Botany. — *Contribution to a theory on the absorption of salts by the plant and their transport in parenchymatous tissue.* By W. H. ARISZ.

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§ 1. *Introduction.*

The problem to be discussed here, has to do with the ability of plant cells to take up salts from their environment. From vegetationexperiments of many investigators, such as TRUE and BARTLETT (1915), PARKER (1927), v. WRANGELL (1928), JOHNSTON and HOAGLAND (1929) and others, it has appeared that plants can absorb anorganic salts even from very dilute solutions. This renders it comprehensible that they can also take up an adequate quantity of food from the soil-solution and from ditchwater. Whereas it was originally thought that the salts are carried along by water that the plant takes up as a result of transpiration, it has become clear in later years that the uptake of salt is a complicated process, which though it may be more or less affected by water-absorption, for the rest takes place independently of it. So it comes to pass that also submerged waterplants, which naturally show no transpiration, yet take up nutrient substances as salts and aminoacids from the environment. This is partly done by their roots, partly by their leaves, as for instance Elodea and Vallisneria (ROSENFELS (1935), ARISZ).

Besides roots and leaves a third group of organs is to be mentioned, which under special circumstances are likewise able to take up salts. Among these are tubers and other organs containing reserve food, which have been cut into discs and as a result of the wounding at their surfaces possess actively synthetizing cells (STEWARD). Moreover there is a fourth group: organs which have the special function of taking up substances from their environment. Of these some instances may be mentioned: 1. The tentacles of the insectivorous Droseras, which have been extensively examined by OUDMAN and ARISZ and 2. the scales on the leaves of Bromeliaceae, the function of which has been investigated by A. HARBRECHT (1942). Finally the lower plants may be mentioned here, of which especially the unicellular algae have been repeatedly examined. (OSTERHOUT, BROOKS, HOAGLAND, COLLANDER and many others.) The processes in such unicellular organisms seem simpler, but they are less suitable for an analysis of the phenomena, because the processes of metabolism are much more intensive here and have a complicating influence on the uptake and transport-processes we are interested in. This makes the analysis by these unicellular plants much more difficult.

It is interesting to trace whether in the above cases we have to deal done by their roots, party by their leaves, as for instance Elodea and

with identical absorption processes. They have in common their dependence on the aerobic respiration of the plant. There is a difference, because the place to which the substance taken up is being carried and the route which is followed, are not the same for every case. In the leafcells of Vallisneria and Elodea and likewise in the discs of reserve organs, the salts chiefly go to the cellsap of the absorbing cells. In the root, however, only part of the substances taken up, will be fixed in the vacuoles of the absorbing cortical cells. A considerable part is carried to the woodvessels in the central cylinder through the cortical parenchyma cells and the endodermis. Especially this latter process has to be considered as the proper task of the root. The well-known experiments of HOAGLAND and BROYER on the absorption of salts by the root have been made in such a way that the first process, in which the substances are secerned into the vacuoles of the cortical cells is much more striking than the second process, the transport to the xylem vessels. This is due to the way in which these experiments have been made. Excised root systems are used, in which the wood vessels have been opened, so that part of the substances given to them, is returned to the liquid nutrient. By a suitable preliminary treatment in a nutrient solution poor in salt, the tissue is low in salt at the beginning of the experiments, while care has been taken that there is a sufficient quantity of reserve food. The result is a strong accumulation in the cortical cells. Owing to this the results of their experiments show a strong resemblance to STEWARD's on accumulation by potato-discs. They are, however, not comparable with the experiments on the absorption of salt by various other investigators who worked with roots with normal salt content that had not been cut off, as for instance those by LUNDEGARDH, where the substances are chiefly given to the woodvessels and the accumulation in the cortical cells is a matter of secondary importance.

We shall revert to the analysis of these processes in the root, when discussing the permeability of the tissue and in § 7. Here we may point out that in all these cases absorption and loss of substances by the protoplasm go together. For though we usually speak of absorption of substances by the vacuole, it is more correct to consider this process from the angle of the protoplasm and to speak of secretion into the vacuole, especially if we have to deal with active processes here. On the one side the protoplasm absorbs the substance from the cell wall and the medium, on the other side releases it to the vacuole. This points to the fact that absorption and secretion are processes experimentally difficult to separate. The secretion of substances by the protoplasm externally, as it occurs in gland cells or in excretory organs such as salt glands and nectaries, may be considered a related process.

Not only are absorption and secretion of substances by the protoplasm processes which are closely connected, but to these may be added the transport of substance in the protoplasm, which can no more be strictly

separated from them. Every absorption and secretion is attended by a movement of the substance in the protoplasm, even in a unicellular organism, where the substance from the environment is carried through the cell wall and the surface zone of the protoplasm to the more inward part of the plasm, whence it can permeate through the tonoplast into the vacuole. With multicellular organisms the movement is more striking, for there the surface layer of the epidermal cells absorbs the substances, whence they are transported to the adjacent cells. Thus transport from cell to cell in the cell walls and the symplasm is possible in the parenchymatous tissue. In the roots too the substances have to be transported over a rather long distance in a radial direction. In the tentacles of Drosera the transport from the glands to the leaf by the cells of the tentacles comes to the fore. These are specialised transport organs (ARISZ 1944). Absorption, secretion and transport therefore are three processes, which are closely related and cannot easily be circumscribed.

§ 2. *Permeability, intrability and transmeability.*

From a great number of researches it has appeared that the absorption of salts into the vacuole occurs on lines entirely different from those followed by most organic substances. Only the dissociated organic substances, as the amino-acids, show some correspondence with the salts (ARISZ and OUDMAN 1938). Before proceeding to set forth the different behaviour of these substances, we have to discuss the terminology of the penetration of substances into the cell. To indicate that a substance passes through the plasm, we usually speak of permeation. The plasm is then called permeable to the substance. If like PFEFFER we consider a plant cell as an osmotic system, the semipermeable membrane is the boundary surface of the protoplasm. There are two of these boundary surfaces to the plasm, one bounding it on the outside and one contiguous to the vacuole. Through H. DE VRIES' fundamental researches, it has become possible to determine the permeability of the plasm for various substances as glycerine and ureum. The *permeability* of the protoplasm which was determined in these researches, therefore, comprised both boundary surfaces and the plasm between them. Later HÖFLER introduced the terms *intrability* and *intrable* to indicate that a substance permeates into the plasm through the surface zone, but cannot go through the tonoplast to the vacuole. Though this terminology is historically comprehensible, it may lead to misunderstanding and trouble. The difficulties are chiefly of two kinds. In the first place we speak of *permeability* by animal cells in which a vacuole is lacking and the same holds good of plant cells without vacuoles, when a substance penetrates the protoplasm. On comparing the permeability of vegetable and animal tissue or cells with and without vacuole, we consequently often compare heterogeneous quantities. The *intrability* of one kind would have to be compared with the *permeability* of another. In the second place confusion may arise

when a substance permeates through a tissue. This may happen without the substance permeating into the vacuoles of the cells. In that case the substance must permeate through the plasmalemma and move in the plasm without proceeding through the tonoplast, after which the substance can leave the plasm of the cell in order to continue its journey in an adjacent cell. If the representation is correct that the plasm of adjacent cells is connected by plasmodesmata, we have to do here with a transport in the symplasm. A fine example of this kind of plasm-permeability is found in the endodermis sheath in the root. According to DE RUFZ DE LAVISON various salts in a high concentration, which causes plasmolysis, permeate into the central cylinder. In doing so they have to pass through the plasm of the endodermis cells, as along the radial and cross walls no substances can be transported, because the cork-bands of CASPARY prevent this, whereas with plasmolysis of the endodermis cells the connection between plasm and cork bands is preserved. (cf. fig. 1.) In such a case we are entitled to speak of plasm-

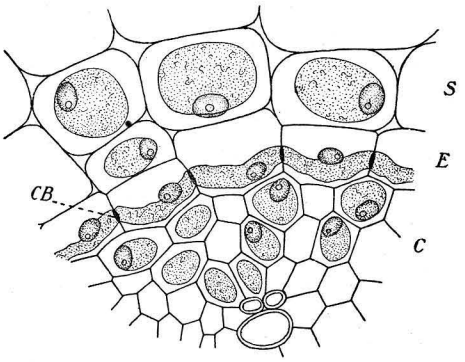

Fig. 1.
Transverse section of a plasmolysed root.
S = cortex. E = endodermis. C = stele. CB = Band of CASPARY.
The plasmolysing solution in penetrating the stele has to pass the plasm of the cells of the endodermis.
(From RUFZ DE LAVISON.)

