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MOLYBDENUM-MANGANESE-IRON ANTAGONISMS IN THE NUTRITION OF TOMATO PLANTS[1]

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Antagonisms and interactions among the essential elements molybdenum, manganese, and iron and their effects on plant growth have been reported by a number of investigators. Millikan (11), for example, with solution culture experiments concluded that molybdenum would alleviate iron deficiency symptoms in flax induced by excess quantities of manganese, zinc, copper, nickel, or cobalt. Relatively high concentrations of molybdenum (5 to 25 ppm added to the nutrient solution) were required. In a subsequent publication, Millikan (12) reported a similar molybdenum-manganese interaction in solution culture experiments with peas, cabbage, and tomatoes, and that in both field and pot experiments manganese toxicity to flax growing in highly acid soils was alleviated by additions of molybdenum.

Other investigators Hewitt (5, 7), Mulder (13) and Warrington (16) obtained results in direct contrast to those by Millikan; molybdenum, rather than alleviating iron chlorosis induced by high concentrations of metals, accentuated the chlorosis and led to further decreases in growth. Later Warrington (17) reported results to some extent contradictory to those obtained earlier and in agreement with Millikan's proposals. In studies of molybdenum-iron interactions, iron chlorosis was apparent in flax growing in solutions containing 0.1 ppm molybdenum and 10 ppm iron whereas at molybdenum concentrations of 40 ppm chlorosis was not observed.

The possibility that high levels of manganese which might be present in some acid soils would induce or accentuate molybdenum deficiency has been considered. Anderson and Spencer (1) found that a heavy application of manganese sulfate reduced the uptake of molybdenum by flax and induced molybdenum deficiency. However, these effects could have resulted from competition between molybdate and sulfate ions for absorption sites on the plant roots (15). When the effects of manganese and sulfate were considered separately in more recent investigations by Anderson and Arnot (2) and Mulder (13), it was found that high concentrations of soil manganese accentuated molybdenum deficiency and decreased the molybdenum content of plant tissue. Mulder, however, was not able to duplicate this interaction between manganese and molybdenum for all plant species tested when grown in soil or with cauliflower when grown in solution culture.

Because of the contradictions to be found in published data relating to molybdenum-manganese-iron interactions and because of the importance of understanding the factors governing the manganese, iron, and molybdenum nutrition of plants, these further

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studies were undertaken. It was hoped that closely controlled experiments coupled with analyses of plant tissue might lead to a better understanding of the nature of these interactions, particularly in regard to the absorption of iron by plants.

MATERIALS AND METHODS

The nutrient medium employed was a slightly modified Hoagland's solution described by Johnson et al (8). The following quantities of the essential elements in microgram atoms per liter are present: N, 16,000; K, 6,000; Ca, 4,000; P, 2,000; S, 1,000; Mg, 1,000; Cl, 50; B, 25; Mn, 5.0; Fe, 4.0; Zn, 2.0; Cu, 0.5; and Mo, 0.1. A portion of the nitrogen is provided as an ammonium salt rather than as nitrate. This was effective in reducing changes in pH in the culture solutions in spite of large variations in the amount of plant growth. For example, in the experiment to be reported in table I, the average pH of the cultures in which maximum growth of 3.67 g developed was 4.66 after a 24 day growth period while in cultures with only 0.20 g of growth the pH was 4.53. Therefore, adjustment of pH during the growth period was unnecessary.

A 0.002 M $FeSO_4 \cdot 7\,H_2O$ solution adjusted to pH 3.5 served as the iron source; molybdenum was added as $(NH_4)_6MO_7O_{24} \cdot 4\,H_2O$; and manganese as $MnCl_2 \cdot 4\,H_2O$. Since the experiments were of relatively short duration and the amount of growth insufficient to deplete the nutrients, the solutions were not changed during the experiments. In some cases, several additions of iron were made. This is indicated in the presentation of the individual experiments.

The molar stock solutions providing the major essential elements were purified of manganese contamination by heating in the presence of calcium phosphate and calcium carbonate precipitates as described by Stout and Arnon (14) and of moylbdenum by the copper sulfide co-precipitation method of Hewitt (6). Double distilled water was employed in all experiments and the culture containers as well as all glassware were thoroughly cleaned by soaking in dilute HCl and rinsing with double distilled water as is customary in micronutrient experiments.

