PLANT RESPONSE TO SALINE SUBSTRATES

II. CHLORIDE, SODIUM, AND POTASSIUM UPTAKE AND TRANSLOCATION IN YOUNG PLANTS OF HORDEUM VULGARE DURING AND AFTER A SHORT SODIUM CHLORIDE TREATMENT

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Summary

Young barley plants, *Hordeum vulgare* cv. Chevron, were subjected to a sodium chloride concentration of 100 m-equiv/l. In a "continued" treatment, the salinity stress was maintained for 15 days. In a "removed" treatment, sodium chloride was removed from the substrate after 5 days, and the subsequent response was studied over a period of 10 days.

Growth was reduced during the sodium chloride treatment, but the growth rates after sodium chloride removal equalled those of the controls. However, leaves 1, 2, and 3 showed higher dry weight increments in the continued than in the removed treatment. This was attributed to continued ion accumulation by the plants treated with sodium chloride.

In the continued plants, the chloride and sodium contents of the individual parts increased during the experiment. Potassium contents decreased, and net losses of potassium were found from all plant parts which had completed their development. No such potassium losses were found for the control plants.

The chloride and sodium contents in the continued plants decreased, as a rule, in the order: sheaths of leaves 1, 2, and 3; leaf 1; leaf 2; leaf 3; younger leaves and sheaths; and roots. Potassium contents, on the other hand, were higher in the younger than in the older plant parts.

After sodium chloride removal, most of the chloride and sodium accumulated during the treatment was retained in the plant as a whole. Leaves 1 and 2 and the sheaths of leaves 1, 2, and 3 did not show any net losses of chloride or sodium. Leaf 3 showed an appreciable loss of chloride but no net loss of sodium. A large proportion of the chloride was lost from the roots, while net sodium losses from this part were very much smaller.

Potassium contents of developed plant parts did not increase appreciably after sodium chloride removal, but the potassium uptake of developing parts was increased to control levels.

It is suggested that the drastic ion changes in the older plant parts, and the much smaller ion changes in the younger parts, are of relevance to the growth of *H. vulgare* on a saline substrate.

I. INTRODUCTION

Ion accumulation by the plant is one important aspect of plant response to saline substrates. Chloride contents of the shoot are usually higher than those of the roots (Arnold 1955). An increase in the external concentration usually leads to increased chloride contents of the plant (Eaton 1942; van den Berg 1952), but the

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amounts accumulated vary markedly with the species (van den Berg 1952; Arnold 1955). Sodium, on the other hand, is virtually excluded by the leaves of some species, even on substrates high in sodium chloride (Richards 1954). The effect on potassium uptake is also dependent on the species.

Much less is known about the ion distribution within the shoot. Arnold (1955) emphasized that the ion content of individual plant parts is of far greater importance than that of the shoot as a whole. On saline substrates, chloride contents of older leaves were found to be higher than those of younger leaves in beets and onions (Yankovitch 1949), grape vines (Woodham 1956), and strawberries (Ehlig and Bernstein 1958). A similar distribution of sodium within the plant was found on non-saline substrates (Effmert 1960). There appears, however, to be little precise information on sodium and potassium distribution within the shoots of plants subjected to a high sodium chloride concentration.

Information on the ion uptake of plants is usually obtained after a lengthy salinity treatment. In such cases the changes in ion content may be not only a direct response to the increased ion concentration of the substrate, but also the result of pronounced changes in plant development and metabolism. Furthermore, most experiments are carried out at a constant salt concentration, while the salt concentration of the soil solution in the field varies greatly with time. It is suggested that more attention should be given to both these aspects.

Part I of this series (Greenway 1962) described the response by several varieties of *Hordeum vulgare* to salinity stresses. Large varietal differences were found for the ion uptake by the shoot as a whole. However, the pattern of ion distribution within the plant, and that of ion translocation after sodium chloride removal from the substrate, was rather similar for all varieties.

This suggested a more detailed study on the response by one variety of *H. vulgare* to both a continuous sodium chloride treatment, and to sodium chloride removal from the substrate after a brief salinity stress. Young plants were used and this paper describes growth and net changes in chloride, sodium, and potassium contents for the whole plant and its individual parts.

II. METHODS

The experiment was carried out in the glasshouse. Water cultures were used to avoid any complication of ion absorption by the leaves, such as might arise in regularly flushed sand cultures (Greenway 1962). Seeds of *H. vulgare* cv. Chevron were sown in river sand on October 10, 1958. After the first leaf had fully expanded the seedlings were transferred to Arnon's standard nutrient solution (see Hewitt 1952; Greenway 1962). To ensure that neither sodium nor chloride would be limiting growth of the controls, sodium chloride at a concentration of 1 m-equiv/l was added to the nutrient solution. Four plants were grown in 2·5 l. of solution and the cans used were of baked enamel finish to prevent corrosion.

Sodium chloride treatment was begun when the second leaf had fully expanded. The concentration was increased to 50 m-equiv/l the first day and to 100 m-equiv/l on the second day. Five days after the commencement of sodium chloride treatment,

half of the treated plants were transferred to standard nutrient solution. This treatment will be referred to as "removed". A second group of plants were grown at the same sodium chloride concentration for the rest of the experiment, and they will be referred to as "continued". All solutions were replaced at 5-day intervals, and before transference the roots were rinsed with the appropriate solution for approximately 30 sec.

Fifteen replicates from all treatments were harvested at 5-day intervals on each of four occasions. These were: H_1, date of sodium chloride application; H_2, date of sodium chloride removal; H_3 and H_4, 10 and 15 days after sodium chloride application, respectively. The plants were separated into leaf 1; leaf 2; leaf 3; the sheaths of leaves 1, 2, and 3 combined, hereafter referred to as "the sheaths"; the younger leaves, sheaths, and the stem (referred to as "the rest of the shoot"); and the roots. Roots were rinsed for approximately 60 sec in distilled water, and all plant parts were dried rapidly at 80°C.

