## PLANT RESPONSE TO SALINE SUBSTRATES

## VI. CHLORIDE, SODIUM, AND POTASSIUM UPTAKE AND DISTRIBUTION WITHIN THE PLANT DURING ONTOGENESIS OF HORDEUM VULGARE

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#### Summary

This paper describes the effects of sodium chloride on H. vulgare during the whole of plant development. Rapid increases in sodium and chloride concentrations occurred during the early tillering, with little further change until grain formation. The net chloride and sodium intake did not change markedly during the major part of plant development, so that increases in sodium and chloride concentrations were prevented by the regulatory effect of rapid growth. During senescence the relative growth rate decreased and there were marked increases in chloride and sodium concentrations.

Throughout the whole of plant development distributions of chloride, sodium, and potassium between plant organs were similar to those found previously during the early tillering stage, i.e. chloride and sodium concentrations increased and potassium concentrations decreased with age.

Concentrations of sodium, potassium, and chloride in the grain were much lower than those in the rest of the plant. Treatment with sodium chloride changed the ion balance of the grain to a certain extent, but compared with the vegetative organs these changes in ion composition were very small.

Potassium retranslocation was not impaired by high concentrations of sodium and chloride in vegetative organs.

In a separate experiment, during the early tillering stage, sodium retranslocation was very slow. and there was no sodium loss from the plant as a whole.

Sodium, chloride, and potassium contents of the grain differed in the same order as retranslocation rates of these ions measured during early tillering.

The data showed that ion regulation in the shoot was achieved both by growth of young organs and by selectivity during retranslocation. It is suggested that this selectivity occurs during uptake into, or transport by, the retranslocation system.

#### I. INTRODUCTION

Previous experiments showed that, during the early tillering stage of *Hordeum* vulgare, tolerance to a saline medium was partly determined by selective ion uptake; for example an ability to exclude sodium and chloride, but take up potassium (Greenway 1962a, 1963; Greenway and Rogers 1963). A further study during the full life cycle of the plant would add to an understanding of this ion regulation. Of particular relevance are the ion relationships of developing fruits as compared with those of vegetative organs, because minerals of seeds are largely supplied by retranslocation (Mason and Maskell 1931). In plants with a marked ion unbalance the

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#### H. GREENWAY ET AL.

degree of retranslocation of various ions would determine the ion balance of newly developing organs, and therefore contribute to the survival of a species on saline media.

During the early tillering stage of H. vulgare, chloride and sodium concentrations of the shoots rose rapidly at the start of treatment with sodium chloride, and this phase was followed by a more gradual, but apparently continuous, increase (Greenway 1962b). At a much more advanced stage of growth *Puccinellia distans* (Lunt, Youngner, and Oertli 1961) and Agropyron elongatum (Greenway and Rogers 1963) were low both in chloride and sodium. Since it is claimed that these species increase in salt tolerance during plant development (Bernstein and Hayward 1958) the drifts in ion concentrations needed a more detailed study. In the present experiments with *H. vulgare*, measurements were made on the chloride, sodium, and potassium uptake by individual parts including the individual organs of fertilized inflorescences. Attention was given to the effects of rapid growth on the resulting chloride and sodium concentrations within the plant.

### II. Methods

### (a) Experiments 1 and 2

Hordeum vulgare var. pallidum (C.P.I. 11083), a salt-tolerant variety, was grown in leached sand cultures. Methods were as previously described (Greenway 1962a) but the nutrient solutions contained 8 m-equiv/l of  $Ca(NO_3)_2$  and 1 m-equiv/l of NaCl.

One plant per container was retained for treatment with sodium chloride which reached a concentration of 125 m-equiv/l on the third day.

(i) *Experiment 1.*—Plants were sown on June 26, 1961, and sodium chloride treatment was begun when the first leaf had fully developed. Harvests were at 32, 50, 69, 83, and 128 days after application of sodium chloride.

At each harvest, six replicates of each treatment were transferred to a dark-room at 7 a.m. Three replicates were pooled, so that all measurements were on two replicates each consisting of three separately grown plants.

