Growth, Water Relations, and Ion Content of Field-grown Celery [*Apium graveolens* L. var. *dulce* (Mill.) Pers.] under Saline Irrigation

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ABSTRACT. We irrigated field-grown celery *(Apium graveolens* L. *var. dulce* [Mill.] Pers. 'Tall Utah') with four concentrations of saline water, NSC (nonstressed control), SW1, SW2, and SW3, corresponding to EC of 0.5, 4.4, 8.5, and 15.7 dS·m⁻¹, respectively, plus a nonirrigated control (NIC) and investigated the effects of the treatments on water relations, yield and ion content. In addition, we compared simultaneously plant response to both salt and drought stress by using a modified version of the threshold-slope model. Increasing salinity of the irrigation water reduced fresh and dry weights of the shoots, but increased the dry matter percentage in shoots. The marketable yield was moderately affected by salinity (25% reduction at EC 8.5 dS·m⁻¹). In contrast, a severe water stress dramatically decreased the marketable yield from 23 t·ha⁻¹ (average of the irrigated treatments) to <7 t·ha⁻¹ (nonirrigated control). Na⁺ and Cl⁻ concentrations increased in salinized plants whereas nitrogen content, K⁺, Ca²⁺, and Mg²⁺ concentrations decreased upon salinization. Midday leaf water potentials (Ψ_t) decreased from –1.48 MPa (0.5 dS·m⁻¹) to –2.05 MPa (15.7 dS·m⁻¹) and –2.17 MPa (nonirrigated control), though the reduction in leaf cellular turgor was less severe. The maintenance of high leaf cellular turgor was positively correlated to a decrease in osmotic potential and to an increased bulk modulus of elasticity. These results indicate that it is possible to irrigate celery with saline water (up to 8.5 dS·m⁻¹) with acceptable losses in marketable yield and confirmed that in the field, this species has the ability to efficiently regulate water and ion homeostasis. In the absence of irrigation, celery plants were unable to cope with the drought stress experienced, although this was comparable, in terms of soil water potential, to the one caused by saline irrigation.

Celery is considered a moderately salt sensitive vegetable crop (Francois and West, 1982; Rhoades et al.,1992). However, this species has a halophitic ancestry (Yamaguchi, 1983) and it has often been used as a model to investigate the physiological and molecular basis for plant salt tolerance (Aloni and Pressman, 1980; 1987; Everard et al.*,* 1994; Francois and West, 1982; Loescher and Everard, 1996; Stoop et al.*,* 1996). Only a few researchers, however, have addressed the question of how this species regulates water and solute homeostasis under saline conditions (Pardossi et al.*,* 1998). Water stress is one of the primary and most common responses of plants to salinity. Therefore, the assessment of plant water relations is critical, first to describe any salt tolerance performance in a physiological context, second to compare plant performance in different environments and, finally, to verify the possibility of growing celery in the field using saline water as an irrigation source. Crop salt tolerance depends to a large extent on the environmental condi-

tions in which such tolerance is evaluated (Dalton et al., 1997; 2000; 2001; Maas and Grattan, 1999). In some coastal areas of Mediterranean regions, saline water is the only source of water available for irrigation. Consequently, in these areas, saline irrigation is often performed in salinized soils that, over time, have encountered significant modifications of their physico-chemical properties. Therefore, the assessment of species- and environment-specific salt tolerance performance is fundamental in order to design cropping systems to optimize the use of local water resources (Rhoades et al.,1992; Pardossi et al., 1999).

In this study we evaluated the overall performance of field grown celery subjected to irrigation with saline water in a long-term salinized soil to better understand its physiological response in this Mediterranean environment.

Materials and Methods

STUDY SITE AND EXPERIMENTAL TREATMENTS. The experiment was carried out in 1998 at the Agronomy farm of the University of Naples (40° 31'N, 14° 58'E) on an experimental field that had been irrigated with saline water for the past 10 years (De Pascale and Barbieri, 1995; 1997; 2000). The experimental field was a clay loam soil with 42% sand, 27% loam, 31% clay and trace amounts of lime. Water contents at field capacity (in situ) and at –1.5 MPa (determined using a pressure plate) are reported in Table 1. The experimental treatments consisted of three sea salt

Table 1. Water content (% volume) at field capacity determined in situ (FC) and water content at –1.5 MPa determined using a pressure plate (WP) in 0 to 30 and 0 to 60 cm soil layers as affected by long term irrigation with saline water. NSC = nonstressed control; NIC = nonirrigated control; SW1 = 4.4 dS·m^{-1}; SW2 = 8.5 dS·m^{-1}; SW3 = 15.7 dS·m^{-1}.

Soil layer (cm)	NIC–NSC		SW1		SW2		SW3	
	FC	WP	FC	WP	FC	WP	FC	WP
0–30	35.5	17.5	34.7	16.8	33.9	16.6	37.2	17.9
30–60	35.9	17.5	35.3	17.6	34.8	16.6	42.8	24.1