To obtain improved estimates of relative growth rates the rating procedure of McIntyre and Williams (1949) was used.

For chemical analysis, the 15 replicates were bulked into three groups of five. Chloride was determined according to Best (1950), and sodium and potassium determined using an "EEL" flame photometer after dry-ashing the samples at 500°C.

III. Results and Discussion

(a) Dry Weight and Relative Growth Rate

(i) *Dry Weight.*—The dry weight of the plant as a whole and its principal parts is shown in Figure 1 and Table 1. For the controls the weights of the individual parts are also plotted additively in Figure 2A, and the individual growth curves for leaves 1, 2, and 3 are shown in Figure 2B.

Throughout the experiment, growth of the plant as a whole was retarded by sodium chloride treatment. The dry weight curve of the removed treatment was intermediate between control and continued treatments. Dry weight curves for the rest of the shoot and the roots were similar to those for the plant as a whole (Fig. 1).

In the controls, leaves 1 and 2 showed relatively little growth during the course of the experiment. The dry weight of leaf 3 increased rapidly between H_1–H_2, but further increases were small (Fig. 2). Sodium chloride treatment somewhat reduced the development of leaves 1, 2, and 3 between H_1–H_2 (Fig. 1; Table 1). Between H_2–H_4, however, the dry weight increments in the continued leaves tended to be higher than in the corresponding leaves of the control. In some instances the dry weight of the continued treatment even reached control level (leaves 1 and 2). Leaves 1, 2, and 3 of the removed plants, on the other hand, were always lower in dry weight than the corresponding leaves of the control and their dry weight increments were less than for the control between H_2–H_4 (Fig. 1; Table 1).

These treatment effects on the individual leaves were rather small, but it was nevertheless difficult to understand why during sodium chloride treatment these leaves should attain a higher dry weight than after sodium chloride removal. However, the

amounts of chloride and sodium in leaves 1, 2, and 3 of the sodium chloride treated plants greatly increased throughout the experiment (Fig. 6), and this would contribute to the continued dry weight increments. It appeared, therefore, useful to deduct the weight of chloride, sodium, and potassium from the experimentally determined dry weight. These "adjusted dry weights"* of leaves 1, 2, and 3, and the sheaths were similar in the continued and removed treatments while the controls
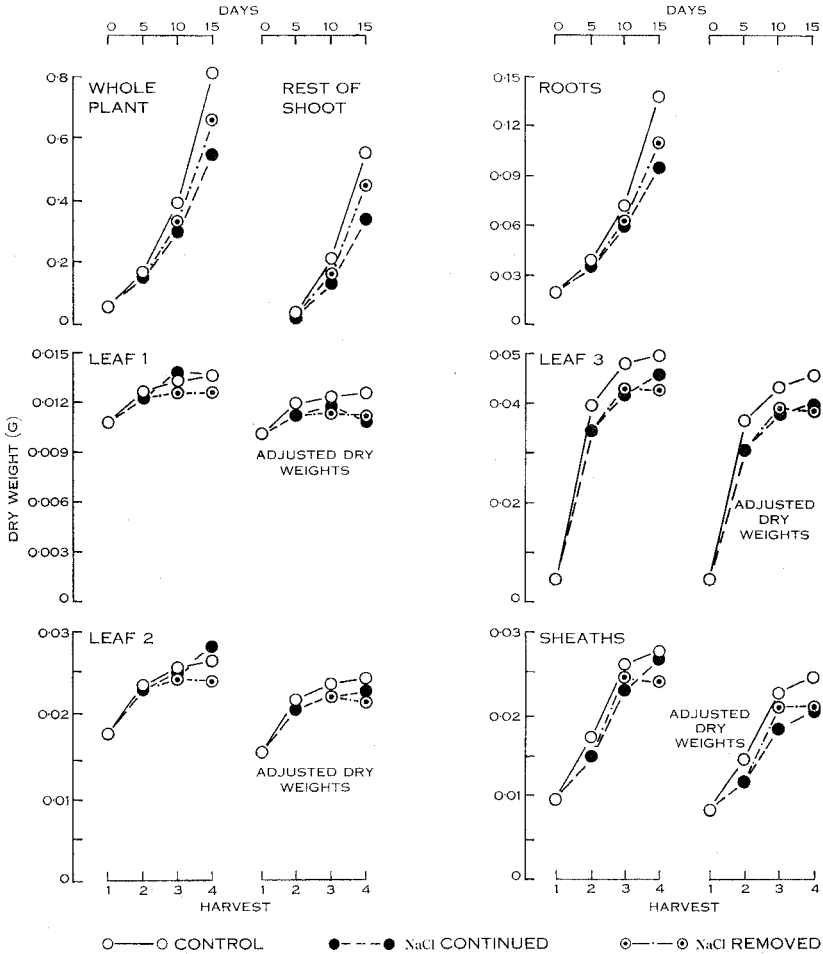

Fig. 1.—Dry weight of the whole plant and its individual parts (see also Table 1). Adjusted dry weights (i.e. determined dry weight minus weight of chloride, sodium, and potassium ions) are also shown for leaves 1, 2, and 3 and for sheaths of leaves 1, 2, and 3 combined.

had a somewhat higher adjusted dry weight (Fig. 1). This indicates that ion accumulation was mainly responsible for the fact that leaves 1, 2, and 3 of the continued treatments had higher experimentally determined dry weight increments than the corresponding parts of the removed treatments.

* As usual the experimentally determined dry weight will be denoted as the "dry weight".

