PLANT RESPONSE TO SALINE SUBSTRATES

I. GROWTH AND ION UPTAKE OF SEVERAL VARIETIES OF HORDEUM DURING AND AFTER SODIUM CHLORIDE TREATMENT

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Summary

A comparative study has been made of the response by varieties of *Hordeum* to high sodium chloride treatment and to sodium chloride removal from the substrate.

In exploratory experiments during the early tillering stage, varieties of *H. distichum* suffered more severe injury, and contained more chloride and sodium, than varieties of *H. vulgare*.

In a second experiment three varieties of *H. vulgare* were treated till full maturity with 125 (S_1) and 250 (S_2) m-equiv/l of sodium chloride. Treatment always reduced the growth of the vegetative shoot, and there were pronounced varietal differences. Moreover, the sensitive variety showed a greatly reduced grain weight ratio at S_1, while no inflorescences were formed at S_2. Grain weight ratios of the two salt-tolerant varieties, on the other hand, were not appreciably affected. Weight of 1000 grains was reduced at S_1 in the sensitive variety, and at S_2 in the resistant varieties.

Chloride and sodium in the inflorescences of the salt-tolerant varieties did not appreciably increase at S_1, while these increases in the sensitive variety were high. In both control and salinity treatments, the chloride and sodium contents of the inflorescences were much lower than those of the vegetative shoots.

Two other experiments with the same varieties of *H. vulgare* were carried out at the early tillering stage (sodium chloride concn. 150 m-equiv/l). It was found that the relative growth rates of the sodium chloride treatments fell more quickly with time than in the controls. After sodium chloride removal from the substrate the relative growth rates increased, but they did not regain control levels. This recovery was less pronounced in the sensitive than in the resistant variety.

The treated shoots of the sensitive variety had higher chloride and sodium, and lower potassium contents, than those of the two resistant varieties. These varietal differences in ion content preceded the varietal differences described for growth.

The data suggest that salt tolerance of varieties of *H. vulgare* is related to an ability to regulate their ion content.

I. INTRODUCTION

In humid climates the occurrence of a high electrolyte concentration in the soil solution is usually confined to the sea-shore. In semi-arid and arid regions saline soils are of more frequent occurrence, both under irrigated and non-irrigated conditions. Response by agronomic species to saline substrates thus becomes important to the utilization of arid lands. Information has become available on the plant physiological aspects of this question, particularly in recent years, but the problem is complex and further studies are required to better the understanding of the physiological characters determining salt tolerance.

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A review of the literature indicates that a combination of the following three factors adversely affects plant growth on saline substrates:

(1) An osmotically reduced water availability in the substrate.

(2) An excessive ion accumulation in the plant tissues.

(3) A reduced absorption of essential elements.

A considerable difference of opinion exists, however, as to the relative importance of these factors. Magistad (1945), and Hayward and Wadleigh (1949) emphasized the reduced water availability in the substrate. Other workers, on the other hand, considered that the relative importance of each factor depends largely on the species and the climatic conditions (Berg 1952), and on the salt composition of the substrate (Kelley 1951).

Most previous experiments either involved a comparison between different species, or a study of one variety within a particular species. Williams and Shapter (1955) suggested that the use of different varieties might help to elucidate the causal factors involved in plant response to water stress. A study of varieties would also have additional agronomic relevance. Maximov (1938) stated that varietal differences in salt tolerance are known to occur, but that information on them is scant.

The majority of data on plant response to a salinity stress have been obtained after a lengthy treatment and often at maturity. Interpretation of such experiments is complicated by the pronounced treatment effects on plant development. Normal selectivity in ion uptake might also be diminished by leaf injury (Greenway 1962), and it is suggested here that senescence might have a similar effect on the selectivity of ion uptake.

To elucidate the sequence of events it is, therefore, essential to make additional measurements on the ion uptake and growth of healthy plants treated during relatively short periods.

Sodium chloride removal from the substrate has been used to simulate concentration fluctuations in the soil solution and to study ion translocation (Groenewegen, Bouma, and Gates 1959). Salt removal also permits a growth study on plants high in chloride and sodium, but removed to a substrate of low osmotic pressure.

The present paper reports the effects of sodium chloride treatments on barley varieties of differing salt tolerance. Measurements involved growth and ion uptake during and after a short salinity treatment at the early tillering stage, as well as yield and ion uptake at maturity. Part II of this series (Greenway 1962) gives a detailed description of chloride, sodium, and potassium uptake and translocation in one variety of *Hordeum vulgare* at the early tillering stage.

II. Materials and Methods

This paper describes the results of four glasshouse experiments. Experiments 1, 3, and 4 were carried out at the early tillering stage, and the plants in experiment 2 were treated till maturity. There were control and sodium chloride treatments, while in experiments 3 and 4 sodium chloride was also removed from the substrate. Further experimental details are given in Section III.

The following barley varieties were used in experiments 2, 3, and 4:

Hordeum vulgare L. var. *pallidum*	C.P.I. 11083
Hordeum vulgare cv. Bolivia	C.P.I. 8315
Hordeum vulgare cv. Chevron	C.P.I. 8320

C.P.I. 11083 was obtained from Algeria, and C.P.I. 8315 and 8320 from the United States of America. The only further available information is on C.P.I. 8320. In 1916, cv. Chevron was selected in the United States from a sample of "four rowed spring barley", an unimproved domestic variety obtained from Switzerland. Plant selection, from later importations of "four rowed spring barley", only resulted in two-rowed types (Åberg and Wiebe 1946).

Sowing dates were April 7, June 20, November 14, and March 19 for experiments 1, 2, 3, and 4, respectively. The plants were grown in cultures of clean river sand. After the first leaf had half-developed the seedlings were thinned to four per can, except in experiment 2 where only one seedling was retained. In experiment 2 large differences in development made it advisable to allocate separate locations to the various treatments, and the position of the individual plants was regularly altered. The treatments occupied the following proportions of the total glasshouse area: control 55%, NaCl (125 m-equiv/l) 33%, and NaCl (250 m-equiv/l) 12%.

Experiment 1 had two replicates per variety, but all the other experiments were carried out with 12 replicates. The nutrient solution was that of Arnon, except that $NH_4H_2PO_4$ concentration was according to Arnon and Hoagland (see Hewitt 1952). It contained (in m-equiv/l): potassium 6, calcium16, magnesium 4, ammonium 2, nitrate 22, dihydrogen phosphate 2, and sulphate 4.

The cans were, as a rule, flushed with fresh solutions at intervals of 2·5–4 hr during the day. However, in the later stages of experiment 2 the intervals were 0·75–1 hr and an extra flushing at 10 p.m. was also included. After ear emergence (expt. 2) the effluent was returned to the 200-l. reservoirs, which were maintained at the desired concentration, and every 6–8 days these solutions were renewed.

The concentration of sodium chloride in the nutrient solution was increased by steps of 50 m-equiv/l per day. Sodium chloride treatments were given particularly liberal flushings to avoid any concentration increases. At salt removal all containers were leached till the chloride content of the effluent from the sodium chloride removed treatments was reduced to that of the control.

In experiments 1, 3, and 4 the plants were transferred to a dark room at 7 a.m. on the day of harvest. In all experiments the harvested plant parts were rapidly dried under forced draught at 80°C. Sand was removed from the roots by rinsing with distilled water.

In experiments 3 and 4 rating procedures were used to obtain improved estimates of relative growth rates (McIntyre and Williams 1949). These growth indices were calculated as "adjusted relative growth rates", by using the dry weight excluding the weight of chloride, sodium, and potassium (see Greenway 1962).

Chemical methods employed were those of Best (1950) for chloride and the "EEL" flame photometer was used for the determination of sodium and potassium.

III. Results

(*a*) *Health and Ion Content of Varieties of* H. vulgare *and* H. distichum (*expts.* 1*A and* 1*B*)

In exploratory experiment 1A 37 varieties were treated with 250 m-equiv/l of sodium chloride. The treatment was commenced at the 1–2-leaf stage; the harvest was 14 days later when 4 leaves and some small tillers had developed.

