SALIENT FEATURES OF THE ROOT SYSTEM RELATIVE TO THE PROBLEM OF SALT ABSORPTION

P. PREVOT AND F. C. STEWARD
(WITH FOUR FIGURES)

Introduction

The problem examined and the system involved

Investigations on salt accumulation which utilize tissue derived from root systems have a double interest. Not only may they contribute to the elucidation of the mechanism of accumulation regarded as a problem of cell physiology, but also to the further question of the absorption of salts envisaged, not merely in terms of individual cells, but of the root as the most effective of salt absorbing organs. The former aspect has been discussed by Hoagland and Broyer (10), and the factors which determine the accumulation of inorganic salts by the cells of barley roots in particular have been outlined. This first discussion concerned only a composite mass of root material which, though accurately reproducible, still comprised cells at all stages of growth and development and of necessity no attempt was made to evaluate their relative efficiency in absorption or to localize along the axis of an individual root those regions most responsible for accumulation. It is the latter aspect of the general problem which is now to be discussed.

The extensive interest (32) in the gross morphology and growth of root systems under field conditions is clearly inspired mainly by their more conspicuous rôle of water absorption. In this connection it is generally recognized that the severe delimitation of the absorbing region for water—due to the presence of fat-impregnated tissues (endodermis, exodermis, or even cork) in the older portions of the root system— involves a clear connection between the ability of a root for growth and its efficiency as an absorbing organ. The maintenance of a root surface free from these restrictions is required. A similar general relation must obtain with respect to salts. With particular reference to water, the extent of the absorbing zone has been discussed notably by PopescO1 (16), and, with emphasis upon anatomical and developmental features, by Scott and Priestley (25).

We are not here concerned with the extent of the absorbing zone for water apart from the expectation that, at least in so far as mere penetration of the superficial tissues is concerned, the absorbing zone for salts would be as restricted as that for water. Statements to the contrary (7), based solely upon the disappearance of solutes from external solutions without examination of the tissues of the root, probably fail to discriminate between the

1 This paper may be consulted for citations to earlier work.
mere chemical reactions between ions of the solution and the deposits in cell walls or upon external surfaces and actual absorption by living cells of the root. The latter is the major problem. Structural features (16, 25) severely limit the absorbing zone for solutes which are unable to penetrate impermeable tissues. It is here that an adequate realization of anatomical features is essential. Since effective utilization by the whole plant demands entry of the salts into the stele, Scott and Priestley (25) rightly stress that, as in the case of water so also for salts, the anatomical status of the endodermis—with respect to the distribution of the completely suberized lamellae and passage cells—together with the extent and distribution of a completely suberized exodermis offers the clue to the problem, at least in so far as penetration of the tissues of the root is concerned. Suggestions concerning mere physical penetration may be derived by experiments involving dyes or qualitative color reactions for iron or nitrates, as the earlier workers implied, but it is clear that quantitative data, lacking when the survey referred to was made, are necessary to localize the zones of active salt accumulation. It will be recalled that while Scott and Priestley recognized that cortical cells may accumulate salts, they particularly emphasized the rôle of the endodermis which, they submitted, represents the functional absorbing surface for salts. As a prelude to entry into the stele, this tissue, it was supposed, accumulated the salts from the dilute external solution which, via the cell walls and intercellular spaces, bathes its external surface. At that time there was little evidence (25, p. 129) that higher concentrations of a given ion could obtain in the stele than in the outer solution, though a gradient of total concentration, for which salts were not held to be chiefly responsible, seemed to be demanded by the problem of water absorption. It was supposed, therefore, that having accumulated the salts the endodermis lost them again internally. Lacking the recent evidence concerning the more definite effects of oxygen concentration in the salt relations of cells, attention was then directed to the possibility that, by analogy with some evidence drawn from the case of Nitella, the higher concentrations of carbon dioxide which may obtain within the stele might be responsible for the loss of solutes internally. Since that time, both with barley and squash, it has been observed repeatedly that the fluid obtained in quantity from within the stele may contain a given solute (KBr) in concentrations much higher than outside the stele (unpublished data of Hoagland and Broyer and of Steward, see also earlier work of Anderssen, Laine, Sabinin, and Steward (1, 13, 23, 29). Quite apart from the rôle of cortex and of endo-

The injection of intercellular spaces with liquid (a common feature of the cortex of roots grown in water and responsible for the translucent appearance described by Popesco) may increase the effective area for diffusion (27) in the cortex, though not in the piliferous layer itself.
dermis respectively in the original absorption, since all solutes which enter
the stele must surely traverse the endodermis, Scott and Priestley's em-
phasis upon this tissue is to this extent justified. The possibility must be
faced, however, that the movement into the stele producing the concentra-
tions observed may be more than a mere passive movement and may itself
demand physiological activity on the part of the tissue concerned. Only a
quantitative approach can form a basis for the solution of these problems.

Not only upon histological grounds, but also upon the basis of current
thought with reference to the mechanism of salt accumulation in cells, it is
to be anticipated that the effective region where salts are not merely ab-
sorbed, but also accumulated, would be confined to a limited zone at the
apex of the root. These views based on evidence derived from Nitella (11),
from storage organs (28, 29, and references there cited), and from roots
(10) have recently been summarized (5). Clearly one of the cardinal
features of actively accumulating cells is a high metabolic rate maintained
by the energy derived from aerobic processes and reflected in the active
carbon dioxide production which ensues. This alone, however, may not be
effective in salt accumulation if the cells in question have become fully
mature, or even senescent, and are unable, by a recrudescence of meriste-
matic activity, to recapture some metabolic process essential for active salt
accumulation and apparently characteristic of cells which are rapidly grow-
ing and developing (5). In short, the normal trend of growth and devel-
opment, which intervenes between meristematic cell on the one hand and
fully expanded, highly vacuolated cell on the other, seems to be associated
with a graded intensity of salt accumulation. Cells exhibit this property to
the maximum degree when they are likewise at the height of their own active
growth and development. This standpoint leads directly to the surmise that
the tissues of the root may display a graded activity in salt accumulation
determined by the stage of development they have attained. To supply the
quantitative data which can alone reveal this fact, many of the experiments
here described were made.