The three oldest tillers were dissected and the rest of the shoot constituted a separate sample. The three oldest tillers were separated into:

Plant Parts	Explanatory Remarks
Leaves 1-4; sheaths 1-4 Leaves 5-8; sheaths 5-8 Leaves 9-10; sheaths 9-10 Leaves $>10$ ; sheaths $>10$ Flag; sheath of flag	Leaf 1 is the oldest leaf, leaf 2 is the second oldest leaf, etc. Most control plants had either 11 or 12 leaves, most sodium chloride- treated plants only 10 or 11 leaves
Stem < 8	Stem below node 8
Stem>8	Stem between node 8 and node of flag
Stem of inflorescence	Stem above node of flag
Inflorescence	Excluding grain and palea
Hulls	Mostly palea
Grain	

(ii) Experiment 2.—This was an experiment with H. vulgare varieties of different salt tolerance (Greenway, unpublished data). For H. vulgare var. pallidum this paper reports only on the ion composition of leaves and inflorescences at the "milk" stage—93 days after application of sodium chloride.

Inflorescences were dissected into rachis, glumen, palea, awn, and grain. The shoot was separated into leaves, sheaths, and stems.

(iii) Experiment 3.—In this water-culture experiment with H. vulgare cv. Bolivia at the early tillering stage, sodium retranslocation was determined. The solutions were labelled with <sup>22</sup>Na during the first 5 days of sodium chloride treatment; non-labelled sodium chloride solutions of the same concentration (100 m-equiv/l) were used after this period. Harvests were taken 5 days after sodium chloride application, and then at 7, 10, and 15 days.

Plants were separated into leaves 1(oldest leaf) - 6, sheaths 1 (oldest sheath) and 2, younger sheaths [tillers 1 (oldest), 2, and 3], and roots.

<sup>22</sup>Na was determined in a Geiger-Müller tube adapted for use with liquids. Other procedures and methods were described in Greenway and Thomas (1965).

## III. Results

(a) Experiment 1: Dry Weights of the Whole Shoot and of Individual Plant Parts

Dry weights of the whole shoot and of individual parts of the three oldest tillers are shown in Figure 1. Growth of the whole shoot was strongly depressed by sodium chloride treatment. In the three oldest tillers, leaves, sheaths, and stems (1-8) were reduced in growth during the early harvests (32-69 days), but these parts of sodium chloride-treated plants reached control levels at the later harvests (83 and 128 days). At this stage there were growth reductions only in young leaves, sheaths, and stems. By contrast growth of inflorescences and grain yield of these three oldest tillers were not affected by sodium chloride treatment.

Leaves and sheaths 1–4 had ceased their rapid development at the first harvest (32 days). Rapid development of younger leaves took place between 32 and 69 days and of stems and younger sheaths between 32 and 83 days. Between 83 and 128 days the principal dry weight increments were in the inflorescences and grain.

## (b) Experiment 1: Chloride and Sodium Concentrations in Whole Shoot and Individual Plant Parts

Chloride concentrations are shown in Figure 2 and sodium concentrations in Figure 3. In the vegetative shoot both chloride and sodium concentrations increased rapidly between 0 and 32 days and then only very slowly between 32 and 83 days. In the three oldest tillers, on the other hand, all vegetative parts showed pronounced increases in both chloride and sodium concentrations.

At any one harvest chloride and sodium concentrations were much lower in younger than in older leaves and sheaths (Figs. 2 and 3). Moreover, during rapid growth phases of leaves and sheaths, chloride and sodium concentrations were lower in leaves and sheaths developed late than in those developed early. For example, leaves 5–8 commenced their rapid development between days 32 and 50 and leaves 9



and 10 between days 50 and 69, and during this phase of rapid development they contained 0.64 and 0.37 m-equiv of chloride per gram dry weight of tissue, respectively.\*

Fig. 1.—Dry weights of the whole shoot and of individual parts of the three oldest tillers (experiment 1). Control plants, 1 m-equiv/l sodium chloride; treated plants, 125 m-equiv/l sodium chloride.

