

EXPERIMENTS ON THE RELATION BETWEEN WATER ABSORPTION AND MINERAL UPTAKE BY PLANT ROOTS

BY

T. H. VAN DEN HONERT, J. J. M. HOOYMANS AND W. S. VOLKERS
(*Botanical Laboratory of the University and Foundation for the Research of Plant Nutrition,
Leiden*)

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INTRODUCTION

During the last decades several investigators have studied the question whether ion absorption in living plants is accelerated by the transpiration stream. Up to 1953 opinions more or less counter-balanced each other. About two thirds of the experiments gave evidence of a measurable promotion of the ion intake by water absorption, whereas one third seemed to prove a more or less complete independence between the two. To the first category belong the results of SCHLOESSING (1896), SORAUER (1880), HAAS and REED (1927), SCHMIDT (1936), FREELAND (1937), BÖTTICHER and BEHLING (1939), VAN DER WEY (1936), WRIGHT (1937) and of PHILLIS and MASON (1940), to the second those of HASSELBRING (1914), KIESSELBACH (1916), MENDIOLA (1922), MUENSCHER (1922), HUBER (1923), GRACANIN (1932), KREYZI (1932) and VAN DEN HONERT (1933). Recently, however, the scale seems to have been turned definitely in favour of the first named view by the investigations of PETRISCHEK (1953), HYLMÖ (1953) and BROUWER (1953, 1954).

PETRISCHEK (1953) and with him HUBER (1954) describe the ion absorption in its relation to water transport as consisting of two parts, the first independent of transpiration, the second proportional to it. This second part, which is indicated by HYLMÖ as "phase III" is shown by this last author to be of prominent importance in the ion intake by pea roots.

BROUWER (1953, 1954) obtained results similar to those of HYLMÖ. However, as will be discussed later on, the two authors differ in their interpretation of the phenomenon.

When considering this question it may be useful to state precisely what we want to know. There is no lack of evidence that the transpiration stream in the xylem carries salts and that by intensification of the transpiration stream the salt transport towards the leaves is increased (HAAS and REED 1927, PETRISCHEK a.o.). These salts are ultimately derived from the roots, which in turn absorbed them from

the medium. Now it is well known that plant tissues in general and roots in particular are able to accumulate ions only to a certain extent. ROBERTSON (1940), SUTCLIFFE (1952), HOAGLAND and BROYER (1942), HUMPHRIES (1952) and others showed that the rate of salt absorption is closely dependent on the salt concentration in the tissues and that a high concentration as a consequence of a previous absorption will hamper a further accumulation of the ions in question. If the transpiration current is effective in expediting translocation of minerals from the roots, it will also be effective in ion absorption because by its action the vacuolar concentration will be lowered. According to authors like PHILLIS and MASON (1940), BROYER and HOAGLAND (1943) and HOAGLAND (1944) it is in this way that ion absorption is promoted by transpiration.

However, we may confine ourselves to the more restricted question, whether, given a certain, constant status of the plant, the rate of entrance of ions from the environment into normally living roots is increased by water absorption. If the problem is stated like this, several investigations usually cited in this connection fail to give us an answer. All those, which are concerned with salt transport inside the plant, either by measuring the accumulation of salts in leaves as influenced by transpiration (HAAS and REED 1927, BÖTTICHER and BEHLING 1940) or by measuring concentration and rate of flow of the xylem sap (PETRISCHEK 1953) may at most give us certain indications.

But also in these cases where, in comparison to the water absorption, the actual intake into the roots was measured, the results are not always decisive. HYLMÖ rightly criticises the experimental procedure in a number of cases, although he limits his criticism to the results which do not agree with his views (l.c. p. 377).

An experiment proving — or disproving — an accelerating influence of water transport on ion intake should meet the following requirements. As stressed by HOAGLAND (1944) and HYLMÖ (1953) the experimental times should be short. During the periods of high and low transpiration to be compared the plant should be kept as much as possible in a constant status as far as vacuolar salt concentration, carbohydrate supply etc. are concerned, not to mention structural differences, which will develop in experiments lasting weeks or months. In other words, when applying high and low transpiration conditions alternately the plants should not have time "to change their minds".

The root environment should be kept constant in respect to temperature and pH and well stirred and aerated. If no stirring takes place the roots may deplete their immediate surroundings, so that ions will have to diffuse through an adhering water layer in order to reach the root surface, which process may limit the rate of uptake. For this reason the results obtained with roots in soil or sand cultures are doubtful. As stated by OLSEN (1953) stirring is the more effective the more the nutrient solution is diluted. HYLMÖ, finding no effect of stirring, used fairly concentrated solutions of 1–16 mM CaCl_2 . It seems probable, however, that SCHMIDT (1936) putting the roots of

his *Sanchezia* plant into a narrow potometer vessel soon brought them into an asphyxiated condition (VAN DEN HONERT 1938). This opinion is not shared by HYLMÖ (l.c. p. 379).

Meanwhile, also several experiments made with a more satisfactory water culture technique, like those of FREELAND (1937) and WRIGHT (1939) give evidence of a decided influence of transpiration on mineral intake. However, "the increase in amount of salt absorbed was by no means proportional to the increase in amount of water absorbed by the more rapidly transpiring plants" (KRAMER 1949).

