

PLANT RESPONSE TO SALINE SUBSTRATES

VII. GROWTH AND ION UPTAKE THROUGHOUT PLANT DEVELOPMENT IN TWO VARIETIES OF *HORDEUM VULGARE*

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Summary

In the main experiment, sodium chloride treatment was imposed on two varieties of *H. vulgare* during early tillering and continued until grain formation.

Relative growth rates did not support the notion that salt tolerance increases during plant development. However, grain formation was not affected by treatment with sodium chloride.

Varietal differences in salt tolerance, and in ionic composition, increased during plant development. In the inflorescences there were particularly large varietal differences in ion content, i.e. higher chloride and sodium, and lower potassium, concentrations in the sensitive than in the resistant variety.

The other two experiments were during early tillering. In the resistant variety, high chloride and sodium, and/or low potassium, were the cause rather than the result of chlorosis of the oldest leaf. Chlorosis commenced when the chloride concentration of the plant water reached 500 m-equiv/l, demonstrating that individual leaf cells are very tolerant to high electrolyte concentrations.

Varietal differences in rate of chloride uptake, over 2-hr periods were related to the different chloride concentrations in all organs throughout plant development; both passive and active chloride uptake were higher in the sensitive than in the resistant variety.

A comparison between halophytes and non-halophytes suggests that ion accumulation, rather than ion exclusion, is the superior adaptive mechanism for growth on a saline habitat.

Certain species show a pronounced sensitivity to chloride accumulation in their dry matter. However, this seems related to low leaf moisture contents, i.e. sensitivity to chloride, expressed as m-equivalents per litre of plant water, is rather similar in most non-halophytes.

I. INTRODUCTION

An increase in salt tolerance during plant development has been claimed for certain species (Bernstein and Hayward 1958; Kovalskaia 1958), and is sometimes attributed to a gradual adaptation of the protoplasm (Kovalskaia 1958). Some species, which increase in salt tolerance during continuous treatment with sodium chloride, might become very sensitive to a sudden application of sodium chloride at a late stage of development (Bernstein and Hayward 1958).

The impression that salt tolerance increases during plant development is based partly on satisfactory seed production, even when the same sodium chloride treatment strongly reduces vegetative development during earlier growth. Examples are barley and cotton (Bernstein and Hayward 1958).

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The present paper reports the response of two varieties of *Hordeum vulgare*, which differ in their salt tolerance, to continuous sodium chloride treatment from early tillering to grain formation. The data support a previous conclusion (Greenway 1962a) that the varietal difference in salt tolerance is due to higher chloride and sodium and/or lower potassium concentrations in the sensitive than in the resistant variety.

At high sodium chloride concentrations in the medium, chloride uptake by *H. vulgare* can be separated into active and passive components (Greenway 1965). These two types of chloride uptake were determined, immediately after sodium chloride application, for varieties differing in chloride concentrations of their tissues after prolonged treatment with sodium chloride.

Chlorosis of developed leaves was found to be due to excessive ion accumulation, and the ion concentration at which chlorosis developed was assessed.

II. METHODS

(a) *Response to Sodium Chloride Treatment throughout Plant Development (Experiment 1)*

The varieties of *H. vulgare* used (cf. Greenway 1962a) were: var. *pallidum* (C.P.I. 11083), and cv. Chevron.

Sand cultures, each carrying one plant, were regularly flushed with treatment solutions, so that concentrations were retained within 10% of the specified levels. The nutrient solution was similar to that used previously (Greenway 1962b), but Ca^{2+} and NO_3^- concentrations were at 8 and 14 m-equiv/l, respectively. Treatment with sodium chloride was begun when the third leaf had commenced development; a concentration of 125 m-equiv/l was attained 3 days later, and then maintained throughout the experiment.

Harvests, of eight replicates per treatment, were taken at 0, 17, 31, 43, 50, 64, and 93 days after sodium chloride application. At 64 days sodium chloride was removed from the medium in one series of plants ("sodium chloride removed") but treatment was continued in another series ("sodium chloride continued").

Plants were separated into leaves, sheaths, stems, and roots. Inflorescences were sampled as "fertilized", "emerged, not fertilized", and "not emerged". At 93 days, two fertilized inflorescences from each plant were separated into grain, palea and lemmae, awn, glumes, and rachis. For other procedures see Greenway (1962a).

(b) *Passive and Active Chloride Uptake by Two Varieties of H. vulgare (Experiment 2)*

Seedlings of cv. Bolivia and cv. Chevron were treated with solutions of different sodium chloride concentration, and chloride uptake was determined over the 2-hr period following sodium chloride application, or for 2 hr after pretreatment with sodium chloride for 6 days. The chloride uptake during the 2-hr test period was determined by measuring ^{36}Cl uptake.

In one experiment, nutrient treatments were imposed during the 2-hr test period.

Passive chloride uptake was measured by addition, during the 2-hr test period, of 2,4-dinitrophenol (DNP) at a concentration of 1 mg/l. Other procedures are described in Greenway (1965).

(c) *Chloride Accumulation in Developed Leaves (Experiment 3)*

In a previous experiment with cv. Bolivia (Greenway and Thomas 1965), sodium chloride solutions had been labelled with ^{36}Cl during two periods: in one series between days 0–5 and in another between days 6–10 after sodium chloride application. Sodium chloride treatment was continued after ^{36}Cl removal. The oldest leaf of some plants became chlorotic after 11 days of sodium chloride treatment, and ^{36}Cl , as well as total chloride, was determined for healthy and chlorotic leaves.

III. RESULTS

(a) *Relative Growth Rates throughout Plant Development (Experiment 1)*

In the controls, dry weight of the whole plant was similar for both varieties throughout plant development (Fig. 1). Varietal differences for individual organs were found only after day 64 when more grain and less vegetative shoots developed in C.P.I.11083 than in Chevron. Stem development commenced at day 50 and inflorescences developed rapidly between days 64 and 93.

