the Institute located about 50 m from the experimental site.

3.0 General features of CERES-Maize model

CERES-Maize is a crop specific model aimed at dynamic simulation of maize growth as affected by climatic, plant and soil properties along with certain farm management practices (Ritchie, 1985). It has been developed as a user-oriented model, so its main features are: a) availability of input information on both soil and crop variety; b) minimal demands in computational time.

Because the scope of CERES-Maize is to provide yield estimation, it deals quite accurately with the factors considered to be most important in determining final yield. These include:

- onthogenesis as related to plant genetics, weather and other environmental factors;
- apical development as related to morphogenesis;
- extension of leaves and stems;
- senescence of leaves;
- biomass accumulation and partitioning;

- impact of soil water and nitrogen deficits on growth, development, biomass accumulation and yield.

3.1. Description of the modifications in CERES-Maize

3.1.1. Estimation of Evapotranspiration

Evapotranspiration is calculated in the original version of CERES-Maize by separating soil evaporation from transpiration (Ritchie, 1972). Potential evapotranspiration is calculated using an equilibrium evaporation concept, as modified by Priestley and Taylor (1972), and an equation which expresses the effect of radiation and temperature on equilibrium evaporation. Potential evapotranspiration is then calculated as the equilibrium evaporation multiplied by 1.1 to account for the effects of unsaturated air. The value of the multiplier is increased (greater than 1.1) to allow for advection when the maximum temperature is greater than 35°C and reduced for temperatures below 5°C to account for the influence of cold temperatures on stomatal closure.

The approach adopted by the original model works well enough in no drought conditions, but underestimates crop evapotranspiration in highly advective environments like lysimeters (Castrignanò *et al*., 1997). We modified the Priestley-Taylor equation, matching the proportionality constant to be a function of both maize phenological stage and maximum air temperature. A thorough description of the proposed method can be found elsewhere (Castrignanò *et al*., in press) and the main modifications used are reported in table 2.

3.1.2. Calculation of salinity stress coefficient

Effects of water stress on plant are simulated by the original CERES-Maize using three soil water deficit factors: SWDF, limiting root growth; SWDF1 limiting photosynthesis and grain filling; SWDF2, limiting tissue expansion and then leaf, stem and ear growth. The coefficient SWDF1 is estimated as the ratio between potential root water absorption and potential transpiration, the latter related to solar radiation, LAI and maximum air temperature. SWDF2 is derived directly from SWDF1 according to the empirical relationship: SWDF2 = $0.67 \times$SWDF1, which means that water stress is more severe in affecting plant growth than photosynthesis.

Table 2.

Modifications made to the subroutine POTEV of CERES-Maize model

Function	Expression	Parameters	Units
1) Estimation of net Radiation from solar radiation	$\tau = \frac{Rn}{Rs}$ τ = 0.70 for ISTAGE = 1[a] τ = 0.67 for ISTAGE = 2 τ = 0.71 for ISTAGE = 3 τ = 0.68 for ISTAGE = 4 τ = 0.59 for ISTAGE = 5	R_n = net radiation R_s = solar radiation	MJm^{-2} per day MJm^{-2} per day
2) Determination of α coefficient of the Priestley and Taylor formula	$ETo = \alpha \frac{\Delta}{\Delta + \gamma} Rn$ α = 0.33 for ISTAGE = 8 α = 0.62 for ISTAGE = 9 α =1.24 for ISTAGE = 1 α =1.40 for ISTAGE = 2 α =1.45 for ISTAGE = 3 α =1.31 for ISTAGE = 4 α =0.89 for ISTAGE = 5	ET_o = potential evapotranspiration R_n = net radiation Δ = saturated vapour pressure-temperature curve's slope γ = psychrometric constant	mm day^{-1} MJm^{-2} per day mbar °C $^{-1}$ mbar °C $^{-1}$
3) Estimation of potential evapotranspiration	IF 5°C $\leq$ TEMPMX $\leq$ 20 °C EO = EEQ $\cdot$ α IF TEMPMX > 20 °C EO = α $\cdot$ EEQ $\cdot$ [(TEMPMX - 20) $\cdot$ 0.05 + α] IF TEMPMX < 5°C EO = α $\cdot$ EEQ $\cdot$ 0.01 $\cdot$ EXP (0.18 $\cdot$ (TEMPMX+20))	EEQ = equilibrium evaporation EO = potential evapotranspiration TEMPMX = maximum air temperature	mm day^{-1} mm day^{-1} °C

[a] ISTAGE = 1 (Seedling); ISTAGE = 2 (juvenile development); ISTAGE = 3 (Panicle initiation); ISTAGE = 4 (Grain filling)
ISTAGE = 5 (Effective grain filling); ISTAGE = 6 (Physiological maturity); ISTAGE = 8 (Sowing); ISTAGE = 9 (Germination).

