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WATER UPTAKE FROM WATER AND SALT SOLUTIONS

BY

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1. INTRODUCTION

The process of water uptake has been investigated very extensively. Especially the work of RENNER (1912, 1915, 1929) and KRAMER (compiled in 1949) has delivered important data on this phenomenon. Quite recently another review of the literature appeared (KRAMER 1956).

Since the investigations of Renner a difference is made between an active and a passive water uptake. At low transpiration rates an effective pressure (root pressure) in the xylem vessels is found, which manifests itself as guttation of the intact plant or as bleeding if the xylem vessels are cut. This root pressure occurs only if a vital intact root system is placed in a well-aerated medium. Various explanations have been given for this phenomenon. At the Botanical Laboratory at Groningen the exudation process has been investigated intensively (VAN NIE, HELDER and ARISZ (1950); ARISZ, HELDER and VAN NIE (1951); VAN ANDEL (1952); VAN ANDEL (1953); ARISZ (1956). There are good reasons to assume, that an active transport of salt or a concentrated salt solution represents the primary part of the process causing a secondary transport of water as a consequence of the osmotic suction of the sap in the xylem vessels. Processes, similar to those involved in the exudation process, can be expected to bring about the root pressure in intact plants. It is still a matter of dispute whether the osmotic water uptake is of any importance for the total water uptake. Most authors do not ascribe an important role to the root pressure in the water transport of the plant. KRAMER (1939) showed that the exudation rate of tomato and sunflower plants amounted to only 1 or 5 % of the transpiration rate. Consequently he assumes that during moderate or high transpiration rates the passive water uptake (i.e. the water uptake induced by shoot transpiration) has such a high value that the solution in the xylem vessels of the root is very diluted so that the osmotic component of the water transport is negligeable. This conclusion is based on the presumption that the exudation rates in intact plants and decapitated plants are the same. As yet this assumption is only a hypothesis.

RUFELT (1956) assumed that the osmotic water uptake and the passive water uptake take place along different tracks, so that they are more or less independent of each other. He found in his experiments with wheat plants, that the transpiration could be diminished by applying either an osmotic counter suction in the root medium (mannitol) or by using sodiumdiethyldithiocarbamate (dieca) as an inhibitor. The decrease in transpiration was ascribed to an elimination of the osmotic water uptake. However, it is equally possible that in his experiments the water conductivity of the roots was decreased. This would have had the same effect as an inhibition of the active water uptake. Similar data of KRAMER (1951, 1940) were interpreted in this way.

TAGAWA (1934) found that the transpiration was greater on a balanced salt solution (Knopp) than on a one salt solution or an isotonic sugar solution. Here again this greater water uptake may be due to an osmotic component or an increased water conductivity.

Except for the indications given above we cannot find many data in literature in favour of the idea that the osmotic water uptake plays an important role in the total water uptake of transpiring plants. It seems desirable, therefore, to get more experimental data about the significance of the osmotic water uptake. These data were obtained using the following phenomenon.

When a root system of an intact transpiring plant is transferred from distilled water to an osmotically active solution e.g. a salt solution, then the water uptake is reduced instantaneously after the transference. Thereafter the water uptake gradually increases until after some time a new constant level is reached. These experiments have been described by BRIEGER (1928), RENNER (1929) and PERIS (1936). The decrease of the water uptake immediately after transference is caused by the osmotic counter suction of the salt solution. The following gradual increase of the water uptake was ascribed to a gradual increase of the suction tension in the xylem vessels (BRIEGER, 1928). The increase of the suction tension mentioned may be a result of:

a. a transport of ions from the medium into the xylem vessels (osmotic suction);
b. an increase of the mechanical suction, or
c. a combination of a and b.

Peris assumed that factor *a* is the most important one. However, data supporting this assumption are still lacking, for nothing is known about the ion concentration of the sap in the xylem vessels in these experiments. The experiments described below give more informations as to the causal factors involved in these transference reactions.

