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Studies on Molybdenum Absorption and Transport in Bean and Rice

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ABSTRACT

The patterns of molybdenum (MoO_4^{2-}) absorption and transport were investigated in intact bean (*Phaseolus vulgaris* L.) and rice (*Oryza sativa* L. cv. I.R.8) plants. The mobility of MoO_4^{2-} absorbed by roots and by leaves was compared with that of a freely mobile element, Rb^+. Although MoO_4^{2-} absorption by bean roots was nearly as high as that of Rb^+, its transport to the shoot was considerably less. When MoO_4^{2-} was fed to one of the primary leaves, most of it was transported to the stem and root. Evidence obtained here showed that MoO_4^{2-} was mobile. Experiments with intact rice seedlings revealed large differences in the absorption and transport of MoO_4^{2-} between the plants grown in $CaSO_4$ and those in Hoagland solution. Molybdate uptake by excised rice roots was suggested to be an active process since it was greatly inhibited by a metabolic inhibitor. The presence of Mn^{2+}, Zn^{2+}, Cu^{2+}, Cl^-, or SO_4^{2-} in the absorption medium reduced MoO_4^{2-} uptake which was markedly enhanced by the presence of Fe^{2+}.

Molybdenum is one of the micronutrient elements essential for plants. Following the early work of Arnon and Stout (1) and Piper (16), the occurrence of its deficiency has been recorded in many soils and crop plants, and remedial measures like soil, foliar, or seed treatment have been widely advocated (7, 17).

Several studies have been made in the past years relating to the mechanisms of absorption and transport of major nutrients and also some micronutrient elements (5, 12). However, information on the mechanisms of micronutrient absorption is still inadequate, and Moore (13) has rightly emphasized the need for a systematic investigation to understand the manner in which the micronutrients, especially boron and molybdenum, are absorbed by plant systems and also the factors which control their absorption and transport. Molybdate absorption and transport have been studied in intact plants and excised roots, and the results are reported here.

MATERIALS AND METHODS

Experiments on the absorption and transport were carried out with bean plants and excised roots or intact seedlings of rice. Beans (*Phaseolus vulgaris* L.) were germinated in sand for 5 days, transferred to 0.5 Hoagland solution No. 1 (8) minus MoO_4^{2-} and grown for 7 to 9 days under a 12-hr photoperiod (500 ft-c) at 25 C. Rice (*Oryza sativa* L. cv. I.R.8) seeds were germinated in trays over 0.5 Hoagland solution minus MoO_4^{2-} for 7 days, and the roots were excised for use.

The absorption medium consisted of ^{86}Rb- or ^{99}Mo-labeled 0.01 mM RbCl or ammonium molybdate [$(NH_4)_6Mo_7O_{24}\cdot 4H_2O$] adjusted and maintained at pH 5.5 with KOH twice during the absorption. Unless otherwise stated, the same but nonradioactive cold (5 C) solutions were used for desorption of the roots at the end of the experimental period. In one experiment, the absorption and transport of MoO_4^{2-} were compared with those for Rb^+. The roots of bean plants were exposed to the absorption medium and removed at different times. Foliar absorption and transport of MoO_4^{2-} and Rb^+ were also measured in another set of bean plants. The isotope solutions (0.2 ml of 0.01 mM RbCl or ammonium molybdate) were placed in a plastic ring 1 cm in diameter (15) which was fixed in the intercostal region on the upper surface of a primary leaf. The transport to different parts was assayed after punching out and discarding the leaf area below the plastic ring.

The patterns of absorption of MoO_4^{2-} by root and transport to shoot were examined in rice seedlings grown in three different media, *viz.* 0.1 mM $CaSO_4$, 0.5 Hoagland or full Hoagland solutions without MoO_4^{2-} for 15 days. For measuring the absorption and transport, sets of 10 seedlings were placed in flasks containing 200 ml of the absorption medium, and removed at different time intervals during a 6-hr period.

