

## Effects of saline irrigation water and heat waves on potato production in an arid environment

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### Abstract

Production of spring potato (*Solanum tuberosum* L. cv. Désirée) on a deep sandy soil in the central highland of the Negev desert of Israel under drip irrigation with saline water (up to  $6.2 \text{ dS m}^{-1}$ ) was studied in the years 1992–1997. The objective of the study was to determine the effects of saline water irrigation on potato production in an arid environment with special focus on the interactions with weather conditions. Although yields were often high, salinity effects were evident in some years. Thus 1992 and 1996 yields were  $6\text{--}7 \text{ kg m}^{-2}$  and showed no significant effect of salinity, while a pronounced drop in yield with increasing salinity was observed in 1993 and 1994. Analysis of weather data for 1993–1994 suggests that the decline in yield was due to interactions between saline irrigation and prolonged heat wave events occurring during crop development. Further experimental work (1997) revealed that tuber yield was most sensitive to combined salt and heat stress when heat waves occurred at 40–60 days after emergence. The combined stress apparently leads to the collapse of mechanisms for avoiding salt accumulation in young expanding leaves, resulting in failure of vegetative growth recovery and a consequent reduction in the leaf area index and canopy functioning. The relationship between tuber sink demand and available photoassimilate supply at certain stages of plant development is discussed with reference to the ability of the potato plant to recover from the combined stress.

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### 1. Introduction

Dryland cultivation of potato (*Solanum tuberosum* L.) is expanding steadily worldwide (Scott, 1997). Since supplies of fresh water in dry regions are by definition limited, irrigation with brackish water is often proposed as an option. In Israel, potatoes consume large amounts of high-quality water every year—water that might be replaced by saline water

drawn from the huge fossil aquifers lying beneath the Negev desert (Issar and Nativ, 1988).

In their comprehensive work, Maas and Hoffman (1977) show that, in terms of relative yield (percentage of the yield under non-saline conditions), the response of any given crop to salinity levels is characterized by a two-phase curve. The authors classify potato as a moderately salt-sensitive crop and define a relatively low soil salinity ( $\text{EC}_e$ ) threshold of  $1.7 \text{ dS m}^{-1}$  for this crop above which the relative yield decreases by 12% per  $1 \text{ dS m}^{-1}$  increase in  $\text{EC}_e$ , based on earlier experiments by Bernstein et al. (1951) on a loamy soil under flood irrigation. While Maas and Hoffman's curve

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provides a general scheme of crop response to salinity, its parameters vary depending on environmental conditions (e.g. soil properties and weather) and agricultural methods (e.g. irrigation methods) (Shannon and Grieve, 1999). Reasonable yields under saline irrigation water have been reported for many crops previously classed as relatively sensitive to salt stress (Pasternak and De Malach, 1995). Furthermore, in some crops (e.g. tomato) the reduction in fresh yield under salinity may be compensated by an increase in fruit dry weight and other quality parameters (Mizrahi and Pasternak, 1985; Mizrahi et al., 1988; Pasternak et al., 1986b). It was shown recently that, under temperate summer conditions and saline water sub-irrigation, potato yields remained unaffected by soil salinities as high as  $3.5\text{--}7.6\text{ dS m}^{-1}$  (Patel et al., 1999, 2001). In the southern Arava valley of Israel, winter potatoes routinely produce substantial yields under saline ( $3.5\text{ dS m}^{-1}$ ) irrigation water. These findings encouraged us to explore the potential of potato production with saline water irrigation as modulated by various factors characteristic of the desert climate.

Irrigation with saline water can be problematic. In heavy, poorly structured soils with low infiltration capacity, it often results in enhanced salinization of the soil (Shainberg and Singer, 1990). Where the water table is high, saline irrigation aggravates pre-existing salinity problems. These problems can be overcome in part by growing the crop on deep sandy soils, which allow water to drain rapidly and retain little salt (Pasternak and De Malach, 1990). In arid zones, however, high evaporative demands exacerbate the low water availability that characterizes sandy soils (Schleiff, 1981), and saline irrigation can intensify rhizosphere salinity, subjecting plants to severe osmotic stress. This unwelcome scenario can be avoided by using appropriate methods of irrigation management (Pasternak and De Malach, 1995). Unlike flood irrigation, drip irrigation leaches salt away from the root zone while maintaining a low soil moisture tension (Pasternak, 1987). Both these effects are best achieved in sandy soils by the pulse irrigation method, as shown in tomato by Pasternak and De Malach (1994).

