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Effects of External Factors on the Transport of Radiophosphorus by the Roots of Intact Barley Plants

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INTRODUCTION

Kinetic studies have been carried out by many investigators on the mechanism of ion absorption in the roots, and they have pointed out that there are the active and passive processes for this mechanism (11, 12, 23, 31, 35, 36, 40). (In the generally accepted terminology, "*passive*" ones stand for the purely physical pathways, such as diffusion, ion exchange, adsorption and combination, and "*active*" ones conceivably play a part in the overall course of events in addition to the metabolically determined, such as anion respiration.)

There are abundant evidences that the processes of absorption and translocation of solutes are closely interrelated in the intact plants; the nutrient content of roots is not only determined by the balance between these processes, but also is in itself an important factor determining their rates (6, 7). STEWARD *et al* (39) suggested that the shoot may provide the stimulus for the removal of salts from the root. WILLIAMS (45) considered that competition between roots and shoots is a important factor in determining the distribution of phosphorus in wheat plants. Evidences have been presented which support the idea that the rate of absorption of mineral ions by root may be considerably affected by the rate of concurrent transpiration (7, 23, 24, 29, 33).

Thus, an understanding of the factors which determine the rate of removal of nutrients from roots to shoots is essential in the interpretation of the nutritional relationships of intact plants. Factors determining the rate and extent of solute absorption may be due either to external or environmental conditions, or to internal controlling conditions. Of the external or environmental conditions, hydrogen ion concentration, temperature, aeration, light intensity, and the content of mineral salts in the plants are important. These conditions may alter and determine the internal physico-chemical conditions and the relative rates of processes, some interrelated with absorption in roots. Therefore, the present investigation was carried out to make sure whether the rate of the transfer of phosphorus absorbed

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previously from roots to shoots is affected by those factors of considerable importance in determining the rate of absorption. Above all, effects of light on the interrelation between translocation of phosphorus and transpiration were investigated, and discussed.

MATERIALS AND METHODS

Barley plant, Fujisaka No. 5, was used as the material. All experiments were performed with the young barley at the third leaf stage which had been grown in nutrient solution in a greenhouse for about three weeks.

The culture methods of the plants were modified ones reported by HOAGLAND and BROYER (15) as following. The seeds were immersed in running tap water overnight. The washed seeds were placed at regular intervals on a stainless steel wire-netting, covered with the other wire-netting and with a sheet of gauze which was immersed in water, and then this apparatus was transferred to the incubator maintained at 25°C. The seeds were germinated in the dark except when the wire-netting and the gauze covering the seeds were taken off on the fourth day. On the fifth day the seedlings were removed out of the incubator, and were kept in the room for four to five hours. The seedlings at this time had grown a length of 2 to 3 cm in hypocotyl. The uniform seedlings were selected, and were supported by a rubber holder with nine slots at regular intervals. The slot in the rubber holder permitted removal of plant without injury. The four rubber holders transplanted were put on one plate, and the plate was fixed on the Wagner pot full of 4.5 liters of nutrient solution.

Until the seedlings grew at the third leaf stage, the plants were raised in a greenhouse with 1/10 strength Hoagland's solution of the following composition: KNO_3 , 0.5 mM; $\text{Ca}(\text{NO}_3)_2$, 0.5 mM; MgSO_4 , 0.2 mM; KH_2PO_4 , 0.1 mM; Fe-tartrate, 5 ppm; MnCl_2 , ZnCl_2 , and H_3BO_3 , trace. The plants in some experiments were grown in full strength Hoagland's solution to compare with low salt plants. The solution was renewed weekly in the 1/10 strength solution, and daily in the full strength. The solution was not aerated, since preliminary experiments indicated that growth was not improved by aeration. To obtain more uniform plants, the plants were removed in a growth chamber for two days before treatments. The light intensity of the growth chamber was 6,000 lux at the level of the 3rd leaf under artificial illumination and the temperature was maintained constantly at 24°C. The light period was ten hours daily.

Nine plants were used as a batch and the experiment was repeated twice at least.

The absorption of radiophosphorus was carried out by dipping the roots in 1/10 strength Hoagland's solution containing 20 $\mu\text{C/l}$ concentrations of $\text{H}_3^{32}\text{PO}_4$ under the conditions of room temperature at 21°C and of artificial illumination of 6,000 lux

for 30 minutes. This treatment was called "*pretreatment*". HAGEN and HOPKINS (13) indicated that both H_2PO_4^- and HPO_4^{--} ions are absorbed under aerobic conditions by excised barley roots, and that the ratio of H_2PO_4^- and HPO_4^{--} ions at pH 6.0 was 93.8 and 6.1 percentage respectively, and that the amounts of phosphate absorbed by excised barley roots was maximal value at this pH when the total phosphate concentration in external solution was 1×10^{-4} *M*. Therefore, the pH value of 1/10 strength Hoagland's solution used for pretreatment was adjusted to 6.0 with 0.1 *N* KOH or 0.1 *N* HCl, as the solution contained phosphate at the concentration of 1×10^{-4} *M*. The radiophosphorus absorbed from roots during pretreatment had been accumulated almost in the roots and slightly in the shoots. Furthermore, the amount of this absorbed radiophosphorus was enough to measure the radioactivity in the roots and shoots after the subsequent treatments. To prevent the contamination of adsorption on shoots during the pretreatment, the upper surface of the rubber holders were sealed with paraffin-lanoline mixture and the lower with agar.

