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Full Paper

Toxic symptoms in rubber tree sapling and its response to manganese application

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Abstract: It is well established that manganese (Mn) is an essential element promoting plant growth. However, in acid soils excessive Mn levels are toxic to crops. We investigate the response in growth and nutrient uptake and the symptoms of toxicity in rubber tree saplings grown in solution culture. The optimal 0.01 mM Mn application rate is found to promote growth and enhance chlorophyll and total non-structural carbohydrate contents. However, excessive Mn levels of 15 and 30 mM inhibit plant growth and uptake of N, K, Ca and Mg nutrients. Moreover, rubber tree saplings grown with excessive Mn levels have symptoms of toxicity, viz. yellowing leaves, root breaks and latex rubber emanating from roots. The highest Mn accumulation is found in the lateral root section. Excessive Mn levels cause nutrient imbalance and decreasing N, K, Ca and Mg uptake. Additionally, 30 mM Mn causes root rot, lateral root rot, latex seepage from the root and change in root colour to dark brown. Therefore, near optimal Mn levels should be used in rubber tree cultivation. Furthermore, soil with high Mn concentration requires a high rate of N, K, Ca and Mg fertiliser application to achieve the optimal level of these elements in the plant.

Keywords: *Hevea brasiliensis*, manganese, toxicity, plant toxic symptoms, rubber tree saplings

INTRODUCTION

Manganese (Mn), a trace element necessary for plant growth, plays a key role in several plant physiological processes, particularly in the release of oxygen during photosynthesis [1]. Mn is involved in pollen germination, pollen tube growth, root cell elongation and resistance to root pathogens [2]. Moreover, it is a component of certain enzymes such as peroxidase, which generates hydrogen peroxide contributing to pathogen resistance [1, 2]. Mn deficiency in a plant reduces its

Maejo Int. J. Sci. Technol. **2021**, *15*(01), 1-12

chlorophyll content which is related to photosynthesis rate and carbohydrate production [1]. On the other hand, Mn is a toxicant when in excess, and may be the main factor limiting crop production [2]. Mn toxicity symptoms in rubber trees include yellowish green colour with distinct green midrib, veins and veinlets in young leaves or top whorl leaves [3]. Different plant species or even varieties within a species have varying tolerance to Mn exposure [1]. The majority of soil Mn are in the forms of the minerals pyrolusite (MnO_2) and manganite ($MnO(OH)$) or in the compounds of manganese oxides (Mn_2O_3 and Mn_3O_4) [4]. The ionic form of Mn^{2+} is the bioavailable form and can be readily translocated to the roots and shoots [4]. In contrast, other ionic forms of Mn such as Mn^{3+} and Mn^{4+} are not available for plant utilisation [4].

Soil Mn concentration is greatly increased under acidic (pH < 5.5) or poor drainage conditions, along with high organic matter content [1]. In Thailand 2-4 mg kg^{-1} extractable Mn in soil has been reported as optimal for rubber tree growth [5]. The majority of soils in Thailand are acidic (pH < 6.5) [6], and the extractable Mn range in cultivated soils is 17-43 mg kg^{-1} [7], resulting in rubber leaf Mn concentrations exceeding 300 mg kg^{-1} [8, 9], whereas the optimal Mn range in leaves is 45-150 mg kg^{-1} [10]. Therefore, soil and leaf Mn levels tend to be higher than optimal for rubber trees. At low concentrations, soil Mn is an essential micronutrient for rubber tree growth, with a positive relationship between soil Mn and latex yield [11], while a high soil Mn concentration is likely to be toxic to the plants [12], resulting in a low latex yield [11].

Although the majority of soils in rubber plantations of Thailand have higher than optimal Mn levels (> 4 mg kg^{-1}) and the bulk of rubber tree leaves have greater than 150 mg kg^{-1} of Mn [10], which may be toxic to rubber trees, still there is no prior report on toxicity symptoms in rubber trees grown in Thailand and their response. In this research the outcome of response, toxicity of Mn on plant growth and nutrients uptake and some parameters related to Mn functions in plants, such as chlorophyll and total non-structural carbohydrate content, are determined and discussed.

