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PHOSPHORUS DEFICIENCY ENHANCES MOLYBDENUM UPTAKE BY TOMATO PLANTS

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ABSTRACT: Water culture experiments are described which provide conclusive evidence that Mo uptake by tomato plants is markedly enhanced by P deficiency. In a longterm experiment, which ran for 11 days, in marked contrast to the uptake of other nutrients, a three fold higher Mo uptake rate was observed after only four days of withdrawal of P from the nutrient medium. In contrast to the gradual increase in pH of the nutrient medium of the plants supplied with P, the pH in the medium of the -P plants fell. Throughout the growth of these plants net H^+ efflux could be accounted for by excess cation over anion uptake, indicating that organic acid extrusion plays no major role in the observed fall in pH.

Further evidence that Mo uptake is enhanced in P deficient tomato plants is provided in short-term nutrient solution experiments (1h and 4h) using radioactive molybdenum (^{99}Mo). Compared with P sufficient plants, the uptake rates of ^{99}Mo by P deficient plants were three to five times higher after 1h and nine to twelve times higher after 4h. Resupplying P during the uptake periods to deficient plants reduced the uptake rate of ^{99}Mo to values similar to those of P sufficient plants. It is concluded that the uptake of molybdate occurs via phosphate binding/ transporting sites at the plasma membrane of root cells. Further support for this conclusion comes from exchange experiments with non-labelled molybdenum, which show a much larger amount of ^{99}Mo exchangeable from the roots of P deficient plants.

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INTRODUCTION

Higher plants respond to a lack of phosphorus (P) by a variety of morphological and physiological changes. Both, root elongation growth (1) and root hair proliferation (12) may be enhanced. In a number of plant species the release of organic acids and particularly citric acid is induced from the roots (13,25,19). As much as 23% of the total dry weight of white lupin plants may be released as citric acid and precipitated as calcium citrate in the rhizosphere of plants grown in a P deficient calcareous soil (8). For other plant species P deficiency is associated with enhanced activities of extracellular phosphatase in the rhizosphere (9,4). All these responses increase the ability of P deficient plants to acquire P from the soil.

Another response of some plant species to a lack of phosphorus is to acidify the nutrient medium or rhizosphere by H^+ excretion (net proton efflux). This response to P deficiency which occurs even when plants are supplied with NO_3-N, is associated with a shift from excess anion over cation uptake by P sufficient plants to an excess cation uptake by the deficient plants (16,27,18,22).

In a recent serial harvest experiment to investigate the response of tomato plants to P deficiency, we observed that molybdenum (Mo) uptake is greatly enhanced when P is omitted from the nutrient solution. In this paper we report the findings of this experiment together with a short-term experiment using labelled Mo (^{99}Mo) to study the kinetics of Mo uptake in P sufficient and P deficient tomato plants in the presence or absence of P in the nutrient medium. By investigating the kinetics of exchange of labelled Mo with non-labelled Mo after termination of uptake we have also been able to obtain further information on the binding and compartmentation of Mo in root cells of P deficient and P sufficient tomato plants.

MATERIALS AHD METHODS

Serial Harvest Experiment

Plant Cultivation: Ten day old tomato plants (*Lycopersicon esculentum* var. Ailsa Craig) were transferred to a circulating NFT (nutrient film technique) system in a controlled environment chamber (25°C day and night, photoperiod 14 hours at 620 $\mu Em^2/s$) This system consisted of four similar units each comprising a tank holding 10 litres of nutrient solution which was circulated, via a pump, along two troughs both of which supported ten plants. Plants received half strength complete nutrient solution (see below) for a four day adaptation period after which the

number of plants per trough was reduced to five. At the end of a further four days in full strength solution, time zero of the experiment, plants were subjected to the two treatments either with P ("+P"= 0.5 mM) or without P ("-P") for 14 days. Two of the four units received a complete nutrient solution ("+P") and the remaining two received the solution without phosphate ("-P"). The composition of the full strength complete nutrient solution was as follows: (mM) 2 $Ca(NO_3)_2$, 0.5 KH_2PO_4, 0.5 K_2SO_4, 1 $MgSO_4$, (μM) 50 FeNaEDTA, 30 H_3BO_3, 2.5 $CuSO_4$, 7.85 $MnSO_4$, 0.9 $ZnSO_4$, and 0.5 Na_2MoO_4. In the "-P" solution 0.5 mM KH_2PO_4 was omitted and replaced by 0.25 mM K_2SO_4. Sulphate was used as a compensating ion as its effect on the uptake of other ions is relatively low. The nutrient solutions were adjusted to pH 6 using a saturated, freshly prepared and filtered solution of $Ca(OH)_2$. In order to maintain the nutrient concentrations throughout the experiment the solutions were renewed daily.

Harvest Procedure: Serial harvests of four plants per harvest were taken from both treatments at day 0, 4, 7, 11, and 14 of the experiment. Plants were separated into roots and shoot and fresh and oven dried (24 hours at 90°C) weights of individual plants were recorded.

Plant Analyses: Dry plant parts were bulked according to treatments and prepared for mineral analyses by ashing at 500°C followed by digestion in HCl (26). Total K, Ca, Mg, P, Fe, Cu, Zn, Mn, B, and Mo were determined on an ICP (ARL 3580).

Total N and S analysis were carried out on the dried and ground plant material. Nitrogen was estimated using a CHN-autoanalyser (Carlo Elba Model 8806) and S was determined using an induction furnace (Leco HF 10).

Xylem Sap Collection and Analysis: Xylem sap was collected after detopping the plants according to the method described by Armstrong and Kirkby (2). The chemical analysis of bulked and diluted samples was carried out on an ICP as described above.