Pretreatment had no sooner finished than the roots were immersed in running tap water for 30 seconds, in order to take off radiophosphorus adsorbed on the surface of the roots. After washing the roots, the plants were removed into ^{32}P -free 1/10 strength Hoagland's solution. The plants were harvested and sectioned at three hours after pretreatment, except the experiments of the time course of translocation. Usually each plant was sectioned into roots and shoots, and fresh and dry weight were measured by usual method.

For radioactive assay, the plant sections were completely dry-ashed by an electric furnace (550-600°C, 8 hours), and the ash was dissolved with HCl and added warm water. The solution was filtrated if the precipitate (probably silicate) were markedly found. The solution or the filtrate were completely removed into a sample pan, and dried by an ultrared lamp. Radiophosphorus activities were determined by a G-M tube (end-window, mica thickness 1.1 *mg/cm*²), so that radioactivities in roots or shoots were calculated as *cpm* per 1 *g* of fresh or dry weight. The transport ratio of radiophosphorus from roots to shoots was expressed in percentage of accumulated phosphorus in the shoots which was translocated from roots.

The amount of water absorption was determined by potometer, and the results were expressed in *ml* per 1 *g* of fresh weight of the whole plant.

RESULTS

Time course. Low and high salt plants that absorbed radiophosphorus with the pretreatment were removed into ^{32}P -free 1/10 and full strength Hoagland's solution (pH 6.0) respectively, and each plant was raised under following conditions: Light intensity, 6,000 lux; room temperature, 23°C. The plants were harvested at 1, 2, 3, 6, 9, 12 hours, and, the transport ratio of radiophosphorus from roots to shoots was determined each time. The results were shown in Fig. 1. In all

experimental periods, the transport ratio showed higher values in low salt plants than in high salt. The transport ratio in low salt plants shows a rapid increment

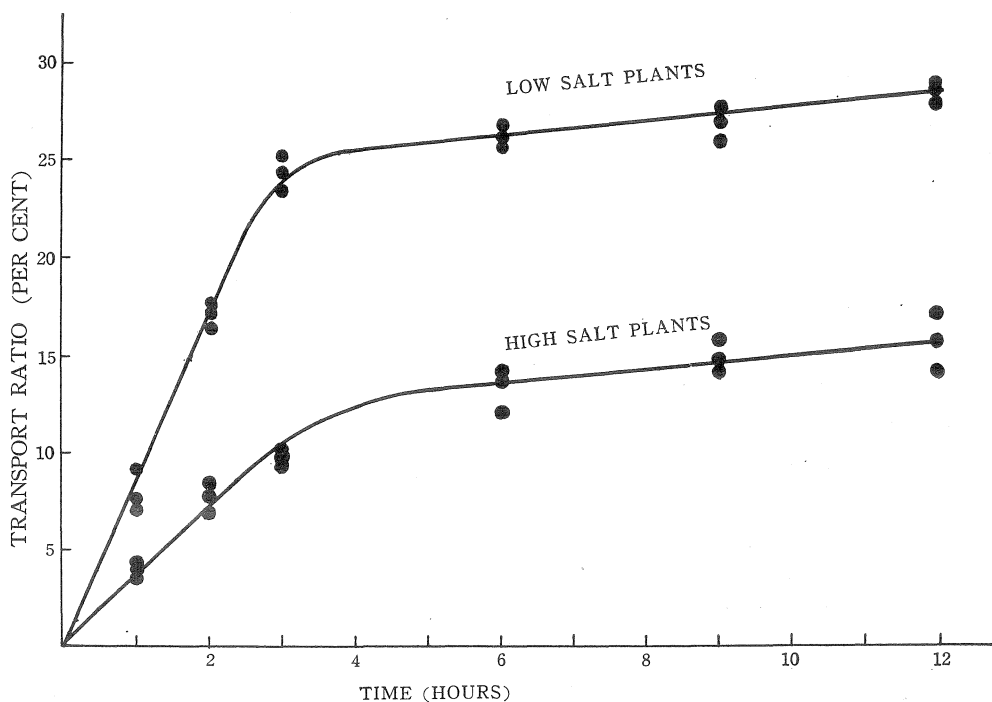


Fig. 1. Time course of translocation of radiophosphorus in high and low salt plants. Each value is the average of 9 individuals of barley plants at the third leaf stage.

till three hours, but the subsequent increase was very slight. The same results were obtained in high salt plants although it was not so clear as in low salt plants. This shows that most of mobile phosphorus fraction which the roots absorbed during pretreatment may be transported from roots to shoots within three hours. Effects of various external factors on the translocation of phosphorus, therefore, were investigated by comparing with the values of transport ratio at three hours after the pretreatment.

Studies with abscised roots of barley (15) have clearly shown the necessity of an aerobic environment for the accumulation of salt. VLAMIS and DAVIS (44), with abscised roots of tomato and rice, found that the accumulation of potassium and bromide clearly reduced at oxygen values below 3-5 per cent. A fairly close correlation exists between these effects of oxygen supply on accumulation, and on total respiration by comparable tissues. The transport ratio of low salt plants at three hours after pretreatment, however, did not show the least difference between aeration and nonaeration, although, in the experiment of time course, the nutrient solution was aerated for experimental periods. This shows that two liters of nutrient

solution contain enough oxygen for the respiration interrelated with translocation. In the following experiments, therefore, the solution was not aerated.