A series of three experiments was carried out with excised rice roots. For studying the action of a metabolic inhibitor on MoO_4^{2-} absorption, excised roots were suspended in the absorption medium at pH 7.4, with or without 10^{-6} M pCF$_3$ O-CCP,[1] and roots (500 mg fresh wt) were removed for assay. In another set, the influence of other ions on MoO_4^{2-} absorption was examined by suspending the rice roots in the absorption medium containing 0.01 or 0.1 mM $FeSO_4$, $MnSO_4$, $CuSO_4$, $ZnSO_4$, NH_4Cl, or $(NH_4)_2SO_4$ for 4 hr. The absorption of MoO_4^{2-} in the presence of 0.01 or 0.1 mM $FeSO_4$ was further investigated with respect to different washing medium. The samples were allowed to absorb MoO_4^{2-} for 4 hr, and then desorbed for 30 min in solutions containing 0.1 mM ammonium molybdate alone, or in combination with either 0.1 mM $FeSO_4$ or FeEDDHA.

In general, the roots were desorbed for 30 min. Low amounts of 0.1 mM $CaSO_4$ or $CaCl_2$ were routinely included in all of the solutions. The plant parts were dried and radioassayed in a gamma ray spectrometer and the results presented are the means of values obtained for five bean plants, three sets of rice seedlings, and five sets of excised rice roots on a fresh wt basis.

RESULTS

Molybdate absorption by roots of intact bean seedlings and transport to the stem, primary and trifoliate leaves were measured during a 24-hr period and compared with those for Rb^+ (Fig. 1). Molybdate absorption by root is slightly less than that of Rb^+, although its transport is considerably less than that for Rb^+. The transport to the trifoliate is the largest, followed by stem and primary leaves in both Rb^+ and MoO_4^{2-}. Furthermore, the absorption and transport of both Rb^+ and MoO_4^{2-} follow a biphasic pattern, with a second phase beginning approximately at 6 hr. The rate of transport of Rb^+ to the trifoliate nearly runs parallel to its

[1] Abbreviations: p-CF$_3$ O-CCP: *p*-trifluoro-methoxyphenylhydrazone; FEEDDHA: ferric ethylenediaminedi(*o*-hydroxyphenyl acetate).

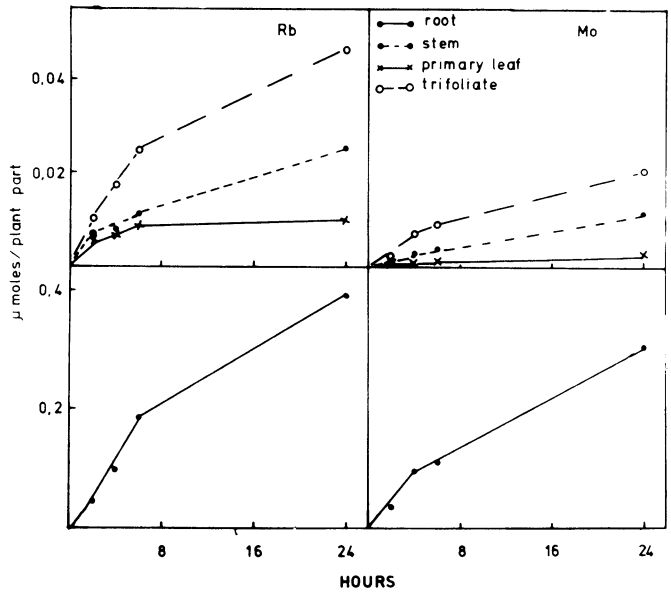

FIG. 1. Course of MoO_4^{2-} and Rb^+ absorption by roots and transport to different parts of intact bean seedlings during 24 hr. The absorption medium contained 0.01 mM RbCl or ammonium molybdate.

Table I. Foliar Absorption and Translocation of MoO_4^{2-} and Rb^+ in Bean Plants

The isotope solution, 0.2 ml of 0.01 mM Ammonium molybdate or RbCl was supplied to one of the primary leaves by means of a plastic ring and after 24 hr the leaf area with the ring was punched out and discarded. The amount transported to the remaining part of the applied leaf and other parts is estimated and given as absolute amounts per plant part.

