

# INTERRELATIONS BETWEEN GROWTH AND PHOTOSYNTHESIS OF SALT BUSH (*ATRIPLEX HALIMUS* L.) GROWN IN SALINE MEDIA

By J. GALE\* and A. POLJAKOFF-MAYBER\*

[Manuscript received April 14, 1970]

## Summary

Plants of *A. halimus* were grown in culture solutions to which NaCl or Na<sub>2</sub>SO<sub>4</sub> was added to different concentrations. The osmotic potential of the sap, growth, morphology, and leaf gas exchange (transpiration and photosynthesis) were studied. At least three different effects of salinity were identified: (1) an increase of leaf area and succulence induced by relatively low concentrations of salt in the growth medium. This resulted in an increase of the leaf area available for transpiration and photosynthesis (and hence growth); (2) an increase of stomatal resistance to water vapour loss and CO<sub>2</sub> uptake. This tended to reduce both transpiration and photosynthesis per unit leaf area; (3) changes in mesophyll resistance to CO<sub>2</sub> uptake ( $r'_m$ ). Relatively low concentrations of NaCl reduced  $r'_m$ , but high NaCl concentrations (i.e. external osmotic potentials lower than -9 atm) and all concentrations of Na<sub>2</sub>SO<sub>4</sub> brought about an increase in  $r'_m$ . In addition to the above effects, salinity may have caused a hormonal imbalance as was indicated by the increased sprouting of lateral buds.

These responses to salinity tend to counteract one another in their overall effect on growth. Which factor will become dominant is determined by the level and type of salinity, and also, possibly, by climatic conditions.

## I. INTRODUCTION

It was previously reported that optimal growth of some *Atriplex* species occurs only in the presence of small amounts of salt (Ashby and Beadle 1957; Black 1958; Blumenthal-Goldschmidt and Poljakoff-Mayber 1968; Greenway 1968;) and very small quantities may be essential (Brownell 1965). When *A. halimus* L. plants were grown in nutrient solutions salinized with NaCl to an external osmotic potential ( $\Pi_e$ ) lower than -8 atm (i.e. higher salt concentration), changes occurred in the submicroscopic structure of chloroplasts and other cell organelles (Blumenthal-Goldschmidt and Poljakoff-Mayber 1968). These changes may be correlated to the general reduction in growth which became significant at this level of salinity. The occurrence of stomatal closure was reported in certain glycophytes if grown under saline conditions, even when the plants were fully adjusted osmotically and leaf turgor was maintained. In these cases both transpiration and photosynthesis were reduced (Gale, Kohl, and Hagan 1967; Meiri and Poljakoff-Mayber 1970). In addition to acting via stomatal closure, salinity may also affect the more basic processes of photosynthesis (Gale, Kohl, and Hagan 1967).

The objective of the present investigation was to study the relations between the growth of *A. halimus* under saline conditions and the changes in the photosynthesis and transpiration of the leaves. A second purpose of the study was to compare the effects of iso-osmotic concentrations of NaCl and Na<sub>2</sub>SO<sub>4</sub> on the growth and gas exchanges of *A. halimus*.

\* Department of Botany, Hebrew University of Jerusalem, Jerusalem, Israel.

## II. METHODS

Seeds of *A. halimus*, gathered from plants growing in the Israel Negev, were germinated in sand. When the seedlings had reached a height of about 6 cm they were transferred to aerated Knop solution (osmotic potential  $-0.25$  atm). Different series of plants were used for the growth and for the gas-exchange experiments.

Each of the plants for the growth experiments was set out in a 1.5-litre container in which the Knop's nutrient solution was changed every 2-3 days. The plants were grown during the spring and summer seasons in Jerusalem, in a greenhouse. Maximum daily temperatures varied between 23 and 32°C.

After 1 week, salinization was begun at a rate not exceeding 1 atm/day. The final osmotic potentials ( $\Pi_e$ ) in the nutrient media were 0, -1, -3, -5, -9, and -15 atm (in addition to the  $-0.25$  atm of the Knop solution). Either 24 m-equiv/l NaCl or 34 m-equiv/l  $\text{Na}_2\text{SO}_4$  was used to obtain each atmosphere of osmotic potential.

