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THE ABSORPTION, TRANSLOCATION AND
ACCUMULATION OF SODIUM IN YOUNG
SQUASH PLANTS.

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THE ABSORPTION, TRANSLOCATION AND ACCUMULATION
OF SODIUM IN YOUNG SQUASH PLANTS

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THE ABSORPTION, TRANSLOCATION AND ACCUMULATION
OF SODIUM IN YOUNG SQUASH PLANTS

ABSTRACT

In most plants the concentration of sodium is much lower in the leaves than in the roots. In other species, however, there seems to be an equal distribution of this element between the shoots and the roots. The squash plant, Cucurbita pepo, used in the present study is an example of the type of plant that in respect to the roots maintains a relatively low sodium concentration in its leaves. When the plants were grown in a medium containing equivalent amounts of sodium and potassium the hypocotyls and leaves contained less sodium than potassium. When the roots were excised or killed by immersion in boiling water similar amounts of both elements moved to the upper portion of the plant. Thus the living roots exerted a large effect in discriminating against the uptake of sodium.

The low amount of sodium in the leaves was accounted for, in part, by translocation of this element from the leaves to the roots. Suspension of phloem activity by steam or localized chilling to girdle the hypocotyl resulted in accumulation of sodium in the leaves and the hypocotyl above the girdle. Similar accumulation resulted from the treatment with 2,4-dinitrophenol, a phosphorylation uncoupling agent.

Calcium was found to reduce significantly the amount of sodium accumulated by excised and intact roots. However, this effect on the roots was not consistently reproduced in the shoot. The predominant anion in the medium seemed to influence the effect of calcium. Thus

under transpiring conditions calcium inhibited sodium translocation to the shoot if the predominating anion in the medium was nitrate. On the other hand calcium increased the amount of sodium in the shoot if the predominant anion was sulfate. Chloride and phosphate did not seem to have any effect on the calcium response.

Under conditions where root pressure was active (decapitated roots or guttating plants), the amount of sodium in the xylem sap was reduced by the presence of calcium in the root medium.

INTRODUCTION

In the classical paper of Collander (1941a) on the selective uptake of ions by plants, he reported the absorption of lithium, sodium, potassium, rubidium, cesium, magnesium, calcium, strontium, manganese and copper by some 21 species of vascular plants. Of all these elements he found that the concentration of sodium in the shoot, expressed as milliequivalent percentage of the total cations, presented the greatest variation. In one case where he grew the plants in the presence of two milliequivalents per liter each of sodium and potassium for some 2 months, he found that Atriplex hortense had a milliequivalent percentage of sodium some 56 times more than Fagopyrum. The large differences among species in the absorption of sodium remained more or less the same despite the variations in the composition of several culture solutions and the fact that the experiments were conducted during different years. When the plants were grown in soil instead of in water culture the differences were further magnified.

Briggs, Hope and Robertson (1961) suggested the following possible explanations for the great differences in the sodium contents of plants: (1) that some plants have many more binding sites within for sodium than others, or (2) that some plants have much more resistance than others to the accumulation of sodium in the vacuole, or (3) that sodium is actively extruded from some plants.

Collander (1941a) found the tissue concentrations of elements other than sodium and manganese varied no more than two- to five-fold among species. Manganese varied from fifteen- to thirty-fold among the species studied. The tissue concentration of manganese in a given species was

subject to large variations resulting from the concentration of this element in the medium and other environmental factors. However, sodium concentration in the tissues of a species was found to be rather insensitive to variations in the environment.

Many plants tend not to transport much sodium to their stems and leaves even though sodium may accumulate in their roots. On the other hand, there are plants that contain more sodium in their shoots than in their roots, while in still others there seems to be little difference in the concentration of this element between the different parts of the plant.

In some species the accumulation of sodium in a particular organ depends on the method of culturing the plant and possibly on the composition of the medium. Thus cotton plants which were grown in sand culture accumulated a much higher concentration of sodium in the roots than in the leaves. The leaves of cotton plants grown in water culture, however, were found to contain more sodium (Joham, 1955). Cooper et al. (1953) also found that sodium accumulated in the roots of cotton plants only "under certain conditions."

In other species the accumulation of sodium in certain organs depends also on the maturity of the plant. Young Suaeda macrocarpa (Binet, 1962) and Laguncularia racemosa (Chapman, 1942) were found to contain a greater amount of sodium in their roots than in their leaves. However, as the plants matured the concentration of sodium in the roots decreased while the amount in the leaves increased.

Of the 16 vascular plants studied by Collander (1941b) 11 had a greater equivalent percentage of sodium in the roots, three had the same

percentage for roots and shoots, and two had a distinctly greater percentage in the shoot compared to the roots. Examples of these types of plants are shown in Table I.

Collander (1941b) also found that potassium, rubidium, cesium and to a lesser extent magnesium tended towards an equal distribution between root and shoot. Surprisingly the element lithium, which generally behaves as sodium in most instances (Steinbach, 1962), was found to act differently from sodium. There was a greater equivalent percentage of lithium in the shoot than in the root. Calcium behaved in the same manner as lithium.

Burstrom (1937) found essentially the same pattern of distribution of the above elements in Avena.

Wallace and Hemaïdan (1963a), using radioactive sodium, concluded that very little of this element was transported from the root to the shoot of bush beans. In radish, however, the transport of sodium to the shoot occurred readily. They found that for beans, whether sodium was supplied to the leaves or to the roots, the same distribution pattern of accumulation in the roots resulted.

Respiratory poisons were found to disturb the distribution pattern of sodium. Poisoned plants accumulated a greater amount of this element in their shoots. Wallace and Hemaïdan (1963b) interpreted this effect of cyanide as "facilitating the transport of sodium to the shoot." Pearson (1962) obtained similar results with 2,4-dinitrophenol but contended that this agent "decreased the retentive capacity of the root for sodium."

There have been several suggestions as to why the sodium concentration is very low in the leaves of many plants, unlike potassium which

TABLE I. EXAMPLES OF DIFFERENCES IN BEHAVIOR OF PLANTS AS EXPRESSED BY DISTRIBUTION OF SODIUM AMONG THEIR ORGANS

Leaf Na $\bar{>}$ Root Na:

| | | |
|--|----------------|----------------------------|
| <u>Beta</u> sp. | Chenopodiaceae | Bower and Wadleigh, 1946 |
| <u>Atriplex hortense</u> | " | Collander, 1941b |
| <u>A. littorale</u> | " | " " |
| <u>Suaeda vulgaris</u> | " | Binet, 1963 |
| <u>S. macrocarpa</u> (mature) | " | " 1962 |
| <u>Chloris</u> sp. | Chlorantaceae | Bower and Wadleigh, 1946 |
| <u>Laguncularia racemosa</u> (mature) | Combretaceae | Chapman, 1942 |
| <u>Lactuca</u> sp. | Compositae | Collander, 1941b |
| <u>Raphanus</u> sp. | Cruciferae | Huffaker and Wallace, 1959 |
| <u>Brassica</u> sp. | " | Truog et al., 1953 |
| <u>Sinapis</u> sp. | " | Collander, 1941b |
| <u>Vicia</u> sp. | Leguminosae | " " |
| <u>Daucus</u> sp. | Umbelliferae | Truog et al., 1953 |

Root Na $>$ Leaf Na:

| | | |
|---|----------------|-----------------------------|
| <u>Salsola</u> sp. | Chenopodiaceae | Collander, 1941b |
| <u>Spinacia</u> sp. | " | " " |
| <u>Suaeda macrocarpa</u> (young) | " | Binet, 1962 |
| <u>Laguncularia racemosa</u> (young) | Combretaceae | Chapman, 1942 |
| <u>Aster</u> sp. | Compositae | Collander, 1941b |
| <u>Helianthus</u> sp. | " | " " |
| <u>Avena sativa</u> | Gramineae | " " |
| <u>Paspalum</u> sp. | " | Bower and Wadleigh, 1948 |
| <u>Zea mays</u> | " | Bange and van Vliet, 1961 |
| <u>Hordeum</u> sp. | " | Sutcliffe, 1957 |
| <u>Persea</u> sp. | Lauraceae | Haas, 1950 |
| <u>Medicago</u> sp. | Leguminosae | Cope et al., 1953 |
| <u>Phaseolus</u> sp. | " | Wallace and Hemaidan, 1963 |
| <u>Pisum</u> sp. | " | Barbier and Chabannes, 1951 |
| <u>Melilotus</u> | " | Collander, 1941b |
| <u>Fagopyrum</u> | Polygonaceae | " " |
| <u>Prunus</u> sp. | Rosaceae | Lilleland, 1946 |
| <u>Prunus</u> sp. | " | Hayward and Long, 1946 |
| <u>Citrus</u> sp. | Rutaceae | Cooper et al., 1952 |
| <u>Nicotiana</u> sp. | Solanaceae | Collander, 1941b |
| <u>Solanum</u> sp. | " | " " |

accumulates in the shoot. Bange and van Vliet (1961) visualized a highly specific transporting carrier of potassium from the root to the shoot. A corresponding model for sodium was believed to be nonexistent.

Truog et al. (1953) went to the extent of opening the roots by shearing off the tips. This treatment, however, did not increase the transport of sodium to the shoot. They implied the possibility of a "restriction at the nodes where iron under certain conditions fails to pass freely and thus accumulates."

Gauch and Wadleigh (1945), on the other hand, attributed the large difference in the sodium content of the shoot and the root to the possibility that "the membranes in the cells of certain extrastelar tissues of the roots may be especially proficient in the exclusion of sodium and operate to withhold it from the vascular system - e.g. the endodermis...."

Sutcliffe (1962) discounted the idea that the accumulation of sodium in roots is due to a preference for sodium by the vacuoles of the root cortex cells allowing an excess of potassium to move into the stele, since excised barley roots exhibit a preferential accumulation of potassium over sodium when both are supplied in the medium (Sutcliffe, 1957).

In the absence of further evidence Collander (1941b) gave two alternative explanations for differences among plants in their site of sodium accumulation. He contended that the transport of this element from the root to the shoot may be more inhibited in some plants than in others. The other explanation he gave was that the transport of sodium from the shoot to the root may be more developed in plants which have low concentrations of this element in their shoots.

MATERIALS AND METHODS

The experiments reported herein were conducted in a room (1.8 x 1.9 x 3.0 m.) in which both temperature and humidity were controlled. The temperature averaged 27° C. during the daytime and about 22° C. during the night. The relative humidity was about 70 percent during the day and near saturation at night. Air was drawn into the room with an electric fan.

Towards the latter part of the study the humidity was about 50 percent during the day and about 80 percent at night. During this latter period the temperature varied little throughout the day with an average near 25° C.

A bunk having lower and upper compartments (each deck was 61 x 122 cm.) each of which housed four 48-inch GE "Power Groove" white fluorescent tubes. Two 15-watt incandescent bulbs provided the longer wavelength of the spectrum. The light intensity at the level of the leaves varied from 500 - 600 foot candles. A 16-hour photoperiod was provided.

Summer squash, Cucurbita pepo (zucchini hybrid 829; lot No. 1438C obtained from the Joseph Harris Company of New York), was the experimental plant used. The seeds were thoroughly washed with tap water for a few minutes then transferred to distilled water in a 4-liter beaker. The seeds were placed in a wire basket immersed about 2 centimeters below the surface. An air pump provided the compressed air for aeration. The water was changed after 12 hours when it became turbid.

After 24 hours the seeds were transferred to germinating pads (10 x 13 cm.) made of plastic-coated 1 centimeter mesh hardware cloth. A piece of nylon net cloth was fitted over this to hold the seeds. Each

pad contained 25 - 30 seeds. Four of the germinating pads were suspended with rubber coated wires over a 6-liter plastic tray painted black on the outside. Six liters of germinating solution was sufficient to reach the germinating pads and thus the seeds were kept moist.

A steel can 6 centimeters tall and 8.5 centimeters in diameter, open at both ends, was placed over the seeds. This held the plants in place during handling.

During the first 4 - 5 days after soaking, the seeds were usually kept in the dark but because of lack of space germination also occurred in the presence of light in some cases. As far as can be determined however, this did not affect the growth of the plants.

The germinating solution contained 0.0005 M each of $\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$, $\text{Ca}(\text{NO}_3)_2 \cdot 4\text{H}_2\text{O}$ and KH_2PO_4 . Iron was supplied at the rate of 5 ppm of the element from FeEDTA. All the known essential micronutrient elements were also supplied at the rate recommended by Hoagland and Arnon (1939).

In some of the experiments it was desired that the sodium content of the plants to be used in the experiments be increased, so 0.0005 M NaH_2PO_4 was incorporated into the germinating solution. The solution was changed after 1 week. The plants remained for 5 days in this new solution before they were used in the experiments. Water loss due to transpiration and evaporation was replaced with distilled water once a day.

The experimental solution, unless otherwise stated, consisted of the primary and secondary phosphate salts of sodium and potassium. The solution was made in such a way that a pH of 5.9 was obtained. The reaction of the solution did not change more than 0.2 pH unit during the

usual 24-hour experimental period. This experimental solution contained 5 milliequivalents per liter each of sodium, potassium and calcium. The calcium was supplied as the chloride salt. The volume of the solution used varied from 1.5 liters per replication in short term experiments of less than 12 hours to 3.8 liters in longer experiments. In no case was there a change in the composition of the solution for any particular ion by more than 20 percent. Aeration of the solution was provided throughout the germination and experimental periods of growth of the plants.