Hydrogen ion concentration. Low salt plants treated with the pretreatment were removed into various hydrogen ion concentration of ^{32}P -free 1/10 strength Hoagland's solution to raise for three hours in light, and the transport ratio of radiophosphorus was determined at each hydrogen ion concentration. As is shown in Fig. 2 the transport ratio was slightly greater at pH 5 and 6 than at other pH

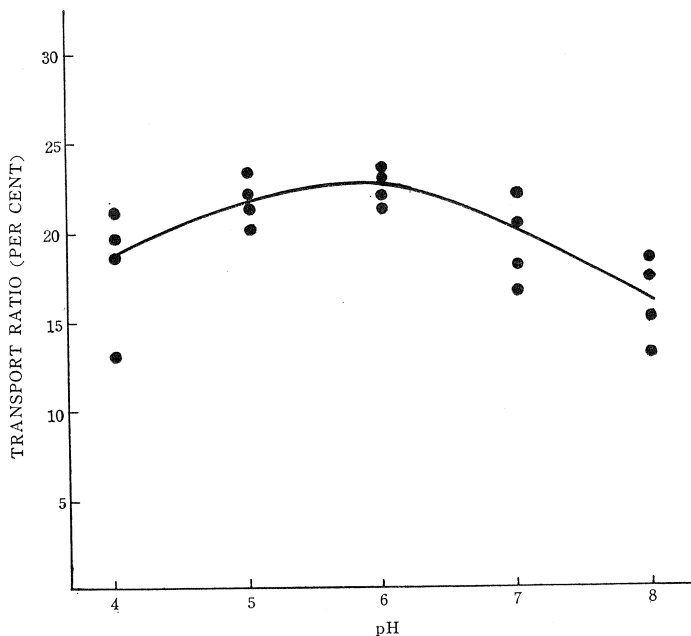


Fig. 2. Effect of hydrogen ion concentration on the translocation of radiophosphorus in low salt plants. Each value is the average of 9 individuals of barley plants at the third leaf stage.

values. In living tissues, a tendency toward modification of the hydrogen ion concentration by a moderate alteration of the pH of the external solution is counteracted within the protoplasm by direct buffer action of constituent compounds, and, possibly, by a similarly effective modification in the rates of some metabolic reaction. Thus, the pH in cells is maintained within rather narrow limits (1). HOAGLAND and BROYER (16) found that the pH values of exudates from decapitated plants were remarkably constant even though the hydrogen ion concentration of the medium bathing the roots varied over a wide range. Therefore, though in this experiment the transport ratio of radiophosphorus was relatively high in pH values from 5 to 6, it should properly be considered not to have a great influence at this limit. Though no marked change of internal conditions occurs with the alteration of external hydrogen ion conditions, some changes of metabolic processes in root tissues may occur in order to maintain constantly hydrogen ion concentration in

root tissues. For example, there is the accumulation of organic anions in root tissues bathed in alkaline solutions (16, 20, 21, 25).

Transport ratio of phosphorus from roots to shoots for three hours was not greatly affected by relatively large changes in the external pH, but values of transport ratio at pH 6 were relatively constant in repeated experiments than at other pH (Fig. 2). Then the subsequent experiments were carried out in the nutrient solution adjusted to pH 6.0.

Temperature. Several investigators have reported on the relationships of temperature of external solution to the absorption of mineral salts in the roots (15, 42, 43). These data indicate that increases in both accumulation and respiration rates are associated with rise in temperature of the medium bathing the tissues. More than double increase in transport ratio for a ten-degree rise in temperature indicates that these processes are of physico-chemical nature. From the concordance of temperature effects obtained between accumulation of inorganic solutes and respiration (especially the enhanced respiration), investigators have generally inferred some interrelation between them. Then, for the purpose to make sure whether these interrelations also occur on the transport of phosphorus from roots to shoots, the following experiment was carried out.

Low salt plants that absorbed radiophosphorus with pretreatment were removed into various temperatures of ^{32}P -free 1/10 strength Hoagland's solution (pH 6.0) to raise in light for three hours. Transport ratio at each temperature was determined, so that the optimum curve with maximum values at 20°C was obtained (Fig. 3).

Light. Light was found by HOAGLAND and DAVIS (17) to be an important factor determining the rates of the absorption of inorganic solute. Then, for the purpose of making sure of the influence of light on the absorption and translocation of phosphorus, low salt plants that exposed in artificial illumination (6,000 lux) for 48 hours absorbed radiophosphorus with pretreatment in light, and were then removed into the ^{32}P -free 1/10 strength Hoagland's solution to raise for three hours in light or dark. And low salt plants kept in dark for 48 hours were

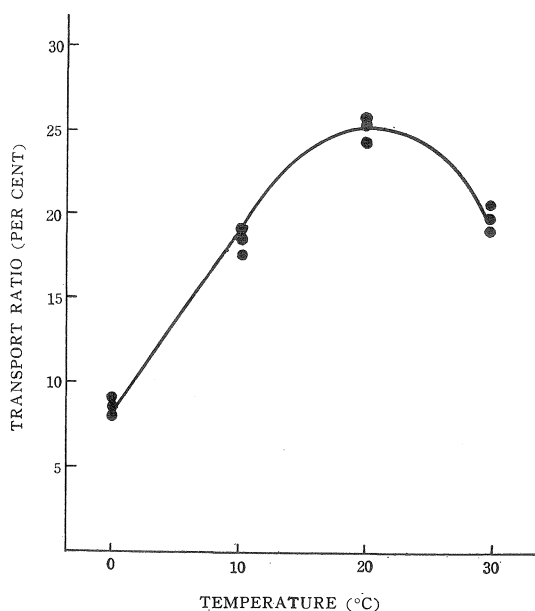


Fig. 3. Effect of temperature of nutrient solution on the translocation of radiophosphorus in low salt plants. The values of each treatment are average values of 9 individuals of barley plants at the third leaf stage.