Dry weight changes in plants absorbing high amounts of ions have evidently to be considered with some caution. Ashby and Beadle (1957), for example, found, that growth of *Atriplex nummularia* was unaffected by sodium chloride concentrations as high as 400 m-equiv/l. However, large amounts of chloride and sodium were

TABLE 1

DRY WEIGHT (G) OF THE PLANT AS A WHOLE AND ITS INDIVIDUAL PARTS

Plant Part	Treatment	Harvest			
		H_1	H_2	H_3	H_4
Leaf 1	Control	0·0108	0·0126	0·0133	0·0135
	NaCl continued	—	0·0125	0·0137	0·0135
	NaCl removed	—	—	0·0126	0·0125
Leaf 2	Control	0·0171	0·0237	0·0257	0·0266
	NaCl continued	—	0·0234	0·0251	0·0285
	NaCl removed	—	—	0·0245	0·0242
Leaf 3	Control	0·0047	0·0391	0·0475	0·0490
	NaCl continued	—	0·0340	0·0422	0·0449
	NaCl removed	—	—	0·0424	0·0417
Sheaths (sheaths of	Control	0·0096	0·0170	0·0260	0·0278
leaves 1, 2, and 3	NaCl continued	—	0·0148	0·0229	0·0268
combined)	NaCl removed	—	—	0·0243	0·0240
Rest of the shoot	Control	—	0·0389	0·2140	0·5541
(younger leaves,	NaCl continued	—	0·0303	0·1379	0·3419
sheaths, and stem)	NaCl removed	—	—	0·1637	0·4477
Root	Control	0·0183	0·0380	0·0708	0·1360
	NaCl continued	—	0·0367	0·0594	0·0938
	NaCl removed	—	—	0·0621	0·1104
Whole plant	Control	0·0604	0·1694	0·3973	0·8070
	NaCl continued	—	0·1516	0·3012	0·5494
	NaCl removed	—	—	0·3297	0·6604

absorbed in these plants, and it can be shown that the 400 m-equiv/l salinity stress had reduced the adjusted dry weight by approximately 15% as compared with a treatment of 50 m-equiv/l.

(ii) *Relative Growth Rate*, R.—Ion accumulation might also be important when relative growth rates are measured over short intervals, particularly when at the start of the interval ion uptake is drastically changed. These R values are therefore presented as "adjusted relative growth rates" in Table 2.

R values of controls declined with time, and the continued treatment reduced R values to approximately the same extent during all harvest intervals. However, expressed as a percentage of the control value, the depression of R values by sodium

chloride treatment became somewhat more pronounced during the later stages of the experiment. After sodium chloride removal, R values temporarily increased and they rapidly returned to control values.

(b) Chloride and Sodium Uptake and Translocation

Chloride, sodium, and potassium contents (m-equiv/100 g dry weight) are presented in Figures 3 and 4. The corresponding absolute data (m-equiv/plant part) are shown in Figures 5 and 6.

(i) *Chloride and Sodium Uptake in Controls.*—In the controls, the relative chloride and sodium contents of the individual plant parts did not change appreciably during the course of the experiment (Figs. 3 and 4). Chloride concentrations were
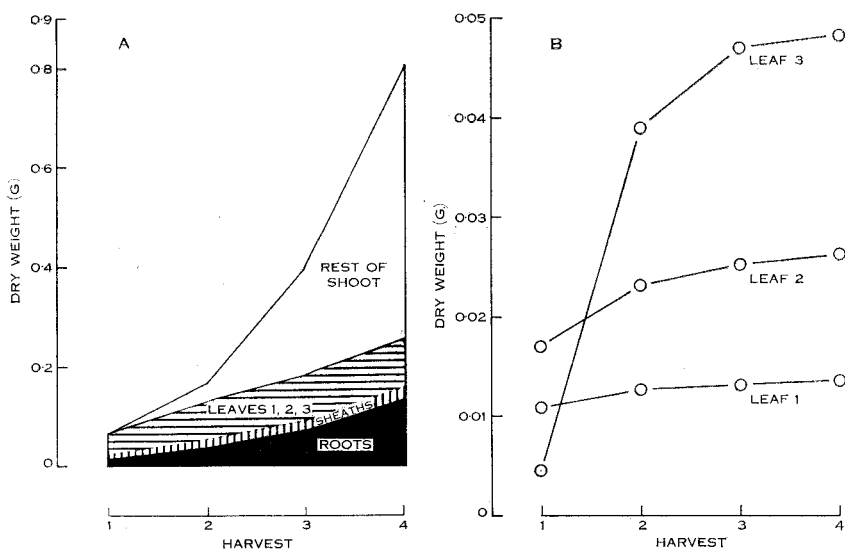

Fig. 2.—Dry weights of parts of control plants: *A*, plotted additively; *B*, plotted individually for leaves 1, 2, and 3.

highest in the sheaths, intermediate in the other parts of the shoot, and lowest in the roots. In all parts of the shoot the sodium contents were much lower than the chloride contents. The roots, on the other hand, had higher sodium than chloride contents (Figs. 3 and 4; Table 4). Net increases in sodium and chloride took place only in developing parts, and no further change occurred after cessation of dry weight increments (Figs. 5 and 6).

It should be mentioned here that in another experiment of the present series net losses of chloride from developed control leaves were observed. The control nutrient solution of that experiment contained 0·1 m-equiv/l of sodium chloride, but all other experimental details were similar. It is shown in Table 3 that the plants of that experiment had considerably lower chloride contents (m-equiv/100 g) than the controls of the main experiment. The developed leaves of these "low

chloride" plants showed a net loss of approximately 50% of chloride (m-equiv/plant part) during a 5-day interval (H_2–H_3).

(ii) *Chloride and Sodium Uptake in Sodium Chloride Continued Treatment.*— In the continued treatment, the plant as a whole and its individual parts showed considerable net increases of chloride and sodium (m-equiv/plant part) throughout the experiment (Figs. 5 and 6). The chloride and sodium contents (m-equiv/100 g) of all plant parts were very much higher in the sodium chloride treatment than in the control (Figs. 3 and 4).