During tillering, relative growth rates were much higher in controls than in sodium chloride-treated plants [harvest intervals 1–3, Fig. 2(a)]. However, declines in relative growth rates during further plant development were faster in controls than in sodium chloride-treated plants. The effects of sodium chloride treatment can be best indicated by expressing relative growth rates as a percentage of control values [Fig. 2(b)]. In Chevron, adverse effects of sodium chloride treatment increased with time during tillering, and then became less pronounced during stem and grain formation. Sodium chloride reduced growth less in C.P.I. 11083 than in Chevron, and in contrast with Chevron the relative growth rate of sodium chloride-treated C.P.I. 11083 exceeded that of the controls during grain formation.

Development of sodium chloride-treated plants was very different from controls, as shown by their dry weights (Fig. 1) and tiller numbers; for example, at day 93 Chevron had formed 168 and 65 tillers in control and sodium chloride treatments, respectively. Between 64 and 93 days, therefore, salt tolerance can be better assessed by comparing the "sodium chloride continued" with the "sodium chloride removed" treatments. Presence of sodium chloride in the medium reduced relative growth rate even during grain formation (Figs. 2(a) and 2(b), 64–93 days), particularly in Chevron.

In previous experiments removal of sodium chloride from the medium during early tillering did not restore relative growth rates to control levels (Greenway 1962a). The present increases over control level, subsequent to sodium chloride removal, are presumably due to the dense development of the controls and the long period over which relative growth rate was measured (29 days as compared with 5 days in Greenway 1962a).

Removal of sodium chloride from the medium resulted in accelerated vegetative growth in both varieties, but inflorescence development was only stimulated in Chevron (Fig. 1). Grain formation was the same in the "sodium chloride removed" and "sodium chloride continued" treatments (Fig. 1).

For each harvest interval the relative development of various organs is best indicated by the dry weight distribution ratios (i.e. the ratio of the increase in dry

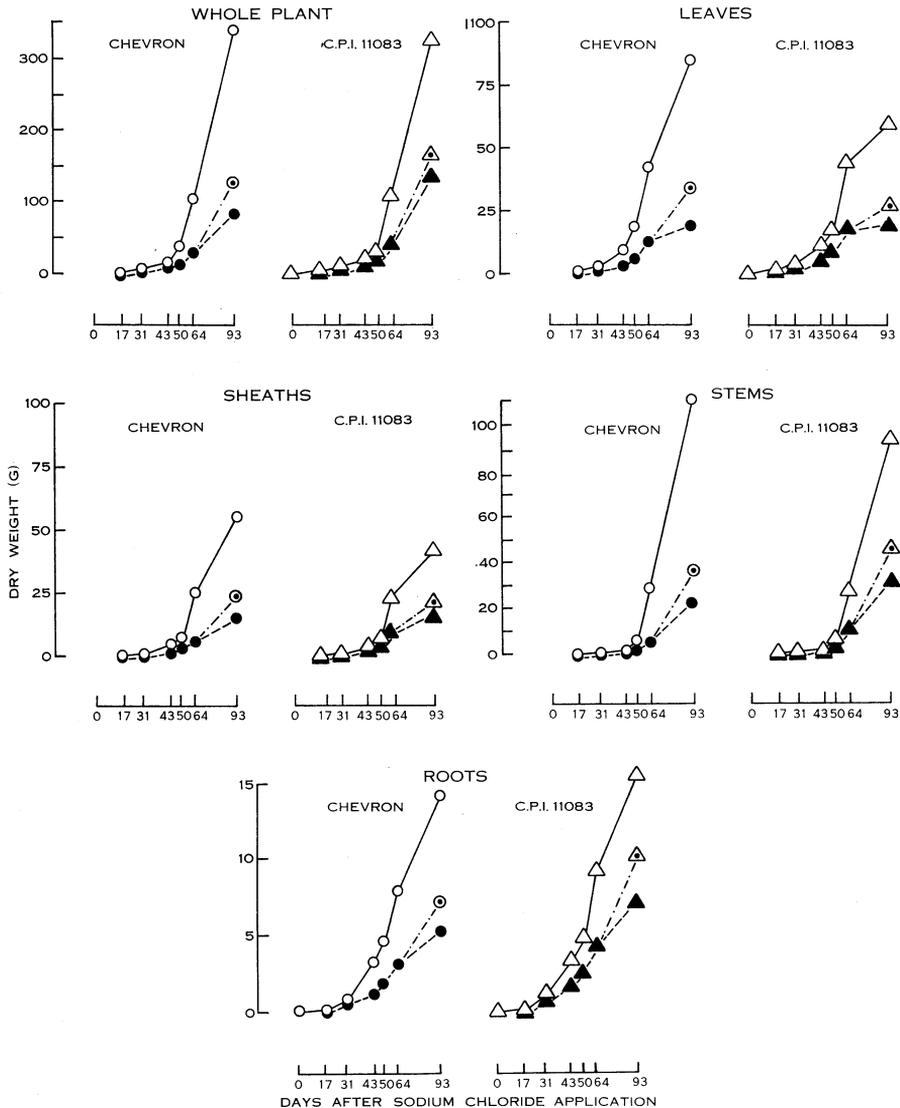


Fig. 1.—Dry weight of whole plant and its individual parts in two varieties (Chevron, C.P.I. 11083) of *H. vulgare* (experiment 1). Dry weights of inflorescences at 93 days are given in the following tabulation. Differences from control values for each variety due to treatment with sodium

[For continuation see opposite page]

weight of the organ to the increase in dry weight of the whole plant—see Fig. 3). Until inflorescence formation commenced (day 64) the effects of sodium chloride on the distribution of dry weight were small, the most marked effect being an increased