Different organs of the same age have very different ion concentrations (Figs. 2 and 3). Inflorescences were very low in both sodium and chloride (Figs. 2 and 3,

\* Similar trends during ontogenesis were found in the potassium concentrations of control leaves and sheaths (Fig. 4).

69–128 days). Usually sheaths contained considerably more chloride and sodium than corresponding leaves, except at senescence (128 days) and except for leaves 1–4 between 69 and 128 days. Above node 8 ion concentrations were highest in the stems, but below node 8 the stems contained less chloride and sodium than leaves 1–4 and sheaths 1–8. Sodium concentrations were higher than those of chloride in older leaves and sheaths (1–8) and in younger leaves during the early stages of development (leaves>8; 50–83 days). In stems chloride and sodium concentrations were about equal, but chloride exceeded sodium in inflorescences and their stems.



Fig. 2.—Chloride concentrations in the whole shoot and in individual parts of the three oldest tillers (experiment 1). Least significant differences indicated are for P = 0.05. Control plants, 1 m-equiv/l sodium chloride; treated plants, 125 m-equiv/l sodium chloride.

# (c) Experiment 1: Chloride and Sodium Concentrations in the Controls

Sodium concentrations were very low in the controls. Trends were similar to those found in the sodium chloride treatments, though the concentration differences between leaves and sheaths of different age were less pronounced.

In contrast with the sodium chloride treatment, chloride concentrations in the controls were higher in younger than in older leaves and sheaths (>8 as compared

with <8). Chloride concentrations of older leaves and sheaths (<8) decreased between 32 and 69 days.

Treatment thus strongly affected the chloride and sodium distribution within the three oldest tillers, which is best shown by the ratio of ion concentration in inflorescences to ion concentration in young leaves (>8). At 83 days this ratio for chloride was 0.5 in the controls and 0.2 in the sodium chloride treatment, and corresponding values for sodium were 0.16 and 0.07.



Fig. 3.—Sodium concentrations in the whole shoot and in individual parts of the three oldest tillers (experiment 1). Least significant differences indicated are for P = 0.05. Control plants, 1 m-equiv/l sodium chloride; treated plants, 125 m-equiv/l sodium chloride.

# (d) Experiment 1: Potassium Concentrations in Whole Shoots and Individual Plant Parts

Potassium concentrations are shown in Figure 4(a) and total potassium content per plant part in Figure 4(b). Sodium chloride treatment strongly reduced potassium concentrations. Control and treated plants differed also in the distribution of potassium within the three oldest tillers [Fig. 4(a)]. For example, at 83 days, the potassium concentration in the controls was highest in the older organs (<8) and lowest in the inflorescences. In the sodium chloride-treated plants, on the other hand, potassium was much more evenly distributed, with lowest concentrations in the older sheaths (1-4) and higher levels in inflorescences, leaves, and stems.

Potassium concentrations of the older leaves did not change appreciably with time in sodium chloride-treated plants. Younger leaves (>8) had relatively high initial potassium concentrations, but these decreased strongly during the subsequent phase of rapid development (69–83 days), and during this period there was little net potassium intake [Fig. 4(b)]. Upon completion of development, however, potassium



Fig. 4.—(a) Potassium concentrations in the whole shoot and in individual parts of the three oldest tillers (experiment 1). Least significant differences indicated are for P = 0.05. (b) Total potassium contents in individual parts of the three oldest tillers (experiment 1). Control plants, 1 m-equiv/l sodium chloride; treated plants, 125 m-equiv/l sodium chloride.

concentrations of younger leaves (>8) rose to higher levels than in older leaves. In the older sheaths (1-8) both potassium concentrations and total content decreased strongly with time (Fig. 4). The decreases in potassium concentrations of sheaths and younger leaves occurred during the rapid development of stems and inflorescences (69–83 days; Fig. 1).