^{99}Mo Experiment

Plant Cultivation: Sixteen day old tomato plants, precultured in a peat/quartz sand mixture (1:1,v/v), were transplanted into 5-L plastic pots (4 plants/pot) which were placed in a growth chamber (22°/20°C day/night temperatures, 16/8 h day/night light regime, light intensity of 220 $\mu Em^2/s$, Sylvania fluorescent tubes FR 96 T). The plants were supplied with 5-L aerated nutrient solution of the same composition as used for the serial harvest experiment. For the first three days,

only a half-strength nutrient solution was provided in order to allow the plants to adapt to the new environmental conditions. For the next four days all plants were supplied with a full-strength nutrient solution. Solutions were changed daily.

On day 24, the beginning of the preculture period, twelve pots were supplied with a minus P ("-P") solution and the remaining twelve with the same solution as before ("+P"). On this day the plants were at a comparable stage to day 0 of the "serial harvest experiment". The period of preculture lasted for six days prior to the short-term uptake experiments with labelled Mo (^{99}Mo). At this time the plants in the "-P" treatment were showing phosphorus deficiency symptoms, including darker green leaves than the controls.

Uptake of ^{99}Mo was investigated over 1 and 4 hour period in plants precultured with or without P as described above, and from nutrient solutions in which P was present or absent. The compositions of the nutrient solutions used in the short-term uptake studies were the same as those used during preculture. The status of P supply during the uptake experiments is indicated as "+Pu" for plants with P supplied as "-Pu" for plants without supply.

The experimental setup of the ^{99}Mo experiment may be summarized as follows:

I. Preculture	"+P"		"-P"	
-for six days				
II. Treatment during the				
uptake period of ^{99}Mo	"+P"	"-P"	"-P"	"+P"
III. Coding				
used in the text	+P+Pu	+P-Pu	-P-Pu	-P+Pu

In both uptake experiments (1h and 4h) there were three replicates for each treatment. Vertical bars in the figures indicate standard deviation.

Short-Term Uptake Experiments: Prior to transfer to the nutrient solution containing ^{99}Mo the roots were dipped four times into distilled water (three seconds for each time of dipping) to remove adhering preculture solution. Each uptake period in the labelled nutrient solutions was terminated by rinsing the roots with distilled water for one minute, followed by dipping the roots four times into distilled water (each time for a period of two seconds) to remove adhering labelled

solution. Afterwards the roots were transferred into 0.5 L cold (+10°C) exchange solution containing only 10 μM non-labelled Mo [$(NH_4)_6Mo_7O_{24}$].

For the 1-hour-experiment the plants were removed from the exchange solution after 15 minutes and, for a further one minute, the solution was allowed to drip from the roots back to the pot. Finally the plants were separated into shoots and roots for fresh weight determination.

For the 4-hour-experiment the exchange solution was changed three times. Solution A represents the first 7.5 minutes of exchange, solution B the second 7.5 minutes and solution C resulted from another 15 minutes of exchange. Thereafter the roots and shoots were separated for fresh weight determination.

After drying the plant material at 65°C for 24 hours, dry weight was determined and the samples prepared for ^{99}Mo measurements.

Following filtration the exchange solutions were dried in a rotary evaporator and the residue dissolved by treating it once with 5 mL HCl (1%) and twice with 5 mL distilled water. ^{99}Mo activity was determined in the bulked concentrated exchange solution.

Production and Measurement of ^{99}Mo: 16.2 mg $(NH_4)_2MoO_4$ (Aldrich Chemical) were activated for 24 hours at a flow density of 10^{14} neutrons cm^2/s and a surface temperature of 20°C at the nuclear reactor (KFA) Julich, Germany.

A stock standard solution containig ~48 MBq total radioactivity was prepared from this activated salt, 52% of the radioactivity originated from ^{99}Mo (half life, $T_{0.5}$: 66.6 hr) and 48% from ^{99m}Tc ($T_{0.5}$: 6.03 hrs). A sample representing 9.6 μg of labelled Mo (^{99}Mo) was taken and used in all measurements as internal standard.

Measurements were carried out using an automatic gamma sample changer (LB MAG 510, Berthold). Two windows were set on the spectra, one for ^{99m}Tc at 150 (+/-100) keV and the second for ^{99}Mo at 760 (+/-300) keV. The counting efficiency was determined with a Ge(Li)-detector (Getac), coupled to a 4096 channel analyser (TN-1710, Tractor Northern) with an incorporated microcomputer (LS I-11) which allowed the on-line evaluation of the spectra.

RESULTS

Serial Harvest Experiment: Witholding P from the nutrient medium markedly depressed P concentrations in shoot and root tissues at all harvests

TABLE 1. Dry weights and P concentrations of shoots and roots obtained in the serial harvest experiment as affected by P supply and day of harvest. Plants cultivated with P (+P = 0.5mM) or without P (-P).

Day of Harvest	Treat-ment	Dry Weight (g plant^{-1}) Shoot	Root	P Concentration (mg P g^{-1} dry wt.) Shoot	Root	P Deficiency Symptoms
0	+P	0.23	0.03	7.5	14.0	
4	+P	0.80	0.12	9.7	14.6	
	-P	0.76	0.14	3.3	5.6	mild
7	+P	1.80	0.26	10.4	15.4	
	-P	1.34	0.29	2.1	3.2	strong
11	+P	4.76	0.61	9.3	14.0	
	-P	1.73	0.40	1.3	2.6	necrosis
14	+P	9.39	1.28	9.1	13.6	
	-P	1.96	0.49	1.2	2.3	severe necrosis

whilst having a much lesser effect on growth in the early stages of the deficiency (Table 1). After only four days of P deprivation when growth was scarcely affected and the plants were showing only mild deficiency symptoms including darker green leaves, the P concentrations of the deprived plants were decreased to about one third of the controls. Growth of roots was less affected by the deficiency than that of shoots and a depression in root growth was not observed until the third harvest at day seven. Phosphorus deficiency symptoms became progressively more intense as P concentrations declined in shoot and root tissues as diluted by growth.