After the final level of salinity had been reached it was maintained throughout the experiment. The solutions were changed every 2-3 days. The plants were harvested at the end of a further 5 weeks of growth and the fresh and dry weights of the leaves, branches, and roots were determined.

There were six replicates of each of the 12 experimental variables (six salt concentrations, two salts). Growth of the plants was not very uniform, due evidently to the heterogeneity of the seed material.

Leaf areas were measured on samples of the leaves of each treatment and the ratio of leaf area to leaf fresh weight was obtained. The total plant leaf area was calculated from this ratio and from the overall leaf fresh weight.

An additional, parallel group of *A. halimus* plants was set out as above. The leaves of these plants were used for the measurement of sap osmotic potentials ( $\Pi_i$ ). The harvested leaves of each treatment were divided into two batches. The first was rapidly frozen (in aluminium foil packages) in dry ice, and then thawed. The sap was expressed with a hydraulic press at 2000 lb/in<sup>2</sup>. The second batch was rinsed for 2 min in tap water in an attempt to remove the salt, which accumulates on the surface of the leaves. After rinsing, the leaves were dried with blotting paper before being frozen. The osmotic potentials of the sap were measured with a cryoscopic osmometer.

The plants for the gas-exchange experiments were grown in 5-litre containers, three to four plants per container. In one series, the medium was salinated with NaCl to give  $\Pi_e$  values of -3, -9, -13, and -21 atm. In a second series the plants were salinated with  $\text{Na}_2\text{SO}_4$  to give  $\Pi_e$  values of -1, -3, -5, -9, and -15 atm. A higher range of NaCl salinities was used in order to increase the effect of the salt, because in previous experiments NaCl appeared to be less toxic than  $\text{Na}_2\text{SO}_4$ .

Gas exchange of single leaves, still attached to the plant, was measured in an apparatus very similar to that described by Gale and Poljakoff-Mayber (1968). Illumination was from a water-jacketed quartz-iodine lamp. Leaf and air temperature, air humidity, wind velocity, and concentration of  $\text{CO}_2$  could be controlled and monitored. Data on photosynthesis given below refer to net  $\text{CO}_2$  uptake. Values given are the averages of five or six measurements taken from different leaves of three or four plants. Only the largest apparently healthy leaves from among the five distal leaves of any branch were used. Illumination was 4000 f.c. at the leaf surface (which for this lamp was found to be equivalent to  $0.4$  cal  $\text{cm}^{-2}$   $\text{min}^{-1}$ ). Leaf temperatures were  $28 \pm 2^\circ\text{C}$  (measured to  $0.1^\circ\text{C}$ ), and relative air humidity over the leaves was approximately 35%. Differences in humidity between ingoing and outgoing air streams could be measured with an accuracy of approximately 0.15% R.H.

Boundary layer and stomatal resistances to water vapour loss and  $\text{CO}_2$  uptake, and mesophyll resistance to  $\text{CO}_2$  uptake, were calculated by standard procedures (Gaastra 1959). Mesophyll resistance to  $\text{CO}_2$  uptake ( $r'_m$ , in units of  $\text{sec cm}^{-1}$ ) was obtained from the equation

$$r'_m = [(C_a - C_c)/P] - (r'_a + r'_s),$$

where  $C_a$  is the concentration of  $\text{CO}_2$  in the air over the leaf (units:  $\text{cm}^3 \text{CO}_2 \text{cm}^{-3}$  air),  $C_c$  is the concentration of  $\text{CO}_2$  in the chloroplast after fixation and is taken to be zero,  $r'_a$  and  $r'_s$  are respectively boundary layer and stomatal resistances to  $\text{CO}_2$  (units:  $\text{sec cm}^{-1}$ ), and  $P$  is net  $\text{CO}_2$

uptake (units:  $\text{cm}^3 \text{CO}_2 \text{cm}^{-2} \text{leaf sec}^{-1}$ ). This equation, as first used by Gaastra (1959), gives a "mesophyll resistance to carbon dioxide" which includes all resistances to the uptake of  $\text{CO}_2$  by the leaf (such as diffusional, transport, excitation, and carboxylation) other than stomatal and boundary layer resistances. It is more an arithmetic convenience, for comparing the relative dimensions of stomatal, boundary, and internal resistances, than a physical reality (Gale and Poljakoff-Mayber 1968).