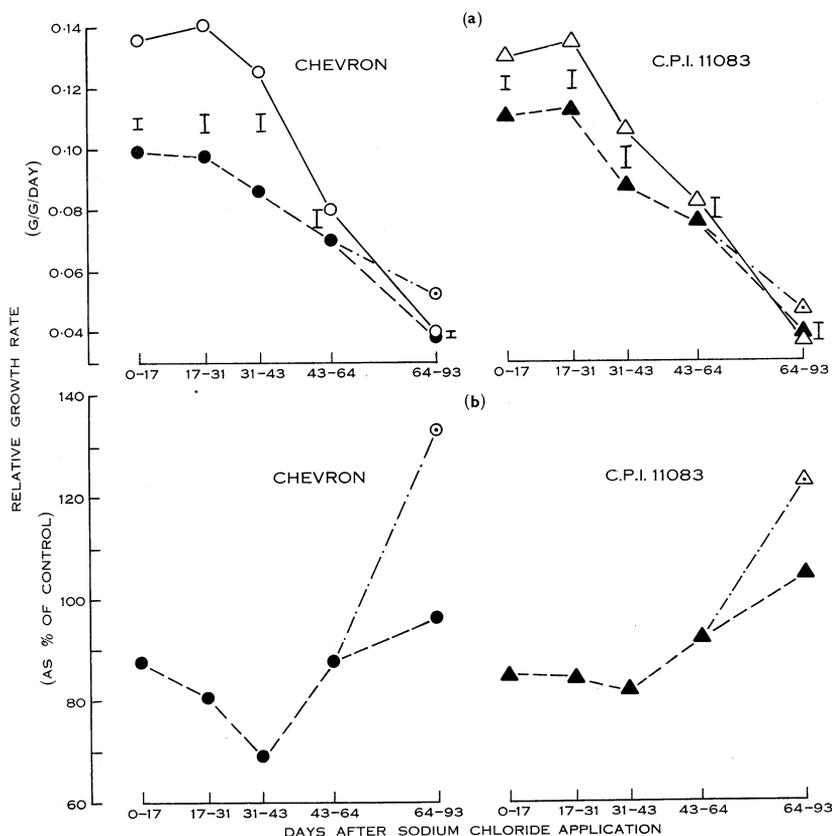


Fig. 2.—Relative growth rates of two varieties (Chevron, C.P.I. 11083) of *H. vulgare* as affected by sodium chloride treatment at 125 m-equiv/l (experiment 1). Least significant differences at $P = 0.05$ are indicated. Symbols as in legend to Figure 1.

Fig. 1 (Continued)

chloride are significant at $P = 0.05$ for the grain and each type of inflorescence. In all controls, sodium chloride concentration was 1 m-equiv/l.

Variety	Treatment	Dry Weight (g) of Inflorescences per Plant			
		Grain	Fertilized Inflorescences	Non-fertilized Inflorescences	Non-emerged Inflorescences
Chevron	Control (○)	30.2	20.8	10.8	2.3
	Sodium chloride, 125 m-equiv/l (●)	10.3	6.1	3.6	0.6
	Sodium chloride removed (○)	10.8	8.6	5.0	1.3
C.P.I. 11083	Control (△)	77.4	26.5	8.7	0.7
	Sodium chloride, 125 m-equiv/l (▲)	39.0	13.4	7.8	1.1
	Sodium chloride removed (△)	41.5	13.5	6.5	0.9

leaf and root growth and a decreased sheath and stem growth in Chevron plants. During grain formation, sodium chloride treatment increased inflorescence and grain development relative to growth of other organs, such as leaves and stems (Fig. 3, both varieties).

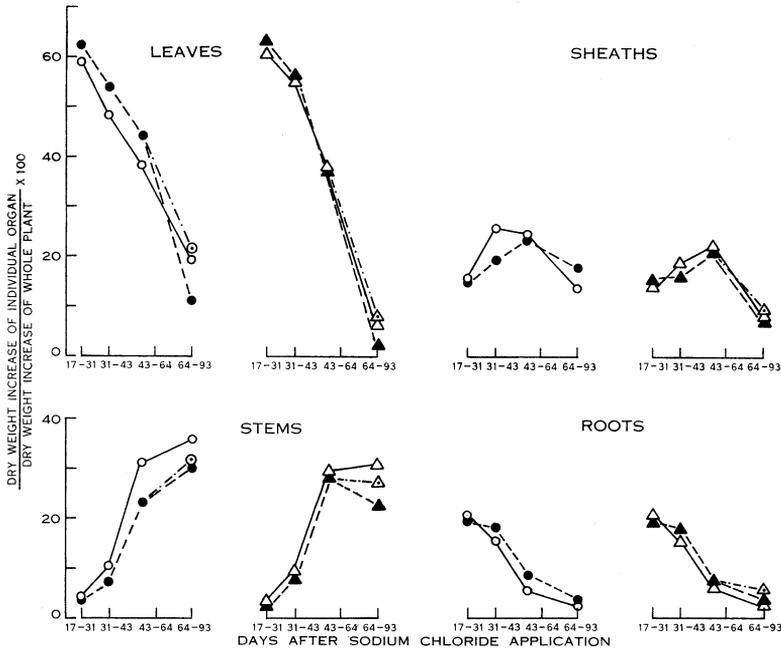


Fig. 3.—Distribution within the plant of dry weight increments over each harvest interval of two varieties (Chevron, C.P.I. 11083) of *H. vulgare* as affected by sodium chloride (experiment 1). During the last interval (64–93 days) dry weight increments for inflorescences and grain were as follows:

Variety	Treatment	Dry Weight Increment (g)	
		Inflorescences	Grain
Chevron	Control (○)	13.5	12.9
	Sodium chloride (●)	16.0	17.5
	Sodium chloride removed (◊)	14.7	10.8
C.P.I. 11083	Control (△)	14.5	34.9
	Sodium chloride (▲)	21.6	40.8
	Sodium chloride removed (◻)	15.6	33.8

(b) *Ion Uptake throughout Plant Development (Experiment 1)*

In the sodium chloride treatments chloride and sodium concentrations were higher in Chevron than in C.P.I. 11083 (Fig. 4). This varietal difference became more pronounced during plant development, until at the end of the experiment sodium concentrations of the shoot organs were twice as high in Chevron as in C.P.I. 11083 (Fig. 4). In the leaves, varietal differences were also pronounced, when ion concentrations were expressed on a plant water basis (Fig. 5).

