

INVESTIGATIONS INTO THE OCCURRENCE OF ACTIVE AND PASSIVE COMPONENTS IN THE ION UPTAKE BY *VICIA FABA*

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I. INTRODUCTION

In previous publications (BROUWER, 1953*b*, 1954*b*) the author described the influence of the water uptake on the ion uptake in *Vicia faba*. It was found that with stronger transpiration the ion uptake was greater than with weak transpiration. Yet water uptake and ion uptake were not absolutely coupled. From the experiments it appeared that:

- a. by the use of inhibitors the ion uptake could be inhibited independent of the water uptake (fig. 1);

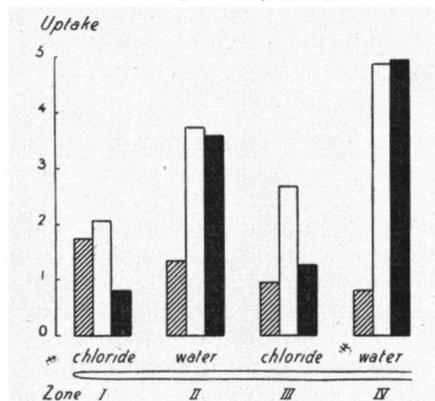


Fig. 1. Influence of 2,4-dinitrophenol, 10^{-8} M, on the water and chloride uptake at high suction tension in the xylem vessels. Chloride and water uptake of the various root zones at low suction tension (shaded blocks), at high suction tension without inhibitor (white blocks) and at high suction tension with inhibitor (black blocks). The nutrient solution contained 5 mM calcium chloride with or without inhibitor. The shoot was constantly illuminated. The suction tension in the xylem vessels of the root was increased by enhancing the osmotic value of the solution in the main vessel (vide Brouwer, 1954). With dinitrophenol in the nutrient solution the chloride uptake was reduced to about 50 % without a reduction of the water uptake. Scale unity 14γ Cl or 200 mm^3 of water per zone per 24 hours.

- b. by an osmotic counter suction in the medium the water uptake could be inhibited without influencing the ion uptake (fig. 2);

- c. in an average of a large number of experiments in which either the water uptake or the ion uptake was determined by the various root zones, the ratio:

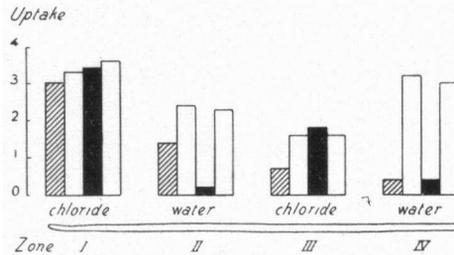


Fig. 2. Influence of an osmotic counter suction with sucrose in the nutrient solution on the water and chloride uptake at high suction tension in the xylem vessels. Chloride and water uptake of the various zones of the root at low suction tension (shaded blocks), at high suction tension without sucrose (white blocks) and at high suction tension with an osmotic counter suction (black blocks) in the medium. The sucrose solution strongly decreases the water uptake without a reduction of the chloride uptake. Scale unity 14γ Cl or 200 mm^3 of water per zone per 24 hours.

$$\frac{\text{chloride uptake at high transpiration}}{\text{chloride uptake at low transpiration}}$$

showed more parallelism with the ratio:

$$\frac{\text{waterconductivity at high transpiration}}{\text{waterconductivity at low transpiration}}$$

than with the ratio:

$$\frac{\text{water uptake at high transpiration}}{\text{water uptake at low transpiration}} \quad (\text{fig. 3}).$$

These facts induced the author to state the hypothesis that the increased ion uptake, as it is found at a higher transpiration, is to be attributed to an increased conductivity for ions in the root tissue, with the turgescence of the tissue as a causal factor for the change in conductivity. The influence of the water uptake on the ion uptake therefore was considered to be of an indirect nature.

Before at the hand of experiments with *Pisum sativum* HYLMO (1953) had developed a theory, in which the influence of the transpiration on the ion uptake was called direct. He distinguished the ion uptake into three components, of which one (phase I) was independent of the water uptake (diffusion and absorption). The accumulation in the root (phase II) appeared to be dependent on the water uptake as far as the chloride uptake was concerned. Finally a third component (phase III) was left, which increased directly proportional to the water uptake and at a water uptake nihil appeared to be practically nihil too. It is this third phase, the salt transport to the shoot, which in Hylmö's experiments strongly determined the whole relation between ion uptake and water uptake, because diffusion and

accumulation in the root tissue were small in proportion to the total ion uptake.

From the experiments it appeared:

- a. that the ion uptake in the range investigated was directly proportional to the water uptake, independent of the way in which the water uptake was varied;
- b. that the measure in which the transpiration stream was diluted with respect to the medium concentration was equal for all concentrations investigated.

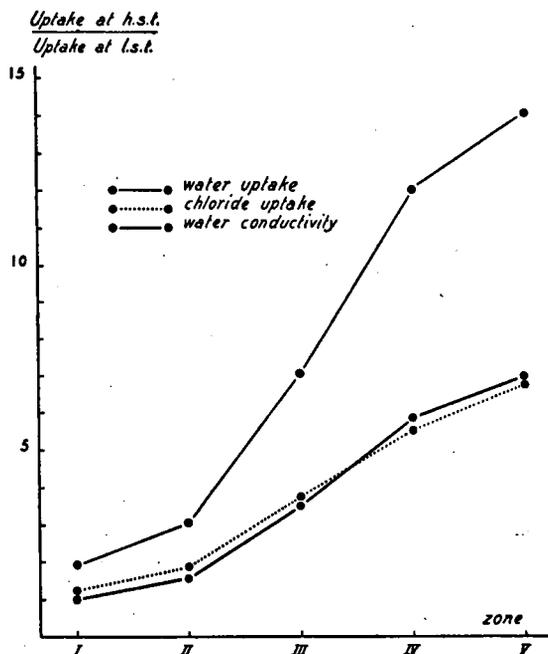


Fig. 3. Comparison of the ratio (mean value from about 40 experiments): $\frac{\text{uptake at high suction tension}}{\text{uptake at low suction tension}}$ for water and chloride by the various root zones with the ratio: $\frac{\text{waterconductivity at h.s.t.}}{\text{waterconductivity at l.s.t.}}$ Experimental conditions as in fig. 1 and 2 (first two periods). The ratio has been calculated by dividing the uptake values at high and low suction tension.

From the above HYLMO concluded that the influence of the water uptake on the ion uptake was direct and according as more water was taken up a proportional extra quantity of ions was carried along passively.

HYLMÖ's (1953) and BROUWER's (1954) experiments therefore correspond in so far that they both show a distinct correlation between transpiration and ion uptake. As was stated above the interpretation varied. This led HYLMO (1955) to examine my experimental results

again. According to HYLMO it would appear from this that it was also possible just as with *Pisum* to distinguish between the active and the passive components of the ion uptake with the aid of the data obtained for *Vicia faba*. The way in which this examination has been made will be critically discussed below. It will appear that the data examined by him yield no proof for his hypothesis concerning the mechanism of the ion uptake in *Vicia faba*. Some new results will be added.

II. COMMENTS ON HYLMO'S PUBLICATION

To discuss the most important items in HYLMO's publication (1955) it may be useful to follow it closely.

In figure 4 (HYLMO, 1955, fig. 1) the correlation between the water uptake and the chloride uptake inhibited or not has been plotted. Hylmö points out that on applying 2-4 dinitrophenol or on stopping

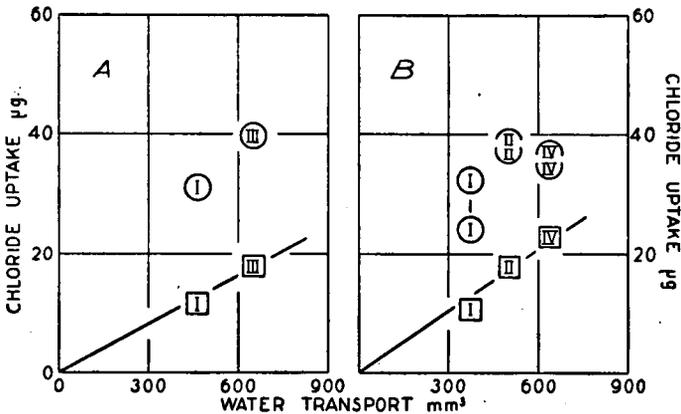


Fig. 4. The influence of 10^{-5} M 2,4-dinitrophenol (A) and of oxygen deficiency (B) on the water and chloride uptake of the different root zones at high suction tension in the vessels. Uptake per 3 cm of root length during 24 hours from a medium of 5 mM calcium chloride. Roman numerals designate the root zones counted from the root tip. A. Circles denote without DNP, squares with DNP. Data from Brouwer 1954 table IX A. B. Circles denote aerated roots, squares without aeration. Data from Brouwer 1954 table X. (Hylmö 1955 fig. 1, page 437).

aeration the chloride uptake is directly proportional to the water uptake, as is to be expected when the active component of this uptake is eliminated. Apparently he assumes that the active uptake is completely inhibited. No evidence however is present for this. Moreover it appears from the data of the non-inhibited uptake that it is also possible to connect this points by a straight line passing through the origin. This would mean that the whole uptake is passive, though sensitive to inhibitors. Here we meet an other objection to this figure, viz. a direct comparison of water and salt uptake of the various root zones, without its first being shown that the correlation between water uptake and salt uptake is equal for all zones.