2. METHODS

A. *The apparatus*

The apparatus used in these experiments was described in detail elsewhere (BROUWER, 1953). The bulk of the roots is placed in the main vessel (fig. 1 A) whereas one root (reference root) is enclosed in two small potometers of 5 cm length each. As these experiments require a constant temperature, the whole apparatus is placed in a thermostat of 40 litres capacity with heating element and stirring mechanism. This set up renders it possible to change the solution in the main vessel independently from the contents of the micropotometers. The water uptake from the main vessel and the micropotometers can be determined separately.

B. *Plant material*

The experiments have been performed with 3-5 week old bean plants (*Phaseolus multiflorus*), which were grown on a Hoagland nutrient solution.

C. *Calculations*

Brieger (1928) showed that the water uptake can be expressed by the formula: $U = k(S_{xylem}\text{-}S_{medium})$. In distilled water the suction tension of the medium (S_m) is zero, whereas on a salt solution the value of the osmotic suction of the medium has to be used. At the very moment of transference from distilled water to a potassium nitrate solution we get:

$$\begin{array}{ll} U_{d.w} = k \times S_x & \\ U_{KNO_3} = k \times S_x - k \times S_{KNO_3} & - \\ \hline U_{d.w} - U_{KNO_3} = k \times S_{KNO_3} & \end{array}$$

In this equation S_{KNO_3} is known and $U_{d.w}$ and U_{KNO_3} are measured. So we can compute k and S_x. It appears from the course of the water uptake on potassium nitrate that U_{KNO_3} gradually increases, probably as a consequence of a change in S_x and perhaps k. The calculation given above, therefore, only applies if the uptake values immediately before and after the transference are used. However, the transference itself takes some time. To get the right uptake values we have made an extrapolation to time zero (fig. 1, 2 and 3 dotted lines). It is clear that some inaccuracy is unavoidable. If after some time the water uptake on potassium nitrate has become constant, this solution in the main vessel is changed for distilled water. Now we see immediately after the transference a highly increased water uptake, which rapidly decreases until after some time a new constant level is reached. At this transference we can use the formulae:

$$\begin{array}{ll} U'_{d.w} = k' \times S'_x & \\ U'_{KNO_3} = k' \times S'_x - k' \times S_{KNO_3} & - \\ \hline U'_{d.w} - U'_{KNO_3} = k' \times S_{KNO_3} & \end{array}$$

From the latter equation we can compute S_x and k'.

It appears that S'_x has a much higher value than S_x, whereas in many occasions k' is greater than k (See Arisz, 1956 page 37).

From Dixon's cohaesion theory we know, that a loss of water from the leaves gives rise to a mechanical suction tension in the xylem vessels not only of the leaves but also of the root. We may expect that on distilled water the suction tension in the xylem vessels represents a mainly mechanic suction. If, however, the root system is placed on a salt solution, a transport of a salt solution into the xylem vessels may be expected and as a consequence of such a salt transport an osmotic suction may occur. The formula of Brieger runs into: $U = k\ (S_{mech} + S_{osm}) - S_{med}$. During the steady state on distilled water the water uptake by the roots will be equal to the water loss by the shoot and we may expect, therefore, a constant S_{mech}, whereas the S_{osm} probably will be about zero. Immediately after transference from distilled water to a salt solution the loss of water due to transpiration is much greater than the reduced water uptake (Arisz, 1956, p. 35-37). This results in an increase of the S_{mech}. Furthermore we expect now an increase of the S_{osm} due to a permeation of salt ions into the xylem vessels. The increase of S_x to S'_x, therefore, can be a consequence of the mechanical component and/or an increase of the osmotic component of the suction tension. We have to consider the following possibilities:

$$S'_x > S_x \qquad \begin{array}{ll} 1 & S'_{x\,mech} = S_{x\,mech};\ S'_{x\,osm} > S_{x\,osm} \\ 2 & S'_{x\,mech} > S_{x\,mech};\ S'_{x\,osm} = S_{x\,osm} \\ 3 & S'_{x\,mech} > S_{x\,mech};\ S'_{x\,osm} > S_{x\,osm} \end{array}$$