concentrations of the irrigation water SW1, SW2, SW3 corresponding to EC of 4.4, 8.5, 15.7 dS·m^{-1} and osmotic potentials (OP) of 0.22, 0.35 and 0.73 MPa, respectively. Furthermore, a nonstressed control (NSC, EC = 0.5 dS·m^{-1}; OP = 0.02 MPa) and a nonirrigated control (NIC) were included. Saline water was obtained by adding commercial sea salt (Na$^+$ 12.3, K$^+$ 3.8, Ca^{2+} 0.02, Mg^{2+} 0.04, Cl$^-$ 14.4, SO$_4^{2-}$ 0.03 mol·kg^{-1}) to the irrigation water (Na$^+$ 0.53, K$^+$ 0.05, Ca^{2+} 1.55, Mg^{2+} 0.84, Cl$^-$ 0.38, SO$_4^{2-}$ 0.15, HCO$_3^-$ 4.73 mol·m^{-3}). Commercial sea salt was used to realistically reproduce the actual composition of the irrigation water available in the experimental area considered, which is contaminated by sea water. The amount of water applied at each irrigation was calculated as the net evaporation over the entire soil surface between two irrigation events as determined using a Class A evaporation pan. Plots were irrigated every 5 d, using a drip irrigation system with 2 L·h^{-1} emitters (4 emitters/m^2). The estimated water consumption was based on a nonstressed crop, therefore all treatments (with the exception of NIC) received the same amount of water. Of course, salinized plants did actually receive higher leaching fractions, as expected, because their growth, and consequently their transpiration (T), was reduced under stress (Hoffman, 1990).

GROWTH CONDITIONS. On 23 Apr., celery seedlings [*Apium graveolens* L. *var. dulce* (Mill). Pers. 'Tall Utah'] were placed 0.22 m apart within rows and rows were planted 0.5 m apart. Before transplanting the seedlings, N at 80 kg·ha^{-1}, P at 75 kg·ha^{-1} and K at 133 kg·ha^{-1} were applied to the soil. After transplanting, plants were side-dressed with additional nitrogen fertilizer (N at 100 kg·ha^{-1}). An initial irrigation (30 mm) with nonsaline water was used to ensure proper establishment of the plantlets. Saline treatments were initiated 41 d after transplant (3 June). The total amount of water applied from the beginning of the salt treatments until harvest was 265 mm (distributed in six irrigation events). Rainfall throughout the growing period was 115 mm (48 at the end of April after transplanting and 67 during May) and mean temperature ranged between 14 °C and 25 °C. Harvest began 84 d after transplanting (16 July), when the control plants had reached the marketable size of small bunches, which according to the European Union Grade Standards is between 150 and 500 g/plant (nonmarketable yield included bunches with heart rot or injuries).

WATER POTENTIAL MEASUREMENTS. At 67 and 82 d after transplanting (DAT), total water potential (Ψ_t) was measured between 12:00 and 1:00 PM on tissue discs punched from the first uppermost fully expanded, healthy and sun-exposed leaf and on excised segments of secondary roots (in the 0 to 25 cm soil layer) taken from nine plants per treatment (three per each replication). Measurements were performed before irrigation, with a thermocouple psychrometer type B (Slavick, 1974). The osmotic potential (Ψ_π) was measured on frozen/thawed samples and pressure potential (Ψ_p) was estimated as the difference between Ψ_t and Ψ_π, assuming a matric potential equal to zero (Hsiao, 1973).

Leaf osmotic adjustment (OA) during the growing season was determined as the difference $\Psi_{\pi o}RWC_o - \Psi_\pi RWC$, where $\Psi_{\pi o}RWC_o$ is the product of [osmotic potential] × [relative water content] of unstressed plants (NSC) and $\Psi_\pi RWC$ is the product of [osmotic potential] × [RWC] of leaves from salinized or nonirrigated plants (Morgan, 1984). In addition, diurnal osmotic adjustment (OA$_d$) in leaves was determined as the difference $^{100}\Psi_\pi RWC_o - (\Psi_\pi RWC$, where $^{100}\Psi_\pi RWC_o$ is the product of [osmotic potential] × [RWC] at full turgor for samples harvested at dawn and $\Psi_\pi RWC$ is the product of [osmotic potential] × [RWC] of comparable leaves sampled at midday. For each measurement, the RWC was calculated as (leaf fresh weight – leaf dry weight)/(leaf saturated weight – leaf dry weight). The osmotic potentials at full turgor were measured via thermocouple psychrometry on distilled water saturated leaves (Turner, 1981).

The bulk elastic modulus of the leaf tissue (ϵ) was calculated according to the relationship (Morgan, 1984): $d\Psi_p/d\Psi_t = \epsilon/(\epsilon - \Psi_\pi)$, where Ψ_p is the leaf pressure potential, Ψ_t is the total leaf water potential and Ψ_π is the leaf osmotic potential. Specifically, ϵ was calculated by rearranging the equation as follows: $\epsilon = \Psi_\pi (d\Psi_p/d\Psi_t)/(d\Psi_p/d\Psi_t - 1)$. For each treatment and for each date, the term $d\Psi_p/d\Psi_t$ was calculated as the slope of the linear relationship between leaf pressure potential and leaf water potentials measured at midday.

SOIL. During the growing season, soil samples from each experimental plot were taken 1 d before and 2 d after each irrigation event at 30-cm depth increments in the 0 to 120 cm soil profile, for measurements of electrical conductivity (EC$_e$) on saturated soil extracts (Kalra and Maynard, 1991). At the same time, soil water content was determined in each plot using a soil neutron probe at 30-cm depth increments in the 0 to 120 cm soil profile. The soil matric potential was calculated in the 0 to 60 cm soil layer from the soil moisture characteristic curves [h (θ)] (Ruggiero et al., 1999). The osmotic potential of the soil water in the 0 to 60 cm soil layer was derived by the EC$_e$ measurements (Rhoades et al., 1992). Total soil water potentials were calculated by adding to the matric water potential values the corresponding osmotic potential values normalized for the actual soil water contents measured before each irrigation event (neutron probe measurements). To minimize potential variability problems that may have been caused by the complexity of salt and soil-water distributional patterns under drip irrigation, soil samples and neutron probe measurements were collected in the middle of two plant rows at approximately 0.15 m from an emitter, which typically had a wetted area radius of 0.3 m.