At the 10th day of treatment the leaves of some varieties were paler green than the corresponding control leaves. The tips of the older leaves became brown and necrotic, then chlorosis of the whole leaf blade developed, followed by the death of the particular leaf. Another group of varieties became darker green than their controls, and if injury developed it was confined to a rather small proportion of the plant.

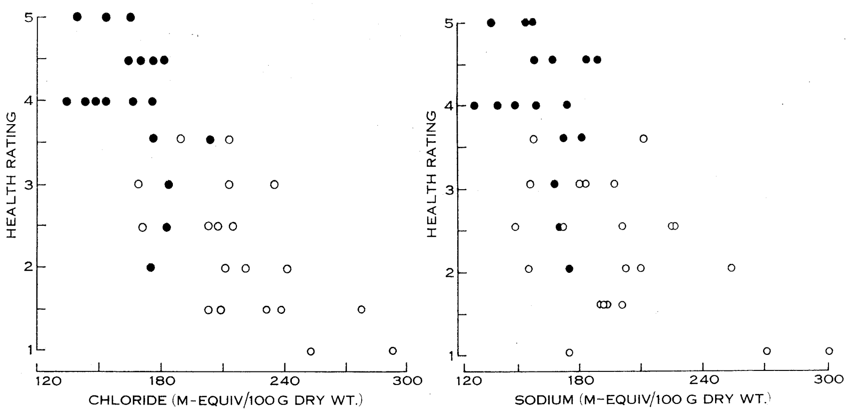

Fig. 1.—Relation between health rating and ion content in sodium chloride treated *H. vulgare* (●) and *H. distichum* (○) at the early tillering stage. Health ratings are as follows: *1*, severe chlorosis; *2*, chlorosis; *3*, severe tip burn; *4*, tip burn; *5*, healthy. Each observation represents a different variety (expt. 1A). Plants were treated for 14 days and a sodium chloride concentration of 250 m-equiv/l was reached at the fifth day. Correlation coefficients are as follows:

	Chloride	Sodium
H. vulgare	$-0\cdot44$ ($P = 0\cdot06$)	$-0\cdot32$ (n.s.)
H. distichum	$-0\cdot65$ ($P<0\cdot001$)	$-0\cdot43$ ($P<0\cdot05$)

Figure 1 shows that varieties of *H. vulgare* tended to be less injured, and contained less chloride and sodium than varieties of *H. distichum* ($P<0\cdot001$). In *H. distichum* injury was related to increasing chloride and sodium contents. This relation was much less pronounced in *H. vulgare*, and this might have been due to the slight difference in health between ratings 4 and 5 (Fig. 1). No relation was found between the health and the potassium contents of the different varieties.

It was found that a sodium chloride concentration of 400 m-equiv/l was a convenient method for selection of varieties (expt. 1B). For instance, after 10 days of treatment cv. Chevron was severely injured and completely chlorotic. Cv. Bolivia showed injury of leaves 1 and 2, but not of leaves 3 and 4. Var. *pallidum* (C.P.I.

11083), on the other hand, was dark green and only showed some chlorosis of the first leaf. This variety survived a further 20 days of treatment, after which the test was terminated. These three varieties were chosen for further experimentation.

(*b*) *Yield and Ion Content of Three Varieties of* H. vulgare *as affected by Sodium Chloride Treatment during the Full Life Cycle* (*expt.* 2)

In this experiment sodium chloride was applied when the first leaf had fully developed. The two concentrations of 125 and 250 m-equiv/l will be referred to as S_1 and S_2.

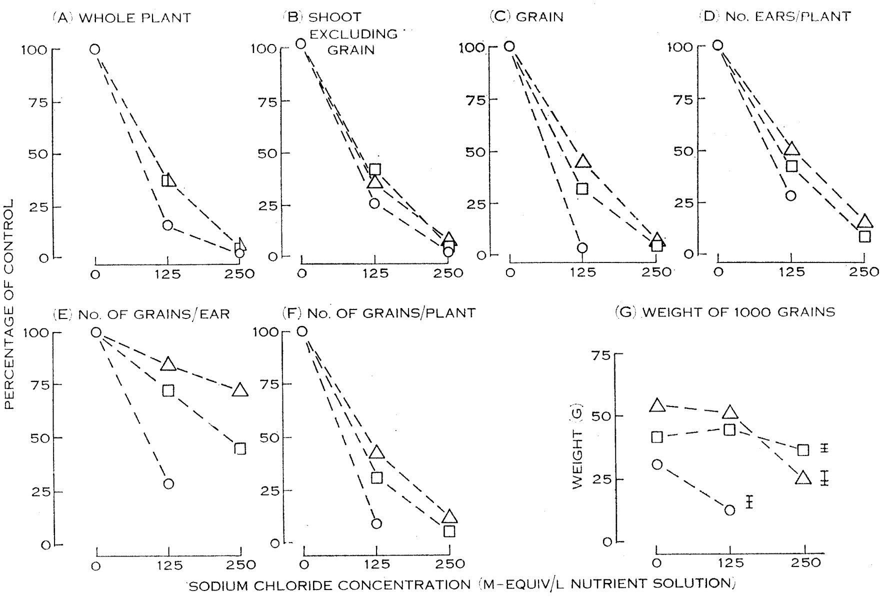

Fig. 2.—Response of three varieties of *H. vulgare*—Chevron (○), Bolivia (□), and C.P.I. 11083 (△)—to sodium chloride treatment till maturity (expt. 2). The actual control values and the significances for the varietal differences in departure from control due to salinity are presented in Table 1.

Growth of C.P.I. 11083 and Bolivia was strongly reduced by S_1 and particularly by S_2 (see Plate 1, Fig. 1). Adverse effects were even more pronounced in Chevron, and at S_2 the plants died before ear emergence (Plate 1, Fig. 2).

The plants were harvested when fully mature and the mean harvest dates of the treatments were as follows:

	Chevron	Bolivia	C.P.I. 11083
Control	November 28	December 8	December 11
S_1	November 25	December 7	December 10
S_2	November 3	November 24	November 23

Early maturity for barley grown on saline land was also found by Ayres, Brown, and Wadleigh (1952).

(i) *Dry Weight and other Growth Characteristics*.—The various growth characteristics are presented in Figure 2 as a percentage of control values. The actual values for the controls are presented in Table 1. The dry weight of the whole plant was decreased markedly by salinity treatment and this effect was most distinct in Chevron (Fig. 2*A*). Varietal differences were more marked in the grain weight than in the weight of the shoot excluding the grain (Figs. 2*B* and 2*C*). The reduction in ear formation was also most pronounced in Chevron. In C.P.I. 11083 ear number was depressed less than the dry weight of the shoot excluding the grain (Figs. 2*B* and 2*D*).

TABLE 1

DRY WEIGHT AND EAR FORMATION IN CONTROLS OF THREE VARIETIES OF H. VULGARE (EXPT. 2)

Statistical significances were calculated after a logarithmic transformation. Salinity effects are shown in Figure 2

	Control Values			P* for Varietal Differences in Departures from Control Values due to Salinity (Bolivia > C.P.I. 11083):	
	Chevron	Bolivia	C.P.I. 11083	At 125 m-equiv/l	At 250 m-equiv/l
Dry weight (g) of whole plant	365	454	417	n.s.	n.s.
Dry weight (g) of shoot excluding grain	218	277	255	n.s.	n.s.
Grain weight (g)	139	166	152	$P<0\cdot05$	n.s.
No. of ears/plant	85	92	68	$P<0\cdot05$	$P<0\cdot01$
No. of grains/ear	50	42	42	n.s.	$P<0\cdot01$
No. of grains/plant	4276	3871	2866	$P<0\cdot05$	$P<0\cdot01$

* For all the plant attributes in this table the departure from control due to salinity in cv. Chevron was always highly significantly greater than in C.P.I. 11083 and in cv. Bolivia.