Each treatment was replicated three times unless otherwise mentioned. Each replication consisted of no less than 5 and no more than 20 plants.

After the experimental periods, the plants were divided into leaves, hypocotyls and roots. The "leaf" sample contained the cotyledons, the first true leaf and the apical bud. The roots were centrifuged at 130 x g. for 2.5 minutes after which its fresh weight was determined. The fresh weights of the leaves and hypocotyls were determined separately. The range in weight of the different organs in grams per plant were: leaves, 1.89 - 2.33; hypocotyls, 0.70 - 0.81; roots, 0.41 - 0.56.

The samples were then placed in paper bags and dried in a forced draft oven. After drying the samples were ground and ashed in a furnace overnight at about 500° C. The ash was taken up in 10 milliliters of 4 N HCl, digested on a hot plate for a few minutes and filtered. The filtrate was made up to 100 milliliters from which dilutions were made when necessary. A Beckman DU spectrophotometer with flame attachment was used to determine sodium and potassium.

Tables incorporated in the text are indicated with Roman numerals while the Arabic numerals denote the tables appended at the end of this

thesis. The range given after each average is the standard error of the mean.

I. The Distribution of Sodium and Potassium in the Plant

The primary objective of this experiment was to determine the variation in the sodium and potassium contents in the different organs of the plant after supplying these ions at several solution concentrations.

Plants used for the 24-hour absorption period were grown as described in the methods. They were transferred to the experimental solution at the age of 13 days and were harvested 24 hours later. In contrast, the plants which were subjected to a 192-hour absorption period were transferred to the experimental solution at the age of 5 days. Both groups were harvested at the same time. The plants for the short term experiments were grown in a total volume of 3.0 liters of germinating solution whereas those for the long term experiments were grown in a total volume of 3.8 liters. The latter plants were also exposed to a higher light intensity.

As a result of the difference in the culture techniques of the two groups, the growth of the plants in the gallon jars was slightly but significantly greater than that of plants in the plastic trays. Both groups were harvested early on their 14th day. Data from this experiment are shown in Table II, and Appendix Tables 1, 1a and 1b.

Plants which were subjected to the earlier treatment contained approximately twice as much sodium and potassium as those given the 24-hour absorption period, except for the sodium content of plants grown in the two lowest concentrations. Surprisingly, the total amount of potassium absorbed by the plants did not seem to be affected by the

TABLE II. THE EFFECT OF THE CONCENTRATION OF SODIUM AND POTASSIUM IN THE NUTRIENT SOLUTION AND THE DURATION OF THE ABSORPTION PERIOD ON THEIR CONCENTRATIONS AND DISTRIBUTION IN THE DIFFERENT ORGANS OF THE PLANT

| Treatments | Meq./kg. fr. wt. | | | | Percentage distribution | | | |
|-----------------------------------|------------------|-------------|------------|------------|-------------------------|----|-------|----|
| | Shoots | | Roots | | Shoots | | Roots | |
| | Na | K | Na | K | Na | K | Na | K |
| <u>24 hour absorption period</u> | | | | | | | | |
| 0 meq. Na/l. | 0.43 | 67.94 | 12.80 | 48.98 | | | | |
| 5 meq. K/l. | ± 0.02 | ± 0.75 | ± 0.10 | ± 0.30 | 13 | 85 | 87 | 15 |
| 5 meq. Na/l. | 0.76 | 66.40 | 18.97 | 49.09 | | | | |
| 5 meq. K/l. | ± 0.04 | ± 0.35 | ± 0.32 | ± 0.29 | 16 | 86 | 84 | 14 |
| 10 meq. Na/l. | 0.87 | 63.85 | 23.88 | 47.30 | | | | |
| 10 meq. K/l. | ± 0.06 | ± 0.92 | ± 0.15 | ± 0.56 | 14 | 86 | 86 | 14 |
| 20 meq. Na/l. | 1.36 | 69.78 | 33.66 | 47.02 | | | | |
| 20 meq. K/l. | ± 0.10 | ± 1.30 | ± 0.16 | ± 0.39 | 15 | 87 | 85 | 13 |
| <u>192 hour absorption period</u> | | | | | | | | |
| 0 meq. Na/l. | 0.67 | 95.70 | 1.14 | 85.08 | | | | |
| 5 meq. K/l. | ± 0.04 | ± 1.10 | ± 0.13 | ± 0.76 | 77 | 86 | 23 | 14 |
| 5 meq. Na/l. | 3.03 | 102.19 | 7.83 | 78.90 | | | | |
| 5 meq. K/l. | ± 0.28 | ± 2.33 | ± 0.27 | ± 1.15 | 65 | 87 | 35 | 13 |
| 10 meq. Na/l. | 5.27 | 105.07 | 15.89 | 78.15 | | | | |
| 10 meq. K/l. | ± 0.26 | ± 1.02 | ± 0.25 | ± 0.80 | 61 | 86 | 39 | 14 |
| 20 meq. Na/l. | 12.00 | 114.14 | 25.43 | 75.75 | | | | |
| 20 meq. K/l. | ± 0.19 | ± 10.68 | ± 0.81 | ± 1.42 | 65 | 88 | 35 | 12 |

The ranges shown are the standard errors of the means of three replications.

concentration of this element in the medium or by the presence or absence of sodium.

Although there seemed to be a trend towards increasing amounts of potassium in the organs of the shoot with increasing concentration in the nutrient medium, the increment was very small considering the several fold increase of the element in the medium. The percentage distribution of this element in the different plant organs was not affected by its concentration in the medium. The length of the absorption period had little or no effect on the distribution of potassium between root and shoot (Table II); however, the percentage distribution among the organs of the shoot was affected greatly (Appendix Table 1b). The total amount in the hypocotyl showed no consistent increase and that in the first true leaf increased only moderately with the longer period of absorption. The greatest increase in total amount with time occurred in the cotyledons. This increase was threefold. The total amount of potassium in the roots increased twofold with the longer absorption period but this quantity remained at about 14 percent of the total amount in the whole plant.

On the other hand the amount of sodium varied greatly with the organs, as the concentration in the medium was varied, and with the duration of the absorption period. An increase in the concentration of this element in the medium and the longer absorption period, usually increased the content of sodium in the various parts. As with potassium, the percentage distribution of sodium in the various parts of the plant was not affected by the concentration of this element in the medium. This is not surprising for potassium since the total amount of this element in the plant remained the same regardless of the treatment.

However, in the case of sodium there was as much as a fifteenfold difference in the total sodium content between the treatment given 20 milliequivalents of sodium per liter and that given no sodium at all. The time factor also affected the distribution of this element in the various parts of the plant. After the 24-hour absorption period about 85 percent of the total sodium was in the roots. Less than 5 percent was present in the leaves and about 10 percent in the hypocotyls. Roughly one-third of the total amount of sodium was present in each of the three organs after the plants had been in the experimental nutrient solution for 192 hours.

The data indicate that sodium increased very slowly in the shoot. The sodium content of the shoots of plants subjected to the 24-hour absorption period was only about one-tenth of that in plants given the longer absorption period. The shoots of plants that were subjected to the 192-hour absorption period contained only twice as much potassium as those subjected to the 24-hour treatment.

II. The Time Course of Absorption and Translocation

Since most of the experiments involved a 24-hour absorption period, the uptake of the elements within this length of time was studied in more detail. The plants used were germinated in the usual manner as described earlier. Sodium was introduced into the germinating medium in the same concentration as potassium. The sampling was carried on up to 48 hours. The results are presented in Figures 1 and 2.

The hyperbolic curve typical of root accumulation was evident for both elements. If the concentration at 48 hours were considered 100 percent, then the 50 percent concentration was attained at 6 hours for

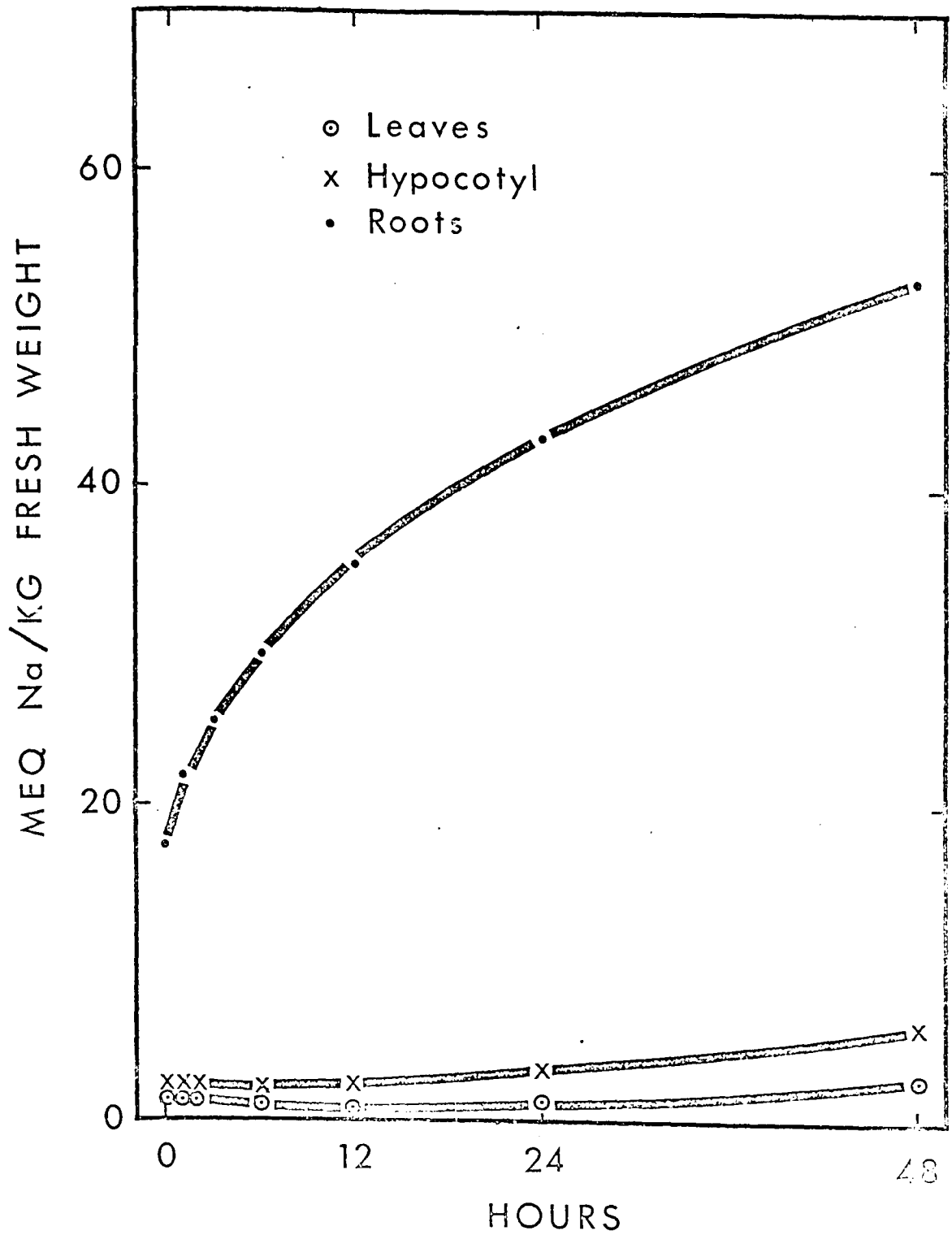


Figure 1. The absorption of sodium by young squash plants from a medium containing 5 meq/l each of sodium and potassium

