Growth and Development of Potatoes under Salinity and Water Deficit

Bruria HeuerA,B and A. NadlerA

A Institute of Soils and Water, ARO, The Volcani Centre, POB 6, Bet Dagan 50250, Israel.
B Corresponding author.

Abstract
The agronomic and physiological responses of potato to salinity and to water deficits were determined. The experiment consisted of five treatments: three salinity levels and two restricted amounts of water. Plant height, leaf area and fresh weight accumulation were significantly affected by the salinity and moisture treatments. Stem number, leaf elongation and the content of dry-matter in leaves, stems and tubers were hardly affected. Harvest index, an important agronomic trait, was markedly improved by the different treatments.

Keywords: water deficit, saline water, Solanum tuberosum, growth.

Introduction
In arid and semi-arid regions, where growth is limited by water shortage or by water of poor quality, the use of saline water for crop production is often unavoidable. Most crops tolerate salinity up to a threshold level above which yields decrease as salinity increases (Maas 1986). In addition, during the dry season, when most crops are irrigated, periods of temporary water deficit may be encountered. Potatoes are classified as moderately salt-sensitive (Maas and Hoffman 1977; Ahmad and Abdullah 1979) and as very sensitive to water stress (Salter and Goode 1967; Kleinkopf 1983). A salinity level as determined by the electrical conductivity of a saturated soil solution extract, in the range of 4·0 dS m⁻¹ or above, usually lowers tuber yields by more than 25% (Maianu 1985). The extent of tolerance to water stress depends on its intensity, the cultivar involved and the developmental stage of the crop (Levy 1986; Miller and Martin 1987; Haverkort et al. 1990). This is also true for salt tolerance (Levy 1992). However, information regarding the effect of salinity on potatoes is limited, rather contradictory and mostly not derived from field trials (Bilski et al. 1988; van Hoorn et al. 1993).

Responses of potatoes to salinity or soil moisture are generally assessed in terms of survival, vegetative growth, tuber size or total tuber production (van Loon 1981; MacKerron and Jefferies 1988; Flowers and Yeo 1989). It is generally accepted that their relatively high sensitivity to water stress demands proper irrigation management for growth and for tuber production, implying frequent soil water measurements (Foroud et al. 1993). Straightforward correlations between soil measurements and plant growth under salt or water stress conditions have
not been found, and therefore possible injury cannot be predicted throughout the entire growth period of the crop, nor can the final yield.

The purpose of the present study was to provide additional information on the growth and development of potato under salinity and under restricted water supply. Further, we looked for the possibility of correlating soil parameters with physiological ones for a better prediction of plant response to stress conditions.

**Materials and Methods**

**Plant Material**

Potatoes (Solanum tuberosum L. cv. Desiree) were planted on 23 February 1993 at Kibbutz Nahal Oz, in the northern Negev, Israel. The soil was a clay loam (Calcic Palexeralf), 17% clay, 36% silt, 47% sand, CEC = 14.5 cmol kg\(^{-1}\), 11% CaCO\(_3\), and a field capacity of 18.5% w/w. The experimental plots had been irrigated with brackish water (EC = 5 dS m\(^{-1}\)) for the last 8 years and were washed and leached before the experiments started. The potatoes were planted in 9 m long beds containing two ridged rows, 1.04 m apart, with four plants per metre of row. The distance between the centres of adjacent rows in the same bed was 96 cm. Before planting, 40 t ha\(^{-1}\) cow manure, 0.9 t ha\(^{-1}\) superphosphate and 5 t ha\(^{-1}\) gypsum were broadcast and incorporated. Urea as N source was applied with each irrigation, supplying a total N amount of 0.45 t ha\(^{-1}\). Drip laterals were laid in the middle of each pair of rows with emitters every 60 cm, delivering 2.2 L h\(^{-1}\). Available water in the soil profile at the beginning of the experiment was estimated at 12-24 cm. This water was sufficient to ensure good emergence of the plants on 23 March. Subsequently, the differential irrigation treatments were started.