PLANT GROWTH. After the first irrigation event with saline water, nine plants per treatment were collected at 10-d intervals until harvest for growth analysis. Leaf area was measured using a leaf area meter (LI-3000; LI-COR, Lincoln, Nebr.). Shoots (leaves and petioles) were dried at 70 °C and weighed. At harvest, plants were cut at the soil surface, counted, weighed, and scored

for their marketability. The plants were then trimmed by removing the oldest external leaves. Yield and growth responses to salt and drought stress were described by using both the threshold-slope model proposed by Maas and Hoffman (1977) and a version of this model modified as follows: $Y_r = 100 - S (T - \Psi_s)$ where Y_r = relative yield expressed as percentage of the yield obtained under nonstress conditions, T = the soil water potential threshold expressed in MPa, S = the yield reduction percentage per unit decrease in soil water potential below the threshold T, and Ψ_s is the time-weighted average total soil water potential in 0 to 60 cm soil layer, where most roots are found and from where roots take up over 80% of the total transpired water (Katerji et al., 1994). Expressing the relative yield (Y_r) as a function of Ψ_s (soil water potential) allowed us to combine the effects of both water and salt stress on plant performance.

Leaf mineral analysis. At 67 and 82 DAT, nine subsamples of dried and ground shoots from each treatment were analyzed for macro- and microelement content. Concentrations of P, K^+, Ca^{2+}, Mg^{2+}, Na^+, and Cl^-, and micronutrients were measured in leaves by atomic absorption spectrophotometry or by a colorimetric assay. Total N was determined using the Kjieldhal method. Sulfur was analyzed by inductively coupled plasma (ICP) atomic emission spectrometry (Walinga et al., 1995).

Experimental design. In 1988, we began a project aimed at evaluating the long-term effect of soil salinization on plant response to saline irrigation. The salinity treatments and relative controls were arranged, at that time, in a randomized block design with three replications. Since the objective of that study was to investigate long-term effects of salinization, the salinity treatments, randomly assigned within each block in 1988, had to be reassigned to the same experimental field plots in the following years. Therefore, from 1988 until 1998, at which time the experiment on celery described in this paper was performed, each experimental plot had received the same EC irrigation water. Data were analyzed by ANOVA, and means were compared by Duncan's multiple range test.

Results

Soil water potential. Figure 1a and 1b display matric and total soil water potentials, respectively, in the 0 to 60 cm soil layer. Matric water potentials were similar for the irrigated treatments, whereas it gradually decayed in the NIC with a sharp drop after 55 DAT (Fig. 1a). For the irrigation treatments, the data indicate first that irrigation always occurred at matric water potential values higher than –0.08 MPa (≈70% of the available soil water for the NSC) and second that the irrigation reestablished water contents to field capacity. The total water potential, which includes both matric and osmotic potentials, decreased at increasing salinity as a consequence of the proportionally higher contribution of the osmotic component in those treatments (Fig. 1b).

Leaf water potential. The midday to-

tal water, osmotic and pressure potentials (Ψ_t, Ψ_π, Ψ_p) decreased during the growing season (Table 2). These parameters were higher in irrigated plants compared to NIC plants and, with the exception of Ψ_p, they decreased linearly with the irrigation water salinity (Table 2). Osmotic adjustment increased during the growing season and it was proportional to the salt concentration of the irrigation water. The osmotic adjustment of NIC plants was intermediate between the SW2 and SW3 salinity treatments. In contrast to the seasonal OA results, the ability to osmotically adjust to diurnal fluctuations of leaf water potential (OA_d) did not change during the growing season and it was more pronounced in SW2 and SW3 compared to NIC plants. Salt stressed plants had significantly smaller ε compared to drought stressed plants, indicating that the former had less rigid cell walls compared to the latter.

Root water potential. Total water potential, osmotic and pressure potentials decreased in roots during the growing season also, and their values were consistent with leaf water potentials, with respect to the level and the type of stress imposed. The $\Delta\Psi_{Root-Leaf}$ was larger in NIC relative to irrigated plants and increased with increasing salinity (Table 2).