TABLE 2

ADJUSTED RELATIVE GROWTH RATES (G/G/DAY) OF CONTROL, SODIUM CHLORIDE CONTINUED, AND SODIUM CHLORIDE REMOVED TREATMENTS

The adjusted relative growth rates were calculated by subtracting the weight of chloride, sodium, and potassium from the experimentally determined dry weight

Treatment	Harvest Interval		
	H_1–H_2	H_2–H_3	H_3–H_4
Control (A)	0·195	0·180	0·145
Sodium chloride continued (B)	0·164	0·145	0·113
Sodium chloride removed (C)	—	0·174	0·142
Differences significant at $P =$	0·001	0·001 (A, $C > B$)	0·001 (A, $C > B$)

Comparison between the ion accumulation in various plant parts were of interest, and to facilitate this the relative data of the continued treatments are presented also in Table 4. The chloride absorption of individual plant parts was rather similar to that of sodium, but the sheaths, the rest of the shoot, and, in particular, leaf 3 usually contained significantly more sodium than chloride.

At H_2, both the chloride and sodium contents decreased in the following order: sheaths, leaves 1–3, rest of the shoot, and roots. During the further course of the experiment the roots showed only a small increase in sodium, while the chloride increase was not significant (Fig. 3). Relative chloride and sodium contents of the shoot as a whole increased considerably between H_2–H_4, but these increases were very much smaller than the initial increase during the H_1–H_2 interval (Fig. 3). The increases between H_2–H_4 were smaller in developing plant parts than in those which had completed their development (Figs. 1, 3, and 4). Particularly large increases took place in the sheaths, in leaf 1 between H_2–H_4, and in leaf 2 between H_3–H_4. At the termination of the experiment (H_4), the relative chloride and sodium contents of these parts greatly exceeded those of the rest of the shoot and the roots, while leaf 3 had an intermediate level of chloride and sodium (Table 4).

High ion accumulation in a particular plant part is often correlated with leaf injury (e.g. Ehlig and Bernstein 1958). Development of injury symptoms during the present experiment is shown in Table 5. It is apparent that the steep increases of chloride and sodium content in leaf 1 between H_2 and H_4, and in leaf 2 between H_3 and H_4 (Fig. 4) coincided with the progressive development of injury.
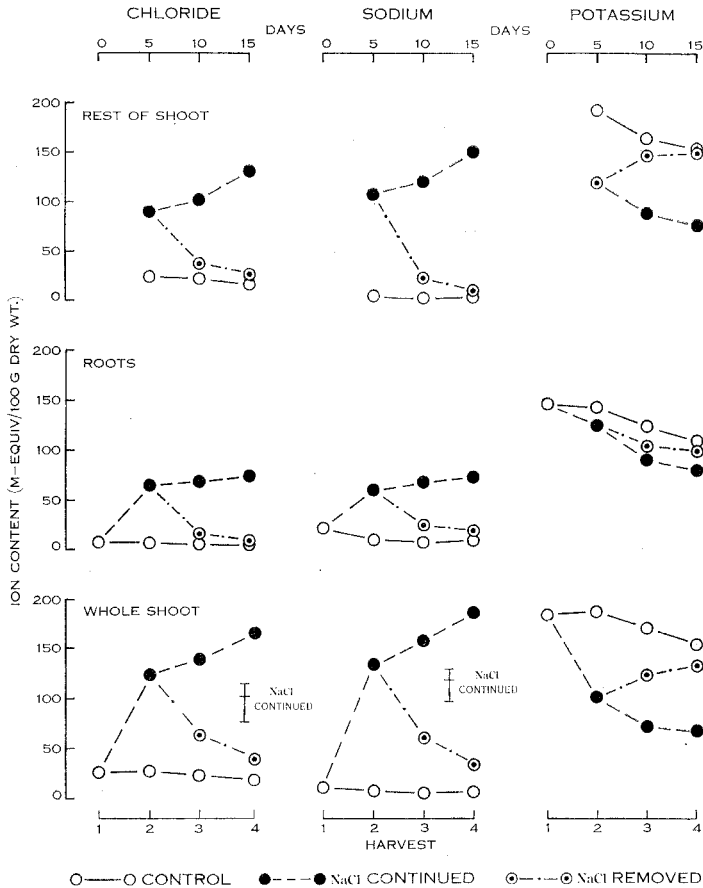

Fig. 3.—Chloride, sodium, and potassium contents of the whole shoot, the rest of the shoot (younger leaves and sheaths and the stem), and the roots of the control, sodium chloride continued, and sodium chloride removed plants.

(iii) *Chloride and Sodium Translocation in Sodium Chloride Removed Plants.*— After salt removal the net change of chloride and sodium in the plant as a whole, and in the rest of the shoot, were not significantly different from the controls (Fig. 5). This suggests that the plant as a whole did not lose any considerable quantities of the chloride and sodium, which had been absorbed during sodium chloride treatment.

