Excess Manganese Disorder in Fruit Trees

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In the cultivation of fruit trees in Japan, a number of disorders, the causes of which are not evidently known yet, are observed. Once such disorders of fruit trees occurred, they cause damage which often lasts for a long period.

In recent orchard management, soil management becomes less intensive due to labor shortage, and continuous application of chemical fertilizers is practiced, resulting in promoting soil acidification. It is considered that these trends may serve, in many cases, as important factors for the occurrence of the disorders of fruit trees. Of many kinds of disorders, the author took up the disorder associated with excess Mn uptake for study. This disorder is observed on plants of satsuma mandarin, apple, Japanese persimmon, etc. On affected satsuma mandarin trees, leaves show brown spots and then fall, i.e., the symptom so-called abnormal defoliation. On apple trees, cracks and depressions appear on the bark of trunks and branches, and the trees lose their vigor, i.e., the symptom of internal bark necrosis. With Japanese persimmon, parts of the fruit rind still remain to be green as green spots at the fruit maturity, i.e., the symptom called greenish spot disorder (Plate 1).

Since it was recognized that all these disorders were associated with apparent increase of Mn content of trees, characteristics of Mn absorption by plants and behavior of Mn in plants were examined in relation to the occurrence of the disorders, with an aim of making clear the cause of the disorders.

Soil characteristic of orchards showing excess Mn disorder

Results of soil analysis of orchards showing abnormal defoliation of satsuma mandarin (hereafter referred to as affected orchards) and those with healthy trees (referred to healthy orchards) are given in Table 1.[1] Soils of affected orchards tend to show lower values for pH, base saturation, and Ca saturation, and higher values for water soluble Mn, 1N ammonium acetate (pH 7) soluble Mn, etc. than healthy orchard soils. Of leaves and fine roots, markedly increased Mn content in leaves was

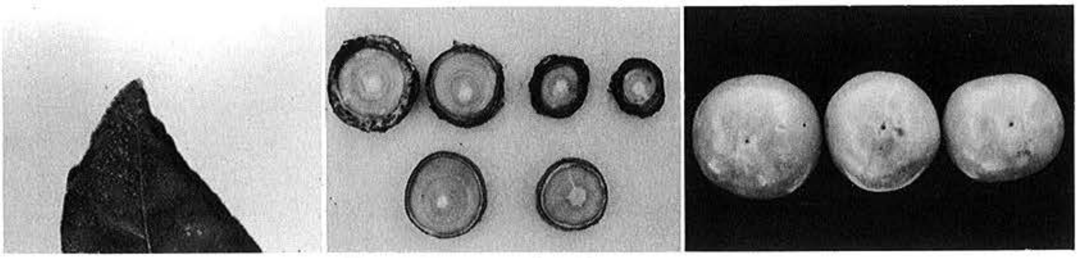

Plate 1. Excess manganese disorder
Left: Abnormal defoliation of satsuma mandarin
Middle: Internal bark necrosis of apple (upper)
Right: Greenish spot disorder of persimmon

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Table 1. The results of soil and leaf analysis in relation to the abnormal defoliation of satsuma mandarin in each soil type

Soil type and orchard		No. of soils	pH (H_2O)	Ca sat. (%)	Water sol. (ppm)		N-NH_4OAc. sol. (ppm)			CEC (me)
					Mn	Al	Mn	Al	Fe	
Granite soils	I[a]	11	5.1	45.7	2.8	2.2	19.1	2.8	8.5	9.33
	N[a]	11	5.7	66.2	0.6	0.8	6.0	1.6	7.1	8.87
Andesite soils	I	15	5.3	59.6	3.3	2.2	60.0	3.5	12.4	20.67
	N	14	5.7	64.5	1.3	0.7	27.3	2.0	10.6	20.15
Clay slate soils	I	5	4.1	19.3	6.0	2.6	17.7	2.2	6.8	13.91
	N	5	4.5	27.4	0.6	1.7	7.5	2.0	4.3	18.24

Soil type and orchard		No. of soils	Exch. cation (me)					Base sat. (%)	Leaf analysis (ppm)			Mn/Fe	(%)
			Ca	Mg	K	Na	Total		Mn	Fe	Al		N
Granite soils	I[a]	11	4.26	0.91	0.63	0.14	5.94	63.7	235.3	147.3	97.1	1.6	3.98
	N[a]	11	5.87	0.93	0.70	0.13	7.63	86.0	73.8	163.0	109.0	0.5	3.61
Andesite soils	I	15	12.32	2.61	1.55	0.15	16.63	80.5	296.8	169.7	113.1	1.7	3.51
	N	14	13.00	2.64	2.19	0.14	17.95	89.1	48.2	194.7	112.0	0.2	3.60
Clay slate soils	I	5	2.69	0.94	0.86	0.07	4.56	32.8	262.4	140.8	145.8	1.9	3.95
	N	5	5.00	1.51	0.93	0.09	7.53	41.3	75.2	148.9	90.0	0.5	3.76

a) I: Affected orchards by abnormal defoliation
N: Normal orchards

Table 2. Comparison of soil chemical properties between normal and affected orchards of apple