## (e) Experiment 2: Ion Contents of Inflorescences

Treatment with sodium chloride increased chloride and sodium concentrations of developing inflorescences and grain over control levels, but these concentration increases were much smaller than in vegetative organs. In both treatments all parts of the inflorescences, but in particular the grain, had much lower chloride and sodium concentrations than the vegetative organs of the same plants (Table 1). These differences were particularly pronounced in sodium chloride-treated plants, as shown by the ratio of the concentration in leaves to that in the grain. For chloride this ratio was 11 in the sodium chloride treatment and 4 in the control; corresponding values for sodium were 25 and 5.

Potassium concentrations of inflorescences and developing grain were not affected by sodium chloride treatment and this was in marked contrast with all other plant organs.

#### TABLE 1

ION CONCENTRATIONS IN INDIVIDUAL PARTS OF FERTILIZED INFLORESCENCES AND VEGETATIVE PARTS OF H. VULGARE: EXPERIMENT 2

Sodium chloride concentration in the medium was 1 m-equiv/l for control plants and 125 m-equiv/l for treated plants

Plant Part	Chloride Concn. (m-equiv/g dry wt.)		Sodium Conen. (m-equiv/g dry wt.)		Potassium Conen. (m-equiv/g dry wt.)	
	Control Plants	Treated Plants	Control Plants	Treated Plants	Control Plants	Treated Plants
Grain	0.056	0.09	0.019	0.039	0.29	0.25
Rachis	$0 \cdot 10$	$0 \cdot 20$	0.055	0.24	0.20 0.23	0.16
Glumen	0.11	$0\cdot 22$	0.042	0.13	0.17	0.26
Palea	$0 \cdot 14$	0.18		0.09		0.30
Awn	$0 \cdot 10$	0.27	0.039	0.10	0.57	0.56
Least significant difference					· · ·	0.00
(P = 0.05) for inflorescences	0.025	(0.018)*	0.018	$(0 \cdot 014)*$	0.053	
Leaves	$0 \cdot 2$	$1 \cdot 0$	$0 \cdot 1$	1.0	$1 \cdot 3$	0.5
Sheaths	$0 \cdot 3$	$1 \cdot 2$	$0 \cdot 1$	$1 \cdot 2$	$1 \cdot 4$	0.6
Stems	$0 \cdot 4$	$1 \cdot 4$	0.15	$1 \cdot 2$	1.4	0.6
Least significant difference						÷Ū
(P = 0.05) for vegetative						
parts	0.055	0.15	0.018	0.09	0.08	0.08

\* Least significant difference for grain.

# (f) Experiment 3: Sodium Retranslocation During the Early Tillering Stage

Dry weight and sodium concentration are shown in Table 2, and total sodium and  $Na_{0-5}$  (sodium absorbed between days 0 and 5) in Figure 5. Results were very similar to those obtained for chloride (Greenway and Thomas 1965) and only main results will be described.

The plant as a whole did not lose any appreciable amounts of  $Na_{0-5}$ , absorbed during the first 5 days, during the subsequent interval of 5–15 days.  $Na_{0-5}$  lost from the roots was mainly transported to the shoots. For example, between days 5 and 15 roots lost and shoots gained about 10  $\mu$ -equiv.  $Na_{0-5}$ .

532

### PLANT RESPONSE TO SALINE SUBSTRATES. VI

Developed leaves 1 and 2 showed pronounced increases in total sodium but very little export of Na<sub>0-5</sub>. In contrast, developed sheaths showed pronounced losses of Na<sub>0-5</sub> during the subsequent period (sheath 1 between days 5 and 15; sheath 2 between days 10 and 15). For the combined sample of leaf and sheath 1 the total sodium intake was  $4 \cdot 3 \mu$ -equiv. per day, while the assessed export was only  $0 \cdot 69 \mu$ -equiv. per day.