Although introduced into diverse climatic regions, potato is a classic summer crop of temperate climate zones. Low temperatures and short photoperiods restrict shoot growth and promote the onset and growth of tubers (Menzel, 1985; Ewing and Struik,

1992). In subtropical countries like Israel, where the winter is quite moderate, potato can be grown successfully in autumn, winter and spring, though not in the warm summer. However, spring and autumn in the Middle East are characterized by unstable weather conditions. Heat waves (locally called *khamseen*), generated by hot dry winds blowing in these seasons from surrounding deserts, are typified by temperatures and vapor pressure deficits that are well above average seasonal values and pose a risk to the normal development of the potato plants. Coming on top of salinity problems, such heat waves can curtail potato yields. Unfortunately, both the frequency and the severity of these events are unpredictable.

In the present study, we demonstrate that high potato yields can be obtained under desert conditions even when the water used for irrigation contains high concentrations of salt ( $\text{EC}_i$  up to  $6.2\text{ dS m}^{-1}$ ). We describe physiological effects of combined salt and heat-wave stresses on the potato plant and discuss the consequences for tuber yields.

## 2. Materials and methods

### 2.1. Location and soil

Field experiments were conducted at the Desert Agro-Research Center at Ramat Negev, on sand dune soil containing over 96% of fine sand grains with a bulk density of  $1.5\text{ g cm}^{-3}$ . The volumetric field capacity of the soil (% water retention at  $-1.5\text{ MPa}$ ) ranged from 0.06 to  $0.07\text{ m}^3\text{ m}^{-3}$ . The 1994 experiment was conducted in a nearby field on a sandy loam soil with a larger silt fraction ( $\sim 10\%$ ).

### 2.2. Climate and weather conditions

In Israel, winter is the wet season. However, average precipitation at Ramat Negev is low—less than 100 mm per year. Minimum temperatures in December–January can drop below  $0^\circ\text{C}$ , precluding potato cultivation in this period. Average maximum temperatures increase rapidly in March–April and reach about  $34^\circ\text{C}$  in June–September. Heat waves lasting several days with a temperature maximum range of  $30\text{--}45^\circ\text{C}$  and relative humidity of less than 25% occur frequently in April–May (and, to a lesser extent, in

September–October). The average evaporative demand on a summer day is about 8–10 mm, but evaporation ( $E$ ) values (measured by a USWB Class A evaporation pan) as high as 14 mm are not infrequent. All the meteorological data were recorded at a station located about 1 km from the field. The daily maximum vapor pressure deficit (VPD) was calculated according to Snyder and Paw (2002). All experiments were conducted from February to June. Sowing took place in mid-February (excluding 1997, as described below).

### 2.3. Plant material and cultivation practices

Prior to sowing, the soil was washed with 200 mm of fresh water ( $EC_i$  at  $1.2 \text{ dS m}^{-1}$ ) to leach away any remains of salt from previous years. The soil was then plowed and fertilized. Seed tubers (cv. 'Désirée') were sown at 20 cm intervals in two rows per 1.93 m wide bed to give a density of 51 000 plants  $\text{ha}^{-1}$ . Each row was mounded afterwards so that the final depth of the tuber seeds was 18 cm.

Sprinkler irrigation was applied twice a week from sowing until emergence, and drip irrigation thereafter. Drippers (Netafim, Israel) were placed at 0.4 m intervals along each row. The daily amount of water, which was applied in three pulses, was calculated from the average evaporation over the previous 10 days, the leaf area index, and the current salt leaching requirements (as recommended by Pasternak and De Malach (1990)). Accordingly, irrigation after sowing was initiated at  $0.4E$  and increased to  $0.9E$  after 80% of the ground was completely covered by foliage. The total amount of water supplied during a season (excluding water used for salt leaching prior to sowing) was about 780 mm. Application of saline water was begun immediately after plant emergence (about 20–40 days after sowing) in all the experiments. On the day when drip irrigation commenced, the field was irrigated with 50 mm of fresh or saline water (depending on the treatment) in order to ensure immediate establishment of a uniform profile of salt distribution in the whole root zone.