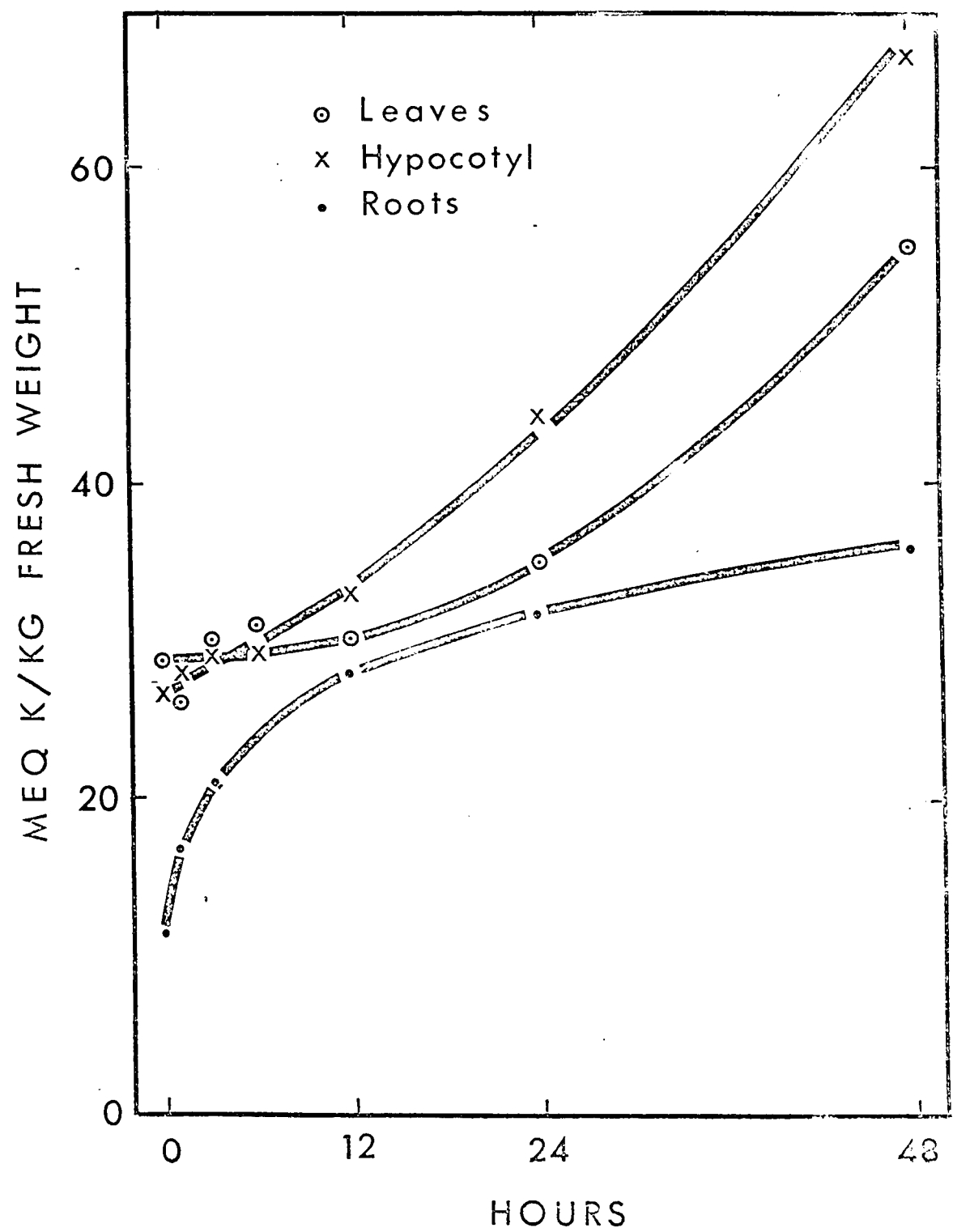


Figure 2. The absorption of potassium by young squash plants from a medium containing 5 meq/l each of sodium and potassium

potassium and 12 hours for sodium. This suggests the relative facility of the absorption and accumulation of these two ions by the root cells.

The translocation of both elements to the shoot showed a definite lag period. Furthermore, the delay seemed to be much longer in the leaf than in the hypocotyl. Bange and van Vliet (1961) obtained similar results for the absorption of the same elements by corn plants.

The ratio of the potassium concentration in the roots to that in the leaves at the different times of sampling ranged from 0.4 - 0.9. Thus at no time was the concentration in the root greater than that in the leaf although unity was approached. On the other hand the concentration of sodium in the root was always higher than that of the shoot. The ratio of the root sodium to the leaf sodium ranged from 12 - 36. Even in plants in which the sodium in the root exceeded potassium, in the leaf there was only one sodium atom to 26 of potassium. With a longer absorption period, as that shown in the earlier experiment, the ratio was even larger.

III. The Accumulation of Sodium and Potassium in Excised Organs

It is logical to suppose that energy is being expended to maintain the large gradient in sodium concentration between the roots and the leaves. It is not known which of the organs maintains this gradient. Does the leaf or shoot produce transport carriers of sodium in the same manner as implied by Bange and van Vliet (1961) for potassium? The direction of movement will of course have to be opposite that for potassium. Or is it due to a greater affinity of the root cells for sodium so that there is actually very little movement of sodium within the plant? In this latter case the root expends the energy to hold the sodium.

It was first thought that these questions could be answered by the use of excised organs. Thus if an excised leaf floating on a sodium solution accumulates as little sodium as an intact one then it could be said that the leaf extrudes sodium. However, as will be seen later, such conclusions could be erroneous.

For this purpose the plants were divided into leaves, hypocotyls and roots. They were then floated in the usual experimental solution containing 5 milliequivalents each of sodium, potassium and calcium. The solutions were contained in white enamel pans. For comparison intact plants were grown with only the roots immersed in the solution. Aeration was provided in all cases. The results from this experiment are shown in Table III.

The data show the tremendous amount of sodium absorbed by the excised leaf compared to that of the intact ones. Some 32 times more sodium was present in the excised leaf. In the case of potassium, however, only about one-sixth of the amount accumulated by the intact leaf was present in the excised organ. The low amount of sodium in the intact leaf indicates that very little sodium was being translocated from the roots. The excised leaf did not show any discrimination against the absorption of sodium. The data indicate that there was even less potassium than sodium entering the cells of the excised leaf. However, this result may have been brought about by the high concentration of potassium originally present in the leaves.

This observation for the leaves seemed to apply to the hypocotyls as well. The amount of potassium that entered the intact hypocotyls was much greater than the amount of sodium. With the excised hypocotyls

TABLE III. COMPARATIVE ABSORPTION OF SODIUM AND POTASSIUM
BY INTACT PLANTS AND EXCISED ORGANS (MEQ./KG. FR. WT.)*

| Treatments | Leaves | | Hypocotyls | | Roots | |
|-------------------------|--------------------|---------------------|--------------------|---------------------|--------------------|---------------------|
| | Na | K | Na | K | Na | K |
| (Initial concentration) | (1.10) | (31.42) | (0.97) | (21.92) | (17.36) | (8.36) |
| Intact plants** | 0.24 ± 0.10 | 31.35 ± 2.17 | 1.42 ± 0.03 | 32.87 ± 4.26 | 4.24 ± 1.30 | 30.80 ± 0.22 |
| Excised organs | 7.70 ± 0.29 | 5.54 ± 0.60 | 3.09 ± 0.20 | -5.22 ± 2.06 | 4.73 ± 0.64 | 26.18 ± 1.91 |

*Values for treatments are the differences between the final and initial concentrations.

**Only the roots were in direct contact with the solution.

The ranges shown are the standard errors of the means of three replications.

there was apparently no net entry of potassium although sodium was absorbed. It should be noted, however, that even after 24 hours in the experimental solution the total concentration of sodium in the excised hypocotyl had not reached the concentration of the ambient solution. The average total concentration of sodium in the excised hypocotyls after the experiment was 4.06 milliequivalents per kilo fresh weight. The corresponding value for the excised leaves was 8.8 milliequivalents per kilo fresh weight. Thus the sodium concentration in the leaf cells provided evidence for accumulation of sodium although the hypocotyl did not indicate any.

At this point it appears that the difference in concentration of sodium between the leaves and the roots was mainly due to the activity of the latter. However, there were several limitations to the preceding experiment that detract from such a conclusion. First is the fact that the shoot organs, which under normal conditions are bathed in air, when excised are in contact with the solution. Secondly, the integrity of the excised system is not the same as the intact one.

To eliminate the second problem, intact plants were floated in solution. For comparison, excised organs were tested at the same time. Results from this experiment are shown in Table IV.

The sodium content of intact leaves was not much different from that of the excised leaves. This means that the exposed vascular system was not responsible for the uptake of sodium into the leaf. Close examination of the sodium contents of the intact and excised organs showed a small but consistent difference. The sodium content of the intact leaves was slightly less than that of the excised leaves. Excised or intact hypocotyls contained equal amounts of sodium.

TABLE IV. COMPARATIVE ABSORPTION OF SODIUM AND POTASSIUM
BY INTACT PLANTS AND EXCISED ORGANS BOTH FLOATED
IN SOLUTION (MEQ./KG. FR. WT.)*

| Treatments | Leaves | | Hypocotyls | | Roots | |
|-------------------------|--------------------|--------------------|--------------------|---------------------|--------------------|---------------------|
| | Na | K | Na | K | Na | K |
| (Initial concentration) | (0.95) | (28.92) | (0.85) | (15.35) | (15.48) | (8.50) |
| Intact plants | 5.26 ± 0.10 | 7.14 ± 0.52 | 2.89 ± 0.15 | 11.78 ± 1.05 | 6.91 ± 0.21 | 25.49 ± 0.44 |
| Excised organs | 5.94 ± 0.14 | 3.49 ± 0.48 | 2.92 ± 0.14 | -1.48 ± 0.20 | 6.00 ± 0.11 | 25.15 ± 0.40 |

*Values for treatments are the differences between the final and initial concentrations.

The ranges shown are the standard errors of the means of three replications.

The sodium content of the roots also showed small but consistent differences. In contrast to the trend observed with the leaves, the intact roots contained more sodium than the excised roots. Since the total amounts of sodium were found to be the same, this was interpreted as an indication that the lower sodium content of the intact leaf was due to the translocation of this element to the root.

IV. The Translocation of Sodium from the Leaves

The previous results indicated that sodium is probably translocated from the leaves to the roots. The outcome was not very conclusive since both organs were in contact with the sodium solution. In another experiment only the leaves were immersed in the solution while the roots were suspended in air wrapped in moist absorbent paper. The wrapped roots were then covered with a beaker to reduce evaporation. This set-up was compared with plants grown in the normal way, that is, only the roots were in contact with the experimental solution. The results from this experiment are shown in Table V.

TABLE V. TOTAL SODIUM AND POTASSIUM CONTENT OF VARIOUSLY TREATED ROOTS (MEQ./20 PLANTS)

| Initial content | | Immersed in solution* | | Roots suspended in air** | |
|-----------------|-------------|-----------------------|-------------|--------------------------|-------------|
| Na | K | Na | K | Na | K |
| 0.118 | 0.080 | 0.172 | 0.313 | 0.213 | 0.132 |
| ± 0.006 | ± 0.008 | ± 0.005 | ± 0.011 | ± 0.018 | ± 0.013 |

*Shoots in air.

**Leaves immersed in solution.

The ranges shown are the standard errors of the means of three replications.

Results from the above experiment showed that indeed there was some movement of sodium from the leaves immersed in solution to the roots suspended in air. The amount contained in these roots was even greater than that contained in the roots which were in the solution containing sodium. Some movement of potassium from the leaves to the suspended roots was also indicated, but movement of this element was much less than that of sodium.

In the above experiment, however, it was noticed that the roots suspended in air had a consistently lower moisture content than the control roots (94 percent versus 96 percent). To eliminate the possibility that the moisture status of the roots may have influenced the above results, another experiment was conducted. This time the roots were placed in distilled water while the leaves were in the experimental solution. Results from this experiment are shown in Table VI.

Results of this experiment again indicate that there was movement of sodium from the leaves to the roots. It should be noticed that this translocation to the roots occurred even when the concentration of sodium was much higher in the roots than in the leaves.

It was thought that the movement of sodium from the leaves might be affected if there were ions moving in the opposite direction, that is, from the roots to the leaves. Thus in another experiment, the roots were placed in 125-milliliter flasks containing 50 milliliters of distilled water or various solutions. The leaves, as before, were immersed in a solution containing 5 milliequivalents per liter each of sodium, potassium and calcium. The results are shown in Table VII.

These results indicated that ions present in the root medium had a definite effect on the movement of sodium from the leaves to the roots.

TABLE VI. SODIUM CONCENTRATION IN THE PLANT ORGANS AS AFFECTED
 BY SUPPLYING THE LEAVES WITH NUTRIENT MEDIA AND IMMERSING
 THE ROOTS IN DISTILLED WATER (MEQ./KG. FR. WT.)

| Treatments | Leaves | | Hypocotyls | | Roots | |
|--------------------------|--------------------|---------------------|--------------------|---------------------|---------------------|---------------------|
| | Na | K | Na | K | Na | K |
| Initial concentration | 0.62 ± 0.05 | 31.83 ± 1.92 | 1.46 ± 0.09 | 40.49 ± 3.59 | 11.51 ± 0.24 | 16.76 ± 0.18 |
| K + Ca | 0.64 ± 0.04 | 39.61 ± 2.54 | 1.47 ± 0.19 | 37.65 ± 4.53 | 11.55 ± 0.39 | 19.98 ± 2.45 |
| Na + K + Ca | 7.12 ± 0.31 | 43.91 ± 4.83 | 4.33 ± 0.32 | 31.65 ± 1.53 | 15.58 ± 1.16 | 16.94 ± 0.65 |

The ranges shown are the standard errors of the means of three replications.

TABLE VII. SODIUM TRANSLOCATION FROM THE LEAVES TO THE ROOTS
AS AFFECTED BY THE COMPOSITION OF THE MEDIUM SUPPLIED
TO THE ROOTS (MEQ./KG. FR. WT.)*

| Medium supplied to the roots | Increase in sodium concentration in the roots | Medium supplied to the roots | Increase in sodium concentration in the roots |
|------------------------------|---|--|---|
| Water | 0.70 ± 0.16 | Calcium (5 meq./1.) | 1.80 ± 0.18 |
| Potassium (5 meq./1.) | 1.06 ± 0.17 | Calcium + potassium (5 meq./1. each) | 2.21 ± 0.44 |

*Values are the differences between the concentration in the roots after the experiment and the initial concentration of 1.47 meq./kg. fr. wt. The ranges shown are the standard errors of the means of three replications.