#### TABLE 2

DRY WEIGHTS OF AND SODIUM CONCENTRATION\* IN THE VARIOUS PLANT PARTS OF H. VULGARE CV. BOLIVIA DURING THE EARLY TILLERING STAGE (EXPERIMENT 3)

Labelled solutions containing  $^{22}$ NaCl at a concentration of 100 m-equiv/l replaced by non-labelled solutions of the same concentration after day 5

	Dry Weight (mg) Days after Application of Sodium Chloride					Sodium Concentration (m-equiv/g dry wt.)				
Plant Part						Days after Application of Sodium Chloride				Least Significant
	0	5	7	10	15	5	7	10	15	Difference (P = 0.05)
Leaf 1 (oldest leaf) Leaf 2	$\frac{18\cdot 3}{3\cdot 6}$	$\begin{array}{c} 24 \cdot 9 \\ 28 \cdot 3 \end{array}$	$24 \cdot 1 \\ 29 \cdot 0$	$\begin{array}{c} 25 \cdot 2 \\ 30 \cdot 2 \end{array}$	$22 \cdot 7$ $31 \cdot 5$	$\begin{array}{c}1\cdot 29\\0\cdot 71\end{array}$	$\begin{array}{c}1\cdot 41\\0\cdot 87\end{array}$	$1 \cdot 99 \\ 1 \cdot 11$	$2.69 \\ 1.96$	$ \begin{array}{c} 1 \cdot 44 \\ 0 \cdot 27 \\ 0 \cdot 27 \end{array} $
Leaf 3 Leaf 4+ tiller 1 (oldest tiller)+		8.1	20.0	33.8	36.3	0.59	0.54	0.75	1.36	0.27
tiller 2 Leaf 5+ leaf 6+			3.6	$32 \cdot 4$	$128 \cdot 5$	-	0.50	0.67	0.85	0.13
tiller 3 Sheath 1 (oldest		-	-	$2 \cdot 7$	$29 \cdot 9$	_	_	0.64	0.67	$0 \cdot 13$
sheath)	$5 \cdot 4$	8.8	7.9	$7 \cdot 2$	7.6	$1 \cdot 73$	$1 \cdot 94$	$2 \cdot 58$	$2 \cdot 90$	0.27
Sheath 2		3.6	$6 \cdot 2$	$7 \cdot 2$	6.7	0.52	0.74	1.51	$2 \cdot 40$	0.27
Younger sheaths		-		$7 \cdot 1$	$25 \cdot 8$		0.20	$1 \cdot 22$	1.21	0 · 27
Whole shoot	$27 \cdot 3$	$73 \cdot 6$	90.8	145.8	$289 \cdot 1$					
Roots	17.6	29.0	32.8	$41 \cdot 3$	81.8	0.46	0.52	0.52	0.31	0.13
Whole plant	44.8	$102 \cdot 6$	123.6	187 · 1	370 · 9					

\* See also Figure 5.

 $Na_{0-5}$  lost from the roots and developed organs of the shoot moved into newly developing organs, such as leaf 3 between days 5 and 10; leaf 4 and tillers 1 and 2 after day 7; and leaves 5 and 6 and tiller 1 after day 10. However, total sodium intake by these organs far exceeded their  $Na_{0-5}$  intake.

#### IV. DISCUSSION

The data presented will be discussed only in relation to the regulation of ion concentrations.

533

# (a) Chloride and Sodium Concentrations as Affected by Growth and Ion Uptake

In the shoots as a whole chloride and sodium concentrations first increased rapidly and then changed little over the long period from early tillering to grain formation (Figs. 2 and 3). During the same period decreases occurred in chloride and sodium concentrations of leaves and sheaths (Greenway 1965). Such observations are



Fig. 5.—Total sodium contents and sodium absorbed between days 0-5 (Na<sub>0-5</sub>) during early tillering (experiment 3). Least significant differences indicated are for P = 0.05. Sodium chloride concentration 100 m-equiv/l.

consistent with the rather low chloride and sodium concentrations found during the later growth stages of other salt-tolerant monocotelydons grown on saline media (Lunt, Youngner, and Oertli 1961; Greenway and Rogers 1963).