The most pronounced arguments in favour of the promoting influence of the transpiration stream on ion intake are found in HYLMÖ's experiments. Working with 20 day-old, intact pea seedlings he stated that the intake of calcium and chloride from 1-9 mM CaCl_2 solutions was roughly proportional to the water absorption and also to the concentration. This would point to a passive intake of ions with the transpiration flow, a wick-like mechanism. However, the concentration of the "transpiration current" proved to be mostly lower than that in the medium. According to HYLMÖ this could be explained by the assumption that cell walls and cytoplasm would permit the passage of both water and salts, whereas the tonoplasts would be permeable to water only.

Apart from this passive mechanism, designated by him as "phase III", HYLMÖ discerns two more absorption mechanisms. "Phase I" is the rapid intake by roots or tissues placed into a more concentrated solution, also proceeding at 0° C and independent of transpiration. It is concerned with the hypothetical "free space" in the tissue which is calculated by HYLMÖ to amount to 8 per cent of the volume of the pea roots. Finally, the process by which ions are accumulated into the vacuoles by means of respiration energy is referred to by him as "phase II". The phase III component, dependent on transpiration, seems to be conspicuously prominent in pea roots.

BROUWER (1954) who, incidentally, could confirm HYLMÖ's results with pea seedlings (l.c. p. 306) studied the intake of water and ions in different zones of secondary roots of intact *Vicia faba* plants. By means of a very elegant experimental procedure he was able to show that by increasing the suction tension of root cells by one means or another the water conductivity of the different root zones investigated was increased to different degrees, so that at higher suction tensions the zone of maximum water absorption shifted away from the root tip, as previously found by BREWIG (1937). However, also the uptake of the anions (nitrate, phosphate and chloride) was influenced in the same way, although to a somewhat less degree. In contrast to HYLMÖ, he considers salt and water uptake as governed by separate mechanisms. In his opinion salt absorption, though its speed is correlated to that of transpiration, still remains an entirely active process. Increased transpiration, by causing an increased suction tension in the living root cells, would promote the rate of ion intake by an increase of "ion conductivity" in these cells.

Although differing in their explanation of the phenomena, both

HYLMÖ and BROUWER lay stress on the pronounced influence of transpiration on ion uptake by plant roots. In this connection it seems appropriate to mention some experiments made in the former Dutch East Indies which escaped attention because they were published in inaccessible periodicals.

Firstly, VAN DER WEY (1936), measuring the intake of water during consecutive hours of the day in aerated water cultures of big tobacco plants and simultaneously following the course of the salt intake by means of conductivity measurements, found a pronounced increase in salt intake during the hours of strong transpiration (Fig. 1).

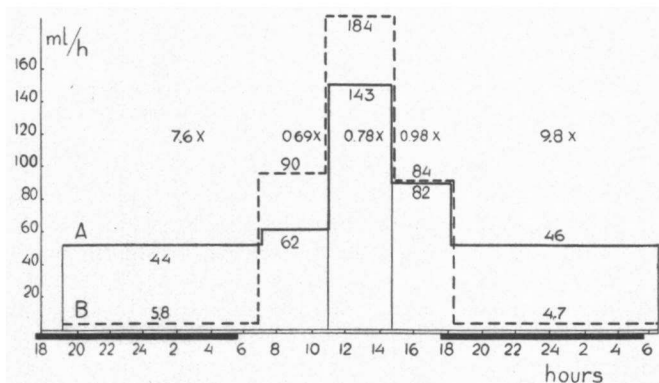


Fig. 1. Tobacco. A. Ion absorption in terms of ml nutrient solution in which the absorbed ions were solved. B. Water intake. Both expressed as ml/h per m² leaf surface. (After VAN DER WEY, 1936).

Also in this case, however, the ion absorption was by no means proportional to the water uptake. The increased ion absorption may have been due partly to an increase in temperature, as no precautions were taken to keep the root temperature constant.

On the other hand, VAN DEN HONERT, working with intact sugar cane plants in water cultures, obtained completely opposite results. He used a method of continuously flowing water cultures (1933), a description of which will be recapitulated in a following publication. The apparatus enabled him to regulate concentrations and pH in the culture solution at will and measure ion and water absorption at the same time. The nutrient solution was stirred and aerated by a constant stream of air. Phosphate absorption was determined by colorimetric analysis of the solution.

With this method he studied the rate of absorption of phosphate in intact sugar cane roots as influenced by environmental factors including concentration, pH, temperature and also transpiration rate. In the experiments mentioned below a pH 6 was maintained throughout.

Firstly, it appeared that the relation between the rate of phosphate absorption and concentration was represented by an asymptotic curve, already reaching a maximum at a phosphate concentration of 1 p.p.m. (Fig. 2). That means that the concentration factor has a negligible influence on the rate of uptake between 1,6 and 2,1 p.p.m.

Keeping the phosphate concentrations between these limits, the rate of phosphate uptake by one sugar cane plant was studied during five consecutive days and nights (Fig. 3). Although during the hours of sunshine the transpiration rate increased to tenfold or more above the night values, the phosphate absorption was but little affected. In these experiments the root temperature was not kept constant but varied as represented in the graph. In a later set of experiments a thermostat was constructed and the influence of temperature on the rate of phosphate absorption was studied, again between the above concentration limits and at pH 6, showing between 25° and 35° C a practically direct proportion to the number of degrees centigrade. Therefore, the variations in the rate of phosphate absorption shown in fig. 3 must have been due mainly to the temperature variations of the roots. It is clear that the influence of transpiration on phosphate