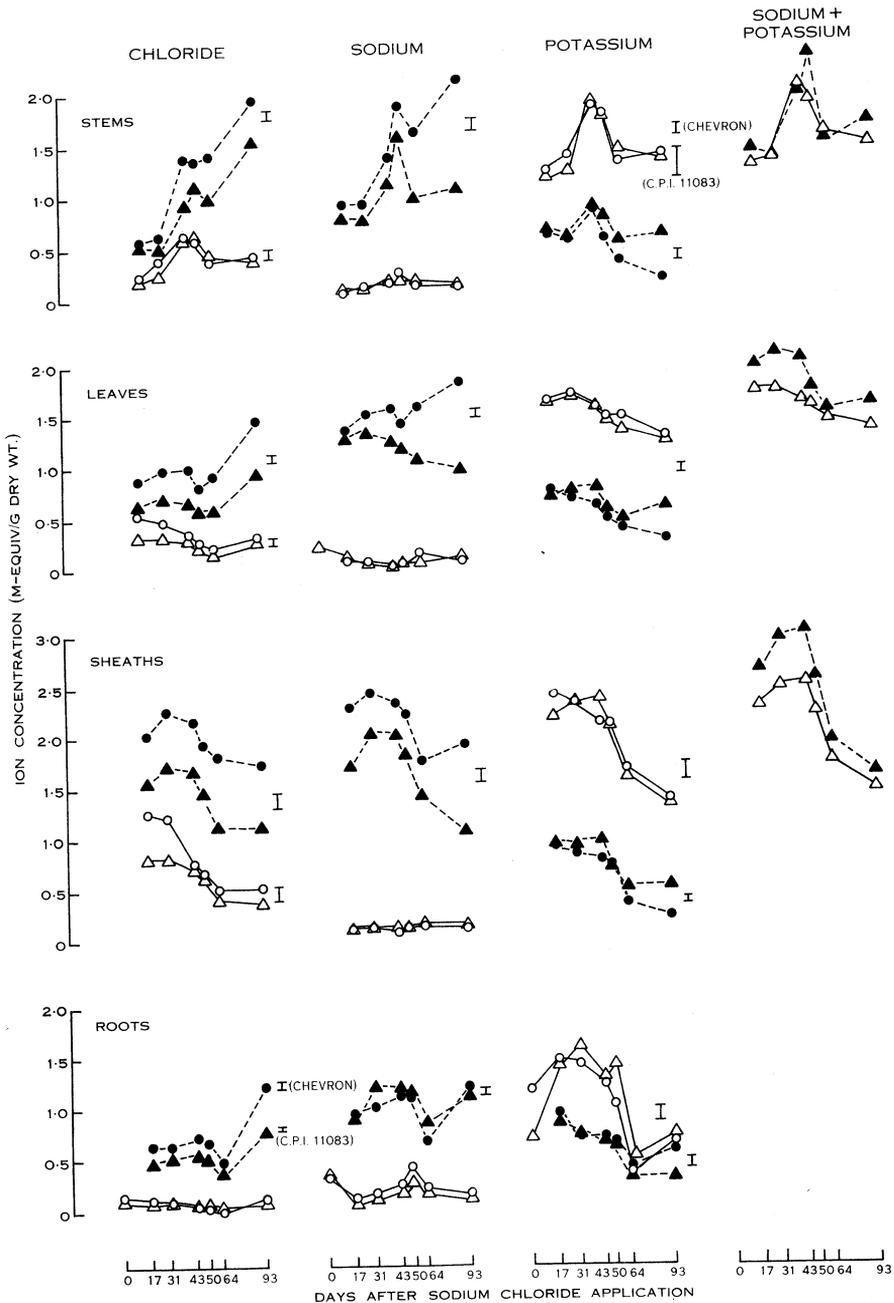


Fig. 4.—Chloride, sodium, and potassium concentrations in two varieties (Chevron, C.P.I. 11083) of *H. vulgare* (experiment 1). Concentrations of these ions (m-equiv/g) in non-emerged inflorescences at 93 days were as follows:

Variety	Treatment	Chloride	Sodium	Potassium
Chevron	Control (○)	0.10	0.03	0.58
	Sodium chloride, 125 m-equiv/l (●)	0.15	0.20	0.55
C.P.I. 11083	Control (△)	0.07	0.04	0.61
	Sodium chloride, 125 m-equiv/l (▲)	0.10	0.05	0.40

Least significant differences ($P = 0.05$): Chloride 0.05, Sodium 0.04, Potassium 0.06

In the inflorescences, sodium chloride treatment increased chloride and sodium concentrations of rachis and glumes, awn, and palea; and the sodium concentrations in particular were much higher in Chevron than in C.P.I. 11083 (Fig. 6). Potassium concentrations were not affected in C.P.I. 11083 but reduced in Chevron.

There were only small effects of sodium chloride on the ion composition of the grain, a much lower sodium concentration in C.P.I. 11083 than in Chevron (Fig. 6) being the only marked varietal difference. Thus chloride retranslocation was probably

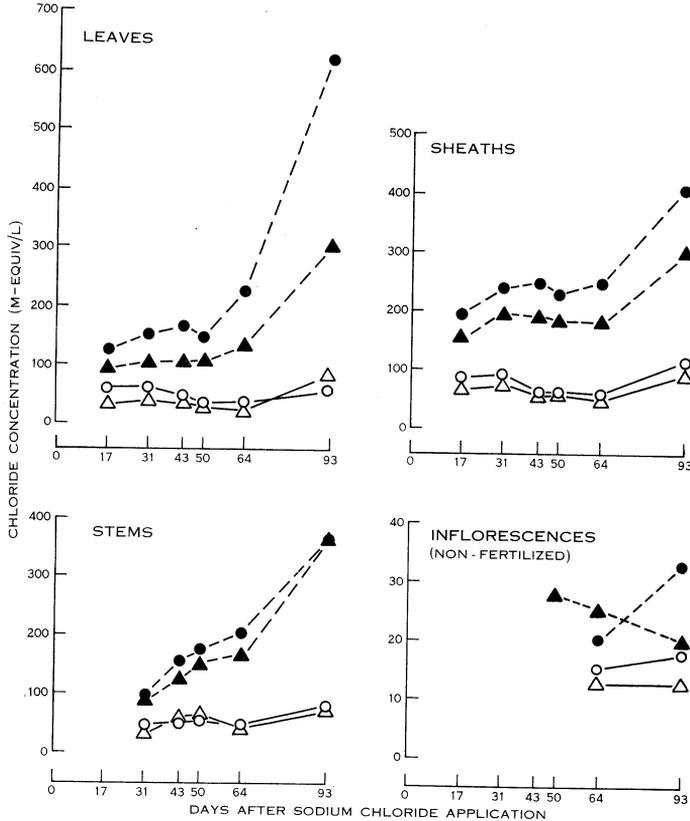


Fig. 5.—Chloride concentrations in plant water of two varieties (Chevron, C.P.I. 11083) of *H. vulgare* (experiment 1):

Variety	Treatment
Chevron	Control (○)
Chevron	Sodium chloride, 125 m-equiv/l (●)
C.P.I. 11083	Control (△)
C.P.I. 11083	Sodium chloride, 125 m-equiv/l (▲)

similar in the two varieties. The total amount of retranslocated sodium was higher in Chevron, but this variety also contained much more sodium in the vegetative organs.