treated with pretreatment in dark, and then removed into the ^{32}P -free 1/10 strength Hoagland's solution to raise for three hours in light or dark. In the same way, high salt plants kept in light or dark for 48 hours were removed into the ^{32}P -free full

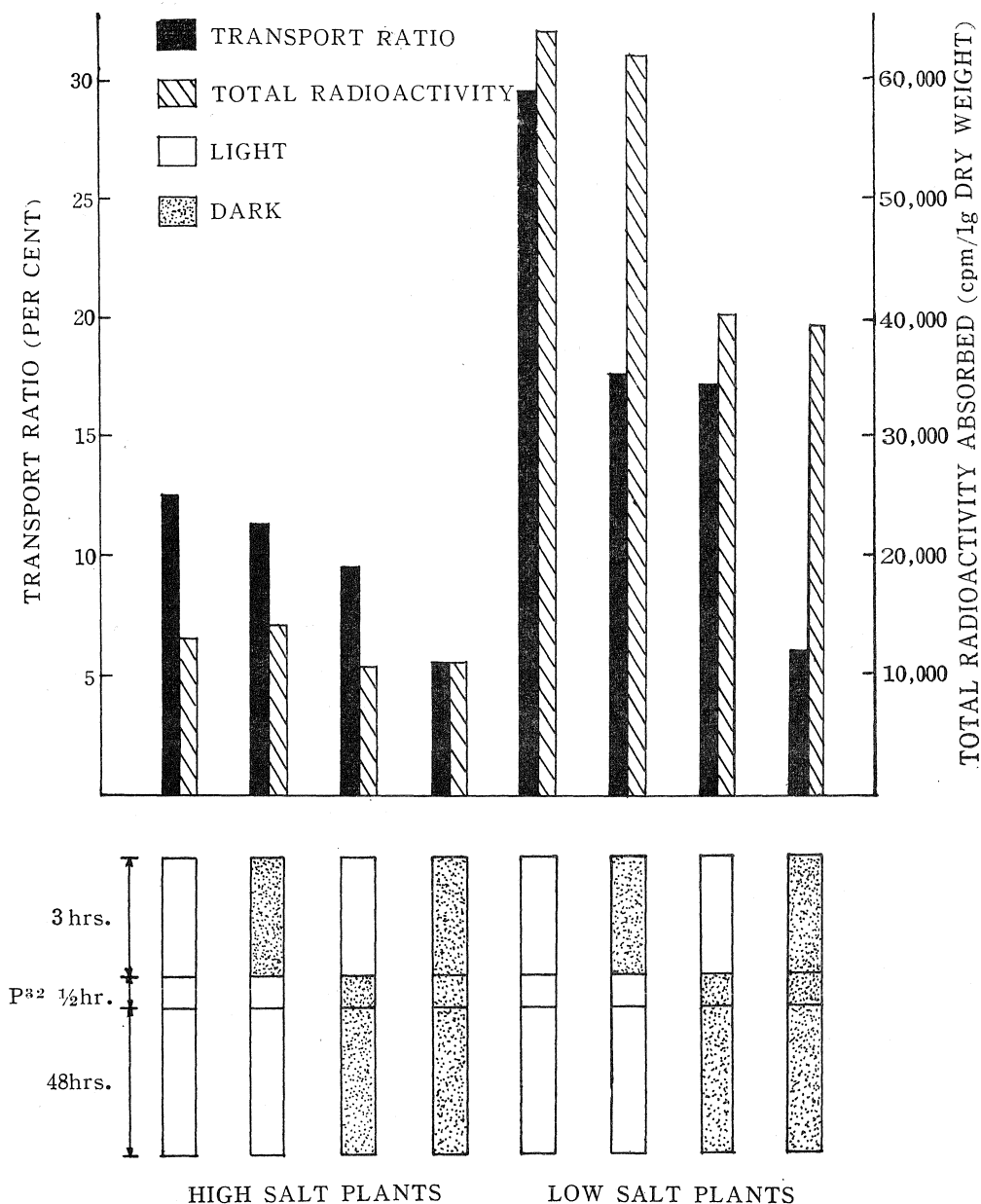


Fig. 4. Effects of light- and dark-treatment on the absorption and translocation of radiophosphorus in high and low salt plants. The values of each treatment are average values of 18 individuals of barley plants at the third leaf stage. The light-treatment was performed with artificial illumination (6,000 lux) and air temperature at 26 °C, and the dark-treatment was kept in the dark room at 25 °C. The culture solution was used 1/10 strength Hoagland's solution in low salt plants and full strength in high salt plants, and the solution temperature was 20 °C.

strength Hoagland's solution to raise in light or dark for three hours after pretreatment. Total absorbed radiophosphorus was determined immediately after the pretreatment, and transport ratio was determined after raising for three hours in light or dark. Total absorbed radiophosphorus in low salt plants was about 1.5 times greater in light than in dark (Fig. 4). It was further observed that total absorbed radiophosphorus in low salt plants, both in light and dark, was much more than in high salt plants, *i. e.*, in light about five times and in dark about four times.