Passing on to figure 5 we see that here too there are various objec-

tions to Hylmö's re-examination. The main objection is that in this figure the data from table I have been compared with the corresponding data from table II. These values have been derived from experiments with different root plants and the values for the chloride uptake of the different roots vary greatly. This appears among other

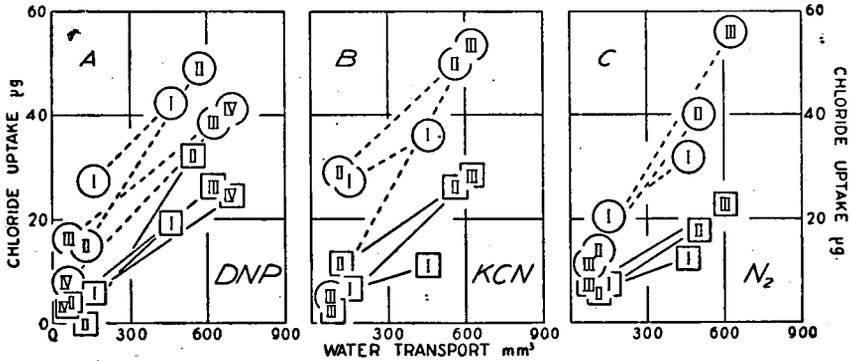


Fig. 5. The influence of 10^{-5} M 2,4-dinitrophenol (A), of $5 \cdot 10^{-6}$ potassium cyanide (B), and of nitrogen bubbling through the medium (C) on the chloride uptake of the different root zones at low and at high water uptake. Uptake per 3 cm of root length during 24 hours from a medium of 5 mM calcium chloride. Roman numerals designate the root zones counted from the tip. Circles denote without inhibitors, squares with inhibitors. Data from Brouwer 1954 table VI. (Hylmö 1955 fig. 2, page 438).

things from the chloride uptake of the various zones without the use of inhibitors as have been given in the first columns of the different sub divisions of tables I and II, of which the most striking differences

TABLE I
Inhibition of the chloride uptake by various inhibitors at low water uptake. Chloride uptake of the different root zones with and without inhibitor

Zone	DNP 10 M			KNC 5.10 M			Nitrogen		
	—	+	% inh	—	+	% inh	—	+	% inh
IV	7	4	43	—	—	—	10	6	40
III	16	4	75	5	2	60	11	7	36
II	15	0	100	29	11	63	13	6	52
I	27	6	78	27	6	78	20	7	66

(Brouwer, 1954 table VI A)

TABLE II
Inhibition of the chloride uptake by various inhibitors at high water uptake. Uptake of the different zones with and without inhibitor

Zone	DNP 10 M			KCN 5.10 M			Nitrogen		
	—	+	% inh	—	+	% inh	—	+	% inh
IV	41	25	40	49	30	40	—	—	—
III	39	26	35	53	28	47	57	23	60
II	49	32	37	59	26	48	40	18	55
I	42	19	55	36	11	70	31	12	61

(Brouwer, 1954 table VI B)

have been italicized. So we see that a great difference in the chloride uptake of the various zones occurs in different experiments. Comparing these experiments with different roots seems therefore not permitted. Besides Hylmö took values for the water uptake which cannot be derived from the experiments from which the figures for the chloride uptake have been derived.

Another objection is just as in the case of the data of figure 4 that Hylmö assumes that the inhibitor concentrations used have just fully inhibited the active component of the ion uptake. He has no other indications for this than a number of data from literature by which this was assumed—though for other material. Side by side with it cases may be mentioned where much higher concentrations did not entirely inhibit the exudation (VAN ANDEL 1953). So Hylmö's figures though clear at first sight are no proof of his argument. As regards Hylmö's criticism concerning the use of sucrose as an osmotic substance to inhibit the water uptake, it is right that sucrose may have a twofold action i.e. beside the osmotic action also an influence on metabolism. I understood this objection as such and therefore used mannitol and magnesium sulphate as osmotica beside sucrose. Mannitol gave, probably owing to impurities in the preparation used by me at that time, no clear results, but magnesium sulphate did (BROUWER 1953*b*, p. 648). It is to be regretted that Hylmö neglected this last fact, just as LONG's observation (1943), who found for tomatoes that by sodium chloride just as by sucrose water uptake could be inhibited for 80 % without influencing the nitrate uptake.

At the conclusion of his paper Hylmö himself occupied with the changes in conductivity for water occurring in the root tissue. The correlation between water uptake and suction tension as it appears from my experiments, is an indication for him that we have to deal here with a phenomenon as was described by ERBE (1933) and PISA (1933) for ultra filters. This would mean that at low suction tensions only part of the microcapillaries in wall and plasm and that the larger ones join in the water transport. The greater the suction the more microcapillaries will join, till finally at a certain suction all microcapillaries are run through. From this moment there is a direct relation between suction tension and water uptake. This means, however, as well that at a low suction tension the water uptake per atmosphere is smaller than at a higher suction tension. Hylmö objects to using the term change in conductivity for this phenomenon. In literature, however, this conception "change in conductivity" has been repeatedly used (RENNER, 1929; BRIEGER, 1928; KOEHNLEIN, 1930; BREWIG, 1937; 1939; and KRAMER, 1949). ARISZ (1956) has pointed out that in physiological literature terms are often being used without there being question of a complete knowledge of the phenomena they refer to. So here too the term conductivity has been used in a purely descriptive way. Therefore in connection with the fact that for the water supply of the plant a higher suction tension per atmosphere suction is more efficient than a low suction tension, we can speak of an enhanced conductivity for water. The question

remains what this enhanced conductivity is based on. It may be due to the joining of a greater number of microcapillaries. The data on the influence of the turgor on the water conductivity, however, as described in a previous publication (BROUWER, 1954a), tell against this.

III. THE INFLUX COEFFICIENT OF THE VARIOUS ZONES

The notion influx coefficient, i.e. "the concentration of the true transpiration stream from the medium to the root in relation to the concentration of the medium", is ascribed great value to by HYLMO (1955, p. 443) when trying to prove the passive nature of the ion uptake. From my experiments with different plant material, however, my experience is that this quantity is most variable, dependent as it is on the salt status of the material. In *Pisum* plants poor in chloride I found an influx coefficient of 0.52, where as the same material when cultivated on a calcium chloride solution for some time after, showed an influx coefficient of 0.03. For rye plants poor in chloride and rich in phosphorus the influx coefficient for chloride amounted to 1.64 and at the same time for phosphate to 0.2. Conversely these values amounted to 0.16 and 1.72 resp. for rye plants rich in chloride and poor in phosphate. From HYLMO's data (1953 fig. 7) there also appears a certain variability. On the whole the influx coefficient decreases with a rising medium concentration and an increasing saturation of the plant with a certain ion.

When examining my experiments on the uptake by the various zones of the root of *Vicia faba* Hylmö arrives at the conclusion that the influx coefficient of the various zones is the same. This conclusion is based on the data given in table III. This table, however, has

TABLE III

The influx coefficients of the different zones as calculated from various experiments

Figure no.	Zone I	Zone II	Zone III	Zone IV
2 A	0.14	0.21	0.16	0.14
2 B	0.09	0.14	0.24	—
2 C	0.10	0.18	0.23	—
3	—	0.12	0.08	0.12
4	0.05	0.08	0.09	0.09

(From Hylmö 1955 p. 443, after tables and figures of Brouwer 1954)

been composed by Hylmö among other things at the hand of the uptake values of figures 4 and 5 discussed above. So the criticism given here is also applicable to the use of this table. Moreover, as already observed by Hylmö, the number of observations is too low to make conclusions possible. A more reliable and at the same time simpler method to get an insight into the influx coefficient of the various zones, is to start from figures 1 and 6. BROUWER, 1954b figs. 6 A and 6 B), as a result of which we get figures 7 A and 7 B. Here data on salt and water uptake determined at the same root have been used. The result is that a difference in values of the influx coefficient can be observed right enough (difference in slope of the

lines). Yet even now a few objections have to be made. The most important being that the regression lines indicating the correlation between water uptake and chloride uptake, just as is the case in Hylmö's figures, pass through two points only.