For plants supplied with the complete nutrient solution a steadily increasing daily net release of OH^- into the solution was measured (Fig. 1). By contrast for plants deprived of P, net release of OH^- occurred only up to day three and thereafter a daily net release of H^+ took place until the end of the experiment. For both treatments and for each of the four growth periods the differences between

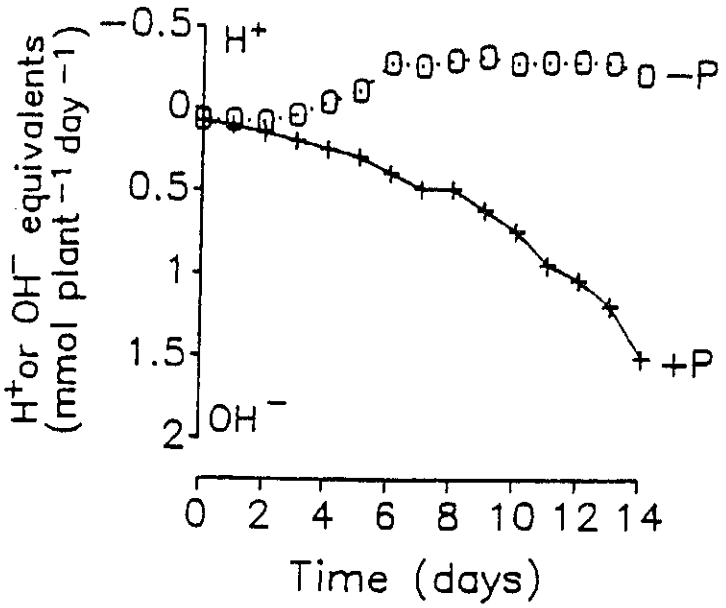

FIGURE 1. Influence of P nutritional status on daily net H^+ or OH^- release per plant as measured by titrations of nutrient solutions obtained from the serial harvest experiment. Plants cultivated with P (+P = 0.5mM) and without P (-P).

cation (K, Na, Ca, Mg) and anion (N, S, P) uptake by the plants were closely balanced by net OH^- or H^+ equivalents released into the nutrient media. This is demonstrated by the cation-anion balance sheet shown in Table 2. For the P sufficient plants the calculated net release of OH^- from the excess anion uptake is in close agreement with the determined value. Analogously the net release of H^+ by the P deficient plants approximates to the excess cation uptake by these plants. This excess was caused by a stronger decrease in anion than cation uptake. The decrease in anion uptake was mainly the result of a much lower NO_3 uptake and its dominating role (~90%) in total anion uptake. Of the cations, the uptake of Mg was much less decreased than either Ca or K.

The striking effect of P deficiency in enhancing Mo uptake rate as compared with other nutrients is shown in Figure 2. For the first three growth periods the Mo uptake rate was about three times greater than that of the control (+P). None of the uptake rates of the other nutrients approached anything like this spectacular increase. Indeed the uptake rates of most nutrients were depressed by P deficiency. Only in the case of Zn for the first and second growth period, S and Fe