Leaves 1 and 2, and the sheaths did not decrease appreciably in chloride and sodium after sodium chloride removal from the substrate (Fig. 6). Leaf 3 also did not show any net loss of sodium, but its chloride content decreased by approximately 25% of the quantity present at date of sodium chloride removal ($P < 0.01$ between H_2–H_3 and between H_3–H_4).
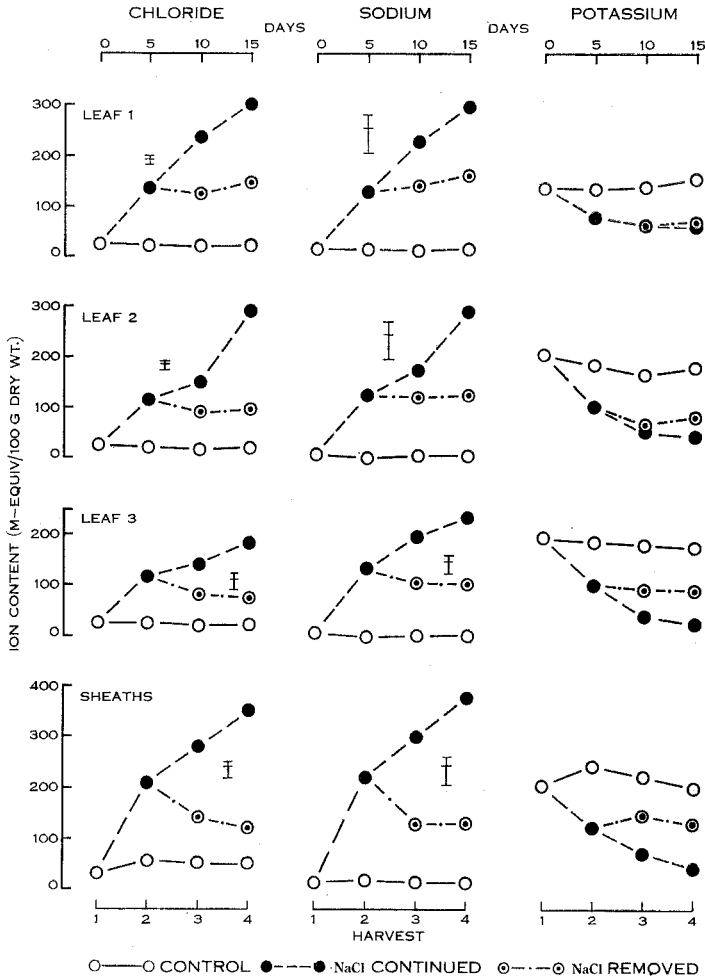

Fig. 4.—Chloride, sodium, and potassium contents of leaves 1, 2, and 3 and of sheaths (of leaves 1, 2, and 3 combined) of the control, sodium chloride continued, and sodium chloride removed plants. Significant differences shown are for sodium chloride continued treatments, and for the chloride content of leaves 1 and 2 they apply only to H_2 and H_3.

The roots were the only part from which net losses in chloride were pronounced. Between H_2–H_3 a significant net loss of sodium also occurred, but this was very much smaller than the chloride loss, and between H_3–H_4 the roots showed a small net increase of sodium (Fig. 5; $P < 0.001$ for differences between chloride and

sodium trends). That cations would have a lower mobility than anions was suggested by Arisz (1958). He postulated that, after accumulation in the vacuole, cations would not exchange with the cations occurring in the cytoplasm, but that such an exchange might occur in the case of anions.

Although in the present experiment the roots lost much more chloride than sodium, nevertheless it was found that at H_4 the amount of chloride in the roots

TABLE 3

NET LOSS OF CHLORIDE FROM THE DEVELOPED LEAVES OF PLANTS GROWN IN A NUTRIENT SOLUTION CONTAINING SODIUM CHLORIDE AT A CONCENTRATION OF $0 \cdot 1$ M-EQUIV/L (SEE TEXT)

Control data of main experiment reported in this paper (sodium chloride concentration $1 \cdot 0$ m-equiv/l) are included for comparison

Plant Part	Sodium Chloride Concentration (m-equiv/l)	Chloride Loss (m-equiv/100 g dry wt.)	
		Harvest 2	Harvest 3
Leaves 1, 2, and 3	$0 \cdot 1$	$4 \cdot 6$	$2 \cdot 2$
	$1 \cdot 0$	$24 \cdot 1$	$21 \cdot 1$
Younger leaves	$0 \cdot 1$	$8 \cdot 9$	$7 \cdot 0$
	$1 \cdot 0$	$25 \cdot 1$	$22 \cdot 9$
Sheaths†	$0 \cdot 1$	$12 \cdot 1$	$9 \cdot 3$
	$1 \cdot 0$	$61 \cdot 7$	$57 \cdot 6$
Roots	$0 \cdot 1$	$3 \cdot 0$	$2 \cdot 0$
	$1 \cdot 0$	$7 \cdot 9$	$7 \cdot 0$
Leaves 1, 2, and 3	$0 \cdot 1$	$1 \cdot 86*$	$0 \cdot 99*$

* Chloride contents expressed as μ-equiv/plant part. Difference between harvests significant at $P < 0 \cdot 05$.

† i.e. sheaths of leaves 1, 2, and 3 combined.

of the removed plants was higher than in those of the control ($P < 0 \cdot 001$). A similar finding was reported by Groenewegen, Bouma, and Gates (1959) for the roots of citrus cuttings 82 days after salt removal. It was suggested that this was due to retention of chloride in the vacuoles of tissues present at date of salt removal, as well as to absorption in newly formed root tissues.

(c) Potassium Uptake and Translocation

(i) *Potassium Uptake (as m-equiv/100 g dry wt.).*—During the course of the experiment, relative contents of potassium decreased in the rest of the shoot and the roots of both control and continued treatments (Fig. 3). Only in the continued treatment were there decreases in leaves 1, 2, and 3 and in the sheaths (Fig. 4). At H_3 and H_4 the potassium contents in the continued treatment decreased in the following order: rest of the shoot, leaf 1, leaf 2, and leaf 3 (Table 4).