In figure 8 the average chloride uptake of all (26) experiments with 5 root zones with low and with high transpiration is plotted

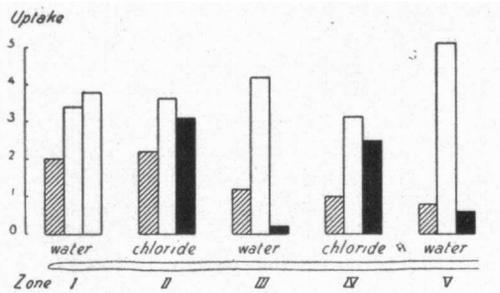


Fig. 6. Influence of an osmotic counter suction with sucrose in the nutrient solution on the water and chloride uptake at high suction tension in the xylem vessels. Chloride and water uptake of the various zones of the root at low suction tension (shaded blocks), at high suction tension without sucrose (white blocks) and at high suction tension with an osmotic counter suction (black blocks) in the medium. The sucrose solution strongly decreases the water uptake without a reduction of the chloride uptake. Scale unity 14 γ Cl or 200 mm^3 of water per zone per 24 hours.

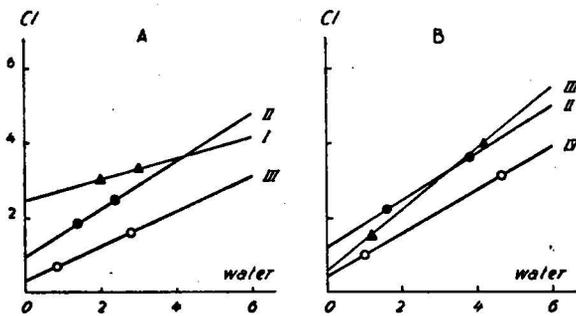


Fig. 7 A. The relationship between water and chloride uptake of the various root zones at low and at high suction tension in the xylem vessels. Data from figure 2 first two periods. Chloride uptake by zone II calculated by interpolation between zone I and III. Water uptake by zone I extrapolated, water uptake by zone II and IV interpolated.

Fig. 7 B. As in figure 7 A. Data from figure 6. Chloride uptake by zone III and water uptake by zone II and IV attained by interpolation. Scale unity vide Figure 1.

against the average values of the water uptake of all (84) experiments with 5 root zones likewise with low and with high transpiration. Because of these greater numbers it may be expected that the result is statistically more reliable than in the four experiments on chloride uptake collected by Hylmö (table III). Also in figure 8 it strikes the

eye that the regression lines for zones I and II are less steep than those of the more basal zones. The influx coefficients from top to base amount to 0.054; 0.074; 0.13; 0.13 and 0.13 resp. So we may conclude from figures 7 and 8 that the correlation between water uptake and chloride uptake for the various zones does not show the same picture. So a uniform filtration of the medium solution over

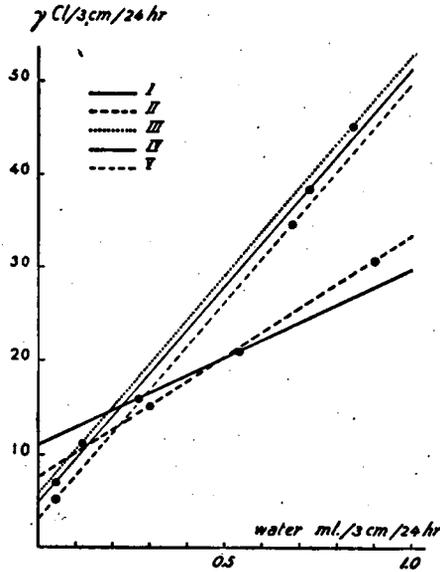


Fig. 8. Mean values of the water uptake by the various root zones versus the mean values of the chloride uptake.

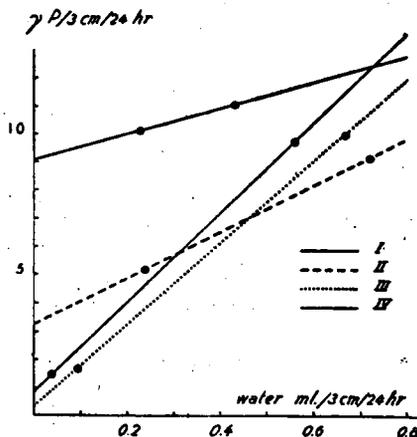


Fig. 9. Mean values of the water uptake by the different root zones versus the phosphate uptake.

the entire root length is out of the question. Figure 9 gives the result of an identical revision of the phosphate experiments. The computed values of the influx coefficient amounted to 0.31; 0.50; 0.91 and 1.0 from top to base. These are much higher than those found for chloride. This is probably due to the fact that the plants had been cultivated on tap water which in contrast to Hylmö's supposition (HYLMÖ 1955, p. 442) did contain chloride and no phosphate. From these phosphate experiments it is again clear that the influx coefficients of the various zones need not be identical.

On the ground of the above we can determine that Hylmö's reexamination of data previously published by me cannot yield any proof for the occurrence in *Vicia faba* of a passive component of the ion uptake linked directly to the waterstream.

Without further preface it is of course a fact that there is a strong correlation between water uptake and ion uptake. The direct causal relation as Hylmö thought to demonstrate from my data has not been proved and continues to be open for discussion. In the following chapters I shall describe fresh experiments (all carried out with *Vicia faba*) and bring up for discussion the interpretation that may be given to them.

IV. THE RELATION BETWEEN WATER UPTAKE AND CHLORIDE UPTAKE

In the previous chapter it appeared that a regression line which is fixed by only two points insufficiently represents the entire correlation between water uptake and chloride uptake. In the experiments described below it has been tried by taking several periods and by varying the water uptake in different ways to meet this objection. The design of these experiments may best be explained by a detailed example as given in figures 10, 11 and 12. Figure 10 gives the chloride uptake of the zones I, II, IV and V from a 5 mM calcium chloride solution for five successive periods (A, B, C, D, and E), the amount of water taken up by zone III in the same periods and from the same solution being measured. The nutrient solution was constantly being aerated and the shoot constantly exposed to light. The suction tension in the plant and as a result the water uptake by the tested root was varied by bringing into the main vessel tapwater (A), 2 atm. sucrose (B), tapwater (C), 3 atm. sucrose (D) and tapwater (E) resp. In addition the growth in length of the apical zone has been plotted as a dotted line in figure 10 A at the foot. As for the uptake we see that the chloride uptake of the zones II, IV and V is correlated in the main with the water uptake by zone III. The chloride uptake by zone I is more related with the growth in length of that zone. It strikes the eye that the growth in length of the top is strongest in the periods in which there is tapwater in the main vessel i.e. at a slight suction in the plant and smallest at a high suction tension in the plant (sucrose in the main vessel). In the right half of figure 10 (B) the chloride uptake of each zone has been plotted for each individual period. With the exception of zone I, in which growth in length occurs, the various zones give very regular pictures. It seems

therefore permitted to compute the chloride uptake by zone III by interpolation of the uptake values of zones II and IV. This chloride uptake by zone III obtained by interpolation has been plotted in figure 11 against the measured water uptake of this zone. Now it appears from figure 11, that the correlation between water uptake and chloride uptake is not directly proportional. The point of