Recent work has shown that failure to measure the gas exchange of the two leaf surfaces separately may cause some error in the partitioning of the individual leaf resistances (Gale and Poljakoff-Mayber 1968; Moreshet, Koller, and Stanhill 1968). However, this error is small in leaves which are almost isolateral, as was found to be the case in preliminary experiments with *A. halimus*. Consequently, in this work, the simpler approach was employed and the gas exchange of the two sides of the leaf were measured together.

The apparatus used for measuring photosynthesis and transpiration is an open-type system. In open systems the rates of gas and vapour exchange have a small feedback effect on the rates of photosynthesis and transpiration. This is due to the modification of the leaf to air,  $\text{CO}_2$ , and water vapour gradients. To overcome this, rates of photosynthesis and transpiration have been calculated to 300 p.p.m.  $\text{CO}_2$  in air, and to a leaf to air vapour density gradient of  $0.02 \text{ cm}^3$  water vapour per cubic centimetre of air. This has been done assuming a 1 : 1 linear relation between gradients and fluxes. Preliminary experiments showed this to be a valid approximation, under the conditions of this experiment, for the small changes in gradients which were involved.

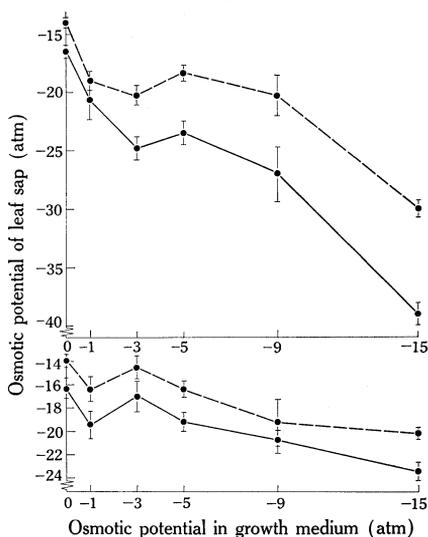


Fig. 1.—Osmotic potential of leaf sap of *A. halimus* plants grown in either NaCl (upper) or  $\text{Na}_2\text{SO}_4$  (lower) salinized culture solutions. — Leaves not rinsed. - - - Leaves rinsed. In Figures 1-4 vertical lines indicate  $\pm$  standard error and the values given for osmotic potential of the nutrient solution are in addition to the  $-0.25$  atm of the Knop solution.

### III. RESULTS

The osmotic potentials of the leaves ( $\Pi_i$ ), from the different treatments, as obtained at the end of the 5-week period of growth, are given in Figure 1. There was a clear difference between the results obtained from plants grown under the two types of salinity. In the rinsed leaves of the plants grown in NaCl salinized media, after an initial rapid decrease of 5-6 atm,  $\Pi_i$  remained fairly constant as long as  $\Pi_e$  was not below  $-9$  atm. From this value of  $\Pi_e$  and on, there was a further decrease in  $\Pi_i$  of 10 atm for a parallel change of  $-6$  atm in  $\Pi_e$ . In the non-rinsed leaves (on which salt crystals could be observed) there was a gradual decrease in  $\Pi_i$  of 23 atm for the overall change of  $-15$  atm in  $\Pi_e$ .

In the plants exposed to  $\text{Na}_2\text{SO}_4$  the osmotic adjustment appeared to be incomplete. The overall decrease of  $\Pi_i$  was only 6–8 atm for the –15 atm change in  $\Pi_e$ . As with the plants exposed to  $\text{NaCl}$ , there was a marked drop in  $\Pi_i$  between the 0 to –1 atm treatment. When  $\Pi_e$  fell below –3 atm there was a steady fall in  $\Pi_i$  which did not, however, equal the change in  $\Pi_e$ .

The effect of  $\text{NaCl}$  and  $\text{Na}_2\text{SO}_4$  salinity on overall growth of *A. halimus*, as expressed by final dry and fresh weights, is shown in Table 1. There are a number of similarities and differences in the growth response of *A. halimus* to the two salts.