In all individual plant parts the reduction in potassium content was smaller than the concurrent increase in sodium. In the plant parts which had completed their development this discrepancy increased during the course of the experiment (Figs. 3 and 4).
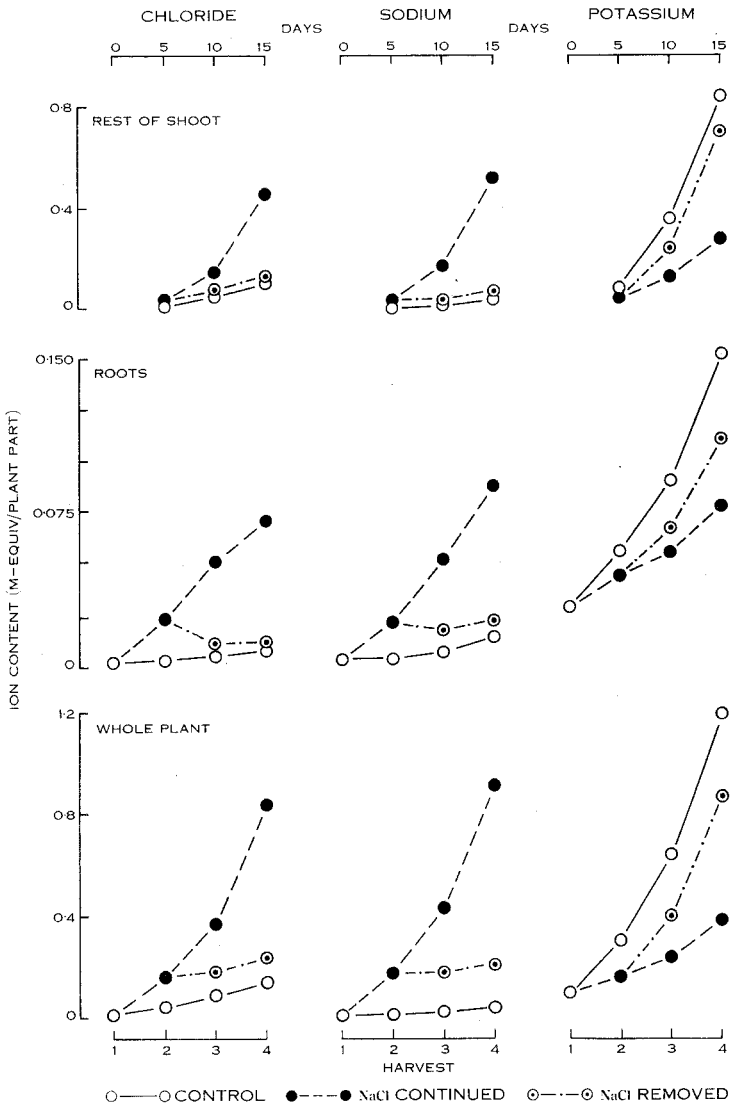

Fig. 5.—Chloride, sodium, and potassium contents of the whole plant, rest of shoot (younger leaves and sheaths and the stem), and roots of the control, sodium chloride continued, and sodium chloride removed plants.

The decrease in the potassium content of sodium chloride treated plants is at variance with data presented by Reifenberg and Rosovsky (1947). These workers did not find any effect of sodium chloride treatment on the potassium content of barley plants which were at the same growth stage as in the present experiment.

It would seem that differences in experimental technique were responsible for this discrepancy. Reifenberg and Rosovsky grew 100 barley seedlings in 500 ml of solution, which was not renewed over a period of 18 days. Twenty-one days after sowing, the dry weight of these plants was somewhat lower than the original seed
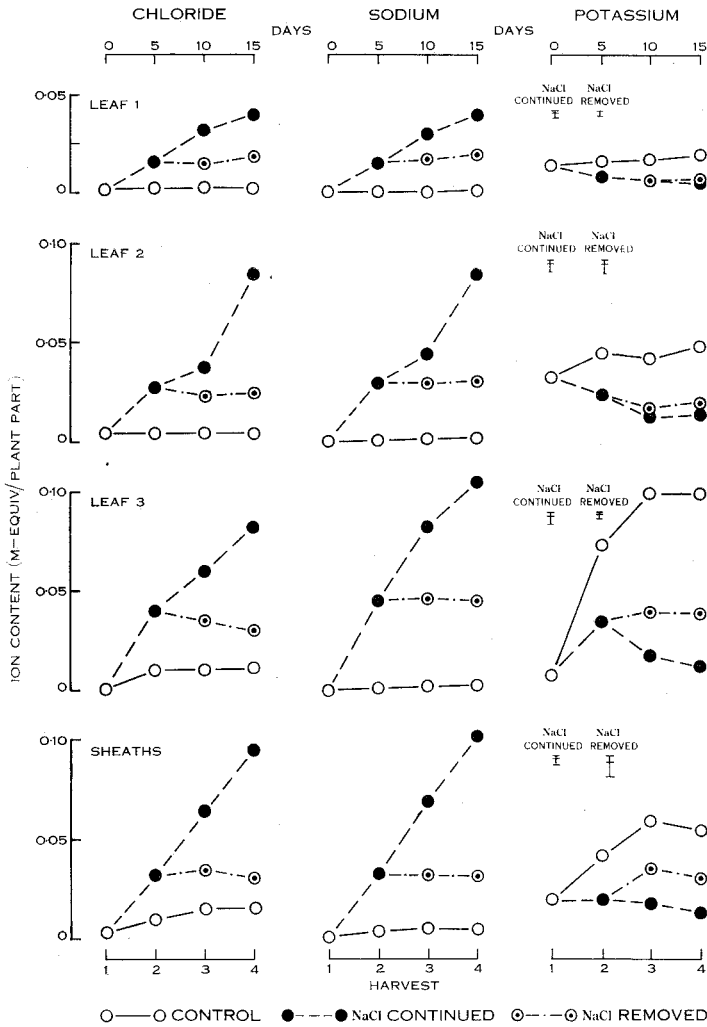

Fig. 6.—Chloride, sodium, and potassium contents of leaves 1, 2, and 3, and the sheaths (of leaves 1, 2, and 3 combined) of the control, sodium chloride continued, and sodium chloride removed plants.

weight. In the present experiment, on the other hand, the plants grew vigorously and they increased, over a period of 21 days, from the original seed weight of 28 mg to 170 mg at H_2.

