

# EFFECT OF SODIUM CHLORIDE SALINITY ON THE WATER BALANCE OF *ATRIPLEX HALIMUS*

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## Abstract

Sodium chloride was found to improve the water balance of *A. halimus* plants under conditions of high evaporative demand. This improvement was expressed by higher values of turgor pressure and percentage saturation value in plants grown in salinized culture solutions (Knop solution to which sodium chloride was added to give final osmotic potentials of from  $-3$  to  $-10$  bars) as compared with plants grown in the control (Knop) solutions.

However, only in leaves of plants grown in saline culture solutions whose osmotic potential did not exceed  $-5$  bars was a constant water potential gradient maintained between the culture solution and the leaf. Furthermore the hydraulic conductivity of the root system appeared to have been impaired by salinity.

The improved water balance of plants which were exposed to salinity could be ascribed to a reduction of transpiration. This was due to some extent to an increase of stomatal resistance but also to a highly significant increase of mesophyll resistance to water loss ( $r_m$ ). Photosynthesis was not affected by  $r_m$ . The ecological implications of the presence of the  $r_m$  factor to the measured transpiration/photosynthesis ratio are discussed.

## I. INTRODUCTION

For optimal growth, *Atriplex halimus* and other halophilic species of *Atriplex* require relatively high concentrations of sodium chloride in the soil or culture medium (Black 1956, 1958; Greenway 1968; Brownell 1965, 1968). Brownell and Jackman (1966) and Gale and Poljakoff-Mayber (1970) showed that small quantities of sodium are essential for the growth of some *Atriplex* species.

Gale, Naaman, and Poljakoff-Mayber (1970) showed that the optimal concentration of sodium chloride in the culture solution for growth of *A. halimus* was a function of environmental conditions. Under conditions of high evaporative demand, the optimal osmotic potential ( $\Pi_{ex}$ ) ranged from  $-3$  to  $-10$  bars. Under conditions of relatively low evaporative demand, all concentrations of sodium chloride in the growth medium depressed growth.

The purpose of the present work was to test the hypothesis that under conditions of high evaporative demand, sodium chloride enhances growth of *A. halimus* by improving the plant's water balance, and if so to study the mechanism whereby this is brought about.

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## II. METHODS

*A. halimus* seeds, gathered from wild plants in the Northern Negev of Israel, were germinated in sand. When the seedlings reached a height of about 5–6 cm they were transferred individually to dark-walled bottles of 125 ml capacity, containing Knop's nutrient solution. The solution was changed every 2 days. After 2 weeks of growth in the "humid" growth chamber (see below) seedlings were transferred to large plastic containers, four seedlings per container. There were 4 litres of aerated Knop solution in each container. Eight containers were placed in each of two growth chambers (ISCO Co. model E-3). Conditions were the same in the two chambers apart from the relative humidity of the atmosphere, which in the "dry" chamber was maintained at  $25 \pm 5\%$  R.H. and in the "humid" chamber at  $75 \pm 5\%$  R.H., during all hours of the day. Other conditions were as follows:

Time of day	Illumination (f.c.)	Total radiation (cal cm <sup>-2</sup> min <sup>-1</sup> )	Temperature (°C)
0600–0800	1100	0.11	23
0800–1200	2900	0.31	29
1200–1400	4600	0.50	29
1400–1600	2900	0.31	29
1600–2200	1100	0.11	23
2200–0600	Dark	—	18

The light source was Metalarc lamps supplemented with incandescent bulbs.

Salinization of the medium with sodium chloride was begun after the plants had grown for 1 week in Knop solution, in the growth chamber. Rate of salinization was such that rate of increase in osmotic potential did not exceed  $-1$  bar per day. The final values of  $\Pi_{ex}$  attained (in addition to the  $-0.25$  bar of the Knop solution) were 0,  $-5$ ,  $-10$  and  $-15$  bars. All the experiments were carried out at least 4 weeks after the final  $\Pi_{ex}$  was reached.

Total water potential  $\psi_w (= \Pi_i + P + T$ , where  $\Pi_i$ ,  $P$ , and  $T$  are osmotic, turgor, and matric potentials respectively) of the plants was measured using the "pressure bomb" as described by Scholander *et al.* (1965).