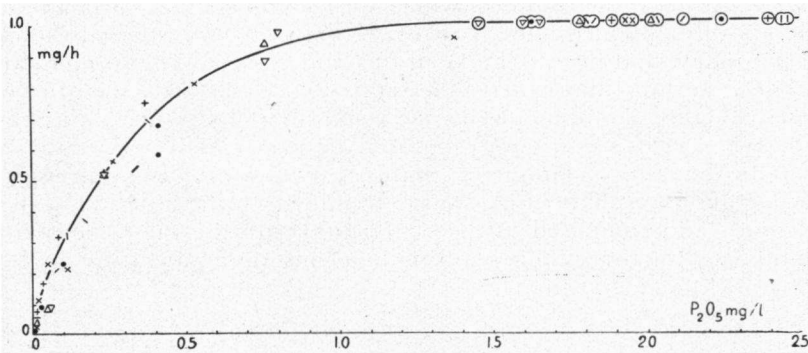


Fig. 2. Sugar cane. Relation between phosphate concentration and rate of phosphate absorption at pH 6. (After VAN DEN HONERT, 1932).

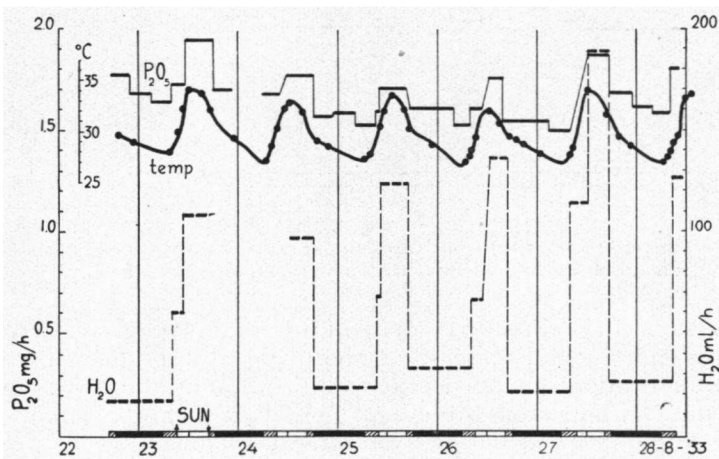


Fig. 3. Sugar cane. Rate of water and phosphate absorption by one plant during several days. Root temperature indicated. (After VAN DEN HONERT, 1932).

absorption in sugar cane roots, if any, is certainly small and hardly exceeds the experimental errors. For this reason the (possibly somewhat premature) general conclusion was drawn that transpiration has hardly any influence on phosphate intake and that the two processes are relatively independent of each other.

Another argument appeared in favour of this view. At very low concentrations (0.01 p.p.m.) and at the lowest transpiration rates during the nightly hours, the rate of phosphate intake appeared to be 500 times that calculated for passive absorption of the unchanged nutrient solution. To use HYLMÖ's terms, it was "phase II" that determined the rate of uptake in these experiments and the contribution of "phase III" to the phosphate uptake was negligible, completely different from HYLMÖ's experiences with *Pisum*.

However, because a few years later SCHMIDT (1936) published his much-cited research on the water and salt intake in the Acanthacea *Sanchezia nobilis*, the results of which were completely at variance with the above mentioned ones, VAN DEN HONERT (1938) studied the rate of phosphate and nitrate intake in this same object. The species name is not a warrant that exactly the same species has been used in both cases, as some confusion seems to be possible especially in this case. The two species studied were in any case very closely related.

With the same technique of continuously flowing water cultures the nitrate and phosphate intake was determined during a period of twice 24 hours and compared to the water intake during the same period. In this case the root system was kept at a constant temperature of 28°C.

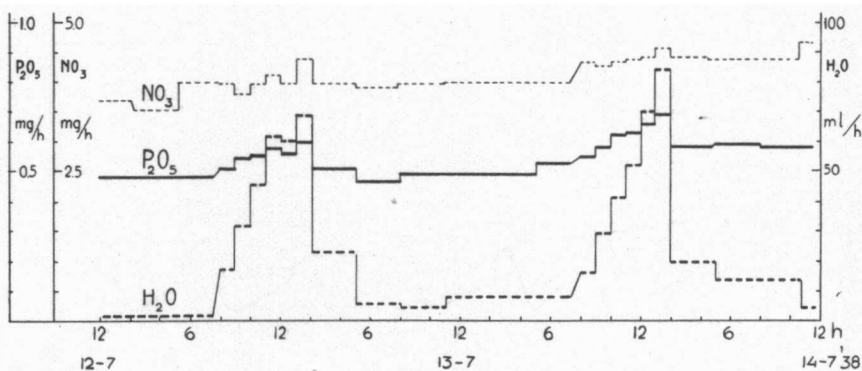


Fig. 4. *Sanchezia nobilis*. Rate of water intake and absorption of phosphate and nitrate by one plant during two days. (After VAN DEN HONERT, 1938).

Again, a ten- to twentyfold increase in water absorption was accompanied by only a small increase in phosphate absorption, whereas the nitrate absorption remained practically constant. Also in this experiment the concentrations were kept low (P_2O_5 below 5 p.p.m., NO_3 below 25 p.p.m.) and the pH was kept at a value 6.

One may wonder why these results differ so much from SCHMIDT's. Admittedly, he determined not only the uptake of nitrate and phos-

phate, but also that of potassium, calcium and magnesium, which ions were left out of account by VAN DEN HONERT. But also for the absorption of the two first named ones he found a strong correlation with the water uptake.