In the vegetative organs of the shoot, sodium chloride treatment decreased potassium and increased sodium concentrations, but for the resistant variety potassium plus sodium concentration was only slightly increased by sodium chloride

treatment. During plant development potassium concentrations in the control followed very similar trends to the sodium, potassium, and the sodium plus potassium concentrations of the sodium chloride-treated plants (shoot organs of C.P.I. 11083, Fig. 4).

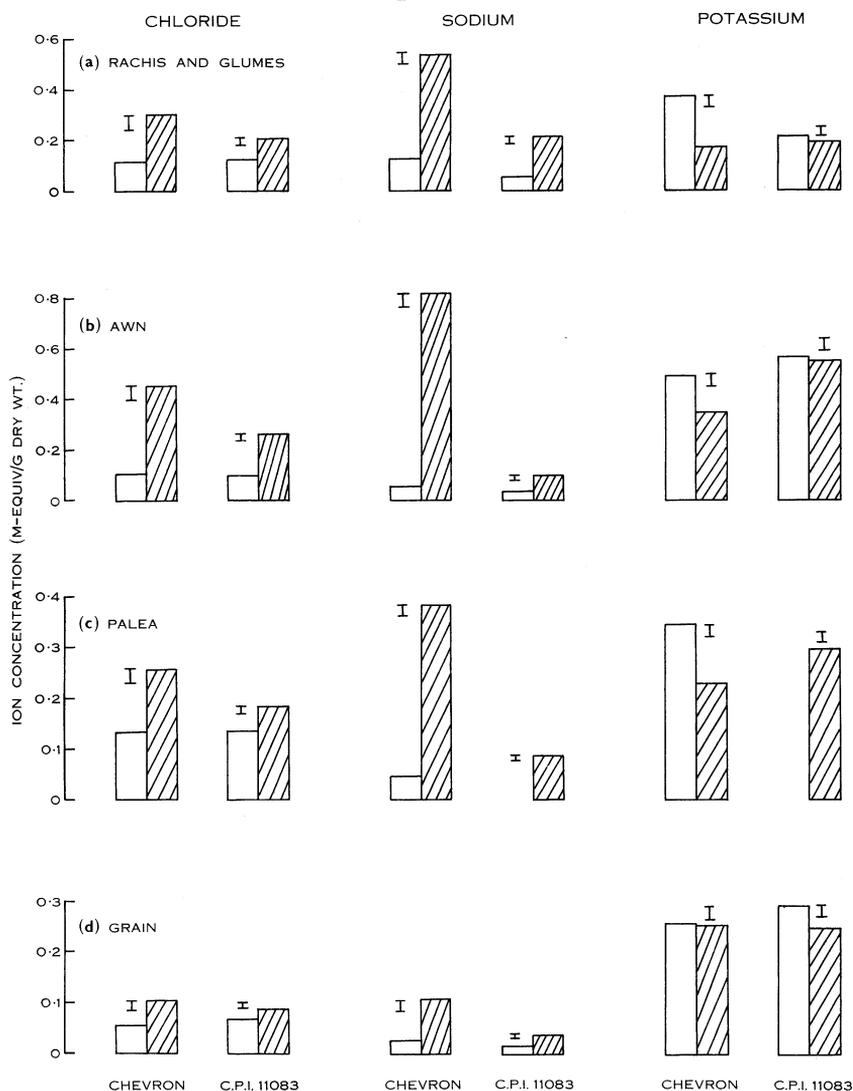


Fig. 6.—Chloride, sodium, and potassium concentrations (at day 93) in individual parts of the inflorescences of two varieties (Chevron, C.P.I. 11083) of *H. vulgare* (experiment 1). As the glumes and rachis had very similar ion concentrations, only the concentrations of the pooled samples are shown. The open rectangles are for treatments with sodium chloride at 1 m-equiv/l, the cross-hatched rectangles for sodium chloride at 125 m-equiv/l.

(c) *Active and Passive Chloride Uptake in Two Varieties of H. vulgare*

In these experiments Bolivia was used as a salt-tolerant variety (cf. Greenway 1962a), because of high interplant variability in C.P.I. 11083. Chloride uptake over

short periods was measured in media of low and high sodium chloride concentration. In an experiment at 5 m-equiv/l, shoots and roots absorbed more chloride in Chevron than in Bolivia, and this was due to the active component of chloride uptake [Fig. 7(a)].