Very pronounced varietal differences were apparent in the number of grains per ear and in the weight of 1000 grains (Figs. 2*E* and 2*G*). Treatment effects on number of grains per ear were particularly small in C.P.I. 11083 (Fig. 2*E*).* In Chevron the weight of 1000 grains was strongly reduced at S_1, but in Bolivia and C.P.I. 11083 only S_2 resulted in a decrease of this value (Fig. 2*G*). The size distribution of the grain was homogeneous for all treatments (unpublished data), and the decreases in mean grain weight were thus due to a general decrease of the weights of the individual grains.

These effects resulted in pronounced differences between the weight ratios of the various treatments (Fig. 3). The grain weight ratio of Chevron was greatly reduced at S_1, but the inflorescence weight ratio was not affected. The inflorescence weight ratio was decreased, however, when expressed in relation to the weight of

* Grains were counted after the ear samples were separated in an aspirator. It is, therefore, possible that in S_1 of Chevron very small grains were lost during this process.

the whole plant excluding the grain (control, 0·22; S_1, 0·12). In C.P.I. 11083 and Bolivia the effects on weight ratios were much less pronounced than in Chevron. S_1 somewhat depressed the grain weight ratio of Bolivia but it even increased this ratio in C.P.I. 11083 (varietal difference significant at $P<0 \cdot 001$). S_2, on the other hand, decreased grain weight ratios and increased inflorescence weight ratios of both Bolivia and C.P.I. 11083.

(ii) *Comparison of Growth Data with those of Agronomic Experiments*.—Ayers, Brown, and Wadleigh (1952) found that under field conditions Chevron was very salt-sensitive, while two other varieties of *H. vulgare* (cv. Atlas and cv. California Mariout) were salt-resistant. These latter varieties were also tolerant in experiment 1A, and the data presented here thus appear of agronomic relevance.

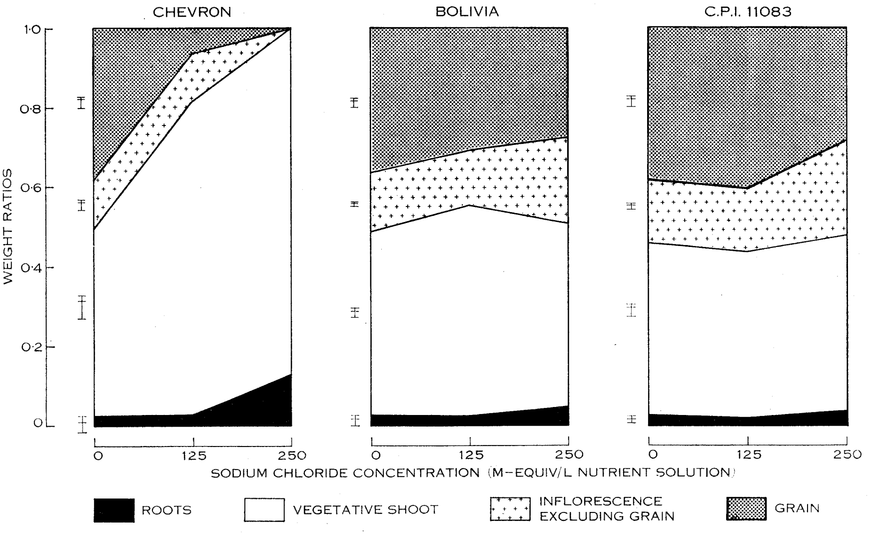

Fig. 3.—Weight ratios for grain, inflorescences, vegetative shoots, and roots of three varieties of *H. vulgare* as affected by sodium chloride treatment (expt. 2).

Ayers, Brown, and Wadleigh (1952), Richards (1954), and others found that tolerant varieties of *H. vulgare* were very little affected by medium salt concentrations, and this is in contrast with the present experiments (C.P.I. 11083 at S_1 in Figure 2 and Plate 1). However, in the present experiments there were optimal conditions for water, nutrient, and light for each individual plant, and this resulted in a prolific development of the controls (Plate 1; Table 1). Adverse effects on tolerant varieties might well be less marked in a dense stand than under the conditions of the present experiments. This view is supported by the small treatment effects on both weight of 1000 grains and on grain weight ratios (Figs. 2*G* and 3), as well as by the smaller glasshouse area occupied by the salt treatments (see Section II). The effect of an additional limiting factor was, for instance, demonstrated by results of Yankovitch (1949), who did not supply optimal moisture and found that salinity treatment increased the grain yield of several wheat varieties.

(iii) *Chloride, Sodium, and Potassium Contents.*—These ion contents are presented in Figure 4. In C.P.I. 11083 and Bolivia chloride and sodium contents of the vegetative shoots were greatly increased, while increases in the roots were very

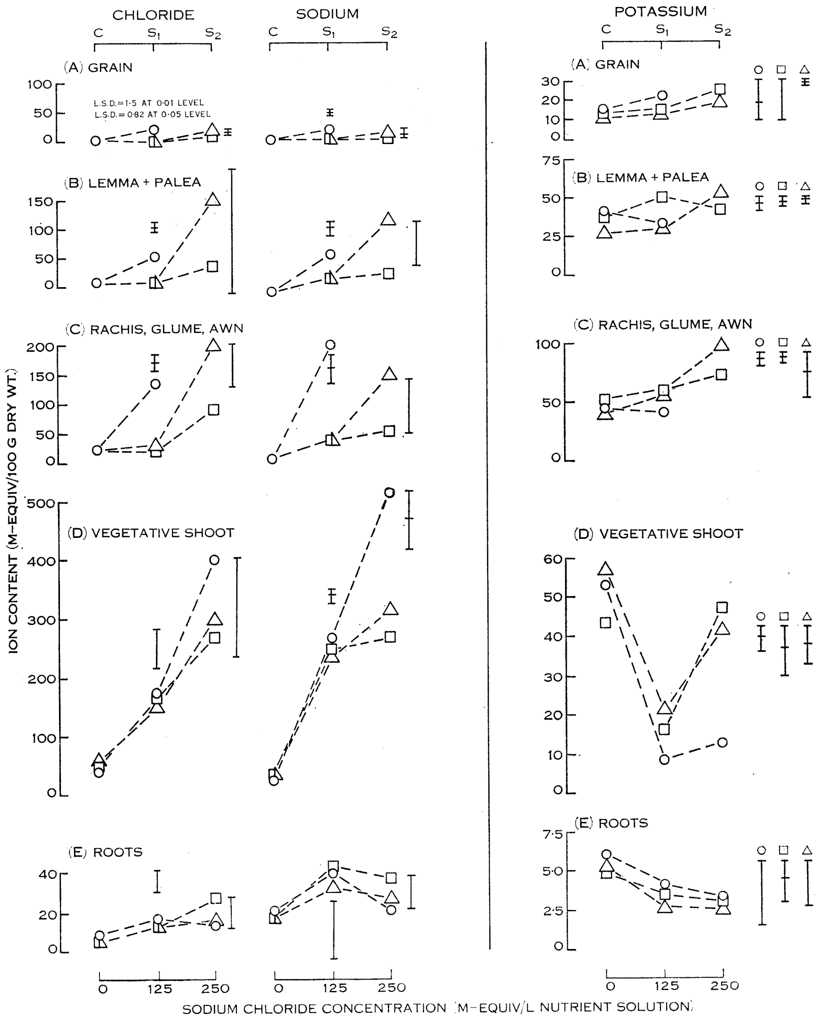

Fig. 4.—Chloride, sodium, and potassium contents in different plant parts of three varieties of *H. vulgare*—Chevron (○), Bolivia (□), and C.P.I. 11083 (△)—as affected by sodium chloride treatment. For chloride and sodium the scale for the roots is larger than for the other parts. Scales for potassium are different from those for sodium and chloride and vary with the plant part. Least significant differences (L.S.D.) for chloride and sodium apply to each individual salinity level, and single values indicate the 0·05 level. L.S.D.'s for potassium are shown for all treatments, but separately for each individual variety.

much smaller. S_1 did not appreciably affect the chloride content of the inflorescences and increases in sodium content were also low. S_2 increased chloride and sodium contents markedly over those of S_1, particularly in the inflorescences of C.P.I. 11083.