Two factors may be responsible for this discrepancy. Firstly, he used concentrations of the order of 50–100 times those used by VAN DEN HONERT. Moreover, he did not aerate his solutions and it seems probable that the asphyxiated condition of his *Sanchezia* roots had something to do with the phenomena he observed. HYLMÖ takes the high nitrate absorption with a relative ion uptake as high as 6 at low transpiration rates as a proof that the roots must have been metabolically active and could hardly have been suffering from oxygen deficiency. However, according to ARNON (1937), nitrate nutrition has the effect of compensating for lack of aeration, probably in connection with the high oxygen content of the nitrate ion.

It appears, therefore, that the evidence in favour of an ion absorption independant of transpiration is not so "astonishingly slight" as HYLMÖ seems to think. More critical experiments seem to be wanted. For this reason a number of short-term experiments were made with maize in water cultures under controlled conditions. The absorption rates of ammonium, nitrate, phosphate and potassium were determined at widely varying rates of transpiration.

MATERIALS AND METHODS

Maize seedlings of a single cross hybrid D × 9 reared from seed obtained from the plant breeding station "Centraal Bureau", Hoofddorp, were cultivated in pots with garden soil up to a size of about 50 cm. The roots were then freed from soil as much as possible by washing and the plants, usually two together, were placed into culture jars of 400–600 ml capacity with a WOODFORD and GREGORY (1948) solution of the following composition.

$\text{Ca}(\text{NO}_3)_2$	0,102 mM	MgSO_4	0,0975 mM
KNO_3	0,277 mM	KH_2PO_4	0,1505 mM

The solutions were continuously aerated and were renewed every three days.

After new roots had developed the still adhering soil was gradually cleared away, together with most of the original roots. After about four weeks a vigorous root system had developed, adapted to the water culture medium and suitable for absorption experiments.

The experimental procedure was very simple. The two plants, together with the wooden cover of the jar on which they were fastened, were lifted out of the solution and placed in another jar in which the desired experimental conditions prevailed. The roots were left there for adaptation during at least 20 minutes, after which a possible "rapid initial intake" was supposed to have been completed. Subsequently, the plants were transferred to another jar with identical conditions. After a certain time, depending on the concentration of

the ion in question and the expected absorption rate, the plant was taken out again.

The transpiration rate was determined by weighing plant and jar together on an automatic scale accurate to 0.3 g at the beginning and the end of every experimental period. The weighing took less than one minute.

As a matter of fact not the water uptake but the water loss from the plant was measured by this method, the evaporation from the surface of the solution being negligible during these short periods used. Now the changes in rate of water absorption by the roots, which are of interest here, will lag behind those of the transpiration loss (KRAMER 1937). However, this time lag is considered not to be of great importance in consequence of the adaptation period used with every change of conditions.

The nutrient solution was stirred and aerated by a continuous air stream. From time to time 1 ml samples were taken for colorimetric determination of the pH. As the solutions were only very slightly buffered care had to be taken not to bring the sample into contact with the air, because by loss of a little CO_2 the pH easily shifts towards the alkaline side. Therefore two drops of indicator solution (bromocresol purple 100 mg to 250 ml H_2O) were added to a 6 mm wide test tube and the sample pipetted into it in such way that while emptying the pipette its tip was kept under the surface of the solution in the test tube. One soon gets experience in mixing the indicator homogeneously in this way.

In the experiments to be described here the pH was kept at the value 6, by addition of a drop of 0.1 M NaOH or by supplying the aerating air stream, whenever necessary, with a small amount of carbon dioxide. The supply of CO_2 from a cylinder with pressure regulator was controlled by means of a needle valve and by observing the velocity of bubbling through a small washing bottle. This simple method appeared to be most helpful in regulating the pH of culture solutions in the range of pH 4.5–7.

The root temperature was kept at 20° C by placing the jars into a water thermostat.

The transpiration was influenced by putting the plants either in a sunny place in a glasshouse in the wind of a ventilator, or in a dark room with still air and with a high relative humidity. The transfer from one place to another took only half a minute. Perhaps it should have been more elegant to change the humidity factor only and to perform all the absorption experiments in the light. But as the greatest transpiration rates were obtained in strong sunlight and the light factor could not be kept constant anyway, this idea was abandoned. For the rest the results showed little evidence of a "change of mind" by the plants under conditions of light and darkness, in other words the status of the plants in respect to the carbohydrate supply of the roots etc., appeared to remain sufficiently constant. Indications of small changes will be discussed later on.

The absorption was measured by analysing samples of the nutrient

solution before and after the absorption period. For ammonium, nitrate and phosphate colorimetric methods were used. Ammonium and nitrate were determined by the Nessler and the phenol disulfonic acid methods respectively (ALLPORT 1947) and phosphate by the molybdenum blue method according to PARKER and FUDGE (1927). Potassium concentrations were determined by means of a BECKMAN flame photometer.

Care was taken to measure the absorption in the asymptotic part of the concentration-absorption curve, i.e. in a concentration range where the concentration factor has only little influence on the rate of absorption.

The influence of concentration on the rate of intake of nitrate, phosphate and ammonium by maize roots in water culture was known from experiments to be described elsewhere. Consequently, unless especially mentioned otherwise, the concentration of the named ions was well between the limits of 50 and 5 p.p.m. The same holds good for potassium, although the exact influence of the potassium concentration on the rate of intake was not yet known.

The desired very short experimental periods likewise made it necessary to use low concentrations, to the effect that within these periods still a considerable part ($1/3$ to $1/2$) of the solute in question was absorbed. A same absorption intensity at higher concentrations either would require a much longer time or would give unreliable results with the use of colorimetric methods.