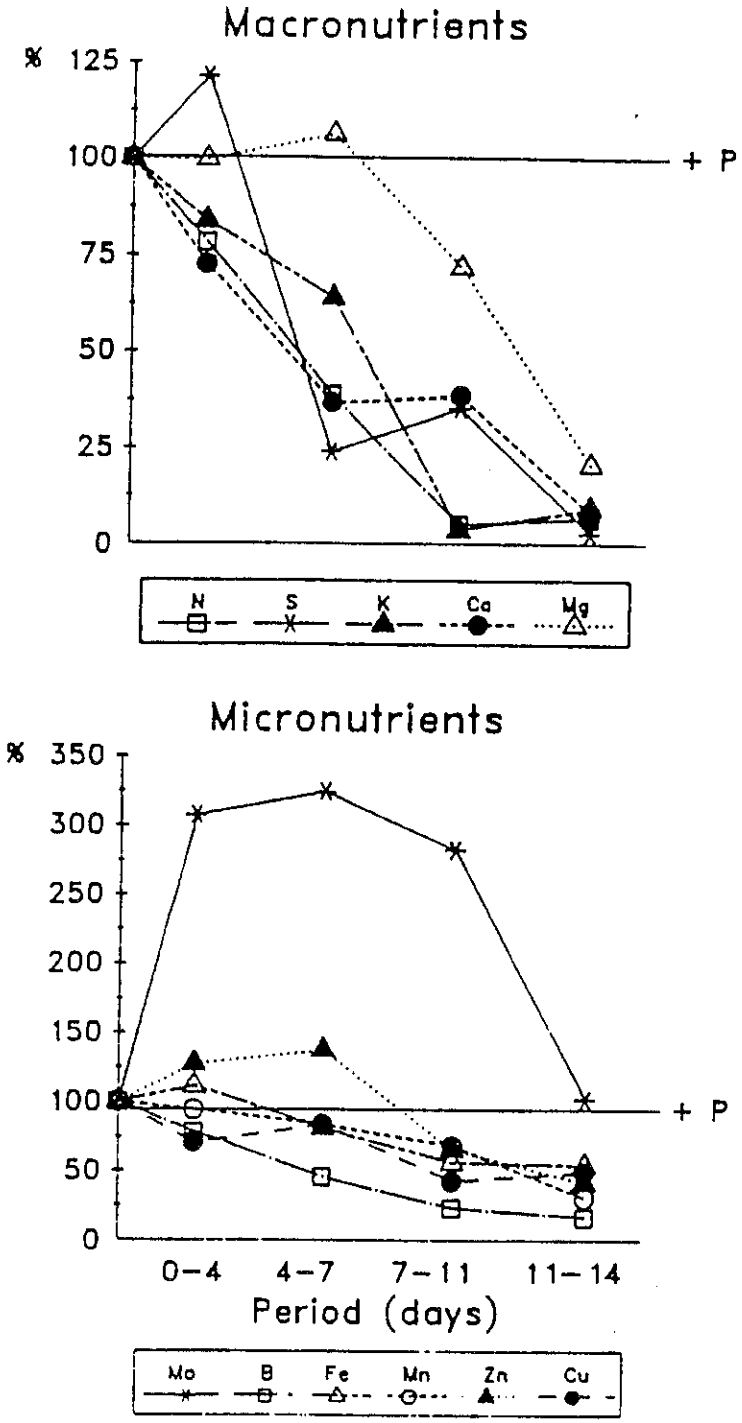

FIGURE 2. Influence of P deficiency on uptake rates of macro- and micro-nutrients per unit root dry weight per day between harvests. Uptake rates of -P-plants are expressed as relative values with uptake rates of the control (+P) set at 100% for each nutrient. Plants cultivated with P (+P = 0.5mM) and without P (-P).

TABLE 2. Uptake of Cations and Anions by Plants Supplied With P (+P = 0.5 mM) or Without P (-P) Between Harvests 2 and 3 (Day 4 to Day 7) of the Serial Harvest Experiment. Excess anion or cation uptake is compared with OH^- or H^+ release as measured by titration.

P Status	K	Ca	Mg	Σ Cat	N	S	P	Σ An	A-C	OH^-	H^+
	(μeq g^{-1} root fresh wt. day^{-1})										
+P	160	139	55	354	390	26	37	453	99	103	
-P	103	51	59	213	153	6	1	160	-53		54

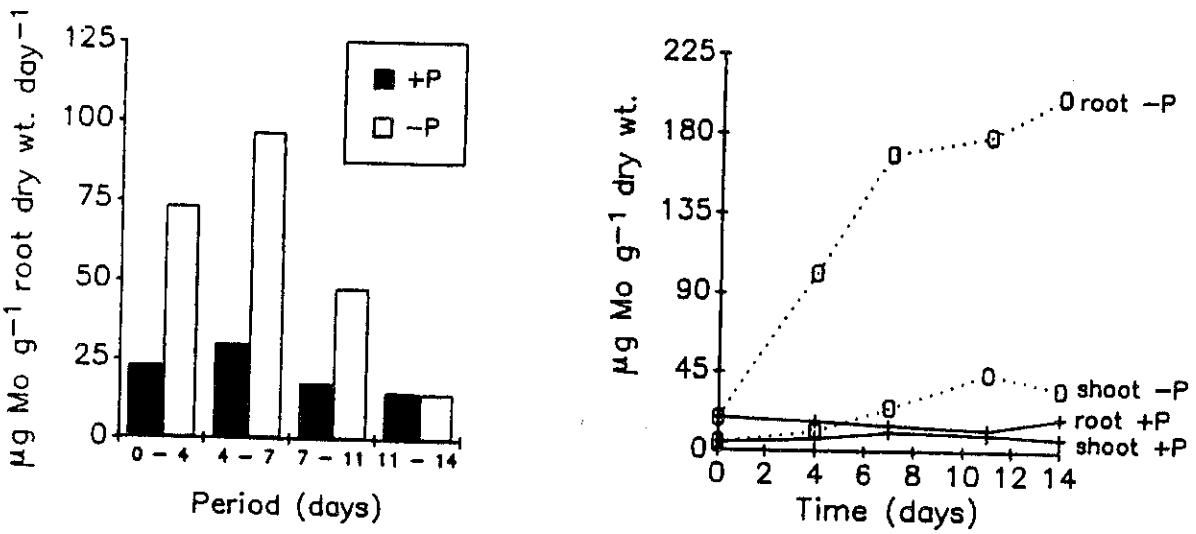

FIGURE 3. Uptake Rates and Concentrations of Mo in Shoots and Roots of Tomato Plants Grown in Nutrient Solutions With P (+P = 0.5 mM) or Without P (-P). Results calculated as an average between two harvests according to Williams (1948).

in the first growth period and Mg in the second growth period uptake rates were somewhat increased.

Absolute values of the enhanced Mo uptake given in Figure 3 show that the highest Mo uptake rate of P deficient plants occurred during the second growth period (days 4-7). The much higher amount of Mo taken up by the P deficient plants was mainly stored in the roots, giving rise to concentrations more than ten times those of the roots of the P sufficient plants (Fig. 3). Accumulation of Mo in the shoots of the P deprived plants, although only about 20% of the concentrations in the roots, were about five times greater than those of the shoots of P sufficient plants (+P).

The transport of Mo and other nutrients to the shoot as measured by rates of xylem sap exudation is shown in Table 3. In contrast to other nutrients, with the exception of Zn, the rate of Mo transport was increased under P deficiency. Even at the onset of P deficiency on day 4 the rate of Mo transport was doubled. Under P deficiency the transport of K and Ca were depressed whereas Mg was little affected. After eleven days of P deficiency the transport of all nutrients was depressed as might be expected, but Mo was less affected than the others.