Orchard	No. of soils	Soil depth	pH (H_2O)	Ca sat. (%)	Water sol. (ppm)		N-NH_4OAc. sol (ppm)			CEC (me)	Exch. cation (me)					Base sat. (%)
					Mn	Al	Mn	Al	Fe		Ca	Mg	K	Na	Total	
I[b]	27	A[a]	5.18	37.40	2.9	2.5	43.0	22.2	7.3	24.65	9.22	1.09	1.53	0.11	11.95	48.48
		B[a]	4.85	28.18	4.3	4.6	42.4	32.1	10.8	20.58	5.80	1.19	0.88	0.14	8.01	38.92
N[b]	18	A	5.45	43.46	0.8	1.9	34.5	12.9	16.1	23.70	10.30	1.37	1.79	0.14	13.60	57.38
		B	5.23	36.23	0.7	1.8	24.9	19.3	12.4	19.32	7.00	1.20	1.09	0.16	9.45	48.91

a) A: Surface soil (0-15 cm)
B: Subsoil (30-40 cm)

b) I: Affected orchard soils by internal bark necrosis
N: Normal orchard soils

Table 3. Soil analysis of Japanese persimmon orchards in relation to the greenish spot disorder

Prefecture	Orchard	Soil depth (cm)	pH		Water sol. Mn (ppm)	N-NH_4OAc. sol Mn(ppm)		N-HN_4OAc.(H)[c] sol. Mn(ppm)	
			H_2O	KCl		pH 7	pH 4.5	pH 7	pH 4.5
Tokushima	D[a]	0~15	5.6	4.8	7.3	85.8	284.3	810	1127
		30~40	4.7	4.0	7.1	45.3	59.0	206	292
	N[b]	0~15	5.9	5.3	2.3	62.7	279.2	604	985
		30~40	5.2	4.3	2.6	28.2	38.0	255	385

a) D: Orchards producing disordered fruits
b) N: Orchards producing normal fruits
c) (H): (IN ammonium acetate +0.2% hydroquinone) soluble manganese

observed in affected orchards as compared to healthy orchards, while no distinct difference was recognized with other inorganic components.

Almost the same tendency as above was recognized with the result of soil analysis for apple orchards showing internal bark necrosis (Table 2)[1] and Japanese persimmon orchards with greenish spot disorder (Table 3).[2] Thus, it was made clear that the soil was acidified at first and then solubility of Mn was increased for the ocurrence of the disorder associated with excess Mn uptake of tops.

Correlations between Mn content of affected leaves and soluble Mn contents of soils by the use of different solvents were determined.[1] In general, the degree of correlation was in the following order: water soluble Mn $>$ 1N ammonium acetate (pH 7) soluble Mn $\geqslant$ Mn soluble in 1N ammonium acetate (pH 4.5) + 0.2% hydroquinone $>$ 1N potassium chloride soluble Mn. This tendency indicates that more easily soluble Mn such as water soluble Mn shows higher correlations to leaf Mn content than easily reducible Mn, measured after adding hydroquinone, which is thought to express potential Mn supplying capacity of soils. The critical point for the occurrence of the disorder of satsuma mandarin was 3 ppm of water soluble Mn, and in case of 1N ammonium acetate (pH 7) soluble Mn, it was 5 ppm for clay slate soils, 20 ppm for granite soils, and about 50 ppm for andesite soils.[1]

Mn absorption and distribution in satsuma mandarin trees

In healthy plants of satsuma mandarin, a large amount of Mn is accumulated in fine roots, and only a small amount of Mn, in general, is translocated into the tops. The author made clear the reason for such distribution of Mn in the healthy plants. Strong activity of oxidase was found in healthy fine roots. Mn^{2+} is oxidized and deposited as MnO_2 in the healthy fine roots (Plate 2, 3, 4).[3] Such oxidation and deposit were not observed in roots slightly treated with heat (80°C, >3 min). Fine roots taken