permeability. This is no intrability, because the substance leaves the plasm again. We may arrive, however, at entirely wrong conclusions, if we compare the results obtained in this way for permeation through the plasm, with those obtained for permeation of the substance through the plasm from environment to vacuole, in which case the tonoplast has to be passed too. In order to avoid confusion, it is desirable to indicate one of the two processes by an other name. In order to maintain the word permeability for cells possessing no vacuole, such as all animal cells, it is desirable to give a different name to the penetration from the environment through the protoplasm into the vacuole. In this case we shall use the terms *transmeability* and *transmeation*. *The protoplasm, therefore,*

that allows a substance to pass through both membranes, through plasmalemma and through tonoplast will be called transmeable here. We then arrive at the following definitions. The general conception penetrable will be expressed by *permeable*. This may obtain for the wall, the plasm or for plasmalemma and tonoplast separately. If an exact indication of the kind of permeation through the plasm is desired, we use *intrable to designate that the substance permeates through the plasmalemma into the plasm and transmeable when the substance passes through plasmalemma as well as tonoplast to arrive in the vacuole.* If the substance does not pass through the tonoplast, but leaves the plasm through the plasmalemma, we speak of *permeable sensu stricto.*

If we abide by this terminology, it may be prevented better than has been the case hitherto, that processes of various nature are put on a level. If we consult summarizing works on permeability, as e.g. Das Permeabilitäts Problem by GELLHORN, it strikes us that not even an attempt has been made to separate the data on intrability from those on transmeability. Indeed the investigators themselves repeatedly leave it undecided which quantity they have determined. This for instance holds good of those, who compare data on Bacteria and other unicellular organisms, which possess no or only small vacuoles with those on higher plants where transmeability has been determined. It may be imagined that in some cases it may occur that the tonoplast is better permeable than the plasmalemma. In that case it will make no difference whether an investigation is made into intrability or transmeability. Instances of cases in which this has actually been investigated, are certainly not abundant. The same objection obtains for a survey by KAHO (1926) in ‚die Ergebnisse der Biologie', where data on intrability in higher plants are being compared to those on transmeability without it being considered that this is not permitted without comment. Also LUNDEGARDH's method (1911) to determine the permeability of the root from the change in length of its apex by permeation of substances, deserves further study, because we are not sure which quantity was determined in these young cells rich in plasm. With this type of experiments it is possible that in older cells transmeability is determined, in the younger cells intrability. The meaning of the terminology proposed here, is to get a better base for comparative observations.

We shall now proceed with the discussion of the permeation of various substances. We already stated that dissociated substances behave differently from non-dissociated ones. About the permeation (here: transmeation) of this latter group of substances we have obtained good information through the researches of HÖFLER and COLLANDER with their collaborators. We know that they can more or less penetrate into the vacuoles of the living cells through diffusion and that this process is dependent on the ‚transmeability' of the protoplasm. The permeation into the vacuole and the exosmosis of the absorbed substance from the vacuole

when the cells are again submerged in water, are diffusion-processes which proceed in the same way in either direction. Transmeation through the protoplasm is determined by the size of the molecules and by the lipoid-solubility of the diffusing substances. In case of equilibrium the substances in the vacuole will be present in the same concentration as in the medium, unless the solubility of the substances in the cell sap is different from that in the external solution or the substances are being chemically converted or fixed. This may cause an accumulation of substance in the vacuole, but it is of a nature quite different from the accumulation which often occurs on accumulation of salts, when the substances are piled up in the vacuole unaltered and are found there in a dissolved condition.

For salts too it is assumed by various investigators that they permeate through the protoplasm. Especially in Beggiatoa mirabilis a great permeability to salts was found by RUHLAND. The researches by FITTING, WEIXL HOFFMAN, JARVENKYLA and MARKLUND have shown that in higher plants salts can permeate through the plasm in a slight degree (permeate used here in the sense of transmeate). It remains, however, uncertain whether in experiments with non-balanced solutions we have to deal with a normal behaviour of the protoplasm. Besides we have to consider that these experiments have often been made with concentrated or fairly concentrated salt solutions, so that they do not prove that very low concentrations, such as act a part in the environment, can pass as well. Objections to plasmolysis-experiments have been repeatedly been raised (RUHLAND, ILJIN, STILES, SCHMIDT, ARISZ and VAN DIJK). We shall see in the next section that there is reason to surmise that from such low concentrations there can penetrate ions into the protoplasm, but that a passive diffusion of dissociated or non-dissociated salt molecules in the vacuole is improbable. This makes us suppose that the positive results obtained with high concentrations of a one-salt-solution might be connected with modifications in the conditions of the protoplasm, which are brought about by the abnormal concentrations of certain ions, after the ions have penetrated into the protoplasm through the intrable outer layer. It is known that one-salt-solutions, such as are used for plasmolysis-experiments, are extremely poisonous as nutrient solutions. Moreover by the use of high osmotic concentrations the plasmolysis method causes alterations in the protoplasm which hinder its normal function, which according to ARISZ and VAN DIJK appears from the fact that the active uptake of asparagine is considerably hampered. In still unpublished researches the great sensitivenous of the active salt uptake has appeared for one-salt-solutions, even in a very dilute solution.

In correspondence with this are the experiences with „Kappen"-plasmolysis, a phenomenon by which the cytoplasm swells strongly. According to HÖFFLER this swelling is brought about by an enhanced intrability of the protoplasm due to the concentrated salt-solution. Different researchers

among whom SEIFRIZ, LEPESCHKIN and HÖFLER assume that the plasmalemma allows ions to pass, the tonoplast does not. Solutions so highly concentrated as are used for permeability-experiments, however, don't act a part in the environment of most organisms. By the absorption of salts from ditch-water or from the soil we have to deal with much lower concentrations 1/10000 to 1/100000 mol and on the question whether such low concentrations permeate or not plasmolysis-experiments can throw no light. To be sure, in the organisms living in the sea the salt-concentrations in the environment are much higher, but it is surprising to find that the composition of the cell sap also in unicellular weeds living in the sea may considerably differ from that of the environment (OSTERHOUT), which surely does not suggest permeability of the plasm for these ions. On the ground of his experiments with unicellular weeds COLLANDER has arrived at the conviction that the plasm as a whole does hardly allow any salts to pass and one should rather be surprised that the protoplasm is so little permeable to salts. By the very impermeability of the protoplasm maintaining a high osmotic concentration in the vacuole is possible. So when we notice that substances which do not permeate are yet accumulated in the vacuole this points to the existence of a process through which these substances are taken up from the environment into the protoplasm and are passed on by the protoplasm to the vacuole. Our intention is to analyse this process of absorption in this article. It may be divided into the following parts which will be treated separately.

They are: 1. the uptake of ions from the environment into the protoplasm.
2. the secretion of ions by the protoplasm into the vacuole.
3. the transport of ions in the protoplasm and from cell to cell.

It is not our intention to give an extensive discussion on the mechanisms of the interchange of ions, of the transport in the protoplasm and of the accumulation in the vacuole. It may, however, be valuable to analyse the combined action of the various processes and to throw some light on some essential points in the salt-absorption of the root.

§ 3. *The uptake of ions into the protoplasm. The permeability of the surface layers of the protoplasm.*

From the great number of experiments made in the last few years with radio-active ions, it has become clear that they are easily taken up into the plant. If a plant with roots is placed in a medium with radio-active ions, their presence in the root can be demonstrated after a short time. Next they penetrate into the wood vessels and they are rapidly spread through the whole plant with the transpirationstream. STOUT and HOAGLAND also found a strong lateral transport through parenchyma-tissue from the wood to the cortex.

From experiments by JENNY, OVERSTREET and AYERS with radio-active ions it appears that the outer layer of the protoplasm is penetrable for ions. If a plant which has taken up radio-active potasium ions, is trans-

ferred to a solution without radio-active potassium ions, there ensues a loss of radio-active potassium ions, if a potassium salt is present in the solution, which is, however, not the case when the medium is pure water or a solution of salts with other cations, as sodium. This points to an interchange of radio-active potassium ions and non-radio-active ones, and it may be concluded from this fact that under normal circumstances potassium ions from the medium are continuously interchanged with potassium ions from the plant. The surface zone of the protoplasm is therefore permeable to these ions. The same obtains according to these investigators for radio-active sodium- and bromine ions. If therefore a plant does interchange radio-active potassium against other potassium-ions, but not against sodium-ions, which are present in the medium, this is not due to the fact that the plant does not allow these ions to pass. but because the conditions for interchange are not present. From this it may be concluded that *the surface layer on the outside of the protoplasm renders interchange of ions possible*. This may be called *interchange-permeability of the surface-layer*.