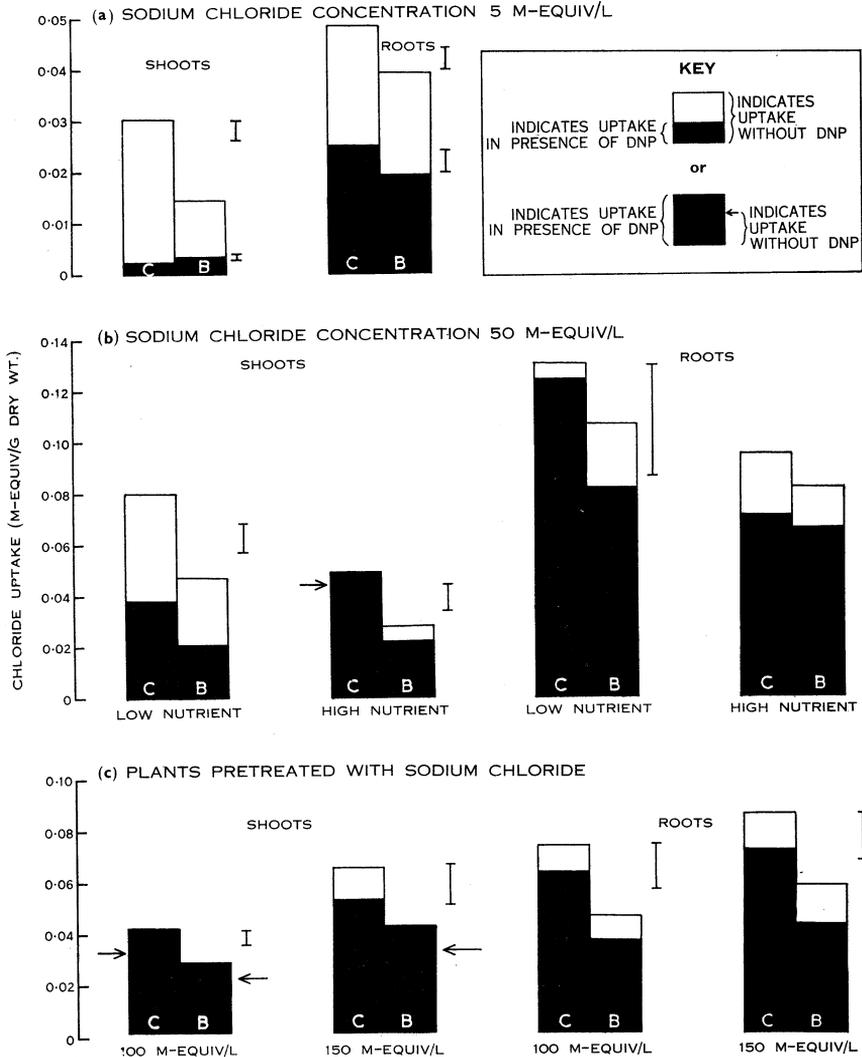


Fig. 7.—Chloride uptake in presence or absence of dinitrophenol (DNP) over a 2-hr interval by Chevron (C) and Bolivia (B) seedlings (first to second leaf stage) of *H. vulgare*: (a) at low sodium chloride concentration (5 m-equiv/l); (b) at sodium chloride concentrations of 50 m-equiv/l at low nutrient (one-fortieth of full strength Hoagland solution) and high nutrient (one-half of full strength Hoagland) levels; (c) seedlings pretreated for 5 days with sodium chloride (m-equiv/l) as follows:

Treatment	Day 1	Day 2	Day 3	Day 4	Day 5
100 m-equiv/l series	50	100	100	100	100
150 m-equiv/l series	50	100	150	150	150

Test performed between 8 and 10 a.m. on day 6.

Both varieties were also tested at low and high nutrient levels with sodium chloride at 50 m-equiv/l in the medium [Fig. 7(b)]. Chloride absorption by both roots and shoots was much higher in the low than in the high nutrient, and in all cases Chevron absorbed more chloride than Bolivia. The increased chloride uptake in the shoots at low nutrient was mainly DNP-sensitive and the varieties differed in both active* and passive components of chloride uptake. At high nutrient level, the entire chloride uptake of the shoot was DNP-insensitive, and again therefore, there was a varietal difference in passive chloride uptake.

Both varieties were also tested after pretreatment with sodium chloride at concentrations of 100 and 150 m-equiv/l [Fig. 7(c)]. Under these conditions the entire chloride uptake from the medium to the shoot was DNP-insensitive, while this component contributed about 70% to the total root uptake. Chevron absorbed much more chloride in its roots and shoots than Bolivia and this varietal difference was mostly due to the passive (DNP-insensitive) component.

In most of the other short-term experiments (Greenway, unpublished data) Chevron absorbed more chloride than Bolivia. However, in two experiments with sodium chloride at 50 m-equiv/l, no varietal difference in chloride uptake was found.

(d) *Chloride Uptake as Related to Leaf Injury (Experiment 3)*

Chloride uptake by the oldest leaf, during the early tillering stage, is shown in Table 1. Chlorotic leaves contained much higher chloride concentrations than healthy leaves; irrespective of harvest all chlorotic leaves contained between 3.0 and 3.5 m-equiv. chloride per gram dry weight. In previous experiments both the oldest and second oldest leaf showed chlorosis and collapse when chloride concentrations reached 3.0 m-equiv. per gram dry weight (Greenway 1962b). Chlorotic leaves also contained much more chloride, supplied to the plant as a whole, prior to the development of chlorosis. The higher Cl_{0-5} and Cl_{6-10} concentrations† in chlorotic than in healthy leaves could be due to:

- (1) A reduced retranslocation once chlorosis developed. However, mean retranslocation rates for the oldest leaf were 18 μ -equiv. Cl_{0-5} /g/day and 21 μ -equiv. Cl_{6-10} /g/day. Thus, retranslocation rates were too small to account for differences in chloride concentrations between healthy and chlorotic leaves at day 13, because these leaves became chlorotic only during the two days preceding harvest.
- (2) A reduced retranslocation even before chlorosis developed. Again, most differences between healthy and chlorotic leaves, were too large to be due solely to retranslocation differences.

The data therefore suggest that high chloride accumulation preceded the development of chlorosis.

* This varietal difference is not significant at $P = 0.05$ because active uptake was determined by difference, and hence would have an increased variance. However, varietal differences in active uptake presented in Figure 7(a) were statistically significant.

† Cl_{0-5} , chloride supplied between days 0 and 5; Cl_{6-10} , chloride supplied between days 6 and 10.

IV. DISCUSSION

(a) *Ion Uptake*

Previous papers have discussed chloride, sodium, and potassium uptake (Greenway 1962a, Greenway *et al.* 1965), and only new aspects will be discussed here.