Plant Parts	MoO_4^{2-}		Rb^+	
	nmoles x 10^2 ± SE	Distribution as % of total	nmoles x 10^2 ± SE	Distribution as % of total
Applied Primary Leaf	6.04 ± 1.4	17.16	3.83 ± 0.1	13.03
Opposite Primary Leaf	6.65 ± 1.1	18.89	2.99 ± 1.2	10.16
Trifoliate Leaf	2.76 ± 0.7	7.84	5.90 ± 0.1	20.05
Stem	10.80 ± 0.7	30.68	4.32 ± 1.2	14.68
Root	8.95 ± 0.1	25.43	12.38 ± 3.1	42.08

absorption by root while this is not so for MoO_4^{2-}. Transport of Rb^+ and MoO_4^{2-} to the primary leaves reached a near maximum at 6 hr and remained at the same level up to 24 hr.

The data on foliar absorption and transport reveal that a considerable amount of MoO_4^{2-} is absorbed and transported within the plant. The total amount absorbed after discarding the site of isotope application is 35.23 and 22.90 nmol/plant for MoO_4^{2-} and Rb^+, respectively (Table I). The pattern of translocation of MoO_4^{2-} is different from that of Rb^+. While MoO_4^{2-} and Rb^+ are nearly equally distributed between the applied and opposite primary leaves, the transport of MoO_4^{2-} is largely downward to the stem and root, and Rb^+ is transported equally to the growing regions, namely trifoliate leaves and the root. Transport of MoO_4^{2-} to shoot is much less than to other parts.

The absorption and transport of MoO_4^{2-} in intact rice seedlings are influenced by the nutrient media used for their culture. The absorption is the lowest in the plants grown in $CaSO_4$ while it is higher in those raised in Hoagland solution (Fig. 2). In contrast, the transport in plants grown in $CaSO_4$ was higher than in those raised in Hoagland solution. The absorption and transport in plants grown in 0.5 and full Hoagland solution did not differ very much.

Studies with excised rice roots show that MoO_4^{2-} absorption is sensitive to the metabolic inhibitor pCF_3 O-CCP (Fig. 3). Furthermore, the presence of Cu^{2+}, chloride, and sulfate inhibited the

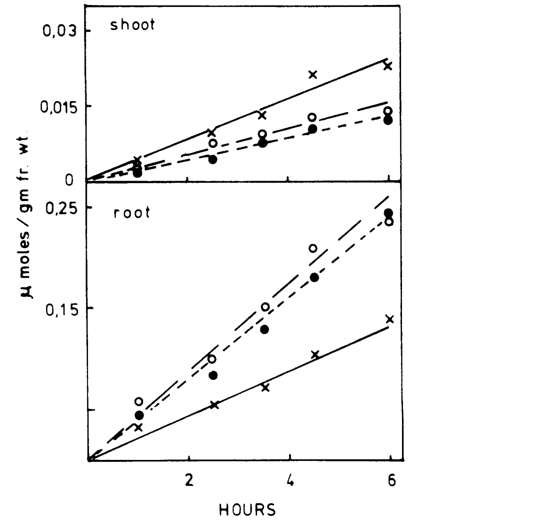

FIG. 2. Absorption and transport of MoO_4^{2-} from 0.01 mM ammonium molybdate in rice seedlings grown in 0.1 mM $CaSO_4$ (×——×), 0.5 Hoagland (○——○), and full Hoagland (●- - -●) nutrient medium. The values are the means of three sets of 10 seedlings each.

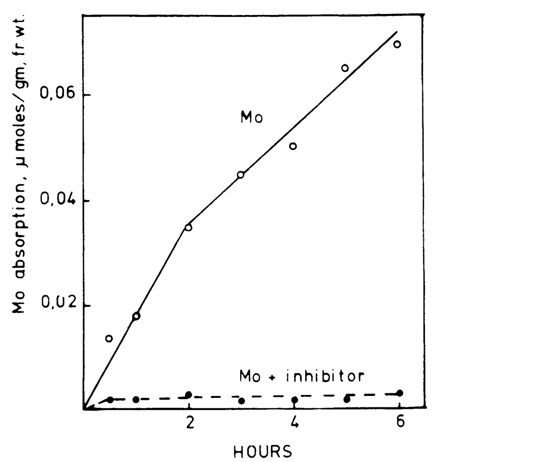

FIG. 3. Effect of 10^{-6} M pCF_3 O-CCP on the absorption of MoO_4^{2-} from 0.01 mM ammonium molybdate by excised rice roots.