Translocation of phosphorus absorbed during pretreatment also was affected by light (Fig. 4). This effect was remarkable in low salt plants. In low salt plants, transport ratio of pre-illuminated plants was higher than that of non-pre-illuminated ones, both in light or dark for three hours. In pre-illuminated plants, transport ratio of plants raised in light for three hours was higher than in dark. In non-pre-illuminated plants the same results were obtained. It is possible that light may be an important factor on the absorption and the translocation of phosphorus through its relation to food synthesis, probably to the sugar content in the plants.

On the other hand, although visible light has no direct effect on evaporation, it greatly modifies the rate of transpiration through its effects on stomatal opening. The stomates of barley plants open by the exposure to light and close in its absence. It is natural that an increase in stomatal opening should lead to increase in stomatal transpiration rate. There are the facts that the rate of absorption of water tends to parallel the rate of water loss in transpiring plants. If phosphate moves passively in water from the root upward to the shoot, as demonstrated by a number of workers (10, 11, 22, 23, 24, 26), translocation of phosphorus also should be affected by light. The results shown in Fig. 4 were quite possible basing on the influence of stomatal transpiration stream rising by light. In order to make sure of some interrelations between translocation of phosphorus and transpiration (especially the water absorption enhanced by light), the following experiments were carried out.

Effects of light intensity on translocation of radiophosphorus and water absorption. Low salt plants that absorbed radiophosphorus with pretreatment were removed into ^{32}P -free 1/10 strength Hoagland's solution (pH 6.0) to raise for three hours under various light intensity. Transport ratio and the amounts of absorbed water at each light intensity were determined as shown in Fig. 5. Transport ratio of radiophosphorus increased linearly to 6,000 lux, but in spite of increase of light intensity the subsequent transport ratio did not. On the contrary, the amounts of absorbed water increased slightly at 3,000 lux, but the subsequent increase was linear with that of the light intensity. Although there was no interrelationship between transport ratio of radiophosphorus and the amounts of absorbed water in high light intensity, there seems to be some interrelationship between them in low light intensity not more than 6,000 lux.

It has been demonstrated experimentally that the rate of water absorption is usually closely correlated with the loss of water, although water absorption tends to

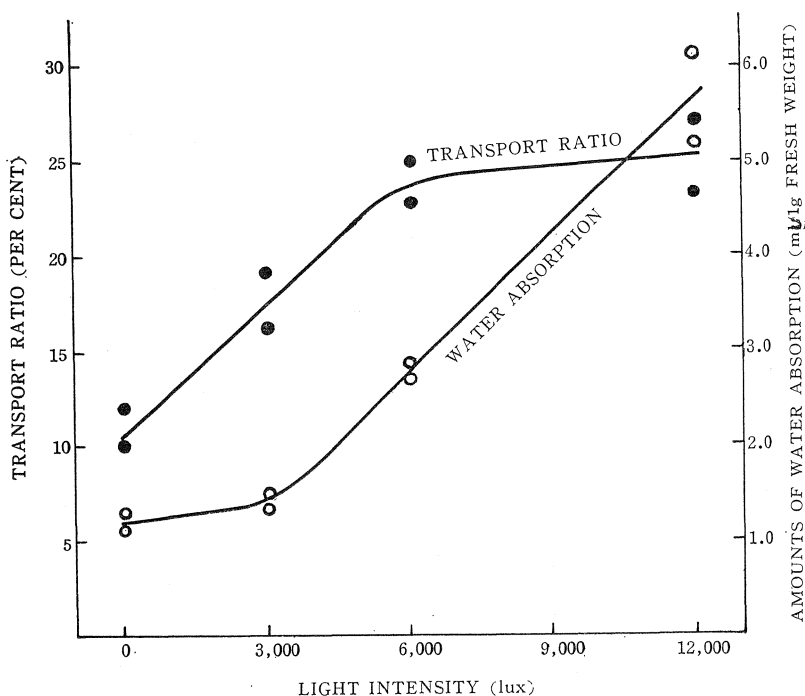


Fig. 5. Effect of light intensity on water absorption and the translocation of radiophosphorus in low salt plants. Each value was obtained from 9 individuals of barley plants at the third leaf stage. Air temperature, 24°C, 1/10 strength Hoagland's solution, 21°C.

have a lag somewhat behind the transpiration. According to KRAMER (27), this lag occurs because the pull that developed by transpiration is not transmitted instantly to the roots, but is delayed by resistance to the movement of water in various parts of its path. If this lag occurs in experiments of effect of light intensity, the rate of transpiration at each light intensity would be larger than the amounts of absorbed water. But the rising tendency of water absorption with increase of light intensity did not undergo a change. Transpiration is affected by those factors which affected the evaporation from the moist surfaces. The most important of these are humidity of the air, temperature of the plant and the air, and wind. As the effect of increasing light intensity on the rate of water absorption in barley plants maintained at a constant temperature and relative humidity is investigated, the values of water absorption obtained are regarded as the amounts of water loss by transpiration, that is, as the increase in water absorption by light that results from increased stomatal aperture. Translocation of radiophosphorus, however, was only slightly higher at 12,000 lux than at 6,000 lux.