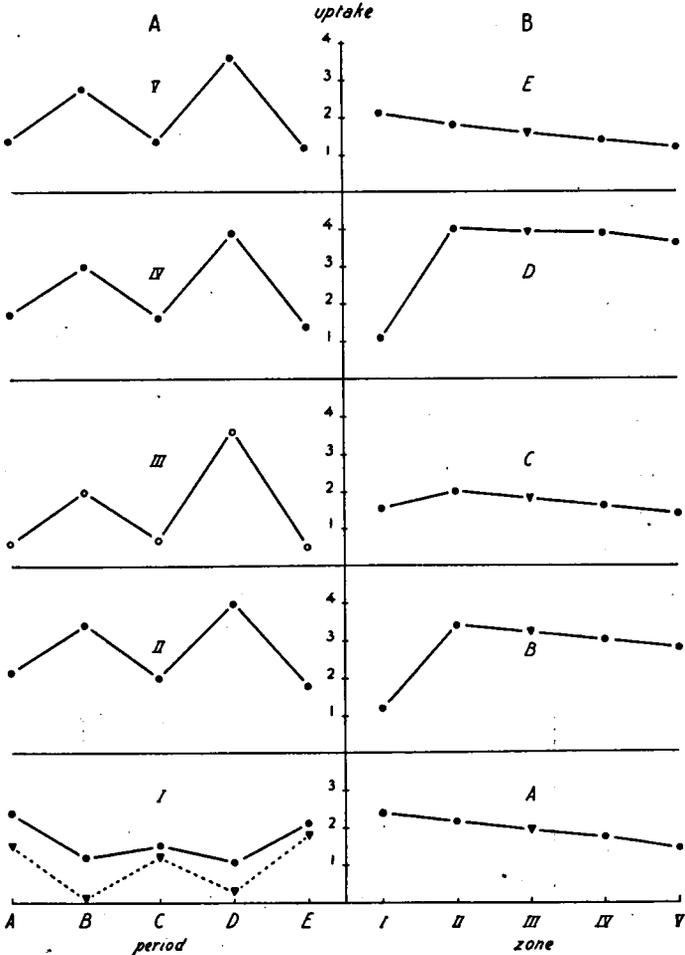


Fig. 10 A. The chloride or water uptake of different zones of the tested root in successive periods (A-E) at various osmotic values of the solution in the main vessel. A, C and E tap water in the main vessel, B 2 atm sucrose and D 3 atm sucrose. ○—○ water uptake; ●—● chloride uptake; ▼—▼ longitudinal growth of the tip zone. Scale unity 14 γ Cl, 200 mm^3 water or 5 mm growth per zone per 24 hour.

Fig. 10 B. The chloride or water uptake as found in fig. 10 A during the different periods. Interpolation of the chloride uptake by zone II and by zone IV gives the chloride uptake by zone III (▼).

intersection of the two regression lines drawn with the y -axis shows great differences in the accumulation in the root to be expected from these lines, viz. 12.0 and 21.5 γ chloride. In figure 12 the chloride uptake have been plotted against the suction tension measured in the xylem vessels (method see BROUWER, 1953a, b). From this it appears that the water uptake follows a course as is to be expected with the occurrence of changes in conductivity, i.e. slight suction tensions are relatively less effective (points under the straight line) than the higher ones. At higher suction tensions the chloride uptake reaches a kind of saturation value (dotted line). The line drawn for the chloride uptake shows a great correspondence with the correlation

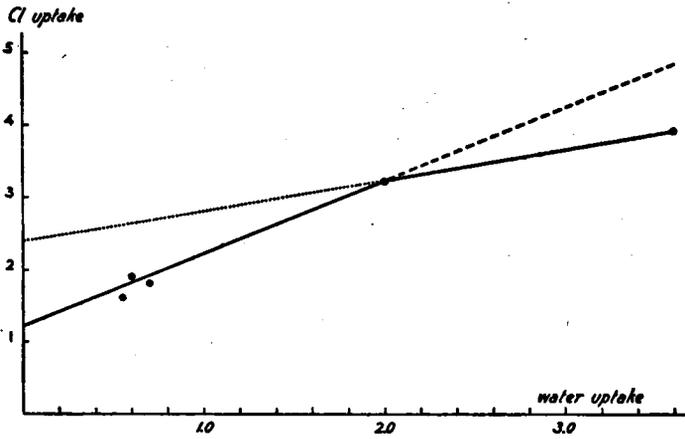


Fig. 11. The relation between the water uptake by zone III from figure 10 A and the chloride uptake by this zone as calculated from figure 10 B.

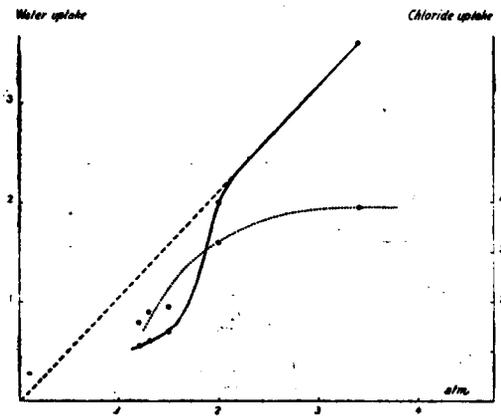


Fig. 12. The water uptake (full line) and the chloride uptake (pointed line) of zone III (vide figures 10 and 11) versus the suction tension in the xylem vessels. The dotted line represents the water uptake as would be expected without changes in water conductivity.

between suction tension and water conductivity (see BROUWER 1954*b*, fig. 2). How great this correspondence is for the case in question, may appear from figure 13 which gives the correlation between suction tension and chloride uptake as a dotted line, the correlation between suction tension and water conductivity as a solid line. A certain parallelism is unmistakable. It seems that with the higher values of the suction tension the chloride uptake relatively increases a little more than the water conductivity. For the significance of this phenomenon I refer to the discussion. Lastly figure 14 may serve as an example to make clear that even three points are not yet sufficient to fix the entire correlation between water uptake and salt uptake. It looks like it that this relation should be rendered by a curved line.

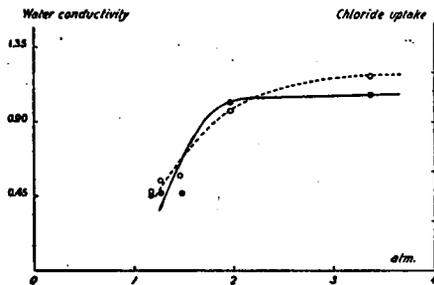


Fig. 13. Chloride uptake (dotted line) and water conductivity (full line) versus suction tension (data from figures 10, 11 and 12). Scale unity 200 mm³ water, 14 γ Cl and 1 mm³/l cm/l atm/20 minutes.

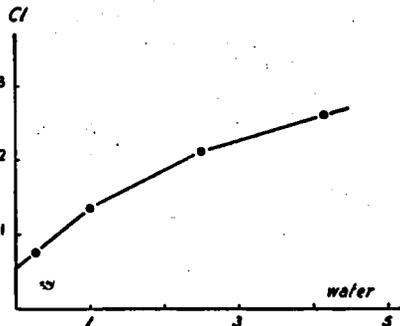


Fig. 14. The chloride uptake by the third zone of another experiment at various levels of the water uptake. Scale unity vide figure 1.

V. THE RELATION BETWEEN WATER UPTAKE AND CHLORIDE UPTAKE WHEN 2,4-DINITROPHENOL (DNP) IS USED

In a previous publication (BROUWER 1954*b*) it was shown that 10⁻⁵ DNP administered for one period inhibited the chloride uptake to about 50% (varying between 35 and 100%) without influencing the water uptake. On prolonged application a further inhibition follows some influence on the water uptake becoming visible as well.

This has been rendered in figures 15 A and 15 B. Here the water uptake (open dots) and the chloride uptake (black dots) of the various zones in successive periods has been plotted. During period A the uptake was determined from a 5 mM calcium chloride solution to which during the following periods DNP was added to a concentration of 10^{-5} M. The data have been obtained from two parallel experiments A and B, in which in the experiment of fig. A the water uptake was

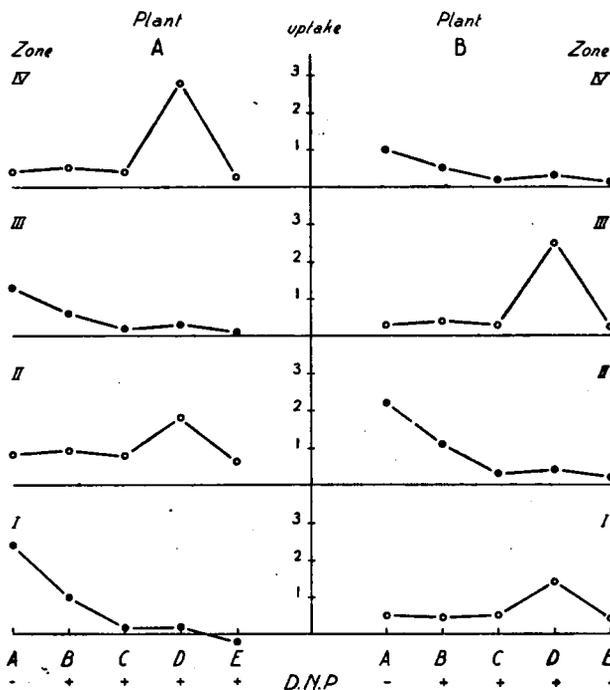


Fig. 15 A and B. The chloride and water uptake by the various root zones of the tested root at low and high suction tension during successive periods from a 5 mM calcium chloride solution (period A) and from this solution with addition of 10^{-5} DNP (periods B-E). Open circles denote water uptake, black dots chloride uptake. Scale unity vide figure 1.