Hoagland and Broyer (10) emphasized the importance of an adequate
realization of the nutritional status of the tissue. With tissue of a given age
and state of development an initial low salt content is accompanied, under
the experimental conditions used, by a high sugar content, and permits a
very rapid subsequent absorption of salt. Hence this attempt to assign the
effective accumulation to any specific region of the root has been made recog-
nizing that this may be modified by the previous nutrition of the root sys-
tem, which determines the salt concentration already attained, as well as by
the rate of metabolism and by histological features.
Experimental results

Technique and Materials

The basic procedure finally adopted resolved itself into the determination of the salt concentration attained, under conditions optimum for accumulation, by root segments the location of which on the axis was definitely known. The segments analyzed were isolated either before or after the absorption period, according to the objective, and a solute not normally present, namely, a bromide (KBr), utilized.3 The technical difficulties demanded that this study be made only with reference to the bromide ion. However, in view of the evidence available in the papers already cited, the conclusions derived may be extended with safety to include cations.4

For practical reasons root segments, free from laterals, were used almost exclusively. An abundance of secondary and adventitious roots, which normally produces an efficient absorbing system and which is a conspicuous feature of the root systems in the condition described (10) in the former paper, merely replicates the potentialities of the root apex and for the purposes in question would have proved confusing. Unbranched roots available in large numbers (over 1000 roots were commonly used in a single experiment) and with the maximum length free from laterals were, therefore, desired. Of the roots which never branch, the one tried (hyacinth) involved difficulties apparent with many potential sources of material and will be referred to later. After preliminary examination of roots grown in water culture from bulbs or from the seeds of legumes or squash these plants were finally discarded, either because of the low order of absorption attained, the difficulty of obtaining a uniform population of roots, or troubles due to contamination with fungi. It is now evident that those plants with large fleshy storage organs, such as bulbs or cotyledons, introduce limitations due to the high content of salt already present in the roots, and, in view of the evidence by Hoagland and Broyer (10), this may be associated with a relatively low sugar content. As described by Steward (29), and Hoagland and Broyer (10), these factors combine to reduce the total absorbing capacity, and, therefore, in some cases (e.g., onion), actual accumulation could rarely be detected in the young roots before the leaves had fully emerged. In the first work these low total absorption figures were regarded as inconclusive, but one may recognize here that for the future study of what may be termed “high salt” roots these

3 The advantages of this solute and the analytical procedure (9) for its determination have been sufficiently emphasized in other writings and need no further reference here. To permit accurate determination of the smaller amounts of bromide special care was taken with the aeration procedure. Freshly standardized 0.001 N thiosulphate—standardized against KBr—was used in a burette, with an appropriate jet, graduated in 0.02 cc. but easily readable to 0.01 cc.

4 See footnote to page 522.
plants may prove useful. Direct evidence that sugar was at least one factor in the minimal activity of these young roots may be derived from the observation that, both for *Allium cepa* and *Vicia faba*, roots excised from plants, the developing leaves of which had been exposed to light, absorbed more salt per unit weight than similar ones exposed only to darkness (table I). It is worthy of record that the roots derived from plants in the light

**TABLE I**

**Effects of illumination of the shoot upon bromide absorption by the root**

<table>
<thead>
<tr>
<th>Plant</th>
<th>Germination conditions</th>
<th>Fresh wt. gm. per 100 roots</th>
<th>Dry wt. gm. per 100 roots</th>
<th>Water content %</th>
<th>Absorption period hours</th>
<th>Br absorbed in milli-equivalents per 1000 gm. fresh wt.</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Allium cepa</em></td>
<td>Light</td>
<td>2.28</td>
<td>0.093</td>
<td>96</td>
<td>24</td>
<td>5.4</td>
</tr>
<tr>
<td></td>
<td>Dark</td>
<td>1.76</td>
<td>0.068</td>
<td>96</td>
<td>24</td>
<td>4.6</td>
</tr>
<tr>
<td><em>Vicia faba</em></td>
<td>Light</td>
<td>2.42</td>
<td>0.115</td>
<td>95</td>
<td>24</td>
<td>13.6</td>
</tr>
<tr>
<td></td>
<td>Dark</td>
<td>2.00</td>
<td>0.095</td>
<td>95</td>
<td>24</td>
<td>11.7</td>
</tr>
<tr>
<td></td>
<td>Light</td>
<td>2.35</td>
<td>0.120</td>
<td>95</td>
<td>24</td>
<td>14.4</td>
</tr>
<tr>
<td></td>
<td>Dark</td>
<td>1.94</td>
<td>0.095</td>
<td>95</td>
<td>24</td>
<td>11.4</td>
</tr>
</tbody>
</table>

were consistently greater in fresh weight per unit length of root and seemed to be composed of larger cells.

Of the dicotyledon roots examined, the secondary roots of *Vicia faba* and roots from cotton (*Gossypium*) plants were the most promising material and some confirmatory evidence derived from these plants is quoted. The difficulty of obtaining a constant supply of uniform roots caused us to reject the relatively thick unbranched roots which can be developed on cuttings of woody plants (*e.g.*, *Salix*) in moist air.

The principal experimental material finally chosen was derived from roots of seedling barley plants (*Hordeum vulgare*) of the strain utilized by Hoagland and Broyer (10) and was restricted to primary roots and those adventitious roots which are always present in the embryo before it germinates and which are identical in structure with the primary root.5

5 It is common knowledge (2) that after the development of the first roots from initials present in the embryo of barley, adventitious roots are produced in conjunction with tillers. These are much thicker, differ in anatomical features, and remain unbranched for several inches. The long unbranched roots which were used in this work must be clearly distinguished from these adventitious roots which form later and which were not employed. Reference may be made to Bryant (6) for some anatomical data on barley roots and a description of the effects of aeration. It will be seen by reference to a recent work upon the Gramineae (2) that comprehensive studies of the anatomy of the roots of barley as affected by environmental conditions are lacking.
The germination technique outlined in the preceding paper (10) was utilized and then the uniform seedling plants were transferred, when 2 or 3 days old, in a compact layer to a cheesecloth screen above a deep dark tank containing either distilled water or Hoagland's nutrient solution. In this way healthy, long, straight roots free from laterals for distances in excess of 6 cm. could be obtained in large numbers. By controlling the period in distilled water or the nutrient solution roots of the high salt or low salt type could be produced at will. Healthy, actively accumulating roots can be grown even in distilled water for a considerable time (up to about 15 days). If unduly prolonged this treatment affects the efficiency of the apical region; although that of the more mature tissues persists. It is worth emphasizing that the technique used on the roots, by the authors of the preceding paper (10), fostered copious branching, whereas the technique used by the authors tended to suppress the formation of laterals. Granted that the lateral roots virtually duplicate the problem presented by the apices of the unbranched segments, it is clear that the data in this paper permit the probable distribution of the salt absorbed by the whole root system to be described. This was a not inconsiderable factor in the choice of experimental material, which was also influenced by the known adaptability of barley roots to water culture. A further point requires emphasis. Since barley, in common with most of the monocotyledons, is free from secondary growth, the attempt to correlate the absorbing and accumulating regions with the progressive maturation of cells and tissues from the growing region was not complicated either by the early development of cambium in the growing roots or by the incipient formation of a cork meristem in the isolated root segments occasionally utilized. Almost exclusively, excised roots have been used. It has to be recognized that the activity of an excised root of barley is not maintained indefinitely under our conditions. The work of Hoagland and Broyer (10), confirmed in the present examination of root segments, revealed that after some hours (approximately 50 to 60 in the present study), a decline, apparently irreversible, in the absorbing capacity occurred. Experiments described in the text show that this point was appreciated in the experiments dealing with the localization of the accumulating region and the major conclusions have been derived from experiments concerned with the period preceding the decline referred to.