Effects of light and humidity on translocation of radiophosphorus and water absorption. To controll the rate of transpiration with humidity of the air and darkness, low salt plants treated with pretreatment were raised for three hours under

following conditions :

Treatment A : light intensity, 6,000 lux ; relative humidity of the air, 35 % ; temperature of the air, 21°C.

Treatment B : light intensity, 6,000 lux ; relative humidity of the air, 90 % ; temperature of the air, 21°C.

Treatment C : darkness ; relative humidity of the air, 35 % ; temperature of the air, 22.5°C.

Treatment D : darkness ; relative humidity of the air, 85 % ; temperature of the air, 22.5°C.

Hoagland's solution used in all treatments was ^{32}P -free 1/10 strength one (pH 6.0) and temperature of the solution was maintained at 20°C.

The results obtained are shown in Fig. 6. Both transport ratio of radiophosphorus and the amounts of absorbed water in treatment A was the highest value compared

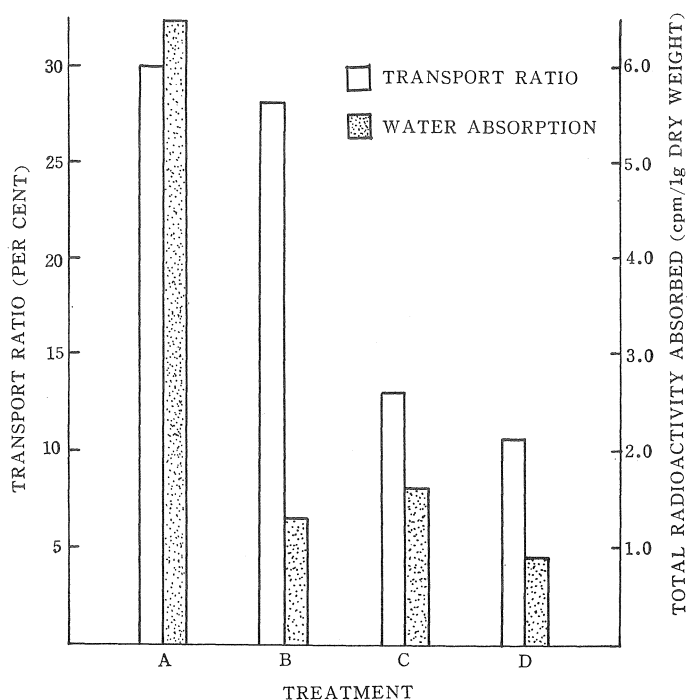


Fig. 6. Effects of light and humidity on water absorption and the translocation of radiophosphorus.

with others. But, in spite of the transport ratio in treatment B was nearly equal to that in treatment A, the amounts of absorbed water showed a decrease to 1/5 as compared with in treatment A. On the contrary, the amounts of absorbed water in treatment C were nearly equal to that in treatment B, but the transport ratio was on the decrease to about 1/2 of that in treatment B. These indicate that the translocation of phosphorus from roots to shoots may be affected by light without reference to transpiration rate.

In comparison with the results of treatment A and C, or B and D, it is observed

that transpiration rate is remarkably affected by light under low humidity of the air, but is not so under high humidity, that is, light greatly modifies the rate of transpiration on that particular condition (such as low humidity of the air) through its effects on stomatal opening.

There were a great deal of absorption of water and of transport of radiophosphorus in treatment C, compared with those in treatment D. The same results were obtained from the comparison between treatment A and B. These results suggest that translocation of phosphorus from roots to shoots may possibly be affected by transpiration above and beyond effect of light. However, there is no comparison between the degree of influence of transpiration and that of light itself on the translocation of phosphorus.

Effects of osmotic pressure of nutrient solution. The absorption of water was controlled by changing the relative humidity of the air, or by treating the plants with light and darkness as described above. Now the water absorption was altered by the increase in osmotic pressure of nutrient solution that was brought about by adding the mannitol.

Low salt plants treated with pretreatment were removed into the ^{32}P -free 1/10 strength Hoagland's solution, with various concentration of mannitol, and raised in light for three hours. The transport ratio of radiophosphorus and the amounts of water absorption were determined at each concentration of mannitol, as shown in Fig. 7. Both the transport ratio and the amount of water absorption decreased

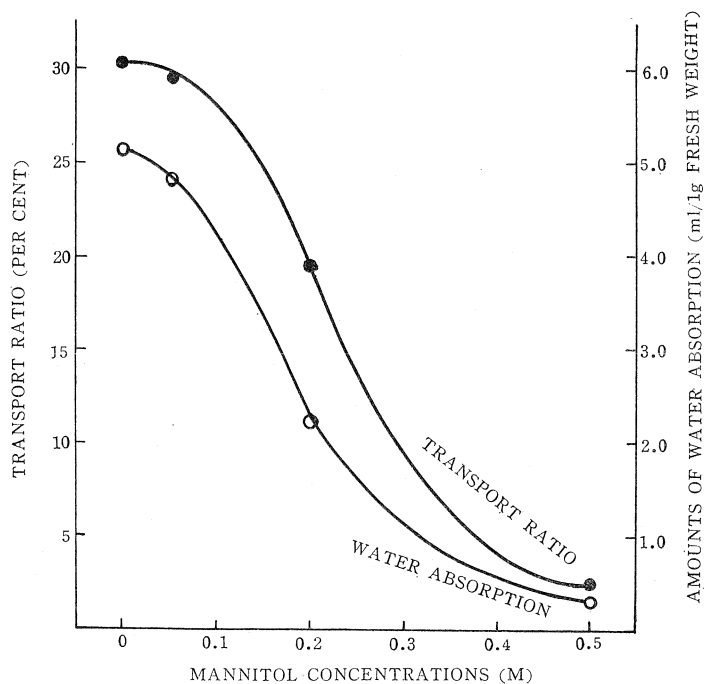


Fig. 7. Effect of osmotic pressure of nutrient solution on the water absorption and the translocation of phosphorus in low salt plants. Each curve is the average curve obtained from 36 individuals of barley plants at the third leaf stage. Light intensity, 6,000 lux, air temperature, 25°C, 1/10 strength Hoagland's solution, 20°C.