MATERIALS AND METHODS

Cultivation of Rubber Tree Saplings

Budded stumps of rubber tree (*Hevea brasiliensis*), RRIT 251 and RRIM 600 clonal varieties (developed by Thailand and Malaysia respectively), were cultivated in an 80-L plastic box (dimension 48 x 75 x 42 cm) inside a greenhouse under a completely randomised design with three replications. $MnSO_4{\cdot}H_2O$ solutions containing 0.01, 15 and 30 mM Mn were applied. The basal applications of N, P, K, Ca, Mg, Fe, B, Zn, Cu and Mo were 15, 2, 15, 25, 10, 2, 0.5, 0.2, 0.01 and 0.005 mg element L^{-1} in the forms of $(NH_4)_2SO_4$, $NaH_2PO_4{\bullet}2H_2O$, K_2SO_4+ KCl, $CaCl_2{\bullet}2H_2O$, $MgSO_4{\bullet}7H_2O$, $FeSO_4{\bullet}7H_2O$, H_3BO_3, $ZnSO_2{\bullet}7H_2O$, $CuSO_4{\bullet}5H_2O$ and $(NH_4)_6{\bullet}Mo7O_{24}{\bullet}4H_2O$ respectively. All nutrient solutions were prepared using purified-grade in deionised water (18.2 MΩ•cm). An air pump was used to provide O_2 for plant growth.

Growth and Symptom Evaluation

Response to and toxic effects or symptoms from Mn exposure were considered. After 40 days, shoot height and stem diameter were measured. The second compound leaf of growing whorl after three months of defoliation was sampled. Total chlorophyll and total non-structural carbohydrate were estimated [13, 14]. Plant sections, namely leaf, stem, primary root and lateral root, were washed with deionised water, separated and oven-dried at 80 ºC for 3 days. These samples were subsequently ground and digested with H_2SO_4 for total N analysis (Kjeldahl method) [13] and with mixed acid (HNO_3:$HClO_4$ = 3:1 v/v) for Mn, P, K, Ca, Mg, Fe, Zn and Cu analyses [13].

Statistical Analysis

All data are presented as mean values of three replications with standard deviations. The data were subjected to one-way analysis of variance (ANOVA) and the significant differences were confirmed using Duncan's multiple range tests (DMRT) at $P \leq 0.05$.

RESULTS AND DISCUSSION

Response to Mn Exposure During Growth of Rubber Tree Saplings

The growth of both RRIT 251 and RRIM 600 varieties is faster with exposure to 0.01 mM Mn than without Mn (Tables 1 and 2). Stem diameters of both RRIT 251 and RRIM 600 varieties receiving 0.01 mM Mn are larger than those without Mn application (Table 1). The stem diameter of RRIM 600 plants receiving 0.01 mM and 15 mM Mn is greater than that without Mn application. Applying 0.01 mM Mn provides the highest growth rate for rubber tree stem in both RRIT 251 and RRIM 600. The height of rubber tree saplings receiving 0.01 mM Mn increases by 11.1 cm and 19.1 cm for RRIT 251 and RRIM 600 respectively.

Table 1. Effects of Mn on stem diameter of rubber tree saplings (RRIT 251 and RRIM 600 clonal varieties)

Mn (mM)	RRIT 251 (mm)			RRIM 600 (mm)		
	Initial	Final	Difference	Initial	Final	Difference
0	4.84	4.98	0.14b	4.98	5.33	0.35b
0.01	4.45	5.09	0.64a	5.03	5.98	0.95a
15	4.84	4.85	0.01b	4.39	4.86	0.47b
30	4.92	4.91	0.01b	4.90	4.97	0.07b
F-test	NS	NS	*	NS	NS	*
C.V. (%)	11.16	10.12	67.11	10.93	9.58	45.65

Note: * = significantly different at $P \leq 0.05$; NS = not significantly different at $P > 0.05$. Different letters in the same column indicate significant differences by DMRT at $P \leq 0.05$.