**Treatments**

The treatments consisted of three salinity levels and two restricted amounts of water, summarized in Table 1. The salinity treatments included irrigation with water from the National Water Carrier (EC\(_i\) = 1.5 dS m\(^{-1}\)), which served as the control for the entire experiment, and with two salinized waters from the Shaphdan (Dan region effluent from an activated sludge treatment plant) having EC\(_i\) of 3 and 6 dS m\(^{-1}\) respectively. The water used contained traces of NO\(_3\), PO\(_4\), heavy metals, etc., but within the usual limits of the concentrations recommended for domestic effluents. Salinization started on 8 April. Irrigation water was applied twice weekly from March to July at a rate dependent on evaporation from a screened USWB Class A evaporation pan (5.0 to 8.3 mm day\(^{-1}\)) and a crop coefficient which varied between 0.6 to 1.0, according to the soil coverage by the canopy. The total amount applied from treatment initiation to harvest was 480 mm for all the salinity treatments. The first restricted-amount treatment (treatment 4) received only 60% of the above amount of water, i.e. 288 mm throughout the growth period; in the second (treatment 5), irrigation was withheld for about 2 weeks, between days 57 and 74 after planting. Although potato plants are grown normally under adequate water supply, short periods of water deficit may occasionally occur. For this reason, treatment 5 was added. The experiment had a completely randomized design with four replications, two beds per plot, and was part of a large commercial field.

<table>
<thead>
<tr>
<th>#</th>
<th>Treatment</th>
<th>Water applied (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Non-saline, 1·5 dS m(^{-1})</td>
<td>480</td>
</tr>
<tr>
<td>2</td>
<td>Saline, 3·0 dS m(^{-1})</td>
<td>480</td>
</tr>
<tr>
<td>3</td>
<td>Saline, 6·0 dS m(^{-1})</td>
<td>480</td>
</tr>
<tr>
<td>4</td>
<td>Non-saline, 60% of water applied</td>
<td>288</td>
</tr>
<tr>
<td>5</td>
<td>Non-saline, irrigation withheld between days 57 and 74 after planting</td>
<td>442</td>
</tr>
</tbody>
</table>
Measurements

Soil water content was measured to a depth of 100 cm with a neutron probe, and soil matric potential was measured with tensiometers, installed at depths of 25, 45 and 75 cm, near the emitters. Soil salinity was obtained from a grid of suction cups installed at the same depths as the tensiometers. Since potatoes are a shallow-rooting crop, most measurements refer to the layer 0-50 cm. Plant growth was estimated by measuring the following parameters: height, leaf elongation, leaf area, stem number, accumulation of fresh and dry weight, tuber yield and harvest index. Soon after salinization had started, 15 young expanding leaves from each treatment (one leaf per plant) were marked and their initial length was measured. The elongation rate of these leaves was determined by consecutive measurements of their length. Leaf shedding took place on 2 July and the crop was harvested 10 days later. Leaf shedding refers to the removal of all the leaves to facilitate crop harvest. Leaf area was determined from the relative dry weights of leaves and of 25 discs randomly removed from them. Ten such measures were made for each sample. Five plants from each treatment were sampled on 6 June, weighed individually and separated into various organs. The height estimate for each plot was obtained by measuring 15 marked plants at different time intervals. Harvest index is usually defined as the ratio of harvested dry matter to total plant dry weight. In the field it is difficult to determine root dry weight, therefore, shoot harvest index is commonly used in agronomic studies. The data are presented with the respective standard error of the mean for each treatment and the least significant difference (L.S.D. 0.05) between treatments, derived from an analysis of variance.

Results and Discussion

Soil Parameters

Irrigation with saline water led to a continuous increase in soil salinity (Fig. 1). In general, owing to frequent irrigation and leaching, a relatively constant soil salinity is maintained in the root zone (Bernstein and Francois 1973). In spite of the fact that the soil had been washed and leached, it contained certain levels of absorbed salts from the preceding experiments with saline water, which could not be removed from the soil profile. Thus, the final values of EC at a depth of 75 cm were 3.83, 7.03 and 10.27 dS m⁻¹ in treatments 1, 2 and 3 respectively, higher than planned at the beginning of the experiment (Fig. 1).

Soil water contents (% volume) in treatments 1-3 were similar and ranged from 24 to 35%, depending on the soil depth (data not shown). Treatment 4 was much drier, especially at the depth of 25 cm with a difference in water content around 10% for most of the growing period. Nevertheless, all the values of soil water content in treatment 4 were above field capacity. The matric potential of the soil at 25-cm depth in treatment 4 was very negative, with an average of -95 kPa (Fig. 2).