according to the increase of molar concentration of mannitol in the nutrient solution. The transport ratio at 0.2 M of mannitol was about 64 per cent of the control (0.0

M) and about 10 per cent was shown at 0.5 M of mannitol. On the other hand, the amounts of water absorption at 0.2 M of mannitol was about 44 per cent of the control and about 2 per cent as at 0.5 M . The upward translocation of phosphorus in low osmotic pressure of external solution was slightly affected, as compared with the rate of water absorption. On the contrary, in high osmotic pressure of external solution the upward translocation of phosphorus was markedly affected as compared the rate of water absorption. Wilting of the shoots were seen in the nutrient solution containing 0.5 M mannitol. The greater the amounts of water absorption, was, the more phosphorus was transported from roots to shoots, although the amounts of transported phosphorus and water absorption were not proportional.

DISCUSSION

There has been many investigations on the role of transpiration in the absorption and translocation of mineral salts in plants. HYLMO (22) and WRIGHT and BARTON (46) reported that the movement of ions from external solution into roots and, in turn, into the shoots, is dependent on the rate of water absorption and of transpiration, and SMITH (38) observed that increasing the rate of transpiration of corn and pea seedlings increased the absorption and translocation of radiophosphorus to the shoots. HOAGLAND and his colleagues (14), however, emphasised the importance of salt accumulation in the root cells as the first step in salt absorption, and claimed that although increased transpiration may sometimes speed up the transport of salt from roots to shoots, it has no direct effect on movement of salt from the external solution into the root xylem. According to the review of RUSSELL and BARBER (36), there are two conflicting views on the mechanisms whereby transpiration can affect the overall process by which ions pass upwards through intact plants: *Review A*, the transfer of ions across the root symplast to the vascular stele is an active process dependent on the release of energy through metabolic processes, and the effect of transpiration is to accelerate the movement of ions in water after they have been released into vascular tissues (2, 4, 5, 7, 14, 18, 37). On the other hand, *Review B*, ions move passively in water from the outer surface of the root upward to the shoot (10, 11, 22, 23, 24, 26).

From effects of light intensity on the rate of water absorption and translocation of radiophosphorus from roots to shoots, there seems to exist some inter-relationships between them in low light intensity not more than 6,000 lux (Fig. 5). It was considered as the increase in water absorption by light from increased stomatal aperture. The rate of water absorption in stomatal transpiration was controlled by light and humidity of the air (Fig. 6), so that the rate of water absorption was greatly modified by light and humidity of the air. And yet, the transport ratio of phosphorus was remarkably affected by light, but was hardly by humidity of the air, that is, the translocation of phosphorus from roots to shoots may be

affected by transpiration above and beyond effect of light, although there is no comparison between the degree of influence of transpiration and of light itself on the translocation of phosphorus. PETRITSCHER (34) found that the concentration of xylem sap did not decrease in proportion to the daily increase in the rate of water movement, *i. e.*, the more rapid the movement of the transpiration stream was, the more salt moved in it, although the amounts of salt and water absorbed were not proportional. It was observed, in experiments on effect of osmotic pressure of nutrient solution, that the greater the amounts of water absorption was, the more phosphorus was transported from roots to shoots, although the amounts of transported phosphorus and of water absorbed were not proportional. Wilting of shoots were seen at 0.5 *M* of mannitol contained in nutrient solution, and the transport of phosphorus to shoots at this point was very slight. These observations indicate that it is necessary for translocation of phosphorus from roots to shoots to flow a proper amount of water from roots to shoots.

If seedlings of barley plants are grown in a limited volume of a standard inorganic nutrient solution (such as full strength Hoagland's), the excised roots are rendered much more activity in subsequent absorption of salt than those which are excised from plants grown with a full and renewed supply of nutrition. HOAGLAND and BROYER (15), give the following explanation: "When the volume and concentration of the nutrient solution does not keep place with the translocation of salt from root to growing shoot, as a consequence the root suffers partial depletion of its salt content low salt root tissues developed under these experimental conditions also have a high sugar content, a point to be discussed presently". Thus, in these cases, the roots of plants growing in water respond to a reduced concentration of total salt, not only by an increase in the relative absorption of the salt, but by an actual increase in their sugar content. To obtain more precise data on these points, RUSSELL and SHORROCKS (37) measured the effect of varying transpiration rate, concentration of external solution, and salt status of the plant on uptake of both phosphate and rubidium by barley plants. With low salt plants and dilute external solutions, uptake was independent of the transpiration or only slightly affected. With high salt plants and more concentrated external solution there was a closer correlation on salt absorption, probably modified by the age, metabolic condition, and salt content of the plant, and especially of the roots (28). In young and actively growing roots, which are grown in the low salt condition, accumulation in root cells and active transport into the xylem are the dominant processes and increased water absorption has little effect on salt absorption, except possibly indirectly by reducing the concentration in the xylem sap. In older roots, especially if high in salt, less accumulation occurs and there probably is less active transport into the xylem and it is possible that some salt is carried into the xylem in the transpiration stream independent of the active transport mechanisms. The possibility of such passive movement in older roots is increased by the concept that 10-30 per cent of root volume