\[
\begin{align*}
\text{Ca(NO}_3\text{)}_2 & \quad 0.005 \text{ M} \\
\text{KNO}_3 & \quad 0.005 \text{ "} \\
\text{MgSO}_4 & \quad 0.002 \text{ "} \\
\text{K}_2\text{HPO}_4 & \quad 0.001 \text{ "}
\end{align*}
\]

The familiar "toxicity of distilled water" is not here in question. Water of the exceptional purity to possess these toxic properties would not retain them in contact with so large a quantity of living tissue.
The only other technical details concern the isolation of the root segments and the conditions adopted for absorption. In all cases the small root segments were cut transversely by hand with a sharp safety razor blade from small batches of roots laid parallel, in a single layer, with their apices alongside. Previously, two brief washings with distilled water removed surface contamination from the bromide solution, and those roots awaiting cutting did so in distilled water. After cutting, the roots were surface dried with drying paper, and subsequently both the fresh and dry weights of the samples were recorded. These operations need considerable care to avoid unnecessary manipulation, or actual loss of sap, but the reproducibility of the blotting technique may be recognized from the estimation that the error in the fresh and dry weights of comparable samples did not exceed 5 per cent. The somewhat greater error in cutting the segments is mainly eliminated by expressing the salt content per segment, not in absolute terms, but per unit fresh weight. The ashing procedure demanded by the bromine determination was done in an electric furnace in the presence of caustic soda.

The bromide content of the roots is expressed as milliequivalents per 1000 gm. fresh weight. Since the water content of the roots is high (over 90 per cent.), this may be compared directly as a concentration with that of the external solution. Only very special purposes and precision greater than that necessary in this paper would demand the calculation of concentrations of absorbed salt in terms of the actual water content of the tissue. The absorption experiments were conducted by growing the roots in a 0.005 M KBr solution with a rapid stream of air in excess of that actually demanded by the needs of the tissue. Both the aeration vessels described by RosenFels (22) and jars containing coiled perforated block tin aerators have been used. Respiration determinations have not been made in this first part of the problem, though they will be clearly desirable in the future.

The Extent of the Absorbing Surface

Examination confirmed that the roots of barley grown in water culture had no suberized superficial tissues even at the level where laterals appeared. All the cells external to the stele were therefore in free contact with the external solution. Some experiments were made to verify the perhaps obvious presumption that salt could enter the superficial tissues over the whole surface of the root. In these experiments the question of accumulation after

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8 No attempt was made to determine the radial distribution of the most actively accumulating regions. For some reference to this problem on the basis of qualitative experiments, see POPESCO (16, figs. 22–25).

9 Caustic soda is preferable to sodium peroxide, especially where dry tissue is concerned.
TABLE II

**Comparison of the Bromide Content of Root Segments Cut Before and After Absorption***

<table>
<thead>
<tr>
<th>PLANTS</th>
<th>SEGMENTS CUT BEFORE ABSORPTION</th>
<th>SEGMENTS CUT AFTER ABSORPTION</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>REGION (0 = APEX)</td>
<td>Br MILLIEQUIVALENTS PER 1000 GM. FRESH WT.</td>
</tr>
<tr>
<td>Barley</td>
<td></td>
<td></td>
</tr>
<tr>
<td>6 days</td>
<td>0 to 4 cm.</td>
<td>33.4</td>
</tr>
<tr>
<td>old</td>
<td>4 cm. to end</td>
<td>30.0</td>
</tr>
<tr>
<td>Barley</td>
<td></td>
<td></td>
</tr>
<tr>
<td>14 days</td>
<td>0 to 3 cm.</td>
<td>27.5†</td>
</tr>
<tr>
<td>old</td>
<td>3 to 6 cm.</td>
<td>32.7</td>
</tr>
<tr>
<td></td>
<td>6 to 9 cm.</td>
<td>30.8</td>
</tr>
</tbody>
</table>

* Absorption period: 15 hours in 0.005 M KBr solution.
† There was some apparent injury to the tissue in this case.

Penetration was not a principal concern and hence the root segments analyzed were comparatively large—too large, in fact, to reveal the longitudinal gradients of accumulation to be discussed in a subsequent section. To facilitate the analytical procedure "low-salt" roots grown in distilled water and capable of marked salt accumulation were used.

The three types of procedure used were as follows:

1. Segments were cut from the barley roots before they were immersed in 0.005 M KBr solution, and after an appropriate period in this solution they were analyzed for bromide. In this case the salt might penetrate via the cut ends (e.g., by the vessels or large, central, vessel-like cavity) or the external piliferous layer. The contribution of the transverse surfaces exposed, in comparison to the total surface, was small.

2. Similar roots were immersed for an identical period but in this case the entire length free from laterals remained intact. Subsequently they were subdivided into lengths identical with those in the preceding treatment and analyzed for bromide. This comparison was made for two separate series which involved plants of different age, namely, 6 days and 14 days (table II). It will be evident from the tables that all the root segments absorbed bromide, and equally so, whether they were present in the intact root or were isolated from it previously. This result strongly suggests that the effect of transverse cuts is negligible and that, granted contact with the bromide solution via the external surface, this solute can penetrate to all portions of the root which can absorb it and that no advantage accrues from contact of the older segments with the younger, or from the direct contact.
of cortical cells, not bounded by a piliferous layer, with the external solution. The absence of intercellular spaces injected with liquid in the latter tissue does not therefore restrict penetration appreciably.