The original CERES-Maize model calculates potential root water absorption rate considering radial flow to single roots and expressing it as a function only of soil water content and root length density. In the model the water potential difference between root and soil is assumed to remain constant at 21 cm of water for all water contents and a flow rate of 0.03 cm^3 cm^{-1} d^{-1} is chosen as an approximate maximum plant-limited flow rate. Root length density and distribution in the soil are estimated on the basis of soil properties and the amount of assimilates partitioned to roots.

If the maximum water uptake exceeds the maximum calculated transpiration rate, the maximum absorption rates from each soil layer are reduced proportionally so that the uptake becomes equal to the transpiration rate. If the maximum uptake is less than the maximum transpiration, the transpiration rate is set equal to the maximum absorption rate.

The estimation of the root growth in the soil is a really weak part of CERES Model as certain assumptions, difficult to verify experimentally, are used for simulation (Ritchie, 1985). In fact, root growth patterns depend on many physical and chemical soil properties, the amounts of assimilates transported to the roots, and soil water content. Therefore, we decided to follow a different approach in estimating the salinity stress coefficient.

In the original CERES-Maize, growth reduction is not directly dependent on plant water status, but rather on soil water status. Expressing the new salinity/water stress coefficients (SWDF1 and SWDF2) as a function of some direct indication of plant water status seemed to be a reasonable assumption. We chose predawn leaf water potential because it is a synthetic parameter related to water status of the plant in equilibrium with the soil (Katerji et al., 1996). The study of the relationship of the ratio between actual evapotranspiration (ETR) and potential evapotranspiration (ETP) (relative evapotranspiration) as a function of predawn leaf water potential (ψ_b), conducted on maize in different experimental conditions, has produced quite similar results (Katerji et al., 1994; Dwyer and Stewart, 1984). We equalised the new stress coefficient SWDF1 to relative evapotranspiration and used the data collected by Katerji et al., 1994 to adapt a non-linear piece-wise function of the following type (fig. 1):

$$SWDF1 = b_0 + \frac{b_1}{[1 - b_2 \times \exp \quad (c)]} \qquad \text{for } \psi_b \leq \text{-1 bar}$$

$$SWDF1 = b_0 + \frac{b_1}{\left[1 - b_2 \times \exp\left(\frac{-c}{\psi_b}\right)\right]} \qquad \text{for } \psi_b > \text{-1 bar} \tag{1}$$

The stress function (1) was calculated using the non-linear fitting procedure (NLIN) of the statistical software package SAS\STAT (SAS, 1997), which provides least-squares estimates and asymptotic standard errors of the coefficients (b_0, b_1, b_2 and c) and mean square error (MSE) of the model. The results of fitting are reported in table 3.