^{99}Mo Experiment: The effect of P nutritional status (preculture +P or -P) on shoot and root dry weight is shown in Figure 4. Compared with the P sufficient plants (+P+Pu; +P-Pu) the P deficient plants (-P-Pu;-P+Pu) were lower in shoot dry weight by about 20% whereas root dry weights were similar.

Uptake of ^{99}Mo was considerably affected by P treatment and each of the four treatments had a characteristic pattern of uptake which was similar after 1 or 4 hours (Fig. 5). For the P sufficient plants (+P) ommission of P during the uptake period (+P-Pu) only slightly increased ^{99}Mo uptake. In the case of the P deficient plants, however, omission of P during the uptake period (-P-Pu) resulted in a 3-5 times (1h) or 9-12 times (4h) higher ^{99}Mo uptake as compared with the P sufficient plants. Resupplying P to the P deficient plants (-P+Pu) for the ^{99}Mo uptake period, decreased the ^{99}Mo uptake to values comparable to those of the P sufficient plants without external P supply (+P-Pu).

After an uptake period of 1 hour only a small amount of the ^{99}Mo taken up was translocated to the shoots regardless of P treatment (Fig. 5) and after a 4 hour uptake period this amount increased about fourfold. By contrast, after the 4 hour uptake period the amount of ^{99}Mo in the roots had increased only in P deficient plants in the absence of an external P supply (-P-Pu). Obviously the capacity of

TABLE 3. Influence of P Nutritional Status on the Translocation Rate of Nutrients in the Xylem Exudate to the Shoot. Results calculated from xylem sap concentrations and exudation rates obtained during the serial harvest experiment and expressed as µmol or mmol per kg root fresh weight per hour. Plants cultivated with P (+P = 0.5 mM) or without P (-P).

Day of Harvest	Mo		Zn		K		Ca		Mg	
	+P	-P	+P	-P	+P	-P	+P	-P	+P	-P
	µmol						mmol			
4	0.64	1.35	11.9	14.9	8.6	8.5	5.2	2.6	2.2	2.8
7	0.27	1.57	8.9	15.7	10.8	4.2	6.8	1.6	2.7	2.5
11	0.73	0.51	7.1	4.3	8.2	1.3	5.5	1.0	2.5	1.0

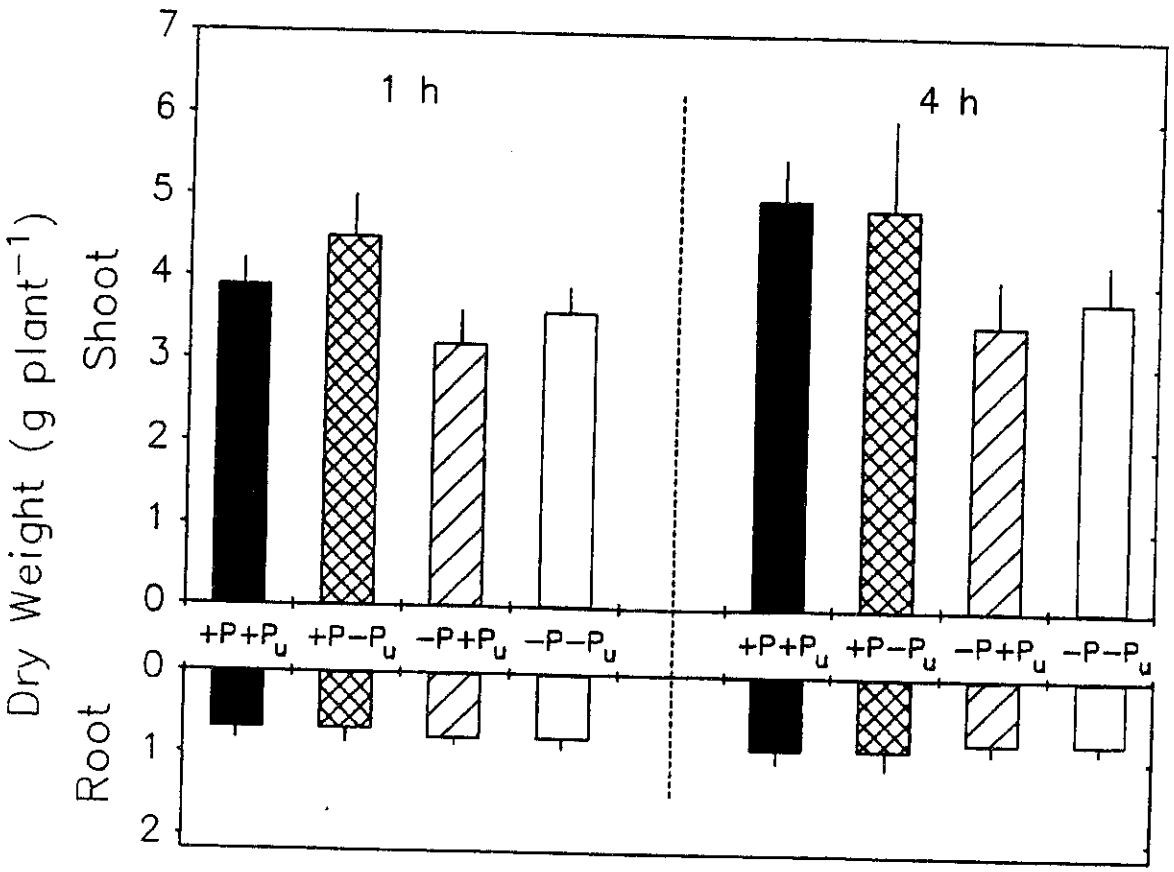

FIGURE 4. Shoot and Root Dry Weights of P Sufficient and P Deficient Plants (Preculture: +P and -P) of the ^{99}Mo Experiment Used for the Short-Term Uptake Studies (1h and 4h) in the Presence (+P_u = 0.5 mM) or Absence (-P_u) of Phosphate.