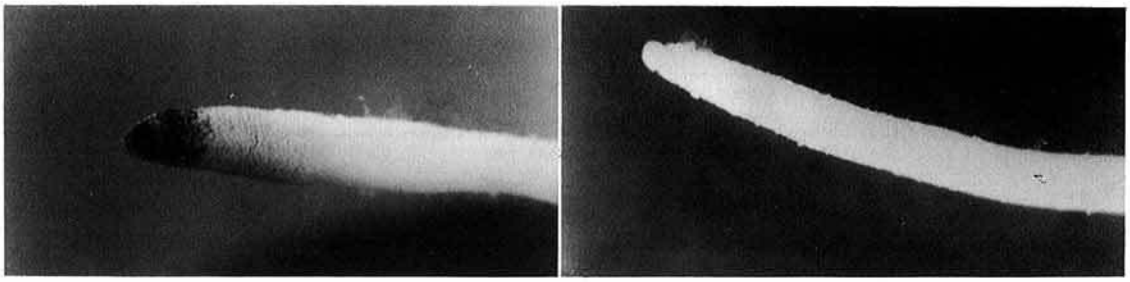

Plate 2. Manganese-oxidized substances on the surface of fine root of satsuma mandarin
Left: Healthy root
Right: Affected root by heat treatment (80°C, 3 min)

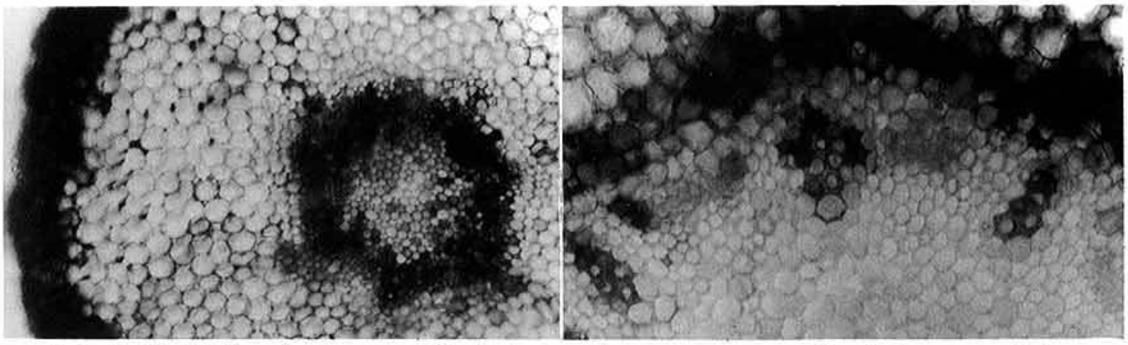

Plate 3. Distribution of manganese-oxidized substances in transverse root section of satsuma mandarin
Left: 5 mm from the apex
Right: 7 mm from the apex (xylem)

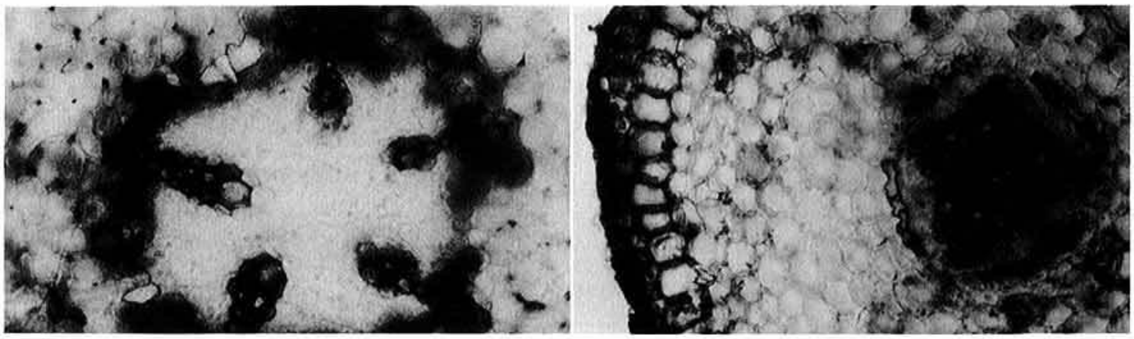

Plate 4. Oxidase activity in healthy fine root of satsuma mandarin
Left: α-naphthylamine staining
Right: Cytochrome oxidase staining