(i) *Potassium and Sodium Uptake during Development*.—Pitman (1965) grew *H. vulgare* (cv. Bolivia) seedlings in media of low ionic concentrations, and concluded that potassium and sodium followed the same pathway during transference to the shoot. This conclusion is supported, for the salt-resistant variety at media of high sodium chloride concentrations, by the pattern of ion uptake for all shoot organs;

TABLE 1

CHLORIDE ABSORBED BY THE WHOLE PLANT DURING DIFFERENT PERIODS AFTER APPLICATION OF SODIUM CHLORIDE AND BY CHLOROTIC AND HEALTHY LEAVES OF *H. VULGARE*, CV. BOLIVIA (EXPERIMENT 3)

Concentration of sodium chloride in the medium 100 m-equiv/l. Chlorosis commenced after 11 days of sodium chloride treatment. Only the oldest leaf became chlorotic, and its chloride concentrations are reported here

Days after Application of Sodium Chloride	Total Chloride at Harvest (m-equiv/g dry wt.)		Chloride Absorbed by the Whole Plant between Days 0 and 5 Found in Oldest Leaf at Harvest (m-equiv/g dry wt.)		Chloride Absorbed by the Whole Plant between Days 6 and 10 Found in Oldest Leaf at Harvest (m-equiv/g dry wt.)	
	Healthy Leaf	Chlorotic Leaf	Healthy Leaf	Chlorotic Leaf	Healthy Leaf	Chlorotic Leaf
13	1.64	3.25	0.47	0.73	0.67	1.30
15	1.84	3.40	0.40 } 0.37 }*	0.54 } 0.52 }*	—	—
18	2.23	3.25	0.34 } 0.39 }*	0.43 } 0.78 }*	0.52 } 0.39 }*	0.43 } 0.67 }*

* Duplicate determinations.

i.e. potassium, sodium, and potassium plus sodium concentrations of sodium chloride-treated plants followed trends similar to potassium concentrations of controls, and the sum of potassium and sodium was not greatly increased by sodium chloride treatment (Fig. 4).

Throughout plant development, ratios of potassium uptake to sodium uptake by the whole shoot were higher in C.P.I. 11083 than in Chevron. In Chevron the K/Na ratio declined during grain formation, indicating a reduced ion selectivity of this variety with the onset of senescence (Table 2).

(ii) *Chloride Uptake by Different Varieties*.—Chloride concentrations in all organs of Chevron were higher than in C.P.I. 11083 throughout plant development (Fig. 4). (For similar differences between Chevron and Bolivia, see Greenway 1962a.)

Such differences in chloride concentration after prolonged sodium chloride treatment could be due to long-term effects, such as differences in metabolism resulting from sodium chloride treatment, retention of chloride at salt saturation of the tissues, and relative growth rates. However, the main cause for the different chloride concentrations was a large varietal difference in rate of chloride uptake, as shown in the short-term experiments immediately following application of sodium chloride (Fig. 7).

TABLE 2
RATIOS OF NET POTASSIUM UPTAKE TO NET SODIUM UPTAKE BY THE
WHOLE PLANT OVER DIFFERENT PERIODS DURING PLANT DEVELOPMENT
(EXPERIMENT 1)

Sodium chloride concentration 125 m-equiv/l		
Days after Application of Sodium Chloride	Plant Variety	
	C.P.I. 11083	Chevron
17-31	0.52	0.47
31-43	0.59	0.39
43-50	0.33	0.30
50-64	0.45	0.16
64-93	1.02	0.14

At high sodium chloride concentrations varietal differences were mainly because of the different rates of passive chloride uptake [Figs. 7(b) and 7(c)] which could be due to:

- (1) An inherent varietal difference in the rate of passive chloride uptake.
- (2) Sodium chloride treatment, leading to an immediate but permanent change in rate of passive chloride uptake, resulting in the varietal difference.

The rate of chloride uptake in the varieties used might be different because of differences in volume of pathway, in rate of flow along the pathway, or both. This question can be resolved only by measuring passive uptake of substances other than Cl^- and Na^+ , preferably non-ionic compounds supplied at low external concentrations.

(b) Growth during Plant Development

Sodium chloride reduced relative growth rates less during inflorescence formation than during tillering (Fig. 2), suggesting that salt tolerance increased during plant development. However, during later growth stages development of controls was far ahead of the sodium chloride-treated plants, and during this period salt tolerance can be better assessed by comparing "sodium chloride continued" and "sodium chloride removed" treatments. This comparison showed that growth reductions, due to sodium chloride, were at least as pronounced during grain formation as during tillering (Fig. 2). Yet the grain, by providing an alternative sink for carbohydrates, could have mitigated adverse effects of sodium chloride on relative growth rates. There was, therefore, no evidence for increased salt tolerance during plant development.

Sodium chloride treatment reduced total grain weight, but grain weight ratios increased (0.28 for C.P.I. 11083 in the "sodium chloride continued" treatment and 0.24 in both "sodium chloride removed" treatment and controls). A satisfactory grain development was also shown by the equal grain yields of plants in the "sodium chloride continued" and "removed" treatments (Fig. 1). In a field experiment, Ayers, Brown, and Wadleigh (1952) also found that sodium chloride, applied at the four-leaf stage or later, did not reduce grain yield of several salt-tolerant varieties of *H. vulgare*. Thus sodium chloride treatment of *H. vulgare* does not reduce photosynthesis and carbohydrate retranslocation below optimum levels, and protein synthesis also remained at a high level (Fig. 8). The only measured adverse effect of sodium chloride treatment was on the formation of new organs.

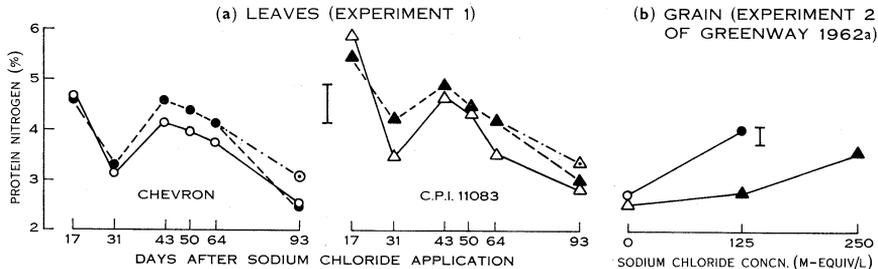


Fig. 8.—(a) Leaf protein nitrogen during plant development as affected by treatment with sodium chloride at 125 m-equiv/l of two varieties (Chevron, C.P.I. 11083) of *H. vulgare* (experiment 1). (b) Protein nitrogen concentrations in grain of both varieties at full maturity (experiment 2 of Greenway 1962a). ○, △ Controls. ●, ▲ Treated with sodium chloride. ○, △ Sodium chloride removed.