To decide which of these three possibilities is realised we started from the following line of thought. If there is distilled water in the main vessel and in the micropotometers a mechanic suction tension will occur in the xylem vessels which is the same for main roots and reference root. After placing the main roots from distilled water in a salt solution an increase of the mechanic suction tension will result in an increasing water uptake both by the main roots and the reference root. The occurrence of an osmotic suction will be restricted to those parts of the root system, which are in contact with the salt solution, and will not influence the water uptake of the reference root. A comparison of the course of the water uptake by main roots and reference root will give an insight into the nature of the increased suction tension.

3. Experimental results

a. *The transference reactions*

The experimental set up and the results of a typical transference experiment are shown in figure 1. After a period of constant water uptake on distilled (demineralized) water present in main vessel and micro potometers a 75 mM calcium chloride solution was brought into the main vessel. From the leap in the water uptake values we computed an S_x of 2.4 atm and a k of 26 $mm^3/3$ min 1 atm. After some time on calcium chloride the water uptake reached a new constant level. Now we changed again the solution in the main vessel and substituted the calcium chloride solution by distilled water. The value of the water uptake from the main vessel shows the normal picture as described in literature. From this leap we computed an S'_x of 5.5 atm and a k' of 27 $mm^3/3$ min 1 atm. We see from these values that the suction tension showed an important increase whereas the conductivity did not change.

If we trace the water uptake by the reference root (fig. 1C) we see that this uptake also showed an important increase after transference of the main roots to the calcium chloride solution and a subsequent decrease after transference back to distilled water. At first sight the course of the water uptake by main roots and reference root is identical. Starting from the supposition that the mechanical suction is equal over the whole root system we may assume that the suction tension in the reference root amounted to 2.4 atm at the beginning of the experiment. Further it seems likely that after transference of the main roots to calcium chloride a migration of ions into the xylem vessels of the reference root did not occur. Thus, the water uptake by the reference root can be used as a measure for the mechanical suction