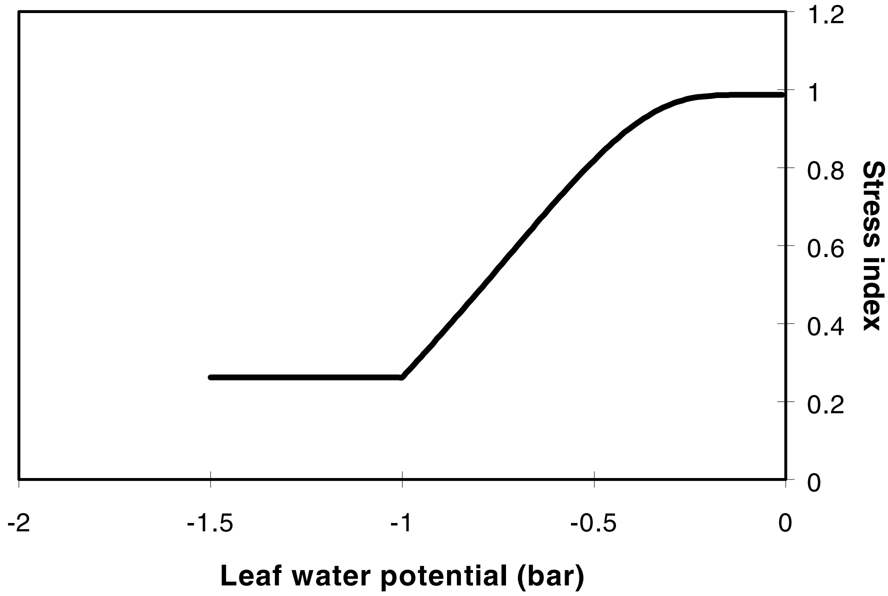

Fig. 1. *Stress coefficient SWDF1 function for maize crop as a function of predawn leaf water potential.*

Then, we calibrated ψ_b as a function of relative total water supply in the soil profile for each type of soil and each salinity level of irrigation water. As regards the salinity levels used, they were chosen because they define the salinity interval of irrigation water used in agriculture.

For each combination of soil type and salinity level, a linear piece-wise model was fitted to the measurements of predawn leaf water potential:

$$\psi_b = a \qquad \text{for } TSW < b \qquad (2)$$

$$\psi_b = e\,TSW + f \qquad \text{for } b \leq TSW \leq d$$

$$\psi_b = c \qquad \text{for } TSW > d \text{ (with } a < c \text{ and } b < d) \qquad (3)$$

where ψ_b is predawn leaf water potential (in bar); TSW is actual soil water supply divided by volumetric soil water content at saturation, varying within the interval (0,1); a, b, c, d, e and f regression coefficients. The standardisation of soil water supply was necessary because maximum soil water content changed as a function of soil type and water salinity. The coefficients were estimated by the linear least-square method (Marquardt, 1983), using lysimetric predawn water potential and soil water content measurements relative to one single drying-up cycle, recorded between two successive irrigation events.

In figure 2 the six calibration curves for each combination soil type × salinity level are reported. The differences between all curves are highly significant, as the standard deviations equal, on average, 0.05 bar (not reported in figure owing to their smallness). As it is clear from the graphs, water availability to crop decreased as salinity level increased.

As regards the other stress coefficients, SWDF2 and SWDF, we retained the original definition in the CERES-Maize model.

Table 3.

Parameter estimates, asymptotically valid standard error of the estimate and mean square error of the stress function.

Parameter	Estimate	Asymptotic Standard Error
B_0	0.986	0.119
B_1	662.686	0.001
B_2	212.113	127.313
C	1.463	0.638

Mean Square Error (MSE) = 0.482

3.1.3. Calibration of input parameters

The input parameters needed to run CERES-Maize are listed in table 4, together with the corresponding values measured directly or calculated, among them the most relevant ones concern genetics and soil. As regards cultivar parameters, the calibrated values were those required to achieve the correct simulation of phenological dates (flowering and maturity) and grain yield, recorded on plants grown in the lysimeters filled with soil A and irrigated with fresh water, according to the method proposed by Ritchie and Alagarswamy (1989). The values thus obtained were then used as input in all simulations.

As regards soil parameters, the values for the lower, drained upper and saturated limits of available soil water (LL, DUL, SAT) were based on those measured in laboratory on soil samples of the two kinds of soil and irrigated with saline water of the same salinity levels used in the experimental trial.