In Part V (Greenway and Thomas 1965) the important regulatory effect of growth on ion concentrations has been discussed. In both the whole shoot and its individual organs the ion concentrations at any one time will not only depend on the net ion uptake but also on the relative growth rate; concentrations being much lower at high than at low relative growth rates. This paper extends these observations to chloride and sodium regulation throughout the life cycle of the plant. Relative growth rates and rates of net chloride and sodium uptake are shown in Figure 6. Chloride and sodium uptake, though decreasing somewhat with time, remained at a high level. Nevertheless ion concentrations were steady (Figs. 2 and 3), i.e. increases in concentrations were prevented by the regulatory effect of continued growth. The calculated maximum chloride concentration (cf. Greenway and Thomas 1965) between 32 and 69 days was 0.82 m-equiv/g dry weight, which was in good agreement with the observed value of 0.92 m-equiv.; and this concentration was maintained till the onset of senescence. During senescence the rates of chloride and sodium uptake were lower than during any other period, but concentrations rose to about 2.2 m-equiv/g dry weight (Figs. 2 and 3), due to a strong decline in relative growth rate (Fig. 6).



Fig. 6.—Relative growth rates (a) and rate of net chloride uptake (b) of the whole shoot (experiment 1). (c) Potassium/sodium ratios of net ion uptake during ontogenesis (experiment 1).

# (b) Chloride and Sodium Uptake by Whole Shoot during Ontogenesis

The decrease in the rate of net ion uptake during plant development could be due to an ion loss from the plant or to a decreased total ion intake. During the early tillering stage there is no appreciable chloride export (Greenway and Thomas 1965). Similarly large losses up till the stage of grain formation are not likely because of the very limited chloride and sodium retranslocation [see Section IV(c)], so total ion uptake, as well as net ion uptake, decreased during plant development. Decreased ion uptake during ontogeny is usual for essential elements absorbed from low external concentrations (cf. Williams 1955), but it is of interest that this decline also occurred for "non-essential" elements supplied at high concentrations.

It was suggested earlier that ion regulation decreases during senescence (Greenway 1962a) and this appears to be supported by the rising chloride and sodium concentrations (83–128 days; Figs. 2 and 3). However, net chloride and sodium intakes were lowest during senescence. Better evidence for a decreased ion regulation during senescence is the decline in the ratio of the potassium uptake to the sodium

uptake. This ratio was remarkably constant during most of plant development, but it decreased strongly during senescence (Fig. 6). Even then this K/Na ratio of uptake by the shoot was high compared to that of the medium.

# (c) Chloride and Sodium Regulation within Individual Tillers during Ontogenesis

During ontogenesis, individual leaves, sheaths, and stems of the sodium chloridetreated plants showed pronounced increases in chloride and sodium (Figs. 2 and 3), leading to much higher concentrations in older than in younger leaves. Furthermore leaves and sheaths formed during later stages of plant development had much lower initial ion concentrations than earlier-formed leaves [see Figs. 2 and 3; also Section III(b)]. This phenomenon could not be due to a decreased net chloride or sodium uptake by the three oldest tillers during ontogeny, as shown by the rate of chloride uptake. This rate declined from 0.062 (m-equiv/g dry wt./day) between 32 and 50 days to 0.052 (m-equiv/g dry wt./day) between 50 and 69 days, the decline being far too small to account for the low initial chloride concentrations of leaves 9 and 10 between 50 and 69 days. Two other possibilities are:

- (1) Later-formed leaves remained wrapped in sheaths of older leaves for a longer period than earlier-formed leaves and so depended more on retranslocation for dry weight increments. Moreover, as long as the leaves have not emerged, transpiration will be low and intake of chloride and sodium would be predominantly by retranslocation, which is slow.
- (2) The stems absorbed and retained large amounts of chloride and sodium, which would diminish the quantities reaching the leaves.

Both these factors become accentuated during ontogenesis and are very pronounced for the inflorescences. The low chloride and sodium concentrations in inflorescences are therefore the culmination of a general trend during ontogenesis and not necessarily, as suggested earlier by Greenway (1962a), due to a specific ability to exclude chloride and sodium.

### (d) Ion Distribution within the Plant

The strong selectivity of younger organs is best demonstrated by the very low K/Na ratios in older organs and the high ratios in younger organs, particularly in inflorescences and developing grain (Table 3).

The following processes could be limiting net ion retranslocation:

- (1) Absorption by the cells of the developing organs, determining net ion transfer from the retranslocation system.
- (2) The degree of ion retention by cells of the older organs, determining availability of ions to the retranslocation system.
- (3) Rate of entry and transport in the translocation system.