OVERSTREET and BROYER investigated into the uptake of radio-active potassium in barley. This may be an active absorption in the sense of STEWARD and HOAGLAND or a cation interchange. At 0° C. radio-active potassium is taken up as well, but as at this temperature no active absorption can take place, the uptake must be entirely based on the interchange of cations under these circumstances. This interchange proved to continue till a limit is reached at which 10 % of the total quantity of potassium present in the roots has been interchanged. The remainder of the potassium is not interchanged. The writers state that the interchangeable potassium "is believed to be associated with the colloidal phases of the protoplasm and cell wall". From this it follows in my opinion that the potassium present in the vacuoles cannot be interchanged at 0° C. If one conceives that the protoplasm of the parenchymatous cells forms one coherent whole, which deserves the name of symplast, this means that from the whole symplast potassium ions can interchange with ions of the medium, but that the potassium present in the vacuoles is not interchangeable.

This makes us surmise that in these experiments the *vacuole-bounds are impermeable to potassium-ions*. It was, however, shown by JENNY and OVERSTREET that in a medium of acid clay colloids (pH 2.9—3.5) the potassium from the vacuole can be replaced by hydrogen as well, because they found that as much as 20 % and even more of the potassium present can be interchanged with H-ions. From this they concluded that all phase-boundaries are permeable to cations in both directions. They, however, inform us that in experiments with acid clays the cells are damaged, so that the permeability of the tonoplast may be founded on its damaged condition. In less acid clays the cells were not damaged irreversibly. Yet in our opinion normal physiologic conditions are out of the question in

these experiments as well, so that it seems possible that here too under the influence of the high concentration of the H-ions in the medium the conditions of the protoplasm and of the surface-layer of the vacuole have been changed in such a way that the tonoplast is no more capable of checking ions.

In connection with these researches we shall discuss here a research of MAZIA's on Elodea, from which it also appears that the tonoplast as contrasted with the plasmalemma is impermeable to certain ions. In Elodea no calcium is present in the vacuole, while calcium that gets into the vacuole immediately crystallizes as calciumoxalate. Indeed there is calcium in the protoplasm; this may be removed from the cell by potassium citrate, without its being irreversibly damaged. If it is subsequently brought into a solution of calciumchloride, the plasm again absorbs calcium ions. The presence of calcium in the protoplasm may be demonstrated by the fact that with certain stimulation reactions (MAZIA and CLARK) calcium is released to the vacuole and crystals of calcium oxalate are formed. The vacuole wall therefore is in this case under normal circumstances impermeable to calcium ions, while the plasm can easily deliver and absorb calcium ions through interchange with other cations Mg, Sr, Ba, K, Na in the medium (MAZIA 1938). These data point to the fact that interchange of ions between *plasm* and *medium* can easiliy take place, but that the *vacuole* cannot allways participate in it, because the tonoplast does not allow all ions to pass. MAZIA, however, like HEILBRON assumes that as a result of the stimulation the plasm sets free Ca-ions, so that they diffuse in the vacuole.

BROOKS and BROOKS (1941) also hold that ions easily penetrate into the protoplasm, provided there are other ions that leave the plasm at the same time. Both ions in the surface zone and ions from the whole plasm, which are combined with proteins there, participate in this.

BROOKS found a similar interchange of ions by Nitella for potassium and rubidium, but not for bromine. He stated (1937) that if a Nitella cell is brought into a solution of radio-active potassium, for the first six hours no radio-active potassium penetrates into the vacuole, whereas already after a few minutes radio-active potassium has penetrated into the protoplasm through interchange of ions. It seems to me that from this fact it may also be concluded that between *vacuole* and *protoplasm* interchange of ions does not occur or with great difficulty. BROOKS himself, however, assumes that ions get from the plasm into the vacuole by a concentration gradient through diffusion. All the above researches therefore support in our opinion the *conception that the protoplasm and its surface zone are permeable to ions, but that certain ions cannot pass into the tonoplast.* Yet we see in some cases that exosmosis of actively absorbed substances from the vacuole occurs. If for instance the protoplasm and the tonoplast are in abnormal circumstances, the surface zone of the vacuole may temporarily become permeable to ions, so that exos-

mosis of ion pairs or interchange of cations and anions may take place. Such an exosmisis was found (ARISZ 1943) as a reversible phenomenon in Vallisneria leaves when after taking up asparagine, they are transported to another solution, pure water or a fresh asparagine solution, in which there are not any salts. Evidently in order to remain in an active condition the protoplasm with its two surface layers needs a medium of a definite composition in which various cations and anions have to be present in an extremely low concentration. By release of ions to the medium the normal condition of the protoplasm is restored after some time; then the protoplasm is again capable of taking up asparagine. This conception corresponds with the data in literature on the toxicity of distilled water and of salt solutions and agrees with the views on antagonism of ions of SEIFRIZ, LEPESCHKIN and HÖFLER.

It has appeared from different experiments that besides through interchange ions can also be taken up without ions of the same charge being released at the same time (LUNDEGARDH, HOAGLAND). In this case in order to maintain the electric equilibrium, ions with an opposite charge must be taken up, either as ion pairs or as BROOKS and LUNDEGARDH suggest, because at certain points cations and at other points anions enter. Now the question will have to be answered whether ions can be taken up into the plasm to an unlimited amount. It is probable that they are partly free, partly bound to the plasm. This binding will probably be of a chemical nature, but it behaves as an adsorption binding. For convenience sake we talk in this case of *adsorbed* ions. All ions in the plasm, except of course those which are built-in in stable chemical compounds, that is both adsorbed and free ions, can be interchanged with ions from the medium.

The concentration of the free ions present in the plasm, is probably determined by Donnan equilibria. In addition the distribution of ions between plasm and medium will also be influenced by the "diffusion effect", studied by TEORELL (1935), in consequence of the diffusion outward of a dissociated substance. The ions in the protoplasm cannot be present in a higher concentration in a free state than the one fitting these equilibria. Otherwise they would leave the cell through the outer layer, which is permeable to ions, whereas from numerous researches it appears that for instance to distilled water no or exceedingly few ions are released.

In order to continue the uptake of ions from the medium as a continuous process, the ions adsorbed to plasmic particles in the surface zone should be removed and leave room for the binding of other similar ions from the medium. From the experiments of JENNY and others with radioactive ions it appeared that simultaneously ions from the plasm go to the medium and vice versa. Owing to the removing of ions from the plasm at a constant speed a streaming of ions will result from the medium to the protoplasm.

This conception of the uptake of ions corresponds very well with the quantitative data on the strength of ion absorption from solutions of various concentrations. In the most varying objects it has always been found that from low concentrations the uptake is relatively greater than from high ones. The curve showing the connection between the concentration of the absorption and the concentration of the solution in the medium has the course of the adsorption isotherm of FREUNDLICH. Various investigators have considered this as an indication that the substances in the cell would be bound by adsorption (STILES, LUNDEGARDH). Others (HOAGLAND, COLLANDER) on the contrary believed that the substances are present in the vacuole in a free state. SCARTH and especially VAN DEN HONERT pointed out that this course of the curve can likewise be explained by the fact that an adsorption process has a limiting effect on the uptake.

So in his experiments on the uptake of phosphates VAN DEN HONERT comes to the conclusion that the ions are adsorbed at the surfacezone and are removed to the vacuole at a constant speed. The amount of ions taken up is on the one side determined by the amount of ions adsorbed at the surface zone, on the other side by the speed of removal. For this purpose VAN DEN HONERT makes use of the image of the conveyor-belt which had already been used by VAN DER WEY for the transport of growth substance before.

The process of the transport of ions in the protoplasm will be discussed in § 5. Below only the first part of the process is treated, the adsorption of the ions to the protoplasm. From the above it may be concluded that there is a tendency to attain an adsorption equilibrium between the ions which are bound in the outward layer of the protoplasm and the active concentration of the ions in the medium. Such an adsorption-equilibrium will generally be rapidly achieved, so that this process develops in most cases so quickly that the adsorption-equilibrium is approached. LUNDEGARDH (1941) found that the formation of the electric potential at the root surface for H-ions was reached in 0.75 sec., while on exchange of a 1/10000 into a 1/1000 m. salt solution, the formation takes place in 1 to 4 seconds, dependent upon the nature of the cation. This longer duration would indicate a diffusion over a distance of 2.9 μ as far as the adsorbing surface zone.