In Chevron chloride and sodium contents showed pronounced differences with those in C.P.I. 11083 and in Bolivia. At S_1 Chevron vegetative shoots had only slightly higher chloride and sodium contents than the other two varieties. However, the inflorescences at S_1 and the vegetative shoots at S_2 contained much more chloride and sodium in Chevron than in C.P.I. 11083 and Bolivia (Figs. 4*B*, 4*C*, and 4*D*).

The ion distribution within the plant was rather similar for all varieties, and to facilitate comparison between parts, the data for C.P.I. 11083 are also presented in Table 2. Chloride and sodium contents in the shoots invariably decreased in the order: vegetative shoots; awns, rachis, and glumes; lemma and palea; and grain. The very small treatment effect on the ion content of the grain is noteworthy. Salt-treated rice also had much lower chloride contents in the grain than in the vegetative shoots and the roots (Ting Tsing and Fang Yi-Hsuing 1957).

Table 2

ION CONTENTS (M-EQUIV/100 G DRY WEIGHT) OF INDIVIDUAL PLANT PARTS OF C.P.I. 11083 (EXPT. 2)

Plant Part	Chloride Ion			Sodium Ion			Potassium Ion		
	Control	NaCl Concn. 125 m-equiv/l	NaCl Concn. 250 m-equiv/l	Control	NaCl Concn. 125 m-equiv/l	NaCl Concn. 250 m-equiv/l	Control	NaCl Concn. 125 m-equiv/l	NaCl Concn. 250 m-equiv/l
Grain	3·2	3·8	17	1·6	4·0	15	13	13	19
Lemma+palea	9·4	16	154	5·6	20	126	27	31	56
Rachis, glume, awn	30	43	202	9·8	42	151	37	56	99
Vegetative shoot	50	152	303	38	227	317	58	22	42
Roots	4·4	12·2	15·9	17	33	26	5·8	2·9	2·6

The high chloride and sodium contents in the inflorescences of the sensitive variety might have been partly responsible for their poor grain formation. Senescence might, however, be expected to diminish the ion regulation of plant tissues. Before considering any adverse effects of the high ion contents it would, therefore, be necessary to obtain data at an earlier growth stage when the inflorescences are still actively functioning. Even at maturity the inflorescences of the resistant varieties had very low ion contents as compared to the vegetative shoots (Fig. 4) and to leaves and sheaths at an earlier growth stage (Figs. 8 and 9). These observations suggest that inflorescences of the resistant varieties are particularly able to exclude chloride and sodium. Matukhin and Boĭko (1957) reported similar low chloride contents for the inflorescences of a number of species grown on saline substrates.

Potassium in the vegetative shoots of Bolivia and C.P.I. 11083 was greatly reduced at S_1, but not at S_2 (Fig. 4*D*). In the inflorescences potassium increased somewhat at S_1, and it usually increased considerably over the control values at S_2 (Figs. 4*B* and 4*C*). Salt treatments strongly reduced potassium contents of

Chevron vegetative shoots, and smaller decreases occurred in the inflorescences. Certain regularities in the potassium distribution within the shoot occurred (Table 2). For example, the grain always had the lowest potassium content. In the controls potassium content of the inflorescences was lower than in the vegetative shoot, but inflorescences of the treated plants were highest in potassium.

In considering the potassium data it has to be remembered that after ear emergence the nutrient supply was limited (see Section II). The high potassium content in the inflorescences at S_2 might thus be due to a relatively more liberal supply of potassium than in the control. In the case of S_1, however, the vegetative shoot was sharply decreased in potassium content, indicating that potassium uptake

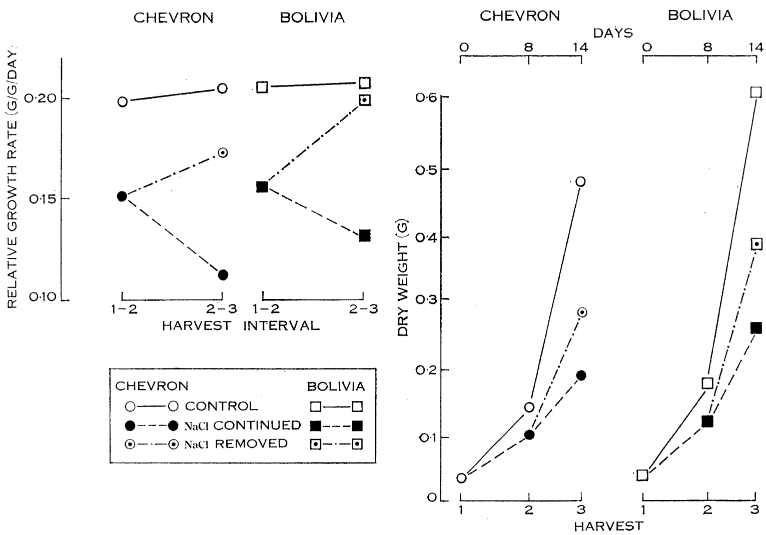

Fig. 5.—Relative growth rate, and dry weight of the whole plant in control, NaCl continued, and NaCl removed treatments of two varieties of *H. vulgare* (expt. 3). Relative growth rates (R values) for the H_2–H_3 interval were corrected by leaf ratings taken prior to harvest 2 (McIntyre and Williams 1949). Significant differences of R for control minus NaCl removed treatments are as follows: Chevron, $P<0\cdot001$; Bolivia, not significant; Chevron minus Bolivia, $P<0\cdot05$.

in the plant was reduced. Yet the potassium content of the inflorescences of the salt-tolerant varieties increased and this again suggests that inflorescences are better protected than vegetative shoots against an ion unbalance of the substrate.

(c) *Growth and Ion Uptake during and after Sodium Chloride Treatment in Three Varieties of* H. vulgare (*expts.* 3 *and* 4)

These experiments were carried out at the early tillering stage and treatments were imposed over relatively short periods to minimize complications of differences in development and of injury to plant parts.

In experiment 3, Bolivia and Chevron were subjected to a sodium chloride stress, which was attained in the usual manner by increments of 50 m-equiv/l each

TABLE 3

DRY WEIGHT (G) OF INDIVIDUAL PLANT PARTS IN TWO VARIETIES OF H. VULGARE AS AFFECTED BY SODIUM CHLORIDE CONTINUED TREATMENT AND SODIUM CHLORIDE REMOVAL FROM SUBSTRATE (EXPT. 3)

Plant Part	Chevron						Bolivia					
	Control			NaCl Continued		NaCl Removed	Control			NaCl Continued		NaCl Removed
	Harvest 1	Harvest 2	Harvest 3	Harvest 2	Harvest 3	Harvest 3	Harvest 1	Harvest 2	Harvest 3	Harvest 2	Harvest 3	Harvest 3
Leaves 1, 2, and 3	0·022	0·083	0·096	0·058	0·079	0·079	0·026	0·099	0·121	0·072	0·108	0·105
Young leaves of main shoot	—	—	0·095	—	0·034	0·056	—	—	0·091	—	0·030	0·058
Sheaths of main shoot	—	0·023	0·082	0·019	0·038	0·055	—	0·028	0·101	0·025	0·052	0·064
Tillers	—	0·007	0·144	0·0004	0·019	0·052	—	0·014	0·198	0·0017	0·041	0·090
Roots	0·009	0·038	0·110	0·030	0·050	0·069	0·011	0·050	0·149	0·035	0·067	0·105
Whole plant	0·031	0·151	0·527	0·107	0·220	0·311	0·037	0·191	0·660	0·134	0·298	0·422

day till the 150 m-equiv/l level was reached. Harvest 2 was taken 8 days after treatment application, and then sodium chloride was removed from the substrate of half of the treated plants. Between harvests 2 and 3 (H_2–H_3), an interval of 6 days, there were thus a sodium chloride removed and a sodium chloride continued treatment. In experiment 4, C.P.I. 11083 and Chevron were similarly treated, but there was no sodium chloride continued treatment during the second interval (H_2–H_3). The control solutions of experiments 3 and 4 contained 0·1 and 1 m-equiv/l of sodium chloride respectively. Data for growth attributes are presented under separate headings for the two experiments.