Fresh water ( $EC_i = 1.2 \text{ dS m}^{-1}$ ) from the national water carrier and saline water ( $EC_i = 4.5$  or  $6.2 \text{ dS m}^{-1}$ ) from local wells were used. Different levels of salinity were obtained by using mixing junctions (Pasternak et al., 1986a) or a modification

Table 1

Concentrations of major cations and anions in fresh and saline irrigation water in Ramat Negev

$EC_i$ ( $\text{dS m}^{-1}$ )	Ion concentration ( $\text{mol m}^{-3}$ )			
	$\text{Na}^+$	$\text{Ca}^{2+}$	$\text{Mg}^{2+}$	$\text{Cl}^-$
1.2	0.1–0.2	0.3–0.7	0.1–0.3	0.5–1.4
6.2	49.3	10.2	3.1	71.4

of the double-line source system (Pasternak and De Malach, 1995). The elemental composition of the waters used is shown in Table 1. Soil salinity was monitored three times per season to depths of 15, 30, and 60 cm. As mean  $EC_e$  only slightly exceeded  $EC_i$  in the 1992–1996 experiments, indicating an almost steady state condition due to effective salt leaching, mean  $EC_e$  per treatment was calculated and used in the results for those years.

After the soil was plowed and prior to sowing, the field received a dressing of Superphosphate at  $1500 \text{ kg ha}^{-1}$ , potassium chloride at  $500 \text{ kg ha}^{-1}$ , and pelleted cow manure at  $5000 \text{ kg ha}^{-1}$ . A complete soluble fertilizer solution (Sheffer1, Fertilizers and Chemicals Ltd., Haifa, Israel), with an NPK ratio of 5:3:8, was injected into the water with every irrigation throughout the growing season until three weeks before harvest. The concentration of N in the water ranged from 70 to  $100 \text{ mg L}^{-1}$ , and total nitrogen application was  $350 \text{ kg N ha}^{-1}$ . The corresponding amounts of P ( $\text{P}_2\text{O}_5$ ) and K ( $\text{K}_2\text{O}$ ) were 210 and  $560 \text{ kg ha}^{-1}$ , respectively.

### 2.4. Experiments

#### 2.4.1. Experimental design

A random block layout with six replications per treatment was used in all the trials. Each experimental plot was composed of three 5 m long rows. Yield was measured only for plants growing in the central row, the outer rows serving as borders.

#### 2.4.2. Experiments in 1992–1996

The experiments differed in the range and number of water salinity levels examined. In 1992 and 1993, waters were used without mixing and only two  $EC_i$  levels were tested, 1.2 and  $6.2 \text{ dS m}^{-1}$ . In 1994 and 1996, fresh and saline waters were mixed to produce

five  $EC_i$  levels within the 1.2–6.2  $dS\ m^{-1}$  range. All other practices were similar among experiments.

#### 2.4.3. Experiments in 1997

Potatoes were sown at three different sowing dates (2 February, 26 February, and 13 March). At the first sowing date, half of the rows were covered with 0.15 mm thick transparent polyethylene sheets immediately after sowing to enhance germination. Soil temperatures at a depth of 0.15 m ranged from 11 to 15 °C in the covered rows, which was 5–7 °C higher than in the bare soil at the same depth and time. Plant emergence occurred about 10 days earlier on covered soil than in the bare rows, so, in all, four plant populations differing in age were obtained. Fresh (1.5  $dS\ m^{-1}$ ) or saline (4.5  $dS\ m^{-1}$ ) water was applied in six replications in a randomized design. All agricultural practices were similar to those described above. Relevant weather parameters during the 1997 season are given in Fig. 1, including the distribution and intensity of heat wave events (a heat wave was considered to have occurred if the daily maximum vapor deficit rose above 4 kPa).

#### 2.5. Measurements

Plant growth and development were monitored in 1996 and 1997 using leaf area index (LAI) measurements. Five whole plants from the borderlines of each plot were sampled at two-week intervals. The plants were divided into leaves, stems, and tubers. About 50 representative leaves were measured for leaf area (Lambda Inst. Corp. type LI-3050A/3), after which they were dried for 48 h in an oven at 70 °C for calculation of specific leaf area ( $m^2\ g^{-1}\ DW$ ). The LAI was calculated by multiplying specific leaf area by total leaf dry weight, then dividing by the ground area occupied by the five plants. Tubers were counted and their fresh and dry weights determined. In 1997 the carbon exchange rate (CER) was measured in both young fully expanded and old leaves in each salinity treatment (15 replications) using a portable IRGA system (LiCor 6200). CER measurements were carried out between 0900 and 1100 h four times per season.