Various investigators have found the laws of adsorption applicable to the uptake of ions by the plant. We only mention STILES 1924, SCARTH 1925, LEMANCZYK 1926, NIKLEWSKI, KRAUSE and LEMANCZYK 1928, WRANGELL 1928, LUNDEGARDH 1932, 1935, 1938, 1940, PERIS 1936, LAVOLLAY 1936. Our own researches on the uptake of substances by the tentacles of Drosera and those on the uptake of substances by Vallisneria pointed to the significance of adsorption processes as well. This can therefore be based on the view that *the first phase of the process of uptake is an adsorption to the plasm and that the concentration of adsorbed ions*

is one of the factors determining the strength of the transport of ions

So in the preceding discussion we arrived at the conclusion that the outer layer of the protoplasm allows ions to pass, whereas the tonoplast may inhibit the passage of certain ions. The question may now be raised whether only ions which are adsorbed by the plasm can penetrate into the protoplasm, or that also ions can be taken up without being adsorbed to the surface zone. No direct data bearing on this subject are known. Though the pores will not be very narrow, because, as will be subsequently discussed, the protoplasm of leaf- and root cells is intrable for sucrose (see pag. 21) it is conceivable that owing to their charge the free ions cannot penetrate through the pores, whereas they will be able to do so, when they are adsorbed by the plasm (cf. PFEFFER and SCHÖNFELDER), because in that case they have a larger part of the pore at their disposal. *On the ground of the above representation that an adsorption process has a limiting influence on the uptake, it is likely that only adsorbed ions can be taken up.* If free ions also penetrated this relation would be impossible. Whether the binding of the inward-directed ions to the plasm already occurs in the surface zone or in a layer lying more inward, cannot be decided and does not matter here. Since in the protoplasm both cations and anions are bound, they may be simultaneously moved in the protoplasm and secreted into the vacuole. The behaviour of the ions discussed here only obtains for very low concentrations, as required for experiments with nutrient solutions. In higher concentrations and especially in such high concentrations as are used in plasmolysis experiments, the physico-chemical properties of the protoplasm will be modified by the entering ions. This gives rise to phenomena as "Kappen"-plasmolysis. Owing to the higher concentration of the medium a new equilibrium of the ions in the protoplasm will be formed. If a one-salt-solution is used, the relative ratio of the different ions in the protoplasm will be altered. As for a normal functioning of the protoplasm the ratio of the different ions must remain within certain limits, the physico-chemical condition will change, when these limits are exceeded. In that case the permeability of the tonoplast may alter likewise. Hence that in plasmolysis experiments results may be obtained about the permeability of the protoplasmic membranes which are different from those obtained in experiments with lower salt concentrations.

If the above conception of the permeability of the protoplasm and its membranes is correct, the accumulation of substances in the vacuole is in many cases an active secretion. The energy required for this process is provided by aerobic respiration. Of course this does not alter the fact that also in the protoplasm in the way indicated by TEORELL and also through chemical reactions substances may be accumulated.

§ 4. *The secretion of ions into the vacuole. The accumulation process.*

In many experiments it is impossible to determine with certainty wether

a substance that has been taken up by a cell, is present in the plasm, in the vacuole or in both. In fact this can only be ascertained for those cells that possess so large a vacuole that the cell-sap can be analytically examined. Only in a few cases the presence of a substance may be concluded from a chemical reaction, which brings about a visible alteration. Therefore experiments with weeds consisting of large cells such as the Characeae, Chara and Nitella and also with Valonia and Halocystis are of great value, because in those the cell sap can be analytically examined. STEWARD, however, drew attention to the fact, and also COLLANDER's observations are in accordance with it, that these cells show a relatively slight accumulation. Though BROOKS contests STEWARD and MARTIN's conception that Valonia is little active, by pointing out that their metabolism is active in proportion to the amount of protoplasm, this does not alter the fact that active accumulation in these cells is slight with respect to the volume of the sap. The experiments with these organisms, however, indicate that by active processes substances can be accumulated in the vacuole. For cells of a tissue we must do with less accurate methods. The investigators who analyse expressed sap from tissues in order to trace whether substances have been taken up, have to face the difficulty of proving that this expressed sap, at least in the main, corresponds with the vacuole sap. It appeared that especially in the last few years there was no unanimity on this head. It may, however, be expected that in cells with little protoplasm the sap, which is being expressed, after the protoplasm has been killed, will in the main correspond with the vacuole sap (STEWARD 1932, BROYER and HOAGLAND 1940).

A third method to trace whether substances are taken up in the vacuole, is the simultaneous determination of the osmotic value of the cell sap and of the amount of substance taken up in the cell. In tracing this a good correspondence between increase of osmotic value expected and found was ascertained in some cases (ARISZ and VAN DIJK, ARISZ 1943). Neither does this method give any certainty, because the change of osmotic value may as well be caused by ana- or cata-tonosis.

On the ground of researches with radio-active ions BROOKS arrived at the conclusion that Nitella first accumulates ions in the protoplasm and does not pass them to the vacuole until later. The accumulation in the vacuole therefore would be a result of a previous accumulation in the protoplasm and would not take place contrary to the concentration-gradient. COLLANDER could not corroborate these data by Nitella. A priori it does not seem probable that in the protoplasm an unlimited accumulation of freely diffusing ions could be maintained, while the outer layer of the protoplasm allows ions to pass. The view we developed in the preceding section that the tonoplast does not allow ions to pass, is conditional for the maintenance of salts in a higher concentration in the vacuole than in the protoplasm and the medium.

Also if one assumes, as has been done here, that for accumulation of

substances in the vacuole a concentration-gradient plasm-vacuole, is not required, the accumulation mechanism will have to be localized in the protoplasm contiguous to the vacuole, and one will after all be able to agree to the conception of BROOKS: "The concept which we wish to bring out, is that the protoplasm is the agent which is important in accumulating electrolytes".

On the nature of the accumulation mechanism, i.e. the uptake of ions by the vacuole various investigators have given theories, see among others BRIGGS, OSTERHOUT, LUNDEGARDH and HOAGLAND and BROYER's criticism (1940). We shall not go further into this in this article and consider this process either a consequence of the accumulation in the protoplasm or a secretion into the vacuole, in the way the protoplasm secretes substances to the vessels or to the medium (active hydathodes). Energy is needed for this performance.

The consequence of this accumulation must be further discussed here. For the organism it means that the osmotic value of the vacuole is being enhanced. For the growth of the cells this is essential, because the pumping in of osmotic substances into the vacuole of growing cells maintains a turgor pressure which is conditional for cell-elongation. This moreover depends on the presence of a number of growth factors, as growth substance and cell building material (cf. pag. 23). To the essential significance of this secretion process BURSTRÖM and FREY-WYSSLING recently also drew the attention.

When the question is asked whether the accumulation in the vacuole is of any consequence for the transport of substances in the tissue of the plant, this question must be answered in the negative, for it seems to be a not very efficient mechanism for this purpose. For instead of making the substances available for transport, they are fixed in the vacuole. The data on root systems of plants of high or low salt-concentration (HOAGLAND and BROYER) show, however, that the accumulation in the vacuole does not continue in an unlimited way and in connection with the enhanced osmotic value there may exist a limit, at which the accumulation decreases or stops. This puts an end to the accumulation in the vacuole, so that the substances become available for the adjacent cells in larger quantities. In this connection it is interesting to point to a supposition we made regarding the transport in the Drosera tentacles (ARISZ 1944). In these typical transport organs the vacuoles would be nearly put out of use through the aggregation of the cells of the tentacles, while the plasm through swelling takes up a volume as large as possible. With these specific transport cells therefore no or hardly any accumulation of the transport-substances into the vacuoles of these cells would take place. For transport purposes the cytoplasm is of pre-eminent importance.

§ 5. *The transport of ions in the protoplasm.*

The experiments with radio-active ions prove that the ions not only

penetrate into the cells contiguous to the medium, in which the radio-active ions are present, but that they are also easily transported from cell to cell and in consequence of this have been spread over large pieces of parenchymatous tissue after a short time. A transport of ions from cell to cell is therefore possible. Now that we have seen that the surface zone of the protoplasm allows ions to pass for interchange and the inner-layer, the tonoplast, may be impermeable to ions, only cell wall and cytoplasm are to be regarded for this transport of ions.