determined of zones II and IV and the chloride uptake of zones I and III, whereas in fig. 15 B just the reverse took place. During the periods A, B, C and E the suction tension was kept low, during period D it was increased. This latter is clearly shown by a strongly increased water uptake, whereas the increase in chloride uptake in this period is slight. Under the influence of DNP the correlation between chloride uptake and water uptake has practically disappeared here. The correlation between chloride uptake and water uptake with and without DNP being administered, has been represented in fig. 16. As for its arrangement this experiment was identical with the experiment plotted in the figures 10 up to and including 13. For five successive

periods the chloride resp. water uptake of the various zones was determined. The chloride uptake of zone III (obtained by interpolation) has been plotted against the measured water uptake of that zone. During periods A and B the uptake was determined from a 5 mM calcium chloride solution only whereas in periods C, D and E DNP had been added. During periods A, C and E there was tapwater in the main vessel, during periods B and D 0.1 M sucrose. From figure 16 it appears that the line through A and B shows the

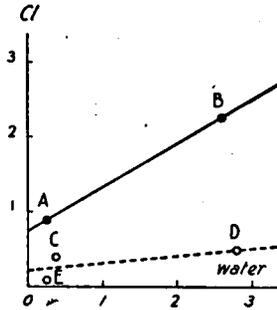


Fig. 16. The relationship between water uptake and chloride uptake with (open circles) and without (black dots) 2,4 dinitrophenol addition to the 5 mM calcium chloride solution. Scale unity vide figure 1.

normal relation between water uptake and chloride uptake. The chloride uptake during period C has been inhibited for about 50 % in respect of that of period A. Indeed during period E, under identical circumstances the chloride uptake has still further decreased. Comparing the average of the uptake in periods C and E with the uptake in the intermediate interim period D seems reasonable. This then shows the correlation between chloride uptake and water uptake in the presence of DNP, as it may be found in figure 16 as a dotted line. There is a great difference in slope between the lines A-B and C/E-D. With an equally strong rise of the water uptake the chloride uptake without inhibitor increases much more than the one with inhibitor. The influx coefficients computed from these lines amount to 11.6 % (A-B) and 1.7 % (C/E-D) of the medium concentration resp.

VI. THE CORRELATION BETWEEN WATER UPTAKE AND CHLORIDE UPTAKE WHEN DIFFERENT OSMOTICA ARE USED

In a previous publication it was shown that when the water uptake was inhibited by sucrose solutions the chloride uptake hardly decreased. It was even proved possible to decrease the water uptake and at the same time increase the chloride uptake in some circumstances by administering sucrose. As an explanation of this phenomenon it was thought at the time that a change in the conductivity for salts, under influence of the osmotic action of the sucrose increases the salt uptake. This was in entire agreement with the observation that sucrose increases the conductivity for water (ROSENE 1941,

BREWIG 1939, BROUWER 1954a) and as a result of an unaltered mechanic suction in the xylem vessels the water uptake as well. In the undermentioned experiments it has been tried to extend the earlier data in that sense that of the same root data were obtained about water uptake and chloride uptake with and without osmotic counter suction in the root medium, both combined with low and high suction tension in the xylem vessels. Besides sucrose there were used as osmotica: lactose, mannitol and magnesium sulphate. This variation was chosen to enable us to separate a possible influence on the metabolism from a purely osmotic influence. Mannitol and magnesium sulphate had also been used for this purpose in the investigation published in 1954, but at the time the results with mannitol were rather variable, so that sometimes even a loss of chloride was found, sometimes, however, the same picture was obtained as in the case of sucrose. A protracted treatment with the mannitol used by me at the time showed a colouring black of the roots, a phenomenon that was never observed when sucrose was used. These experiments have now been repeated and extended. The results of some of these experiments have been plotted in figures 17 and 18. Just as in the previous chapters the interpolated value of the chloride uptake has been plotted in these figures against the water uptake measured. Points 1 and 2 have been obtained at a low

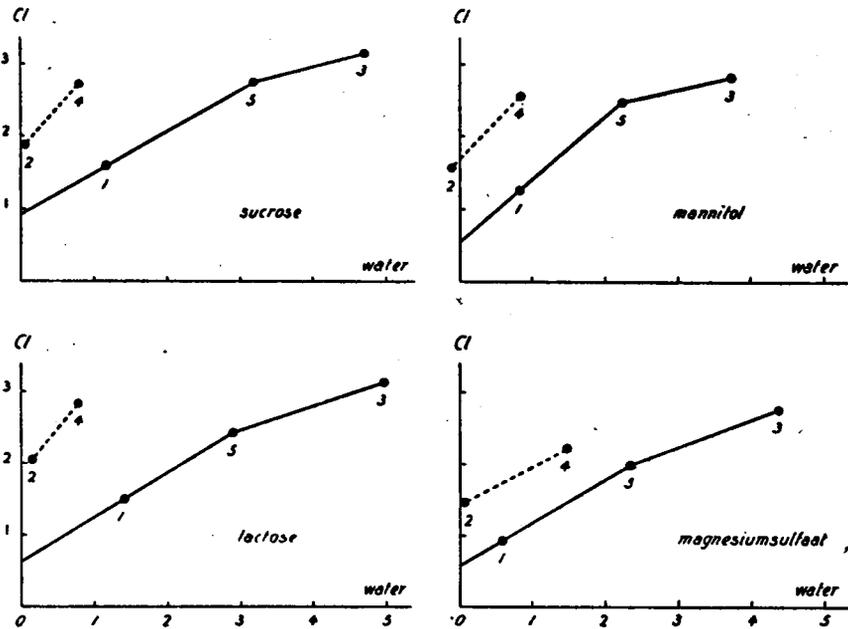


Fig. 17. Water and chloride uptake by zone III at various levels of the suction tension with or without an osmotic counter suction in the medium. The water uptake has been measured directly, the chloride uptake has been attained by interpolation. Scale unity vide figure 1.

mechanic suction in the xylem vessels, 4 and 5 at a higher one and 3 at the highest. During periods 1, 3 and 5 the uptake was determined from a 5 mM calcium chloride solution on addition of the osmoticum to a concentration corresponding with 2.5 atm. On comparison of the points 5 and 3 with 2 and 4 resp. (fig. 17) we see that owing to the osmotic counter suction in the medium the water uptake has been greatly diminished, much more than the chloride uptake. This holds good both for sucrose and for lactose, mannitol and magnesium sulphate. In all these cases therefore the chloride uptake is much higher than might be expected on the ground of the regression lines through the points 1, 5 and 3 with the water uptake of periods 2 and 4. So the first result from these experiments is that by applying osmotically active substances of a various nature the chloride uptake is higher than fits the inhibited water uptake. Further the points 2 and 4 have been connected by a line. These lines give the correlation

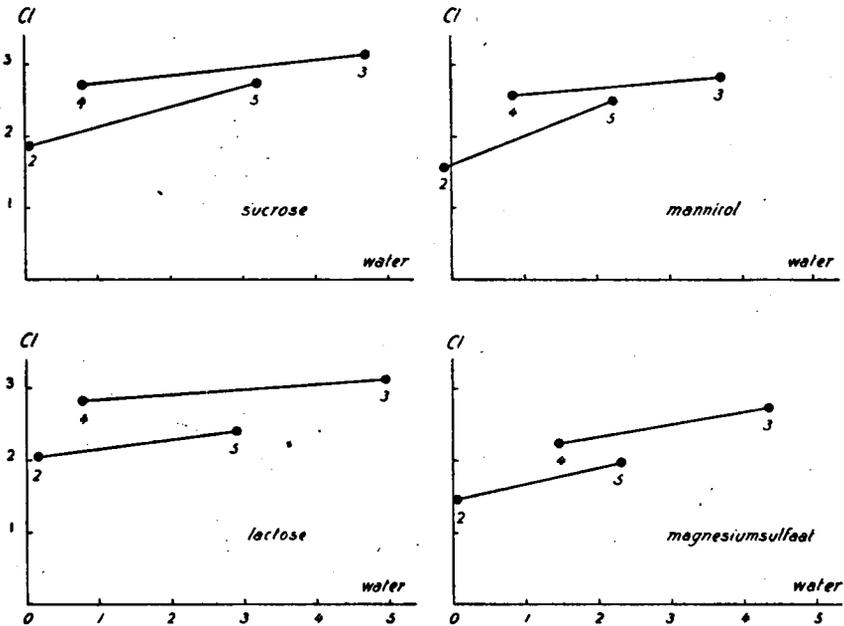


Fig. 18. The same data as given in figure 17.

between water uptake and chloride uptake at an osmotic counter suction in the medium. Here we also see that according as more water is taken up there is a greater ion uptake. The slope of these lines is steeper for sugars than that of the lines through points 1, 5 and 3. This is not the case for magnesium sulphate. We have now compared the relation between water uptake and chloride uptake with and without counter suction in the medium. In figure 18, four of the five points of figure 17 have been laid off again. Now the points 4 and 3 and 2 and 5 resp. have been joined. The train of thought

underlying this is that these points in twos correspond with about equal suction tensions in the root tissue. For the points 2 and 5 it will amount to about 2.5 atm. for the points 4 and 3 rather more than 3 atm. We now see that under these circumstances there also exists a correlation, be it less pronounced, between water uptake and chloride uptake.