In calculating the quantities absorbed no corrections were needed for the decrease in the available volume of nutrient solution caused by the sampling for the pH determination (usually not more than 6 ml on a volume of 600 ml in every experiment), although the transpiration (determined as loss of weight) was corrected for it.

The loss of volume of the solution caused by the water absorption through the roots (taken equal to the quantity transpired) was duly taken into account in the computation of the ion absorption rates.

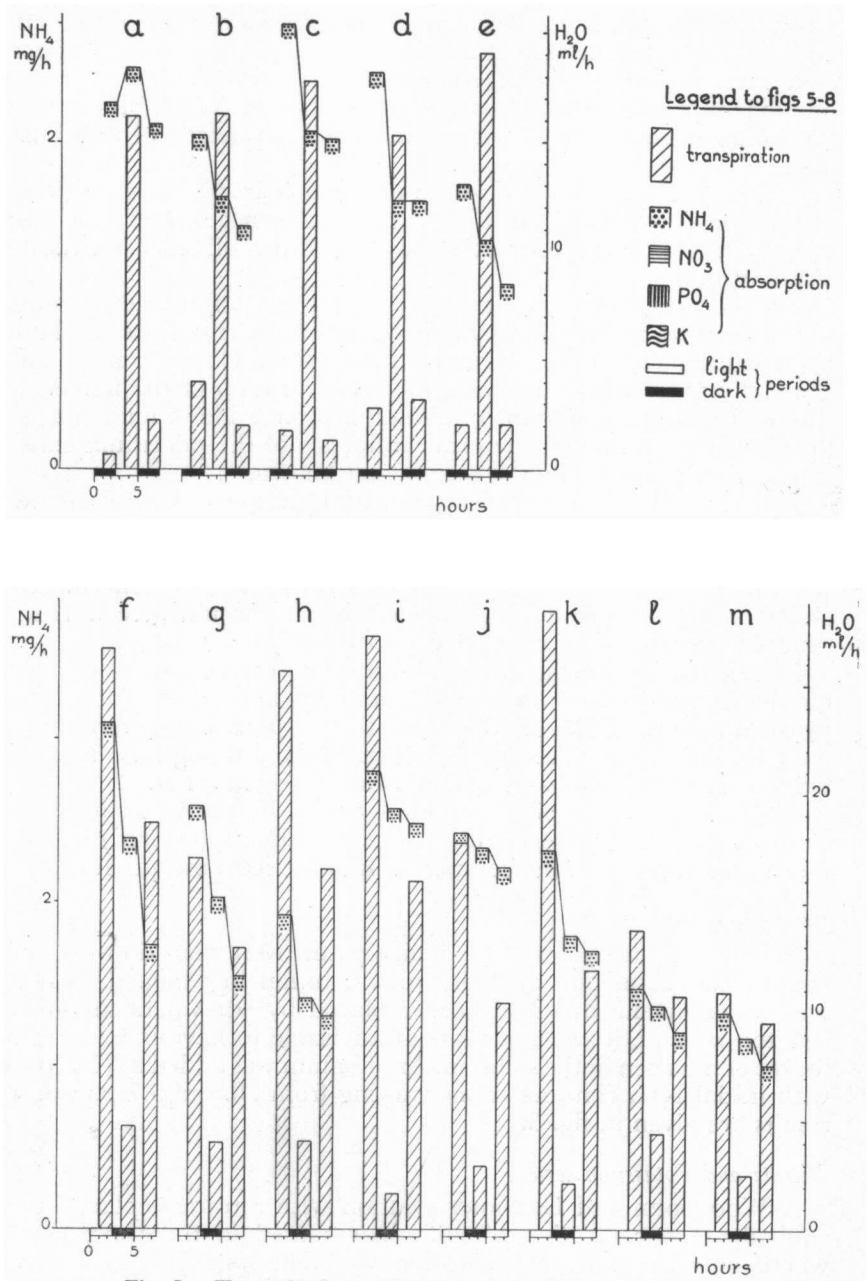
Ammonium series

In this series the roots of the maize plants were placed in the above mentioned WOODFORD and GREGORY solution in which the calcium and potassium nitrates had been replaced by equivalent amounts of sulfates, because it was not thought advisable to have more than one source of nitrogen in the solution. Ammonium was added as $(\text{NH}_4)_2\text{SO}_4$ with initial NH_4 concentrations varying from 20.5 to 9.7 p.p.m. The results are given in fig. 5.

Nitrate and Potassium series

A WOODFORD and GREGORY solution with nitrates replaced by an equivalent concentration of sulfates was used in those experiments where only the nitrate absorption was determined (Fig. 6, a, b). The necessary nitrate was supplied as KNO_3 with an initial NO_3 concentration of 47-48 p.p.m.

In the combined nitrate and potassium experiments (fig. 6, c-f)



a one-salt solution of KNO_3 was used in order to avoid the necessity of special precautions in the flame photometric determination of potassium. Here the initial K and NO_3 concentrations varied between 32–27 and 51–43 p.p.m. respectively.