Fig. 1. Soil matric (**A**) and total (**B**) water potentials in the 0 to 60 cm soil layer during the growing season. Samples were taken 1 d before and 2 d after each irrigation event. NSC = nonstressed control; NIC = nonirrigated control; SW1 = 4.4 dS·m⁻¹; SW2 = 8.5 dS·m⁻¹; SW3 = 15.7 dS·m⁻¹. Each point is the mean of nine samples. Vertical bars represent ±se.
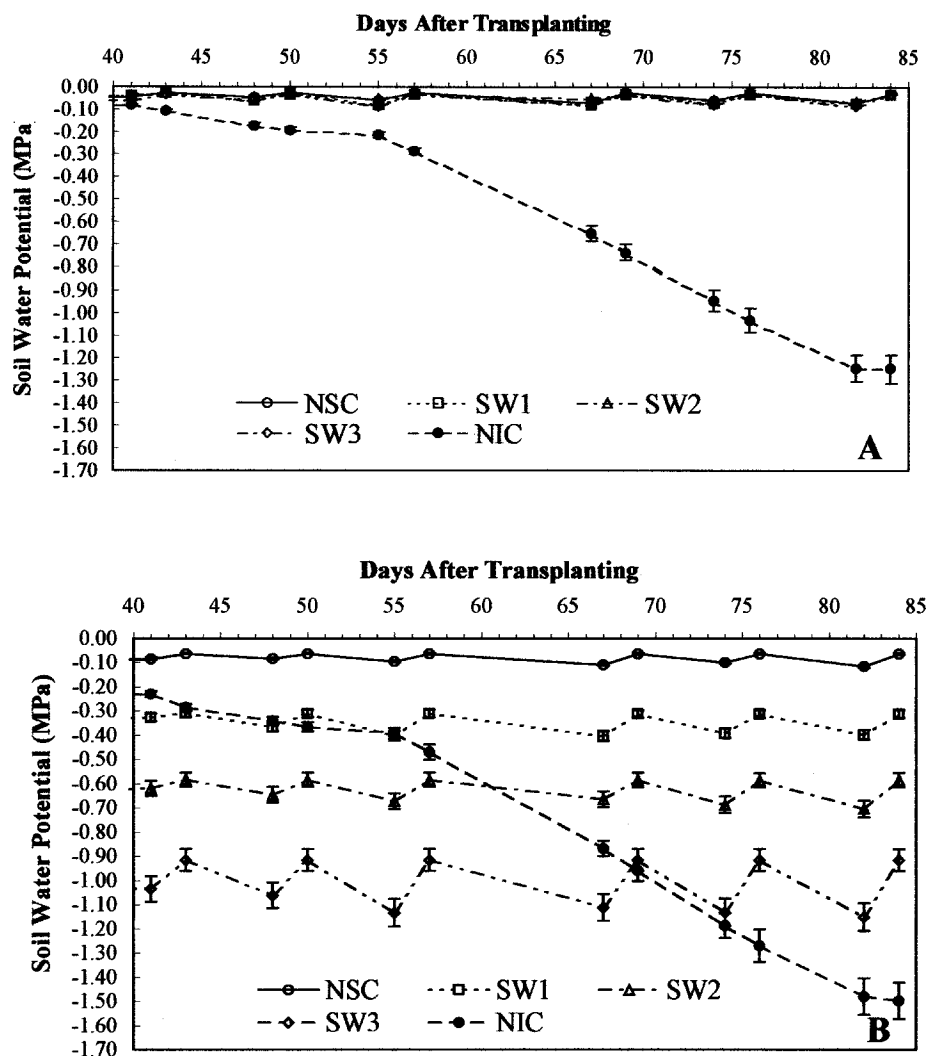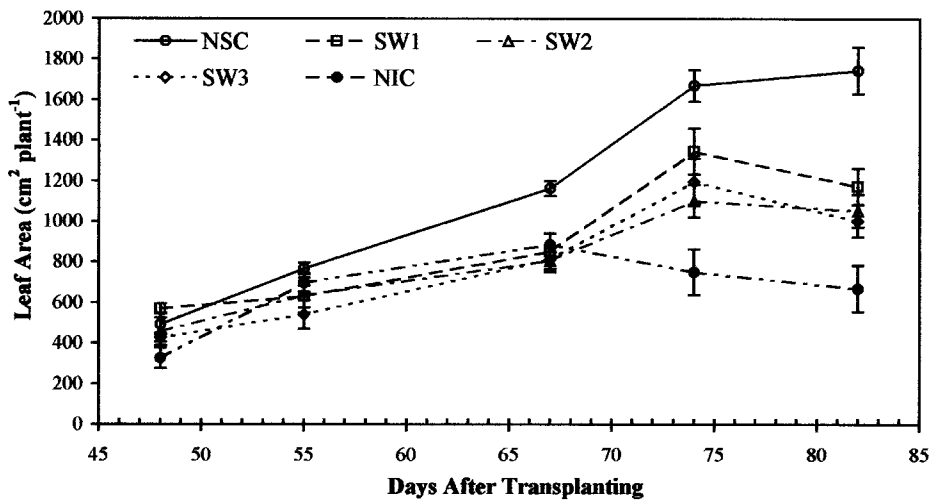
Table 2. Water relation parameters (MPa) in leaves and roots of nonstressed and salinized celery plants. OA = leaf osmotic adjustment during the growth season; OA_d = diurnal osmotic adjustment in leaves; DAT = days after transplanting; NSC = nonstressed control; NIC = nonirrigated control; SW1 = 4.4 dS·m^{-1}; SW2 = 8.5 dS·m^{-1}; SW3 = 15.7 dS·m^{-1}.

	Leaves						Roots			$\Delta\Psi$
Parameter	Ψ_t	Ψ_π	Ψ_p	OA	OA_d	ε	Ψ_t	Ψ_π	Ψ_p	Root–Leaf
67 DAT	−1.69	−2.28	0.59	0.29	0.42	2.46	−0.94	−1.66	0.72	0.75
82 DAT	−2.15	−2.47	0.32	0.65	0.43	2.57	−1.13	−1.43	0.30	1.02
	**	**	**	**	NS	NS	**	**	**	**
NIC	−2.31 a[z]	−2.63 a	0.32 c	0.52 b	0.38 c	2.81 a	−1.30 a	−1.76 a	0.46 b	1.01 a
NSC	−1.43 d	−1.95 d	0.52 a	–	0.31 c	2.06 c	−0.74 d	−1.33 c	0.59 a	0.70 c
SW1	−1.75 c	−2.23 c	0.48 ab	0.27 d	0.40 bc	2.36 bc	−0.95 c	−1.44 b	0.49 b	0.80 bc
SW2	−1.91 b	−2.42 b	0.51 a	0.40 c	0.56 a	2.58 ab	−1.01 c	−1.50 b	0.49 b	0.90 ab
SW3	−2.22 a	−2.64 a	0.42 b	0.65 a	0.48 ab	2.77 a	−1.18 b	−1.73 a	0.55 a	1.03 a
Interaction										
DAT × salinity	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS

[z]Mean separation within columns by Duncan's multiple range test at $P \le 0.05$.

ns,*,**Nonsignificant or significant at $P \le 0.05$ or 0.01, respectively.