Marglobe variety tomatoes were used in all experiments. After germination in one tenth Hoagland's solution of the major elements, 3 seedlings were transplanted to each of the 2 quart polyethylene containers which served as culture vessels. The nutrient solutions were aerated continuously. Plaster of Paris lids served both as covers for the plastic containers and support for the plants. The translucent containers were covered with aluminum foil to eliminate

TABLE I

EFFECTS OF VARYING CONCENTRATIONS OF MOLYBDENUM AND MANGANESE ADDED TO THE CULTURE MEDIUM ON THE YIELD, IRON, MANGANESE, AND MOLYBDENUM CONTENT, AND THE DEVELOPMENT OF IRON DEFICIENCY CHLOROSIS OF TOMATO PLANTS

TREATMENT	ADDED TO CULTURE SOLUTION, PPM		AVE DRY WT OF PLANTS PER CULTURE, G	ANALYSIS OF LEAF AND STEM TISSUE, PPM			SEVERITY OF Fe DEFICIENCY CHLOROSIS *
	Mo	Mn		Fe	Mn	Mo	
A	0.7	0.27	2.73	96	45	19	None
B	"	5.4	2.05	60	527	14	None
C	"	10.8	2.09	51	990	16	None
D	"	21.6	0.22	..	...	...	+++++
E	3.35	0.27	3.67	56	31	445	None
F	"	5.4	1.53	29	680	573	+++
G	"	10.8	0.64	33	1148	898	++++
H	"	21.6	0.20	..	...	...	+++++
I	13.4	0.27	2.50	39	41	1796	None
J	"	5.4	0.32	33	932	3404	++++
K	"	10.8	0.30	46	1007	2485	+++++
L	"	21.6	0.15	...	...	...	+++++
M	33.8	0.27	1.11	44	60	4399	+
N	"	5.4	0.45	...	...	...	++++
O	"	10.8	0.29	...	...	...	+++++
P	"	21.6	0.18	...	...	...	+++++
Q	67.0	0.27	0.23	...	...	...	++
R	"	5.4	0.16	...	...	...	+++
S	"	10.8	0.15	...	...	...	+++
T	"	21.6	0.12	...	...	...	+++

The growth period was 24 days. Iron was added (0.22 ppm as $FeSO_4 \cdot 7\,H_2O$) to each culture 6 times during this period.

* The degrees of iron chlorosis associated with these designations are: +, faint, mottled chlorosis on the terminal leaves; ++ and +++, increasing proportion of the terminal leaves chlorotic except the veins which remained green; ++++, the terminal growth was completely chlorotic; +++++, in large areas of the terminal growth the chlorotic tissue had become necrotic. Similar designations are employed in table II.

light and reduce temperature changes. All experiments were carried out in a conventional greenhouse. Every treatment in each experiment consisted of duplicate cultures. The plants from each culture were harvested separately; divided into roots and tops; the roots were washed thoroughly in distilled water; and all samples were dried at 65° C.

To avoid contamination due to grinding, the entire samples were wet-ashed in a nitric-perchloric-sulfuric acid mixture. Iron was determined as an *o*-phenanthroline complex; manganese by oxidation to permanganate; and molybdenum as the amber colored complex of quinquevalent molybdenum and thiocyanate. Each of the duplicate samples from a specific treatment was weighed and analyzed separately. The values reported in tables I and II are averages of these determinations. Of the treatments producing more than 0.5 g growth, in only one did the individual dry weight values vary from the average reported by more than 15 %. Among the chemical analyses, the duplicate determinations for iron in 1 treatment, for manganese in 2 treatments, and for molybdenum in 5 treatments of the total reported exceeded the average values by more than 15 %. The molybdenum analyses, therefore, were considerably less consistent than the iron and manganese.

Experimental Results

Molybdenum-Manganese-Iron Interactions: The initial experiment was an attempt to reproduce with the tomato plant Millikan's results which had shown molybdenum capable of offsetting manganese toxicity in several plant species. Table I shows the treatments tested which included 5 concentrations of molybdenum varying from 0.07 to 67.0 ppm with each level of molybdenum combined with manganese concentrations of 0.27, 5.4, 10.8, and 21.6 ppm. The highest concentrations of molybdenum or manganese were chosen to be within suspected toxicity ranges.

The highest levels of manganese obviously were toxic as shown by the marked, successive decreases in growth in treatments A to D and E to H. If the results agreed with those reported by Millikan, the injurious effects resulting from a specific level of manganese would have diminished as the concentration of molybdenum in the culture solution increased. Exactly the opposite was obtained in all cases. For example, in Treatments B, F, and J all of which contain 5.4 ppm manganese, but 0.07, 3.35, and 13.4 ppm molybdenum respectively, growth decreased from 2.05 to 1.53, and to 0.32 g of dry tissue. Similarly in Treatments C, G, and K containing 10.8 ppm manganese but increasing molybdenum, growth decreased from 2.09 to 0.30 g.