(i) *Dry Weights and Relative Growth Rates*: *Experiment* 3.—Dry weight and relative growth rate of the whole plant are presented in Figure 5 and the dry weight of the individual plant parts in Table 3. At H_2 and H_3 the dry weight of the whole plant decreased in the order control, removed, and continued treatments. At H_2 the shoots mainly consisted of leaves 1, 2, and 3. In the control shoots the subsequent dry weight increases occurred primarily in the young leaves of the main shoot and tillers. In the continued and removed treatments, on the other hand, leaves 1, 2, and 3 showed considerable dry weight increases during the H_2–H_3 interval. At H_3 the main treatment differences for the leaves were found in the young leaves of the main shoot and the tillers.

Relative growth rates (R values) of both varieties were markedly reduced by sodium chloride treatment during the first interval. In the controls R values did not change with time, but they declined with time in the continued treatments, and this decline was more distinct in the case of Chevron (Fig. 5).

In considering this decline of R values it has to be remembered that it might have been partly due to the lower salinity levels during the first days of the salinity treatment. The proper comparison would, therefore, be between the last 6 days of the first interval and the whole of the second interval. No data are available to establish R values over the last 6 days of the first interval. Their minimum values can, however, be assessed by assuming that no adverse effects had resulted from the first 2 days of salinity treatment. R still declined with time as shown by the following values:

Chevron		Bolivia	
Recalculated R	R	Recalculated R	R
((H_1+2 days)–H_2)	(H_2–H_3)	((H_1+2 days)–H_2)	(H_2–H_3)
0·141	0·112	0·146	0·131

After salt removal R values of Bolivia increased, but they did not reach the control level. A much smaller increase occurred in Chevron, and R values of this variety were well below the control value.

The relative water contents* are presented in Figure 6. In the controls Bolivia had higher values than Chevron. The continued treatment usually reduced the relative water contents, with the notable exception of the young leaves of the main

* Relative water contents were also calculated by excluding chloride and sodium from the dry weight. In the treated plants these "adjusted" relative water contents were somewhat higher than the conventional values. However, trends were similar and the conventional values are sufficient for the purpose of the present paper.

shoot of Chevron at H_3. Relative to the controls these decreases were usually less pronounced in Chevron than in Bolivia; for example at H_2 leaves 1, 2, and 3 were reduced to 93% in Chevron, but to 84% in Bolivia. Sodium chloride removal resulted in relative water contents which generally exceeded the control values.

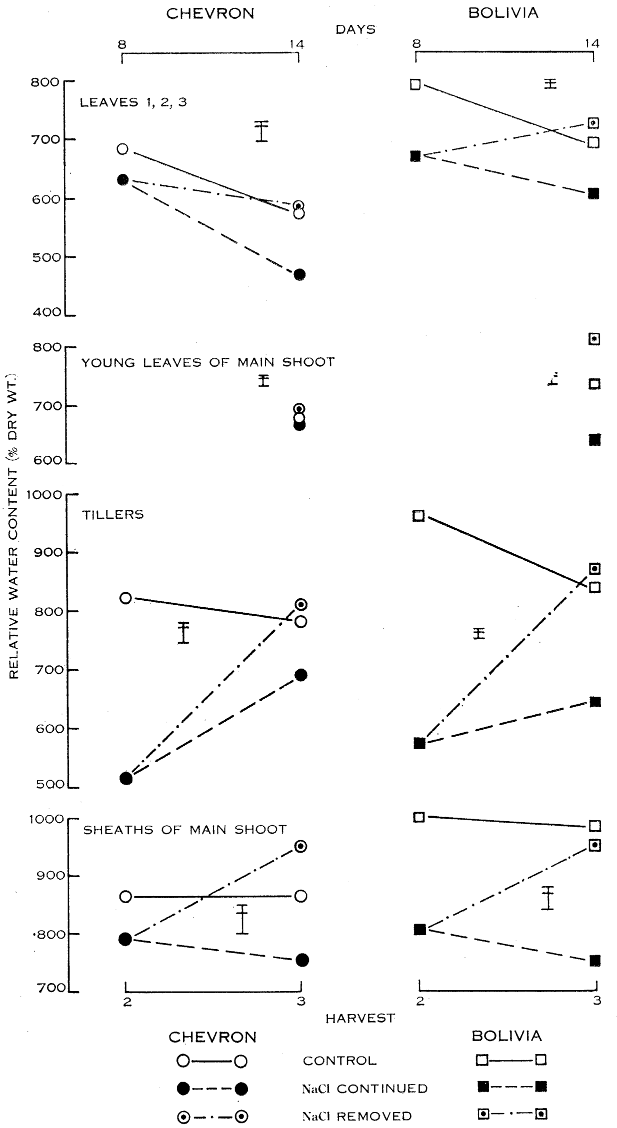

Fig. 6.—Relative water contents of two varieties of *H. vulgare* as affected by control, NaCl continued, and NaCl removed treatments (expt. 3).

(ii) *Dry Weights and Relative Growth Rates: Experiment* 4.—In this experiment plants were separated into leaves 1, 2, and 3; rest of the shoot; and roots.

Dry weights are shown in Figure 7 and relative growth rates in Table 4. Sodium chloride treatment depressed R values in both varieties (H_1–H_2). The decline in

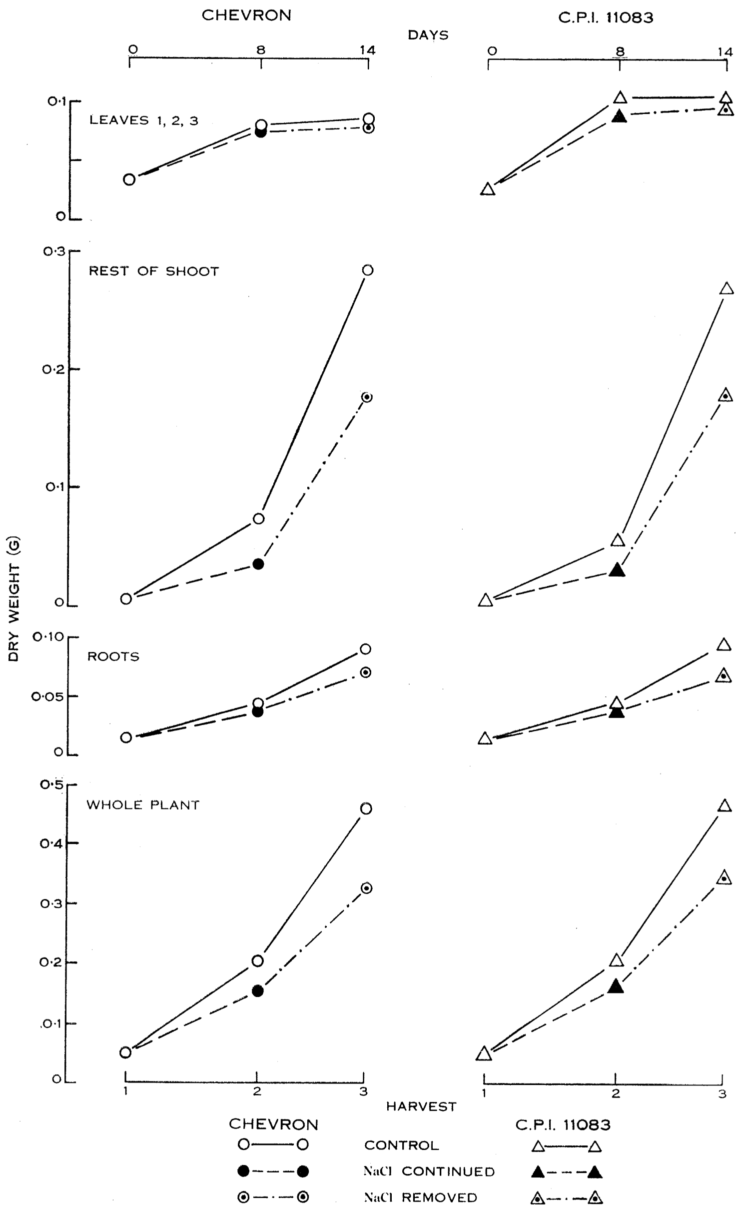

Fig. 7.—Dry weight of the whole plant and its individual parts in two varieties of *H. vulgare* as affected by NaCl continued and NaCl removed treatments (expt. 4). The scale for the whole plant is smaller than those for the individual parts.