Fig. 2. Leaf area development during the growing season. NSC = nonstressed control; NIC = nonirrigated control; SW1 = 4.4 dS·m^{-1}; SW2 = 8.5 dS·m^{-1}; SW3 = 15.7 dS·m^{-1}. Each point is the mean of nine samples. Vertical bars represent ±SE.

PLANT GROWTH AND YIELD. Irrigation with saline water resulted in a significant reduction in leaf area and dry matter accumulation (Figs. 2 and 3). The negative effect of salinization on leaf area development was evident after one week of irrigation (55 DAT) and it became more significant by the end of the growing season (Fig. 2). We did not find significant differences in leaf area among salinity treatments. The accumulation of dry matter followed a pattern similar to the leaf area development pattern (Fig. 3). However, by the end of the growing season, the dry matter accumulation of SW1 plants was higher compared to the other salt treatments (Fig. 3). In contrast, the absence of irrigation caused a reduction in plant growth. Specifically, at soil water potentials above about –0.8 MPa (67 DAT) NIC plants were similar in terms of leaf area and dry matter to salt stressed plants. At soil water potentials below about –0.8 MPa, both parameters began to decrease in NIC plants. By the end of the season, leaf area and dry weight were 38% and 36% smaller in salt stressed plants (average of the three treatments) respectively, compared to NSC plants, whereas NIC plants were 60% and 64% smaller than NSC plants, respectively. Plants survival at harvest was not affected by irrigation or salinity treatments. In contrast, plant fresh weight and marketable yield were both significantly affected by salinization (Table 3). The absence of irrigation did not allow NIC plants to reach the minimum quality standard. For the NIC treatment, virtually no marketable plants were obtained. Reduced dry matter production in salinized plants was mainly caused by a reduced leaf area (Fig. 2) because the number of leaves per plant were similar among plants in different salt treatments (Table 3). NIC plants had a significantly reduced number of leaves compared to irrigated plants, whereas the net assimilation rate (NAR) was unaffected (Table 3).

The relative marketable yield (Y_r) was directly correlated to the soil water potential (Ψ_s) for the salinity treatments ($r = 0.998^{**}$) (Fig. 4a). Drought stressed plants appeared to be more affected than salt stressed plants at similar Ψ_s, indicating that a decrease in Ψ_s due to a decrease in soil matric potential (Ψ_m) may be relatively much more deleterious for plant growth than a

Fig. 3. Dry matter accumulation during the growing season. NSC = nonstressed control; NIC = nonirrigated control; SW1 = 4.4 dS·m^{-1}; SW2 = 8.5 dS·m^{-1}; SW3 = 15.7 dS·m^{-1}. Each point is the mean of nine samples. Vertical bars represent ±SE.
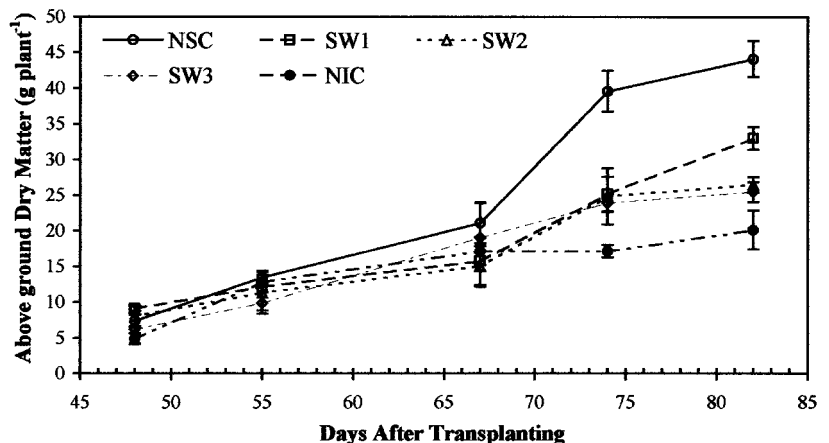
Table 3. Growth parameters in nonstressed and salinized celery plants. FW = mean plant fresh weight; MY = trimmed bunch marketable yield; NAR = net assimilation rate; NSC = nonstressed control; NIC = nonirrigated control; SW1 = 4.4 dS·m⁻¹; SW2 = 8.5 dS·m⁻¹; SW3 = 15.7 dS·m⁻¹.

Parameter	Plants (no./m²)	FW (g/plant)	MY (t·ha⁻¹)	NAR (g·dm⁻²·d⁻¹)	Leaves (no./plant)
NIC	8.8	115.5 c[z]	6.2 c	0.082 b	7.7 b
NSC	9.0	372.2 a	29.4 a	0.101 a	9.7 a
SW1	8.8	324.4 a	25.7 a	0.080 b	9.4 a
SW2	8.8	326.1 a	22.4 a	0.075 b	9.2 a
SW3	9.0	226.0 b	16.4 b	0.080 b	8.9 ab

[z]Mean separation within columns by Duncan's multiple range test at $P \leq 0.05$.

similar decrease in osmotic potential (Ψ_π) (Fig. 4a). Alternatively, we may consider that the responses of salt and drought stressed plants to variations in soil water potentials cannot be superimposed. Nevertheless, when the relative marketable yield was plotted vs. leaf water potentials (and leaf water potential components) of the combined drought and salt stressed plants, we identified significant correlations between yield and both total water potential ($r = 0.929^*$) and turgor potential ($r = 0.959^*$), whereas the correlation between yield and osmotic potential was not significant ($r = 0.868^{ns}$) (Fig. 4b).