Osmotic plus matric potentials were also measured with the pressure bomb. Procedure was as follows: A twig was cut and weighed and quickly transferred to the bomb. The water potential was measured and the pressure in the bomb was then released via a gas-release valve. This valve was connected to a temperature-controlled lithium chloride hygrometer. A regulated flow of dry nitrogen was then passed through the chamber. The level of the humidity in the nitrogen, after passing over the twig, was used to calculate the water loss of the twig. From time to time the nitrogen efflux was arrested and the water potential of the twig was again determined. About six such measurements were made on each twig. From these data a curve describing the water potential as a function of water content was obtained. The curvature of this plot changes when the turgor potential reaches zero. The water potential at zero turgor (osmotic plus matric potentials) is obtained from the intersection of the two tangents to the two sections of the curve. Hence, assuming  $\Pi_i V = K$ , and  $T V = K'$ , where  $V =$  volume, the initial value of  $\Pi_i + T$  can be calculated.  $\Pi_i + T$  value was corrected by adding the value of the osmotic potential of the expressed xylem sap, obtained independently with a cryoscopic osmometer. This method is tedious but is the only one suitable for plants which accumulate or secrete salt. Preliminary experiments comparing this method to cryoscopy of expressed sap, showed good agreement for glycophytic plants (Kaplan and Gale, unpublished data).

Hydraulic resistance to the passage of water through the roots was also measured with the pressure bomb, as described by O'Leary (1969). Pressure of 10 bars was used and exudate was collected for 5 min.

Water content of twigs was measured by a modification of the method of Stocker (1929). Instead of being placed in pure water, each twig was equilibrated in culture solution of the same composition as that in which the entire plant had been grown. The twigs were covered with polyethylene bags. Equilibrium was attained in 48 hr. Results of these measurements are expressed as percentage saturation value. This value was calculated in the same manner as Stocker's "saturation deficit".

Gas-exchange measurements of single attached leaves were made in apparatus similar to that described by Gale, Poljakoff-Mayber, and Kahane (1967). Measurements were made at a radiant flux density of  $0.39 \text{ cal cm}^{-2} \text{ min}^{-1}$ , obtained from a quartz-line lamp. These measurements were used to calculate rates of photosynthesis and transpiration, and diffusional resistances to water loss and to  $\text{CO}_2$  uptake. Two modifications were introduced into the system:

- (1) Two fans were placed in the chamber, one over each leaf surface. The fans were turned by a motor-driven magnet situated beneath the chamber. The fans minimized the transport resistance in the turbulent phase of the boundary layer. Under these conditions boundary layer resistance can be assumed to be confined to the diffusional phase within the laminar layer adjacent to the leaf. This allows for the calculation of the stomatal resistance to carbon dioxide diffusion from the stomatal resistance to water vapour diffusion, using the ratio of the coefficients of diffusion of carbon dioxide and water vapour in air, thus eliminating the necessity of introducing the rather uncertain, 0.66 power, correction coefficient.

Due also to the efficient stirring, the concentrations of the different gases over each of the two leaf surfaces are homogeneous. Consequently the concentrations of carbon dioxide, water vapour, and helium in the air leaving the two halves of the chamber may be assumed to be close to the average values over the leaf. This increases the accuracy of the estimation of the water vapour and carbon dioxide gradients from leaf to air and of the helium gradient from the bottom to top surface of the leaf.

- (2) Helium was present in the air stream passing over the lower side of the leaf, at a concentration of 5.7% (v/v). Aliquots of helium-containing air, from the upper chamber, were introduced periodically into the gas chromatograph through an in-line sampling valve. The chromatogram peak areas were measured with a disk integrator.