The decreases in growth induced by moderate levels of manganese and accentuated by molybdenum, for example Treatment F in comparison with Treatment J, correlated with observations on the degree of iron chlorosis and indicated that both elements were capable of affecting iron availability. When a leaf which was very chlorotic and much reduced in size from a plant of Treatment G was painted with a ferrous sulfate solution near the conclusion of the experiment, a normal green color was quickly restored, thus substantiating that the observed chlorosis was due to iron deficiency. The significance of the reduced chlorosis associated with the highest concentration of molybdenum (Treatments Q to T) will be discussed in a subsequent section.

With very high levels of manganese (Treatment H) or of molybdenum (Treatment T) additional symptoms not normally associated with iron deficiency were apparent. For manganese toxicity, this consisted of a brown, necrotic spotting and streaking of lower leaves, stems, and petioles; for molybdenum toxicity, a golden pigmentation of the newest growth and extreme stunting of leaf size near the growing point, particularly the basal leaflets.

Where sufficient material was available, the plant tissue was analyzed for iron, manganese, and molybdenum. The results correlate well with the weight data and visual observations of iron chlorosis. Increasing concentrations of manganese in the culture solution resulted in much higher concentrations in the plant tissue and at the same time a decrease in iron content, from 96 to 51 ppm in Treatments A, B, and C and from 56 to 33 ppm in Treatments E, F, and G. The effect of increasing concentrations of molybdenum in the culture medium on the molybdenum and

Table II

Ability of Relatively Low Concentrations of Molybdenum Added to the Nutrient Solution to Induce Iron Deficiency in Tomato Plants

Treatment	Added to culture solution, ppm		Ave dry wt of plants per culture, g		Fe content of tissue, ppm		Mo content of tissue, ppm		Severity of Fe Chlorosis *
	Mo	Fe	Tops	Roots	Tops	Roots	Tops	Roots	
A	0.067	0.11	3.28	0.63	29	34	11	115	+
B	0.67	0.11	2.52	0.72	29	29	54	1195	++
C	3.35	0.11	0.82	0.37	28	99	930	2710	+++
D	6.70	0.11	0.39	0.14	30	171	1270	2785	+++++
E	0.067	1.10	3.17	0.65	55	780	12	48	None

The growth period was 25 days. Iron was added to Treatments A, B, C, and D only at the start of the experiment, but to cultures of Treatment E (0.22 ppm) 5 times during the growth period.

* See table I for explanation of symbols.

iron contents of tissue can be evaluated from the data from Treatments A, E, and I. The molybdenum content increased from 19 to approximately 1800 ppm while the iron content, rather than increasing or remaining constant as might be predicted from Millikan's results, decreased from 96 to 39 ppm.

The possibility that an interaction between molybdenum and manganese might also be observed through the capacity of increasing concentrations of either element to accentuate the symptoms due to a deficiency of the other was investigated. Cultures were prepared from which molybdenum was omitted and manganese varied from 0.27 to 5.4 ppm and from which manganese was omitted but molybdenum varied from 0.067 to 3.4 ppm. There was no indication that increasing levels of either manganese or molybdenum had any effect whatsoever in inducing or accentuating a deficiency of the other element. This is in agreement with results reported by Mulder (13) from nutrient culture experimentation.

MOLYBDENUM-IRON INTERACTIONS: In the experiment reported in table II, the capacity of molybdenum to affect iron availability was further evaluated with manganese added to all cultures at a low concentration and thus omitted as a variable. Except for the control, the concentration of iron employed was relatively low, 0.11 ppm added at the start of the experiment. This resulted in plants which were mildly chlorotic by the end of the growth period in cultures receiving even the lowest level of molybdenum, but growth was not affected as shown by a comparison of yields from Treatment A and the control cultures of treatment E which received a total of 1.10 ppm iron during the course of the experiment. Molybdenum concentrations varied from 0.07 to 6.70 ppm, far below the maximum tested in the initial experiment.

Molybdenum was surprisingly effective in accentuating iron deficiency for although only 0.67 ppm molybdenum was present in Treatment B, top growth decreased to 2.52 g from the maximum of 3.28 g in Treatment A. Further increases of molybdenum reduced growth to 0.82 and 0.39 g in Treatments C and D respectively. These decreases correlated with marked intensification in the terminal chlorosis characteristic of iron deficiency.