In 1997, special attention was paid to the effects of heat wave events on the vegetative parts of the plant. Weather forecasts were monitored to enable plant sampling just before as well as four days after heat

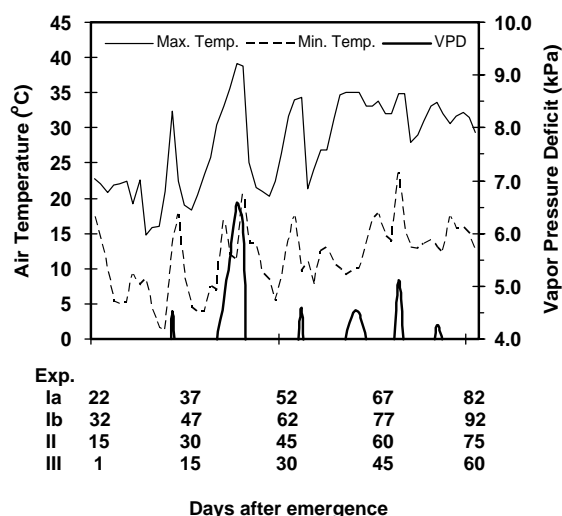


Fig. 1. Daily maximum and minimum temperatures and maximum VPD values (above 4 kPa) recorded 1 km from the experimental field in Ramat Negev in April–May 1997. Corresponding time after emergence for each experiment is plotted below the graph (see Section 2).

wave events. The leaf population was divided into three categories: young-expanding, fully expanded, and old leaves. Fresh and dry weight and leaf area were determined separately for each leaf category and for stems and tubers. Samples were then ground to fine powder, burnt to ash in a 500 °C furnace, and dissolved in distilled water. The concentration of Na was determined using a flame photometer (Corning–EEL, Scientific Instruments). Chloride concentration was analyzed using a Metrohm 655 Dosimeter.

Unless otherwise specified, tubers were usually harvested at about 140 days after sowing (DAS). Samples comprising all the tubers from one row-meter were taken from each experimental plot at the rate of two samples per plot, producing 12 yield replications per treatment. Tubers were cleaned of sand and their fresh weight was determined.

### 3. Results

#### 3.1. Salinity and weather effects on tuber yields of 1992–1996 experiments

Cultivation of spring potatoes under desert conditions using saline irrigation water ( $EC_i$  up to

Table 2

'Désirée' tuber yields obtained under different soil extract salinities ( $EC_e$ ) in 1992–1996 together with timing and duration of heat wave events ( $VPD > 4$  kPa)

Year	Yield (kg m <sup>-2</sup> )						Days with VPD > 4 kPa		
	EC <sub>e</sub> (dS m <sup>-1</sup> )						DAE		
	1.6	2.4	4.2	5.0	6.6		0–40	40–60	60–80
1992	6.7	–	–	–	6.3	NS <sup>a</sup>	1	0	4 (1)
1993	6.3	–	–	–	4.5	**	1	6 (2)	3 (2)
1994	4.9	4.8	3.4	2.9	2.3	**	2 (2)	10 (5)	10 (2)
1996	6.8	7.0	6.3	6.5	6.7	NS	6 (5)	2 (2)	8 (2)

Values in parentheses represent the number of heat wave events DAE, days after emergence.

<sup>a</sup> Non-significant.

\*\* Significant at  $P \leq 0.01$ .

$6.2\ dS\ m^{-1}$ ) often produced high yields. However, there were large year-to-year variations in the crop's response to salinity (Table 2). In 1992 and 1996, 'Désirée' tuber yield was practically unaffected by soil salinities ( $EC_e$ ) as high as  $6.6\ dS\ m^{-1}$ . By contrast, in 1993, and particularly in 1994, tuber yields dropped substantially as soil salinity increased. We note that the conditions of cultivation (soil, variety, sowing date, water and fertilizer amounts, irrigation management) were identical in all the trials, with the sole exception of 1994 when the trial was conducted on sandy loam instead of sand. On the other hand, weather, and more especially the incidence of heat wave events, differed significantly among the four years. In 1992–1994, tuber yields under saline water irrigation appeared to be negatively correlated with the number of heat wave days. In 1996, however, numerous heat wave days failed to bring about a reduction in yields (Table 2).

### 3.2. The 1997 experiment: heat wave timing and duration versus tuber yield

The experiments conducted in spring 1997 were designed to facilitate analysis of potato performance under saline water irrigation ( $4.5\ dS\ m^{-1}$ ) in relation to the heat waves experienced at different stages of crop development. In the early sown experiment (2 February), application of plastic mulch to some of the rows moved plant emergence forward by 10 days, providing two groups of plants with separate developmental courses. One significant heat wave event occurred in the spring of 1997. It lasted 4 days, and  $VPD$  values exceeded 6 kPa (Fig. 1). The early sown experiments experienced that event as late as at 40–60 days after emergence (DAE), whereas the late-sown experiments were exposed to it at earlier stages of plant development (Table 3). The other heat wave events were shorter and relatively weak (Fig. 1).