TABLE 1  
FRESH WEIGHT OF *A. HALIMUS* PLANTS GROWN FOR 5 WEEKS IN DIFFERENT CONCENTRATIONS OF SALINIZED CULTURE SOLUTIONS

Values given are means  $\pm$  standard error

$\Pi_e$ (atm)*	Salinized with $\text{NaCl}$			Salinized with $\text{Na}_2\text{SO}_4$		
	Fresh Weight (g)	Dry Weight (g)	$\frac{\text{Fresh Wt.}}{\text{Dry Wt.}}$	Fresh Weight (g)	Dry Weight (g)	$\frac{\text{Fresh Wt.}}{\text{Dry Wt.}}$
0	15.0 $\pm$ 1.8	2.4 $\pm$ 0.43	6.3	15.0 $\pm$ 1.8	2.5 $\pm$ 0.41	6.0
– 1	22.8 $\pm$ 3.6	3.8 $\pm$ 0.56	6.0	18.5 $\pm$ 3.0	3.2 $\pm$ 0.55	5.8
– 3	22.5 $\pm$ 2.4	3.2 $\pm$ 0.35	7.0	31.8 $\pm$ 5.0	4.4 $\pm$ 0.58	7.2
– 5	22.8 $\pm$ 2.6	3.4 $\pm$ 0.37	6.7	19.5 $\pm$ 1.6	2.8 $\pm$ 0.20	7.0
– 9	23.5 $\pm$ 2.7	3.3 $\pm$ 0.28	7.1	15.0 $\pm$ 3.5	2.2 $\pm$ 0.20	6.8
–15	19.4 $\pm$ 2.1	2.8 $\pm$ 0.43	6.9	9.1 $\pm$ 0.8	1.6 $\pm$ 0.12	5.7

\* In addition to –0.25 atmospheres of Knop nutrient solution.

Growth was very significantly stimulated by low concentrations of either of the salts. This stimulation was greater for  $\text{Na}_2\text{SO}_4$  than for  $\text{NaCl}$  but, due to the considerable variability, the difference between the effect of the two salts is of low statistical significance ( $P > 0.05$ ). However, the data indicate a more defined optimum at about –3 atm for  $\text{Na}_2\text{SO}_4$  and a broad optimum between –1 and –9 atm for  $\text{NaCl}$ . Further decrease in  $\Pi_e$  reduced the overall growth and the reduction was much more pronounced in the  $\text{Na}_2\text{SO}_4$  than in the  $\text{NaCl}$  series.

An analysis of the fresh to dry weight ratios of the plants confirmed previously reported findings and showed that one effect of salinity, whether of the  $\text{NaCl}$  or  $\text{Na}_2\text{SO}_4$  type, was on succulence. An optimum curve for fresh to dry weight ratios was obtained for the entire plants grown in  $\text{Na}_2\text{SO}_4$ , plants grown in  $\text{NaCl}$  showing a much smaller change (Table 1). Changes in succulence were more pronounced in the leaves than in the entire plant. In the leaves the fresh to dry weight ratio rose from 7.2 in the controls to 9.5 at –5 atm  $\Pi_e$   $\text{NaCl}$  and to 8.3 at –3 atm  $\Pi_e$   $\text{Na}_2\text{SO}_4$ . Succulence declined at higher levels of salinity. At a  $\Pi_e$  of –15 atm (for both types of salinity) fresh to dry weight ratio of leaves was equal to that of the controls. There was a highly significant decrease in the fresh to dry weight ratio of the roots, from 9.3 to 6 ( $P < 0.01$ ) between the non-saline controls and the plants exposed to –1 atm  $\Pi_e$  due to either  $\text{NaCl}$  or  $\text{Na}_2\text{SO}_4$ . This decrease was due entirely to an increase in root dry weight. However, at salt concentrations above –1 atm an optimum curve was obtained for root succulence.

As could be expected from the effect of salinity on growth and succulence, the curves for leaf area per plant were of a similar pattern (Fig. 2). Significantly larger leaf areas were found in the plants exposed to NaCl salinities up to  $-9$  atm than in the controls, whereas in the plants exposed to  $\text{Na}_2\text{SO}_4$  the leaf area fell sharply if  $\Pi_e$  was lower than  $-3$  atm, which was also the optimal salt concentration for other parameters of growth.