Analyses for iron and molybdenum show that in spite of the sharp decreases in growth in Treatments B, C, and D, the iron content of the leaf and stem tissue remained constant at approximately 30 ppm. This would seem to indicate that 30 ppm is the critical iron content for growth under the conditions of this experiment, and that yield was determined by the availability to the plants of sufficient iron to maintain the content of the tops at this level.

The iron content of the roots also was approximately 30 ppm in Treatments A and B. However, with higher molybdenum concentrations in the culture solution in Treatments C and D, the amount of iron rather than remaining constant as in the top growth increased markedly to 99 and 171 ppm.

An attempt was made to determine if the reverse of the effect described above also could be demonstrated, that is if increasing concentrations of iron added to the culture medium would accentuate molybdenum deficiency. When molybdenum was omitted from the culture solution and iron added in concentrations of 0.66, 1.32, and 3.30 ppm, the results presented in table III were obtained. The weights of tissue from the duplicate cultures rather than average yields are included to show that except for one culture of Treatment B, the results definitely show that as the iron concentration in the culture medium increased growth decreased from a maximum of approximately 2.8 g in Treatment A to only 0.2 g in Treatment C. Visible observations indicated these decreases to be due to molybdenum deficiency.

The most likely explanation for the inconsistency in Treatment B would seem to be that one culture had become contaminated with molybdenum. The experiment was repeated employing a wider range of iron concentrations, and during early stages of growth there were visual indications of effects similar to those reported in table III. Unfortunately, these differences disappeared by the conclusion of the experiment and equally severe molybdenum deficiency symptoms were present in all treatments. It may be significant that growing conditions were quite different during the two experiments. In the initial trial, cloudy and cool weather prevailed; during the second, temperatures were very high and sunlight intense. Possibly there is only a relatively slight difference in molybdenum availability associated with varying iron supply and this is reflected in growth differences only if a minimum rate of supply of molybdenum to the top growth is necessary during periods of slow growth.

TABLE III

EFFECTS OF INCREASING IRON CONCENTRATIONS IN THE CULTURE MEDIUM IN ACCENTUATING MOLYBDENUM DEFICIENCY

TREATMENT	CONC ADDED TO CULT SOLN, PPM		OVEN-DRY WT OF TOPS AND ROOTS (G) IN DUPLICATE CULTURES	
	Fe	Mo	A	B
A	0.66	0.00	2.72	2.92
B	1.32	0.00	0.99	7.68
C	3.30	0.00	0.23	0.23
D	0.66	0.01	4.97	6.02

The culture period was 27 days. The indicated concentrations of iron were added to the cultures 3 times during this interval.

DISCUSSION

An increase in the concentration of any constituent of a culture medium to levels far in excess of normal probably will result in essential element interactions

which contribute to reduced growth. These interactions are of significance only when element concentrations reasonably close to those employed in routine culturing of plants are involved as in the present situation in which as little as 0.67 ppm molybdenum accentuated iron deficiency. The nature of this interaction is of immediate interest, particularly because a cation and anion are involved thus making unlikely the possibility of a direct competition in the activation of an iron containing enzyme as sometimes is proposed for iron-manganese antagonisms. Inactivation of the iron through formation of an iron-molybdenum precipitate of very low solubility is a possibility and is supported by the data in table II showing a constant iron content in top growth although root contents increased as higher molybdenum levels were added to the culture solution. Warrington (17) also suggests that molybdenum affects the upward translocation of iron. It is difficult to determine by analyses of the roots whether the proposed iron-molybdenum precipitate adhered to the roots after forming in the culture medium or formed in the roots following absorption of the iron and molybdenum. However, since very low concentrations of the 2 elements are involved (0.11 and 0.67 ppm of iron and molybdenum added to the culture medium) it seems more likely that through absorption and accumulation the concentrations of these elements within the plant are raised to the values reported by Jones (10) to be necessary for ferric molybdate precipitation. The mechanism involved would be similar to that reported by Biddulph (4) for formation of iron-phosphate precipitates in plant tissue which result in reduced iron availability.

It is impossible to evaluate definitely the reasons for the directly contrasting results presented in this paper and those obtained by Millikan. However, a possible explanation is suggested by the data from Treatments Q to T in table I. Cultures in this series received 67 ppm molybdenum, a very toxic concentration as shown by almost complete lack of growth, but the chlorosis observed was less than in cultures receiving much lower concentrations of molybdenum. Apparently the effects of the molybdenum were so severe that after transplanting the seedlings to the culture solutions, symptoms of molybdenum toxicity masked the iron chlorosis or growth ceased before iron chlorosis developed. On the basis of observations alone, this could have been interpreted as a beneficial effect of molybdenum. However, it seems doubtful that practical significance should be attached to this effect unless it results in plant growth comparable to control cultures and is produced by lower concentrations than the 5 to 25 ppm reported by Millikan.