After sodium chloride removal the relative potassium contents in the rest of the shoot increased rapidly, and at the termination of the experiment potassium

TABLE 4

ION CONTENTS OF THE INDIVIDUAL PLANT PARTS OF THE SODIUM CHLORIDE CONTINUED TREATMENTS

Plant Part	Chloride Content (m-equiv/100 g dry wt.)				Sodium Content (m-equiv/100 g dry wt.)				Potassium Content (m-equiv/100 g dry wt.)			
	H_1 (control)	H_2	H_3	H_4	H_1 (control)	H_2	H_3	H_4	H_1 (control)	H_2	H_3	H_4
Sheaths†	37	217	282	356	17	225*	303*	382*	206	128	76	48
Leaf 1	23	136*	239	301	16	127	228	298	135	79	61	59
Leaf 2	28	117	152	293	7·6	129	176*	293	206	106	55	46
Leaf 3	29	120	144	185	9·4	133	199***	235**	196	102	43	30
Rest of shoot‡	—	91	102	131	—	109**	121**	150**	—	119	88	78
Roots	8·6	66	70	75	22	61	69	77	146	125	92	82
Least significant differences ($P = 0.05$) between individual plant parts		6	11	43§		15	15	16		9	11	15

* $P < 0.05$ ⎫
** $P < 0.01$ ⎬ For differences between the chloride and sodium contents of the individual plant parts at any particular harvest.
*** $P < 0.001$ ⎭

† Sheaths of leaves 1, 2, and 3 combined.
‡ Younger leaves, sheaths, and stem.
§ Leaves 1 and 2 were excluded from the statistical analysis at H_4.

was approaching control levels. The difference in root potassium between removed and control plants was also reduced (Fig. 3). In leaves 1, 2, and 3, and in the sheaths; on the other hand, no such recovery in potassium occurred, although the decreases with time were arrested (Fig. 4).

(ii) *Potassium Uptake (as m-equiv/plant part).*—During the course of the experiment, net increases of potassium took place in most of the individual parts of the controls. Even the oldest part (leaf 1) did not show any potassium loss (Figs. 5 and 6).

TABLE 5

LEAF SYMPTOMS IN LEAVES OF SODIUM CHLORIDE
CONTINUED PLANTS AT DIFFERENT HARVESTS

Symptoms denoted by numerals as follows:
1, healthy; 2, tipburn; 3, chlorosis; 4, half of leaf
collapsed; 5, whole leaf collapsed

Leaf No.	Harvest 2	Harvest 3	Harvest 4
1	1	3·1	3·8
2	1	1	2·1
3	1	1	1

In the continued treatment, net potassium contents of all the individual plant parts were much lower than those of the control (Figs. 5 and 6). Some parts suffered a net potassium loss after salt application (leaf 1 between H_1 and H_2, and leaf 2 between H_1 and H_3, Fig. 6). These leaves had completed their development at H_1, the date of sodium chloride application. Leaf 3, which had nearly completed its development at H_2 (Fig. 1), subsequently showed a net potassium loss between H_2 and H_4 (Fig. 6).

After sodium chloride removal the net uptake of potassium increased in the plant as a whole, the rest of the shoot, and the roots. However, potassium contents in these parts did not reach control levels (Fig. 5). Only little change occurred in the potassium content of plant parts which had ceased development at date of sodium chloride removal (Fig. 6). There was a small net decrease in leaf 2 between H_2 and H_3, and a small net increase in leaf 3 during the same period.

IV. GENERAL DISCUSSION

(a) *Ion Distribution within the Plant and its Relevance to Growth*

It has been shown that the older parts of sodium chloride treated plants have a drastically changed ion content as compared with the control. In younger plant parts, however, sodium and chloride were increased to a smaller extent, and potassium remained at a higher level. Arnold (1955) described a similar situation in a group

of halophytes, of which the older leaves accumulated excessive amounts of ions and subsequently died, while new organs were still formed. He contrasted this "accumulation" type of halophyte with the "regulation" type, which regulates the ion concentration even in the older plant parts. This ion regulation is often achieved by an increase in succulence, thus maintaining a moderate concentration in the cell sap even during continued ion accumulation. In barley a combination of ion accumulation and decreases in water content resulted in exceedingly high chloride concentrations in the plant water of the older leaves (Greenway 1962).

The removed treatment of the present investigation indicates that differences between older and younger parts will be amplified, if fluctuations in the concentration of the substrate occur. In these treatments the ion contents of the older plant parts remained virtually unaltered. Rapid dry weight increments in the developing parts, on the other hand, diluted the relative sodium and chloride contents considerably, while potassium uptake in these organs was resumed at control levels.

This strong selective ion uptake of younger parts could be important to plant growth on saline substrates. In the present experiment, for example, development of younger parts proceeded, although at a reduced rate, during the salinity stress and there was a rapid recovery after salt removal. If the younger parts had not been as well protected against ion changes in the substrate, much more severe effects on growth might well have followed.

Study of salinity effects is often confined to the shoot as a whole, or alternatively to a certain part of the shoot. Eaton (1942), for example, analysed the expressed sap from the whole shoot, or from leaves which were sampled irrespective of their age. Van den Berg (1952) analysed samples of the whole shoot and only supplemented these with some comparisons between injured and healthy parts of individual leaves. The present data show that information on ion distribution within the shoot is needed for an understanding of growth response.

(b) Ion Uptake and Redistribution

It is well known that ion uptake by plants can be greatly influenced by the experimental technique used. The validity of the data presented here is strengthened by the fact that in other experiments of the present series similar results were obtained, even though these experiments included sand and water cultures in which the solutions were changed much more frequently (Groenewegen and Mills 1960; Greenway 1962).

(i) *Chloride and Sodium Uptake in Sodium Chloride Continued Treatment.*— In this treatment the older plant parts contained very high amounts of chloride and sodium, and they were severely injured. The steep increases in the ion content of leaves 1 and 2 coincided with progressive development of injury (Fig. 4; Table 5). It is thus impossible to establish whether the excessive ion accumulation caused the injury or, on the contrary, injury had impaired the selectivity of ion uptake. Similar considerations apply to many correlations between leaf injury and ion accumulation, as, for example, those reported by Woodham (1956) and van den Berg (1952).