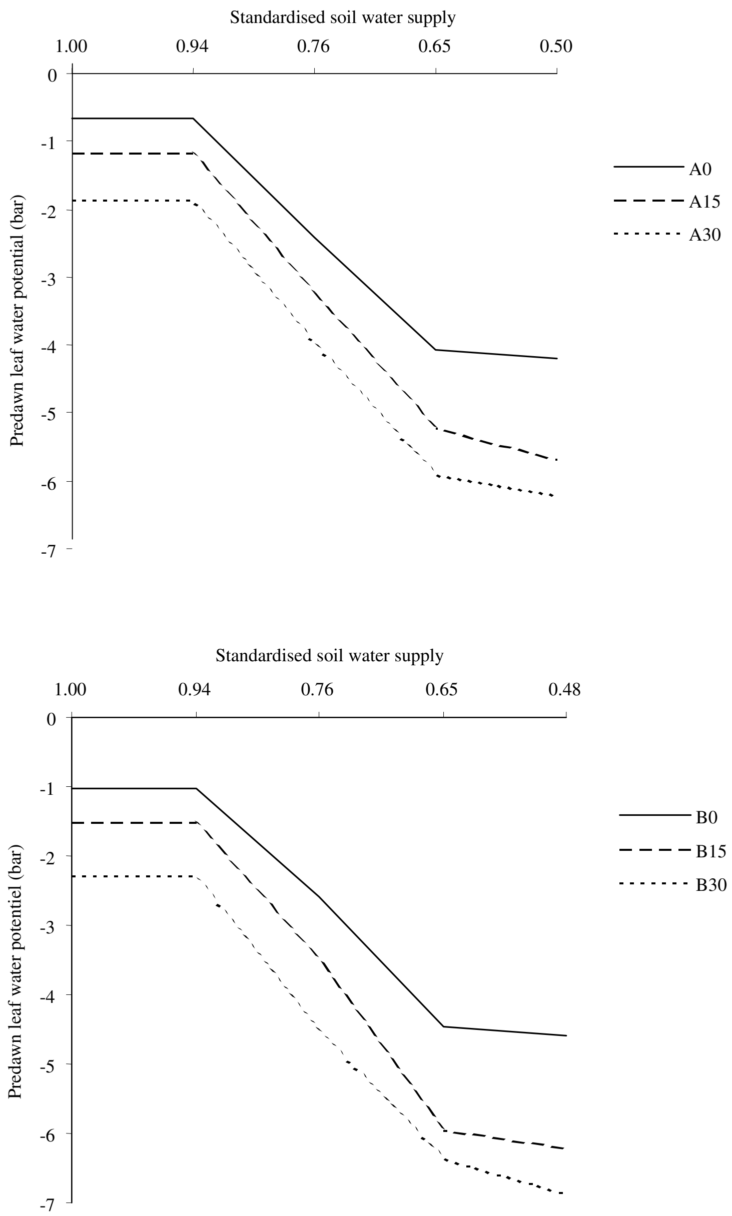

Fig. 2. *Calibration curve of predawn leaf water potential vs. standardised soil water supply for each saline treatment and soil type.*

4.0 Model evaluation

Cumulative crop evapotranspiration, cumulative above-ground biomass, LAI, estimated at the different dates of observation, and final grain yield were chosen as response variables to value model performance.

A linear regression between mean predicted and measured values for each of the variables under study was made and two Student's tests were applied to verify the following two "null" hypotheses: intercept=0 and slope=1.

5.0 Results and Discussion

Some results of simulations, compared with corresponding measurements, are reported for each combination soil type x water salinity level in table 5. As regards the fresh water treatment for the soil A, the simulation was quite good in terms of yield, above-ground biomass and maximum LAI. On the contrary, the model overestimated grain yield and biomass of the fresh water treatment for the soil B. Using the same cultivar coefficients for both soils does not then allow to account for a decrease in productivity of the soil B compared with the soil A. That is quite probably caused by differences in texture composition between the two soils and a related less water availability in the soil B. From this first comparison between the two soils, we can then verify a low sensitivity of model cultivar parameters to soil texture differences, heritage of the original model because differences in model performance between the two soils were also found in the fresh water treatments.

Simulation differed sensibly from reality as concerned phenology, as simulated dates for both flowering and physiological maturity lagged five days behind, regardless of treatment. Moreover, as regards saline treatments, an underestimation (10%-20%) of maximum LAI was observed, reflected then in the same proportion in above-ground biomass.

To evaluate model performance, time paths of simulated evapotranspiration, above-ground biomass and LAI, compared with observed data, are reported on a daily scale for all treatments and for each soil type in figures 3, 4 and 5 respectively. The overall matching between evapotranspiration simulations and measurements (fig. 3) was satisfactory for both soils and all saline treatments, with a slight overestimation during the central phase of the crop cycle for the more stressed treatment. The greatest deviations were observed early in the growth period, from sowing to about day of year 223, when the soil was mostly uncropped and in correspondence to irrigation events. After irrigation, simulated evapotranspiration decreased very quickly from unrealistic high values, becoming very low within one or two days at most, unlike a natural process which develops more gradually.