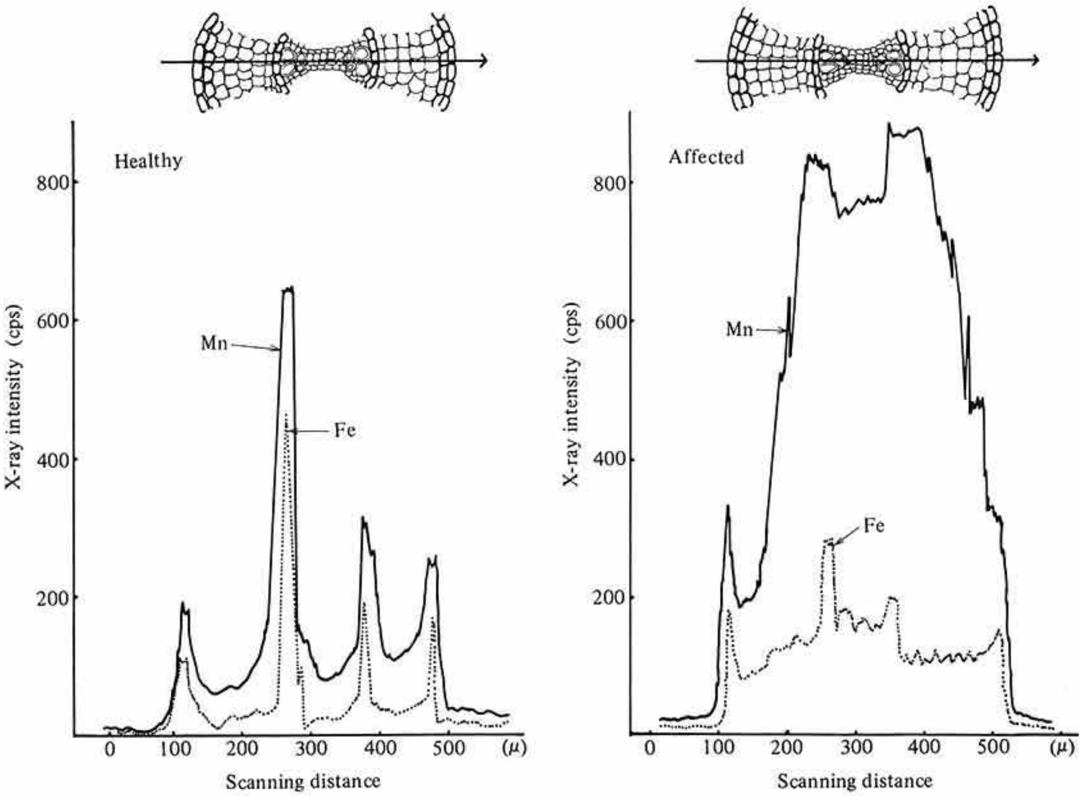

Fig. 1. Line scan profile for Fe and Mn in satsuma mandarin fine roots sampled in Nagasaki Prefecture
Left: Root of healthy plant
Right: Root of affected plant

from affected orchards showed lower values of oxygen uptake, α-naphthylamine oxidation, and H_2O_2 decomposition as compared with fine roots from healthy orchards, indicating lowered activity of the former.[4] Furthermore, it was apparently observed that Mn^{2+} entered into the inner portion of the roots more rapidly in the former than the latter, showing a strong evidence of Mn^{2+} distribution throughout an affected root[5] (Fig. 1). Thus, it was made clear that the healthy fine roots of satsuma mandarin are

Table 4. Distribution of manganese (^{54}Mn) in satsuma mandarin

Treatment	Root (%)				Root total (%)	Top (%)							Top total (%)	Transpiration (g/cm² day)
	Fine root	Medium root	Large root	Root cap		New leaf	Old leaf	Leaf total	Current shoot	1 year old branch	2, 3 years old branch	Branch total		
Mn 100 ppm	66.67	2.83	3.46	5.19	78.05	8.99	1.46	10.45	2.85	3.97	4.63	11.50	21.95	0.147
Mn 100 ppm +KCN10^{-4}M	72.95	1.71	0.89	2.19	77.74	10.36	1.82	12.18	3.22	4.21	2.65	10.08	22.26	
Mn 100 ppm +KCN10^{-3}M	71.29	2.59	0.99	2.30	77.17	12.70	0.85	13.55	2.81	3.22	3.25	9.28	22.83	0.127