Table 2. Effects of Mn on height of rubber tree saplings (RRIT 251 and RRIM 600 clonal varieties)

Mn (mM)	RRIT 251 (cm)			RRIM 600 (cm)		
	Initial	Final	Difference	Initial	Final	Difference
0	21.5	29.1	7.6	22.4	38.0a	15.6ab
0.01	26.8	37.9	11.1	27.6	46.7a	19.1a
15	21.0	21.3	0.3	21.3	21.9b	0.6b
30	22.4	22.6	0.2	21.6	22.1b	0.5b
F-test	NS	NS	NS	NS	*	*
C.V. (%)	28.81	32.19	68.05	25.06	17.99	40.09

Note: * = significantly different at $P \leq 0.05$; NS = not significantly different at $P > 0.05$. Different letters in the same column indicate significant differences by DMRT at $P \leq 0.05$.

Maejo Int. J. Sci. Technol. **2021**, *15*(01), 1-12

RRIT 251 plants without Mn application display the highest total chlorophyll content (3.3 mg dm^{-2}) and so do RRIM 600 saplings receiving 0.01 mM Mn (3.7 mg dm^{-2}). In both RRIT 251 and RRIM 600 plants the carbohydrate content in the leaves decreases with increasing Mn application rate with RRIT 251 suffering a more severe decrease (Table 3). Dry weights of leaves, petiole, stem and lateral root of both RRIT 251 and RRIM 600 saplings receiving 0.01 mM Mn are higher than those of untreated samples (Tables 4 and 5). Both RRIT 251 and RRIM 600 plants receiving Mn higher than 0.01 mM display significantly higher plant Mn concentrations in all parts studied with the uptake increasing with Mn application rate (Table 6). However, the majority of plant Mn uptake is found in primary roots, lateral roots and stems of rubber tree saplings (Figure 1).

Table 3. Effects of Mn on total chlorophyll and total non-structural carbohydrate in rubber leaves (RRIT 251 and RRIM 600 clonal varieties)

Mn (mM)	Total chlorophyll (mg dm^{-2})		Total non-structural carbohydrate (g kg^{-1})	
	RRIT 251	**RRIM 600**	**RRIT 251**	**RRIM 600**
0	3.3a	3.4	172a	173
0.01	2.4ab	3.7	136ab	136
15	1.9ab	3.1	158a	172
30	1.5b	3.0	95b	128
F-test	*	NS	*	NS
C.V. (%)	35.87	22.94	19.12	21.99

Note: * = significantly different at P ≤ 0.05; NS = not significantly different at P > 0.05. Different letters in the same column indicate significant differences by DMRT at P ≤ 0.05.

Table 4. Effects of Mn on leaf, petiole and stem dry weight of rubber saplings (RRIT 251 and RRIM 600 clonal varieties)

Mn (mM)	Leaf dry weight (g)		Petiole dry weight (g)		Stem dry weight (g)	
	RRIT 251	**RRIM 600**	**RRIT 251**	**RRIM 600**	**RRIT 251**	**RRIM 600**
0	3.6a	4.9a	0.6ab	1.2a	1.5	2.0b
0.01	5.1a	5.3a	0.9a	1.3a	2.0	3.3a
15	2.8ab	2.4b	0.4b	0.5b	1.2	1.2c
30	1.1b	1.6b	0.4b	0.3b	1.0	1.1c
F-test	*	*	*	*	NS	*
C.V. (%)	28.32	33.03	38.75	32.61	32.66	17.59

Note: * = significantly different at P ≤ 0.05; NS = not significantly different at P > 0.05. Different letters in the same column indicate significant differences by DMRT at P ≤ 0.05.

Maejo Int. J. Sci. Technol. **2021**, *15*(01), 1-12

Table 5. Effects of Mn on dry weight of primary root and lateral root of rubber tree saplings (RRIT 251 and RRIM 600 clonal varieties)

Mn (mM)	Primary root dry weight (g)		Lateral root dry weight (g)	
	RRIT 251	RRIM 600	RRIT 251	RRIM 600
0	21	26	1.2ab	1.4ab
0.01	29	25	2.1a	2.6a
15	30	22	0.7b	1.0b
30	29	35	1.0ab	0.7b
F-test	NS	NS	*	*
C.V. (%)	33.87	36.88	40.81	47.03

Note: * = significantly different at P ≤ 0.05; NS = not significantly different at P > 0.05. Different letters in the same column indicate significant differences by DMRT at P ≤ 0.05.