The experiments with radio-active ions are not the only examples of such a transport. We know that also under the influence of clays saturated with bases, in which the active concentration of the cations at the surface is very high (JENNY), interchanges of ions with large tissue-complexes take place. With these experiments it cannot be doubted that the ions which are present in the plasm are replaced by ions from the medium. In the experiments of various investigators, regarding the excretion by the roots of ions coming from the shoot (PRIANISCHNIKOW, ACHROMEIKO, SCHMIDT, LUTKUSS and BÖTTICHER) this process must take place through large strands of parenchymatous tissue. It is not known how far the release of ions from the above mentioned parts is based on a transport along special tracks (phloem), but partly this will no doubt be a transport through parenchymatous tissue. Also the radial transport of radio-active ions, which STOUT and HOAGLAND found in the stalk, must be transport in parenchymatous cells.

These phenomena therefore make the impression that through the plasm ions can be easily moved along fairly long distances and it seems likely that the adjacent cells are bound by plasmatic connections and form a symplasm (MÜNCH). *In the symplasm ion transport can easily take place.*

If, however, we don't hold by MÜNCH's symplasm hypothesis, we shall have to assume that the transport does not occur in the cytoplasm of the cells, but that in addition the cell-wall and the outer layer of the protoplasm will have to be passed. As the cell-wall is comparatively thin and the outer layer of the plasm allows the ions to pass, the ion transport will in principle take place in the same way as in a symplasm, but it will be greatly retarded by the diffusion from cell to cell.

The mechanism of the ion transport in the plasm is too hypothetical as yet to be treated extensively. In a previous publication (ARISZ 1944) we pointed out when discussing the transport in Drosera tentacles that the transport of ions in the cytoplasm through binding to the protoplasm is conceivable in two ways. It may be imagined 1. that *the ions bound to protoplasmic particles* are transported by the streaming protoplasm, so that we have to deal with *protoplasmic streaming*; 2. that the ions first bound to the outer layer of the protoplasm proceed to other plasmic-particles and from these again to others, etc., so that therefore *the ions are transported in the plasm, each time bound to other particles of protoplasm.*

The first hypothesis was also discussed by LUNDEGARDH in 1932. He says on p. 227: :"Durch solche Massenströmungen würde natürlich ein Durchtritt von gelösten Körpern auch in dem Fall stattfinden können, wenn die Diffusionspermeabilität sehr gering oder gleich Null ist. Wenn nämlich der gelöste Körper durch chemische Bindung oder Adsorption von den Partikeln der äusseren Grenzschicht des Kolloids aufgenommen wird, so kann es bei Konvektionsbewegung der Kolloidpartikeln doch durch die Schicht hindurchgehen. Dieser theoretisch denkbare Fall von Konvektionspermeabilität scheint bisher nicht berücksichtigt worden zu sein."

LUNDEGARDH points in this connection to the theoretically conceivable case that ions are taken up without permeating into the plasm (cf. LUNDEGARDH 1940 p. 263). As, however, interchange of ions also takes place at a low temperature, at which the protoplasmic streaming ceases, this possibility should in my opinion not be considered as an explanation of the passing of the surface layer.

A transport of substances bound to protoplasmic particles virtually resolves itself into HUGO DE VRIES' old theory on the influence of protoplasmic streaming on the transport. According to this the movement of the plasmic particles causes the transport of substances.

The second hypothesis that the ions go from one plasm-binding to another, has certain advantages, especially if the conception of a symplasm is correct. For in that case the ions can be spread over the whole symplasm in the same way. If, however, the symplasm-hypothesis is not correct, we shall have to assume that the ions get from one cell into the other by diffusion and in the case of polar transport by electric forces as well, by which each time both the outer layer of the protoplasm and the cell wall have to be passed.

Indeed there is not a very great difference between the two hypotheses, as probably the invisible transport of ions will bring about visible protoplasmic streaming, as VAN DEN HONERT (1932) has proved likely by means of model experiments. In that case protoplasmic streaming is not the cause of the transport of substance, but an attending phenomenon. FITTING's researches with Vallisneria leaves on chemodinesis of various substances would indicate that owing to the emersion of a leaf in a solution containing a chemodinetically working substance, the latter is taken up in the cells and causes a microscopically perceptible streaming in the protoplasm. When after some time the substance is equally distributed over the complex of cells, the protoplasm again settles down. This is not the place to point out the many points of correspondence between protoplasmic streaming and transport of substance, both in the transport of growth substance (BOTTELIER, DU BUY and OLSON, THIMANN and SWEENEY) and in the transport of salts (ARISZ, tentacles of Drosera and still unpublished researches on salt transport in Vallisneria). The theory of JENNY and OVERSTREET (1939 cf. fig. 2) on transport along

surface boundaries indicates a possibility, how transport of ions along surfaces can rapidly take place (cf. LUNDEGARDH 1940, p. 369). If the ions in the plasm are bound to substances like proteins, they may also interchange in a similar way between adjacent ion-binding areas. If, however, the ions are more firmly attached to the proteins, so that such

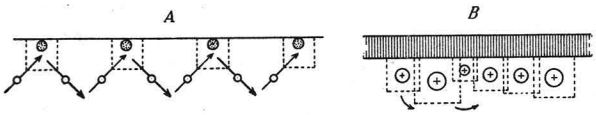

Fig. 2.
A. Schematic representation of diffusion of ions in colloids.
The dotted lines circumscribe the oscillation spaces of the adsorbed ions.
B. Scheme of the movement of a positive ion along a boundary.
The oscillation spaces of the adsorbed ions partly coincide, which makes a faster movement possible.
(From JENNY and OVERSTREET.)

an interchange cannot easily take place, we may be reminded of the short life of these proteins, as it appears from newer data on substances containing radio-active atoms, in which the ions are set free, when the protein is decomposed. May be rhythmical processes as JANSSEN imagines by the synthesis of substances in the organism, may act a part in these ion movements. The cause of these ion movements will have to be found in concentration differences which are caused either by a higher active concentration in the medium or by a lower active concentration in the regions of growth and synthesis in the plant. In § 8 this will be further discussed. Seeing the transfer of unequal amounts of cations and anions would cause an accumulation of electrical charges, a simultaneous transport of anions and cations in the protoplasm will as a rule have to be assumed. In how far in synthesis processes cations and anions can locally be used up in unequal quantities and the levelling of the difference in charges may take place at a different point in the plant, we cannot express an opinion on. BREAZEALE (1923) seems to have conceived something like this.

§ 6. *Permeability of tissues.*

It appears from the preceding discussion that in order to understand the transport of ions in tissues and particularly in the root, we must get away from considering the behaviour of separate cells. We must consider the parenchymatous tissue as one whole and therefore we speak of the permeability of a tissue in distinction of the permeability of a cell or of the plasm of one single cell. The phenomenon of the plasm-transmeability (see the definition on p. 25) is very material from the standpoint of *cell* physiology, because it defines what substances diffuse in the vacuole. From the standpoint of *tissue* physiology, however, this cellular phenomenon is less important. Here we are not concerned with

the introduction of substances into the vacuole, but with the permeability of the plasm in that sense that substances can pass the plasm of the whole tissue. The permeability of the tissue concerns the penetration into the protoplasm (intrability), the further transport through the plasm from cell to cell and the possible release of the substance. In this process the outer surface layer of the plasm is passed at any rate ,but this need not be the case with the tonoplast, so that the being taken up into the vacuole or not is of no consequence. Hence the fact that from experiments from which it appears that a tissue is permeable, we may at most draw conclusions as to the intrability of the cytoplasm, but not as to its transmeability, while it must be considered whether the substance may be transported along the cellwall without concerning the protoplasm. An instance, making this clear, has already been discussed viz. the permeating of concentrated salt solutions through the endodermis sheath of the root (cf. p. 4). Here we still wish to discuss K. PERIS' experiments (1936). She found that roots of Phaseolus multiflorus, which suck up water from a potetometer with a constant speed, take up less liquid from the moment when the water is replaced by a salt solution. It is comprehensible that the suction tension of the salt solution retards the uptake of water (BRIEGER 1928). After some time, however, the uptake of water increases without reaching its original strength. This increase in water absorption she explains by permeation of the salt solution into the cells of the root and she makes use of this phenomenon to compare the permeation of various salt solutions. By permeation she means the penetration of substances through the plasm into the vacuole. Let us assume that this phenomenon is indeed connected with the penetration of salts into the tissue of the root. [1]) It is then permitted to speak of plasm permeability, as only the penetration of the salts into the protoplasm (symplasm) in the direction of the woodvessels is concerned. If this takes place the resistance of the symplasm decreases and the absorption of fluid must increase. Only the cell wall and the plasmalemma need be passed. From these experiments, therefore, we may at most draw a conclusion about the *intrability* of the plasm and the ability of special substances to be transported through the symplasm of the root cells. On the *transmeability* of the plasm and the permeability of the tonoplast these experiments can certainly not give us any information. That is why a comparison of the results of these experiments with those of FITTING, BARLUND and HÖFLER. who investigated into the transmeability, is not permitted. Similar confusions are repeatedly found in literature (cf. p. 424).