LEAF MINERAL CONTENT. Salinity affected leaf mineral contents (Table 4). Na^+ and Cl^- concentrations increased during the growing season and with increasing salinity. In contrast, Ca^{2+} and Mg^{2+} and S decreased upon salt treatment. A moderate drop of K^+ was measured in drought stressed plants also where, in contrast, the level of Ca^{2+} slightly increased. Micronutrients were not affected by salt or drought stress, with the exceptions of B and Mn^{2+} which decreased and increased, respectively, in both drought stressed and salt treated plants. The K^+/Na^+, Ca^{2+}/Na^+ and Mg^{2+}/Na^+ molar ratios decreased with salinity possibly because of competition effects of Na^+ vs. K^+, Ca^{2+} or Mg^{2+} (Table 5).

Discussion

The objective of this study was to evaluate growth and various physiological responses of field-grown celery in a Mediterranean environment and to specifically compare the yield response to various levels of saline irrigation vs. absence of irrigation. Plant response to increasing soil salinity may greatly depend on the environmental conditions (Dalton et al., 1997, 2001). Therefore, it is of critical importance to assess the environment-specific salt tolerance performance of the species considered, especially when such assessment is used to optimize cropping systems in environments where the water resource is limited (Rhoades et al.,1992). Although irrigation with saline water significantly reduced leaf area and dry matter accumulation of celery, it caused an acceptable decrease of the final marketable yield (10% and 25% reductions at 4.4 and 8.5 dS·m⁻¹, respectively).

Based on the Maas–Hoffman relationship we identified an EC_e salinity tolerance threshold of 1.41 dS·m⁻¹. These results are consistent with those of Francois and West (1982) who reported an EC_e threshold value ≤1.8 dS·m⁻¹. However, in our experimental conditions each unit increase in salinity above 1.4 dS·m⁻¹ resulted in a 5.4% reduction in relative marketable yield. This value is slightly lower than the slope value identified by Francois

and West [6.2% (dS·m⁻¹)⁻¹], possibly as a consequence of different experimental conditions.

In general, plant growth in saline environments is limited by both water stress (caused by a decreased water potential of the soil solution) and ion toxicity. According to a model proposed by

Fig. 4. (**A**) Relative yield (Y_r) decrease at decreasing soil water potential (Ψ_s). See text for details on the modified Maas-Hoffman model adopted in this study. (**B**) Relative yield (Y_r) decrease at decreasing leaf water potentials. Each point is the mean of 9 samples. Open symbols indicate leaf total (○) osmotic (□) and turgor water (△) potentials of salt stressed plants and closed symbols indicate leaf total (●) osmotic (■) and turgor water (▲) potentials of drought stressed plants.
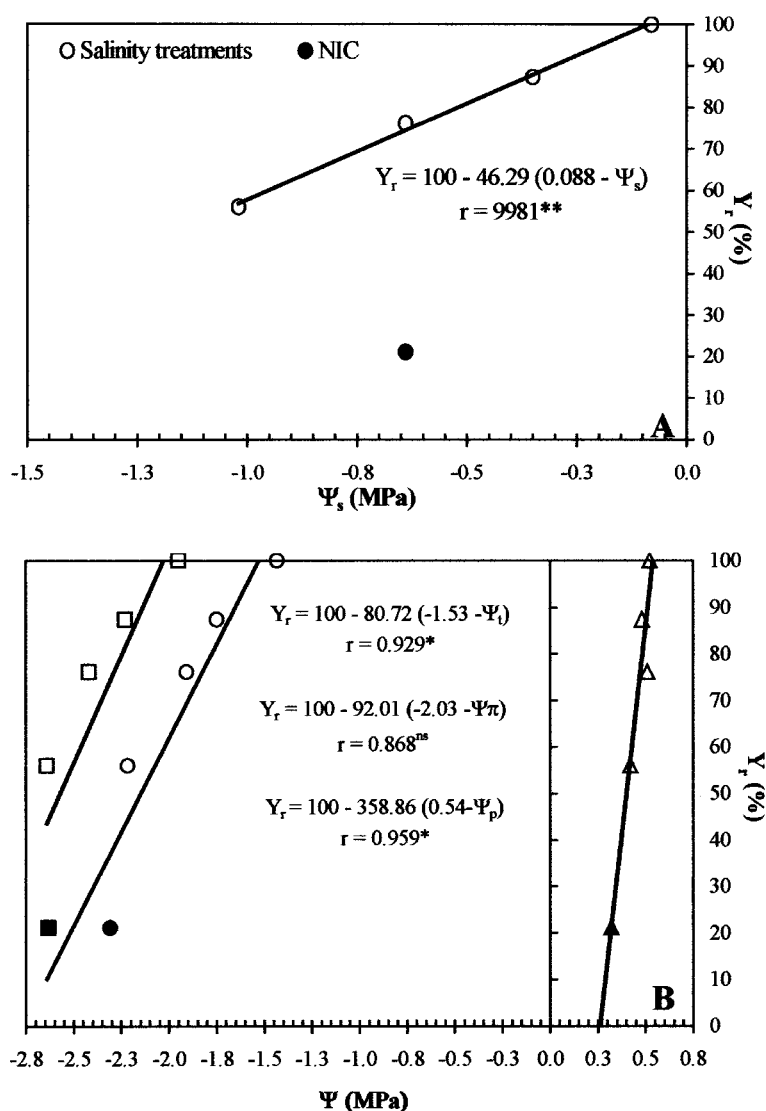