### III. RESULTS

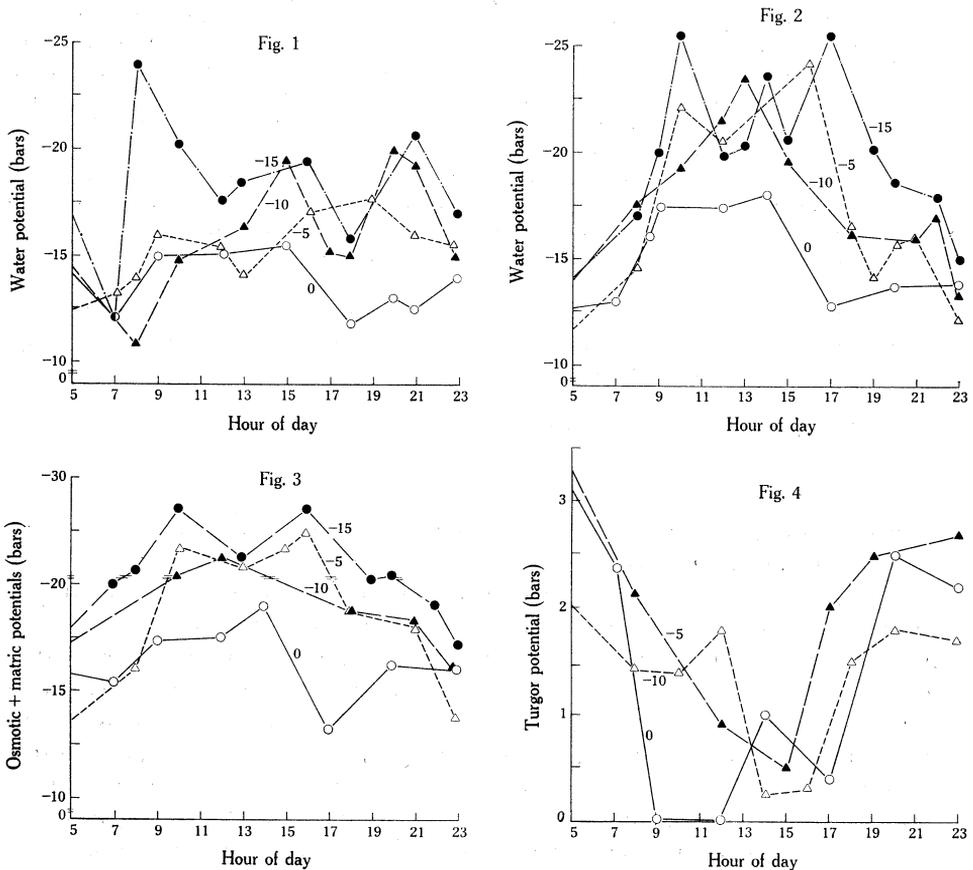
Total water potential,  $\psi_w$ , was measured during the day in plants taken from the two growth chambers. Results are shown in Figures 1 and 2.

Despite the large fluctuations in  $\psi_w$  during the day, as can be seen, a number of conclusions may be drawn: (1) in the "humid" chamber (Fig. 1) the  $\psi_w$  of the moderately salinized plants ( $\Pi_{ex}$  of  $-5$  and  $-10$  bars) differed only slightly from that of the controls during the morning hours. Later on, the  $\psi_w$  of these plants decreased considerably, i.e. the  $\psi_w$  value became more negative. The higher the salinity in the medium, the earlier was the decrease of  $\psi_w$ . The  $\psi_w$  of the plants grown in a solution in which  $\Pi_{ex}$  was  $-15$  bars was consistently lower than that of the controls throughout the day. (2) In the dry chamber all the plants grown in salinized media had similar values of  $\psi_w$  throughout the midday hours, at a level approximately 5 bars below that of the controls. Consequently only those plants grown at a  $\Pi_{ex}$  of  $-5$  bars showed a complete "osmotic adjustment", i.e. they maintained a constant water potential gradient from the outside solution to the leaves ( $\psi_w - \Pi_{ex} = \text{constant}$ ).

Measurement of the osmotic plus matric potentials ( $\Pi_i + T$ ) in the plants growing in the "dry" chamber (Fig. 3) showed that the changes in  $\psi_w$  which appeared in the course of the day could be ascribed to changes in these two parameters (here measured together).