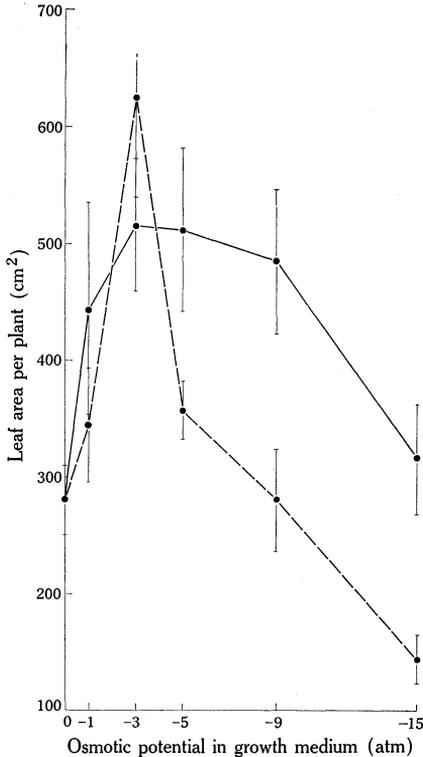


Fig. 2.—Leaf area of *A. halimus* plants grown in either NaCl (—) or  $\text{Na}_2\text{SO}_4$  (---) salinized culture solutions.

The higher the concentration of NaCl in the nutrient solution (i.e. lower  $\Pi_e$ ) the greater was the “leafiness” of the plants, due to the sprouting of leaf buds. In plants exposed to  $\Pi_e$  of  $-15$  atm NaCl, the leaf to stem fresh weight ratio was almost twice that found in the control plants ( $P < 0.01$ ). Most of this increase occurred between 0 and  $-3$  atm. This effect was much less apparent in the plants exposed to  $\text{Na}_2\text{SO}_4$  salinity.

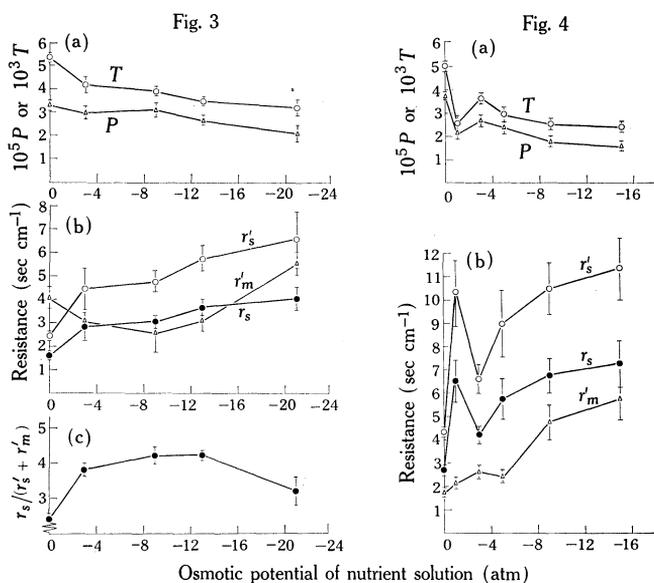
The effect of salinity on net photosynthesis, transpiration, and calculated leaf resistances for plants grown in NaCl-salinized media is given in Figures 3(a) and 3(b) and for plants grown in  $\text{Na}_2\text{SO}_4$  in Figures 4(a) and 4(b).

It is apparent from the data of Figures 3(b) and 4(b) that one of the main ways in which salinity affected gas exchange was by increasing stomatal resistance to water vapour ( $r_s$ ) and to  $\text{CO}_2$  ( $r'_s$ ) diffusion. The data for plants exposed to  $\text{Na}_2\text{SO}_4$  salinity [Fig. 4(b)] show that the effect on stomata was especially great between 0 and  $-1$  atm  $\Pi_e$ . Unfortunately this point on the curve ( $-1$  atm) is lacking in the NaCl treatment in which the plants were grown in a somewhat wider range of  $\Pi_e$  (see Section II).