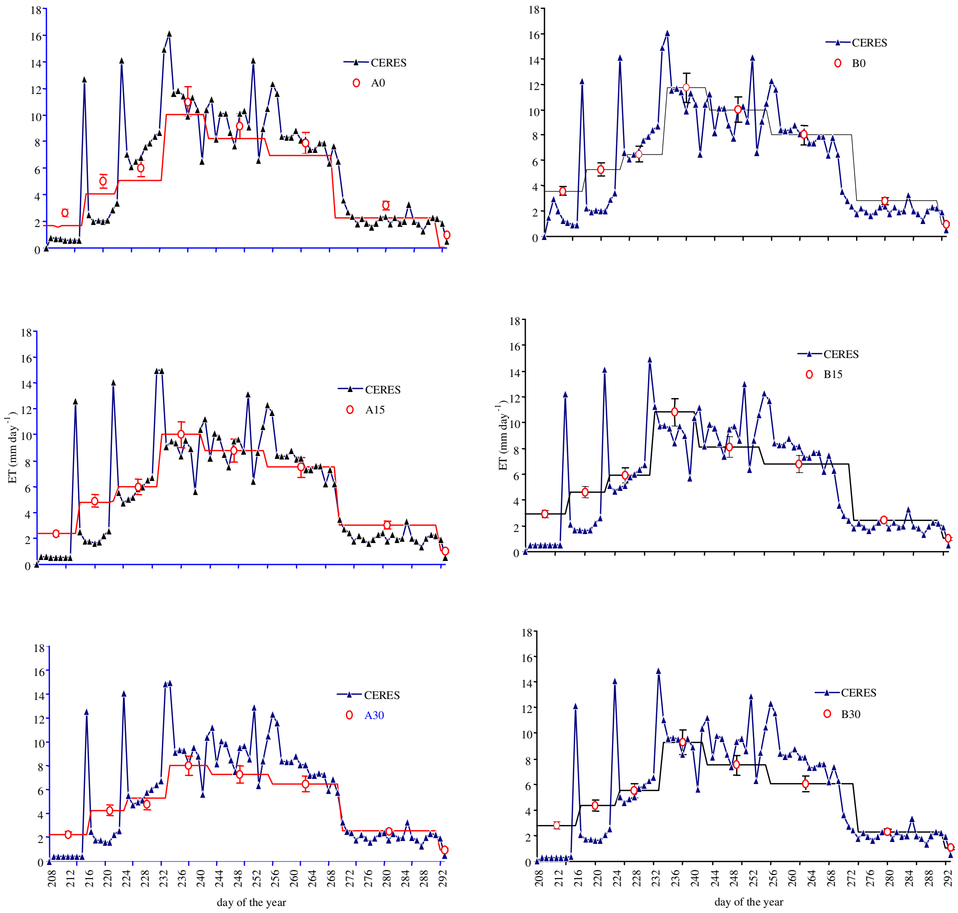

Fig. 3. *Comparison between measured and predicted daily evapotranspiration as simulated by CERES-Maize.*

TABLE 4.
Some input data required for CERES-Maize simulation model (Jones and Kiniry, 1986).

Parameter or Variable	Acronym	Units	value	
Location data				
Latitude	LAT	degrees	41	
Planting data				
Sowing depth	SDEPTH	cm	5	
Plant population	PLANTS	plant m^{-2}	6	
Climatic data				
Year	IYR	-		
Day	JDATE	day of year		
Maximum temperature	TEMPMX	°C		
Minimum temperature	TEMPMN	°C		
Solar radiation	SOLARD	MJ m^{-2}		
Rainfall	RAIN	mm		
Cultivar data				
Cultivar name	NAME	-	Hybrid Asgrow 88	
Thermal time from emergence to end of juvenile stage	P1	°C day	80	
Photoperiod sensitivity coefficient	P2	day h^{-1}	0.30	
Thermal time from silking to physiological maturity	P5	°C day	500	
Potential kernel number	G2	kernels $plant^{-1}$	720	
Potential kernel growth rate	G3	mg $kernel^{-1}$ per day	11	
Soil data			Soil A	Soil B
Soil albedo	SALB		0.13	0.14
Stage-1 soil evaporation coefficient	U	mm	11	10
Whole-profile drainage rate coefficient	SWCON		0.60	0.40
Runoff curve number	CN2		83	81
Lower limit of plant-extractable water	LL	cm^3 cm^{-3}	0.250	0.277
Drained upper limit	DUL	cm^3 cm^{-3}	0.436	0.464
Saturated water-content	SAT	cm^3 cm^{-3}	0.590	0.619