3. As a further proof that bromide penetrates freely through the external surface of the root and that neither the cut ends of the root nor the apex are more efficient for penetration than the intervening region, the third procedure, which exposed only a median zone leaving the proximal and distal ends out of direct contact with the bromide solution, was adopted. Long unbranched roots (6 cm.) were bent into a loop, their cut ends and apices penetrating a thin agar plate, (fig. 1) which prevented contact between

![Diagram](https://example.com/diagram.png)

**Fig. 1.** Illustration of method of studying the surface available for absorption by roots (see table III): A, glass plate; B, agar plate; C, root; D, potassium bromide solution; E, drop of water.

the apex or cut end and the bromide solution. The bromide content was determined separately upon the median portion in direct contact with the solution (1.5 to 4.5 cm. from apex) and the combined proximal and distal remnants. Comparison was then made with control root pieces entirely immersed in the usual way and subsequently cut into segments of the same size. In the roots treated by the procedure of figure 1 some bromide migrated into the proximal and distal portions which were not in direct contact with the bromide solution. It can be shown that if this bromide had remained in the median segment it would have had bromide content almost identical with that of the roots completely immersed. In other words, as much bromide passed through this portion of the root surface by one procedure as by the other. In the roots totally immersed, the available surface for bromide penetration was the whole root surface (the volume for accumulation the same in both cases),
## TABLE III

The root surface available for salt absorption

<table>
<thead>
<tr>
<th>Experiment</th>
<th>Absorption* conditions</th>
<th>Root segment</th>
<th>Br absorbed in milliequivalents per 1000 gm. fresh wt.</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>6 cm. of primary root immersed</td>
<td>Median 1.5 to 4.5 cm.</td>
<td>18.8</td>
</tr>
<tr>
<td></td>
<td>Median zone only immersed</td>
<td>Median 1.5 to 4.5 cm.</td>
<td>11.2</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Median, but corrected for Br which migrated</td>
<td>17.2</td>
</tr>
<tr>
<td>B</td>
<td>6 cm. of primary root immersed</td>
<td>Median 1.5 to 4.5 cm.</td>
<td>24.0</td>
</tr>
<tr>
<td></td>
<td>Median zone only immersed</td>
<td>Median 1.5 to 4.5 cm.</td>
<td>16.8</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Median, but corrected for Br which migrated</td>
<td>22.9</td>
</tr>
</tbody>
</table>

* Roots from barley plants 12 days old grown in distilled water. Absorption period: 16.3 hours in 0.005 M KBr solution.

and therefore the total absorption was greater than in the case illustrated in figure 1. These facts can be discerned in table III. The data also imply that in these detached roots the bromide can reach the accumulating cells more readily by direct penetration of the external surface than it can by longitudinal migration from bromide solutions applied at other points along the root axis. The absorbed bromide is mainly in the cortex and if the movement which does occur is restricted to that unspecialized tissue this result would be intelligible.

These results can be summarized by saying that for barley roots grown in water culture the whole root surface between the apex and the emergence of secondary roots represents a potential absorbing surface for salts. This is in harmony with the complete absence of suberized superficial tissues. Data are not available for unbranched roots with a suberized exodermis. In roots previously deprived of salts, bromide can be accumulated even at distances exceeding 5 cm. from the apex at which level, in these "low-salt" roots especially, the endodermis is completely suberized and has much thickened radial and inner tangential walls. Whether the salt accumulated by the cortical cells at this level can be available for the tissues within the stele is an open question.
DISTRIBUTION OF ACCUMULATION IN ROOTS

The aspect of the problem which involves the distribution of accumulation in roots is in many respects the most important one. It follows that in the immersed roots just discussed the bromide solution can penetrate freely to the accumulating cells, and that any differences of concentration attained along the longitudinal axis reflect the capacity for accumulation in the cells concerned, and that the factor of penetration of the superficial tissues need not be considered further.

The data of tables IV, V, VI, VII, and VIII comprise the results of absorption experiments in which the roots were cut into segments at the end

<table>
<thead>
<tr>
<th>TABLE IV</th>
<th>DISTRIBUTION OF ABSORBED BROMIDE IN SEGMENTS OF ROOTS* FROM ‘‘LOW-SALT’’ PLANTS</th>
</tr>
</thead>
<tbody>
<tr>
<td>Absorption period</td>
<td>Distance of segment from apex</td>
</tr>
<tr>
<td>0-1 CM.</td>
<td>1-2 CM.</td>
</tr>
<tr>
<td>hours</td>
<td>Br in milliequivalents per 1000 gm. fresh weight</td>
</tr>
<tr>
<td>5</td>
<td>14.2</td>
</tr>
<tr>
<td>10</td>
<td>31.8</td>
</tr>
<tr>
<td>24</td>
<td>49.5</td>
</tr>
<tr>
<td>30.3</td>
<td>51.5</td>
</tr>
<tr>
<td>47</td>
<td>62.8</td>
</tr>
<tr>
<td>101</td>
<td>49.2</td>
</tr>
</tbody>
</table>

* Barley roots from plants 9 days old grown in distilled water. External solution for absorption period: 0.005 M KBr.
† Value open to question.

<table>
<thead>
<tr>
<th>TABLE V</th>
<th>DISTRIBUTION OF ABSORBED BROMIDE IN SEGMENTS OF ROOTS* FROM ‘‘HIGH-SALT’’ PLANTS</th>
</tr>
</thead>
<tbody>
<tr>
<td>Absorption period</td>
<td>Distance of segment from apex</td>
</tr>
<tr>
<td>0-1 CM.</td>
<td>1-3 CM.</td>
</tr>
<tr>
<td>hours</td>
<td>Br in milliequivalents per 1000 gm. fresh weight</td>
</tr>
<tr>
<td>9</td>
<td>15.8</td>
</tr>
<tr>
<td>23</td>
<td>20.0</td>
</tr>
<tr>
<td>50.5</td>
<td>27.1</td>
</tr>
<tr>
<td>79</td>
<td>29.3</td>
</tr>
</tbody>
</table>

* Barley roots from plants grown 15 days in nutrient solution. External solution for absorption period: 0.005 M KBr.
### TABLE VI
**Distribution of Absorbed Bromide in Segments of Roots* of Low Absorbing Capacity**

<table>
<thead>
<tr>
<th>Absorption Period</th>
<th>Distance of Segment from Apex</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>0–1 cm.</td>
</tr>
<tr>
<td>hours</td>
<td>Br in milliequivalents per 1000 gm. fresh weight</td>
</tr>
<tr>
<td>10</td>
<td>14.4</td>
</tr>
<tr>
<td>65.3</td>
<td>4.27</td>
</tr>
</tbody>
</table>

* Barley roots from plants grown in half-strength nutrient solution. External solution for absorption period: 0.005 M KBr.