This was particularly true when the medium contained calcium. The sodium translocation to these roots was significantly higher than that to roots in water or potassium solutions.

From the several experiments described it may be concluded that sodium can be translocated from the leaves to the roots even against a concentration gradient. Moreover, the above results also indicated that ions in the root medium have an influence on this translocation.

It was shown earlier, e.g., in the time course absorption study (Figure 1) that little sodium accumulated in the leaves when supplied to the roots, yet the amount in the shoot increased with time. Since sodium has just been demonstrated to move from the leaves to the roots, the mobility of this element in the plant body is apparent. From the results presented thus far it was suspected that the reason for the low amount of sodium in the intact shoot may be the translocation of this element back to the roots as it gets to the leaf, as Collander (1941a)

had speculated. The next series of experiments was done to test this possibility further.

V. The Effect of Girdling on the Translocation of Sodium

If it is true that the reason for the low amounts of sodium in the leaves is due to its being translocated back to the roots, then it should be possible to induce the leaf to accumulate greater amounts of this element if the downward movement is suppressed. Girdling is one of the most common experimental methods used in studies of this nature. It is a way of stopping the movement of translocates in the phloem.

Because of the bicollateral nature of the vascular bundles of the squash hypocotyl the phloem cannot be separated easily from the xylem as is commonly done with woody dicots. Therefore steam girdling was the method employed to terminate phloem activity. The total effect of steam girdling is more than just the abolition of phloem activity since the steam kills all the cells at the point of application.

A jet of steam was directed onto the rotating hypocotyl for a minute or two. A loss of turgor and a change in color to darker green was observed at the place of steaming. In a few hours this portion of the hypocotyl shrank to the size of a completely dried hypocotyl. No sign of wilting of the leaves was observed for 48 hours or more. Furthermore water loss from the medium supplied to the roots of the plants was not decreased as a result of girdling. Hence the xylem system apparently functioned normally or nearly so.

After the experimental period, the plants were divided into leaves, hypocotyl tissue above girdle, hypocotyl tissue below the girdle and roots. Inasmuch as some plants were not girdled the terminology that

will be used subsequently will be "apical hypocotyl" and "basal hypocotyl" for that part above or below the girdle, or above or below a corresponding point in an ungirdled hypocotyl.

The results from the first experiment conducted in this series are shown in Table VIII. The amount of sodium in the leaves was higher in the girdled than in the ungirdled plants, although the difference is not significant.

In the plants that were harvested at the beginning of the experiment, there was apparently no difference in sodium or potassium concentration between the apical and basal hypocotyls. After 24 hours of absorption by ungirdled plants sodium was higher in the basal than in the apical portion of the hypocotyl. In the case of the plants that were girdled sodium accumulated above the girdle in the apical hypocotyls. The apical hypocotyls of the girdled plants had more than twice the concentration of sodium found in the corresponding part of the ungirdled plants.

When sodium contents of the leaves and apical hypocotyls are added together and the girdled and ungirdled plants compared (Table VIIIA) it can be seen that there was a definite accumulation of sodium above the girdle, and that there was no similar effect on the distribution of potassium.

The higher concentration of sodium in the apical hypocotyls than in the leaves of the girdled plant was looked upon as a consequence of a mechanism which tends to move sodium from the leaves towards the roots. It is possible that in a more prolonged experiment a saturation point in the apical hypocotyls would be reached beyond which further movement of the element out of the leaves would be prevented.

TABLE VIII. THE EFFECT OF GIRDLING THE HYPOCOTYL ON THE CONCENTRATION OF SODIUM AND POTASSIUM IN THE DIFFERENT ORGANS OF THE PLANT (MEQ./KG. FR. WT.)

| Treatments | Water loss (ml.) | Element | Leaves | Apical hypocotyls | Basal hypocotyls | Roots |
|------------------------|---------------------|---------|---------------------|----------------------|---------------------|---------------------|
| Initial concentrations | - | Na | 0.73 ± 0.09 | 1.69 ± 0.29 | 1.43 ± 0.19 | 7.44 ± 0.36 |
| | | K | 39.03 ± 0.94 | 49.20 ± 2.30 | 50.44 ± 7.48 | 30.29 ± 2.93 |
| Not girdled | 113 ± 9 | Na | 2.85 ± 0.41 | 3.94 ± 0.15 | 4.98 ± 0.13 | 11.24 ± 1.13 |
| | | K | 54.82 ± 2.53 | 70.98 ± 2.25 | 60.43 ± 1.89 | 26.44 ± 0.52 |
| Girdled | 115 ± 13 | Na | 3.90 ± 0.39 | 8.89 ± 0.75 | 4.93 ± 0.17 | 10.53 ± 0.38 |
| | | K | 45.61 ± 1.09 | 70.69 ± 1.49 | 55.72 ± 1.43 | 25.48 ± 1.45 |

The ranges shown are the standard errors of the means of three replications.

TABLE VIII. THE EFFECT OF GIRDLING ON THE SODIUM AND POTASSIUM CONTENT ABOVE AND BELOW THE GIRDLE (MEQ./5 PLANTS)

| Treatments | Element | Leaves + apical hypocotyls | Roots + basal hypocotyls | Whole plants |
|-------------------|---------|-------------------------------|-----------------------------|----------------------|
| Initial amount | Na | 0.017 ± 0.002 | 0.033 ± 0.001 | 0.050 ± 0.001 |
| | K | 0.77 ± 0.02 | 0.30 ± 0.03 | 1.06 ± 0.01 |
| Not girdled | Na | 0.064 ± 0.002 | 0.052 ± 0.012 | 0.116 ± 0.010 |
| | K | 1.25 ± 0.15 | 0.33 ± 0.06 | 1.58 ± 0.17 |
| Girdled | Na | 0.101 ± 0.008 | 0.046 ± 0.003 | 0.147 ± 0.009 |
| | K | 1.07 ± 0.07 | 0.28 ± 0.01 | 1.36 ± 0.07 |

The ranges shown are the standard errors of the means of three replications.

Table VIII A also shows that the total amount of sodium per plant was slightly more in the girdled than in the ungirdled plants. The amount of sodium in its basal regions was not significantly less in girdled than in ungirdled plants.

It was proposed earlier that a possible reason for the very low amount of sodium in the leaves could be the very small amount of this element being translocated from the roots to the leaves. Evidence in support of this is the observation that leaves floated on a solution containing sodium absorbed more of this element than did leaves of plants which had only their roots in contact with the solution containing sodium.

To test further the effect of roots on upward transport of sodium, girdled and ungirdled plants whose roots had been excised were used. For comparison plants with intact roots were also used in the same experiment. The results are shown in Table IX.

Upon comparing the two treatments in which the plants were girdled, the selectivity exerted by the roots against sodium transport to the tops is evident. The concentration of sodium in the apical hypocotyls of plants without roots was nearly three times as high as that in the same parts of the plants with roots.

It is not valid to compare the treatments without roots because the plants that were not girdled exhibited a loss of their turgor despite the fact that the roots were excised under water. The xylem vessels may have been plugged by phloem exudate to some extent. Partial blocking of the transpiration stream would result in less sodium and potassium moving up the shoot. That this was true appears to be confirmed by the lower amounts of sodium and potassium present in the leaves and apical hypocotyls.

TABLE IX. THE EFFECT OF ROOT EXCISION AND GIRDLING ON THE CONCENTRATION OF SODIUM IN THE DIFFERENT ORGANS (MEQ./KG. FR. WT.)*

| Treatments | Leaves | | Apical hypocotyls | | Basal hypocotyls | |
|---------------------------|---------------|----------------|-------------------|----------------|------------------|----------------|
| | Na | K | Na | K | Na | K |
| (Initial concentration) | (0.79) | (40.10) | (1.70) | (50.45) | (1.56) | (49.20) |
| Intact plants girdled | 1.83 ±0.15 | 42.09 ±1.62 | 5.30 ±0.08 | 46.37 ±0.99 | 4.11 ±0.22 | 27.52 ±2.97 |
| Roots excised girdled | 7.45 ±0.10 | 42.86 ±1.41 | 15.01 ±1.52 | 56.79 ±2.48 | 13.59 ±2.54 | 43.02 ±3.61 |
| Roots excised not girdled | 0.93 ±0.24 | 35.12 ±1.58 | 4.20 ±0.74 | 42.68 ±3.44 | 14.65 ±0.51 | 40.78 ±4.12 |

*Values for treatments are the differences between the initial and final concentrations.

The ranges shown are the standard errors of the means of three replications.

The high amount of sodium in the basal hypocotyls of the plants without roots was something that was not anticipated. This sodium could not have come from the leaves since the basal hypocotyls of girdled plants were also high in sodium. This is likely due to the fact that the xylem was open and in contact with the solution.

The above experiment was repeated with modifications designed to prevent the loss of turgor by the ungirdled plants whose roots were excised. The plants were covered with transparent plastic bags. This prevented detectable loss of turgor in these plants. Results from this experiment are shown in Table X and Appendix Table 2.

In all cases covered plants absorbed less sodium and potassium than the uncovered ones. Thus, in this study transpiration had a great effect on the ions absorbed.

Data for the covered intact plants show the same trend as found previously (Table VIII) for apical portions of girdled and ungirdled plants. Again the main difference was in the apical hypocotyls. Unlike the data of Table VIII these data clearly show lower sodium values in portions below the girdle. The basal hypocotyls of the ungirdled plants had a concentration of 4.28 milliequivalents of sodium absorbed per kilo fresh weight as compared to 2.76 milliequivalents sodium per kilo fresh weight of the girdled plants. For the roots the amount was 9.20 milliequivalents for the ungirdled plants and 7.32 milliequivalents for the girdled plants.

The excised root systems had a sodium concentration of 8.91 milliequivalents per kilo fresh weight, whereas the roots of the uncovered intact plants had 12.99 milliequivalents per kilo fresh weight. This

TABLE X. THE EFFECT OF GIRDLING, CONTROLLED TRANSPIRATION AND ROOT EXCISION ON THE CONCENTRATION OF SODIUM IN THE VARIOUS ORGANS (MEQ./KG. FR. WT.)*

| Treatments | Water loss (ml.) | Leaves | Apical hypocotyls | Basal hypocotyls | Roots |
|---|---------------------|--------------------|----------------------|---------------------|---------------------|
| (Initial concentration) | - | (0.15) | (0.70) | (0.60) | (2.94) |
| Intact plants not girdled without cover | 168 ± 15 | 2.34 ± 0.66 | 4.00 ± 0.69 | 5.57 ± 0.72 | 12.99 ± 0.61 |
| Intact plants not girdled with cover | 50 ± 6 | 1.06 ± 0.24 | 1.67 ± 0.25 | 4.28 ± 0.28 | 9.20 ± 0.16 |
| Intact plants girdled with cover | 48 ± 12 | 1.47 ± 0.20 | 5.37 ± 0.47 | 2.76 ± 0.12 | 7.32 ± 0.03 |
| Without roots not girdled without cover | 78 ± 1 | 0.83 ± 0.08 | 3.85 ± 0.31 | 13.41 ± 0.30 | - |
| Without roots not girdled with cover | 32 ± 4 | 0.76 ± 0.10 | 2.02 ± 0.17 | 9.70 ± 0.62 | - |
| Without roots girdled with cover | 33 ± 6 | 1.16 ± 0.13 | 6.99 ± 0.95 | 9.79 ± 1.39 | - |
| Without roots girdled without cover | 53 ± 3 | 1.22 ± 0.31 | 9.54 ± 0.54 | 10.77 ± 0.34 | - |
| Excised roots only | - | - | - | - | 8.91 ± 0.62 |

*Values for treatments are the differences between the initial and final concentrations.

The ranges shown are the standard errors of the means of three replications.

highly significant difference showed that as much as a third of the sodium in the roots of the intact plants can be accounted for by sodium translocated from the leaves. The amount of potassium present in the roots did not seem to be affected by the shoot.

Table X also shows that plants without roots behaved in a manner similar to intact plants insofar as the effect of girdling and controlled transpiration is concerned. In the present experiment the uncovered plants did not lose their turgor as much as those of Table IX. Also the high concentration of sodium in the plants without roots observed in the earlier experiment (Table IX) was not found here. However, when another experiment was performed (Table XI and Appendix Table 3) the trend obtained was essentially the same as in Table IX.

All the experiments that have been presented so far were performed with plants germinated in very dilute nutrient medium. In most cases the plants were transferred to the experimental solution and allowed to remain there for only 24 hours prior to their harvest. The question arose, would the results obtained earlier be consistent if girdling were done on plants that are in a steady state of ion absorption?