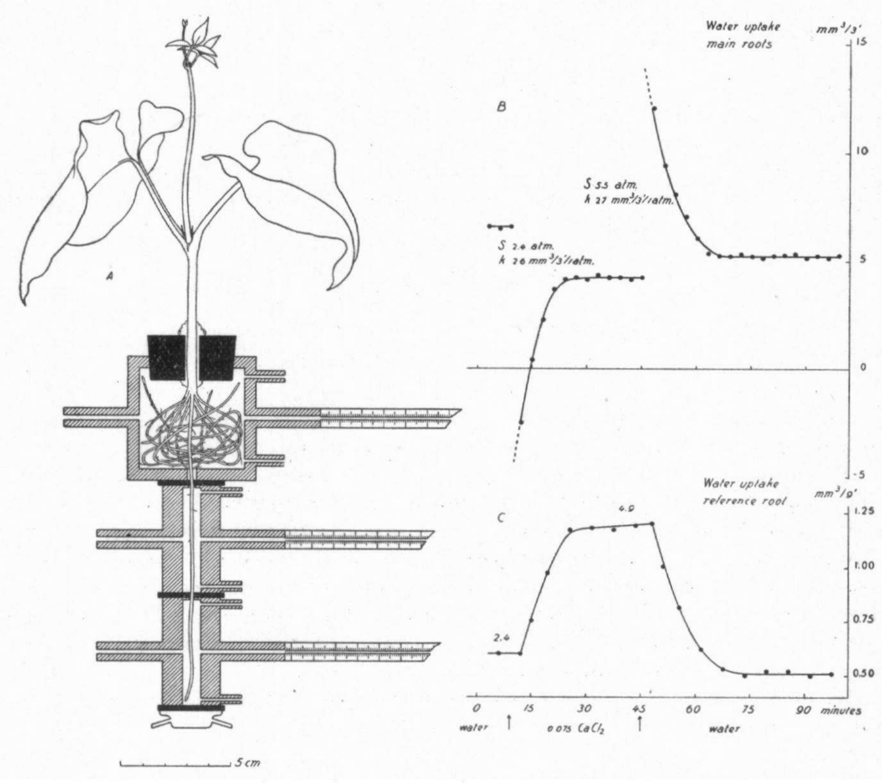

Fig. 1. A. The experimental set-up. A bean plant placed on a perspex vessel, the main roots in a large vessel (main vessel) and the reference root in two micropotometers; B. The course of the water uptake by the main roots at transference from distilled water to a salt solution and at transference from the salt solution back to distilled water; C. The course of the water uptake by the reference root on distilled water at the transference of the main roots to a salt solution and back to distilled water

tension. This is the more likely because the conductivity of the root system remained unchanged. In this way we find a mechanical suction tension of 4.9 atm. The total suction tension in the main roots amounted to 5.5 atm (see above). The difference between total suction tension and mechanical suction tension (5.5 — 4.9 = 0.6 atm) represents the osmotical component of the suction tension in the main roots.

From these values we may conclude that the increase of the water uptake after transference to a calcium chloride solution by far the greatest part is caused by an increase of the mechanical component of the suction tension. The osmotic component of the suction tension causing the osmotic water uptake amounted to only a 10 %, even on such a concentrated salt solution. The assumption of PERIS (1936) that the whole phenomenon was due to a permeation of ions into the root must be discarded.

b. *Comparison of different concentrations of the same salt*

Figure 2 gives the course of the water uptake at transference from distilled water to a 5.0 atm potassium nitrate solution and to a 2.5 atm

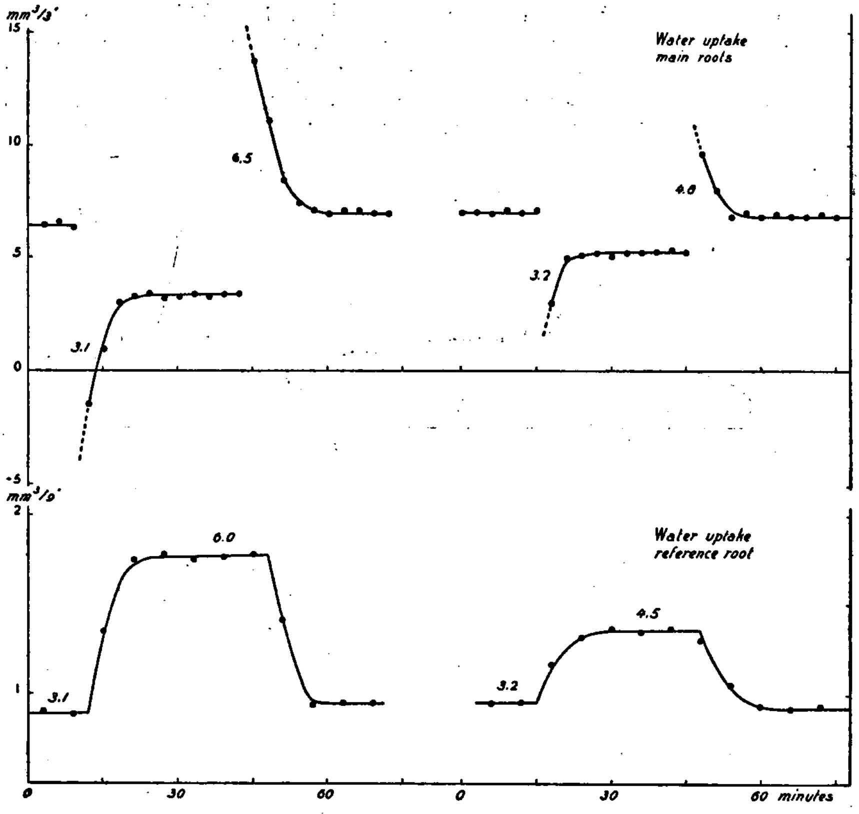

Fig. 2. The course of the water uptake by main roots and reference root on distilled water, and after transference of the main roots to a salt solution and back to distilled water