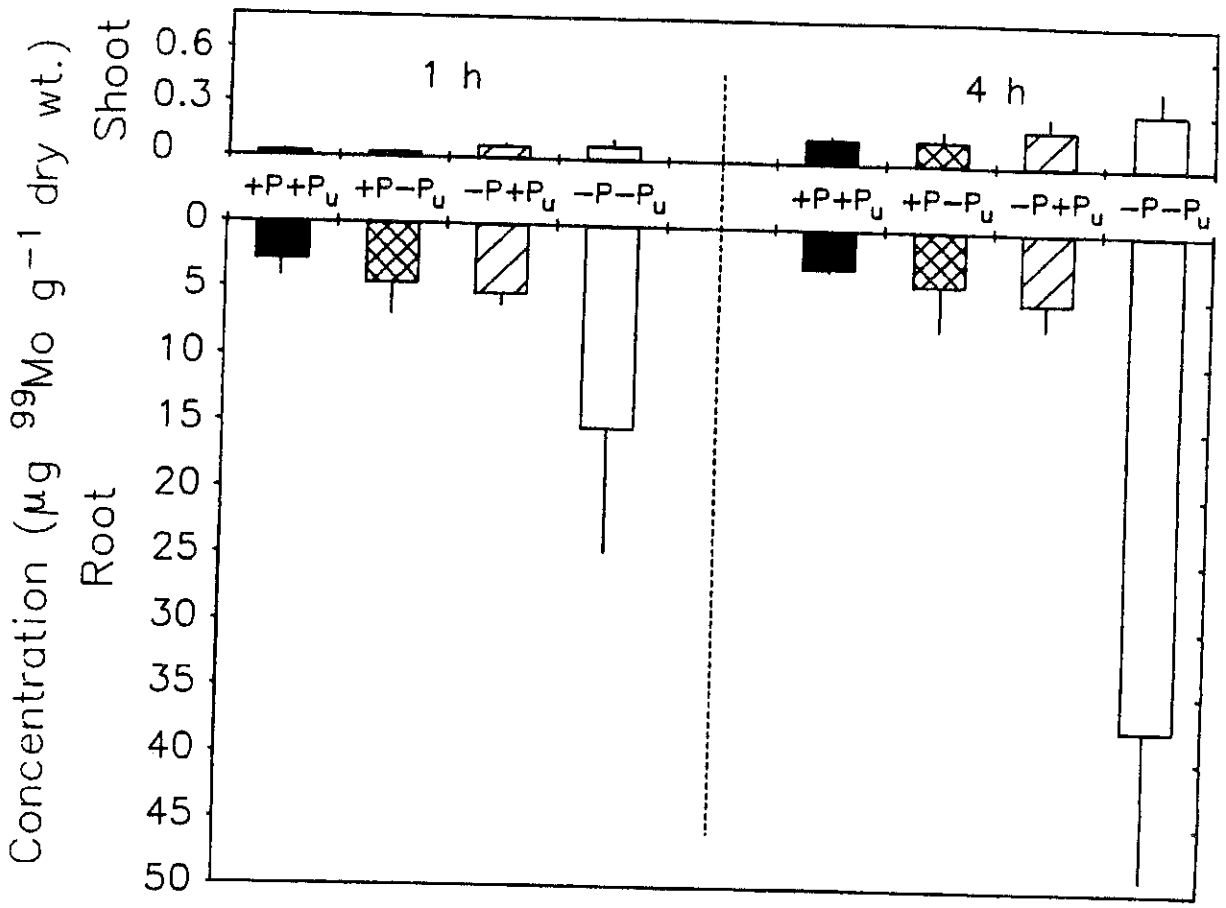

FIGURE 5. ^{99}Mo Concentrations in Shoots and Roots of P Sufficient and P Deficient Plants as Affected by Presence (+Pu = 0 5 mM) or Absence (-Pu) of Phosphate During the Uptake Periods of ^{99}Mo. Root concentrations include exchangeable ^{99}Mo. Note the different scales for root and shoot ^{99}Mo concentrations.

the roots to accumulate ^{99}Mo must have been almost saturated during the first hour of uptake except in P deficient plants without P in the nutrient medium over the uptake period.

In order to characterize the localization and binding state of ^{99}Mo in the roots, a study was made of the kinetics of exchange of ^{99}Mo in the roots with non-labelled Mo (10 µM) from the external solution. The results were similar for both uptake periods. Only the results of the 4-hour-experiment are therefore shown (Fig. 6). In principle, the amount of ^{99}Mo exchanged reflects the differences in ^{99}Mo content of the roots, i.e. the ^{99}Mo exchange was several times higher in the P deficient plants when P was also ommitted from the external