Plant Growth

Plant height was significantly affected by salinity and water restriction (Fig. 3). Within the first 20 days after treatment initiation, plant height was reduced by about 17% in treatments 3 and 4 compared with the control treatment. This inhibition of plant growth remained more or less constant throughout the entire growth period. However, withholding of irrigation for 2 weeks reduced final plant height by 25% (treatment 5). None of the treatments influenced stem number (Table 2). Leaf length was slightly affected by salinity at the beginning of the field experiment; it fully recovered later (Fig. 4). In contrast, water deficit severely affected leaf development. For example, on 9 May, reductions of 27.5
Bruria Heuer and A. Nadler

Fig. 1. Electrical conductivity (EC) of the soil layer extracts obtained with suction cups.

Fig. 2. Soil water potential measured with tensiometers.
and 62.1% in leaf length were found in treatments 4 and 5, respectively. A marked decrease in leaf area was observed when the crop was irrigated with the more saline water or with restricted amounts of water, 62 and 59% respectively (Table 2). The greatest effect was obtained in treatment 5, in which leaf area was reduced by 76%. Although not measured, we assume that leaf number was also affected. For example, in treatment 4, the area of an individual leaf was
reduced by 28% and the area of all leaves by 59%, the difference resulting from a different leaf number. Jefferies (1993) also reported that drought significantly reduced the final size (area) of potato leaves. Leaf expansion is first reduced by the decrease in the soil water potential (Munns 1993). Later, a salt-specific effect appears as salt injury in the old leaves, leading to their death. Loss of only a few leaves does not affect plant growth, but if the rate of leaf death approaches the rate of new leaf production, a substantial drop in the supply of assimilates to the growing leaves can occur, leading to a significant suppression in plant growth. In our experiment, leaf death which reduced leaf number was responsible for the decrease in leaf area. Levy (1983) suggested that the ability to maintain leaf expansion under increasing soil-moisture deficit is correlated with the capacity for osmotic adjustment. This being the case, our results suggest that partial or full osmotic adjustment was induced by the salinity treatments. Furthermore, we found some accumulation of sugars and proline in leaves of treatment 3 and the ion content in these leaves corresponded to 15% of their dry weight (Nadler and Heuer 1995).

Table 2. The effect of salinity or water deficit on leaf area and stem number of potatoes
Measurements were taken on 7 June. Means±s.d. (n = 15 plants per plot)

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Leaf area (m² plant⁻¹)</th>
<th>% of control</th>
<th>Number of stems per plant</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>4.74±0.15</td>
<td>100</td>
<td>2.75±0.83</td>
</tr>
<tr>
<td>2</td>
<td>4.38±0.20</td>
<td>92</td>
<td>3.25±0.43</td>
</tr>
<tr>
<td>3</td>
<td>1.80±0.11</td>
<td>32</td>
<td>2.63±0.69</td>
</tr>
<tr>
<td>4</td>
<td>1.94±0.09</td>
<td>41</td>
<td>2.87±0.68</td>
</tr>
<tr>
<td>5</td>
<td>1.15±0.07</td>
<td>24</td>
<td>2.50±0.50</td>
</tr>
<tr>
<td>l.s.d.(0.05)</td>
<td>0.39</td>
<td></td>
<td>1.45</td>
</tr>
</tbody>
</table>

Leaf and especially stem fresh weights were markedly decreased by salinity and water stress (Fig. 5). In spite of this, wilting of leaves was not enhanced by the treatments. Tuber yield was not affected by the treatments imposed or by the history of field exposure to salinity (Nadler and Heuer 1995), similar to the results obtained in other field trials (Plaut and Carmi, pers. comm.). The same was true for tuber dry weight (Fig. 6). The percentage of dry matter in the leaves or stems was almost the same in all treatments, but significantly greater in the tubers of water-stressed plants (Table 3).

Yield depends on accumulation of dry matter and on its partitioning into tubers as well as on the tuber dry matter content. Dry matter production and its accumulation in the tubers are important quality criteria and important parameters for assessment of adaptation to stress conditions. It was previously shown that water stress resulted in a preferential supply of assimilates to the tubers (Munns and Pearson 1974).

There are two possibilities to explain the lack of tuber yield response: (a) a relatively low tuber dry weight production in the control treatment; and (b) a real increase due to or in coincidence with, the stress imposed. This would appear to be the case here for salinity stress too. If calculated per unit leaf area, the production of total dry matter (leaves+stems+tubers) was doubled under high
Fig. 5. Accumulation of fresh weight in potatoes as a function of salinity or water deficit. Wilted leaves = brown, dead leaves, still attached to the stems. Vertical bars indicate s.d. of the means. l.s.d.₀·₀₅ = 46, 96, 23 and 191 for green leaves, stems, wilted leaves and tubers respectively.