$$Y_r = 100 - 46.29 (0.088 - \Psi_s)$$
$$r = 9981^{**}$$

$$Y_r = 100 - 80.72 (-1.53 - \Psi_t)$$
$$r = 0.929^*$$

$$Y_r = 100 - 92.01 (-2.03 - \Psi_\pi)$$
$$r = 0.868^{ns}$$

$$Y_r = 100 - 358.86 (0.54 - \Psi_p)$$
$$r = 0.959^*$$

Table 4. Ion content on dry weight basis (mmoles kg^{-1}) in nonstressed and salinized celery shoots. DAT = days after transplanting; NSC = nonstressed control; NIC = nonirrigated control; SW1 = 4.4 dS·m^{-1}; SW2 = 8.5 dS·m^{-1}; SW3 = 15.7 dS·m^{-1}.

Parameter	N	P	K$^+$	Ca^{2+}	Mg^{2+}	S	Na$^+$	Cl$^-$	Mn^{2+}	Fe	B
67 DAT	1857	149	645	527	156	156	587	559	1.55	5.02	3.89
82 DAT	1557	139	657	640	177	143	700	686	1.62	5.75	3.89
	**	NS	NS	**	**	NS	*	*	NS	NS	NS
NIC	1771 ab^z	104 c	609 ab	787 a	189 a	187 a	204 d	186 d	1.44 b	5.52	3.33 b
NSC	1879 a	136 b	716 a	667 ab	193 a	174 a	243 d	223 d	1.33 b	5.29	4.17 a
SW1	1764 ab	142 ab	701 a	542 b	160 b	131 b	626 c	593 c	1.35 b	4.78	3.89 a
SW2	1629 ab	159 a	652 ab	500 b	152 b	134 b	883 b	876 b	1.62 b	5.95	3.89 a
SW3	1543 b	162 a	558 b	525 b	152 b	143 b	1035 a	1014 a	2.13 a	5.48	3.98 a
Interaction											
DAT × salinity	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS

^{z}Mean separation within columns by Duncan's multiple range test at $P \leq 0.05$.
ns,*,**Nonsignificant or significant at $P \leq 0.05$ or 0.01, respectively.

Table 5. Ion content ratios (mol·mol^{-1}) in nonstressed and salinized celery shoots. DM = shoot dry matter; DAT = days after transplanting; NSC = nonstressed control; NIC = nonirrigated control; SW1 = 4.4 dS·m^{-1}; SW2 = 8.5 dS·m^{-1}; SW3 = 15.7 dS·m^{-1}.

Parameter	DM (%)	Na$^+$/Cl$^-$	K$^+$/Na$^+$	Ca^{2+}/Na$^+$	Mg^{2+}/Na$^+$
67 DAT	16.4	1.08	1.70	1.57	0.43
82 DAT	15.9	1.03	1.42	1.47	0.39
	NS	NS	NS	NS	NS
NIC	19.7 a^z	1.11	2.99 a	3.91 a	0.93 a
NSC	14.6 c	1.10	3.09 a	2.90 a	0.83 a
SW1	15.3 b	1.06	1.12 b	0.89 b	0.26 b
SW2	15.5 b	1.01	0.75 b	0.58 b	0.17 b
SW3	15.8 b	1.03	0.55 b	0.52 b	0.15 b
Interaction					
DAT × salinity	NS	NS	NS	NS	NS

^{z}Mean separation within columns by Duncan's multiple range test at $P \leq 0.05$.
ns,*,**Nonsignificant or significant at $P \leq 0.05$ or 0.01, respectively.

Munns and Termaat (1986), after an initial water stress, an excessive concentration of toxic ions (mainly Na$^+$ and Cl$^-$) will negatively interfere with the normal plant metabolism. The excessive concentration of toxic ions can be counteracted by an active accumulation/translocation of these ions into the older leaves. The abscission of prematurely senesced ion-loaded leaves removes the excess of toxic ions, while actively preserving dividing meristems and younger leaves from toxicity problems. A drawback of this physiological strategy, however, is an early reduction of the photosynthesizing leaf area which will eventually cause yield loss. Everard et al. (1994) and Pardossi et al. (1998) have documented a severe leaf abscission in salinized celery (300 mM NaCl) and a significant drop in NAR at moderate salinity levels (50 and 100 mM NaCl), which are both consistent with our results. However, the parameter that seemed to be more sensitive to salt stress in our experimental conditions was the leaf area, which was significantly smaller (≈38%) compared to the leaf area of NSC plants even at a salinity level of (30 mM NaCl (EC = 4.4 dS·m^{-1}). In contrast, Pardossi et al. (1998) found only a moderate reduction (≈15%) in leaf area at salinity levels below 10 dS·m^{-1} (≈130 mM) in greenhouse grown celery plants. A comparison between our data sets and those of Pardossi et al. (1998), however, reveals that at similar levels of EC of the irrigation water, plants grown in the field have correspondingly reduced values for leaf water potential compared to greenhouse plants grown in hydroponic culture. These findings indicate that field-grown plants may experience more severe levels of stress compared to greenhouse-grown plants even when roots are exposed

to the same level of salinity and suggest that yield reduction is possibly related more to the average salinity in the shoot than the average root zone salinity (Dalton et al., 1997; Maggio et al., 2002).

