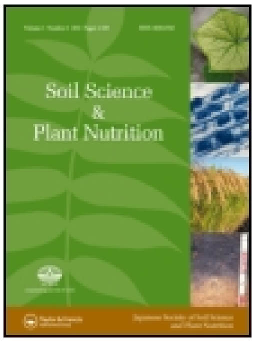

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INTERACTION BETWEEN IRON AND MANGANESE IN THE RICE PLANT

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The importance of the ratio of iron to manganese in plant tissue has been pointed out by several workers and data have been presented suggesting that a ratio of 1.5 to 2.5 is required for normal growth (1).

In oats, manganese deficiency symptoms have been reported to be identical to those of iron toxicity, and iron chlorosis has been produced by increasing the manganese level (2). Chlorosis caused by manganese excess was corrected by the addition of iron. In this case the chlorotic and the normal plants had the same iron content, indicating that manganese had not limited iron uptake but rather had reduced the activity of iron in the plant (3). In soybean, the optimum ratio of soluble manganese was found to be about 2, both in the growth medium and in the tissue (4). The same investigators claimed that the symptoms of iron deficiency or manganese toxicity appear when the ratio is lower than 2 and iron toxicity or manganese deficiency appears when it is higher. They further stated that the iron content of plants is higher at a low than at high manganese level in the growth media, indicating that iron and manganese show reciprocal relations in absorption. Manganese in the rice plant decreases as iron supply increases (5). In lespedeza, application of iron reduced the degree of manganese toxicity by depressing manganese uptake (6). In rice an increase in the level of iron in the culture solution caused a decrease in manganese content (7).

It has been reported that excess manganese hinders the translocation of iron by causing the iron in the plant to be converted into an insoluble form (8, 9). It was suggested that with a low level of manganese in the plant, iron is in the ferrous form and may cause iron toxicity, while at a high manganese level iron may be in the ferric form and iron deficiency may result (4).

In the rice plant, iron toxicity is characterized by the development of brown pindots on the interveinal tissue of lower leaves. They may develop, in more serious cases, into brown discolorations all over the leaf (10). Manganese deficiency is evidenced by chlorotic interveinal areas on the lower leaves. As the deficiency becomes more advanced, these may develop into brown streaks (11). Thus, iron excess and manganese deficiency can be easily differentiated. Similarly, iron deficiency and manganese toxicity can be easily differentiated; the former is indicated by a chlorosis of the young leaves (12), and the latter by the development of brown spots on the leaves (especially on the veins of lower leaves) and by the rolling of the leaves (11).

The rice plant is noted for its resistance to high levels of iron and manganese and its susceptibility to iron chlorosis. Apparently, it is susceptible to iron chlorosis because of the oxidizing power of the root system which serves to oxidize the element from its ferrous to the ferric form (12). The plant on submerged soils may suffer from an excess of iron if an extremely high iron concentration is reached in the solution (13). Manganese content of the rice plant growing under submerged conditions is often very high because of a high manganese concentration in the soil solution, and yet the plant shows no signs of any abnormality (11).

These observations suggest that the interaction between iron and manganese in the rice plant may be different from that in other crops. The following experiments were designed to examine this possibility.

Experimental Methods and Results

Effect of iron level on manganese content of the plant

Two-week old Peta seedlings were transplanted to 4-liter pots containing a standard culture solution

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Table 1. Manganese content of rice plants as affected by iron and manganese levels in culture solution.

Mn level (ppm)	Fe level (ppm)	Mn content (ppm)	
		Shoot	Root
1	0	430	125
	0.1	300	35
	10.0	230	24
	40.0	150	13
40	0	2130	1880
	0.1	1680	1630
	10.0	1200	1380
	40.0	850	860

at pH 5.0. These were subjected to varying levels of iron at 1 and 40 ppm (Table 1) with manganese supplied as $MnSO_4$ and iron as $FeCl_3$. The culture solutions were renewed weekly and the plants harvested after a 45-day treatment. The shoots and roots were separated and analyzed for manganese.

Manganese content of the shoot as well as of the roots decreased with increases in iron level in the culture solution at both manganese levels. At 1 ppm Mn the decrease was more noticeable in the roots than in the shoot.

The data demonstrate that manganese uptake is depressed by iron. The higher the iron level, the less the manganese uptake, and at a low manganese level, manganese translocation from the roots to the shoot is promoted by higher iron levels.

Effect of manganese level on iron content of the plant

Sixty-day old Peta plants grown in a standard culture solution were subjected to varying levels of manganese at 1 ppm Fe as $FeCl_3$. The culture solution, kept at pH 4, was changed every week. After 36 days the plants were harvested, separated into young leaves, old leaves, culm, and roots, and analyzed for iron.