Inflorescences and the grain contained about the same amount of potassium in control and sodium chloride-treated plants, despite much lower potassium concentrations in the vegetative organs of the latter plants (Table 1). Thus potassium retranslocation was not impaired by the high sodium concentrations of the source (developed organs). Since the ion content of the grain is mainly supplied by retranslocation (Mason and Maskell 1931) a comparison between grain content and retranslocation rates determined during early tillering is worth while, particularly as the exporting organs contained similar concentrations of ions. [Sodium and chloride concentrations in the vegetative organs of sodium chloride-treated plants were similar to potassium concentrations in the controls, and about the same level of ions occurred in the oldest leaf during the early tillering stage (potassium, see Greenway and Pitman 1965; chloride, see Greenway and Thomas 1965; sodium, see Table 2).] With this level as the source,

#### TABLE 3

K/Na ratios in the vegetative shoots of h. vulgare cv. bolivia 69 and 83 days after application of sodium chloride (experiment 1), and in the vegetative shoots and inflorescences 93 days after sodium chloride application (experiment 2)

Sodium chloride concentration in the medium was 1 m-equiv/l for the control plants and 125 m-equiv/l for the treated plants

K/Na Ratios: Experiment 1*					K/Na Ratios: Experiment 2			
Plant Part	Control	Control Plants		l Plants	Plant Part	Control Plants	Treated Plants	
	69 Days	83 Days	69 Days	83 Days		93 Days	93 Days	
					Vegetative shoot			
Leaves 1–8	28	21	0.22	0.23	Leaves	13	0.5	
Sheaths 1–8	29	23	0.14	0.08	Sheaths	14	$0 \cdot 4$	
Leaves > 8	45	21	0.77	0.54	Stems	9	$0 \cdot 4$	
					Inflorescence			
${\it Sheaths}\!>\!8$	30	17	0.48	0.33	Rachis	14.5	0.7	
Stems	21	17	0.41	0.33	Glumen	4.1	0.5	
Ears	19	43	$3 \cdot 5$	$5 \cdot 8$	Palea		$3 \cdot 3$	
Stem ears		27		$1 \cdot 6$	Awn	$15 \cdot 2$	$5 \cdot 6$	
					Grain	$15 \cdot 4$	$6 \cdot 4$	

\* The three oldest tillers were used in this experiment.

concentrations in the developing grain were 0.29 m-equiv/g dry weight for potassium, 0.09 m-equiv/g for chloride, and 0.04 m-equiv/g for sodium (Table 1). In comparison, daily retranslocation rates during the early tillering stage were 3.1 m-equiv/leaf/day for potassium (Greenway and Pitman 1965), 1.6 m-equiv/leaf/day for chloride (Greenway and Thomas 1965), and 0.69 m-equiv/leaf/day for sodium\* (Fig. 5). Thus retranslocation rates for the different ions varied in the same order as grain content, suggesting that during the full life cycle of the plant chloride and sodium retranslocation was slow compared with potassium.

\* Assessment of retranslocation rates can only be approximate, but the differences are large enough to make valid comparisons with grain contents. The quoted rates are all "assessed estimates" (see Greenway and Thomas 1965), these being most suitable because of the short half-life of  $^{42}$ K. For chloride and sodium, estimates made some time after tracer removal were also used, these being in substantial agreement with the assessed estimates.

537

The low chloride and sodium mobility could be due to a strong retention by individual cells of developed organs, i.e. these ions were not readily available to the translocation system. Alternatively, entry into the retranslocation system was the rate-limiting step in chloride and sodium retranslocation.

A rate-limiting step in sodium retranslocation is suggested by the faster  $Na_{0-5}$  loss from sheaths than from leaves (Fig. 5). In the sheath, released ions could be exported via the transpiration stream, i.e. export would not be limited to the translocation system. Another possibility is that leaf and sheath cells released ions at different rates.