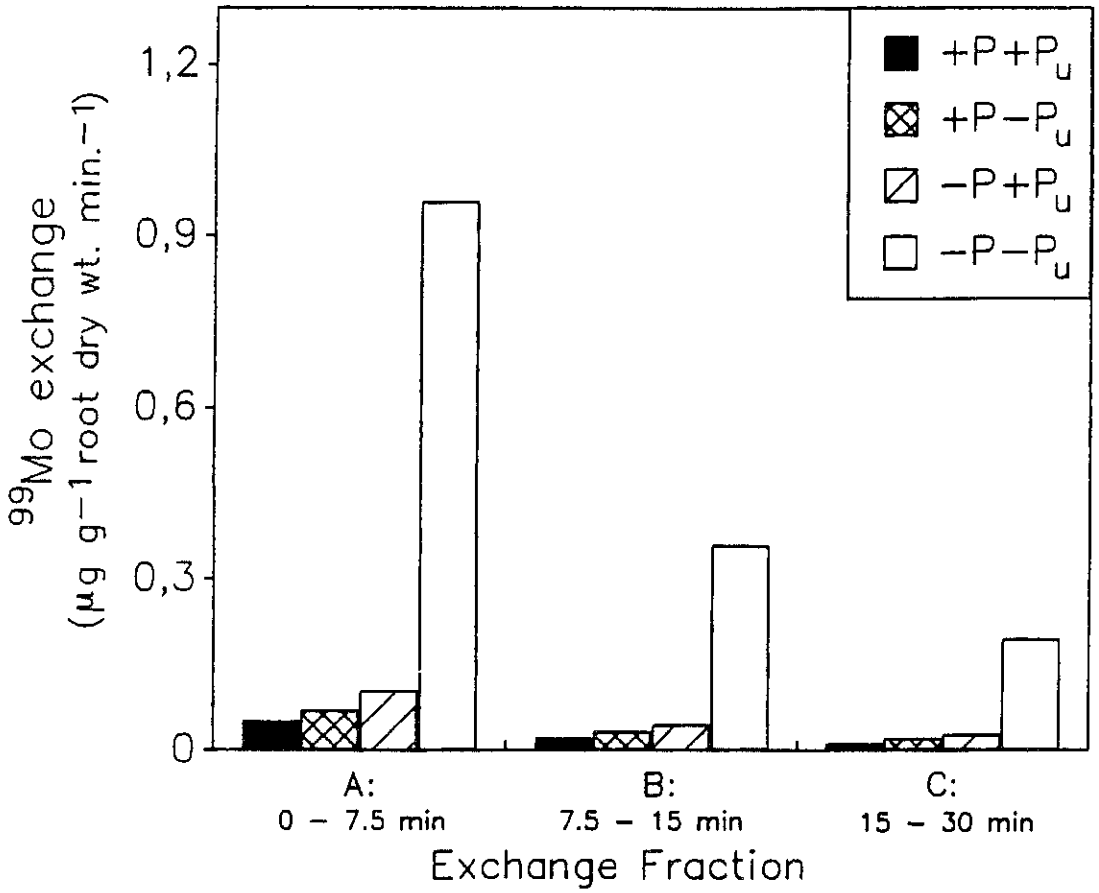

FIGURE 6. Kinetics of ^{99}Mo Exchange from Preloaded Roots (4-Hour Uptake Period) by Non-Labelled Mo (10 µM) in Tomato Plants with Different P Nutritional Status and Different P Treatment During the Preloading Period. Results obtained in the ^{99}Mo experiment.

solution during the uptake period (-P-Pu). Regardless of the P treatment, ^{99}Mo exchange declined rapidly with time.

The percentage ^{99}Mo exchanged in each fraction of the total root ^{99}Mo (see Fig. 5) is mainly independent of treatment (Table 4). Only fraction A of the -P-Pu treatment was larger than the other treatments. For all treatments the total ^{99}Mo exchanged as a percentage of the root ^{99}Mo after the termination of the uptake period was in the range of 25 to 30%.

DISCUSSION

Both the serial harvest experiment and the ^{99}Mo experiment clearly demonstrate that Mo uptake is markedly enhanced in P deficient tomato plants

TABLE 4. Exchange of ^{99}Mo by Non-Labelled Mo in Roots of Tomato Plants of Different P Nutritional Status and Subjected to Different P Treatments During the ^{99}Mo Loading (4h). Exchanged ^{99}Mo expressed as percentage of total ^{99}Mo in roots at the termination of the short-term uptake period with ^{99}Mo. Numbers in brackets give the standard deviation of the mean of three replicates.

Exchange Fraction	Treatment			
	$+P+P_u$	$+P-P_u$	$-P+P_u$	$-P-P_u$
A 0 - 7.5 min	12.6 (4.1)	13.6 (2.5)	14.0 (2.2)	19.1 (0.5)
B 7.5 - 15 min	5.4 (0.4)	6.2 (1.1)	6.1 (0.7)	7.2 (0.3)
C 15 - 30 min	6.0 (1.6)	7.5 (1.2)	7.7 (0.1)	7.8 (0.4)

(Figures 2, 3, and 5) and that the Mo taken up is largely accumulated in the roots (Figures 3 and 5). The plants responded very rapidly to a lack of P in the nutrient medium. After only 4 days in the P deficient medium, though growth of plants was scarcely affected and only mild P deficiency symptoms were visible, the concentrations of P in plant tissues had fallen drastically and a switch from net OH^- efflux to net H^+ efflux from the roots became evident (Table 1, Fig. 1). Even at that early stage, Mo uptake and to a lesser extent transport were greatly enhanced by P deficiency (Fig. 3).

A fall in pH in the nutrient medium in response to P deficiency is a well-known phenomena (16,3,28,18,22). From our results it may be concluded that since differences in cation and anion uptake were balanced by net OH^- or H^+ efflux in P sufficient and deficient plants respectively (Table 2), organic acid extrusion from roots plays no major role in the observed fall in pH induced by the P deficient plants. In this respect tomato plants behave differently from white lupin (13,8) or rape (19).