An experiment to answer this question was performed on plants grown in a manner similar to that used in the 192-hour absorption experiment shown in Table II. The seeds were germinated in the usual medium. Seven days later the plants were transferred to gallon jars containing the usual medium and, in addition, varying amounts of sodium. Thirteen days after soaking the seeds, one-half of the plants were girdled while the rest were left intact. The girdled and ungirdled plants were then returned to their original solution. Both groups of plants were har-

TABLE XI. THE EFFECT OF GIRDLING, CONTROLLED TRANSPIRATION AND
ROOT EXCISION ON THE CONCENTRATION OF SODIUM
IN THE VARIOUS ORGANS (MEQ./KG. FR. WT.)*

| Treatments | Water loss (ml.) | Leaves | Apical hypocotyls | Basal hypocotyls | Roots |
|---|------------------------|--------------------|----------------------|---------------------|---------------------|
| (Initial concentration) | - | (0.18) | (0.40) | (0.42) | (1.10) |
| Intact plants not girdled without cover | 138 \pm | 1.55 ± 0.05 | 3.53 ± 0.16 | 3.80 ± 0.18 | 12.32 ± 0.19 |
| Intact plants girdled with- out cover | 137 ± 7 | 2.10 ± 0.09 | 6.31 ± 0.44 | 3.27 ± 0.23 | 10.95 ± 0.18 |
| Without roots not girdled without cover | 48 ± 3 | 0.20 ± 0.01 | 2.36 ± 0.14 | 14.70 ± 0.89 | - |
| Without roots girdled with- out cover | 62 ± 1 | 3.69 ± 0.26 | 11.29 ± 0.50 | 14.72 ± 1.01 | - |
| Without roots not girdled with cover | 13 ± 1 | 0.13 ± 0.03 | 1.25 ± 0.03 | 7.03 ± 0.07 | - |
| Without roots girdled with cover | 13 ± 1 | 0.47 ± 0.04 | 3.72 ± 0.08 | 7.53 ± 0.33 | - |

*Values for treatments are the differences between the initial and final concentrations.

The ranges shown are the standard errors of the means of three replications.

vested 24 hours later. The results obtained from this experiment are shown in Table XII and Appendix Table 4.

The present results show that many of the comparisons between corresponding parts of girdled and ungirdled plants lack statistical significance. In all cases, however, the organs above the girdle tended to show a higher concentration of sodium compared to the corresponding part in the ungirdled plant. It should also be taken into consideration that the experiment was conducted for 24 hours and that with experiments like this, the longer the absorption period, the greater would be the differences between treatments.

The only instance in which leaves had a higher concentration of sodium than the roots is shown in Table XII. This happened as a result of interference with the rootward movement of sodium by girdling.

The earlier observation that doubling the concentration of sodium in the medium approximately doubled the concentration of sodium in the organs was again observed. The potassium content of the shoot (Appendix Table 4) does not seem to have been affected by the concentration of sodium in the medium or in the tissues. That of the root decreased with an increase in concentration of sodium in this organ.

.VI. Further Evidences on the Downward Translocation of Sodium

If the hypothesis that sodium travels upward by way of the transpiration stream before moving back to the root is correct, then greater differences in the sodium content of the blade should be obtained if girdling were performed on the petiole. It is to be remembered that steam girdling as shown in previous data resulted in greater differences in the sodium content of the apical hypocotyls than of the leaf blades.

TABLE XII. THE EFFECT OF GIRDLING PLANTS IN A STEADY STATE
OF ION ABSORPTION ON THE CONCENTRATION OF SODIUM IN
THE DIFFERENT ORGANS (MEQ./KG. FR. WT.)

| Treatments | Leaves | Apical hypocotyls | Basal hypocotyls | Roots |
|--------------------|------------|----------------------|---------------------|------------|
| <u>Not girdled</u> | | | | |
| 0 meq. Na/l. | 0.57 | 0.86 | 0.90 | 2.64 |
| 5 meq. K/l. | ± 0.06 | ± 0.17 | ± 0.13 | ± 0.26 |
| 5 meq. Na/l. | 3.11 | 8.62 | 12.26 | 12.64 |
| 5 meq. K/l. | ± 0.28 | ± 1.30 | ± 1.58 | ± 0.87 |
| 10 meq. Na/l. | 5.81 | 16.23 | 23.18 | 21.24 |
| 5 meq. K/l. | ± 0.57 | ± 2.09 | ± 4.24 | ± 1.70 |
| 20 meq. Na/l. | 19.94 | 39.57 | 55.09 | 35.72 |
| 5 meq. K/l. | ± 5.29 | ± 8.06 | ± 8.43 | ± 1.10 |
| <u>Girdled</u> | | | | |
| 0 meq. Na/l. | 0.99 | 1.39 | 1.22 | 2.67 |
| 5 meq. K/l. | ± 0.19 | ± 0.23 | ± 0.25 | ± 0.39 |
| 5 meq. Na/l. | 4.74 | 12.98 | 8.08 | 11.08 |
| 5 meq. K/l. | ± 0.25 | ± 1.14 | ± 0.58 | ± 0.35 |
| 10 meq. Na/l. | 9.31 | 26.53 | 18.75 | 19.33 |
| 5 meq. K/l. | ± 0.53 | ± 1.84 | ± 4.36 | ± 1.38 |
| 20 meq. Na/l. | 39.04 | 45.33 | 40.13 | 31.66 |
| 5 meq. K/l. | ± 4.89 | ± 3.61 | ± 3.74 | ± 1.95 |

The ranges shown are the standard errors of the means of three replications.

Thus, in one experiment the petiole of the first true leaf was girdled.

Data from this experiment are shown in Table XIII.

TABLE XIII. THE EFFECT OF GIRDLING THE PETIOLE OF THE FIRST TRUE LEAF ON THE SODIUM AND POTASSIUM CONCENTRATION IN THE BLADE (MEQ./KG. FR. WT.)

| Element | Initial concentration* | Not girdled** | Girdled* |
|---------|------------------------|---------------|--------------|
| Na | 0.27 ± 0.06 | 0.98 ± 0.11 | 2.25 ± 0.45 |
| K | 8.45 ± 0.09 | 13.83 ± 0.30 | 14.54 ± 0.50 |

*Three replications.

**Two replications.

The ranges shown are the standard errors of the means.

The data show that the amount of sodium retained within the 24-hour experimental period in the blade of the leaf whose petiole had been girdled was significantly greater than that in the blade of the leaf whose petiole was not girdled. The above observation is an indication that under normal transpiring conditions some of the sodium may move up to the leaf blades before it moves back to the roots. There is no evidence, however, to prove that downward movement does not occur with sodium ions that have not reached the leaf.

Another experiment elaborating the downward movement of sodium was with the split root technique. The method consisted essentially of putting half of the root system of the plant in a medium containing sodium while the other half was placed in another medium not containing this element.

The squash plant has a main tap root from which long secondary roots branch out. It was impossible to divide the root system into equal parts.

Partition of the roots was then made at an arbitrary point on the root where the upper secondary roots would be just about equal to the rest of the tap root and the lower secondary roots. In a given replication with several plants, it was made a point that half of the plants had their main tap root in one medium while the other half of the plants had their main tap root in the other medium. Results from this experiment are shown in Table XIV.

TABLE XIV. SODIUM CONCENTRATIONS IN DIVIDED ROOT SYSTEMS GROWN IN THE PRESENCE OR ABSENCE OF THIS ELEMENT (MEQ./KG. FR. WT.)

| Treatments | Initial concentration | Roots in medium without sodium | Roots in medium with sodium |
|----------------|-----------------------|--------------------------------|-----------------------------|
| Intact plants | 9.63 \pm 0.21 | 25.82 \pm 0.57 | 39.58 \pm 4.12 |
| Excised roots* | - | 17.91 \pm 0.88 | 25.95 \pm 1.58 |

*Include about 1 cm. of the hypocotyl.

The ranges shown are the standard errors of the means of three replications.

The initial amount of sodium in the roots was 9.63 milliequivalents per kilo fresh weight. After 24 hours, the roots placed in the medium containing sodium had 39.58 milliequivalents per kilo fresh weight; the roots placed in the medium without sodium contained 25.82 milliequivalents of sodium per kilo fresh weight. The data thus indicate that sodium moved from the roots that absorbed the element from the medium to the roots that did not have sodium in their medium. Similar results had been obtained with peas (Barbier and Chabannes, 1951) and beans (Wallace and Hemaidan, 1963).

The set-up for the split root experiments, particularly with plants having tap root systems is such that there will always be the doubt that capillary action could occur in the bundled roots. If this happens, the element in question would travel to the other half of the roots and get absorbed there. Because of this possibility another set-up was made where the shoots, except for the basal 1 cm. of the hypocotyls were excised. If capillary action were a major factor involved, the amount of sodium in the roots placed in the medium without this element would be the same regardless of the presence or absence of the shoot. It is to be recalled that roots of intact plants had been found to contain more sodium than excised roots (Table X).

The data for the roots placed in the medium without sodium show a value of 17.91 milliequivalents of sodium per kilo fresh weight and 25.82 milliequivalents of sodium per kilo fresh weight for the excised and intact roots, respectively. This difference in sodium content between the excised and intact roots can be accounted for if we assume that the transpiring shoot took up more solute. As was shown earlier (Table X) transpiration had a great influence on the absorption of ions by the present experimental plants. With a greater amount of sodium in the shoot, a greater amount of this element could be translocated to the root.

This result is further evidence that the element sodium was translocated downward to the roots from the shoots. At the same time the data for the excised roots indicate that sodium may move back to the root without having reached the leaves.

If the translocation of sodium is an active process, inhibitors of respiration will affect it. An experiment was conducted for 6 hours to

determine the effect of the phosphate uncoupler 2,4-dinitrophenol on the sodium content of girdled and ungirdled plants. The results are shown in Table XV.

TABLE XV. THE EFFECT OF GIRDLING AND TREATMENT WITH DNP ON THE CONCENTRATION OF SODIUM IN THE PLANT (MEQ./KG. FR. WT.)*

| Plant part** | Initial concentration | Not girdled | | Girdled | |
|------------------------------|-----------------------|---------------|---------------|---------------|---------------|
| | | Control | DNP*** | Control | DNP*** |
| Leaves and apical hypocotyls | (0.49) | 0.17 ±0.03 | 1.11 ±0.11 | 0.40 ±0.04 | 1.19 ±0.04 |
| Roots | (23.61) | 8.36 ±1.01 | 6.49 ±1.41 | 4.46 ±0.57 | 3.25 ±1.57 |

*Six hours absorption period.

**Values for treatments are the differences between the final and initial concentrations.

*** 10^{-4} M.

The ranges shown are the standard errors of the means of three replications.

Data for the plants which were not treated with the uncoupler verify the earlier findings of accumulation of sodium above the girdle and a lower amount of the element in the organs below the girdle.

The incorporation of 10^{-4} M DNP into the root medium increased the amount of sodium translocated to the shoots and retained there to the same extent in girdled and ungirdled plants. This increase in the amount of sodium in the shoots was, however, accompanied by less accumulation in the roots although neither of the comparisons between control and DNP treatments showed statistically significant differences in sodium accumulation by the roots.

Assuming that the effect of DNP in accumulation of sodium in the roots is real, although lacking statistical significance, the results may be interpreted as DNP poisoning two active processes involving sodium. First was the loss of the integrity of the root in discriminating against the transport of sodium. Thus the poisoned plants acted in a way similar to those shown in Table XVIII where the roots were killed by immersion in boiling water. Secondly, since the amounts of sodium in the apical hypocotyl and leaves were the same for girdled and ungirdled plants, downward movement was evidently stopped by DNP in the ungirdled plants.

When such experiments were prolonged to 24 hours, the plants started to lose their turgor and almost all of the sodium in the roots was lost while the amount in the leaves increased to a much higher value.

As additional support for the hypothesis that sodium moved downward through the phloem another method of girdling was used. If the transport of sodium is really through the phloem then the living protoplasm must be involved. If this is the case sodium transport should be affected by temperature. Cold water girdling was therefore adapted in this experiment. Unlike steam girdling which kills the phloem together with the adjacent cells, cold temperature girdling reduces the activity of the living protoplasm.

Tygon plastic tubing having an inside diameter of 1 centimeter was used. Holes were made through the tube with the use of a cork borer. Through these holes were inserted glass tubes 2 centimeters in length having an inside diameter of 4 millimeters. The diameter of the

hypocotyl of the experimental squash plant was slightly smaller than this. The plants were inserted through the glass tubes and held in place with water-saturated absorbent cotton. The tygon tubing led to a cold water reservoir inside the freezer compartment of a refrigerator.

A pneumatic liquid pump circulated cold water through the jackets and back to the reservoir. A thermometer inserted into the input jacket showed a temperature range of 3° C. - 7° C. during the experiment. Another thermometer on the output jacket registered a range of 8° C. - 12° C. The temperature in the jackets from the start to the termination of the experiment probably averaged less than 10° C. A corresponding set-up making use of tap water at a temperature of 25° C. was used for comparison. In both cases five plants composed a replication.

Due to pump malfunctioning the experiment was terminated after 10 hours instead of the desired 24 hours. The plants were cut just above the jacket, dried and analyzed (Table XVI) for their sodium and potassium contents.

TABLE XVI. SODIUM AND POTASSIUM CONCENTRATION IN THE LEAVES AND APICAL PART OF HYPOCOTYLS AS AFFECTED BY VARIOUS TYPES OF GIRDLING (MEQ./KG. FR. WT.)

| Initial concentration* | | Cold water girdle* | | Steam girdle** | | Tap water girdle** | |
|------------------------|--------|--------------------|--------|----------------|--------|--------------------|--------|
| Na | K | Na | K | Na | K | Na | K |
| 0.22 | 32.89 | 1.12 | 36.47 | 1.19 | 39.71 | 0.54 | 35.35 |
| ±0.03 | ± 0.60 | ±0.27 | ± 1.11 | ±0.08 | ± 1.79 | ±0.08 | ± 0.76 |

*Three replications.