potassium nitrate solution and back to distilled water. On 5.0 atm potassium nitrate the osmotic component of the suction tension amounted to 6.5 — 6.0 = 0.5 atm and on 2.5 atm potassium nitrate to 4.8 — 4.5 = 0.3 atm. The osmotic component is higher at the more concentrated solution. It is essential that such experiments are performed with the same plant in time periods as short as possible. This is self evident because different plants show different transpiration rates. The osmotic component is most probably an indication of the salt concentration in the xylem vessels. The total salt transport, therefore, amounts to water uptake times concentration. The water uptake on the more concentrated solution is lower than on the more diluted one. The product water uptake times concentration is about the same in both cases. Many experiments with different salts, performed in this way, have given the same picture.

c. *Comparison of the same concentration of different salts*

The results of a comparison of potassium chloride with potassium nitrate (4.2 atm) are plotted in figure 3. On potassium chloride we see an increase of the suction tension from 2.8 to 5.8 atm, whereas the mechanical component increased from 2.8 to 5.6 atm. The osmotic component amounts here to 0.2 atm. With the same plant the osmotic component on potassium nitrate amounted to 0.4 atm i.e about twice as great as on potassium chloride. The water uptake values are about

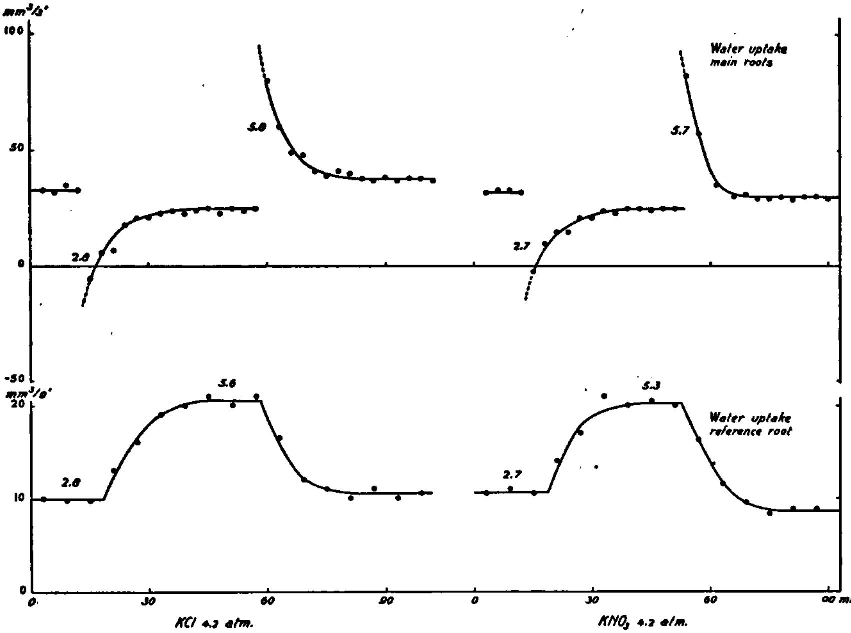

Fig. 3. The course of the water uptake by main roots and reference root on distilled water, after transference of the main roots to a salt solution and after transference back to distilled water.

the same in both cases. So the salt uptake is greater in the latter case. With all plants this appeared to be true. The mean ratio: $\frac{KNO_3}{KCl}$ amounted to 1.82.

By comparing in the same way potassium chloride with calcium chloride it appeared that the osmotic component was greatest on potassium chloride.