is "*free space*", into and out of which, ions can move by diffusion (8,9,19). Therefore, it is possible that low salt plants treated with pre-illumination for 48 hours may have the highest content of sugars than low salt plants kept in darkness for 48 hours and high salt plants in light or dark (Fig. 4). Thus absorption of phosphorus in the root was affected by light, probably through its relation to the sugar content in the plants. In the same way, light was found to be an important factor determining the rates of translocation of phosphorus with no relation to transpiration stream (Fig. 4 and 6).

It was found with low salt plants that the large differences in transpiration rate have little influence on salt movement to the shoot; on the other hand, with high salt plants, which show a low initial capacity for salt absorption, variations in rate of transpiration had a marked effect on salt movement. These agree with the opinion of BROYER and HOAGLAND (7) that the over-all transfer of ions from an external medium to the shoot is not controlled by transpiration, although with high salt plants some step in this transfer (which may become limiting) can be influenced by the rate of transpiration. This independence of transpiration and salt uptake or salt transfer, at least under some conditions, makes it unlikely that salt moves into the xylem through the free space. A factor apparently ignored in all considerations of the route and mechanism of movement into the xylem is that all nutrients do not occur in the xylem sap in the inorganic form in which they are absorbed from the exterior. In bleeding sap collected from a number of species which had been growing in culture solution containing radiophosphorus, three radioactive compounds were detected by chromatography (41). One of these was inorganic phosphate and the other was identified as phosphoryl choline (32). Of the radiophosphorus in the bleeding sap, up to 6 per cent in barley and 20 per cent in tomato was present as this compound. This might be taken as an indication that some phosphorus is transported through the plants as phosphoryl choline; but in later work (30), choline, added to the culture solution in which plants were growing, increased the phosphoryl choline in the roots, but decreased the transport of phosphorus to the shoot. All the nitrogen in the xylem sap of many plants occurs in organic combination (3). This clearly means that in its passage across the root these elements have been exposed to the action of a sequence of enzymes. Our knowledge of cell structure and function is not sufficient to enable us to say whether such changes could be brought about during passage of the element through the free space of a cell or whether accumulation of the element into some cell organelle is necessary for these changes. It appears likely, however, that transport of nutrient from roots to shoots cannot ignore the concurrent metabolic changes the absorbed nutrients may undergo. The facts that transport ratio was remarkably affected by temperature (Fig. 3) and slightly by hydrogen ion concentration (Fig. 2), suggest that metabolic processes occur in over-all processes of ion translocation from roots to shoots. It is possible that light on the translocation of phosphorus may be an important factor through its relation to food syntheses, especially sugar contents, as

effects on the absorption of phosphorus in roots. The cause was not cleared whether sugar content rising by light affected on an active process depend on the release of energy through metabolic processes for the transfer of phosphorus across the root symplast to the vascular stele, or whether light affected on phosphorus uptake from vascular tissues into mesophyll.

SUMMARY

1. The effects of external factors, such as hydrogen ion concentration, temperature, and light, on the transport of phosphorus from roots to shoots, were investigated with the young barley plants at the third leaf stage which had been grown in full or 1/10 strength Hoagland's solution.

2. The results was obtained in low salt plants that most of mobile phosphorus fraction which the roots absorbed during thirty minutes was transported from roots to shoots within three hours, but the subsequent increase was very slight. The same results were obtained in high salt plants although the rate of translocation of phosphorus was lower than in low salt plants.

3. The transport of phosphorus from roots to shoots for three hours was not greatly affected by the pH of external solution, but the rate of transport at pH 6.0 were slightly high than at other pH. In experiments of effect of temperature, the optimum curve with maximum values at 20°C was obtained. These results show that the translocation of phosphorus from roots to shoots may be affected by metabolic processes.

4. The plants exposed with artificial illumination (6,000 lux) for forty eight hours absorbed larger amounts of phosphorus during thirty minutes than non-illuminated plants, and total absorbed radiophosphorus in low salt plants, both in light and dark, was much more than in high salt plants. The translocation of phosphorus absorbed during thirty minutes was also increased by pre-illumination or light-treatment after thirty minutes.

From these results, it is possible that light on the absorption and translocation of phosphorus may be an important factor through its relation to food synthesis, probably to the sugar content in the plants.

5. The idea that absorption and translocation of phosphorus were affected by light, was quite within the bounds of possibility basing on the influence of transpiration stream causing by light. To make sure of some interrelations between translocation of phosphorus and transpiration (especially the water absorption enhanced by light), influences of light intensity, humidity and the osmotic pressure of nutrient solution on transport of phosphorus were investigated.

Consequently, light was found to be an important factor determining the rates of translocation of phosphorus with no relation to transpiration stream. The translocation of phosphorus from roots to shoots, however, may be affected by transpira-

tion above and beyond effect of light, although there is no compararison between the degree of influence of transpiration and that of light itself on the translocation of phosphorus. It was shown that it is necessary for translocation of phosphorus from roots to shoots to flow a proper amount of water from roots to shoots.

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