A probable explanation of such mismatching might be that before crop closing, canopy evapotranspiration is largely affected by soil evaporation, the estimation of which is generally quite difficult since it involves the calibration of some critical coefficients controlling soil drying. Another very likely cause of disagreement between simulation and reality might be the difference in the time interval used to calculate simulated and observed data: the former were predicted daily, whereas the latter were expressed as daily averages over the period between two successive irrigation events. However, the prediction of seasonal evapotranspiration was generally good enough.

TABLE 5.

Comparison between predicted and observed data for each combination salinity level × soil type.

Variable	Units	A_0		A_{15}		A_{30}	
		predicted	observed	predicted	observed	predicted	observed
Anthesis date	(d.o.y*)	258	253	258	253	258	253
Maturity date	(d.o.y)	298	293	298	293	298	293
Grain yield	(kg/ha)	6837	6783	5597	6740	5470	5331
Kernel weight	(kg)	0.230	0.244	0.212	0.254	0.212	0.232
Grains per m²	-	2994	2766	2655	2666	2600	2301
Grains per ear	-	498.98	521.00	442.49	486.00	433.33	505.00
Max LAI	-	3.52	3.42	2.43	3.08	2.41	2.78
Biomass	(kg/ha)	14652	14661	10766	13873	10585	12696
ETR	(mm)	524	520	488	494	484	424

Variable	Units	B_0		B_{15}		B_{30}	
		predicted	observed	predicted	observed	predicted	observed
Anthesis date	(d.o.y*)	258	253	258	253	258	253
Maturity date	(d.o.y)	298	293	298	293	298	293
Grain yield	(kg/ha)	6854	5477	5616	4858	5570	4141
Kernel weight	(kg)	0.230	0.221	0.212	0.226	0.212	0.212
Grains per m²	-	2998	2467	2662	2150	2646	1951
Grains per ear	-	499.67	526.00	443.64	486.00	441.04	441.00
Max LAI	-	3.53	3.43	2.43	2.98	2.38	2.72
Biomass	(kg/ha)	14683	13236	10794	11915	10715	11332
ETR	(mm)	529	571	484	492	480	448

As regards dynamic evolution of cumulative biomass (fig. 4), there were no significant differences between the two kinds of soil, with the exception of a more dramatic effect of simulated salinity stress on the plants cropped in soil B. The agreement between simulation and reality was quite good as regards fresh water treatments; on the contrary, the simulated reduction of biomass caused by salinity stress was too severe, mainly for the less stressed treatment. This disagreement between prediction and reality might be caused either by partial crop adaptation to saline conditions or as this level of stress is still too weak to perceptibly affect first photosynthesis and then biomass accumulation.

LAI prediction showed the same weakness observed for biomass (fig. 5). Model fitting was quite good for the fresh water treatments, except after flowering when actual leaf senescence developed more quickly than in simulation. A quite reasonable cause of that was the poor simulation of leaf senescence in the original CERES model (Carberry et al., 1989 ; Carberry, 1991 ; Lahrouni et al., 1993), which produced an overestimation of the amount of green leaf tissues, actively photosynthesizing. Again, matching was the worst for the less stressed saline treatment and, very likely, the same explanation given for biomass might still hold.