VII. THE FATE OF THE IONS IN THE PLANT

The experiments described above in which the ion uptake of individual root zones was compared with the water uptake of those zones, do not give a direct insight into the distribution of the absorbed ions in the plant. In order to get an impression of this, some experiments will be described here, in which this is the case. These experiments were made with rubidium chloride in which the rubidium was labelled. For the rest the arrangement of the experiments was such that the whole root system was put in the nutrient solution. To this nutrient solution sucrose was added or not, the influence of aeration being examined with presence and absence of sucrose. In a previous publication it was already indicated that experiments in which the whole root system was put in the nutrient solution also showed a distinct correlation between water and chloride uptake. At the same time the influence of sucrose and magnesium sulphate on the chloride uptake was examined. The results of such an experiment have been plotted in figure 19. The regression line has been determined by measuring the chloride uptake (analysis of the medium) and the water uptake of plants 1 and 2 in the case of low (1.2) and

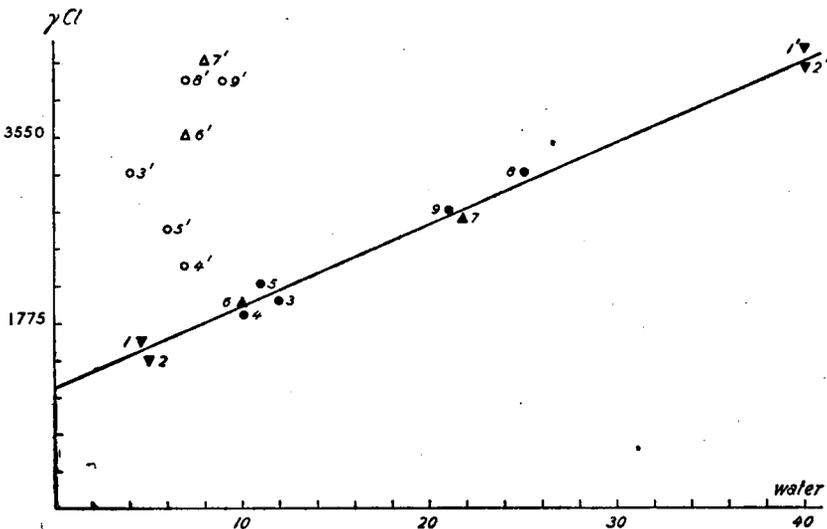


Fig. 19. Water and chloride uptake by the whole root system of *Vicia faba* plants in two successive periods. Each numeral corresponds to one plant. Nutrient solution: plant 1-9 and 1'-2' 5 mM CaCl_2 , 3', 4', and 5' 5 mM CaCl_2 + 2 atm sucrose, 8' and 9' 5 mM CaCl_2 + 2.7 atm sucrose, 6' and 7' 5 mM CaCl_2 + 2.7 atm MgSO_4

in the case of moderate (1', 2') transpiration. Of plants 3, 4, 5 the uptake from a 5 mM calcium chloride solution has first been determined and in the second period from the same solution with addition of 2.0 atm. sucrose (3', 4', 5'). It appeared that this treatment reduced the water uptake and increased the chloride uptake (points over the line). With plants 8 and 9 the same method was followed, but now I used in the second period 2.7 atm. sucrose (8', 9') instead of 2.0. We see a relatively more strongly reduced water uptake and a still greater chloride uptake. With plants 6 and 7 magnesium sulphate (2.7 atm.) was added to the calcium chloride solution instead of sucrose in the second period. Here too we see a result corresponding with that obtained with sucrose, a reduced water uptake and a relatively increased chloride uptake (6', 7'). It always strikes us that on our using an osmotic counter suction in the medium the chloride uptake is higher than corresponds with the water uptake concerned without counter suction. So the correlation between water uptake and salt uptake is modified by this treatment.

Before passing on to the results of the rubidium experiments we should point out that results obtained with rubidium do not simply hold good for chloride as well. The plants used in the experiments were cultivated on Rb free but Cl containing nutrient solution (tap water). Especially the fixing in the root may be for Rb different from what it is for Cl (cf. Hylmö's results with Ca and Cl in *Pisum*). Further in all previous experiments uptake values of one plant or of one zone have always been compared (with each other) in successive periods. In order to follow the fate of the ions in the plant, the plants must be sacrificed. In the results therefore the variability of the plants

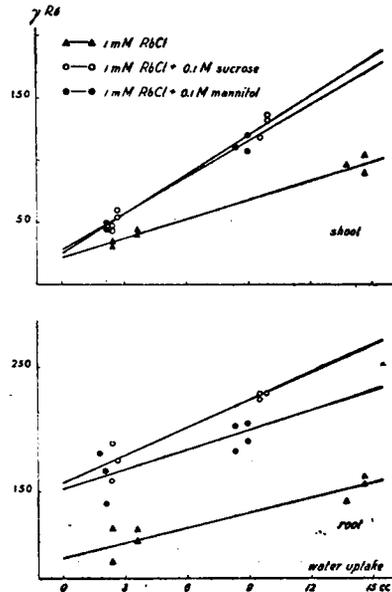


Fig. 20. Water uptake and rubidium uptake (root and shoot separated) by intact *Vicia faba* plants. Each dot represents the mean uptake by 4 selected plants.

Nutrient solution:
 ▲ — ▲ 1 mM RbCl,
 ○ — ○ 1 mM RbCl + 0.1 M sucrose
 ● — ● 1 mM RbCl + 0.1 M mannitol

is included. In order to limit these differences as much as possible averages of 4 plants strictly selected for the experiment were used for each observation. As nutrient solution 1 mM Rb Cl was used; the plants were constantly exposed to the light. The water uptake was determined by weighing. The duration of the experiment was 20 hours, the root systems being washed after that on distilled water for 1½ hours to remove Rb that could be washed out. Figure 20 gives the results of an experiment in which the Rb uptake into the plant and the distribution over root and shoot was traced at low transpiration (under a glass bell) and at evaporation free in the air. The nutrient solution was 1 mM Rb Cl without addition (triangles) with addition of 2.5 atm. mannitol (black dots) or with addition of 2.5 atm sucrose (open dots). Both sucrose and mannitol give an increased accumulation in the root together with an accelerated transport to the shoot. The correlation between rubidium uptake and water uptake is more pronounced on addition of sucrose and mannitol than without these substances. Figure 21 gives the result of an experiment in which

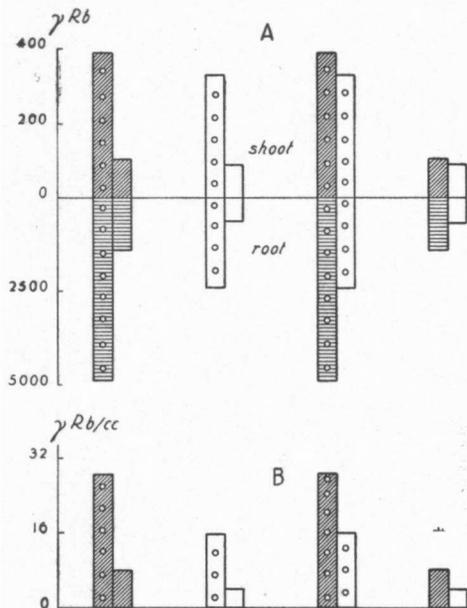


Fig. 21 A. The rubidium contents (roots and shoots) of *Vicia faba* plants after an uptake period of 20 hours on 1 mM rubidium chloride at moderate transpiration with (bubbles) and without aeration, both with (shaded) or without (white) 0.1 M sucrose.