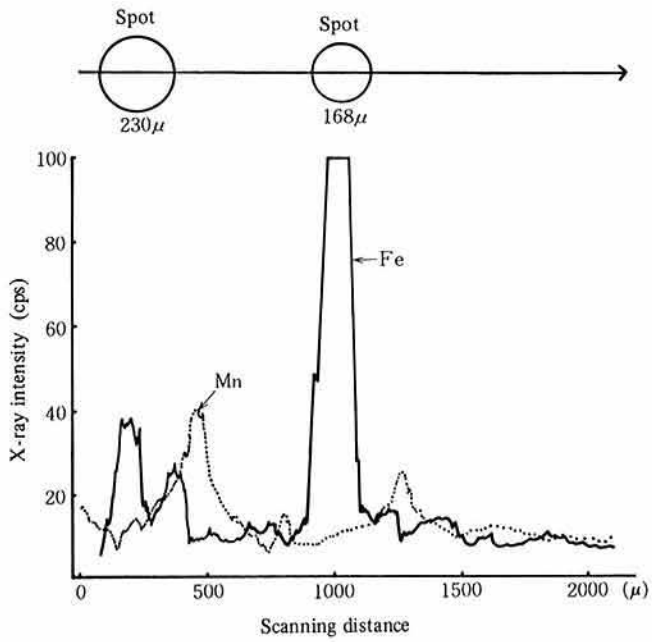

Fig. 2. Line scan profile for Fe and Mn across brown spots of satsuma mandarin leaves containing excess manganese sampled in Nagasaki Prefecture

capable of oxidizing Mn^{2+} and regulating the amount of Mn translocating into tops by depositing the oxidized Mn mainly in epidermis and endodermis of the fine roots. On the contrary, in the fine roots taken from affected orchards, these activities are lowered, so that Mn enters rapidly into roots in response to Mn concentration in rhizosphere, causing the increased Mn content in roots and increased Mn translocation to the top.

Although these results were obtained by histochemical examination of fine roots, the same tendency was recognized in the experiment on ^{54}Mn absorption by fine roots with oxidase activity inhibited by KCN treatment (Table 4). Namely, the amount of α-naphthylamine oxidation, H_2O_2 decomposition, and activities of catalase and ascorbic acid oxidase were reduced 20-30% by 1×10^{-4}M KCN, and about 40-50% by 1×10^{-3}M KCN.[6] Under such conditions, distribution of absorbed Mn to the top (new leaves) was increased, in spite of decreased transpiration.

A large number of small brown spots appeared on the surface of leaves which received excess Mn. Accumulated Fe was observed inside the spots, whereas Mn tended to accumulate outside the fringe of the spots (Fig. 2). Since polyphenol compounds increased markedly in amount in the leaves which absorbed excess Mn,[7] it can be considered that the combination of oxidized polyphenols and Fe^{3+} produced dark brown substances in portions of leaf tissue suffered from Mn toxicity,[3] and after that these substances prevent further entrance of translocated Mn into the tissue portions (brown spots), so that Mn accumulated outside the spots.

Uptake and distribution of Mn in apple trees

Excess Mn disorder found in apple trees is internal bark necrosis. Its occurrence varies with different cultivars and rootstocks. The use of *Malus sieboldii* Rehd as rootstock apparently increases the occurrence compared to *Malus prunifolia* Borkh. var. ringo Asami. It occurs in cultivars, Starking Delicious, Rolls Janet, Fuji, etc. but not in American Summer Pearmain, McIntosh Red, etc.

Fig. 3 shows ^{54}Mn uptake and translocation compared between the 2 rootstocks.[8] *Malus prunifolia* shows apparently higher ^{54}Mn content in fine roots, but smaller amount of ^{54}Mn translocated into leaves. The Mn oxidase activity of the fine roots of *M. prunifolia* was as high as that of satsuma mandarin. It seems, therefore, that a large amount of MnO_2 is deposited in fine roots, resulting in reduced amount of Mn translocation into leaves.

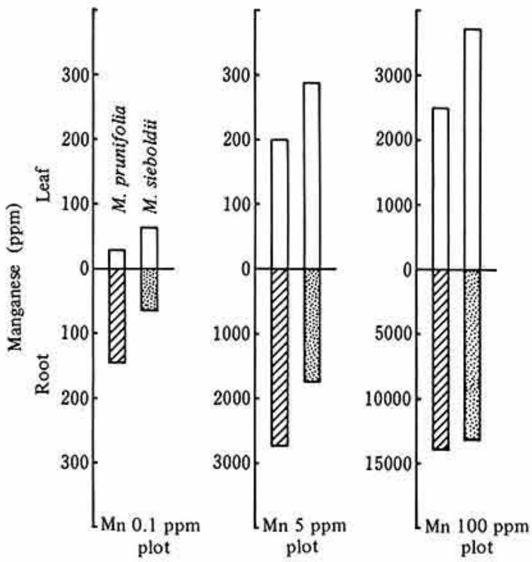

Fig. 3. Uptake and translocation of ^{54}Mn in 2 apple rootstocks, *Malus prunifolia* Borkh. var. ringo Asami and *Malus sieboldii* Rehd