#### TABLE 4

CHLORIDE CONCENTRATION IN INDIVIDUAL PARTS OF H. VULGARE CV. BOLIVIA 69 and 83 days after application of sodium chloride (experiment 1)

The three oldest tillers only were used. Control and treated plants were grown in solutions containing sodium chloride at concentrations of 1 and 125 m-equiv/l, respectively

	Chloride Concentration (m-equiv/l plant water							
Plant Part	Control	Plants	Treated Plants					
	69 Days	83 Days	69 Days	83 Days				
Leaves 1–4	35	355*	610	5000*				
Leaves 5–8	12		155	297				
Leaves 9–10	12	36	94	161				
Leaves > 10	15	40	71	144				
Flags		39		59				
Stems<8	44	49	200	308				
Stems > 8	55	66	170	251				
Inflorescences	24	25	30	44				
Stems of inflorescences		32		113				
Sheaths 1–4	21	68	213	628				
Sheaths 5–8	22	36	189	258				
Sheaths 9–10	33	55	170	331				
Sheaths > 10	43	73	120	300				
Sheaths of flags		68		137				

\* Leaves completely collapsed at time of harvest.

That retranslocation is the rate-limiting step in sodium and chloride export from developed leaves is also indicated by the similar amounts of ions exported from leaves of control and sodium chloride-treated plants. Ion concentrations at the source did not greatly affect the amounts of ions retranslocated, i.e. chloride and sodium concentrations of vegetative parts were very different in control and treated plants, yet similar amounts were retranslocated to the grain (Table 1). Moreover, in plants of low chloride content high rates of chloride retranslocation were found: during the early tillering stage of H. vulgare (Greenway 1962b), in tomatoes (Woolley, Broyer, and Johnston 1958), and in red kidney beans (Greenway and Thomas, unpublished data). A high mobility of the total ion pool in plants of low chloride and sodium content was also indicated by the rather uniform distribution between parts of control plants, as contrasted with the high concentrations in developed organs of sodium chloride-treated plants (Table 4).

Thus increasing ion concentration at the source resulted in a decrease of the relative amounts of ions retranslocated (i.e. when expressed as a percentage of the amounts available). Selectivity during retranslocation was also shown by the K/Na ratio of the translocated ions, which was largely independent of the K/Na ratio of the developed organs (Table 1).

The above-described pattern of ion mobilities could be due to absorption by individual cells of the source. However, it is then necessary to assume that the degree of ion retention by leaf cells, or their ability to absorb further sodium and chloride, increased with increasing ion concentration of the leaf. Such a pattern of ion accumulation is not likely because it would be contrary to all existing evidence obtained with other plant cells (see Briggs, Hope, and Robertson 1961), i.e. ratios of ion concentrations inside cells to concentrations outside are much higher at low than at high ionic concentrations of the medium. If this general pattern also applied to ion accumulation by individual leaf cells, then increasing ion concentrations of the leaf would result in an increased availability of ions to the translocation system (i.e. expressed as a percentage of the total amounts of ions in the leaf).

Chloride, sodium, and potassium retranslocation thus has similar characteristics to active ion uptake by disks of tissue and excised roots, in which a maximum rate of uptake is reached with increasing external concentration, and potassium is absorbed preferentially to sodium in most species, including barley. As shown above it is very unlikely that such a selectivity would result from ion absorption by cells of the source. Evidence that the sink is not the determining factor in this selectivity has been discussed in Part V (Greenway and Thomas 1965), and this conclusion, based on movements in intact plants, is supported by observations with isolated segments of willow stem (Peel 1963). The phloem of these stem segments also showed a preferential intake of potassium as compared with sodium. These considerations suggest that ion selectivity during retranslocation is located either in the sieve tubes themselves, or in cells secreting ions actively into the phloem. This suggestion applies only to ionic relationships of the present experiments, and under different conditions, or with different ions, absorption by cells of either source or sink might become rate-limiting.

In plants grown in media of high sodium chloride concentration, chloride concentrations of the young organs are regulated both during transfer of ions from the root to the shoot, and during retranslocation (Greenway and Thomas 1965). This conclusion is equally valid for the regulation of the K/Na ratio of the young organs.

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