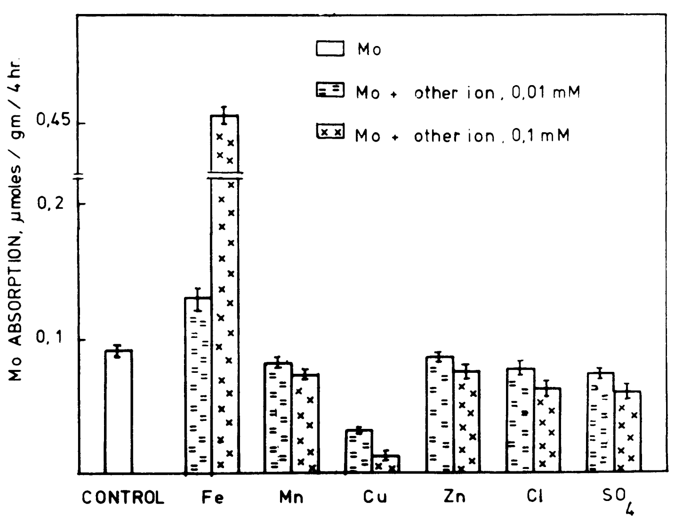

FIG. 4. Absorption of MoO_4^{2-} from 0.01 mM ammonium molybdate by excised rice roots, in the absence and presence of 0.01 or 0.1 mM $FeSO_4$, $MnSO_4$, $CuSO_4$, $ZnSO_4$, NH_4Cl, and $(NH_4)_2SO_4$.

Table II. Effects of $FeSO_4$ and FeEDDHA on the Absorption of MoO_4^{2-} from 0.01 mM Molybdate by Excised Rice Roots

Excised roots were suspended in ^{99}Mo labelled 0.01 mM Ammonium molybdate in the absence and presence of $FeSO_4$ or FeEDDHA for 4 hr, and samples were allowed to desorb for 30 min in solutions containing molybdate alone, or in combination with $FeSO_4$ or FeEDDHA.

Absorption Medium	Desorption Medium		
	0.1 mM Molybdate	0.1 mM Molybdate + 0.1 mM $FeSO_4$	0.1 mM Molybdate + 0.1 mM FeEDDHA
	nmoles/g ± SE	nmoles/g ± SE	nmoles/g ± SE
0.01 mM Molybdate	54.91 ± 4.08	32.07 ± 1.92	49.98 ± 3.49
0.01 mM Molybdate + 0.01 mM $FeSO_4$	51.26 ± 3.16	53.98 ± 1.80	48.83 ± 0.99
0.01 mM Molybdate + 0.1 mM $FeSO_4$	337.45 ± 22.55	334.45 ± 11.68	292.27 ± 25.14
0.01 mM Molybdate + 0.01 mM FeEDDHA	58.10 ± 5.03	50.20 ± 4.63	50.96 ± 2.72
0.01 mM Molybdate + 0.1 mM FeEDDHA	58.32 ± 4.09	46.89 ± 3.86	59.52 ± 3.30

absorption (Fig. 4). There is also a less marked reduction in the uptake in the presence of Mn^{2+} and Zn^{2+}. The presence of low concentrations of $FeSO_4$ (0.01 mM) enhanced MoO_4^{2-} uptake and this enhancement was even greater at high concentrations (0.1 mM). Additional experiments revealed that this enhancement occurred in the presence of 0.1 mM $FeSO_4$ and not FeEDDHA (Table II). When the roots treated with 0.01 mM $FeSO_4$ were desorbed with high concentrations of ammonium molybdate (0.1 mM) no enhancement of MoO_4^{2-} absorption was observed. However, $FeSO_4$ increased the uptake and this is also observed when the desorption medium contained molybdate and $FeSO_4$ (0.1 mM). High concentrations of $FeSO_4$ (0.1 mM) enhanced MoO_4^{2-} absorption and there was no effect of the presence of $FeSO_4$ or FEEDDHA in the desorption medium.