R values with time was less pronounced in the removed than in the control treatment, but the removed plants had nevertheless a lower R value than the controls. Chevron

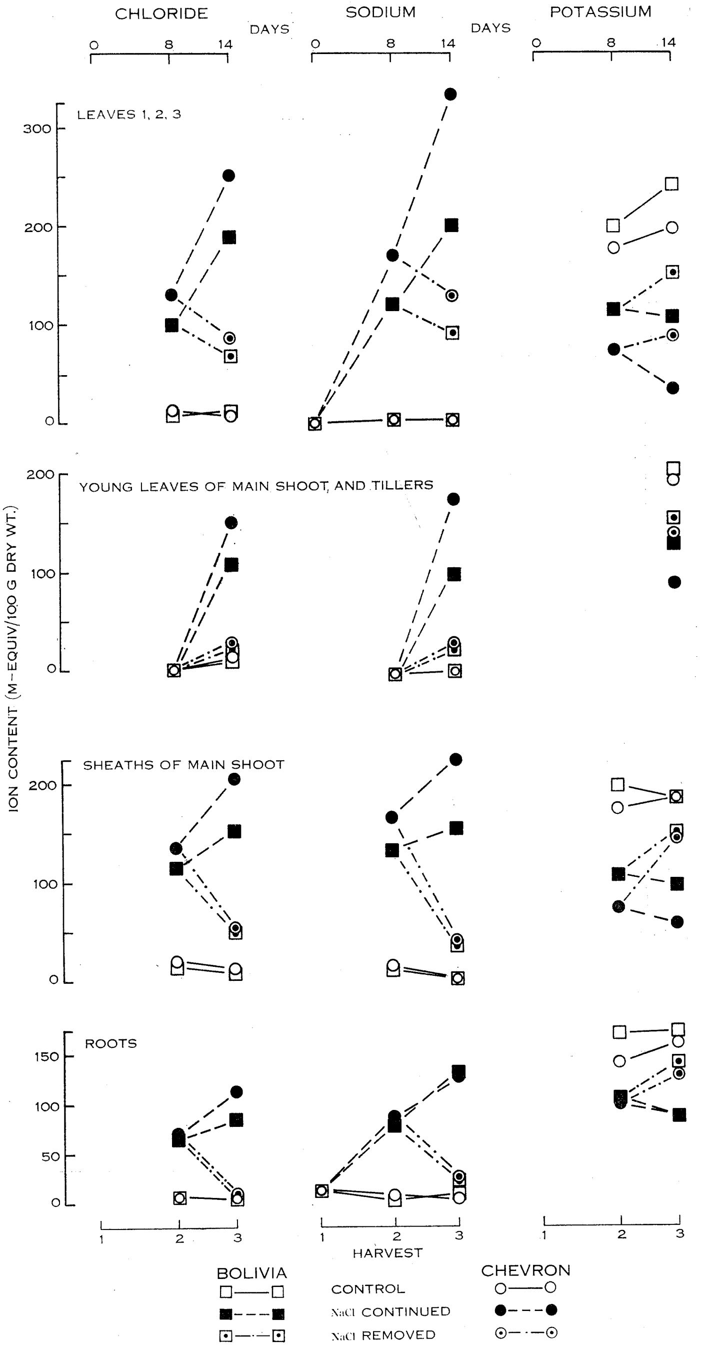

Fig. 8.—Ion content of various parts of two varieties of *H. vulgare* for control, NaCl continued, and NaCl removed treatments (expt. 3). The ionic content of the young leaves of the main shoot and the tillers were very similar and only the average value is presented. Significant differences from control due to treatments (Chevron > Bolivia) are as follows: for NaCl continued—

[*For continuation see opposite page*]

removed plants showed a somewhat less pronounced recovery than those of the other variety, but the varietal difference was less distinct than in experiment 3.

(iii) *Ion Contents of Experiments* 3 *and* 4.—In Part II of this series, detailed data on ion content will be presented for cv. Chevron grown in water culture. Accordingly, only varietal differences will be considered for the two sand-culture experiments presented here. In sand culture there is always the danger that the oldest leaf may absorb ions by contact with the flushing solution. But this was avoided in the water-culture experiment described in Part II (Greenway 1962) and it will be noted that this data is similar to that presented here. An appreciable effect of leaf absorption on the results of the present experiments appears thus unlikely.

TABLE 4

RELATIVE GROWTH RATES (G/G/DAY) OF TWO VARIETIES OF H. VULGARE AS AFFECTED BY SODIUM CHLORIDE TREATMENT AND SUBSEQUENT SODIUM CHLORIDE REMOVAL (EXPT. 4)

	Chevron		C.P.I. 11083	
	H_1–H_2	H_2–H_3	H_1–H_2	H_2–H_3
Control	0·165	0·135	0·162	0·133
Treated with NaCl till H_2, then NaCl removed	0·130	0·120	0·134	0·124
Significances H_2–H_3	Control—NaCl removed, $P<0\cdot05$		Control—NaCl removed, n.s.	

In experiment 4 the control shoots of Chevron contained appreciably more chloride than those of C.P.I. 11083 (Fig. 9), but no such varietal difference was apparent in the controls of experiment 3 (Fig. 8).

In the sodium chloride treated plants all parts of the Chevron shoots had considerably higher chloride and sodium contents than the corresponding parts of Bolivia (Fig. 8) and of C.P.I. 11083 (Fig. 9). In both control and sodium chloride treatments, potassium contents of Chevron were, as a rule, lower than those of the other two varieties. Sodium chloride treatment greatly depressed potassium contents and there was, in most cases, a significant varietal difference. The potassium depression from control values was, then, greater in Chevron than in the other two varieties (Figs. 8 and 9). There was no varietal difference in response to treatment in the roots, where salinity increased both sodium and chloride contents, but decreased potassium (Figs. 8 and 9).

Fig. 8 (*Continued*)

$P<0\cdot05$, $0\cdot01$, or $0\cdot001$ for all plant parts of the shoot for Na^+, Cl^-, and K^+ but excluding Cl^- and K^+ contents of sheaths at harvest 2; for NaCl removed—$P<0\cdot05$ for Cl^- in leaves 1, 2, and 3 and sheaths, $P<0\cdot01$ for Na^+ in leaves 1, 2, and 3.

The general pattern of ion accumulation in the different plant parts of the three varieties was very similar. In experiment 3, chloride and sodium contents in the continued treatments increased with time. At the final harvest the contents decreased in the order leaves 1, 2, and 3, sheaths, young leaves of the main shoot and tillers, and roots (Fig. 8).