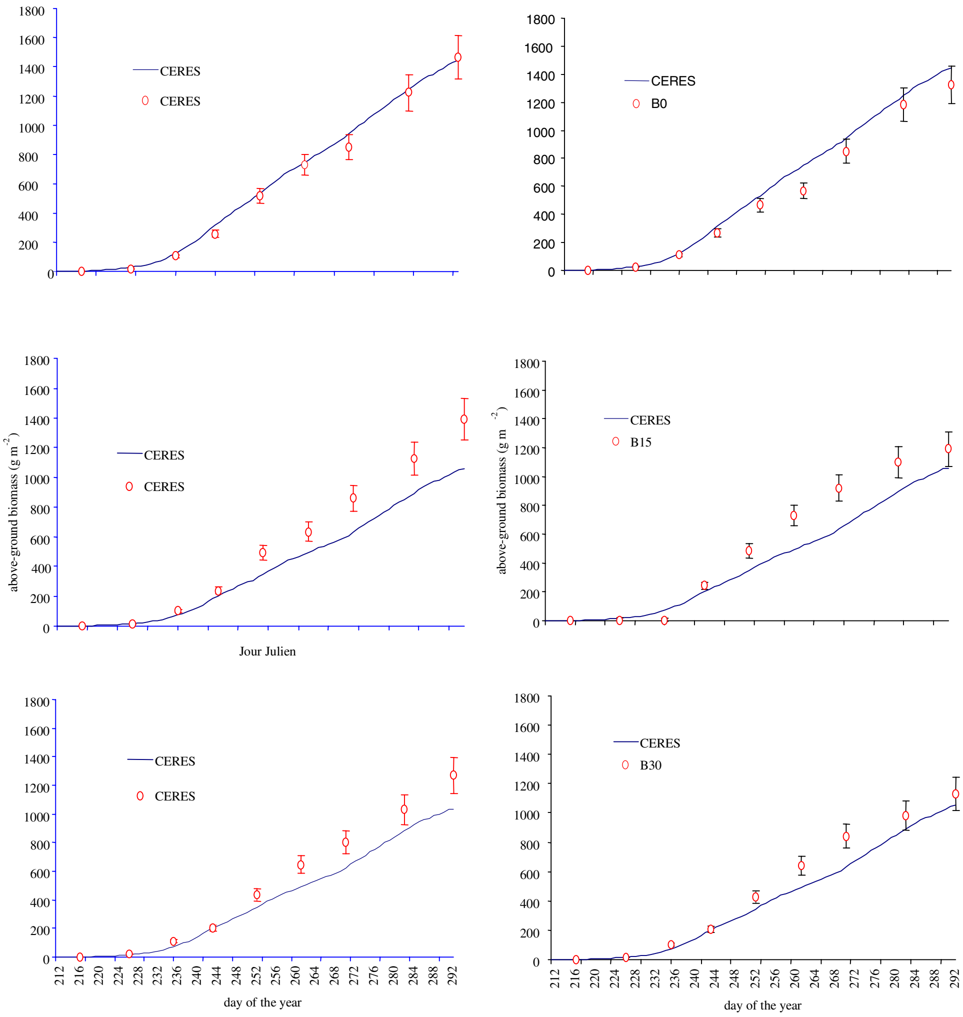

Fig. 4. *Comparison between measured and predicted biomass as simulated by CERES-Maize.*