With increase in manganese level in the culture solution, the iron content of the leaves and roots decreased. The decrease was more pronounced in the roots and was smaller in the old leaves than in the young ones. In the culm, the trend was reversed and the highest Fe contents were associated with the highest levels of Mn in the solution (Table 2).

These data indicate that the iron content of the roots decreases with increases in manganese level of the solution. At a high manganese

Table 2. Iron content of various organs of rice plants as affected by manganese level of the culture solution.

Mn level (ppm)	Fe content (ppm)			
	Young leaf blades	Old leaf blades	Culm	Roots
0	184	187	581	2316
0.5	154	179	543	2800
100.0	88	145	998	1092
500.0	88	130	1372	890

level, more of the iron passing through the roots is deposited in the culm and less is translocated to the new growing leaves.

Interaction of pH, iron form, and manganese level

Thirty-five-day old Peta plants grown in 40-liter pots, two plants each, were divided into 20 treatments. Treatments were factorial of two iron forms, ferric and ferrous sulfates at 100 ppm Fe; two manganese levels, 1 and 50 ppm as $MnSO_4$; and five pH values, 3, 4, 5, 6, and 7. The pH values of the culture solution were checked every day. The culture solutions were renewed once during the treatment and the experinent was discontinued after 45 days. The shoots and roots were separated and analyzed for iron and manganese.

At pH 3, with ferrous iron, the plants were almost dead, while with ferric iron they were stunted, the older leaves were dead, and the young leaves were dark green. At pH 4 the plants with ferrous iron at the low manganese level displayed scattered brown spots, characteristic of iron toxicity, during the early stages of growth, but these disappeared at later stages. At pH 5, all plants were healthy. At pH 6, slight iron chlorosis was observed with ferric iron at the high manganese level. At pH 7, the plants with ferric iron were chlorotic, especially at the high manganese level where scattered light brown spots were observed on the chlorotic leaves. There was no chlorosis with ferrous iron.

The plant weight was greater with ferric iron at low pH values, and with ferrous iron at high pH values (Table 3). With ferric iron the plants grew well between pH 4 and 6 at the low manganese level, but growth was retarded slightly by high manganese at pH 6. With ferrous iron good growth was obtained between pH 5 and 7. The optimum pH was higher when the man-

Table 3. Dry weight and iron and manganese contents of rice plants grown at various pH values with ferric and ferrous iron at each of two manganese levels.

Iron source	Mn (ppm)	pH	Plant weight (g/plant)	Content in shoot (ppm)		Fe/Mn
				Fe	Mn	
Ferric	1	3	8	508	75	6.77
		4	91	154	294	0.52
		5	107	140	550	0.25
		6	102	146	663	0.22
		7	45	112	731	0.15
	50	3	10	595	806	0.74
		4	114	112	1413	0.08
		5	103	118	3123	0.04
		6	91	100	5700	0.02
		7	14	72	5563	0.01
Ferrous	1	3	5	1785	69	25.80
		4	58	236	99	2.39
		5	89	140	313	0.45
		6	86	146	562	0.26
		7	84	140	438	0.32
	50	3	5	1085	200	5.42
		4	82	218	969	0.22
		5	95	124	1794	0.07
		6	89	132	3875	0.03
		7	83	110	3775	0.03

ganese concentration in culture solution was low.

With increase in pH, the iron content of the shoot decreased sharply from pH 3 to 4 and then slightly from pH 4 to 7. It was higher with ferrous than with ferric iron and was higher with the low than with the high manganese level in the culture solution. The manganese content increased with increase in pH and was consistently higher with ferric than with ferrous iron. The content was much higher at the high manganese level than at the low manganese level.

In general, conditions which caused manganese content to increase resulted in a decrease in iron content. However, the changes of manganese content with the change of pH or iron form were greater than the changes in iron content.

The Fe/Mn ratio in plant tissue varied from 0.01 to 25.8. The ratio was not simply correlated with the symptoms in the plant. Plants at pH 7 with ferric iron at 1 ppm Mn were chlorotic and the Fe/Mn ratio was 0.15, whereas those with ferrous iron at 50 ppm Mn and pH 6 and 7 were normal and green although the Fe/Mn ratio was below 0.03. Likewise, iron or manganese contents alone were not closely correlated with the degree of chlorosis.

With ferric iron at 50 ppm Mn and pH 7, the leaves were chlorotic and light brown spots, which may have been a type of manganese toxicity symptom, were observed. The iron and manganese contents were 72 ppm and 5563, respectively.

These data indicate that the iron deficiency and the manganese toxicity symptoms are different from each other and develop independently. Because there is an antagonism between the uptake of the two elements, the symptoms frequently appear simultaneously.