Table 6. Effects of Mn exposure on Mn concentration in leaf, petiole, stem, primary root and lateral root of rubber sapling (RRIT 251 and RRIM 600 clonal varieties)

Mn (mM)	Leaf	Petiole	Stem	Primary root	Lateral root
	Mn (mg kg^{-1})				
RRIT 251					
0	115b	419b	225b	58c	300c
0.01	169b	596ab	299b	59c	383c
15	171b	1,291a	1,146a	756b	14,473b
30	301a	1,288a	1,094a	1,655a	27,715a
F-test	*	*	*	*	*
C.V. (%)	19.01	41.72	58.36	25.90	30.89
RRIM 600					
0	147b	702c	332b	62b	178c
0.01	217b	743c	382b	70b	251c
15	863a	2,665b	2,075a	1,122a	8,786b
30	874a	3,761a	1,891a	1,412a	31,130a
F-test	*	*	*	*	*
C.V. (%)	26.73	23.89	24.97	47.92	7.34

Note: * = significantly different at P ≤ 0.05. Different letters in the same column indicate significant differences by DMRT at P ≤ 0.05.

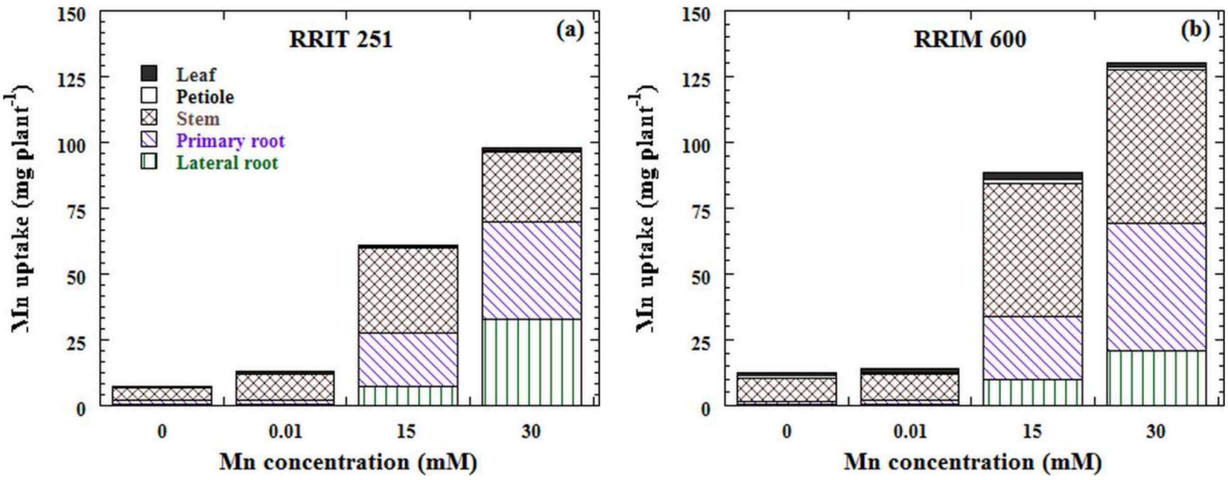

Figure 1. Effects of Mn exposure on Mn content in leaf, petiole, stem, primary root and lateral root of RRIT 251 (a) and RRIM 600 (b) clonal varieties

Tables 7 and 8 show that both RRIT 251 and RRIM 600 clones receiving 0.01 M Mn have higher N and P concentrations in the leaf and petiole than in untreated plants. Mn application causes leaf Mn concentration to increase relative to that without Mn application (Table 7) to a higher level than the optimal leaf Mn of 45-150 mg kg^{-1} [9]. The optimal Mn application (0.01 mM) promotes root growth of rubber tree saplings (Table 5 and Figure 3a). This is similar to the findings in grape [15]. Mn is associated with the synthesis of indoleacetic acid (IAA) which induces cell elongation and cell division, with consequent plant growth and development. Mn also controls IAA activities; in soils with low Mn levels Mn application can improve productivity and grain biofortification [14].