(c) Causes of Adverse Effects of Sodium Chloride on Growth

(i) *Varietal Differences in Salt Tolerance.*—Varietal differences in salt tolerance, as measured by reductions in relative growth rates due to sodium chloride treatment, increased during plant development, and became particularly pronounced during inflorescence formation (Fig. 2).^{*} Inflorescence formation itself was also more strongly reduced in Chevron than in C.P.I. 11083 (Fig. 1). A previous experiment indicates that this trend continued, i.e. at full maturity Chevron had a much lower grain weight ratio than C.P.I. 11083—0.05 and 0.42, respectively (Greenway 1962a).

Varietal differences in sodium and chloride concentrations also increased with time, and had become very pronounced at the last two harvests (Figs. 4 and 5). Moreover, inflorescences contained more chloride, and particularly more sodium, in the sensitive than in the resistant variety (Fig. 6). The presented data, therefore, strongly support a previous suggestion (Greenway 1962a) that differences in salt tolerance of *H. vulgare* varieties are related to higher chloride and sodium, and/or lower potassium, concentrations in the sensitive than in the resistant variety.

The increased osmotic pressures of the medium might also have contributed to growth reductions in both varieties. Water stress effects are particularly likely during formation of new organs, because these contained very low chloride concentrations [inflorescences (Fig. 5); leaves (see Greenway and Rogers 1963)] and therefore could be subjected to similar conditions as imposed during water stress.

* "Sodium chloride continued" compared with "sodium chloride removed" treatments.

(ii) *Leaf Injury and Ion Accumulation*.—For a salt-tolerant variety of *H. vulgare* the data strongly suggest that chloride accumulation preceded the development of chlorosis (Table 1); if so, then the changes in ionic composition were the cause rather than the result of the injury. Concurrent with the chloride accumulation there would have been increases in sodium and decreases in potassium concentrations (Fig. 4). The chlorosis was, therefore, not necessarily due to excessive chloride, but could also have been due to high sodium, low potassium, or a combination of these factors.

The level of sodium chloride at which chlorosis occurs, if expressed on a plant water basis, would be about 400–500 m-equiv/l. This demonstrates a remarkably high resistance of leaf cells to the accumulation of chloride and sodium. Of course, general metabolic activity of the cells might have been adversely affected before chlorosis developed, i.e. at concentrations lower than 400 m-equiv/l.

V. GENERAL DISCUSSION

In many non-halophytes, a high ion accumulation aggravates the adverse effects of high salt concentrations in the medium. This is particularly shown by the higher concentrations of chloride or sodium (or both) which are found in sensitive than in resistant varieties of many species. Examples were given earlier (Greenway 1962*a*). However, halophytes* often contain high chloride and sodium concentrations (Adriani 1958). Thus ion accumulation appears superior to ion exclusion as an adaptive mechanism (i.e. in terms of both growth and survival) on a saline habitat, provided that the species are tolerant to high internal chloride and sodium concentrations. Rapid ion accumulation would facilitate rapid osmotic pressure adjustments (Hayward and Wadleigh 1949). Osmotic pressure adjustments of whole organs are usually adequate even in non-halophytes (Bernstein 1961, 1963), but a high rate of ion absorption could still be vital to rapid development of new cells (Greenway and Thomas 1965). Thus, it should be established whether the different rates of ion accumulation by non-halophytes and halophytes also occur for their growing cells.

Salt tolerance would depend on resistance to high internal ion concentrations, as well as on rapid osmotic pressure adjustments. Pronounced sensitivity to high internal chloride concentrations has been claimed for stone fruits, vines, and citrus (Bernstein and Hayward 1958). This conclusion was based on chloride concentrations of dry matter, but concentrations expressed as milliequivalents per litre of plant water, though not ideal, would be more relevant. Table 3 shows that leaf injury occurred at much lower chloride concentrations (when expressed as m-equiv/g dry wt.) in salt-sensitive than in salt-tolerant species. However, these differences in chloride concentrations between species became much smaller when expressed as milliequivalents per litre of plant water; and then might be due to the usage of indefinite characteristics like "leaf damage" and leaf water content. Thus species of non-halophytes might not differ greatly in tolerance to high internal chloride concentrations.

* The term "halophyte" is used here in the ecological sense of high tolerance to a saline medium.

Some halophytes are very tolerant to high chloride accumulation (*Atriplex vesicaria* in Table 3; Adriani 1958). This might be due to a high resistance of the protoplasm, or alternatively to a pronounced chloride exclusion from the protoplasm; for example by accumulation in the vacuoles. A further understanding of salt tolerance, therefore, requires a study of ion distribution between compartments of individual cells, in both halophytes and non-halophytes.

TABLE 3
CHLORIDE CONCENTRATIONS IN LEAVES SHOWING INJURY OF SALT-SENSITIVE AND SALT-RESISTANT SPECIES

Species	Degree of Salt Tolerance	Leaf Chloride Concentration:	
		As Milliequivalents per Gram Dry Weight	As Milliequivalents per Litre of Plant Water
Apricot and peach*	Low	0.4–0.6 (Brown, Wadleigh, and Hayward 1953)	200–300 (Moiseev 1963)
Citrus*	Low	0.4–0.8 (Cooper, Gorton, and Olson 1952)	210–410 (Lenz, unpublished data)
Vines*	Moderate	0.9–1.0 (Ravikovitch and Bidner 1937)	360–400 (Doelle, unpublished data)
Barley	High	3.0 [Section III (d), this paper]	400–500 [Section III (d), this paper]
<i>Atriplex hastata</i> †	Very high	1.4 (Black 1956)	200 (Black 1956)
<i>Atriplex vesicaria</i> †	Very high	6 (Black 1956)	900 (Black 1956)

* No leaf water contents reported for these species in first-mentioned reference. Leaf water contents used were for leaves of similar age, as given in second reference.

† No leaf injury.

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