### TABLE VII
**Distribution of Bromide in Different Segments of Roots* of *Vicia faba***

<table>
<thead>
<tr>
<th>Absorption Period</th>
<th>Distance of Segments from Apex</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>0–2 cm.</td>
</tr>
<tr>
<td>hours</td>
<td>Br in milliequivalents per 1000 gm. fresh weight</td>
</tr>
<tr>
<td>24</td>
<td>10.5</td>
</tr>
</tbody>
</table>

* Roots from plants grown in sand irrigated with distilled water.

### TABLE VIII
**Distribution of Bromide in Different Segments of Roots* of *Gossypium sp***

<table>
<thead>
<tr>
<th>Absorption Period</th>
<th>Distance of Segments from Apex</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>0–1 cm.</td>
</tr>
<tr>
<td>hours</td>
<td>Br in milliequivalents per 1000 gm. fresh weight</td>
</tr>
<tr>
<td>20.3</td>
<td>22.0</td>
</tr>
</tbody>
</table>

* Roots from plants grown in nutrient solution. External solution for absorption period: 0.005 M KBr.

of the absorption period. It will be observed that the longitudinal distribution of accumulation has been assessed for plants with both the "high-salt" and "low-salt" type of nutrition, referred to previously, and also at various times after the roots were excised and introduced to the absorption conditions.

In table IV, for plants of the "low-salt" type, which ultimately absorb bromide to high concentrations, a pronounced longitudinal gradient of accumulation along the axis of the root is evident (fig. 210). The highest

10 Note that in the figure the sap concentrations are plotted at the mid-point of the segment concerned. The curves were drawn to give a smoothed fit.
concentrations were attained in the samples nearest the apex (their mid-point at 0.5 cm. from the tip), and they decrease progressively and consistently to the oldest tissue examined. It should be stressed that this effect is discernable at the earliest periods when samples were taken, and it persists consistently throughout. Subsequent to 47 hours and prior to 101 hours, the onset of the decline mentioned earlier in this paper causes actual decrease in the bromide content of the tissue samples, and not till then do irregularities appear in the series.\textsuperscript{12}

By contrast with table IV, the data of table V refer to roots of the "high-salt" type. This explains the lower concentrations of bromide which were attained. To compensate for this, larger tissue samples were necessary, and, to avoid a too unwieldy total number of roots, these had to be obtained by

\textsuperscript{12} Irregularities arise only when the apical region is definitely injured by nutritional or other causes.

\textsuperscript{12} Examination of the roots before and after the experiment revealed that a progressive suberization of the endodermis occurred during the experiment so that the stage definitely recognizable at 4 cm. from the tip before the absorption period had encroached to 0.5 cm. by the end of it.
increasing the size of the segments. Even so the evidence for the longitudinal gradation of accumulation is clear from the earliest period (9 hours) to the latest (79 hours).

It is evident that the graded activity in accumulation, which coincides with the progressive development of cells and tissues along the axis of the root, surmounts those factors of sugar content, previous salt nutrition, etc., which determine the total level of salt absorption attained. An extreme example of the persistence of this gradation of activity can be derived from one set of data (table VI) obtained from roots which effected so little total absorption that the primary purpose of the experiment failed. These roots were obtained from plants grown in nutrient solution for 15 days and were excised when the plants were probably unusually low in sugar (4 A.M., and after a period of relatively dull days). It may be noted that, although the tissue (which was analyzed after intervals of 4, 10, 14, 30, 58, and 65 hours) increased progressively in its bromide content, it merely attained, in 65 hours, a level of concentration which the active tissue used in the experiment of table IV reached in 5 hours. Whatever the ultimate explanation of the low total absorption, the interesting point is that the segments nearest the apex retain, relative to those more remote, their greater activity in salt accumulation. This was also evident at other intervals than 65 hours and it should be noted that only in those segments near the apex did actual accumulation occur. In other words, where the special features of the root do not permit it to accumulate salts throughout its whole mass this may still be possible near the apex where new growth can occur. This was also evident in those earlier experiments described with roots from other plants in which only low total absorption was attained. The figures (table VII) obtained with the secondary roots of *Vicia faba* illustrate this point. Of particular interest concerning the gradation of accumulation normally operative in roots growing under standard conditions of water culture with aerated solutions are the data supplied for cotton plants (table VIII). The roots were obtained from plants growing successfully in the greenhouse for other purposes, and they again revealed a similar longitudinal gradation of salt accumulation—albeit associated with the relatively low degree of accumulation which would now be anticipated from the high level of nutrition they received during growth.

The fact of the longitudinal gradation of accumulation\(^\text{13}\) is then established as a general property of roots, and this persists concomitant with either a high or a low total capacity for salt absorption determined by other variables.

\(^{13}\) Since the completion of the work here reported Mr. J. A. Harrison of Birkbeck College, University of London, has collaborated with the authors. By the application of a quantitative spectroscopic technique it has been possible to demonstrate the longitudinal gradation of accumulation of potassium in barley roots, and also of rubidium absorbed during experiments similar to those in this paper.
Figure 3 correlates the principal anatomical features of barley roots grown in water with their activity in salt accumulation. The horizontal histograms represent at three selected levels (data in tables IV and V at 24 and 23 hours respectively) the absorption by roots of both the "high-salt" and "low-salt" type. The distribution of stele and cortex at these levels may be discerned in the scale diagrams shown and the status of cortex (nos. 1, 2, and 3) and of stele (nos. 4, 5, 6, and 7) is apparent from the scale diagrams, which were obtained from camera lucida drawings at the magnification indicated on the figure. Root hairs are omitted from the diagrams, although they were plentiful on the roots used—especially those grown in full nutrient solution. For a further discussion of these structural features and for some data relative to the longitudinal plane, the section headed histological evidence may be consulted.

**INTERRELATIONS IN THE EFFECTS OF NUTRITION, SUGAR CONTENT, TIME, AND DEVELOPMENTAL FACTORS**

From the paper by Hoagland and Broyer (10) it is clear that roots of the "high-salt" and "low-salt" types differ greatly in their sugar content. The probable rôle of sugar as a determinant of the observed longitudinal gradation of salt accumulation must be considered. Direct evidence of the efficacy of an external supply of sugar may be seen in figure 3, which also serves to re-emphasize the form of the absorption/time curves usually obtained in this work with the excised roots (fig. 4 and tables IV and V). With a slight lag, probably due to the time taken for sugar itself to penetrate, the low total absorption of the "high-salt," low-sugar roots used in this experiment was raised almost exactly to that of the "low-salt" roots by an external sugar (glucose) concentration of 2 per cent. This suggested that an external sugar supply might raise the absorption obtained by the roots of bean, onion, etc., to the order of that of the sugar-rich, "low-salt" barley roots. Although 2 per cent. glucose in the external solution raised the absorption from 8.75 to 12.3 milliequivalents per 1000 gm. fresh weight in secondary roots of Vicia faba, the high values characteristic of the barley plants referred to were not realized. From the data of figure 4 it is also clear that the factors responsible for the ultimate decline of excised barley roots are not such that they can be corrected by an external supply of sugar. On the contrary, there is evidence that, despite their low sugar content, the "high-salt" roots are able to continue absorption (albeit at the low level characteristic of them) for a still longer period. The onset of this decline, which is accentuated by the extensive sugar metabolism (10) in the "low-

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14 Note that the longitudinal and transverse scales are different.