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[1]) Here we may point to the possibility that as a result of decreased water supply, the suction tension in the leaf cells, which is the cause of water transport, increases. As for bleeding SABININ found a similar phenomenon, it is probable that the penetration of salts also acts a part.

§ 7. *Salt-transport in the root.*

In the preceding discussion the process of ion-transport has only been discussed in its simplest form, as it will proceed in a symplasm or in a complex of identical cells. We already discussed in § 1 that in the root two processes take place side by side: 1. an accumulation of substances into the vacuoles of the parenchymatous cells of the cortex and 2. a transport of substances to the central cylinder and secretion to the wood vessels. By the root hairs of the epidermal cells salts are absorbed from the environment. They must be transported through the plasm of the cortical cells to the central cylinder, but on their way there the plasm of the cortical cells may be able to secrete salts into the vacuoles of these cells. This does not preclude that salts also penetrate into the root through the walls of the parenchyma cells of the cortex. Together with the absorbed water they are transported in the intermicellar spaces of the cell walls (STRUGGER and ROUCHAL) and may penetrate into the plasm of the cortical cells. This renders it comprehensible that with a stronger water-absorption more salts are taken up, because in that case not only the whole surface of the epidermal cells, but also that of the cortical cells adjoins the external solution. Of course this is only material if the concentration in the external solution is very low, so that the strength of the absorption is also determined by the extension of the absorbing surface.

The salts which are transported in the cell walls and in the plasm of the cortical cells of the root, arrive through the endodermis in the central cylinder and are there given off to the wood vessels. The concentration in these vessels can become considerably higher than in the medium (HOAGLAND and BROYER). Together with the water present in the vessels the salts are transported to other parts of the plant and again taken up into the plasm and the vacuole by the living cells of leaves and branches. Part of the salts is absorbed in the growing parts by the synthesis of protoplasmic substances, another part is being secerned in the vacuoles the remainder would be transported to the basal parts of the plant through the sieve vessels. According to MASON and MASKELL (1931) nitrogen, phosphor and probably also potassium and some other ash-constituents would take part in this transport, while calcium remains in the leaves and is not transported in the phloem.

The process in which salts are absorbed from the medium and excreted to the wood vessels, requires a further discussion. CRAFTS and BROYER gave an interesting explanation of this. According to them the external conditions, especially the oxygen supply would be for the cortical cells different from what it is for the cells lying inside the central cylinder, because the former tissue is well-supplied with oxygen through air canals, whereas in the central cylinder the cells fit together without intercellular spaces and are consequently badly provided with oxygen. Under these circumstances the cortical cells would take up salts actively; but the cells

of the central cylinder release salts. It is quite possible that this theory of CRAFT and BROYER's is based on a correct thought. It assumes, however, an active salt accumulation by the cortical cells in the protoplasm. According to STEWARD, HOAGLAND and others, the active accumulation in the cortical cells is based chiefly on the accumulation in the vacuole and this is of no consequence for a transport to the central cylinder (cf. § 4).

The salt transport from medium to woodvessels can't be a simple diffusion process, because the concentrations of cations and anions in the xylem vessels may be higher than in the medium, so that the uptake and transport of ions to the wood may occur contrary to a concentration gradient. This cannot but imply that we have to deal with an active mechanism. This mechanism, may be, as we saw, the accumulation mechanism of the cortical cells, but there is also another possibility which will be discussed here.

In this connection we may remind of the fact that in experiments on the influence of the environment on the composition of the bleeding sap, a similar result was obtained, viz. that the ions in the bleeding sap may be present in a higher concentration than in the environment. LAINE (1934) found that here the same connection exists between the concentration of the bleeding sap and that of the environment as with an adsorption process between the amount of adsorbed substance and the concentration of the environment, so that FREUNDLICH's formula holds good, $s = k\, c^{\frac{1}{n}}$ in which s = concentration of the bleeding sap and k and n represent constants which are different in the case of potassium, calcium and manganese. This points to the fact that the process of bleeding, by which substances from the environment are absorbed and transported to the xylem conforms to the same law as the absorption by the root and the leaves. In § 3 we ascribed this phenomenon to the adsorption-binding of the ions from the environment to the protoplasm and the removal of the adsorbed ions at a constant speed. With the secretion of substances into the vacuole the cause of the transport of ions is to be found in an active process that secretes the ions into the vacuole. Here a similar active process may assert itself which removes the ions from the surface layer and which is the cause of their transport in the symplasm of the cortical cells. As a result new ions are continuously adsorbed from the environment, next transported and finally given off to the woodvessels. The concentration of the ions in the woodvessels can then rise above that in the environment. The situation therefore is such that in the symplasm and the cell walls of the central cylinder a higher salt concentration may prevail than in that of the surrounding tissue.

Now it is known from anatomical data that on the boundary line of cortex and central cylinder the endodermis sheath is found. This can only allow the salts to pass through the plasm of the cells (DE RUFZ DE LAVISON 1911). The bands of CASPARY prevent a flow of the salt ions

from the central cylinder through the walls of the endodermis cells to the cortex and environment, so that here only transport of ions through the plasm of the endodermal cells can take place. It is therefore obvious to look in the endodermis for the cause of the active transport of ions, though it is not excluded that other cells in the central cylinder have the same function. If this conception should be correct, the cells of the endodermis would have a secretory function (cf. URSPRUNG 1925, GUTTENBERG). There are several data that indicate that this function varies specifically for different ions. Some ions are easily transported between environment and wood vessels, others less easily. WIERSUM's experiments, which have been made in this laboratory and have not yet been fully published, show this. WIERSUM (1944) traced bij roots of Vicia Faba how salts brought into the woodvessels can permeate through the central cylinder and the cortex to the environment. He found that calcium-ions pass well and potassium-ions less easily. These are experiments in which the permeability of the root tissue was examined, and from which it appears that calcium-ions can be easily transported through the root tissue in a radial direction. In WIERSUM's experiments the uptake of water proceeded in a direction opposite to that of the salt transport. The transport, therefore, need not be a passive carrying along by a watercurrent, but may very well be based on diffusion and ion movements in the cytoplasm.

SCHMIDT (1936) found that the uptake of ions in Sanchezia nobilis is accelerated by transpiration. This obtains for calcium, magnesium, nitrate and phosphate, but not for potassium. BÖTTICHER and BEHLING found for maize that transpiration but slightly accelerates the uptake of potassium and phosphate, but strongly accelerates that of calcium. All these experiments show that calcium can fairly easily be transported through the system: environment-cortex-endodermis-centralcylinder-woodvessels, but that potassium behaves differently. It may be taken into consideration, whether the different behaviour of these ions is dependent on the more or less active transport of these ions.

Though not in a direct way concerned with the permeability of salts, yet it is worth while pointing out in this connection that also organic substances behave in the same way. Both PERIS and WIERSUM state that *sucrose* permeates fairly easily through root tissue. This result shows that *the surface layer of the cytoplasm is permeable for sucrose*. Evidently we have methods in hand here to ascertain the *intrability* of the plasm for various substances.

Of course it need not be added that the permeability of the tonoplast for sucrose is a problem in itself. In the case of sugar it may be expected that the outerlayer is permeable, the tonoplast is not. The plasm therefore is intrable for sucrose. WEEVERS already defended this conception in 1931 (cf. also NATHANSON and BENECKE and JOST I. p. 32, 1924) and could explain both the phenomena in plasmolysis through a sucrose-solution and the formation of starch in the cells of leaves that floated on a sugar

solution. If sugar is found in the vacuole, this must be a result of metabolic processes, in which the sugars are accumulated or perhaps more exactly secerned into the vacuole, so that an accumulation may be brought about there.