Table 3

The effect of a single heat wave event in the spring of 1997 on tuber yield of potato ('Désirée') plants irrigated with fresh ( $1.5\ dS\ m^{-1}$ ) or saline ( $4.5\ dS\ m^{-1}$ ) water

Sowing date	Plastic mulch	Heat wave event (DAE)	Harvest (DAS)	Yield ( $kg\ m^{-2}$ )	
				Fresh water	Saline water
Ia (2 February)	–	43–46	140	9.25 a	7.36 b
Ib (2 February)	+	53–56	140	7.81 a	5.83 b
II (26 February)	–	36–39	123	6.98	6.73
III (12 March)	–	21–24	116	5.47	4.66

Four distinct groups of plants differing in date of emergence were followed, of which the heat wave encountered at a different stage of development, as indicated by days after emergence (DAE). Different letters indicate significance at  $P < 0.05$  (within rows). DAS, days after sowing.

Saline water irrigation caused significant reduction (20–25%) in tuber yields from both early- and late-emerging plants of the early sown experiment (Table 3). In the late-sown experiments (26 February and 12 March) the differences in yield between plants irrigated with saline or fresh water were insignificant (Table 3). We note that the very late sowing produced substantially lower yields than the earlier trials under both water qualities.

### 3.3. Effects of combined salt and heat wave stress on canopy development

Saline water irrigation resulted in noticeable changes in the potato plant canopy; leaf color was darker, canopy structure was more compact, and the LAI was slightly, though not always significantly, lower than that of fresh water plants. The differences

in LAI were more pronounced following heat wave events. While heat waves occurring earlier than 40 DAE merely reduced the rate of LAI increase in saline irrigated plants, heat wave days occurring after that stage caused a marked decline in the absolute LAI in those plants (Fig. 2).

On a typical heat wave day, all plants—fresh- and saline-water irrigated—tended to wilt before noon but recovered at night. When heat wave days succeeded each other, however, many young leaves on saline irrigated plants failed to recover, remaining wilted and eventually drying up, a phenomenon not observed among fresh water plants. Furthermore, while fresh water plants resumed their vegetative growth a few days after severe heat wave events, regeneration was much slower or practically absent in the saline treatments, as indicated by a marked decline in the proportion of young expanding leaves (Fig. 3). Carbon

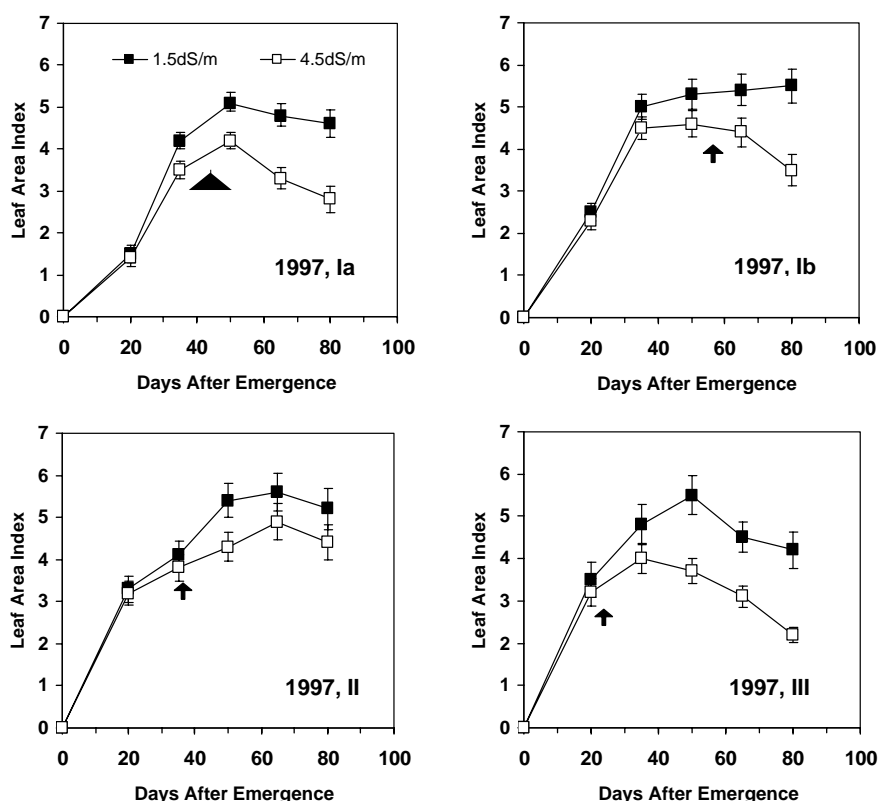


Fig. 2. Variation of leaf area index in potato plants irrigated with fresh or saline water ( $1.5$  or  $4.5 \text{ dS m}^{-1}$ ) during the 1997 growing season. Four distinct groups of plants differing in date of emergence were followed (see Section 2). Arrows indicate timing of heat wave events as expressed in days after emergence.