Effect of manganese level on the susceptibility to iron toxicity

Twelve-day old Peta plants, grown in 16-liter pots, two plants each, were subjected to five levels of manganese: 0, 0.01, 0.05, 0.10, and 10 ppm Mn as

Table 4. Effect of manganese level on iron content of rice plants at varying levels of iron.

Levels in culture solution		Dry weight of shoot (g/plant)	Fe content		Mn content	
Fe	Mn		Shoot (ppm)	Roots (%)	Shoot (ppm)	Roots (ppm)
2	0	10.1	305	0.28	10	0.4
	0.01	10.5	280	0.28	35	4.0
	0.05	10.5	221	0.23	85	7.0
	0.10	13.8	179	0.23	111	28.0
	10.00	14.4	179	0.23	1500	969.0
75	0	6.8	861	6.99	14	Trace
	0.01	8.7	805	5.59	26	Trace
	0.05	9.2	672	4.09	38	50.0
	0.10	12.3	645	2.98	33	26.0
	10.00	9.5	595	3.96	782	119.0
150	0	6.2	5126	16.9	Trace	Trace
	0.01	6.1	1204	14.7	11	Trace
	0.05	6.3	1288	13.7	23	Trace
	0.10	6.5	1064	21.3	33	Trace
	10.00	6.1	690	20.0	605	80.0

$MnSO_4$. Six pots were assigned to each level of manganese. After 30 days, the plants at each manganese level were divided into three groups. Each group was subjected to the following iron levels: 2, 75, and 150 ppm Fe as $FeSO_4$. The culture solution was adjusted to pH 4.0. A sample taken 17 days after the start of the iron treatments was analyzed for iron and manganese.

At all iron levels, the iron content of the shoot decreased with the increase of manganese level (Table 4). At 2 and 75 ppm Fe, but not at 150 ppm Fe, there was a tendency for the iron content of the roots to decrease with increases in manganese level of the culture solution.

At 0 and 0.01 ppm Mn, manganese deficiency symptoms were apparent before iron was introduced as a variable treatment. Iron toxicity symptoms developed at 75 and 150 ppm Fe regardless of manganese level of the plant. The manganese-deficient plants did not show any greater susceptibility to iron toxicity than the normal plants. At 150 ppm Fe, the iron toxicity symptoms were more apparent at 10 ppm Mn than at lower iron levels.

These results indicate that when the manganese content of the plants is high, iron uptake is depressed. However, if the iron level of the substrate is very high, even plants which are high in manganese suffer from iron toxicity. The manganese-deficient plants are not necessarily more susceptible to iron toxicity.

Discussion

The existence of a number of interactions between iron and manganese was demonstrated in these studies. It was observed that an increase of iron or manganese in the growth media causes a decrease of manganese or iron content of the plant, respectively. The change is most noticeable in the roots, possibly indicating that these elements are competing for absorption sites.

An increase of manganese level causes an increase of iron content in the culm and a decrease in the young leaves. Thus, the distribution pattern of iron in the plant is changed by the level of manganese.

Generally speaking, conditions which caused iron content to increase (low pH, ammonium nitrogen, and a ferrous iron source) caused manganese content to decrease.

All these trends suggest interaction between iron and manganese in the development of toxicity or deficiency symptoms. However, the Fe/Mn ratio of the plants did not give a clear-cut picture as to the critical condition at which symptoms develop.

It appears that iron chlorosis and manganese toxicity symptoms are completely different from each other and are caused by a low level of iron or a high level of manganese, respectively. However, because of antagonistic reactions in the uptake of these elements, the two types of symptoms frequently develop on the same plant.

Iron toxicity and manganese deficiency symtoms are also different from each other. A high level of manganese may interfere with iron uptake and reduce the possibility of iron toxicity.

The root environment causing one set of symptoms to appear may also result in the occurrence of the other, but it seems unlikely that the plant mechanisms involved are interrelated. Since there is an antagonistic effect between iron and manganese uptake, addition of iron or manganese may aggravate or depress the development of symptoms. However, the range within which the symptoms may be controlled in this way is rather narrow.

Increasing the manganese content of the soil solution may counteract iron toxicity. However, iron toxicity on a submerged soil is frequently accompanied by low soil pH and the iron level in the soil solution is very high. Thus, large amount of manganese is needed to counteract the high level of iron and such applications may induce manganese toxicity. Manganese toxicity is not frequent, and application of iron to prevent it would rarely have practical significance.

Summary

1) An increase of iron or manganese level in the growth media causes decrease of manganese or iron content of the rice plant, respectively.

2) Iron toxicity symptoms are different from manganese deficiency symptoms, and similarly, manganese toxicity symptoms are different from iron deficiency symptoms.

3) The range within which iron toxicity can be remedied by manganese application appears to be rather narrow, and manganese toxicity is rare. Thus the practical implication of iron-manganese antagonism may not be as important in rice as it has been said to be in other crops.

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