15 Since the data for potassium are lacking it is not possible to state how much of the bromide absorbed was accompanied by potassium. Data for potassium content would have given precision to the term "high-salt" roots and permitted a closer comparison between these data and those in the earlier paper than is now possible.
Fig. 3. Right, anatomy of barley root (''low-salt'' type), at different distances from apex, in relation to bromide accumulation. Nos. 1, 2, 3, cortex and piliferous layer without suberized exodermis. No. 4, 0.6 mm. from root apex. Differentiation of vascular strands quite evident. No. 5, 5 mm. from root apex. Unsuberized endodermis. No. 6, 1 to 3 cm. from root apex. Endodermis suberized but with passage cells opposite xylem groups. No. 7, 3 to 5 cm. from root apex. Endodermis suberized, without passage cells, and, at extremity of segment, also thickened. Ep, piliferous layer; E, endodermis; X, xylem; Ph, phloem; P, passage cell; C, central cavity (axile vessel).

Left, □ 'low-salt'' roots: bromide absorbed by segments; data of table IV; ▢ 'high-salt'' roots: bromide absorbed by segments; data of table V.

''low-salt'' roots and appears with some consistency at approximately 60 hours with barley, must be conditioned by some factor peculiar to excised roots, and until this can be completely specified it must suffice to contrast it with the maintained ability for absorption of attached roots—a property which must surely be identified with their continued growth as well as with the translocation of salt from root to shoot referred to by Hoagland and Broyer (10). It is not unreasonable that the ''low-salt'' excised roots from plants on the verge of actual deficiency symptoms would be the more quickly limited in regard to continued growth than those of the ''high-salt'' type.

At this point a comparison16 with the form of other similar curves may

16 The root experiments in this section were made by withdrawing random samples from a composite batch of root material at the times stated. They were not made only on uniform roots free from laterals as heretofore.
be profitable. In figure 4 data for potato discs in much more dilute solution (0.00075 M KBr) are plotted (28, p. 230). The potato discs are clearly constituted of cells already high in salt, and which maintain their supply of soluble carbohydrate from starch hydrolysis, and are known to be capable of a renewed and protracted activity in growth which eventually (and especially if the tissue is in moist air) culminates in cell division. The slope and general similarity between this curve and that for barley roots of the "high-salt" type requires little comment. Surely both reflect the maintained and progressive activity of the constituent cells at a level fixed alike by their sugar and initial salt content, oxygen supply, and their ability to continue the processes of growth. The similar curve, also shown in figure 4 for potato roots from plants grown in sand culture, suggests two distinct phases. In the first phase (complete by 24 hours) a rapid increase of bromide concentration is reminiscent, though less striking because the nutrient conditions were not so extreme, of the "low-salt" barley roots. The implication is that in both cases (potato roots and "low-salt" barley roots), during the first phase of contact with the potassium bromide, the "low-salt" condition in the initial tissue (now known to be associated with high sugar content) permits a more rapid salt entry than would otherwise obtain. In this first phase, which is really determined by the conditions during previous development, further growth and development of the root cells probably plays but a minor rôle. The second phase is clearly homologous with the behavior in time of the tuber tissue, and of the "high-salt" barley roots and must surely be identified with the slow but maintained processes of growth at least until over 100 hours. During this period the average concentration of the reference element (bromide) in the whole tissue system17 increases steadily as successive cells mature, thus increasing the proportion of tissues which have passed through their most active periods of salt accumulation in the presence of

17 This must be clearly distinguished from the total content of salt in the root system.
bromide. Apart from the failure of some fundamental aspect of the vital machinery, the roots of the "low-salt" type would have shown, after their first rapid intake, either a similar slow but progressive increase in the average bromide concentration or, alternatively, a steady average concentration (the maximum attainable) in which the high concentrations in new cells developing in contact with bromide counteract the declining concentration of those more mature. In other words, the rapid onset of decline, particularly evident in roots of the "low-salt" type, is probably associated with the failure of those very attributes of growing cells which, both in the apex of the root and at the cut surface of storage tissues (5, 29), determine their conspicuous ability for salt accumulation, and it is therefore in harmony with the general thesis here outlined. Further confirmation is obtained when the data of table IV are plotted as time curves when it becomes clear that the apical segments, where the capacity for growth lingers longest, retain their salts until somewhat after the onset of decline in the older tissues.

Since excised roots can remain capable of protracted growth, and presumably of salt accumulation, for almost indefinite periods in sterile nutrient solutions, or on agar, containing sugar and yeast extract (20, 21, 33, 34), the question arises whether yeast extract would have any effect upon salt accumulation by excised roots of barley and particularly their apical segments. Briefly, in these relatively short experiments, no effects on salt accumulation due to yeast extract have yet been observed which could not be ascribed to its sugar content.19

Experiments were done to ascertain the effect of sugar upon the longitudinal gradation of accumulation. These admittedly suffered from the use of too large individual segments (4 cm.) and are not given in detail. Although positive effects due to sugar were obtained (6-day-old plants), they did not alter the relative efficiency of the different segments (0 to 4 cm., and 4 to 9 cm.), but, instead, raised the capacity for absorption of the root as a whole. Indeed the very fact that the longitudinal gradation of accumulation is most pronounced when the roots have highest sugar content and show least response to an external sugar supply ("low-salt" roots) eliminates the possibility that this gradation is due merely to a similar gradient of sugar concentration in the cells.

DISTRIBUTION OF METABOLIC ACTIVITY

One further clue to the metabolic basis for the observed gradation of accumulation in the root can be derived from the fact that the regions of most active accumulation apparently exhibit the greatest avidity for oxygen.

18 This condition is not to be confused with death since the cells in question may still produce carbon dioxide (10) and complete loss of solutes only appears at a later stage of decline.