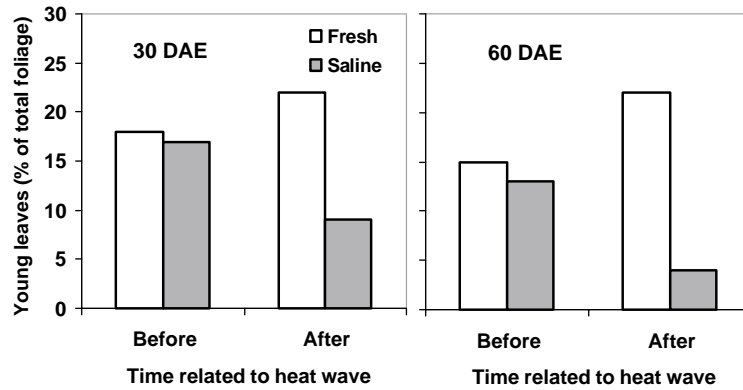


Fig. 3. Proportion (%) of young expanding leaves in foliage of potato plants irrigated with fresh or saline water ( $1.5$  or  $4.5 \text{ dS m}^{-1}$ ) before and a few days after heat wave events that occurred in 1997. Measurements were carried out 30 and 60 days after plant emergence.

exchange rates (CER) recorded for young fully expanded leaves was twice as high as that of older leaves ( $18.5 \mu\text{mol m}^{-2} \text{s}^{-1}$  versus  $9.2 \mu\text{mol m}^{-2} \text{s}^{-1}$ ), with no significant differences between saline and fresh water plants.

Concentrations of sodium were generally higher in stems and old leaves than in younger leaves (Fig. 4), and accumulation of this ion proceeded much faster

under saline water irrigation. A similar pattern was observed for chloride, although chloride concentrations were almost twice as high (data not shown). It is noteworthy that in young expanding leaves, sodium concentrations remained very low even after 60 days of saline water irrigation (Fig. 4). Nevertheless, a few days following a significant heat wave event, sodium concentration measured in young expanding leaves

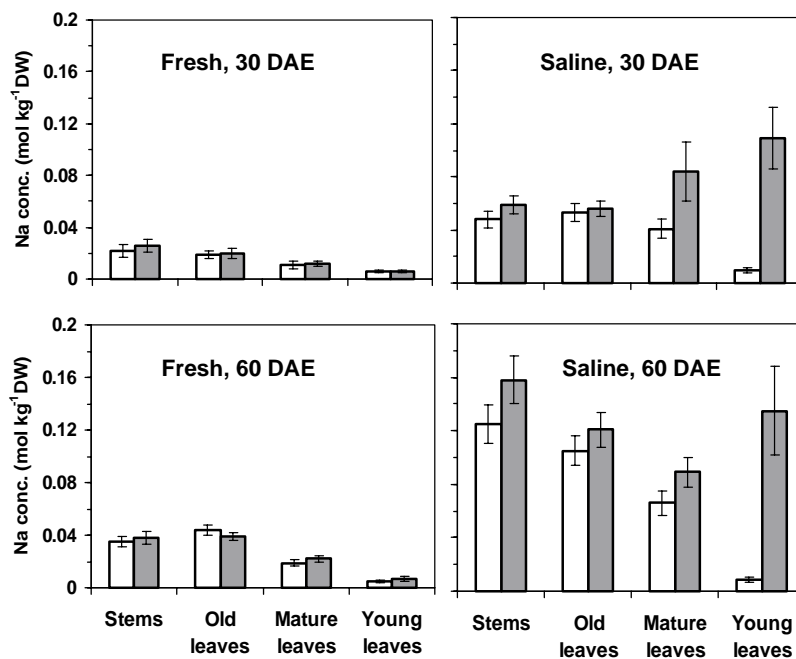


Fig. 4. Sodium concentration in stems and leaves of potato plants irrigated with fresh or saline water ( $1.5$  or  $4.5 \text{ dS m}^{-1}$ ) before (white bars) and a few days after (grey bars) heat wave events that occurred in 1997. Measurements were carried out 30 and 60 days after plant emergence.



increased dramatically as compared to mature leaves and organs (Fig. 4).