**Two replications.

The ranges shown are the standard errors of the means.

The data show that both cold water and steam girdling resulted in a greater amount of sodium in the organs above the girdle than did the tap water girdle.

VII. The Effect of Calcium on the Amount of Sodium Translocated to the Shoot

Jacobson et al. (1961) and Epstein (1961) found calcium to promote the selective accumulation of potassium by excised barley roots. In the presence of calcium, sodium accumulation is depressed while potassium uptake is accentuated. The fact that less sodium is accumulated by the roots suggests that less sodium may be translocated to the shoot. The data of Table VII show that calcium present in the root medium can promote the downward translocation of sodium. Calcium translocated to the shoot from the root probably displaced some sodium from its binding sites in the shoot. This could contribute to a lower sodium content in the shoot.

In one experiment, plants which were supplied with only salts of sodium and potassium were compared with plants which were supplied with a calcium salt in addition. To eliminate the secondary effects of the downward movement of sodium, the plants in one set were girdled. To eliminate the effect of root selectivity another set of girdled plants had their roots excised. The results from this experiment are shown in Table XVII.

The roots of the ungirdled plants in the absence of calcium absorbed about two atoms of sodium to one of potassium. However, the presence of calcium reduced the amount of sodium absorbed to only a quarter. At the same time the amount of potassium absorbed increased by about 50 percent.

TABLE XVII. THE EFFECT OF CALCIUM ON THE CONCENTRATION OF SODIUM AND POTASSIUM IN THE PLANT (MEQ./KG. FR. WT.)*

| Treatments | | Leaves + apical hypocotyls | | Roots | |
|--|-------------|-------------------------------|-----------------------|-----------------------|-----------------------|
| | | Na | K | Na | K |
| (Initial concentration) | | (1.24) | (41.23) | (15.73) | (14.69) |
| Intact plants; not girdled | Na + K | 0.68 <u>+0.16</u> | 24.09 <u>+3.74</u> | 36.24 <u>+0.89</u> | 24.38 <u>+1.97</u> |
| | Na + K + Ca | 0.99 <u>+0.15</u> | 43.62 <u>+1.51</u> | 9.73 <u>+0.63</u> | 36.46 <u>+1.10</u> |
| Intact plants; hypocotyls girdled | Na + K | 1.76 <u>+0.08</u> | 8.77 <u>+2.76</u> | 25.29 <u>+0.53</u> | 20.81 <u>+1.61</u> |
| | Na + K + Ca | 1.52 <u>+0.15</u> | 16.43 <u>+3.06</u> | 9.68 <u>+0.25</u> | 21.82 <u>+1.01</u> |
| Roots excised; hypocotyls girdled | Na + K | 4.41 <u>+0.47</u> | 6.20 <u>+0.30</u> | 20.69 <u>+1.17</u> | 24.79 <u>+0.33</u> |
| | Na + K + Ca | 9.44 <u>+2.95</u> | 13.16 <u>+1.21</u> | 6.69 <u>+0.56</u> | 29.54 <u>+1.29</u> |

*Values for treatments are the differences between the initial and final concentrations.

The ranges shown are the standard errors of the means of three replications.

This effect of calcium is reflected in the data showing about four atoms of potassium to every one of sodium absorbed. Thus the data suggest that calcium inhibits the absorption of sodium and in general promotes the uptake of potassium by the roots.

The effect of calcium on the absorption of potassium by the shoot was consistent with that of the root. That is, a greater transport of potassium to the shoot was brought about by the presence of calcium. In none of the treatments, however, did calcium significantly inhibit the transport of sodium to the shoot. This result was contrary to expectation considering the large effect calcium had in inhibiting the absorption of sodium by the roots.

In another experiment, the roots of the plants were killed by immersion in boiling water for about 3 minutes (Table XVIII). The presence of calcium in the medium did not affect the amount of sodium or potassium translocated to the shoot. The ratio of these two elements in the shoot was very close to unity.

It may be seen that even the dead cells of the boiled roots exhibited some selectivity due to calcium. In the absence of calcium the roots retained the original amount of sodium. The presence of calcium in the medium reduced this amount to one-half. In the case of potassium, the absence of calcium reduced the original amount to one-tenth, while in its presence, the amount of potassium was reduced to only one-third.

An experiment was also conducted to determine whether the predominating anion in the root medium has an effect on the translocation of sodium and potassium to the shoot. The chloride, nitrate, sulfate and phosphate salts of sodium and potassium were used. Results from this experiment are shown in Table XIX.

TABLE XVIII. THE EFFECT OF CALCIUM ON THE AMOUNT OF SODIUM
AND POTASSIUM ABSORBED IN THE ORGANS OF THE PLANT
AFTER KILLING THE ROOTS BY IMMERSION
IN BOILING WATER

| Treatments | Shoots (meq./kg. fr. wt.)* | | | Roots (meq./5 plants) | |
|-------------------------|----------------------------|-----------------------|----------------------|------------------------|------------------------|
| | Na | K | K/Na | Na | K |
| (Initial concentration) | (0.22) | (30.45) | - | (0.024) | (0.033) |
| Na + K | 16.03 <u>±0.74</u> | 18.10 <u>±2.86</u> | 1.13 <u>±0.15</u> | 0.025 <u>±0.001</u> | 0.003 <u>±0.001</u> |
| Na + K + Ca | 15.79 <u>±0.19</u> | 15.19 <u>+1.34</u> | 0.96 <u>±0.09</u> | 0.010 <u>±0.001</u> | 0.011 <u>±0.001</u> |

*Values in the shoots for the treatments are the differences between the final and initial amounts.

The ranges shown are the standard errors of the means of three replications.

TABLE XIX. THE EFFECT OF CALCIUM CHLORIDE ON THE ABSORPTION OF SODIUM AND POTASSIUM FROM SEVERAL OF THEIR SALTS (MEQ./KG. FR. WT.)

| Treatments | Shoots | | Roots | |
|--|--------------------|---------------------|---------------------|---------------------|
| | Na | K | Na | K |
| (Initial concentration) | (1.59) | (30.78) | (16.12) | (15.29) |
| NaCl + KCl | 0.86 ± 0.11 | 7.82 ± 0.75 | 15.98 ± 0.89 | 10.26 ± 0.41 |
| NaCl + KCl + CaCl ₂ | 0.70 ± 0.09 | 20.46 ± 1.38 | 2.43 ± 0.18 | 21.99 ± 0.17 |
| NaNO ₃ + KNO ₃ | 1.95 ± 0.45 | 20.51 ± 1.30 | 27.14 ± 1.04 | 12.69 ± 0.90 |
| NaNO ₃ + KNO ₃ + CaCl ₂ | 1.43 ± 0.11 | 23.16 ± 2.25 | 11.43 ± 1.55 | 26.27 ± 2.83 |
| Na ₂ SO ₄ + K ₂ SO ₄ | 0.60 ± 0.02 | 8.19 ± 0.89 | 21.44 ± 1.26 | 7.02 ± 0.25 |
| Na ₂ SO ₄ + K ₂ SO ₄ + CaCl ₂ | 0.79 ± 0.03 | 8.61 ± 1.28 | 5.24 ± 1.24 | 19.45 ± 0.85 |
| NaH ₂ PO ₄ + KH ₂ PO ₄ | 0.44 ± 0.04 | 10.30 ± 1.67 | 18.06 ± 0.97 | 14.21 ± 0.10 |
| NaH ₂ PO ₄ + KH ₂ PO ₄ + CaCl ₂ | 0.48 ± 0.33 | 17.43 ± 1.35 | 1.46 ± 1.00 | 21.77 ± 0.97 |

*Values for treatments are the differences between the initial and final concentrations.

The ranges shown are the standard errors of the means of three replications.

The results show that of the four pairs of salts used, in general, the nitrates favored a greater absorption of sodium and potassium. When nitrate was the predominant anion, the presence of calcium chloride in the medium tended to inhibit the translocation of sodium to the shoot. However, the difference between the sodium content of shoots grown in the presence or absence of calcium was not significant. On the other hand when sulfate was the predominant anion the presence of calcium in the medium seemed to promote the upward movement of sodium although again in this case the difference is not significant. In the case of phosphate as found earlier along with chloride, the presence of calcium did not seem to affect the upward translocation of sodium.

The upward translocation of potassium when supplied as either nitrate or sulfate was not apparently affected by calcium chloride. However, in the case of the chloride and phosphate salts, the presence of calcium chloride in the medium promoted the translocation of potassium to the shoot.

In the case of the roots, regardless of the anion in the medium, calcium chloride invariably inhibited sodium absorption and promoted potassium accumulation.

With the results obtained so far, it still can not be stated whether calcium has an effect on the upward translocation of sodium. Under ordinary field conditions many workers have shown that a lesser uptake of sodium results from application of calcium to the soil. Jones et al. (1952) showed that the sodium content of citrus leaves decreased with the application of gypsum to the soil. The improvement of plant growth in alkali soils calls for application of gypsum (Ratner, 1935; Richards, 1954). Replacement of the exchangeable sodium from the clay surfaces

followed by leaching is the explanation offered. It was only recently that calcium was shown to inhibit sodium absorption in the absence of clays in a purely liquid medium (Jacobson et al., 1961; Epstein, 1961). The "antagonistic" effect between these two ions in biology and colloids, however, has been known for a long time (Bernstein and Hayward, 1958).

Perhaps the experimental period of 24 hours was too short to reflect in the shoot the effect of calcium on the root. To overcome the possibility of a secondary effect of the shoot, experiments were performed to determine sodium and potassium translocated upward via xylem exudates. In one experiment the plants were decapitated soon after they were transferred to the experimental solution, leaving a stump 2 - 4 centimeters long. Liquid appearing on the cut end during the first hour was discarded. After the first hour, the exudates were collected with individual 1 milliliter syringes from time to time for about 10 hours. The results from this experiment are shown in Table XX.

TABLE XX. THE EFFECT OF CALCIUM ON THE AMOUNT OF SODIUM AND POTASSIUM IN SQUASH EXUDATES

| Treatments | Exudate collected (ml.) | Na | | K | |
|-------------|-------------------------|------------------------|---------|------------------------|---------|
| | | meq. X 10 ⁴ | meq./l. | meq. X 10 ⁴ | meq./l. |
| Na + K | 2.43 | 37.80 | 1.55 | 209.46 | 8.65 |
| Na + K + Ca | 3.30 | 27.39 | 0.73 | 407.40 | 10.91 |

The results show that insofar as the composition of the exudate is concerned calcium did promote the uptake of potassium and concurrently inhibited the upward movement of sodium. Of equal or greater significance is the fact that the concentration of sodium in the exudate was

less than that in the medium bathing the roots. Hence this is a good demonstration of the selectivity of the roots with regard to sodium. This contrasts markedly with the potassium concentrations of the exudate which were in both cases higher than in the external solution.

Since decapitation or wounding is an undesirable feature of the above experiment it was thought that the above results should be compared with the water of guttation from intact seedlings. For this purpose rice seedlings were used since squash seedlings had never been observed to guttate under the present conditions of growing them. The rice seedlings were used when their first true leaves were just coming out of the coleoptiles. The liquid accumulating at the tips of the coleoptiles and leaves was collected. At this stage of development each of the seedlings had only one root 5 - 10 centimeters long. In one treatment the root tips were cut a centimeter from the tip. Results from this experiment are shown in Table XXI.

Similar to the case of the squash exudates, the data on the composition of the water of guttation from rice seedlings show that calcium inhibited the upward movement of sodium and promoted the uptake of potassium. The only apparent effect of cutting the root tips was the lower total amount of guttation compared to that from intact plants. This is probably the reason for the slight but insignificant increase in the concentration of ions in the guttate.

It should be noticed that in both experiments the concentration of sodium was much lower than potassium in the xylem sap. The potassium concentration in each case represented an accumulation, whereas the sodium concentration was lower than that of the external medium.



TABLE XXI. THE EFFECT OF CALCIUM ON THE SODIUM AND POTASSIUM CONTENT OF RICE SEEDLING GUTTATES

| Treatments | No. of collections* | Meq./1000 c.c. of guttate | |
|---------------|---------------------|---------------------------|------------------|
| | | Na | K |
| Na + K | 5 | 2.22 \pm 0.25 | 9.48 \pm 0.73 |
| Na + K + Ca | 5 | 1.41 \pm 0.10 | 11.86 \pm 0.89 |
| Na + K + Ca** | 4 | 1.56 \pm 0.12 | 12.65 \pm 1.21 |

*Collections were made within a 10 hour period.

**Root tips were excised to 1 cm. from tip.

The ranges shown are the standard errors of the means of the collections.

From the results of the last two experiments it is clear that calcium promoted the selectivity of upward transport insofar as the upward movement was due to root pressure. It can not be ascertained whether similar results would be obtained in cases where the xylem sap is moving upward due to a transpirational pull. In any case it is also possible that the observed selectivity promoted by calcium under some field conditions may be due to that governed by the long time effects of root pressure.

DISCUSSION

In many plants the concentration of sodium in the leaf cells is very low relative to that of the root cells. In the foregoing experiments attempts were made to find the physiological mechanism responsible for preventing the build-up of sodium in the leaves.