19 No reflection upon the validity of White's work (33, 34) is here intended.
This may be observed readily by an indirect procedure based on observations of *Lund* and *Kenyon* (14). The apical region of roots of barley, as used in this work, stains deeply with methylene blue,20 whereas the older tissues stain lightly and more superficially. The deep staining of the apical region responds to external conditions, but not so the superficial stain further back. In oxygen-free water, in nitrogen or a vacuum, the apical segment rapidly becomes colorless, and transfer to air proves that this is reversible. In heat-killed tissue, on the other hand, the deeply stained apex is unaffected by an anaerobic environment. These simple tests strongly suggest that the apical segment is a center of more intense oxidation (reducing the dyestuff under anaerobic conditions) than the older tissues. In view of the emphasis recently placed upon the relation between accumulation and aerobic metabolic processes (28, 29, 30) this has particular significance. So much so that confirmation by direct oxygen measurements, not yet available, would be of value.21 *Lund* (14) and his coworkers believe that electrical measurements which can apparently be correlated with oxidation also indicate the gradation of metabolic activity along the axis of the root.

**HISTOLOGICAL EVIDENCE**

The previous paragraph offers tentative but direct evidence in support of the presumption that the region of greatest activity in accumulation is also conspicuous for its activity in metabolism. However, histological evidence is adequate in support of this position.

Practical considerations prevented the use of root segments shorter than 1 cm. Even so, satisfactory analytical data demanded very large numbers of roots. It will be recalled that even a distance of 1 cm. behind the apex includes not only the meristem but also the first and the most conspicuous stages of cell extension. Current views no longer restrict entirely the cell divisions to the apical meristem (18) but recognize that cells which have already enlarged and become conspicuously vacuolated may still remain capable of division, though they do so only infrequently. The apical segment, therefore, where the activity in accumulation is most intense, comprises a limited zone of conspicuous cell division but is mainly composed of cells in which growth by extension predominates over division and which, for present purposes, may be described as at the height of their growth and

20 Acknowledgment is made to Dr. M. M. Brooks for a supply of pure methylene blue.

21 Henderson (8), who reported data for oxygen consumption in conjunction with water absorption, did not distinguish between different portions of the root surface.

22 It is apparent that the need for an even more intimate examination of the apical segment suggests itself. This, however, must await a technique, possibly based on the rapidly developing methods of micro-incineration, which can yield with certainty quantitative data for individual cells so that their activity in accumulation may be more closely related to their development. The more qualitative observations of Penston (15) relative to potassium are suggestive in this connection.
development. The rapid histological changes which occur therein are perhaps the best testimony to their metabolic activity.\footnote{Poesco (16, p. 57) says: ‘‘Le maximum de pénétration du nitrate de potassium, dans la racine de Soja hispida, à lieu entre 1 et 4 mm. de la pointe, où il n’y a pas de poils radicaux. À partir de ce point, la pénétration du sel dans la racine diminue progressivement, pour s’arrêter presque complètement à partir de 10 mm.: à ce niveau l’endoderme paraît brun.’’}

The great activity of the apical segment is therefore to be identified not with the apical meristem, but rather with cells already possessed of large aqueous vacuoles and in which the evident ability for further extension and division prompted the term "vacuolating dividing cells" applied by Priestley (18). It is an interesting, but as yet an open question, whether the vacuole, in the form in which it may now be revealed by special cytological methods in meristematic cells, can also be associated with salt accumulation. Neither the staining experiments of Poesco (which no doubt reflect in the apex of the root the distribution of large vacuoles rather than the intrinsic ability of cells to accumulate), nor the impermeable properties of the root apex inferred by Priestley and Tupper-Carey (19) (on the basis of its resistance to flow and to alternating electrical current) are necessarily incompatible with the ability of the meristem to accumulate salts. Poesco's experiments, which excluded the meristem from the absorbing region, did, it is claimed, reveal the most intense absorption near its low limit\footnote{Poesco (16, pp. 56, 57, and 130). However, as inferred elsewhere, the detailed treatment of the meristematic region is outside the scope of the quantitative methods at present available, but since it occupies so small a proportion of the apical segments used, the quantity of salt it could contain would have little effect upon the quantitative comparisons reported in this paper.} (16, pp. 56, 57, and 130). However, as inferred elsewhere, the detailed treatment of the meristematic region is outside the scope of the quantitative methods at present available, but since it occupies so small a proportion of the apical segments used, the quantity of salt it could contain would have little effect upon the quantitative comparisons reported in this paper.

The following data in table IX were derived from actual measurements of cell sizes from roots, as used in these experiments, which were embedded in paraffin and examined in serial section for both transverse and longitudinal planes. The figures serve to stress the location on the axis of the most conspicuous enlargement of cells. At levels far enough from the apex for stele and cortex to be distinguishable, they were measured separately. Since the proportion of cortex to stele (even including the central cavity or axile vessel) in the roots is high, of the order of 9:1 (fig. 3), the accumulation data are reflected mainly by the cortex and therefore the

\begin{table}[h]
\centering
\begin{tabular}{|c|c|c|c|c|c|}
\hline
Distance from apex (mm.) & 0.24 & 0.6 & 1.2 & 2.4 & 7.4 & 35.0 \\
\hline
Mean length per cell (\(\mu\)) & 11.0 & 17.4 & 42.6 & 46.5 & 150.0 & 198.0 \\
\hline
Mean diameter per cell (\(\mu\)) & 20.3 & 26.1 & 15.6 & 19.2 & 33.0 & 22.8 \\
\hline
\end{tabular}
\caption{Dimensions of cells at different distances from the root apex of barley}
\end{table}
At present, and enlarging the specify scope of this root fore the this (24, dermis rather of the concerned reflect features of cortical which is proportion to be sought in the division neither of cent. is divisions cell of tension, did length at 7.4 even for figures over paper, the results
The basis, therefore, of cortical cells. The demarcation of the functional absorbing zone, by reference to stages of vascular differentiation and of the development of the endodermis (24, 25), utilizes an indirect relation which is not a causal one, and which is of value only in so far as these more easily recognized structural features reflect the condition of the cortical cells which are more directly concerned with salt accumulation. With respect to the problem of the translocation, rather than the absorption of salts, the importance of the histology of the endodermis still remains, since the solutes must surely enter the stele where this tissue is not completely suberized. However, full discussion of the factors which govern the removal of salts from the root is outside the scope of this paper.