4. Discussion

From the experiments described above, it is evident that under the given experimental circumstances the water uptake is mainly determined by a mechanic suction tension in the xylem vessels of the root. Even on such concentrated salt solutions the osmotic component amounts to only 4-10 %.

These results are in agreement with the supposition given by Kramer. In view of the experiments of Rufelt (1956) with wheat plants, it may be that a generalisation of this principle is not allowed.

The question arises in how far a lack of aeration during the application of the salt solutions (30-45 minutes) inhibited the development of a higher osmotic component. At the beginning of the application the solutions were air-saturated, whereas after 45 minutes about 40 % of the oxygen was utilised. We can not speak, therefore, of a large lack of oxygen. Comparative experiments with this material showed that the transpiration on salt solutions with and without aeration did not differ very much, this in contrast with barley plants. The difference was of the same order as the osmotic component calculated from the experiments described above. An example of such an experiment is given in figure 4. However, very soon after stopping the aeration and the subsequent decrease of transpiration the transpiration showed

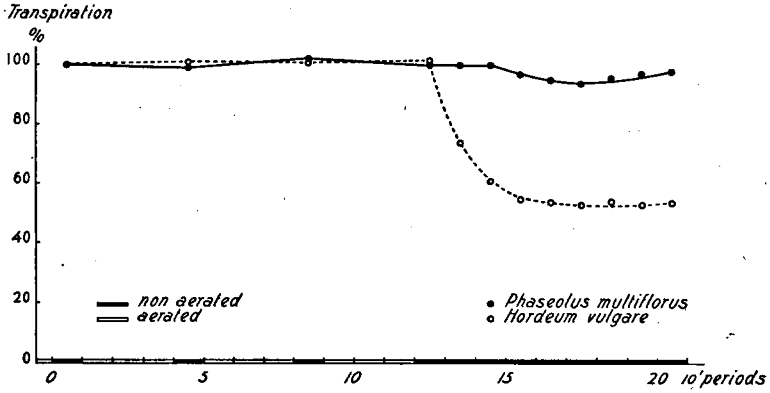

Fig. 4. Comparison of the transpiration rates on a 2.5 atm potassium nitrate solution with and without aeration. The transpiration was determined by weighing during 10 minutes periods. Aerated means alternating 10′ without aeration (weighing) and 30′ with aeration. Non-aerated means without aeration throughout the whole period

an increase regulated by the shoot's suction. However, the osmotic component seems to be a real thing.

Furtheron the experiments showed that the mechanic water uptake, as occurring on distilled water, can be reduced by an osmotic counter suction in the medium. This osmotic counter suction reduces the water uptake immediately to very low values. It is true that we get after transference a gradually increasing water uptake but the subsequent steady state level is lower than the level on distilled water as is the transpiration (see Arisz 1956 fig. 27). These observations are contrary to the supposition of Rufelt that the mechanical water uptake can not be inhibited by an osmotic agent in the medium because the mechanic uptake takes place via non-semipermeable root parts. If this assumption is correct, the water uptake can not be expected to decrease when the plant is transferred from distilled water to a salt solution.

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SUMMARY

The aim of the investigation was an analysis of the transference reactions (Überführungsreaktionen).

These reactions were studied with bean plants.

At transference of the root system of an intact transpiring plant from distilled water to a salt solution the water uptake decreases instantaneously. Thereafter a gradual increase is found until a new constant level is reached. At transference from a salt solution to distilled water the water uptake increases and shows a gradual decrease to a constant level.

It is shown that this course of the water uptake by far the greatest part is regulated by the mechanical suction tension in the xylem vessels and that only a small fraction of the water uptake is due to osmotic forces.

The experimental set-up rendered it possible to make a separation of these two mechanisms.

It appeared to be possible to inhibit the nearly fully mechanic water uptake by means of an osmotic counter suction in the medium.

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