The findings indicate that the relatively low concentration of sodium in the upper parts of the plant as compared to that of potassium is due to the selectivity exerted by the roots. Thus, excision of the roots or killing the roots by immersion in boiling water resulted in movement of equivalent amounts of sodium and potassium to the tops of the plants.

The relatively low concentration of sodium in the leaf cells can be partially explained by translocation of this element back to the roots. Evidence for this was obtained from experiments on girdling. Steam girdling as well as localized chilling of the hypocotyl resulted in the accumulation of sodium above the girdle or the chilled portion. Furthermore, the sodium content of the roots of the girdled plant or of excised roots was found to be less than the sodium content of roots of intact plants. The phosphate uncoupler 2,4-dinitrophenol also stopped the downward translocation. Girdling the hypocotyl of poisoned plants did not have any effect on the amount of sodium above the point of girdling.

Because of the large effect calcium has in reducing the absorption of sodium by the roots, it was first thought that this element may also play a role in keeping the amount of sodium in the shoot low. However, the 24-hour experiments conducted here failed to reveal this effect of

calcium. Only when the upward movement was due to root pressure, as in the case of exudation from a cut stump or guttation from an intact seedling, were consistent results obtained. In this latter case calcium reduced the amount of sodium translocated to the shoot.

Quantitatively the amount of sodium retained above the girdle in excess of that retained above the same point in ungirdled plants, which is taken to be the amount supposed to be translocated back to the roots in a normal intact plant, can account for the maintenance of a low amount of sodium in the leaves to a considerable extent. In some 20 experiments comparing girdled and ungirdled plants supplied with various concentrations of sodium and for various lengths of time, the ratio of the total amount of sodium in the leaves and apical hypocotyls of girdled plants to that of ungirdled plants ranged from 1.2 - 7.2 with an average of 2.1 (Table XXII).

Peel and Weatherly (1959) found about 2 percent potassium and only "traces of sodium" in the phloem sap of Salix. If "traces" means somewhere around one-fiftieth the concentration of potassium, then this is still within the ratio of the two elements in the shoot of the present experimental plants. Ratios of up to more than 100 between these two elements in the leaves have been obtained in the present study. Furthermore the concentration of sodium in the phloem sap is not expected to be high if the feedback mechanism of internal sodium control is functioning. It might be high if and when the mechanism is stopped such as by poisoning, or when the concentration of sodium getting into the leaves is beyond the load capacity of the control mechanism.

TABLE XXII. SODIUM AND POTASSIUM IN THE LEAVES AND APICAL HYPOCOTYLS
OF PLANTS FROM THE VARIOUS GIRDLING EXPERI-
MENTS (MEQ./5 PLANTS)

| Experi- ment No.* | Na | | | K | | |
|-------------------------|-----------|---------|-----------------------------|-----------|---------|-----------------------------|
| | Ungirdled | Girdled | <u>Girdled</u> Ungirdled | Ungirdled | Girdled | <u>Girdled</u> Ungirdled |
| 1 | 0.064 | 0.101 | 1.58 | 1.25 | 1.07 | 0.86 |
| 2 | 0.015 | 0.072 | 4.80 | 0.22 | 0.31 | 1.41 |
| 3 | 0.033 | 0.058 | 1.76 | 0.97 | 0.77 | 0.79 |
| 4 | 0.025 | 0.050 | 2.00 | 0.72 | 0.73 | 1.01 |
| 5 | 0.029 | 0.043 | 1.48 | 0.62 | 0.71 | 1.15 |
| 6 | 0.046 | 0.063 | 1.37 | 1.27 | 1.02 | 0.80 |
| 7 | 0.014 | 0.101 | 7.21 | 0.70 | 0.88 | 1.26 |
| 8 | 0.011 | 0.023 | 2.09 | 0.74 | 0.68 | 0.92 |
| 9 | 0.011 | 0.018 | 1.64 | 1.71 | 1.73 | 1.01 |
| 10 | 0.066 | 0.100 | 1.52 | 1.68 | 1.76 | 1.05 |
| 11 | 0.124 | 0.180 | 1.45 | 1.79 | 1.55 | 0.87 |
| 12 | 0.367 | 0.711 | 1.94 | 1.60 | 1.75 | 1.09 |
| 13 | 0.007 | 0.016 | 2.29 | 0.43 | 0.54 | 1.26 |
| 14 | 0.008 | 0.012 | 1.50 | 0.27 | 0.21 | 0.78 |
| 15 | 0.009 | 0.011 | 1.22 | 0.35 | 0.24 | 0.69 |
| 16 | 0.019 | 0.037 | 1.95 | - | - | - |
| 17 | 0.004 | 0.007 | 1.75 | 0.49 | 0.47 | 0.96 |
| 18 | 0.007 | 0.014 | 2.00 | 0.43 | 0.44 | 1.02 |
| 19 | 0.009 | 0.013 | 1.44 | 0.48 | 0.43 | 0.90 |
| 20 | 0.015 | 0.026 | 1.73 | 0.61 | 0.42 | 0.69 |
| Average | | | 2.14 | | | 0.97 |

*Comparisons between experiments are not possible due to the drastically differing treatments involved.

Relevant to maintenance of the sodium gradient is a knowledge of which organ of the plant is responsible for it. Do the shoot cells extrude sodium, or do the root cells attract and accumulate sodium?

The translocation of solutes from the leaves to the roots is a very much studied phenomenon, particularly for organic substances. Not only assimilates from photosynthesis (Mason and Maskell, 1928; Vernon and Aronoff, 1952; Hartt et al., 1963, 1964; Shiroya et al., 1962) and exogenously applied naturally occurring substances such as amino acids (Nelson and Gorham, 1959) are translocated to the roots but also substances which are not of plant origin such as herbicides or urea (Chlor et al., 1962; Crafts, 1961).

Pristupa and Kursanov (1957) showed that in 22-day old pumpkin plants 18 - 48 percent of the C^{14} introduced to a leaf appeared in the roots within 2 hours. Nelson and Gorham (1959) refer to this as a "pull" or a "demand" of the root. At the same time they admit that translocation is still predominantly downward even in plants which had their roots removed.

The present author believes it is the cells in the shoot which are responsible for keeping the sodium content very low. The evidence for this is as follows. First of all it should be noted that as Collander (1941b) had found the large variation in sodium content of plants was only in their shoots. Although the sodium content of the shoots of various species differed as much as 50 times, that of the roots differed only about 3 times.

Secondly, evidence from the present findings showed that even in girdled plants with roots removed, the translocation of sodium was still

predominantly downward as shown by the accumulation of this element above the girdle.

The third evidence is based on data from scion-rootstock combinations obtained by other workers. Smith, Reuther and Specht (1949) studied the effect of six rootstocks on the mineral composition of the leaves of Valencia oranges. They found that among the elements nitrogen, phosphorus, potassium, calcium, magnesium, manganese, copper, iron, boron, zinc and sodium, only the sodium content of the leaves was not significantly influenced by any of the rootstocks. In other words, the entry or accumulation of any of the above elements into the root thence to the shoot, with the exception of sodium, is a property of the cells of the particular rootstock.

Cooper, Gorton and Olson (1952) studied the mineral composition of the leaves of Valencia orange and Shary Red grapefruit scions each grafted to a Cleopatra Mandarin or sour orange rootstock. They found a significantly greater accumulation of sodium in leaves of the grapefruit compared to leaves of orange. This was true on both rootstocks. Quite different results were obtained for boron, chloride, calcium, potassium and magnesium.

Much has been said about the absorption and translocation of sodium in the plant, but of what importance is this element to the plant?

There are scattered claims in the literature of the essentiality of sodium for the growth of some plants (Holt and Volk, 1945; Harmer and Benne, 1945; Lehr, 1941; Osterhout, 1912; Hopkins, 1950; Williams, 1960; Brownell and Wood, 1957). However, the present consensus of opinion is that sodium can be dispensed with in the growth of the higher plants.

When Sachs (1860) formulated the first synthetic growth media for plants, sodium chloride was one of the constituent salts, and was considered essential. However, he later (1887) recognized this as "superfluous".

Based on the criteria of essentiality of an element for plant growth as formulated by Arnon (1950), certainly sodium can not be considered essential. It has been demonstrated in many instances that its presence in the medium increased the growth and yield of crop plants (Andrews and Coleman, 1939; Lunt and Nelson, 1951, Truog et al., 1953; Cope et al., 1953; Cooper et al., 1953). In some blue-green algae, an obligate requirement for sodium has been shown (Kratz and Myers, 1955). However, with the higher plants this has never been demonstrated.

Despite its non-essentiality for the growth of higher plants the presence of sodium in plants is ubiquitous. Analysis of some 450 species of flowering plants collected from France, Switzerland, Italy and England showed the invariable presence of this element in the plant body (Bertrand, 1951; also Bertrand and Perietzeanu, 1928; compare however with Wallace et al., 1948). This is because sodium is omnipresent in soils.

Damage due to the accumulation of sodium in excessive quantities is not as frequent as damage caused by some other elements (e.g., chloride). Necrosis of the leaves due to the build-up of sodium has been reported for plums, almonds, peaches, citrus and avocado. The situation is probably such that the amount of sodium entering the plant is much beyond the capacity of the control mechanism. The damage would undoubtedly be greater if the control mechanism were stopped as by girdling.

More detailed information regarding the mechanism of sodium toxicity is not available. Even studies on the physiology of salt tolerance do

not reveal much information on the nature of sodium toxicity or tolerance to this element. The work of Niemann (1962) on the response of 12 crop plants to increasing concentrations of sodium chloride revealed that lack of photosynthate does not generally limit the growth of salt-stunted plants. He found that respiration increased in both salt-resistant and salt-sensitive species with increase of salt in the medium. However, the increase in respiration was generally greater and occurred at lower levels of salt in the salt sensitive species. He further found that respiration of the roots of both resistant and sensitive species failed to indicate any consistent effect of the treatment. Hence root cells appear to be less sensitive to high sodium concentrations in terms of respiration rate as well as in terms of toxic effects.

The property of discriminating against the accumulation of sodium is a characteristic that has evolved from the very early sea-floating ancestors of the present day vascular plants. Steinbach (1962) speculated that in the origin of life, the discrimination against the accumulation of sodium may even have preceded the formation of plasma membranes and considers the development of ion gradients as the step at which cells first become responsive to environmental changes.

Some higher plants have partially or completely lost this property of internal sodium control. The first group of plants shown in Table I are probably such examples. The concentration of sodium in their leaves is equal to or greater than that in their roots. Most of these plants under normal conditions would probably show a growth response to the application of sodium to the medium. Truog et al. (1953) and Larson and Pierre (1953) noted that plants which respond to sodium application

are those that show a relatively large increase in sodium content in their leaves.

The shoots of most vascular plants, however, still possess this property of selectivity against the accumulation of sodium. Thus the concentration of sodium in the shoots of the second group of plants in Table I is much lower than the concentration in the roots. These plants apparently retain the internal sodium control mechanism preventing the inevitable rise in sodium in the transpiring leaf.

It thus appears that the large variability in the sodium content of plants compared to that of other elements (Collander, 1941a) may be due to the loss of the internal sodium control mechanism in some species and the retention in others.

It should also be noticed that plants of the first group in Table I are generally resistant to high concentrations of sodium in the medium while those of the second group are not. Collander (1941a) contended that "probably this specific lack of power to exclude sodium ions is a character which in some way enables the halophytes to thrive on saline substrates not suited to requirements of the glycophytes."

There are, however, some notable exceptions to the above generalization. For example, alfalfa and possibly other plants belonging to the second group of plants in Table I are fairly resistant to saline conditions of the medium.

SUMMARY

When squash plants were grown in equivalent concentrations of sodium and potassium, the amount of sodium absorbed by the plants was much less than potassium. When the roots were excised or killed by immersion in boiling water, the amount of sodium translocated to the shoot increased while potassium decreased compared to that of intact plants. An equal amount of these two elements was translocated to the shoot when the living roots were absent.

The concentration of sodium in the squash plant was found to be higher in the roots than in the shoots. When sodium was introduced into the leaves there was movement of this element to the roots.

Subsequent experiments in which phloem activity was abolished or suppressed by steam or cold temperature girdling showed that sodium accumulated above the girdle. It was thus inferred that the low amount of sodium in the shoot is largely due to the active translocation of sodium to the roots. The phosphorylation uncoupler DNP destroyed the selective property of the roots and at the same time stopped the downward translocation of sodium.

The amount of sodium accumulated by excised and intact roots was reduced when calcium was present in the medium. However, under transpiring conditions, this effect on the root cells was not consistently reproduced in the shoots. Under conditions where root pressure was active, the concentration of sodium in the xylem sap exuded by decapitated plants or guttated by intact rice seedlings, which was already at a level below the concentration in the external solution, was reduced even further by the presence of calcium in the root medium.