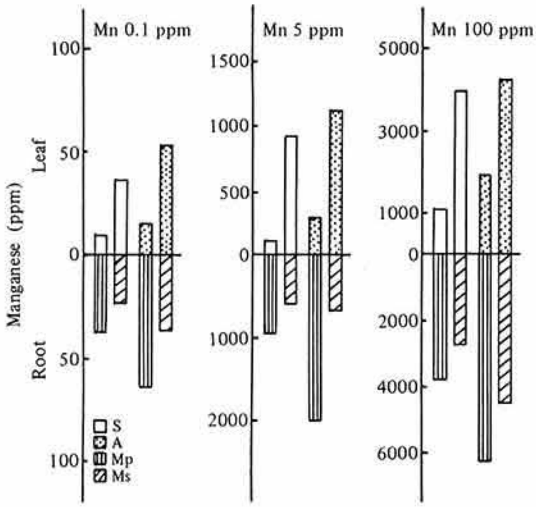

Fig. 4. Effects of rootstocks and cultivars of apple on uptake and distribution of ^{54}Mn
S: Starking Delicious
A: American Summer Pearmain
Mp: *Malus prunifolia* Borkh. var. ringo Asami
Ms: *Malus sieboldii* Rehd

Each of the 2 cultivars, Starking Delicious, susceptible to excess Mn disorder, and American Summer Pearmain, which is not susceptible, was grafted on the 2 kinds of rootstocks, and ^{54}Mn uptake was examined (Fig. 4). When *M. prunifolia* was used, Mn concentration in various parts of the top was apparently low, and that in fine roots was high. On the contrary, when *M. sieboldii* was used, the reverse relation was obtained. Mn uptake of different cultivars grafted on the same rootstocks revealed the fact that Mn content of American Summer Pearmain (not susceptible) was rather higher, than that of Starking Delicious (susceptible cultivar).

Thus, it was made clear that the rootstock, which is apt to cause the disorder, causes translocation of more Mn to the top, and that the disorder occurs in the susceptible cultivar even when the Mn content of the plant is lower than that of the non-susceptible cultivar. It indicates that the occurrence of the disorder is related to the lower tolerance of the top to excess Mn.

Uptake and distribution of Mn in Japanese persimmon trees

The greenish spot disorder, which is caused by excess Mn uptake in Japanese persimmon, occurs most frequently in a cultivar, Matsumotowasefuyu, followed by Fuyu. Results of analysis of leaves and fruits of affected plants are shown in Table 5.[2] In affected fruits, only Mn content apparently increased, particularly fruit rind showed a higher rate of increase. Comparison of Mn contents in leaves and fruits between affected and healthy orchards showed that there is a risk of occurring the disorder in Matsumotowasefuyu at the Mn contents higher than ca. 700 ppm in leaves, 70 ppm in rind, and 50 ppm in flesh.[2]

Uptake of ^{54}Mn was compared between Matsumotowasefuyu (susceptible) and Hiratanenashi (non-susceptible). Like the case of apple trees, the amount of Mn translocated into the top was rather smaller in Matsumotowasefuyu than in Hiratanenashi.[2]

Mn contents of healthy plants of cultivars, Matsumotowasefuyu, Jiro, and Fuyu, cultivated in a same field of a healthy orchard were determined (Table 6). Matsumotowasefuyu, which is most liable to the disorder, showed lower Mn content than other cultivars. This result is quite similar to the case of apple trees, already described. It suggests that susceptible cultivars are less tolerant to Mn.

Table 5. Chemical analysis of Japanese persimmon Matsumotowasefuyu in relation to the greenish spot disorder in Tokushima Prefecture

Organ	Tree	N	P	K	Ca	Mg	Mn	Fe	Cu	Zn
				(%)				(ppm)		
Leaf	D[a]	2.50	0.12	1.29	1.60	0.24	831 (1.92)[c]	75	37	56
	N[b]	2.76	0.18	1.40	1.69	0.26	432 (1.00)	93	25	59
Peel	D	0.74	0.07	0.88	0.11	0.05	94 (2.69)	25	7	8
	N	0.81	0.09	0.87	0.11	0.07	35 (1.00)	27	8	11
Flesh	D	0.63	0.08	0.94	0.06	0.04	57 (1.90)	23	4	8
	N	0.63	0.09	0.92	0.06	0.04	30 (1.00)	24	4	8
Calyx	D	1.03	0.08	0.84	0.69	0.05	281 (1.55)	20	7	19
	N	1.09	0.07	0.73	0.85	0.09	181 (1.00)	19	7	20
Seed	D	1.59	0.55	0.89	0.05	0.13	182 (1.46)	20	7	9
	N	1.61	0.63	0.92	0.08	0.14	125 (1.00)	21	8	10
Fine root	D	1.73	0.17	0.90	1.91	0.15	155 (1.20)	654	153	214
	N	1.65	0.31	1.08	2.07	0.23	129 (1.00)	782	212	234

a) D: Trees bearing disordered fruits
b) N: Trees bearing normal friuts
c) ( ): Ratio for N average