§ 8. *Schematic representation of the processes for the uptake of electrolytes by the plant.*

In the preceding sections the different sides of the problem, how ions are taken up, have been discussed. We shall now proceed to treating a scheme on the uptake of salts and other electrolytes by the plant, which gives a summary of the insight obtained and consequently links up with the conceptions of other investigators.

Such a schematic representation offers the advantage that various points must be accurately formulated, in doing which it may appear how far we are still removed from a correct insight into these intricate processes.

The process of the uptake of ions may be divided into various phases. The first two phases are the uptake of the ions into the outer layer of the protoplasm, their binding at certain points and the movement of the ions in the protoplasm or in the symplast. If the temperature in which the organism is, is low or the vital processes are inhibited in another way, only an interchange of ions is possible. This occurs when the plant is transferred to an environment of a different composition. If, however, the plant is active, a third phase appears, in which ions are removed from the plasm by several causes. The local consumption of ions causes a disturbance of equilibrium in the symplasm, of which a movement of ions is the result and which ultimately causes an uptake of fresh ions from the environment. In this case an equal amount of cations and anions will have to be removed or if either of them preponderates, ions from the plant will have to be given off to the environment at the same time.

Removal of ions from the symplasm may take place in *three* different ways, viz. by *consumption of ions through the synthesis of new substances, through secretion of ions to the vacuole,* and *through actively secerning cells.* For the development of these processes in the living organism a protoplasm functioning normally is required. Besides both synthesis and secretion are dependent on respiration, because both are processes using up energy. As a result these processes will no more proceed normally in case of withdrawal of oxygen.

After all it is of little consequence whether we identify the active uptake of substances with the whole process of the uptake of ions from the outer layer to their consumption, or whether we will only give this name to part of this process, viz. the secretion to the vacuole. We shall speak of active uptake, when ions are withdrawn from the medium and they are fixed in either of the above ways by secretion to the vacuole or to other places or by using up by synthesis.

It has been indicated in the scheme (fig. 3) that between medium M and vacuole V the cytoplasm is found with its surface layers plasmalemma P_1 and tonoplast P_2. With the active uptake by a cell adjoining the outer solution, the ions will have to pass these layers in order to be taken up into the vacuole. The scheme shows that the accumulation in the vacuole

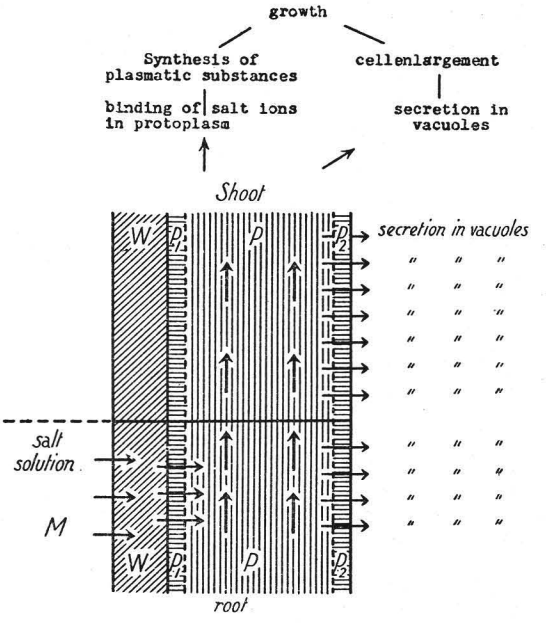

Fig. 3.

The uptake and transport of salts in parenchymatic tissue of root and shoot.

W = cell wall.
P = symplasm.
P_1 = plasmalemma.
P_2 = tonoplast.
M = outersolution.

may take place by secretion of ions by the cytoplasm into the cell sap. In this process the tonoplast does not allow these ions to pass through diffusion. Ions being in the protoplasm may be moved in the protoplasm without needing to pass plasmalemma or tonoplast. This is expressed by the conception symplast.

In the symplast a movement of ions can take place and in every cell-vacuole ions can be accumulated by a mechanism lying in the adjoining protoplasm.

In addition the scheme shows that in growing parts ions are fixed. Growth is dual: growth of plasm owing to synthesis of cell substances, when ions are fixed, and besides growth in volume by stretching of the cellwall.

The process of cell enlargement is based on turgor, active intussusception, growth substance and cell building material (cf. p. 14). The

tendency to maintain the turgor pressure and the taking up of water by the vacuole must be the result of simultaneous secretion of osmotically working substances in the vacuole, which causes water to be taken up. I can not agree with FREY WYSSLING who postulates an active uptake of water. As both the tonoplast and the plasmalemma are permeable to water this process would have no influence at all. I consider the active uptake of water, which has been demonstrated by the experiments of Miss REINDERS in this laboratory as a consequence of the active secretion of osmotic substances into the vacuole. Active secretion of substances into the vacuole is therefore conditional for the growth of the cell.

Both for synthesis and secretion ions are withdrawn from the symplast. By synthesis of amino-acids and proteins nitrogen in the form of NH_4 or NO_3 will be withdrawn from the symplast and S- and P-ions can also be fixed. The colloidal substances formed will moreover adsorb ions such as K, Mg, Ca, etc.

In growing parts therefore anorganic ions are absorbed directly and indirectly through synthesis, while besides a continuous secretion to the vacuoles takes place. The influence of the endodermis on the transport of the salts in the root has not been shown in this scheme (cf. § 7). The scheme only refers to parenchymatous tissue in general.

Summary.

An analysis is given of the uptake of salts by plants. This is a general physiological phenomenon common as well with unicellular organisms as with higher plants. Besides there are organs which have the special function of absorption and transport e.g. the tentacles of Drosera.

The root takes up salts from the surrounding solution or from the soil and moves them to the xylem-vessels and to the young growing cells at its apex. Moreover the cortical cells are able to accumulate salts in their vacuoles. This process is characteristic for most living cells, it requires energy that is produced by aerobic respiration.

The problem is considered whether the boundaries of the protoplast, the plasmalemma and the tonoplast are pervious to salts. Experiments with plasmolysis seem to prove this. Arguments are given that under normal conditions the plasmalemma is permeable to ions but that the tonoplast behaves differently and may be impermeable to certain ions. The data about the permeability of the boundary layers of the protoplasm are insufficient to give a definite opinion on this point.

The consequence of the impermeability of the tonoplast for certain substances or ions is that there must be an active secretion process in order to accumulate them into the vacuole.

The opinion is given that the ions in the peripheral layer of the protoplasm are bound to plasmatic substances and that there exists an adsorption-equilibrium between the ions in this layer and in the surrounding solution. The consequence of a change in the composition or

strength of this solution is a change not only in the peripheral layer of the protoplasm but also in the whole symplasm of the communicating cells.

If ions bound to protoplasmic particles are removed somewhere in the symplasm by local consumption, there results a transport of ions and new ions from the medium wil be bound. The strength of this ion-transfer is limited by the adsorption equilibrium at the surface layer.

The movement of the ions in the plasm is a submicroscopical process. which becomes perceptible in the microscopically visible protoplasmic streaming. This explains the parallelism between both processes, that has also been found with the transport of growth-substance.

The cause of the removal of ions from the symplasm may be

1. their use in synthetizing new compounds in the protoplasm and the binding of ions by the newly formed substances;
2. the secretion of ions out of the protoplasm to the vacuole;
3. the secretion of ions out of the protoplasm to the exterior e.g. to the xylem-vessels.

An accumulation of salt-ions in plant cells may be caused by different processes. It may be an accumulation in the cell-wall, in the protoplasm or in the vacuole. The ion-content of the protoplasm wil probably depend on Donnan equilibria and on the diffusion effect studied by Teorell. The accumulation of ions into the vacuole must be considered as an active secretion-process by the contiguous protoplasm, if the tonoplast is impermeable to these ions.

The above-exposed theory of salt uptake is in harmony with our knowledge about the salt content of the plant. The uptake of ions depends on the constitution of the surrounding solution though by specific adsorption by the protoplasm the ions can be absorbed in other ratio than they are present in the medium. The ions are transported for a great deal to places where they are used for the building or enlarging of young cells. As a consequence the quantity of ions present in the plant depends as well on the composition of the outer solution as on the specific properties of the various tissues.

LITERATURE.

Papers published in the allied countries after May 1940 could not be consulted. Only a small number of the titles mentioned in the text will be given here. The rest can be found easily in the well known works on permeability.