Fig. 21 B. The rubidium transport to the shoot per ml water transpired (data from figure 21 A divided by the amount of water taken up).

under constant circumstances for the shoot (light, free to the air), the Rb distribution was examined after an uptake period on Rb Cl without addition (white blocks) and one with addition of 2.5 atm. sucrose (shaded blocks) both with and without aeration.

Figure 21 A gives the distribution of Rb over root and shoot under the various circumstances. Sucrose (left half of the figure) gives a greatly increased accumulation in the root and a somewhat greater transport to the shoot. The influence of the aeration, both on the accumulation in the root and on the transport to the shoot is very clear (right half of the figure). In figure 21 A the water uptake has been left out of consideration. The water uptake was almost equal with or without aeration, sucrose causing a 35 % reduction in the water uptake. In figure 21 B the concentration of the transpiration stream has been given, i.e. the amount of rubidium finding its way into the shoot per ml water which has been evaporated. This figure 21 B is most interesting for our problem. If we first examine the sucrose influence (left half of the figure), it appears that on addition of sucrose both with and without aeration the concentration of the transpiration stream is nearly doubled. Sucrose therefore has a very pronounced influence on the concentration of the transpiration stream, a fact already apparent from the slope of the regression lines of figure 20. Even stronger than by the sucrose influence we are here struck by the influence of aeration (right half of figure 21 B). Both on application of sucrose and without it the concentration of the transpiration stream has been reduced to less than a third by our leaving out aeration. It strikes us in figure 21 A that an increase in Rb uptake going together with aeration or administration of sucrose, has benefited root and shoot in about the same degree. It may be concluded therefore that the concentration of the transpiration stream may be considerably increased by sucrose and mannitol and may be considerably reduced by putting a stop to aeration.

VIII. DISCUSSION

In literature we find no uniformity of opinion on the mechanism of ion uptake by the root. Treating the various theories is outside the purpose of this investigation. In a previous article (BROUWER 1954*b*), just as in HYLMÖ's (1953, 1955), PETRITSCHKE's (1954) and VAN DEN HONERT's (1955) papers a special study was made of the transpiration on the ion uptake. ARISZ (1945, 1956), BURSTRÖM (1954, 1955) and HUBER (1953) have also paid special attention to this phenomenon in reviewing articles. Except van den Honert the above mentioned investigators found a distinct correlation between water uptake and salt uptake. As for the question why in some cases this correlation is lacking, van den Honert submits different possibilities for consideration, while the author on the ground of various experiments (BROUWER, 1953*b*), especially looks for an explanation via the state of the ions in the plant. This point will not be considered here any further. We start, however, from the supposition that the ion uptake can show a pronounced correlation with the water uptake.

Now the interesting point is whether the experiments described above can give some further indications on the nature of this correlation. For the question is whether this correlation is based on the occurrence of a passive component in the ion uptake, or if a

relation is found between the active ion uptake as well. According to Hylmö the water uptake promotes the accumulation in the root only if it contains but little of the ions concerned. If there is a promotion of accumulation this should be attributed to a penetrating of ions to root parts which would not be reached without a strong water uptake. Beside it the transport of ions to the shoot is nearly completely passive. A removal of ions from the root accelerated by transpiration, ions which were actively fixed there beforehand or were actively taken up, is rejected by him. Petritschek on the other hand finds facts which indicate that ions which have been fixed in the root at night, are given off to the transpiration stream in the day time and next transported to the shoot. As explained in the introduction, I thought to be allowed to conclude from my experiments that the correlation between water uptake and ion uptake was based on a rise in active uptake. Though Hylmö does not accept this view in its general tendency, he himself comes to the conclusion (HYLMÖ, 1955, p. 442) that in my experimental results there are indications which render an increase in bleeding (active uptake different from accumulation in the root) parallel to the increased transpiration possible. In his final conclusions however, Hylmö does not revert to this, so that his article as a whole arouses the impression that an increase of the active transport to the shoot at increasing transpiration should be entirely rejected in his opinion. On the other hand I thought I had to explain the whole phenomenon exactly in this way. Further it is also possible that both factors act a role while finally the possibility should be considered if all plants behave in the same way (ARISZ, 1956).

The meaning of this new research was to gather further data on a possible separation between active and passive components in the ion uptake of *Vicia faba*. For this especially those experiments are important that render a determination of the ion transport to the shoot possible. In first instance they are the experiments taken with rubidium. In those the direct transport to the shoot was determined. Now it appears from figure 21 that by stopping the aeration of the root medium the concentration of the transpiration stream is reduced to $\pm 30\%$. This indicates that at any rate some 70% of the ions, owing to a mechanism controlled or started by metabolism lands into the transpiration stream. Probably this percentage is still higher, seeing through stopping the aeration the oxygen concentration does not become nihil. The latter as follows from the fact that under these circumstances accumulation can still be observed in the root tissue. So it looks as if an active component also acts an important part in the ion transport to the shoot. In the same direction points the influence of sucrose on the concentration of the transpiration stream. Figure 21 B gives direct data of this too. Applying sucrose doubles this concentration. Here too the most obvious explanation is that an active process is to a high degree responsible for the ion concentration in the xylem vessels. In the experiments plotted in figure 20, a comparison has been made between sucrose and mannitol, in which

the phenomenon occurs that these two substances have a similar but it not quite equivalent effect. We do not directly expect mannitol to influence metabolism. ARISZ and SOL (1956) however also find in *Vallisneria* a stimulating effect of mannitol on the chlorid accumulation. So we must consider an influence on metabolism possible.

The experiments discussed above refer to rubidium transport which as has been said could be determined directly. This was not the case in the chloride experiments. Yet in those we can also get an impression of the chloride transport to the shoot from the correlation between chloride uptake and water uptake. Figure 16 clearly shows that by the use of 2.4 dinitrophenol the correlation between water uptake and ion uptake gets much smaller. This points distinctly to a decrease in concentration of the transpiration stream by inhibitors. Here too the conclusion is obvious that a considerable part of the ions is landed into the transpiration stream by an active mechanism. In the same way figure 17 shows clearly that sucrose, lactose and mannitol increase the slope of the regression lines i.e. they raise the concentration of the transpiration stream.

In order to give an impression of the quantitative relations at issue here, the concentrations of the transpiration stream computed from the various experiments have been gathered in the subjoined table IV. In the centre column the concentration has been given found simply on using the aerated nutrient solution. The concentration of the transpiration stream oscillates in this case between 9.2 and 18.8 % of the medium concentration. If aeration is stopped or an inhibitor given, this concentration falls considerably viz. to 1.7–4.7 %

TABLE IV

Influence of inhibitors and sucrose on the concentration of the transpiration stream as percentages of the medium concentration

	Nutr. sol non aerated	Nutr. sol + DNP	Nutr. sol aerated	Nutr. sol + 0.1 suc. aerated	Nutr. sol + 0.1 suc. non aerated
Cl-uptake		1.7	11.6		
Cl-uptake			12.1	26.6	
Cl-uptake	4.1		14.7		
Rb-uptake			9.2	18.8	
Rb-uptake	4.7		18.8	33.8	9.4
Rb-uptake	3.5		14.7	25.3	6.9
Rb-uptake			10.1	19.5	

of the medium concentration. This means that this concentration with respect to the control has been decreased by 70–80 %, the ion transport with equal water uptake being inhibited to this percentage. Conversely it appears from the values in the fourth column that sucrose about doubles the concentration, while the fifth column shows that the inhibition in the presence of sucrose again amounts to 70 %. In my opinion these data clearly show that at least 85–70 % of the ions is landed in the transpiration stream by an active process.