Estimations of turgor pressure obtained by subtracting  $\psi_w$  from ( $\Pi_i + T$ ) are not very reliable due to the relatively high error inherent in the two measurements, as compared to the small numerical values of turgor pressure. Nevertheless this was attempted for the plants grown in the dry chamber. Figure 4 shows results for the control plants and plants grown at two levels of salinity. Bearing in mind the

reservation noted above, the data indicate that whereas by 9 a.m. the turgor of the control plants had rapidly fallen to almost zero, at least some turgor was maintained throughout the day in plants growing in salinized media. In the "humid" chamber the control plants maintained turgor of between 1 and 3 bars throughout the day, whereas the turgor of the plants grown in salinized media was slightly lower, varying between 1 and 2 bars.



Figs. 1 and 2.—Water potential of *A. halimus*, as a function of sodium chloride concentration and hour of day, under "humid" (Fig. 1) and "dry" (Fig. 2) conditions. In Figures 1-5 the osmotic potentials attained in the culture solution (0, -5, -10, -15 bars), in addition to the -0.25 bars of the Knop (control) culture solution, as a result of varying the sodium chloride concentration are indicated.

Fig. 3.—Osmotic plus matric potential of *A. halimus*, as a function of sodium chloride concentration and hour of day, under "dry" conditions. Note change of scale on the ordinate.

Fig. 4.—Calculated turgor pressure of *A. halimus* as a function of sodium chloride concentration and hour of day, under "dry" conditions.

Further evidence for an improved water status in the plants grown in salinized media in the "dry" chamber was obtained from the percentage saturation value (PSV) of control plants and those grown at a  $\Pi_{ex}$  of -5 and -10 bars (Fig. 5). While

the PSV of the control plants varied during the day between 70 and 75%, the PSV of the plants grown in salinized media was between 80 and 85%.

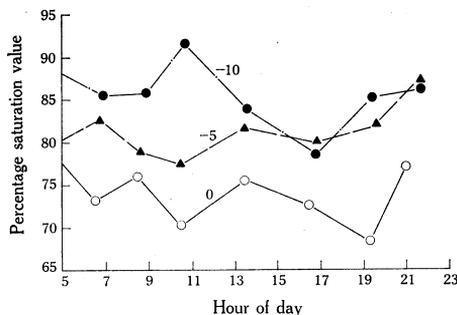


Fig. 5.—Percentage saturation value of *A. halimus*, as a function of sodium chloride concentrations and hour of day, under “dry” conditions.

Measurements of the hydraulic conductivity of the root system (Table 1) as affected by sodium chloride salinity in the growth medium showed that (1) plants grown in the “dry” chamber had a somewhat lower conductivity than those grown in the “humid” chamber; and (2) sodium chloride depressed conductivity under both dry and humid conditions, although there was no significant difference between the levels of salinity.

TABLE 1

EFFECT OF AIR HUMIDITY AND SODIUM CHLORIDE IN THE CULTURE MEDIUM DURING GROWTH ON THE HYDRAULIC CONDUCTIVITY OF THE ROOT SYSTEMS OF *A. HALIMUS*

Osmotic potential of culture solution (bars)	Growth chamber conditions	Hydraulic conductivity*	Supply of water to tops†
0‡	Humid	10.1 ± 1.2	2.4
-5	Humid	5.5 ± 0.7	0.8
-10	Humid	6.7 ± 1.1	1.1
0‡	Dry	8.4 ± 0.4	1.8
-5	Dry	4.0 ± 0.6	0.6
-10	Dry	5.3 ± 0.4	0.8

\* Expressed as milligrams exudate per gram fresh weight of roots per minute at a pressure of 10 bars. Each value given is the average and standard error of at least six plants.

† Expressed as milligrams exudate per gram fresh weight of tops per minute, and are estimates based on ratios of tops to roots obtained in a parallel experiment.

‡ Control.

Photosynthesis, transpiration, and diffusion resistances were measured on plants grown in the dry chamber at a  $\Pi_{ex}$  of 0 and -10 bars. Results obtained are summarized in Table 2 and show that the plants grown at a  $\Pi_{ex}$  of -10 bars had a

considerably larger overall resistance to water vapour loss ( $\Sigma r$ ) than the control plants.\*  $\Sigma r$  averaged  $4.15 \text{ s cm}^{-1}$  for the controls and  $12.7 \text{ s cm}^{-1}$  for the salinized plants. When  $\Sigma r$  was partitioned into its component resistances, as shown in Table 2, salinity is found to have had no significant effect on  $r_s^u$  but a large effect on  $r_s^l$ . Overall leaf stomatal resistance,  $r_s$ , was  $2.1 \text{ s cm}^{-1}$  in the controls and  $5.8 \text{ s cm}^{-1}$  in the salinized plants.