Healthy plant parts also differed in ion contents: for example, leaf 3 contained considerably more chloride and sodium than the younger parts (rest of the shoot in Table 4). In addition the chloride and sodium contents of these parts increased with time (H_2–H_4, Figs. 3 and 4). These facts might have been caused by an inward ion movement which appreciably exceeded any outward movement. This possibility is indicated by the data of Long (1943), who showed that no significant translocation of chloride and sodium counter to the direction of the water movement occurred in tomatoes of high chloride and sodium contents. In such a case the continued inward ion flow, via the transpiration stream, would lead to a gradual increase in chloride and sodium concentration, particularly in terminal organs which had completed their development (leaves 1, 2, and 3, see Fig. 4).

Another possibility is, however, that the age of a plant part affected its ion accumulation. Sutcliffe and Counter (1959) found that slowly growing carrot tissues absorbed more sodium and less potassium than actively growing tissues. It is noteworthy that similar trends in sodium and potassium contents were found for the older and younger barley leaves (Table 4). Further information is required to ascertain which of these mechanisms was responsible for the high ion accumulation in the older plant parts.

(ii) *Chloride and Sodium Redistribution in Sodium Chloride Removed Plants.*— The plant as a whole did not show any appreciable net losses of chloride and sodium after reduction of the sodium chloride concentration in the substrate. A similar finding was reported by Groenewegen, Bouma, and Gates (1959), who studied chloride redistribution in citrus cuttings.

The possibility that reabsorption of ions, temporarily lost to the nutrient solution, may have contributed to the results of the present experiment cannot be entirely excluded. However, similar results were obtained in other barley experiments with regularly flushed sand cultures (Greenway 1962), and a significant contribution of reabsorption appears unlikely.

It was shown also that only small net losses of both sodium and chloride occurred from leaves 1, 2, and 3, and the sheaths, the parts which had already developed at the time of salt removal (Figs. 1, 2, and 6). This small net loss has to be considered in relation to the large concentration gradient between these developed and the developing plant parts, such as the rest of the shoot and the roots (Figs. 3 and 4). Under similar conditions only relatively small amounts of chlorides were lost from developed leaves of widely different species, such as citrus (Groenewegen, Bouma, and Gates 1959) and lupins (Gates, personal communication).

A considerable net chloride retranslocation was, on the other hand, found in tomatoes of low chloride content (Woolley, Broyer, and Johnson 1958). In the present experiments developed leaves of barley plants, which were very low in chloride, also showed a net loss of 50% over a 5-day period. These findings are not contradictory, because in the sodium chloride treated plants the actual amounts of chloride involved were much higher than in the low-chloride plants. For example, 5 days after sodium chloride removal, the actual amount of chloride lost from leaf 3 was six times greater than that lost from the developed leaves of the low-chloride barley plants (Fig. 6 as compared with Table 3).

(iii) *Potassium Uptake and Translocation.*—When grown on saline substrates some species increase in potassium content. Heimann (1958) suggested that this was confined to sodium-sensitive species, and his data indicated that it became particularly pronounced in those species which excluded sodium. Other species, which absorb high amounts of sodium, are reduced in potassium content and it has been shown that barley belongs to this group.

Developed plant parts, such as leaves 1 and 2, showed a net loss of potassium present at the date of sodium chloride application. Net losses of potassium caused by the uptake of other ions have seldom been reported in the literature. Elgabaly (1955) found a large net removal from barley plants as a whole, when they were grown on a potassium-free exchange resin. In the present experiment, sodium chloride treatment affected the potassium content of the older leaves much more strongly than of the younger leaves and of the roots (Table 4).

The decreased potassium content of the shoot as a whole might be due to a sodium competition for a potassium uptake mechanism. Such a competition has been found for excised barley roots (Jacobson *et al.* 1950; Epstein and Hagen 1952*), and for intact maize seedlings (Bange 1959). Sutcliffe (1956) suggested that sodium and potassium uptake of the shoot is selectively controlled during movement into the rootstele. A severe competition of this nature might, of course, result in a potassium deficiency of the shoot as a whole. The net loss of potassium from the developed leaves in the present experiment would then be due to potassium retranslocation from older to younger parts. Such a net translocation of potassium has been observed in a number of cases (Williams 1955), and it was found to be particularly pronounced in potassium-deficient wheat seedlings (Ward 1958).

Experiments on ion uptake have usually been carried out over short periods, and with low-salt plants or tissues. In the present study over longer periods, and with high ion levels even in the control substrate, an additional factor of competition for an accumulation site has to be considered (Scharrer and Mengel 1960). In the present experiment such a competition for an accumulation site might also have contributed to the net losses of potassium from the developed leaves, and the failure of these parts to increase in potassium after salt removal. This would have involved an increase in the outward ion movement, rather than a decreased inward movement as in the case of competition for a carrier.

Further information is required to establish whether the net ion uptake of plants is primarily determined by selectivity during ion movement into the stele, or by ion regulation of individual parts.

(c) *Measurement of Ion Uptake and Loss*

Williams (1955) emphasized that net ion changes in individual plant parts are of relevance to the study of plant growth. He also pointed out that much of the recent work with radioactive tracers does not determine the net results of inward and outward ion movements.

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* Only at high sodium levels in the substrate.

It is also considered that a descriptive study, as reported in this paper, facilitates the formulation of relevant problems requiring the separate measurement of ion uptake and loss. As examples can be given:

(1) The sudden increase in chloride and sodium concentration in the whole shoot after sodium chloride application, followed by the much more gradual increases with time (Fig. 3).

(2) The fate of the potassium lost from the developed leaves (Fig. 6), and the possibility of any considerable potassium losses to the saline substrate. Such and other determinations might clarify the nature of the sodium chloride effect on potassium uptake.

In conclusion it is suggested that a general study on the inward and outward ion movements of plants, subjected to high salt concentrations, is essential to an understanding of tolerance to saline substrates.

V. ACKNOWLEDGMENTS

VI. REFERENCES

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