Surveying these results, we have therefore settled that there exists

a very distinct correlation between water uptake and ion uptake, but at the same time that a passive carrying along of the ions in the transpiration stream must be very much limited. How can we then explain this correlation? In 1954 I ascertained that there exists a strong correlation between the increase in chloride uptake and the increase in water conductivity as it may appear from figure 3 and is corroborated by the results laid of in figures 12 and 13. As to the nature of this correlation we are in the dark. The hypothesis, however, was made that the increased ion uptake was due to an enhanced conductivity for salts, just as an enhanced conductivity for water increases the water uptake per atmosphere suction. Now we know of the water conductivity that on a rise in suction tension it initially increases rapidly to reach a maximum value at last. This maximum value is attained in the suction tension range of 2.5–3.0 atm. But before it had already been found that the apical zone on a rise in suction tension after an initial rise in conductivity showed a fall (fig. 22 A). At the time I attributed this to an injury to the apical zone when closed in. Afterward it appeared to be a reversible phenomenon which may also be found in zone II (fig. 22 B). The

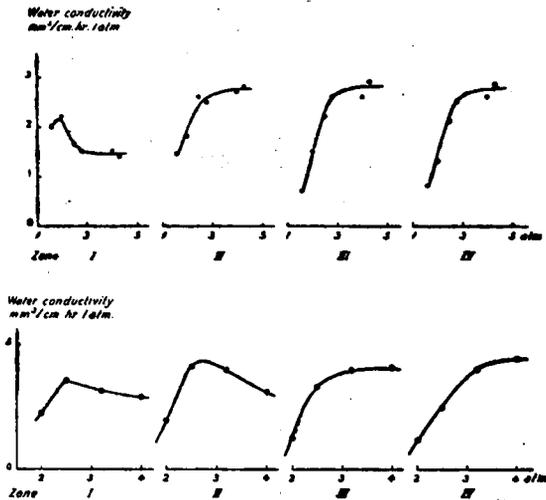


Fig. 22 A en B. Relationship between water conductivity of the various root zones and the suction tension in the xylem vessels. This relation has been plotted for each zone separately. All the values plotted are determined at a steady state, the water uptake and the suction tension being constant for several hours. (fig. 22 A from Brouwer 1954 fig. 2 and fig. 22 B from Arisz 1956 fig. 15)

relation between suction tension and water conductivity is therefore probably given by an optimum curve. I have never succeeded in increasing the suction tension in such a way, that the water-conductivity of the more basal zones also started decreasing. If the salt uptake is quite or for the greater part determined by the conductivity for salts and if the supposition is true that conductivity for

water and for salts are effected in the same sense and in the same measure by the suction tension in the tissue, it is to be expected that in the range of the high suction tensions the salt uptake does not increase any more at a rising suction tension whereas the water uptake does. This means that at a high suction tension no correlation is expected between salt uptake and water uptake. The chloride uptake as plotted in figures 11 and 12 is in agreement with this expectation. The salt uptake increases strongly in the suction tension range in which the water conductivity also strongly increases, but alters little in the higher suction tension sphere. This tallies with the result of the experiment laid of in figure 14. The correlation between water and salt uptake is strongest with lower values of the water uptake (low suction tension range) and decreases with greater water uptake (high suction tension sphere). Figure 18 also gives an indication in this direction. Here points are connected of which it may be supposed that the suction tension in the tissue is about equal. The highest suction tension we found at points 4 and 3. The slope of the line giving the relation between water uptake and chloride uptake under these circumstances, corresponds with an average influx coefficient of 2.27 % (sucrose 2.3 %; lactose 1.4 %, mannitol 1.75 % and Mg SO 3.7 %). The slope of the lines through the points 2 and 5 is averagely somewhat greater and corresponds with influx coefficients of averagely 4.7 % (sucrose 4.6 %; lactose 2.6 %; mannitol 7.8 % and Mg SO 3.7 %). If the salt uptake should be completely determined by factors which also determine the water conductivity we should not expect here a rise with increasing water uptake and the lines would have to run horizontally. This is not quite the case, there is only question of a strong reduction of the influx coefficient. Comparison of the results as they have been plotted in figures 17 and 18, gives the values of the influx coefficients given in table V for the various lines. From top to base the suction tension range lies higher and entirely in correspondence with the influx coefficient lower.

TABLE V
Influence of the suction tension on the influx coefficient (figures 17 and 18)

Regression line	Influx coefficients			
	sucrose	lactose	mannitol	MgSO/
1-5	11.2	12.0	16.4	12.3
5-3	5.3	6.6	4.0	7.1
2-5	4.6	2.6	7.8	4.8
4-3	2.3	1.4	1.75	3.7
2-4	18.6	23.0	21.0	10.3

From the fact that the salt uptake with increasing water uptake, also in the suction tension range where changes in the water conductivity can no more be expected, continues rising, we must conclude that the conductivity is not the only factor determining the salt uptake, but that beside it a passive component of the ion uptake directly linked to the waterstream occurs. According to table V this

would correspond with an influx coefficient of 1.4–3.7 %. This percentage approaches the influx coefficient, as it was found after the use of inhibitors (table IV). From these experiments it would appear that about 70–85 % of the ions in the transpiration stream is landed into it via a mechanism dependent on metabolism and that the correlation between water uptake and salt uptake, which is found here too is based on an increased salt uptake as a result of an increased conductivity for ions. In literature different cases are known from which the turgescence is deemed to affect the water conductivity (BREWIG 1937, 1939, ROSENE 1941, PERIS 1936, BROUWER 1953, 1954) but that this would also be the case for ion transport appears besides this investigation and the one published in 1954, from the bleeding experiments of VAN NIE, HELDER and ARISZ (1950), ARISZ, HELDER and VAN NIE (1951) and from researches by ARISZ and SCHREUDER (1956).

Moreover it appears from the experiments described here that part of the ions is landed into the transpiration stream by a mechanism not controlled by metabolism, i.e. it is not to be inhibited by a protracted treatment with inhibitors. May be this is a component of the ion uptake directly linked to the waterstream. Quantitatively this component is small in *Vicia faba* with respect to the active component.

If we survey the whole ion uptake in these experiments we can distinguish three components all of which are influenced by the water uptake.

- A. The accumulation in the root increases with rising water uptake (fig. 20). Inhibitors reduce the accumulation (figs 16 and 21), whereas osmotica sucrose, lactose, mannitol as well as magnesium sulphate show an increase. Both the increase due to an increased water uptake and the one caused by osmotica indicates an easier penetration of the ions into the root.
- B. As has been explained above the bleeding process is in these experiments the most important factor in the supply of ions for the transpiration stream. The strengthening of this process by the transpiration stream may be partly based on the concentration in the xylem vessels being constantly kept low (Hoagland) but on the other hand it shows so great a correlation with changes in conductivity, that an explanation at the hand of this phenomenon is obvious.
- C. A component linked direct to the water stream which in Hylmö's experiments must be taken as the most important factor for the determination of the concentration in the transpiration stream, is present here, but acts a very minor part. This "passive" influx coefficient amounts here to 2–5 % of the medium concentration. This is the concentration which cannot be further reduced by the ruling out of metabolic processes. It seems therefore that only ± 20 % of the total ion transport to the shoot is brought about in this way.

In the whole ion transport we have therefore this basis concentration,

which is more or less increased by the bleeding mechanism (cf. HUBER 1953). No increase appears after a protracted treatment with inhibitors, a strong increase when sugar is administered. We might wonder whether an uptake mechanism on account of its dependence on metabolism should be called active or not. From a viewpoint of energy it is clear that energy is required for all those processes in which the concentration in any part of the plant grows higher than the one in the medium solution. With the Rb accumulation in the root this is the case. The question remains whether the ion transport to the xylem vessels is passive or active. It is a fact this transport can be retarded by inhibitors and accelerated by sucrose and other osmotica. This, however, also obtains for the water transport, be it at higher concentrations of the inhibitors. Yet we assume that the water uptake, at least in *Vicia faba*, is an almost completely passive process. With the influence of inhibitors on the water uptake we think of a change in conductivity. This possibility must also be left open for the ion uptake. Penetration then may be a question of diffusion, possibly accelerated diffusion. This penetrating is easier on application of osmotica, more difficult when inhibitors are used. Words as changes in permeability or changes in conductivity may then be used. They do not do more, however, than giving a name to a phenomenon that is in any case controlled by the living protoplasm. For the present, however, we can share the general conception and call this salt uptake dependent on metabolism active.

SUMMARY

The relation between water uptake and ion uptake has been investigated at various experimental conditions using 5-7 weeks old *Vicia faba* plants. Taking the uptake from a calcium chloride solution as a control, the relation between ion uptake and water uptake could be modified by using sugars and inhibitors. Applying sugars to the nutrient solution the concentration of the transpiration stream could be enhanced. Using inhibitors this concentration decreased.

The concentration of the transpiration stream amounted to about 13 % of the concentration in the outer solution on aerated calcium chloride solution, to about 24 % on calcium chloride solutions with sugar addition and to about 2-4 % using dinitrophenol addition or a non-aerated solution.

It is assumed that these facts indicate that a dominant part of the ions in the transpiration stream arrives there by means of a process dependent on metabolism. Only a small percentage of the total ion transport seems to be due to a passive carrying along with the transpiration stream.

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