The results of this perhaps too cursory anatomical treatment are therefore in accord with the view that the relative efficiency of the tissues nearest the root apex must be ascribed to the preponderance of active cells rapidly enlarging and even dividing. No doubt it will be possible eventually to specify the metabolic significance of these general histological comparisons. At present, it is possible only to note the implied and suggestive parallelism
(and the evidence does not warrant any stronger statement yet) between the activity of the cells of the root in protoplasmic (protein) synthesis and their corresponding activity in salt accumulation. Previous investigations with storage tissues, though concerned with tissue tending to re-approach rather than recede from the condition of active cell division, have also shown that salt accumulation is most intensely exemplified by those cells whose vital activity is such that it would normally culminate in division. A broad survey (29) of the accumulation displayed by many types of cells and tissues reveals that as these vital activities decline so also does the capacity for salt accumulation and especially so with respect to the absorption of ions of both signs which has been designated "primary absorption." With this point of view the present evidence of the longitudinal distribution of accumulation on the axis of the root is in full accord. The consistent fact which emerges is that cells which are capable of most active growth, which are at the peak of their own vacuolation and extension, attain the greatest degree of salt accumulation. Though external factors may control the total absorption obtained, this does not counterbalance that graded activity which is an inevitable consequence of factors operating in the progressive development and maturation of cells from the root apex.

**Rôle of root cortex**

The survey of the root as an absorbing organ, to which earlier reference was made (Scott and Priestley, 25), implies that under the conditions which obtain in water culture the rôle of cortical cells, and of root hairs when they are present, would be secondary. When, as in the earlier account cited, the endodermis is endowed with the ability both to accumulate salts and to release them to the stele, attention may be focused upon this tissue to the exclusion of the cortex—the probable rôle of which may be thereby unduly restricted. The very technique which produces active "low-salt" roots testifies to the ready removal of solutes from these cortical cell to the growing plant. This possibility was rejected by Priestley and this led to the emphasis upon the endodermis as the functional absorbing surface. It is clear that in the experiments of Hoagland and Broyer (10), as in ours, the bulk of the solute absorbed and accumulated was present in cortical cells which, there is every reason to suppose (see section on the extent of the absorbing surface), absorbed it directly from the external solution. The results here presented suggest that the "low-salt, high-sugar" type of root contains cortical cells capable of accumulation even at levels where the endodermis may commonly be suberized and even free from passage cells. Though affected somewhat by nutrition, the endodermis of barley at 3 cm. from the root apex is commonly suberized, but usually has passage cells which have disappeared completely at 5 cm. An interesting problem is here presented as to whether or not the salt content of the cortex at this level can be withdrawn by the more active regions
and subsequently enter the stele. Though the experiment described by Prevot (17) emphasizes how readily attached roots which have accumulated bromide can subsequently lose it when the conditions for removal and translocation obtain, even at levels some distance from the apex (4 to 5 cm.), it does not establish conclusively that bromide can move out of the older cortical cells to the stele across an endodermis which is definitely and completely suberized. In short, the cells of the root cortex of attached roots function for a considerable period after their formation for the temporary storage of inorganic salts and remain capable, reversibly, of accumulation from the external solution and rapid loss to the presumably more active tissues of the growing shoot. Clearly, the contribution of the root cortex to the functional absorbing system is intimately related to the balance between the demands of the shoot and the external supply. No doubt, complementary to the cycles of salt content, fluctuations of organic constituents would be revealed upon examination. Apparently these properties can be retained for at least 3 weeks, and at distances of over 6 cm. from the apex. The elucidation of those factors which in the intact plant cause this ready removal of electrolytes from root cells which have already accumulated them, and which in excised roots would necessitate drastic treatment with perhaps even irreversible changes, represents one of the most difficult and certainly one of the most fundamental of the outstanding problems. In other words, the difficulty which Priestley and Scott faced with respect to the endodermis really applies very strikingly to all the cortical cells. Even if the suggestion they tentatively advanced (based on the effect of an acid reaction in the stele due to carbon dioxide concentration) could be adequately harmonized with present views of the accumulation mechanism or with unpublished data of the effects of carbon dioxide tension upon it, this explanation could hardly apply to the cortex. Having dealt but incompletely with the mechanism by which the root cells accumulate the salts, the problem of their rapid withdrawal and the conditions which determine this can merely be noticed and left unsolved. The evidence, already referred to, that high concentrations in the stele are obtained only if the roots are aerated suggests that this movement also is not unconnected with the metabolism of living tissues.

Summary

1. The absorption of salts by roots is reviewed with special reference to current views upon salt accumulation on the one hand, and physiological anatomy on the other.

24 During 24 hours' contact with a bromide-free medium, bromide moved to the leaves and the segments near the apex (even as far back as 2 cm.) were almost entirely depleted of the bromide they had previously absorbed (35 milliequivalents per 1000 gm. of fresh weight).

25 This question has been studied quantitatively in extensive experiments on translocation of bromide in barley plants in the Division of Plant Nutrition, University of California.
2. Quantitative experiments are recorded in which long, unbranched roots of barley (Hordeum vulgare), secondary roots of broad bean (Vicia faba), and roots of cotton (Gossypium sp.) were employed.

3. In roots of barley grown in water culture the potential absorbing surface extends back from the apex to the place where secondary roots appear. The functional absorbing zone is limited by factors which operate upon the cortical cells. The histology of the endodermis and the incidence of vascular differentiation may serve to define the region of most rapid removal, but they are not concerned directly with absorption and accumulation of salts by roots.

4. A pronounced longitudinal gradation in the capacity for salt accumulation has been observed. The segments near the apex attain higher concentrations than those more remote. This fact is established for barley plants with both "high-salt" and "low-salt" type of nutrition, secondary roots of bean, and roots of cotton, all of which were grown in water culture.

5. The metabolic and developmental factors involved in the longitudinal gradation of salt accumulation are discussed, and it is concluded that this gradation is an inevitable consequence of the progressive development of cells from the root apex.

6. Interrelations between effects of time, nutrition, and salt accumulation are described. The features common to these and other representative types of absorption/time curves are emphasized. All the time effects are interpreted in terms of the previous nutrition, and the capacity for further growth of the system concerned.

7. Special attention is directed to the probable rôle of the root cortex and to certain outstanding problems which it presents.

These experiments were done in the Division of Plant Nutrition, University of California. Grateful acknowledgment is made to this Division for the facilities provided. The work described relates closely to extensive investigations upon roots then in progress in the Division under the direction of Professor D. R. Hoagland. We have utilized unpublished information and technique derived from these investigations which we now gratefully acknowledge.

The authors' collaboration resulted from a joint stay in the Division of Plant Nutrition during which one of us (Prevot) held a Fellowship under the Commission for Relief in Belgium, Educational Foundation, and the other (Steward) a Rockefeller Foundation Fellowship. The second author accepts the final responsibility for any critical or controversial statements in this presentation.

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