Table 6. Comparison of manganese contents among Japanese persimmon cultivars: most susceptible cv. 'Matsumotowase-fuyu', less susceptible 'Fuyu' (normal tree), and tolerant 'Jiro' (normal tree)

Prefecture	Cultivar		Manganese (ppm)		
			Leaf	Peel	Flesh
Nara	Fuyu	(2)[c]	1313	91	70
	D[a]	(9)	1270	167	102
	N[b]	(6)	755	72	54
Tokushima	Fuyu	(2)	847	84	64
	Jiro	(2)	1248	83	64
	D	(5)	827	90	75
	N	(3)	432	35	30
Fukuoka	Fuyu	(1)	476	22	22
	D	(1)	635	62	31
	N	(1)	364	17	11
Average	Fuyu	(5)	959	77	59
			(1.55)[d]	(1.35)	(1.31)
	Jiro	(2)	1248	83	64
			(2.02)	(1.46)	(1.42)
	D	(15)	1080	134	89
			(1.74)	(2.35)	(1.98)
	N	(10)	619	57	45
			(1.00)	(1.00)	(1.00)

a) D: Matsumotowasefuyu trees bearing disordered fruits
b) N: Matsumotowasefuyu trees bearing normal fruits
c) ( ): Sample numbers
d) ( ): Ratio for N average

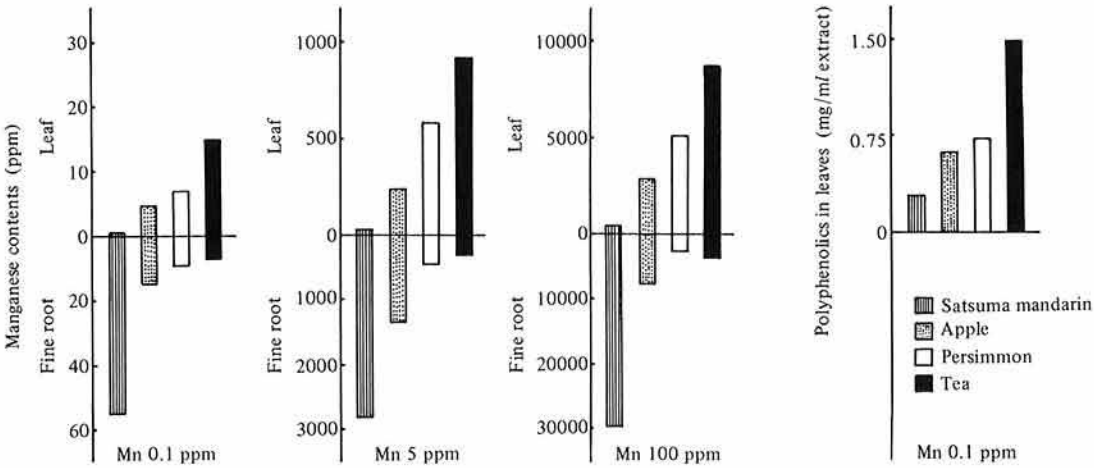

Fig. 5. ^{54}Mn uptake and water soluble polyphenolics in leaves of several fruit trees

Relationship between tolerance to Mn and polyphenol compounds

Varietal differences in the tolerance to Mn are already shown with apple and Japanese persimmon. Different tree species also differ in the tolerance to Mn. For example, the excess Mn disorder occurs in satsuma mandarin at leaf Mn contents exceeding 100 ppm, and in apple (Starking Delicious) at leaf Mn contents higher than 300 ppm, whereas no abnormality occurs in tea plants at leaf Mn contents above 3,000 ppm. It seems that highly tolerant plants may have some mechanism to suppress Mn toxicity.

The fact that more Mn is translocated into the top of tolerant tree species was already mentioned with apple and Japanese persimmon. Fig. 5 shows the result of a solution culture experiment in which satsuma mandarin, apple (Starking Delicious), Japanese persimmon (Fuyu), and tea plants (Yabukita) were treated with 0.1, 5, 100 ppm of Mn.[11] In this case, too, the amount of Mn uptake by leaves was greatest in tea plants (most tolerant), followed by Japanese persimmon, apple, and satsuma mandarin in that order. On the other hand, Mn contents in roots was highest in satsuma mandarin, followed by apple, Japanese persimmon, and tea in that order. Since fine roots of tea showed markedly low activity to oxidize Mn^{2+} ion,[10] the majority of Mn absorbed by roots seems to be translocated into the top. On the contrary, fine roots of satsuma mandarin have strong oxidase activity by which Mn^{2+} is oxidized and deposited as MnO_2 in epidermis and endodermis of the fine roots. Therefore, only few Mn is translocated to the top, thus preventing the occurrence of excess Mn disorder.