#### 4. Discussion

Reasonable yields of spring potato can be obtained using saline water ( $EC_e < 7 \text{ dS m}^{-1}$ ) irrigation, as indicated by our experimental results in the years 1992–1996 (Table 2). In fact, the relative yields attained in those experiments were usually higher than predicted by Maas and Hoffman (1977) definitions for potato (Fig. 5), with the exception of 1994, in which year there was a good match between our results and the authors' predictions. In the light of these findings and of other recent studies (Patel et al., 1999, 2001), it would seem that potatoes are less salt-sensitive than earlier believed. However, there were large year-to-year variations in the crop's response to salinity (Table 2), and these call for an explanation. Among the factors that might induce such variations, weather conditions—and more especially the incidence of heat wave events, which differed significantly among the four years—seemed worth examining as a key determinant.

At first glance, our findings suggest that the decline in tuber yields under saline irrigation was related to the number of heat wave events experienced during the growing season (Table 2). The correlation seems convincing when 1992 is set against 1993 and 1994. The exceptionally warm spring of 1994, officially declared an agricultural disaster (Gat and Horowitz, 1995), was blamed for the very low potato yields obtained under fresh water irrigation throughout the country. Yet in 1996, a year that witnessed many heat wave days in spring, salinity had no deleterious effects on potato yields (Table 2). Clearly, some additional factor was at work.

In order to help elucidate the interrelation between salt and heat wave stress, a further experiment designed to facilitate analysis of the relationship between heat wave timing and crop development was conducted in the spring of 1997. The results of these trials demonstrate that a single but substantial heat wave event can affect tuber yield in different ways depending on the stage of plant development involved (Table 3). Yields under saline irrigation declined when plants were exposed to significant heat

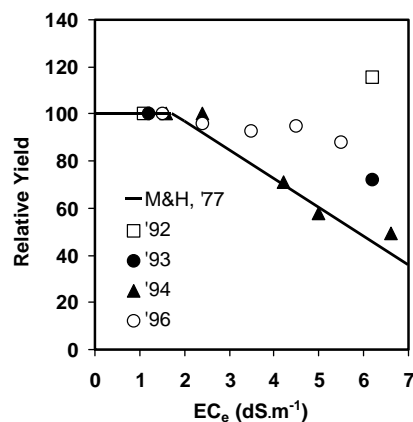


Fig. 5. Relative yields of 'Désirée' potato tubers in response to increasing salinity levels in soil extract as obtained in experiments carried out in the years 1992–1996. Relative yield is expressed as a percentage of the yield under fresh irrigation water in the same year. Solid line indicates potato response to salinity as predicted by Maas and Hoffman (1977).

wave events at 40–60 days after emergence (DAE): that was the case with the early-sown experiments in 1997 (Table 3), as well as in 1993 and 1994 (Table 2). Yields were not affected when plants were exposed to heat spells at an earlier stage of development, for instance in the late-February sowing in 1997 (Table 3) and in 1996 (Table 2), nor when exposure occurred at a later stage, that is beyond 60 DAE, as in 1992 and 1996 (Table 2).

The sensitivity of tuber production to heat waves at this particular developmental stage—40–60 DAE—may be interpreted in terms of the effects of combined stress on vegetative growth. The canopy of potato plants, and especially young organs, tend to wilt during heat waves. Although the severity of the VPD and temperature obviously affects post-stress plant performance, duration of stress appears to be a more important determinant of damage to the shoot, judging by the fact that the effect of single heat wave days was usually transient (data not shown). However, while in plants irrigated with fresh water the LAI was hardly affected even after severe heat wave events, it often declined very substantially in saline water plants (Fig. 2). This marked decline may be linked to the disappearance of the pre-existing population of young leaves, as well as to a limited ability to resume young vegetative growth. Either factor—or the two acting in combination—could account for the drastic decline in



the proportion of young expanding leaves that occurred in saline water plants following pronounced heat wave events (Fig. 3).