Several possible applications of the results obtained to agriculture are apparent. In the first place, the data indicate that molybdenum application would not be a practical means of alleviating manganese toxicity in very acid soils and probably toxicity due to other metals. However, the capacity of relatively low concentrations of molybdenum to directly affect iron availability might be of importance in alkaline soils in which molybdenum availability is at a maximum but iron at a minimum. As reported in table II, iron chlorosis was associated with tissue contents of molybdenum as low as 54 ppm, and the results of Barshad (3) show that the molybdenum content of a number of plant species collected from the field exceeded this value. While the results are inconclusive the possibility that high levels of iron may accentuate molybdenum deficiency also has been indicated in this paper. This could be a contributing factor to the generally decreased availability of molybdenum to plants in acid soils even though Stout et al (15) have shown that in nutrient cultures decreasing pH promotes the capacity of plants to absorb molybdenum. This effect would be associated with quantities of iron far less than provided in experiments by Jones (9) showing molybdenum availability in soils to be affected by the soil ferric oxide content.

Summary

In direct contrast to results reported by other investigators, molybdenum was found to accentuate iron chlorosis in tomatoes induced by excess concentrations of manganese in the nutrient medium. Tissue contents of iron, manganese, and molybdenum correlated closely with visual observations and growth data, for the iron content decreased with increasing concentrations of either manganese or molybdenum in the external medium. Further experiments on iron-molybdenum antagonism showed that as little as 0.67 ppm molybdenum added to the culture medium induced iron chlorosis and reduced growth. It is proposed that this interaction is due to formation of an iron-molybdenum precipitate of very low solubility in the root tissue which makes iron unavailable to the top growth. The results also indicate that high concentrations of iron may accentuate molybdenum deficiency. The significance of the results in terms of plant nutrition and agriculture are discussed.

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FURTHER STUDIES ON COMPARATIVE MOBILITY OF LABELED HERBICIDES[1,2]

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The primary object of the work described in this paper was to study comparatively the absorption and translocation of several herbicides. The fate and toxic action will be the subject of future work. Consequently the various labeled molecules were used at the lowest dosage level that would produce satisfactory autographs, in order to keep toxicity at a minimum. For this reason, these labeled materials may be looked on as simply a variety of isotopic tracers employed to discover the inherent differences in behavior of different molecules as they penetrate plant tissues and move in the vascular channels.

We have learned from previous work (5, 10) that different herbicides move in different quantities and at different rates in whole plants and in potato tuber tissue. Low mobility may result from active accumulation by living cells (9) at points of application, or from lack of an active sink. High mobility may result from lack of active accumulation or metabolism at the point of application. It also requires rapid movement of food materials in the plant. The complex interaction of these several variables suggests a detailed study of mobility as a function of age and leaf maturity, and of other factors that regulate food movements in plants.

Some may question the use of radioautographs as evidence for movement of specific compounds pointing out that the compound applied may undergo decomposition or chemical rearrangement during penetration or translocation. It is true that many compounds do, of which urea is a well known example. There is evidence, however, that many of the herbicides are quite stable in plants. For instance, 2,4-D has been shown to persist in plants for months or even for years. In the use of labeled 2,4-D we often find typical formative effects in the regions of high accumulation as shown by autographs. And certain studies are showing that dalapon is very stable in the cotton plant (7). In the present exploratory work, factors responsible for distribution of the labels are under investigation. When these are understood, studies on the fate of the applied chemicals can be pursued on a more logical basis for, from radioautographs, one has an indication of where an applied chemical is located and hence he may sample his treated plants intelligently.

METHODS[3]

Barley, Zebrina, and cotton plants were grown in nutrient solutions in the greenhouse. Tracer solutions of 2,4-D*, ATA*, MH*, IAA*, urea*, and monuron* were made up in 50 % ethyl alcohol con-

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[3] The following abbreviations and trade names are used: ATA, 3 amino,-1,2,4 triazole; dalapon, sodium 2,2 dichloropropionate; IAA, indole acetic acid; MH, maleic hydrazide; monuron,3,(*p*-chlorophenyl)-1,1-dimethylurea; 2,4-D, 2,4-dichlorophenoxyacetic acid. Labeling in all cases was with C^{14}. The asterisk implies "radioactive."