As mentioned above, the amount of Mn translocation into the top is controlled by the activity of oxidizing Mn^{2+} in roots. Then, what is the mechanism of the tolerance against Mn translocated into the top?

Paying attention to the fact that polyphenol content is generally high in tolerant tree species, the polyphenol content of leaves of satsuma mandarin, apple, Japanese persimmon, and tea was determined (Fig. 5).[11] It was shown that tea and Japanese persimmon, which are apparently more tolerant to Mn than satsuma mandarin, contained more polyphenol compounds.

Toxicity of Mn^{2+} to cells was studied using epidermal cells of onion scale.[10] All of the cells were killed by the treatment of 1×10^{-2}M Mn^{2+} ($MnCl_2$) for 10 hr, whereas their survival period was extended by co-existence of epigallocatechin or catechin + gallic acid, abundantly contained in tea

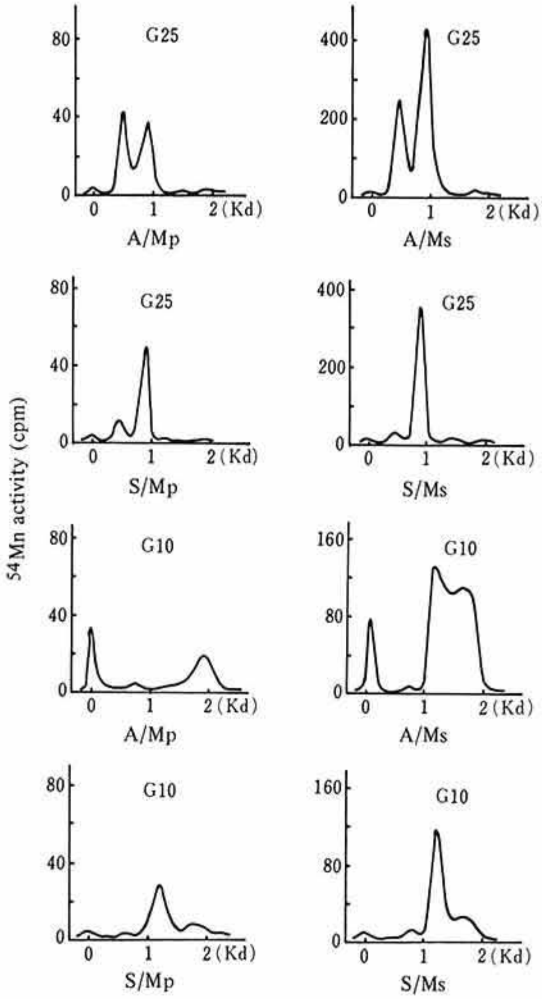

Fig. 6. Sephadex G10 and G25 gel chromatography of ^{54}Mn in centrifugal supernatant liquid (174,000×g) of apple leaves
A: American Summer Pearmain
S: Starking Delicious
Mp: *Malus prunifolia* Borkh. var. ringo Asami
Ms: *Malus sieboldii* Rehd

leaves.

By using the centrifugal method, Mn in leaves was separated into successive fractions: 200×g, 600×g, 10,000×g, 174,000×g, and final supernatant S. The fraction S was further separated by Sephadex G10 and G25.[9] With both apple cultivars, American Summer Pearmain (highly tolerant) and Starking Delicious (susceptible), the S fractions contained 60-70% and the 200×g fractions contained 30-35% of the total amount of Mn in leaves: both fractions occupied nearly 95% of the total. The result of the separation by Sephadex is given in Fig. 6. American Summer Pearmain showed a peak of eluted Mn at around Kd 0.5 in G25 fraction, and 2 peaks at around Kd 0 and 1.7 in G10 fraction. Since the position of these peaks is quite different from the position of Mn^{2+} separation, it is considered that in highly tolerant plants Mn behaves in the form of complex compound with molecular weight of about 500-1,000.

The result completely the same as above was obtained with the tea plant which is also highly tolerant to Mn.[10] From the facts that these tree species contain a large amount of polyphenols, and that the Mn toxicity to cells is suppressed by the presence of polyphenols which are found in tea leaves, it can be considered that there is a mechanism by which Mn is combined with polyphenols to form complex compounds to suppress the toxicity of excess Mn.

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