The depression in anion and therefore in NO_3^- uptake appears to be the main factor leading to the switch from net OH^- efflux to net H^+ efflux from the roots of P deficient plants. There are several possible reasons for this lower uptake of NO_3^-. The net uptake of NO_3^- in particular is dependent on influx and efflux of NO_3^- across the plasma membrane, and increasing rates of efflux depresses net NO_3^- uptake (7). Factors that impair the plasma membrane structure and function such as a lack of P by restricting phospholipid synthesis enhance efflux and thus also restrict net NO_3^- uptake. Additionally, P deficiency inhibits protein synthesis which in turn depresses NO_3^- uptake (28). Since Mo uptake is enhanced by P deficiency, it is unlikely that nitrate reductase activity limited by Mo is a factor in lower net NO_3^- uptake.

The uptake of Mg is least affected of the mineral cations by P deficiency, an effect which has also been observed in chickpea (22). It may be supposed that organic acid anions accumulating in vacuoles under P deficiency bind Mg in preference to K and Ca thus creating a demand for Mg uptake.

The marked effect of P deficiency in increasing Mo uptake in comparison with other nutrients suggests a direct relationship between P deficiency and enhanced Mo uptake. It is well documented that when P is resupplied to plants suffering from P deficiency a rapid uptake of P occurs which may even induce P toxicity (5). This enhanced uptake capacity of P deficient plants results from an increased number of binding sites for P at the plasma membrane or a higher turnover rate of these sites. Since phosphate and molybdate are anions with similar physico-chemical properties we suppose that they may be interchangeable and, therefore, in the absence of phosphate in the nutrient medium, molybdate uptake is enhanced by the higher P uptake capacity of the roots of P deficient plants. In support of this suggestion, a similar enhanced uptake of arsenate, another phosphate analogue, has been observed in P deficient barley roots (23). Furthermore the highest Mo uptake rate in our serial harvest experiment was found to coincide with the period of highest P uptake capacity in the P deficient roots of tomato in the experiment of Clarkson and Scattergood (5).

The much higher uptake rates of Mo in P deficient tomato plants found in the serial harvest experiment were confirmed in the short term ^{99}Mo experiment (Fig. 5) where the uptake rate of ^{99}Mo was studied during the period of highest uptake capacity of P. The higher ^{99}Mo uptake rates could be strongly depressed, even within 1 hour, when P was supplied together with ^{99}Mo in the external solution

(Fig. 5). This rapid response affirms that molybdate is bound and transported across the plasma membrane by phosphate binding and transport sites, rather than the result of cross metabolic changes in root metabolism during the recovery from P deficiency.

If molybdate is taken up in tomato plants by the binding and transport sites for phosphate, in general, ommission of P from the external solution should also enhance Mo uptake in plants adequately supplied with P. We observed, however, only a small increase (Fig. 5). Such a finding is to be expected under the experimental conditions of our study for two reasons. In the first place, transferring P sufficient plants into P free solutions (+P-Pu) results in a substantial efflux of P (11) and thus also an increase in its concentration in the free space of the root cortical cells. Since the external ^{99}Mo concentration is low (0.5 μM), the P concentration at the uptake sites of the plasma membrane therefore, most likely, by far exceeds that of Mo after short-term ommission of P from the external solution. Secondly, when P sufficient plants are transferred to a nutrient solution without P, the plants must be starved of P for several days in order to obtain enhanced uptake rates of P when P is resupplied (24,5). Uptake of Mo by the +P-Pu plants is thus likely to be depressed because of the relatively higher concentration of P at the root surface and the lower P uptake capacity as compared with the -P-Pu treatment.

To our knowledge the results presented are the first report suggesting that molybdate and phosphate use the same carrier sites in ion uptake. Clearly in most cases the P concentration is so much higher than Mo at the root surface that competition is not observed. However, in our experiments by choosing a period after the onset of P deficiency when the capacity for P uptake was high the competition was also pronounced (Fig. 5). Contrary reports that P favours the uptake of Mo (29,30) may perhaps be accounted for by different experimental conditions (*e.g.* very high P concentrations in nutrient solution). In experiments involving soil a further complication arises from the presence of anion exchange reactions at the soil/root interphase (31)

Despite similarities in uptake, P and Mo behave very differently in terms of transport within the plant. In contrast to the rapid P transport to the shoots of plants suffering from P deficiency (5), Mo was largely retained in the roots of plants in both experiments when P was withheld (Figures 1 and 3) even though the rate of transport of Mo from root to shoot was enhanced (Table 3).

Unlike P, Mo may be bound to organic molecules such as phenolics so that movement within the plant might be restricted and this may well account for the reported unequal distribution within root tissues (17,15). Our findings indicate that the rate of transport from root to shoot is independent of the uptake rate and influenced mainly by the Mo concentration in the roots and the period of time available for transport (Figures 3 and 5).

Some conclusions on the compartmentation of ^{99}Mo within roots can be drawn from the kinetic studies of ^{99}Mo exchange by non labelled Mo (Fig. 6). The somewhat steeper decrease from exchange fraction A to B in the P deficient plants (-P-Pu; -P+Pu) indicates a higher proportion of readily exchangeable ^{99}Mo in fraction A of these plants. This is to be expected if ^{99}Mo binds to P uptake sites in the root plasma membrane. The similar pattern from exchange fraction B to C in all treatments suggests only a minor importance of a vacuolar pool of Mo during the short-term uptake periods of ^{99}Mo. It implies as well, that binding of Mo to organic structures might have taken place in the -P-Pu treatment.

Reports that sulphate application depresses molybdate uptake (30,14) are also of relevance to the results presented. In the present study sulphate was used as a compensating anion in the nutrient solution, replacing P in the P deficient treatments. The observed enhancement of Mo uptake in the P deficient plants may therefore even be under-estimated by sulphate competition. It would be of interest to know whether the enhanced capacity of roots of sulphur deficient plants for binding and transporting sulphate (20,6) leads to a similar increase in the rate of Mo uptake, as reported here for P deficient tomato roots.

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