Mesophyll resistance to  $\text{CO}_2$  uptake,  $r'_m$  (see p. 938), behaved differently in the two treatments [Figs. 3(b) and 4(b)]. On exposure to NaCl up to a  $\Pi_e$  of  $-9$  atm, this resistance was reduced.  $r'_m$  only increased in plants grown at  $\Pi_e$  lower than  $-9$  atm NaCl. In plants grown in  $\text{Na}_2\text{SO}_4$ -salinated media, the rise of  $r'_m$  with increasing salinity was steep and continuous; the small decrease in  $r'_m$  at  $-5$  atm was not significant.

The  $r'_m$  values for the control treatments of the NaCl and  $\text{Na}_2\text{SO}_4$  series were not equal. However, the plants were grown in two separate batches and the significance of this is discussed below.

The rise in leaf diffusion resistances in response to salinity is calculated from the measured gradients and from the reduction of both transpiration and photosynthesis [Figs. 3(a) and 4(a)]. This reduction was more pronounced in the plants exposed to



Figs. 3 and 4.—(a) Photosynthesis  $P$  (units:  $\text{cm}^3 \text{CO}_2 \text{cm}^{-2} \text{sec}^{-1}$ ) and transpiration  $T$  (units:  $\text{cm}^3 \text{water vapour cm}^{-2} \text{sec}^{-1}$ ) and (b) diffusion resistances of *A. halimus* plants grown in nutrient solutions salinized with either NaCl (Fig. 3) or  $\text{Na}_2\text{SO}_4$  (Fig. 4). In Figure 3(c) the ratio of stomatal resistance to water vapour diffusion ( $r_s$ ) to the sum of the stomatal ( $r'_s$ ) and mesophyll ( $r'_m$ ) resistances to  $\text{CO}_2$  diffusion is given.

$\text{Na}_2\text{SO}_4$  than in the plants exposed to NaCl. Between 0 and  $-15$  atm  $\Pi_e$ , photosynthesis in the  $\text{Na}_2\text{SO}_4$  treatments was reduced by 58% and transpiration by 52%, while the respective values were 26% and 36% for the NaCl treatments. In these latter plants, photosynthesis was not significantly reduced by salt concentrations between 0 and  $-9$  atm as the reduction in  $r'_m$  at these levels of  $\Pi_e$  compensated for the rise in  $r'_s$ .

The potential efficiency of a plant's use of water may be expressed by the ratio of the resistances to water loss and to  $\text{CO}_2$  uptake. This has been plotted in Figure

3(c), for the plants exposed to NaCl. Small amounts of NaCl seem to increase this ratio, indicating a potentially more efficient use of water. The same data for plants exposed to  $\text{Na}_2\text{SO}_4$  showed no consistent pattern.

#### IV. DISCUSSION

The effects of the presence of either NaCl or  $\text{Na}_2\text{SO}_4$  in the growth medium on the growth and morphology of *A. halimus*, as found in this work (Table 1 and Fig. 2), are similar to those reported for other species of *Atriplex* (Ashby and Beadle 1957; Brownell and Wood 1957; Black 1958; Greenway 1968). Overall growth was stimulated and total leaf area was increased by low concentrations of either NaCl or  $\text{Na}_2\text{SO}_4$ . However, both were depressed by salt concentrations causing  $\Pi_e$  values to fall below about  $-5$  atm.

The response to the two types of salinity operated apparently through different mechanisms. In the plants exposed to NaCl salinity there appeared to have been an osmotic adjustment and a decrease in  $\Pi_i$  equal in magnitude to the decrease in  $\Pi_e$ ; in the plants exposed to  $\text{Na}_2\text{SO}_4$  salinity only a partial adjustment was achieved. However, it must be emphasized that measurements of  $\Pi_i$  of leaf sap of *Atriplex* spp. are very difficult to interpret, due to the accumulation of salt in the hypodermal cells and its presence on the leaf surface. The relation of the true  $\Pi_i$  to the measured values is not known. Attempts to rinse off the salt which accumulates on the leaf surface, as has been done here, are at best arbitrary.