DISCUSSION

Bukovac and Wittwer (4) investigated the mobility of several nutrient elements by leaf disc removal technique and placed Fe^{2+}, Mn^{2+}, and MoO_4^{2-} in the partially mobile group. However, others reported that Fe^{2+} (3) and Mn^{2+} (10) were absorbed by roots and readily translocated to the shoot. We have examined the mobility of molybdenum as an element in comparison with a freely mobile element, rubidium, and it is not our interest to study the mechanisms of uptake of molybdate which enters the plant as anion. Molybdate transport from the root to shoot was less than that of Rb^+, despite the fact their absorption by the roots was nearly the same (Fig. 1). Molybdate supplied to the primary leaf was translocated to other parts, although most of it was in the stem and root. Differences occurred between MoO_4^{2-} and Rb^+ only in the per cent transport to the trifoliate leaves (Table I). The absorption and transport of a moderately mobile element Fe^{2+} were studied earlier (11), and although the experimental techniques differed, some meaningful comparison could still be made between the mobility of Fe^{2+} and MoO_4^{2-}. Only 0.06 μmol out of 4.2 μmol of Fe^{2+} absorbed by bean roots was translocated to shoot, while 0.002 μmol was transported to other parts out of 0.3 μmol of Fe^{2+} absorbed by the primary leaf. In comparison with Fe^{2+}, MoO_4^{2-} appears to be more mobile.

The patterns of absorption and transport of nutrient elements were much altered by the medium of growth of the plants (9, 10). Molybdate absorption by rice roots grown in Hoagland solution was greater than in those raised in$CaSO_4$ (Fig. 2). It is possible that MoO_4^{2-} absorption in seedlings grown in Hoagland solution relates to the entry into vacuole, on the basis of the argument that cytoplasmic sites get saturated during growth in nutrient medium (9). However, more precise experiments are needed to confirm this explanation.

The absorption of MoO_4^{2-} is influenced by the presence of both cations and anions, which are all inhibitory, with the exception of Fe^{2+} (Fig. 4). It is rather surprising that Fe^{2+} is found to enhance the absorption, and this effect is great when $FeSO_4$ is 0.1 mM. It is equally interesting that this enhancement is consistently absent when FeEDDHA is used instead of $FeSO_4$. Molybdate may possibly combine with Fe^{2+} dissociated from $FeSO_4$ and enter as iron molybdate. This does not, however, offer an explanation of why more MoO_4^{2-} is absorbed. The effect of Fe^{2+} on MoO_4^{2-} absorption appears to be a direct one. Berry and Reisenauer (2) studied the influence of MoO_4^{2-} on the uptake and distribution of Fe^{2+} by tomato, and found that MoO_4^{2-} enhanced the plant's ability to absorb Fe^{2+}. Gerloff *et al* (6) reported that MoO_4^{2-} and Mn^{2+} were capable of affecting Fe^{2+} availability in tomato. These authors have examined the effects of MoO_4^{2-} on the absorption of cations and anions. Stout and Meagher (18) obtained evidence for increased translocation of MoO_4^{2-} by phosphate in culture solution. Furthermore, they found from radioautographic studies that the distribution of molybdenum in the leaves was distinctly different from that of potassium. In the review of interactions between MoO_4^{2-} and other cations and anions (14) mention has been made of the enhancement of MoO_4^{2-} deficiency by Cu^{2+} and the inhibition of MoO_4^{2-} uptake by sulfate. Our studies, on the other hand, reveal the effects of both cations Mn^{2+}, Zn^{2+}, and Cu^{2+} and anions Cl^- and SO_4^{2-} on the absorption of MoO_4^{2-}.

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