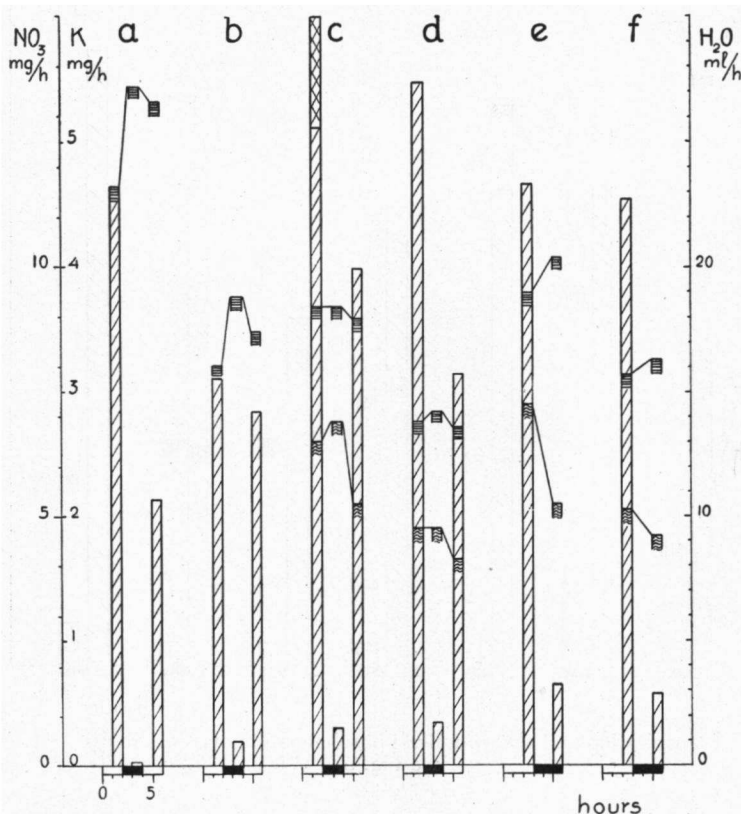


Fig. 6. Transpiration and absorption of nitrate and potassium in maize. Legend see Fig. 5.

Phosphate and Potassium series

In those cases where only the phosphate intake was studied (fig. 7, d–g) a WOODFORD and GREGORY solution was used with an initial PO_4 concentration of 7.8 p.p.m.

For combined determinations of phosphate and potassium absorption a two-salt solution of KNO_3 and KH_2PO_4 was used for the reason mentioned in the preceding paragraph. The initial K and PO_4 concentrations were 53 and 12.9 p.p.m.

As is often done, the phosphate absorption rate has been calculated in terms of mg PO_4 per hour. It should be kept in mind, however, that maize roots absorb phosphate only in the form of monovalent H_2PO_4^- ions, as could be shown in experiments to be published elsewhere. In this respect, therefore, maize behaves exactly like sugar cane

(VAN DEN HONERT, 1932) and shows similarity to rye and *Helodea canadensis* (OLSEN, 1953).

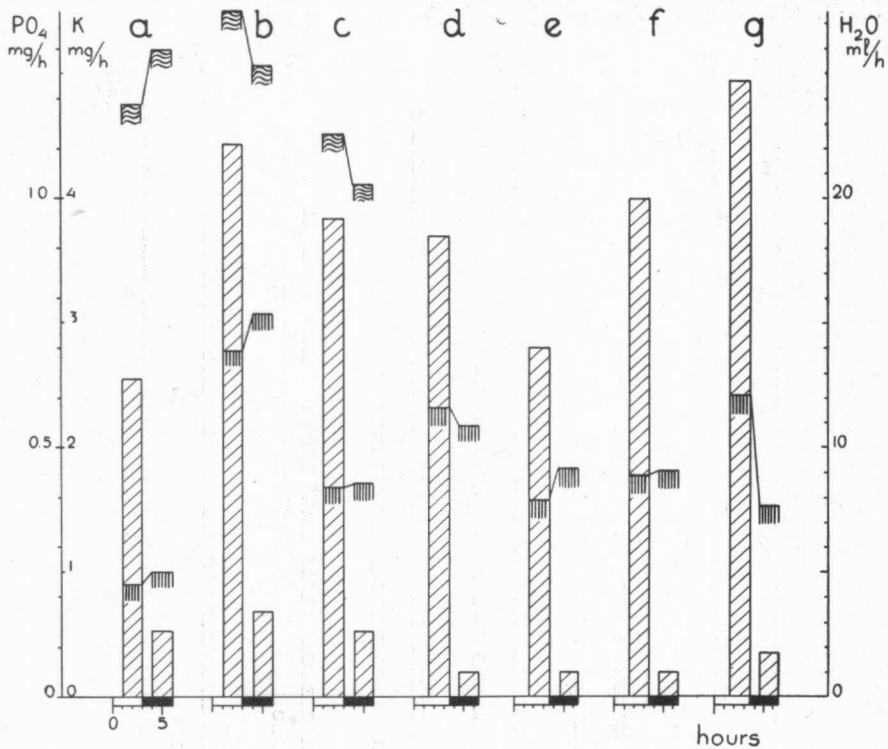


Fig. 7. Transpiration and absorption of phosphate and potassium in maize. Legend see Fig. 5.

Nitrate and phosphate series

Here the $\text{Ca}(\text{NO}_3)_2$ in the WOODFORD and GREGORY solution was replaced by an equivalent concentration of CaSO_4 . KNO_3 and KH_2PO_4 were given in such a way that the initial NO_3 and PO_4 concentrations varied between 46–42 and 6.8–5 p.p.m. respectively.

In this series (see Fig. 8), as well as in the previous one, rather long absorption periods of 2–2.5 hours were used, because otherwise it would not have been possible to determine the fairly slow uptake of phosphate with sufficient accuracy.