TABLE 2

PHOTOSYNTHESIS, TRANSPIRATION, AND DIFFUSION RESISTANCES OF LEAVES OF CONTROL AND SALINIZED *A. HALIMUS* PLANTS GROWN UNDER CONDITIONS OF HIGH EVAPORATIVE DEMAND  
Values given are the average of at least six leaves  $\pm$  standard error

Parameter	Leaf surface	Control (Knop culture solution)	Salinized culture solution*
Photosynthesis ( $\text{mg dm}^{-2} \text{ hr}^{-1}$ )	Upper	$11.7 \pm 0.6$	$10.4 \pm 0.4$
	Lower	$9.7 \pm 0.6$	$6.7 \pm 0.6$
Transpiration ( $\text{mg dm}^{-2} \text{ hr}^{-1}$ )	Upper	$433 \pm 29$	$289 \pm 15$
	Lower	$750 \pm 28$	$289 \pm 15$
Stomatal resistance, $r_s$ ( $\text{s cm}^{-1}$ )	Upper	$9.6 \pm 1.6$	$10.7 \pm 1.1$
	Lower	$2.7 \pm 0.8$	$12.5 \pm 2.1$
Mesophyll resistance, $r_m$ ( $\text{s cm}^{-1}$ )	Upper and lower	$3.4 \pm 0.5$	$13.9 \pm 1.9$

\* Osmotic potential of culture solution  $-10$  bars.

The most interesting finding, however, was that a relatively large mesophyll resistance to water vapour loss ( $r_m$ ) was present in the controls ( $3.4 \text{ s cm}^{-1}$ ) and that this resistance was significantly increased (to  $13.9 \text{ s cm}^{-1}$ ) in the salinized plants. It should be noted that whereas there was a large increase in water vapour diffusion resistance between the controls and the salinized plants (whose transpiration rate was only 50% of that of the controls) the rate of photosynthesis in the salinized plants was reduced by only 20%.

#### IV. DISCUSSION

The data presented here on the water potential, percentage saturation value, and estimated turgor pressure of *A. halimus* show that, under conditions of high evaporative demand, moderate levels of salinity ( $\Pi_{ex} = -5$  to  $-10$  bars) improve the plant water balance (Figs. 1-5).

Differences of PSV between control and salinized plants will have been even higher than appears in Figure 5 because the salt secreted on the surface of the leaves absorbed water during the equilibration period. Although the leaves were wiped before weighing, some moisture always remained at the leaf surface and this decreased the calculated PSV of plants, especially of plants exposed to salinity.

\* It may be shown that

$$\Sigma r = (r_s^u + r_m)(r_s^l + r_m) / (r_s^u + r_s^l + 2r_m),$$

where  $r_s$  and  $r_m$  are stomatal and mesophyll resistances to water vapour, and  $u$  and  $l$  refer to the upper and lower leaf surface respectively.

Three factors may contribute to the maintenance of the water content of the plant under conditions of high external osmotic concentration and high evaporative demand. These are: reduced resistance to water uptake, reduced leaf water potential (to maintain the soil solution to leaf water potential gradient), and increased resistance to water loss.

In the present experiments there appeared to have been a much decreased hydraulic conductivity of the root system in response to salinity (Table 1). These findings are similar to those of O'Leary (1969) for bean plants, grown in saline media, but differ from those of Lopushinsky (1964) for tomato plants. Graziani and Livne (1971) also reported a decrease of hydraulic conductivity through tobacco leaf mesophyll tissue, in response to low water potential. If these results reflect the true root resistance to normal water uptake, then salinity is detrimental to the plant's water balance at the level of the roots. However, it is not certain whether a hydraulic gradient may be equated with the water potential gradient normally operative between the root xylem and soil solution.