To obtain an indication of the ion concentration in the plant fluids ion contents can be best expressed as m-equiv/l in the plant water (Black 1960). These values

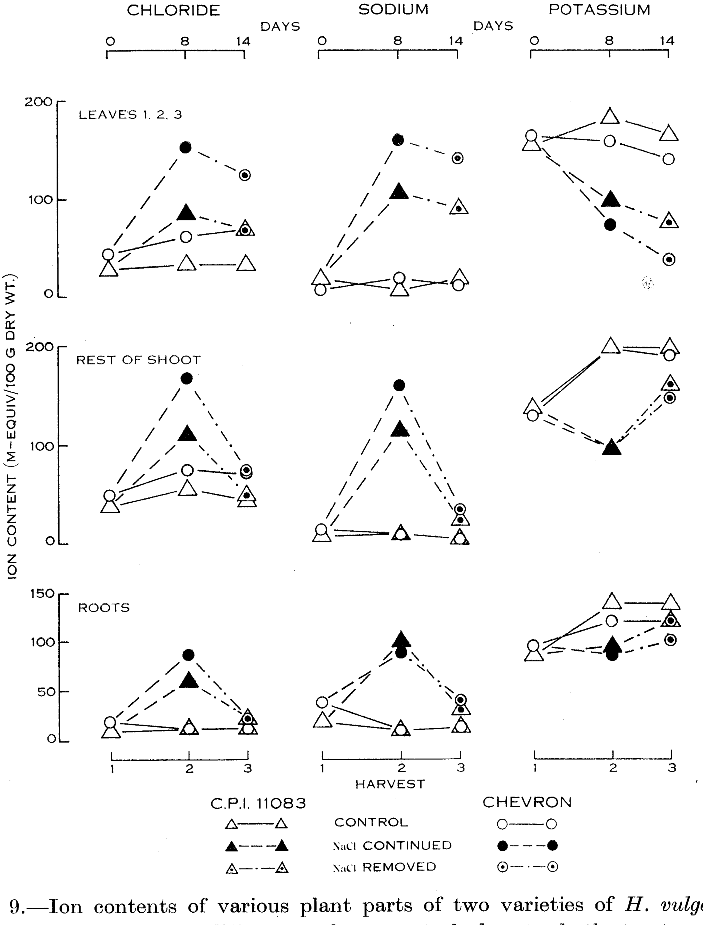

Fig. 9.—Ion contents of various plant parts of two varieties of *H. vulgare* (expt. 4). Significant differences from control due to both treatments (Chevron > C.P.I. 11083) are as follows: for Cl^- and Na^+—$P<0 \cdot 01$ for all parts of the shoot but excluding rest of shoot at harvest 3, which was not significant; for K^+—$P = 0 \cdot 05$ for leaves 1, 2, and 3 at harvest 2 and rest of shoot at harvest 3, $P<0 \cdot 01$ for leaves 1, 2, and 3 at harvest 3.

for some of the relevant chloride data of the continued treatments of experiment 3 are shown in Table 5. At H_3 much higher chloride concentrations occurred in the plant fluids of leaves 1, 2, and 3 than in those of the young leaves and tillers (Table.) 5 This was a result of both a lower relative water and a higher chloride content in the dry matter of leaves 1, 2, and 3 (Figs. 6 and 8). The chloride concentration in the plant fluids was similar to that of the substrate in the case of the young parts of sodium chloride treated Bolivia, such as leaves 1, 2, and 3 at H_2; and tillers and young

TABLE 5

CHLORIDE (EXPRESSED AS M-EQUIV/L) IN THE PLANT WATER OF SODIUM CHLORIDE CONTINUED AND SODIUM CHLORIDE REMOVED TREATMENTS (EXPT. 3)

NaCl concentration of substrate 150 m-equiv/l

Plant Part	Chevron			Bolivia		
	NaCl Continued		NaCl Removed	NaCl Continued		NaCl Removed
	Harvest 2	Harvest 3	Harvest 3	Harvest 2	Harvest 3	Harvest 3
Leaves 1, 2, and 3	206	533	150	150	307	96
Young leaves of main shoot	—	226	—	—	160	—
Tillers	—	218	—	—	159	—

leaves at H_3. In Chevron, on the other hand, the chloride concentrations of the plant fluids were always appreciably higher than that of the substrate.

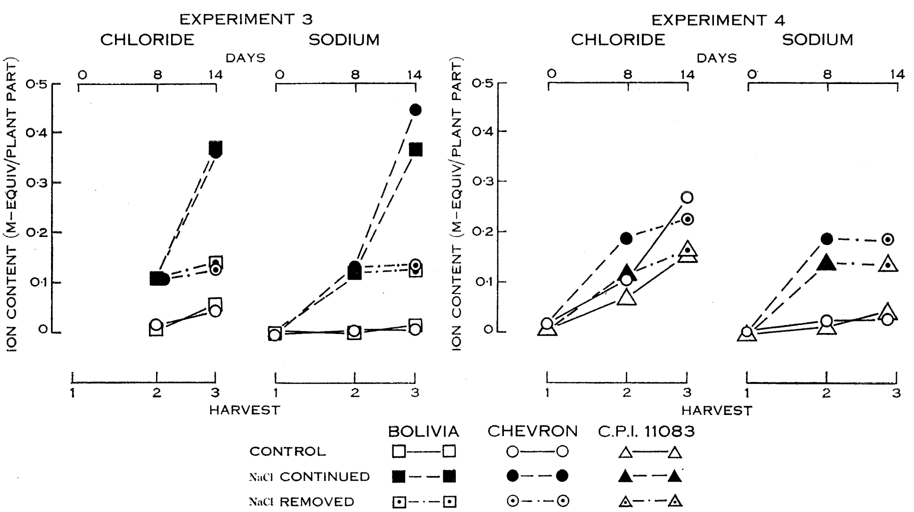

Fig. 10.—Chloride and sodium content for the whole shoot of three varieties of *H. vulgare* (expts. 3 and 4).

Varietal differences in chloride concentration of the plant water were similar to those of the dry matter in the continued treatment, but for the removed treatments they were more pronounced if expressed on a plant water basis (Table 5; Fig. 8).

Absolute chloride and sodium contents (m-equiv/ plant) for the whole shoot are shown in Figure 10. In experiment 3 Bolivia and Chevron had very similar absolute chloride and sodium contents, with the exception of higher sodium contents in the Chevron continued shoots at H_3. Experiment 4 showed, however, that the varietal differences in ion accumulation might occur in the absolute amount of ions, as well as in the earlier-described differences for ion concentration in the dry matter (m-equiv/100 g, Figs. 8 and 9). Figure 10 also amplifies that varietal differences in ion accumulation were not solely confined to the salinity treatments, but that there were also large varietal differences in the chloride content of the control shoots of experiment 4 (see also Fig. 9).

IV. Discussion

(a) *Varietal Differences in Salt Tolerance*

In the present investigation *H. distichum* was found to be much more salt-sensitive than *H. vulgare*. Varietal differences also occur in *Triticum*, and Maximov (1938) stated that the "soft" varieties are more tolerant than the "hard" varieties.

The present experiments showed that varietal differences were only apparent in certain characters. These were:

(1) Survival at a very high concentration at the early tillering stage (400 m-equiv/l (expt. 1B)).

(2) Recovery after salt removal at the early tillering stage (Fig. 5).

(3) Growth and seed production at a medium concentration (125 m-equiv/l (Figs. 2 and 3)).

(4) Survival and seed production at a high salt concentration (250 m-equiv/l (Figs. 2 and 3)).

These characters would be important to the ecology of species on saline soils, particularly since concentrations of the soil solutions tend to fluctuate widely.

Varietal differences in grain formation were particularly pronounced (expt. 2). The sensitive variety was more strongly reduced in number of grains than in weight of assimilating organs such as inflorescences and shoots (Figs. 2*B* and 2*F*). This variety showed also a strong decrease in the weight of 1000 grains. In relation to these results it should be mentioned that the treated plants of this variety developed severe chlorosis, particularly during the shooting stage, and shortly after anthesis this chlorosis also became apparent in the inflorescences. The plants of the salt-tolerant varieties retained their healthy green colour, particularly at the 125 m-equiv/l level. At this salinity level grain weight ratios and weight of 1000 grains of these varieties were not affected and this indicates a good assimilating capacity of inflorescences and shoots.