It appears that in potato plants the young expanding leaves benefit from special protection against salt accumulation, since sodium concentrations remained very low even after 60 days of saline water irrigation (Fig. 4). Ion compartmentalization among organs and tissues is one of the basic mechanisms for maintenance of ion homeostasis in plants (Apse and Blumwald, 2002; Greenway and Munns, 1980; Läuchli and Epstein, 1990; Serrano, 1996; Zhu, 2001). Excess ion accumulation is avoided, especially where steady metabolic functioning is essential for plant persistence or reproduction, such as in young leaves (Hasegawa et al., 2000; Munns, 1993; Niu et al., 1995) and fruits (Apse and Blumwald, 2002). However, in potato plants these compartmentalization mechanisms seemed to collapse during heat waves, as indicated by the dramatic upsurge of sodium concentration measured in young expanding leaves a few days after the event (Fig. 4). This salt accumulation was obviously responsible for the lethal consequences of severe heat waves on the population of young expanding leaves among our saline water potato plants. Indeed, synergistic effects of different environmental stresses on plants have often been described (Levitt, 1980; Munns, 2002).

While the direct deleterious effect of combined stress on an existing population of young leaves could explain short-term, transient, reductions in the LAI, it cannot account for a steady decline in the index. Moreover, the concurrence of a persistent decline in the LAI with heat waves occurring after 40 DAE (Fig. 2) calls for an explanation. The ability of the potato plant to resume vegetative growth following substantial foliar damage may be analyzed from a whole-plant perspective. Vegetative growth resumption requires reallocation of assimilates. While tubers are formed during the first 40 DAE, in this period they are too small (Fig. 6) to influence shoot growth, which is vigorous enough to overcome stress damage and replace lost leaf area. However, the tubers grow rapidly in size, and towards 40 DAE and thereafter become the dominant sink for dry matter (Fig. 6). Strong tuber demand for any available photoassimilate might inhibit the emergence of substitute shoot growth at this time, simultaneously causing reduction in the

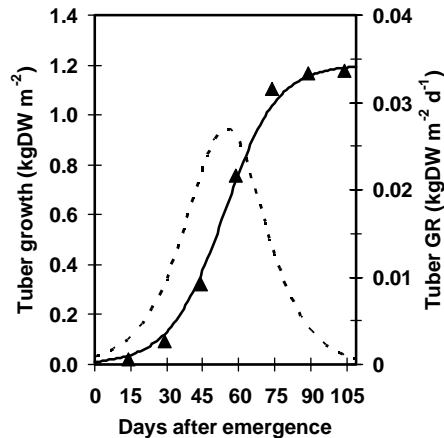


Fig. 6. A schematic display of potato ('Désirée') tuber growth (solid line) and growth rate pattern (dashed line) from emergence to harvest. Tuber yields were sampled every 15 days during the 1996 season to obtain real data (triangle symbols) for curve fitting of a logistic growth function. The derived growth rate (GR) curve indicates that dry matter demand for tuber growth peaks at 55 days after emergence and then declines.

LAI (Fig. 2), increase in foliar age (Fig. 3), and consequent decline in photoassimilate supply.

Sufficient leaf area and an adequate supply of photoassimilates are prerequisites for the production of substantial tuber yields. A current photoassimilate supply is especially crucial during tuber growth enhancement at 40–60 DAE, as supported by evidence showing that other forms of foliar damage occurring at this stage, such as hail, frost, or pruning, can also reduce potato yields (Dar, 1985; Khurana and McLaren, 1982). Therefore it would be reasonable to suppose that salt- and heat-stress induced canopy impairment occurring at that particular stage might lead to decreased tuber yield. On the other hand, during the last third of crop development (70 DAE–harvest), declining tuber growth relies on remobilization of reserves rather than on current photosynthesis (Moorby and Milthorpe, 1975), and therefore damage to the leaves at that late stage has only a marginal influence on yield.

In conclusion, we show here that reasonable potato yields can be obtained using saline irrigation water ( $EC_i < 7 \text{ dS m}^{-1}$ ) on deep sandy soils as long as extreme weather events do not interfere. Combined heat wave and salt stress, if it occurs at 40–60 DAE, causes irreversible canopy impairments that may lead

to significant reduction in tuber yield. Early planting (and mulching with transparent polyethylene to enhance plant emergence) reduces the chances of encountering heat waves at this sensitive stage of potato plant development. Similarly, early maturing potato cultivars could prove advantageous (Bustan, unpublished). In addition, in frost-free areas saline water could safely be used to irrigate potatoes grown on sandy soils as early as October (northern hemisphere) as well as throughout the winter, as is already widely practiced in Israel. This could significantly extend the potato growing season in, for instance, the arid and semiarid lands around the Mediterranean basin.

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