TABLE 3

MEASURED VALUES OF PHOTOSYNTHESIS AND TRANSPIRATION OF *A. HALIMUS* LEAVES AND VALUES AS CALCULATED ASSUMING MESOPHYLL RESISTANCE TO WATER LOSS ( $r_m$ ) EQUALS ZERO

Parameter	Control (Knop) culture solution	Salinized culture solution
Experimental values		
Transpiration (mg dm <sup>-2</sup> hr <sup>-1</sup> )	1175	578
Photosynthesis (mg dm <sup>-2</sup> hr <sup>-1</sup> )	21	17
Ratio of transpiration to photosynthesis	56	34
$r_m$ (s cm <sup>-1</sup> )	3.4	13.9
Calculated values, assuming $r_m = 0$		
Transpiration (mg dm <sup>-2</sup> hr <sup>-1</sup> )	1910	1216
Photosynthesis (mg dm <sup>-2</sup> hr <sup>-1</sup> )*	21	17
Ratio of transpiration to photosynthesis	91	72

\* Photosynthesis is assumed not to change in relation to  $r_m$ .

Water potential gradients ( $\psi_w - \Pi_{ex}$ ) were maintained in the plants growing in sodium chloride salinized culture solutions with a  $\Pi_{ex}$  of  $-5$  bars. This was due to the reduced osmotic plus matric potential (Fig. 3) and may be considered to be the "osmotic adjustment" as described by Bernstein and Hayward (1958) and others. However, at high levels of  $\Pi_{ex}$  the  $\psi_w - \Pi_{ex}$  gradient was not maintained. This finding is in agreement with those of Mozafar, Goodin, and Oertli (1970) although the experimental procedure was different. The low values of  $\Pi_t + T$  in the control plants were, perhaps, due to high concentrations of organic acids, as found by Mozafar, Goodin, and Oertli (1970) for oxalate.

Limitation of water loss appears to have been the main mechanism whereby salinity operated to improve the plant's water balance, under conditions of high evaporative demand (Table 2). This was achieved in two ways: (1) by the increase of stomatal resistance—as has already been described by Gale, Kohl, and Hagan (1967) and by Meiri, Mor, and Poljakoff-Mayber (1970) for glycophytes and by Gale and Poljakoff-Mayber (1970) for *A. halimus*; and (2) by the increase of mesophyll resistance to water loss.

In order to evaluate the contribution of this mesophyll resistance to the rate of transpiration and to the ratio of transpiration to photosynthesis, the experimental values shown in Table 2 were recalculated, for the same environmental conditions, but this time assuming the absence of the  $r_m$  factor. Results are given in Table 3 and show that  $r_m$  was a very significant factor in the water balance of the plant. Under the conditions of this experiment  $r_m$  reduced transpiration by 38% in the controls and by 52% in the plants grown in saline media. As photosynthesis is independent of  $r_m$  the ratio of transpiration to photosynthesis is also calculated to have been decreased significantly by the presence of the  $r_m$  factor, from 91 to 56 in the controls and from 72 to 34 in the plants grown in saline media.

The presence of this factor ( $r_m$ ) capable of reducing transpiration without affecting photosynthesis is of considerable ecological significance. Previously (Slatyer and Jarvis 1966; Gale, Kohl, and Hagan 1967; and Jarvis and Slatyer 1970) it has been very difficult to rely on values obtained for  $r_m$ , due to the very large experimental error inherent in the methods available for its estimation. However, in the present work there were very large and physiologically significant differences in the values of  $r_m$  obtained in the same experimental system from plants which had been grown under different conditions of salinity. Furthermore, for plants grown in saline media, only the presence of a factor, such as  $r_m$ , could explain the considerable increase of overall leaf resistance to water loss, while there was only a small reduction in photosynthesis (which could be ascribed to changes in  $r_s$ ).

In conclusion it appears that at least one way in which increased sodium chloride levels ( $\Pi_{ex}$  values of between  $-5$  and  $-10$  bars) help *A. halimus* to grow under conditions of high evaporative demand is by improving the plant water balance. This is achieved by reducing the water loss from the leaves in a manner which only slightly reduces photosynthesis per unit leaf area. The greater leaf turgor, as found here in the plants grown in saline media, may then lead to the larger leaf area, as previously reported by Gale and Poljakoff-Mayber (1970). The greater leaf area is then available for increased photosynthesis and growth.

#### V. ACKNOWLEDGMENT

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