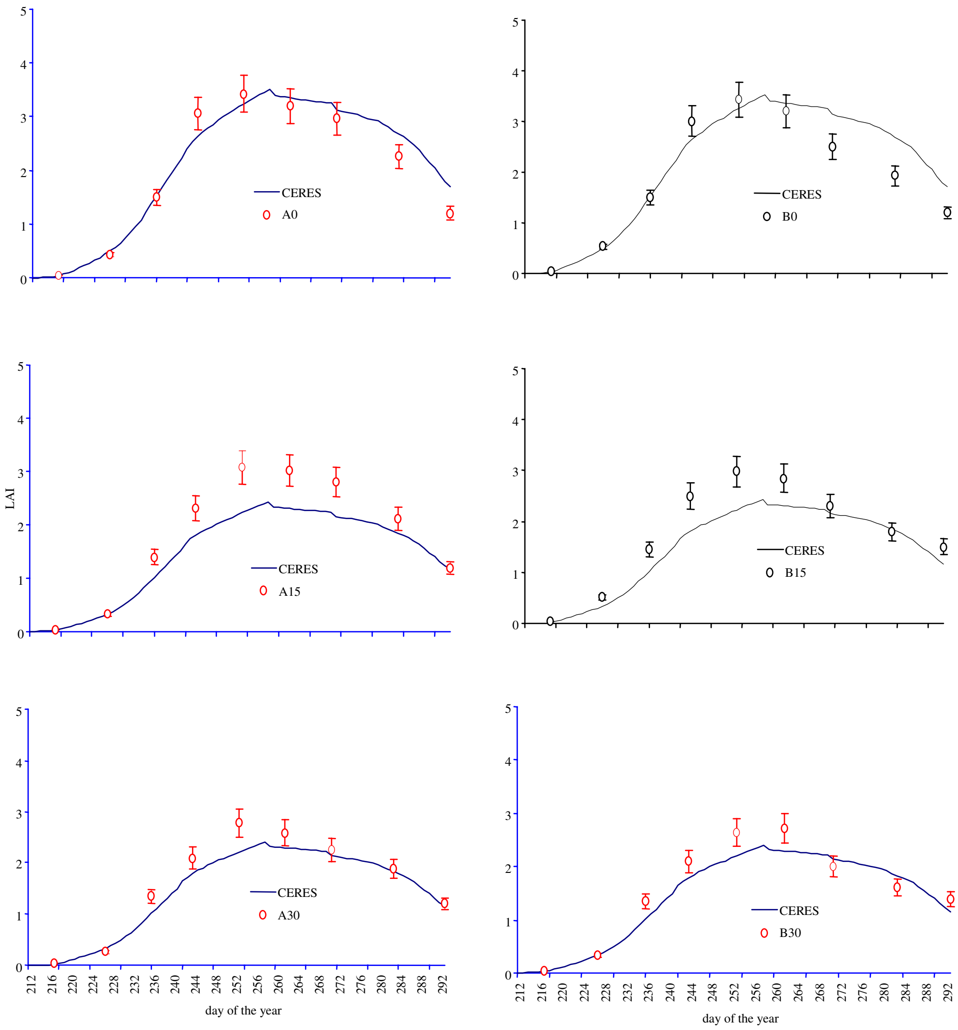

Fig. 5. *Comparison between measured and predicted Leaf Area Index as simulated by CERES-Maize.*

For a more objective comparison between simulation and reality, a linear regression was performed between the averaged values of predictions and experimental data, in relation to the following response variables: final grain yield, cumulative crop evapotranspiration, cumulative above-ground biomass and LAI. The results of this analysis are reported in table 6. As regards final grain yield and LAI, the simulation was quite good, because the intercept and the slope were not significantly different from 0 and 1, respectively. On the contrary crop evapotranspiration was biased at low values and overestimated of about 8%. The prediction of above-ground biomass was better, because it resulted not biased and slightly underestimated (less than 1%).

The quite high determination coefficients (R^2), with the only exception for LAI, seem to suggest that the modified CERES-Maize model reproduces well enough the mean performance of a maize crop irrigated with water of salinity ranging within the interval commonly used in Mediterranean agriculture.

In conclusion, the preliminary results of the test of the modified CERES-Maize model can be considered quite satisfactory and encouraging. However, the model needs to be improved in the following points : increasing model sensitivity to soil type, as it failed to simulate the less productivity of the soil B (more clayey), even in no-stress conditions, due to a reduction in water availability for plants; redefining the stress function in the light of further experimental evidence, either in terms of threshold values or analytical form; modifying the simulation of the rate processes of leaf-growth and senescence, which will also result in better simulation of biomass and grain yield.

Table 6. ***Results of the regression between the averaged values of predicted and measured data of final grain yield, cumulative evapotranspiration, cumulative above-ground biomass and LAI.***

Parameter	Intercept		Slope		R^2 and
	Estimate	Standard Error	Estimate	Standard Error	n(5)
Final Grain yield	-0.204 ns	0.585	1.082(1)	0.115	0.96 (6)
Evapotranspiration	23.488(2)	7.75	0.924(3)	0.027	0.96 (17)
Above-ground biomass	25.273 ns	1.146	1.077(4)	0.035	0.95 (20)
Leaf Area Index	0.135 ns	0.092	1.002(1)	0.048	0.88 (20)

(1) the slope is not significantly different from 1

(2) the intercept is significantly different from 0 for p<0.001

(3) the slope is significantly different from 1 for p<0.01

(4) the slope is significantly different from 1 for p<0.05

(5) the numbers within the brackets represent the number of observations

ns, The intercept is not significantly different from 0

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