Table 3. Percentage dry matter in leaves, stems and tubers and harvest index as affected by salinity or water stress

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Leaves (%)</th>
<th>Dry matter (%)</th>
<th>Stems</th>
<th>Tubers</th>
<th>Total (%)</th>
<th>Harvest index (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>9.99</td>
<td>8.45</td>
<td>16.21</td>
<td>13.87</td>
<td>79.87</td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>10.44</td>
<td>8.61</td>
<td>18.67</td>
<td>13.99</td>
<td>86.08</td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>10.73</td>
<td>8.10</td>
<td>19.56</td>
<td>16.02</td>
<td>91.15</td>
<td></td>
</tr>
<tr>
<td>4</td>
<td>10.26</td>
<td>9.63</td>
<td>18.36</td>
<td>16.31</td>
<td>90.53</td>
<td></td>
</tr>
<tr>
<td>5</td>
<td>9.88</td>
<td>7.67</td>
<td>17.61</td>
<td>15.42</td>
<td>94.36</td>
<td></td>
</tr>
<tr>
<td>l.s.d.₀·₀₅</td>
<td>0.53</td>
<td>0.88</td>
<td>0.60</td>
<td>1.41</td>
<td>1.59</td>
<td></td>
</tr>
</tbody>
</table>

A significant increase in the harvest index was obtained in all the treatments imposed, suggesting a better water-use efficiency (WUE) under saline or water-stress conditions (Table 3). This is an important finding, which may play a leading role in breeding programs. Water use efficiency is defined as the ratio between dry matter production and the amount of water transpired by a crop. Salinity, as well as drought conditions, are responsible for temporary closure of stomata, leading to an increased WUE (Viets 1966; Fischer and Turner 1978; Plaut 1989). If harvest index is increased, the ability of the reduced photosynthetic surface per sink organ to supply assimilates is improved and so is net photosynthesis rate per unit leaf area (Table 4).
The effect of salt or water stress on the accumulation of dry weight in potato plants. Sampling as in Fig. 5. Vertical bars indicate s.d. of the means. l.s.d.0.05 = 4, 11 and 30 for leaves, stems and tubers respectively.

Table 4. The effect of irrigation regimes on total dry matter production and total CO$_2$ uptake per unit leaf area

Total CO$_2$ uptake was calculated using a conversion factor of 0·645 g dry matter per g CO$_2$ (Jones 1992)

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Total dry matter per leaf area (g m$^{-2}$)</th>
<th>CO$_2$ uptake per leaf area (g CO$_2$ m$^{-2}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>52·95±1·55</td>
<td>16·63±0·48</td>
</tr>
<tr>
<td>2</td>
<td>55·84±3·71</td>
<td>16·44±1·09</td>
</tr>
<tr>
<td>3</td>
<td>111·03±3·34</td>
<td>20·88±0·62</td>
</tr>
<tr>
<td>4</td>
<td>103·00±7·16</td>
<td>17·68±1·22</td>
</tr>
<tr>
<td>5</td>
<td>140·14±1·41</td>
<td>17·55±1·76</td>
</tr>
<tr>
<td>l.s.d.0·05</td>
<td>10·67</td>
<td>3·00</td>
</tr>
</tbody>
</table>

Total tuber number was not changed (data not shown). The number of tubers per plant is the product of the number of stems per plant, which was also unchanged (Table 2), and the number of tubers per stem. We assume that the reason for the similar tuber number is that at the beginning of the season (up to about 2–4 weeks after emergence), the soil water potential was similar for all the treatments (Fig. 4). MacKerron and Jefferies (1986) also showed that the number of tubers per stem was reduced when water stress was imposed very early in the growing season, at the time of tuber initiation, but not when it was imposed later. Following their observations, we may suppose that although treatment 4 received 60% less water than the control, water stress was not present at the early stages of growth, but only much later. Haverkort et al. (1990) showed
that once stolons are initiated, they produce tubers regardless of a subsequent drought period.

The results obtained in our experiment highlight the mismatch between parameters of plant growth and crop yield. Soil measurements and plant growth appear to be highly correlated, but none of the measurements during crop growth could be used to predict final yield. It seems, that the amounts of water usually supplied to potatoes are superfluous. A substantial reduction is recommended.

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References


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