ARISZ, W. H., Absorption and transport by the tentacles of Drosera capensis. I. Active transport of asparagine in the parenchyma cells of the tentacles. Proc. Ned. Akad. v. Wetensch., Amsterdam, **45** (1942).

———, II. The activation of the transport of different substances by oxygen. Proc. Ned. Akad. v. Wetensch., Amsterdam, **45** (1942).

———, III. De absorptie van aminozuren en zouten door binding aan het plasma. Verslagen Ned. Akad. v. Wetensch., Amsterdam, Afd. Natuurkunde **53** (1944).

———, IV. Gelijktijdige absorptie van verschillende stoffen. Verslagen Ned. Akad. v. Wetensch., Amsterdam, Afd. Natuurkunde **53** (1944).

ARISZ, W. H., Het actief en passief opnemen van stoffen door Vallisneria. Verslagen Ned. Akad. v. Wetensch., Amsterdam, Afd. Natuurkunde **52** (1943).

——— and P. J. VAN DIJK, The value of plasmolytic methods for the demonstration of the active asparagine intake by Vallisneria leaves. Proc. Kon. Ned. Akad. v. Wetensch., Amsterdam, **42** (1939).

BÖTTICHER, R. und L. BEHLING. Licht, Transpiration, Salzaufnahme und Blattstruktur. Flora N.F. 34 (1939).

BREAZEALE, J. F. Nutrition of plants, considered as an electrical phenomenon. Jour. Agric. Res. 24 (1923).

BROOKS, S. C. and BROOKS, M. M. The permeability of living cells. Protoplasmamonographiën 19, Borntraeger, Berlin (1941).

BROYER, T. C. and R. OVERSTREET. Cation exchange in plant roots in relation to metabolic factors. Amer. Journ. Bot. 27 (1940).

BURSTRÖM, H. Die osmotischen Verhältnisse während des Streckungswachstums der Wurzel. Ann. Agric. Coll. Sweden 10 (1942).

COLLANDER, R. Permeabilitätsstudien an Characeen III. Die Aufnahme und Abgabe von Kationen. Protoplasma 33 (1939).

———, Die Elektrolyt-Permeabilität und Salzakkumulation pflanzlicher Zellen. Tabulae Biologicae, Vol. 19, pars 2 (1942).

———, Diffusion und adenoïde Tätigkeit bei der Ionenaufnahme pflanzlicher Zellen. Die Naturwissenschaften 30 (1942).

FREY-WYSSLING, A. Das Streckungswachstum der pflanzlichen Zellen. Arch. Klaus-Stiftung. Ergänz. Bd. zu Bd. 20 (1945).

CRAFTS, A. S. and T. C. BROYER. Migration of salts and water into xylem of the roots of higher plants. Am. Jour. Bot. 25 (1938).

GELLHORN, E. et J. RÉGNIER. La permeabilité en physiologie et en pathologie générale. Masson et Cie, Paris (1936).

HARBRECHT, A. Untersuchungen über die Ionenaufnahme der Bromeliaceen. Jahrb. w. Bot. 90 (1942).

HOAGLAND, D. R. and T. C. BROYER. Hydrogen-ion effects and the accumulation of salt by barley roots as influenced by metabolism. Am. Jour. Bot. 27 (1940).

HÖBER, R. Some Experiments on the osmotic properties of glands. The collecting Net 9 (1934).

HÖFLER, K. Das Permeabilitätsproblem und seine anatomischen Grundlagen. Ber. D. Bot. Ges. 49 (1931).

———, Kappenplasmolyse und Ionenantagonismus. Protoplasma 33 (1939).

———, Salzquellung des Protoplasmas und Ionenantagonismus. Ber. D. Bot. Ges. 58 (1940).

HOMÈS, M. V. La perméabilité de la cellule végétale aux sels mineraux. Archives de Biologie 47 (1936).

HONERT, T. H. VAN DEN. On the mechanism of the transport of organic materials in plants. Proc. Kon. Akad. v. Wetensch., Amsterdam, **35** (1932).

———, Onderzoekingen over de voedingsphysiologie van het suikerriet, II. Mededeelingen van het Proefstation v. d. Java-Suikerindustrie 23 (1933).

———, Over de eigenschappen van plantenwortels, welke een rol spelen bij de opname van voedingszouten. Natuurkundig Tijdschrift voor Ned. Indië, 97 (1937).

JANSSEN, L. W. Biosynthesis and the outlines of protein structures. Protoplasma 33 (1939).

JENNY, H. and R. OVERSTREET, Surface migration of ions and contact exchange. Jour. Phys. Chem. 43 (1939).

JENNY, H., R. OVERSTREET and A. D. AYERS. Contactdepletion of barley roots as revealed by radioactive indicators. Soil Sc. 48 (1939).

KAHO, H. Das Verhalten der Pflanzenzellen gegen Salze. Ergebnisse der Biologie 1 (1926).

LAINE, T. On the absorption of electrolytes by the cut roots of plants and the chemistry of plant exudation sap. Acta Bot. Fenn. 16 (1934).

LAVOLLAY, J. Considérations sur la fixation et l'échange des cations chez les êtres vivants. Bull. de la Soc. de chimie biol. 18 (1936).

LUNDEGÅRDH, H. Die Nährstoffaufnahme der Pflanze. Jena 1932.

————, Investigations as to the absorption and accumulation of inorganic ions. Annals agr. Coll. Sweden 8 (1940).

————, Bleeding and sap movement. Arkiv för Botanik 31 A (1943).

LUTTKUS, K. und R. BÖTTICHER, Ueber die Ausscheidung von Aschenstoffen durch die Wurzeln. Planta 29 (1943).

MAZIA, D. Cation exchange in Elodea. Jour. cell. comp. Physiol. 11 (1938).

———— and J. M. CLARK. Free calcium in the action of stimulating agents on Elodea cells. The biol. Bulletin 71 (1936).

OVERSTREET, R. and T. C. BROYER. The nature of absorption of radioactive isotopes by living tissues as illustrated by experiments with barley plants. Proc. Nat. Acad. Sc. 26 (1940).

PERIS, K. Zur potetometrischen Bestimmung der Permeabilität der Wurzeln intakter Pflanzen. Protoplasma 26 (1936).

REINDERS, DIRKJE E. Intake of water by parenchymatic tissue. Recueil trav. bot. Néerl 39 (1942).

RUFZ DE LAVISON, J. DE. Du mode de pénétration de quelques sels dans la plante vivante. Role de l'endoderme. Revue Gén. de Bot. Vol. 22 (1910).

————, Recherches sur la pénétration des sels dans le protoplasme et sur la nature de leur action toxique. Ann. d. sciences nat. 9 sér. Bot. 14 (1911).

RUHLAND, W., ULLRICH, H. und YAMAHA, G. Über den Durchtritt von Elektrolyten mit organischem Anion und einwertigem Kation in die Zellen von Beggiatoa mirabilis. Planta 18 (1932).

SCARTH, G. W. The penetration of cations into living protoplasm. Am. Jour. Bot. 12 (1925).

SCHMIDT, O. Die Mineralstoffaufnahme der Pflanzen als Funktion einer Wechselbeziehung zwischen inneren und äusseren Faktoren. Zeitschr. f. Bot. 30 (1936).

SCHÖNFELDER, S. Weitere Untersuchungen über die Permeabilität von Beggiatoa mirabilis. Planta 12 (1931).

STEWARD, F. C. and J. C. MARTIN. The distribution and physiology of Valonia at the Dry Tortugas, with special reference to the problem of salt accumulation in plants. Carnegie Inst. Washington Publ. No. 475 (1937).

STILES, W. Permeability. New Phytologist Reprint 13 (1924).

TEORELL, T. Studies on the "Diffusion Effect" upon ionic Distribution I Some theoretical considerations. Proc. Nat. Acad. Sci. 21 (1935).

WEEVERS, TH. Aufname, Verarbeitung und Transport der Zucker im Blattgewebe. Rec. trav. bot. Néerl. 28 (1931).

WEIXL-HOFMANN, H. Beiträge zur Kenntnis der Salzpermeabilität des Protoplasten. Protoplasma 11 (1930).

WIERSUM, L. K. Een methode van doorstrooming der houtvaten in de wortel in verband met het stoftransport in radiale richting. Versl. Ned. Akad. v. Wetensch., Amsterdam, Afd. Nat., 53 (1944).

WILBRANDT, Die Permeabilität der Zelle. Ergebn. der Physiologie 40 (1938).