APPENDIX

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TABLE 1. THE EFFECT OF INCREASING CONCENTRATIONS OF SODIUM AND POTASSIUM IN THE MEDIUM AND ABSORPTION PERIOD ON THEIR CONCENTRATION IN THE DIFFERENT ORGANS OF THE PLANT (MEQ./KG. FR. WT.)

| Treatments | Concentration of Na and K (meq./kg. fr. wt.) | | | | | | | | | |
|--------------------------------------|--|--------|---------------------|---------|-----------------------|--------|------------|-------|-------|-------|
| | Cotyledons | | Blade 1st true leaf | | Petiole 1st true leaf | | Hypocotyls | | Roots | |
| | Na | K | Na | K | Na | K | Na | K | Na | K |
| <u>24-hour absorption period**</u> | | | | | | | | | | |
| 0 meq./l. Na | 0.26 | 49.56 | 0.29* | 107.42* | - | - | 0.93 | 70.20 | 12.80 | 48.98 |
| 5 meq./l. K | | | | | | | | | | |
| 5 meq./l. Na | 0.36 | 42.78 | 0.32 | 118.51 | - | - | 1.95 | 72.53 | 18.97 | 49.09 |
| 5 meq./l. K | | | | | | | | | | |
| 10 meq./l. Na | 0.18 | 39.57 | 0.37 | 110.03 | - | - | 2.72 | 78.75 | 23.88 | 47.30 |
| 10 meq./l. K | | | | | | | | | | |
| 20 meq./l. Na | 0.38 | 41.83 | 0.95 | 113.31 | - | - | 3.75 | 96.98 | 33.66 | 47.02 |
| 20 meq./l. K | | | | | | | | | | |
| <u>192-hour absorption period***</u> | | | | | | | | | | |
| 0 meq./l. Na | 0.25 | 100.66 | 1.56 | 144.56 | 2.01 | 122.07 | 1.10 | 60.06 | 1.14 | 85.08 |
| 5 meq./l. K | | | | | | | | | | |
| 5 meq./l. Na | 1.62 | 100.78 | 2.84 | 136.72 | 3.88 | 126.22 | 6.42 | 84.69 | 7.83 | 78.90 |
| 5 meq./l. K | | | | | | | | | | |
| 10 meq./l. Na | 2.75 | 103.37 | 3.77 | 142.13 | 4.70 | 141.56 | 13.33 | 84.90 | 15.89 | 78.15 |
| 10 meq./l. K | | | | | | | | | | |
| 20 meq./l. Na | 4.85 | 119.50 | 6.10 | 168.28 | 5.63 | 158.66 | 26.61 | 69.71 | 25.43 | 75.75 |
| 20 meq./l. K | | | | | | | | | | |

*Includes the petiole.

**Transferred to experimental solution on 13th day.

***Transferred to experimental solution on 5th day.

TABLE 1a. THE EFFECT OF INCREASING CONCENTRATIONS OF SODIUM AND POTASSIUM IN THE MEDIUM AND ABSORPTION PERIOD ON THEIR UPTAKE IN THE DIFFERENT ORGANS OF THE PLANT (MEQ. X 10²/10 PLANTS)

| Treatments | Total amounts of Na and K (meq. x 10 ² /10 plants) | | | | | | | | | | | |
|--------------------------------------|---|-------|---------------------|-------|-----------------------|------|------------|------|-------|------|-------------|-------|
| | Cotyledons | | Blade 1st true leaf | | Petiole 1st true leaf | | Hypocotyls | | Roots | | Whole plant | |
| | Na | K | Na | K | Na | K | Na | K | Na | K | Na | K |
| <u>24-hour absorption period**</u> | | | | | | | | | | | | |
| 0 meq./1. Na | 0.37 | 70.0 | 0.19* | 68.2* | - | - | 0.7 | 50.3 | 8.6 | 32.9 | 9.9 | 221.0 |
| 5 meq./1. K | | | | | | | | | | | | |
| 5 meq./1. Na | 0.49 | 61.0 | 0.18 | 66.8 | - | - | 1.5 | 54.4 | 11.4 | 29.5 | 13.5 | 221.8 |
| 5 meq./1. K | | | | | | | | | | | | |
| 10 meq./1. Na | 0.30 | 64.0 | 0.22 | 69.0 | - | - | 2.1 | 60.1 | 15.6 | 31.0 | 18.3 | 222.8 |
| 10 meq./1. K | | | | | | | | | | | | |
| 20 meq./1. Na | 0.58 | 63.9 | 0.52 | 61.4 | - | - | 2.7 | 69.7 | 21.0 | 29.4 | 24.8 | 224.4 |
| 20 meq./1. K | | | | | | | | | | | | |
| <u>192-hour absorption period***</u> | | | | | | | | | | | | |
| 0 meq./1. Na | 0.59 | 237.6 | 0.57 | 53.3 | 0.41 | 25.0 | 1.1 | 58.6 | 0.8 | 59.7 | 3.4 | 434.2 |
| 5 meq./1. K | | | | | | | | | | | | |
| 5 meq./1. Na | 3.73 | 230.1 | 1.01 | 49.4 | 0.74 | 24.1 | 5.8 | 75.1 | 5.9 | 59.1 | 17.1 | 437.8 |
| 5 meq./1. K | | | | | | | | | | | | |
| 10 meq./1. Na | 6.86 | 257.3 | 1.48 | 55.8 | 0.90 | 27.1 | 11.5 | 73.5 | 13.4 | 65.8 | 34.1 | 479.6 |
| 10 meq./1. K | | | | | | | | | | | | |
| 20 meq./1. Na | 10.24 | 252.9 | 2.41 | 65.6 | 1.09 | 30.5 | 24.0 | 62.9 | 19.6 | 58.4 | 53.8 | 462.2 |
| 20 meq./1. K | | | | | | | | | | | | |

*Includes the petiole.

**Transferred to experimental solution on 13th day.

***Transferred to experimental solution on 5th day.

TABLE 1b. THE EFFECT OF INCREASING CONCENTRATIONS OF SODIUM AND POTASSIUM
IN THE MEDIUM AND ABSORPTION PERIOD ON THEIR PERCENTAGE
DISTRIBUTION IN THE DIFFERENT ORGANS

| Treatments | Cotyledons | | Blade 1st true leaf | | Petiole 1st true leaf | | Hypocotyls | | Roots | | |
|--------------------------------------|------------|----|------------------------|----|--------------------------|---|------------|----|-------|----|--|
| | Na | K | Na | K | Na | K | Na | K | Na | K | |
| <u>24-hour absorption period**</u> | | | | | | | | | | | |
| 0 meq./1. Na | | | | | | | | | | | |
| 5 meq./1. K | 4 | 32 | 2 | 31 | - | - | 7 | 23 | 87 | 15 | |
| 5 meq./1. Na | | | | | | | | | | | |
| 5 meq./1. K | 4 | 29 | 1 | 32 | - | - | 11 | 26 | 84 | 14 | |
| 10 meq./1. Na | | | | | | | | | | | |
| 10 meq./1. K | 2 | 29 | 1 | 30 | - | - | 12 | 27 | 86 | 14 | |
| 20 meq./1. K | | | | | | | | | | | |
| 20 meq./1. K | 2 | 28 | 2 | 27 | - | - | 11 | 31 | 85 | 13 | |
| <u>192-hour absorption period***</u> | | | | | | | | | | | |
| 0 meq./1. Na | | | | | | | | | | | |
| 5 meq./1. K | 17 | 55 | 16 | 12 | 12 | 6 | 31 | 13 | 23 | 14 | |
| 5 meq./1. Na | | | | | | | | | | | |
| 5 meq./1. K | 22 | 52 | 6 | 11 | 4 | 6 | 33 | 17 | 35 | 13 | |
| 10 meq./1. Na | | | | | | | | | | | |
| 10 meq./1. K | 20 | 54 | 4 | 12 | 3 | 6 | 34 | 15 | 39 | 14 | |
| 20 meq./1. Na | | | | | | | | | | | |
| 20 meq./1. K | 19 | 55 | 4 | 13 | 2 | 6 | 41 | 14 | 35 | 12 | |

*Includes the petiole

**Transferred to experimental solution on 13th day.

***Transferred to experimental solution 5th day.

TABLE 2. THE EFFECT OF GIRDLING, CONTROLLED TRANSPIRATION
AND ROOT EXCISION ON THE CONCENTRATION OF POTASSIUM IN
THE DIFFERENT ORGANS (MEQ./KG. FR. WT.)*

| Treatments | Water loss (ml.) | Leaves | Apical hypocotyls | Basal hypocotyls | Roots |
|---|------------------------|---------------------|----------------------|---------------------|---------------------|
| (Initial concentration) | - | (32.35) | (29.35) | (16.63) | (15.92) |
| Intact plants not girdled without cover | 169 ± 15 | 23.76 ± 0.26 | 32.61 ± 3.63 | 34.54 ± 3.91 | 26.70 ± 0.13 |
| Intact plants not girdled with cover | 50 ± 6 | 6.67 ± 0.65 | 22.23 ± 0.62 | 35.56 ± 0.74 | 28.25 ± 0.64 |
| Intact plants girdled with cover | 48 ± 12 | -2.00 ± 0.94 | 13.11 ± 0.60 | 21.80 ± 0.64 | 24.39 ± 0.98 |
| Without roots not girdled without cover | 78 ± 1 | -0.31 ± 0.07 | 11.47 ± 1.95 | 27.00 ± 2.18 | - |
| Without roots not girdled with cover | 32 ± 4 | 2.31 ± 1.96 | 7.63 ± 1.49 | 19.95 ± 0.91 | - |
| Without roots girdled with cover | 33 ± 6 | 0.19 ± 0.96 | 12.36 ± 2.83 | 17.92 ± 2.79 | - |
| Without roots girdled with- out cover | 53 ± 3 | 12.43 ± 2.10 | 26.08 ± 7.43 | 29.58 ± 6.91 | - |
| Excised roots only | - | - | - | - | 27.59 ± 0.94 |

*Values for treatments are the differences between the final and initial concentrations.

TABLE 3. THE EFFECT OF GIRDLING, CONTROLLED TRANSPIRATION
AND ROOT EXCISION ON THE CONCENTRATION OF POTASSIUM
IN THE DIFFERENT ORGANS (MEQ./KG. FR. WT.)*

| Treatments | Water loss (ml.) | Leaves | Apical hypocotyls | Basal hypocotyls | Roots |
|---|------------------------|---------------------|----------------------|---------------------|---------------------|
| (Initial concentration) | - | (34.43) | (26.08) | (14.10) | (15.64) |
| Intact plants not girdled without cover | 138 ± 1 | 24.81 ± 2.51 | 27.49 ± 1.64 | 29.37 ± 0.85 | 21.98 ± 0.56 |
| Intact plants girdled without cover | 137 ± 7 | 10.56 ± 1.52 | 26.96 ± 0.66 | 16.72 ± 0.67 | 19.69 ± 0.92 |
| Without roots not girdled without cover | 48 ± 3 | 1.24 ± 0.31 | 20.75 ± 0.77 | 28.52 ± 0.27 | - |
| Without roots girdled without cover | 62 ± 1 | 6.69 ± 1.76 | 18.16 ± 1.34 | 17.54 ± 0.11 | - |
| Without roots not girdled with cover | 13 ± 1 | -0.94 ± 1.06 | 4.01 ± 0.55 | 14.81 ± 0.52 | - |
| Without roots girdled with cover | 13 ± 1 | -1.12 ± 1.06 | 11.20 ± 0.92 | 13.40 ± 0.11 | - |

*Values for treatments are the differences between the final and initial concentrations.

TABLE 4. THE EFFECT OF GIRDLING PLANTS IN A STEADY STATE OF ION ABSORPTION ON THE CONCENTRATION OF POTASSIUM IN THE DIFFERENT ORGANS (MEQ./KG. FR. WT.)

| Treatments | Leaves | Apical hypocotyls | Basal hypocotyls | Roots |
|--------------------|------------|----------------------|---------------------|------------|
| <u>Not girdled</u> | | | | |
| 0 meq./l. Na | 93.23 | 118.72 | 103.33 | 71.93 |
| 5 meq./l. K | ± 0.06 | ± 0.17 | ± 0.13 | ± 0.26 |
| 5 meq./l. Na | 94.73 | 116.93 | 94.17 | 64.11 |
| 5 meq./l. K | ± 0.28 | ± 1.30 | ± 1.58 | ± 0.87 |
| 10 meq./l. Na | 98.60 | 111.60 | 80.21 | 60.12 |
| 5 meq./l. K | ± 0.57 | ± 2.09 | ± 4.24 | ± 1.70 |
| 20 meq./l. Na | 95.85 | 102.78 | 87.45 | 58.67 |
| 5 meq./l. K | ± 5.29 | ± 8.06 | ± 8.43 | ± 1.10 |
| <u>Girdled</u> | | | | |
| 0 meq./l. Na | 95.15 | 106.13 | 95.17 | 59.12 |
| 5 meq./l. K | ± 0.19 | ± 0.23 | ± 0.25 | ± 0.39 |
| 5 meq./l. Na | 94.62 | 108.45 | 95.02 | 54.47 |
| 5 meq./l. K | ± 0.25 | ± 1.14 | ± 0.58 | ± 0.35 |
| 10 meq./l. Na | 93.06 | 107.51 | 89.16 | 46.49 |
| 5 meq./l. K | ± 0.53 | ± 1.84 | ± 4.36 | ± 1.38 |
| 20 meq./l. Na | 96.61 | 106.49 | 87.56 | 42.18 |
| 5 meq./l. K | ± 4.89 | ± 3.61 | ± 3.74 | ± 1.95 |

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