In the last two experiments (Fig. 8, h and i) the plants were put under a bell glass during the light period in order to diminish the transpiration rate, so that the light factor constituted the only important difference between the two periods.

It must be mentioned that in some of these experiments the final phosphate concentrations at the end of the light and dark periods had decreased well below the asymptotic part of the absorption curve.

After the light periods of experiments g, fig. 7 and g, fig. 8 the PO_4 concentration was in both cases ± 2.0 p.p.m. This is still high enough to maintain a rate of phosphate intake 75 per cent of maximal.

EXPERIMENTAL RESULTS

The results of the experiments represented in Figs 5–8 are summarized in Fig. 9. In this figure the abscissa represents the “transpiration percentage” (i.e. dark transpiration rate in per cent of light transpiration rate) whereas the ordinate indicates the “ion absorption percentage” (i.e. the dark ion absorption rate in per cent of light ion absorption rate.).

At first sight it is clear that the majority of the “ion absorption percentages” cluster around the value of 100. In order to ascertain whether any significant relation between transpiration and ion absorption is present the data obtained were submitted to a statistical treatment.

The “ion absorption percentages” were averaged over the different kinds of ions separately and the standard errors of these means calculated. Both these computations were made on the assumption that the method of observation (light-dark-light, light-dark, etc.) is without influence on the ion absorption percentage. (That this assumption was not contradicted by the data themselves was shown by an analysis of variance).

The results are shown in the following table.

Table 1. (Low “transpiration percentages”)

Ion	Average ion absorption percentage	Standard error	Number of degrees of freedom	Confidence limits ¹	
NH_4	101	2.78	12	95	107
NO_3	107	1.66	13	103	111
K	97	5.65	6	83.2	111
PO_4	93	5.8	14	80.6	105

From the confidence limits it is evident that only the nitrate average differs significantly from 100; the difference is, however, in the opposite direction from the one to be expected. It is therefore reasonable to ascribe this difference not to the influence of water absorption but to some concomitant factor, e.g. to the strong illumination used to stimulate the water absorption during the light period. In order to check this hypothesis two experiments were made in which the plants were kept in a humid atmosphere during the illumination; the “transpiration percentages” were accordingly high. (See Fig. 8, h and i and Fig. 9, encircled symbols). The results are given in Table 2.

It is easily seen that there is no significant difference between the means of Table 1 and Table 2; moreover, the nitrate mean is signifi-

¹ We may expect with 95 per cent probability that the “true” mean lies within these limits.

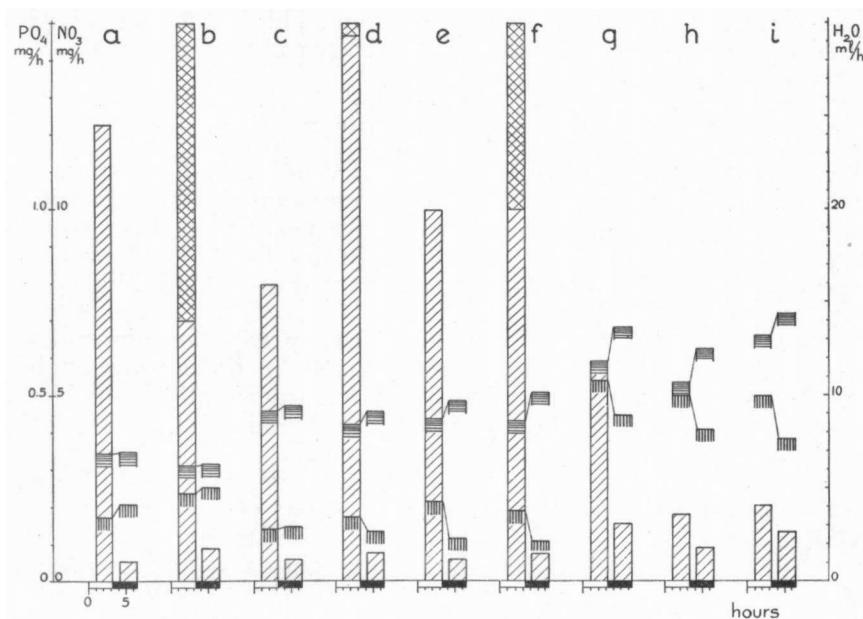


Fig. 8. Transpiration and absorption of nitrate and phosphate in maize. Legend see Fig. 5. The double hatching in b, d and f indicates a transpiration exceeding 30 ml/h .

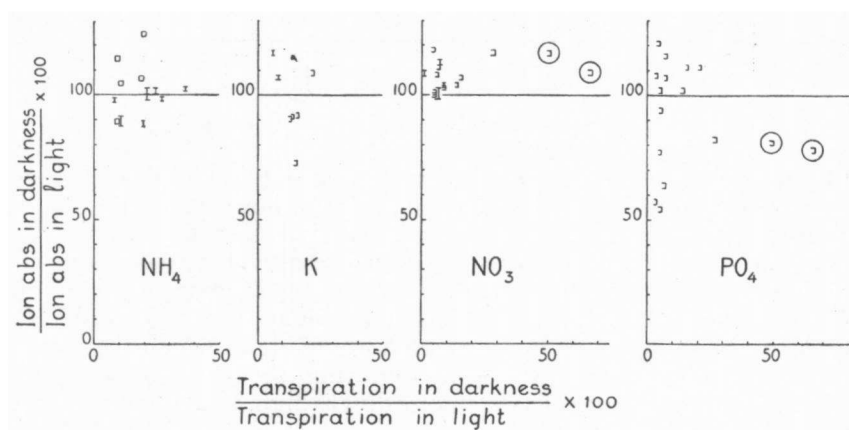


Fig. 9. Summary of the results represented in Fig. 5-8. Sequence of light and dark periods indicated as follows: \square dark-light-dark, I light-dark-light, J light-dark. The encircled symbols refer to experiments h and i in Fig. 8.

cantly greater than 100 in either table. So we can say that the data do not indicate any influence of water absorption on ion absorption. This result was confirmed by the analysis of variance mentioned above. It would have been desirable to make a greater number of the last named experiments. However, the season became too far advanced.