(b) *Varietal Responses to Saline Substrates as Related to Ion Uptake*

In a comparison between various agronomic species Berg (1952) concluded that their salt tolerance was related to an ability to regulate their ion uptake. Matukhin and Boĭko (1957) found that the adaptation of certain species to saline substrates was related to a reduced chloride uptake. Sensitive varieties, or species, absorbed more chloride than resistant ones in wheat varieties at maturity (Yankovitch 1949), in vine varieties (Ehlig 1960), and in trefoil subspecies (Hayward and Wadleigh 1949). Sensitive cotton varieties contained more sodium than resistant ones (Richards 1954). Ehlig (1960) found that vine varieties differed in chloride content before leaf injury became apparent. In most of the abovementioned experiments, however, considerable leaf injury had developed (Richards 1954; present paper, expt. 1), or alternatively harvests were only taken at a late stage of growth (Berg 1952; Yankovitch 1949; present paper, expt. 2). It has been emphasized earlier that under such conditions any interpretation of the data would be hazardous.

To minimize such complications, in the experiments reported here, ion uptake was also studied in young plants, which did not show any obvious leaf injury (expts. 3 and 4). Under these conditions the shoots of the sensitive variety absorbed much more chloride and sodium, and were usually more severely depressed in potassium, than the resistant varieties (Figs. 8 and 9). These varietal differences in ion content preceded those for growth. For example, in experiment 3 leaves 1, 2, and 3 of Chevron had, at H_2, considerably more chloride and sodium than those of Bolivia, yet relative growth rates over the period H_1–H_2 had been reduced to an equal extent in both varieties (Figs. 5 and 8). This suggested that an ability to regulate the ion contents of the tissues is an important factor in determining the salt tolerance of varieties of *H. vulgare*.

Ion accumulation in the plant has been considered to alleviate the stress caused by the increased osmotic pressure of the substrate (Eaton 1942; Terra 1955). Hayward and Wadleigh (1949) also suggested that the high ion absorption of most halophytes has an important bearing on their salt tolerance. Between H_2–H_3 leaves 1, 2, and 3 of the continued treatments accumulated large amounts of chloride and sodium (expt. 3 in Fig. 8). These leaves formed the major portion of the shoot, as is demonstrated by the weight ratios of the Chevron continued treatment in Figure 11. Relative growth rates during the same period decreased, however, and this decline was more distinct in the variety with the highest ion accumulation. This variety (Chevron) had much higher chloride concentrations in its plant water than those occurring in the substrate (Table 5) and it would, therefore, be expected to be least affected by the high osmotic pressure of the substrate. It thus seems reasonable to suggest that the decreases in R values with time were related to an adverse effect of the increased ion content in the plant tissues.

That excessive ion accumulation was at least partially responsible for the reduced growth on saline substrates is further indicated by the lower R values of the removed treatments as compared to the controls (Table 4; Fig. 5). This finding is in contrast with experiments on water stress. Gates (1955), for instance, found that upon rewatering tomato plants, which had been subjected to moisture stress, higher R values than the controls were attained. Amer and Williams (1958) reported similar phenomena in a number of species. In the present experiments leaves 1, 2, and 3 retained their high chloride and sodium contents after sodium chloride removal (Figs. 8 and 9). These leaves formed a considerable portion of the whole shoot (Fig. 11), and it is suggested here that their high ion contents were responsible for the lower R values in the removed as compared to the control treatments.

This view receives strong support from the fact that the variety which suffered the most pronounced change in ion content also showed the least marked recovery after sodium chloride removal (Fig. 5, Chevron as compared with Bolivia). An observation of similar nature was made during a study on germination of lucerne seeds (Uhvits 1946). She found that, both during and after treatment, sodium chloride affected germination more drastically than mannitol solutions of the same osmotic pressure.

The data at maturity are in keeping with the conclusion that, in varieties of *H. vulgare*, low rather than high ion contents mitigated the adverse effects of

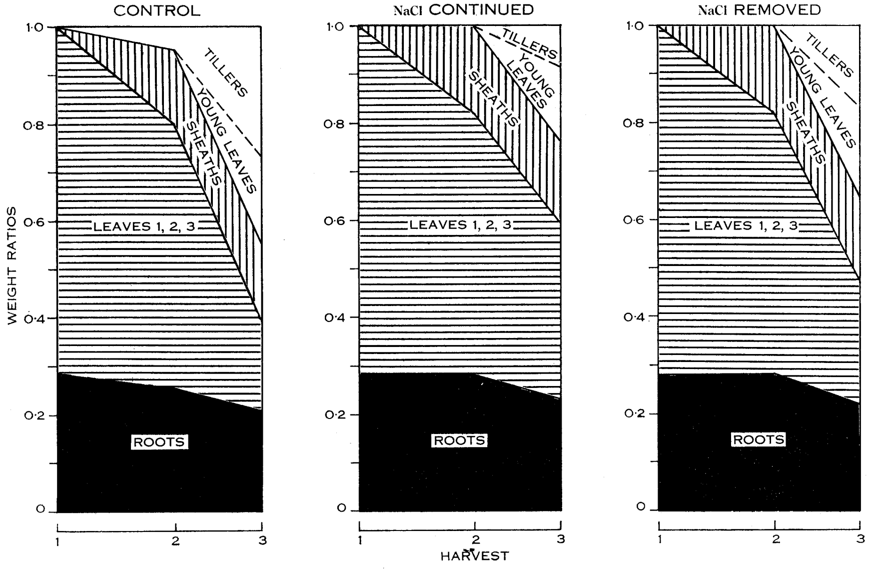

Fig. 11.—Weight ratios of the various plant parts of Chevron variety of *H. vulgare* for control, NaCl continued, and NaCl removed treatments (expt. 3).

a salinity stress. For instance, the satisfactory grain formation of the resistant varieties might have been due, at least partially, to the low chloride and sodium contents of their inflorescences.

The presented data do not permit a more specific suggestion as to the particular ion which would be mainly responsible, and even potassium deficiency cannot be excluded. In certain species increased sodium uptake is known to mitigate the effects of potassium deficiency. However, in the case of barley it has been shown that sodium accumulation became detrimental under conditions of potassium deficiency (F. J. Richards 1956).

Apart from ion effects there were, in the present experiments, indications of additional effects by the high osmotic pressure of the substrates, for example the reduced stem elongation (Plate 1). Kelley (1951) states that it is impossible to clearly separate between the individual effects of the osmotic and ion content factors. This difficulty would be reduced if osmotic stress could be imposed without the complication of solute absorption. An attempt to use mannitol for this purpose was, however, unsuccessful (Groenewegen and Mills 1960).

Salinity and water stresses have been considered identical by several workers. Richards and Wadleigh (1952) defined total soil moisture stress as the summation of soil moisture tension and the osmotic pressure of the soil solution. Bernstein and Pearson (1954) used sodium chloride solutions to simulate drought stresses in soils. The validity of such procedures is rendered extremely doubtful by the evidence presented in this paper. This conclusion is supported by the finding of Gates (personal communication) that primordial initiation in lupins was inhibited by moderate water stresses, but not by salinity treatments.

The data indicate that further study on varietal responses to saline substrates would be advantageous. It would, for instance, be of interest to establish whether varietal differences in other species are also related to differences in regulation of ion uptake. Study of varieties of the same species, but of different salt tolerance, might also assist in the elucidation of the causal factors responsible for the adverse effects of ion accumulation within the plant.

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PLANT RESPONSE TO SALINE SUBSTRATES. I

Effect of various concentrations of sodium chloride on growth of two varieties of *Hordeum vulgare*: var. *pallidum* (C.P.I. 11083) (Fig. 1); cv. Chevron (Fig. 2). Subscript letters and numerals represent respectively control and sodium chloride concentrations of 125 and 250 m-equiv/l.