The highly significant correlation between relative marketable yield and leaf (Fig. 4b) and root water potentials points to a similar conclusion and emphasizes that yield responds better to the internal (plant water potential) rather than to the external (root zone soil water potential) plant environment. The relationship between yield and external variables, such as soil water potential, may overlook the different ability of salinized and drought stressed plants to osmotically adjust (Table 2, OA$_d$) and may account for the observed yield response discrepancy of combined salt and drought stressed plants (Fig. 4a).

One clear response that celery plants exhibit with increasing salinity is their pronounced ability to maintain high cellular turgor in the presence of hyperosmotic stress (Table 2 and Fig. 4b). Under salinity stress, Na$^+$ and Cl$^-$ are readily available and plants use these to maintain turgor. In contrast, drought stressed plants have a limited access to Na$^+$ and Cl$^-$ and they may divert sugars and other metabolic compounds for osmotic adjustment at the expense of growth. This may provide a further explanation for higher yield of salinized vs. drought stressed plants at similar levels of soil Ψ_s (SW2 vs. NIC) (Fig. 4a). However, Na$^+$ and Cl$^-$ contributed only partly to maintain high turgor [34% of the SW2 cellular osmolality estimated according to the van't Hoff relationship (Nobel, 1999)], suggesting that the biosynthesis of other organic solutes (compatible solutes) also participates to further

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decrease the cellular osmotic potential. This process is likely to be coordinated with the compartmentation of toxic ions (Na^+ and Cl^-) in the vacuole (Hasegawa et al., 2000). Importantly, the closer correlation of yield vs. turgor potential compared to yield vs. osmotic potential also indicates that accumulation of solutes is not the only physiological response essential for acclimation in hyperosmotic environment, yet other parameters involved in turgor maintenance, such as cell wall modifications (O'Neill, et al., 2001) and protection of cellular and subcellular membrane integrity (Riga and Vartanian, 1999) may also actively contribute in preserving yield. Interestingly enough, when the relative yield was plotted vs. root water potential and its relative components, yield appeared more closely related to total ($r = 0.954^*$) and osmotic ($r = 0.937^*$) potentials than to turgor potential ($r = 0.595^{NS}$) (data not shown), indicating that different mechanisms may be involved in root and shoot stress adaptation (Maggio et al., 2001).

The functional relationship between maintenance of cellular turgor and growth is still a controversial issue. Munns and Termaat (1986) and Munns (1993) proposed that a reduction in leaf cellular turgor is not the main cause for a reduction in stomatal conductance, NAR, and limited leaf expansion in saline environments. Nevertheless, we did find a correlation between leaf pressure potential (cellular turgor) and leaf area ($r = 0.87^{**}$), which may indicate that in field grown celery the ability to maintain high turgor is an important physiological adaptation to ensure relatively sustained growth rates upon salinization. Although this correlation cannot unequivocally assess a cause–effect relationship (Munns, 1993), it is at least consistent with the observed decrease in cell wall elasticity (high ε of salinized leaf tissue, which also contributes to high turgor maintenance in saline environments (Table 2).

Osmoregulation plays a fundamental role in salt stressed celery, as indicated by the degree of osmotic adjustment measured in leaves of salinized plants (Table 2). Everard et al. (1994) have shown that accumulation and compartmentation of Na^+ and Cl^-, together with possible de-novo synthesis of compatible solutes (mannitol), play key roles for salt stress tolerance in celery. These results are consistent with the OA values measured in both nonirrigated and salinized plants. Furthermore, we found a significantly improved ability of salinized plants to adjust to the midday water deficit (OA_d), a condition of extreme stress often experienced by plants grown in the field in Mediterranean environments. Our results indicate that the ability to efficiently accomplish diurnal osmotic adjustments is an important adaptive feature, which seems to be much more developed in salinized compared to drought stressed plants. Seasonal and diurnal OA may be due to different regulatory mechanisms and may accomplish different physiological functions. Diurnal values of solute accumulation for celery were similar to those reported for other crops such as soybeans (0.4 MPa), sunflower (0.6 MPa), and sorghum (0.7 MPa) (Takami et al, 1982; Turner and Jones, 1980; Wenkert et al., 1978). An improved ability to cope with diurnal fluctuations of vapor pressure deficit (VPD) by facilitating the maintenance of a favorable water potential gradient may counteract the detrimental effects due to the superimposition of different stresses (midday water stress on salt stressed plants). This response was confirmed by a positive correlation we found between osmotic adjustment and $\Delta\Psi_{Roots-Leaves}$ ($r = 0.930^{**}$), which has been documented by other authors also (Pardossi et al., 1998).

The reduced uptake of N, Ca^{2+}, Mg^{2+} and K^+ in salt treated plants is consistent with other reports (Pardossi et al., 1999) and

it may have been one cause of reduced market quality at high salinity (plants subjected to salinity stress tended to develop heart rot and leaf injuries). We did not find detrimental effects of salinity on the concentration of any of the micronutrients analyzed, which indicates that micronutrients deficiency was not a major cause of reduced marketable yield.

Identifying environment- and species-specific salinity tolerance economic thresholds is necessary for optimizing farming and soil reclamation strategies in environments subject to salinization and to design precision agriculture guidelines. For Mediterranean environments, we therefore conclude that it is possible to cultivate celery in the field using saline water (up to 8.5 dS·m^{-1}) with an acceptable yield reduction. In the absence of irrigation, however, the ability to osmotically adjust to diurnal fluctuations of leaf water potential is significantly reduced in this species and it is possibly one of the reasons for low yield in absence of irrigation.

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