Table 2. (High "transpiration percentages")

Ion	Average ion absorption percentage	Standard error	Number of degrees of freedom	Confidence limits ¹
NO ₃	113	4.23	13	104 122
PO ₄	79.5	15.4	14	46.5 113

Meanwhile, the general tendency of the nitrate absorption percentages in the dark to be higher than those during the preceding light period throws doubt on the assumption that during the short experimental periods used the plants remained in a completely constant status. Evidently the periods were long enough for the plants to have "changed their minds" already to a small extent. The same holds true for the phosphate absorption, where the variations seem to have something to do with the season. All the "ion absorption percentages" below 90 per cent (Fig. 9) were obtained in the autumn of 1954 after August 31th. Perhaps the carbohydrate content of the roots of the maize plants grown during shortening days was insufficient for a constant phosphate absorption during a dark period of three hours or more. If this were true the question remains why nitrate and phosphate behave differently.

Another phenomenon to be mentioned here is the rather steady decline of the ammonium absorption during practically all of the experiments (see Fig. 5). It is a phenomenon generally observed in those cases where maize roots grown in a solution containing nitrate as the only source of nitrogen were brought into an ammonium containing solution.

As mentioned before, the concentrations in the experiments were generally kept such, that the concentration factor had little influence on the ion absorption rate. Nevertheless, the ratio between the rates of absorption of two different ions determined simultaneously varied between wide limits, as shown in Table 3.

Table 3. Ratio of ion absorption rates determined simultaneously.

Values obtained	NO ₃ /K	NO ₃ /PO ₄	K/PO ₄
highest	3.08	72.3	53.4
average	2.47	34.2	31.6
lowest	2.09	16.2	15.9

This gives evidence of a certain independence between the different ion absorption mechanisms involved.

¹ We may expect with 95 per cent probability that the „true” mean lies within these limits.

DISCUSSION

The conclusion from these experiments cannot be otherwise than that in maize roots in water culture, under the experimental conditions described and within the experimental errors, no influence of transpiration on the rate of absorption of ammonium, potassium, nitrate and phosphate could be demonstrated. The question arises why other authors, especially HYLMÖ and BROUWER, obtained completely different results.

In the first place they used different objects. It is possible that there are differences in protoplasmic or cell wall structure between roots of pea and broad bean on the one hand and maize roots on the other hand. It is imaginable, for that reason, that the transpiration-dependent part of the ion uptake (HYLMÖ's phase III), prominent in pea and broad bean, is negligible in maize. Besides, it is not certain that in maize calcium and chloride uptake would give the same picture as that of ammonium, potassium, nitrate and phosphate.

However, our results seem to be contradictory to some observations of BROUWER's (1953, *l.c.* p. 644), who stated a decided increase also of nitrate and phosphate absorption in young maize plants at higher transpiration rates. Two reasons may be advanced for this discrepancy. BROUWER used a HOAGLAND solution with higher phosphate and nitrate concentrations (44 and 158 p.p.m. respectively) than used in the present experiments. Also in BROUWER's experiments with broad bean and in those of HYLMÖ with peas, higher — mostly much higher — concentrations were applied than those used by the present authors. As in HYLMÖ's experiments the rate of "phase III" was found to be strongly dependent on the salt concentration, it might well be possible that such a transpiration-dependent ion absorption would become measurable also in maize at higher concentrations. The results thus far available seem to be in accordance with the assumption that the ratio between "phase II" and "phase III" is much higher in maize than in pea or broad bean, so that only at higher concentrations the influence of "phase III" might become apparent in maize. This would mean a quantitative rather than a fundamental difference between the two types of plants.

It might, however, also be surmised that the low concentrations used by the present authors would not permit the detection of "phase III", even if maize roots were identical with pea roots. However, if the "transpiration stream" taken up by the roots had the composition of the culture solution without dilution, the excess ion intake should have been apparent at the highest transpiration rates we measured. This maximal intake was calculated to be of the order of magnitude of 20, 30, 40 and 250 per cent for ammonium, potassium, nitrate and phosphate respectively. Therefore, unless a considerable dilution took place (*cf.* HYLMÖ) this surmise seems to be unlikely. Nevertheless, this last argument does not seem conclusive as yet.

SUMMARY

Maize plants in water cultures were submitted to conditions of high transpiration in the sun and low transpiration in the dark. Transpiration rates were determined together with those of ammonium, potassium, nitrate and phosphate absorption from solutions at pH 6 and 20° centigrade.

No significant influence of transpiration on ion absorption was found. These results seem to be at variance with those obtained by HYLÖ with peas and by BROUWER with broad beans. However, the ion concentrations used were considerably lower than those used by HYLÖ and BROUWER. Moreover, the possibility is discussed that the concentration- and transpiration-dependent component of the ion absorption might be great in pea and broad bean and small in maize. The seeming contradiction would then be reduced to a quantitative difference.

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