In the calculations of leaf resistances to gas and vapour exchange [Figs. 3(b) and 4(b)], mesophyll resistance to water vapour loss ( $r_m$ ) has been assumed to be negligible. However, the tendency to accumulate salts in the hypodermal layers of the leaf, to saturation, implies the possibility of salt accumulation in other parts of the leaf. If, for instance, salt accumulates at the evaporating surface of the mesophyll cells then  $r_m$  may not be negligible, in which case stomatal resistances ( $r_s$  and  $r'_s$ ) will be overestimated and mesophyll resistance to  $\text{CO}_2$  uptake ( $r'_m$ ) will be underestimated (Gale and Poljakoff-Mayber 1968).

In plants grown in media having NaCl concentrations of up to  $-9$  atm the ability of the mesophyll to take up  $\text{CO}_2$  appears to have been increased, i.e.  $r'_m$  was reduced [Fig. 3(b)]. Higher concentrations of NaCl in the growth medium and all concentrations of  $\text{Na}_2\text{SO}_4$  induced a rise in  $r'_m$ —which is an expression of increasing salinity damage. As noted above  $r'_m$  values of the non-salinized plants of the two series of experiments were not the same. This may have been due to small climatic differences during the growth period (Gale, Naaman, and Poljakoff-Mayber 1970).

The upward trend in  $r'_m$  of the plants exposed to NaCl salinity starting from a  $\Pi_e$  of  $-9$  atm coincides with the changes in submicroscopic structure (mainly swelling of chloroplasts) which were reported to appear at this level of salinity (Blumenthal-Goldschmidt and Poljakoff-Mayber 1968).

The increase of stomatal resistance in the plants of both series with decreasing  $\Pi_e$  [Figs. 3(b) and 4(b)] is similar to that reported for glycophytes grown in NaCl-salinized media (Gale, Kohl, and Hagan 1967; Meiri and Poljakoff-Mayber 1970) and may have been due to a lack of osmotic adjustment of the guard cells relative to adjacent epidermal cells, as reported by Bearce (1968). Such a situation could easily come about in *Atriplex*, where salt accumulates on the epidermis.

In the plants exposed to NaCl, the reduction of  $r'_m$  at  $\Pi_e$  up to  $-9$  atm compensated for the increased  $r'_s$ . This resulted in net photosynthesis per unit leaf area remaining fairly constant at salt concentrations below this level. In the  $\text{Na}_2\text{SO}_4$ -treated plants each increment in salt concentration further reduced net photosynthesis. It follows that the increased growth of the plants, when grown in media salinized with either NaCl or  $\text{Na}_2\text{SO}_4$ , at  $\Pi_e$  of up to about  $-5$  atm (Table 1), was not due to an increase of photosynthesis per unit leaf area but to an increase in total leaf area (Fig. 2). A similar conclusion was reached by Greenway, working with *A. nummularia*, from estimates of net assimilation rates (Greenway 1968).

The evaluation from measurements of single leaves of the transpiration and photosynthesis of the plants salinized with  $\text{Na}_2\text{SO}_4$  is slightly biased. This is because gas exchange of only apparently healthy leaves was measured, whereas there was a larger percentage of chlorotic and necrotic leaves on the plants exposed to  $\text{Na}_2\text{SO}_4$  than on those exposed to NaCl.

The plants growing in media salinized with NaCl up to a level of  $-13$  atm showed a higher potential efficiency for the use of water [Fig. 3(c)]. This may be ecologically advantageous for survival under conditions of moderate salinity and shortage of water, a situation common in the arid saline regions where *A. halimus* grows. No such consistent trend was found for the plants grown in media salinized with  $\text{Na}_2\text{SO}_4$ .

An increased leafiness was observed in plants grown in NaCl-salinized media. This was due to sprouting of lateral leaf buds, a phenomenon suggestive of a breakdown of hormone-induced apical dominance. Such hormonal imbalance has already been implicated in salinity damage of plants (Itai, Richmond, and Vaadia 1968).

#### V. ACKNOWLEDGMENTS

This work was supported by a grant (PL-480, Project No. A10-SWC-7) from the United States Department of Agriculture. Our thanks are due to Mr. M. Forte of the Negev Research Institute for supplying the seeds of *A. halimus*.

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