In both RRIT 251 and RRIM 600 plants receiving 0.01 mM Mn, P and Mg concentrations in stems are higher than untreated ones (Table 9). Table 10 shows that the lateral root in both RRIT 251 and RRIM 600 saplings receiving 0.01 mM Mn displays higher P and K root concentrations than these of untreated plants. Increasing Mn application rate, however, decreases not only K uptake but also Ca concentration in the lateral root.

Table 7. Effects of Mn on nutrient concentration in leaf of rubber saplings (RRIT 251 and RRIM 600 clonal varieties)

Mn (mM)	Leaf nutrient								
	N	**P**	**K**	**Ca**	**Mg**	**Mn**	**Fe**	**Zn**	**Cu**
	(g kg^{-1})					(mg kg^{-1})			
RRIT 251									
0	37ab	2.8b	12	3.6c	2.6a	115b	90b	43b	5.4a
0.01	40a	4.0a	10	5.9a	2.3ab	169b	67b	33b	4.6a
15	32ab	2.1b	11	3.6c	2.2ab	171b	66b	35b	4.6a
30	25b	2.1b	11	5.0b	1.9b	301a	155a	124a	3.3b
F-test	*	*	NS	*	*	*	*	*	*
C.V. (%)	20.24	15.03	19.01	8.98	11.69	19.01	12.35	15.59	11.30

Maejo Int. J. Sci. Technol. **2021**, *15*(01), 1-12

Table 7. (Continued)

Mn (mM)	Leaf nutrient								
	N	P	K	Ca	Mg	Mn	Fe	Zn	Cu
	(g kg^{-1})					(mg kg^{-1})			
RRIM 600									
0	35ab	2.6ab	11ab	5.9	1.9	147b	69	41	5.2b
0.01	39a	3.3a	12a	5.7	2.5	217b	62	34	7.1a
15	37ab	2.5b	11ab	5.5	2.0	874a	91	45	3.6b
30	28b	1.5c	8b	7.1	2.3	863a	109	44	4.3b
F-test	*	*	*	NS	NS	*	NS	NS	*
C.V. (%)	13.27	15.66	17.25	23.52	18.13	26.73	28.23	11.36	16.21

Note: * = significantly different at P ≤ 0. 05; NS = not significantly different at P > 0. 05. Different letters in the same column indicate significant differences by DMRT at P ≤ 0.05.

Table 8. Effects of Mn on nutrient concentration in petiole of rubber saplings (RRIT 251 and RRIM 600 clonal varieties)

Mn (mM)	Petiole nutrient								
	N	P	K	Ca	Mg	Mn	Fe	Zn	Cu
	(g kg^{-1})					(mg kg^{-1})			
RRIT 251									
0	14	1.2b	16a	5.6	1.7	595ab	38a	31	3.8bc
0.01	18	3.5a	15ab	7.1	1.4	418b	19ab	29	3.0c
15	19	1.3b	13b	5.4	1.4	1,291a	15b	29	5.9a
30	14	1.2b	12b	6.1	1.6	1,288a	19ab	40	5.1ab
F-test	NS	*	*	NS	NS	*	*	NS	*
C.V. (%)	20.31	10.95	14.66	17.92	36.28	41.72	35.51	37.89	14.75
RRIM 600									
0	14b	2.4b	14ab	8.2	0.9b	702c	30ab	33	2.8b
0.01	20a	3.8a	16a	6.7	1.3a	742c	24b	31	5.5a
15	16b	1.7c	11ab	9.7	0.8b	2,665b	56ab	30	2.4b
30	14b	1.4c	8b	7.5	1.0b	3,761a	74a	34	2.6b
F-test	*	*	*	NS	*	*	*	NS	*
C.V. (%)	15.78	13.49	19.69	59.37	21.49	23.89	46.92	19.75	10.76

Note: * = significantly different at P ≤ 0. 05; NS = not significantly different at P > 0. 05. Different letters in the same column indicate significant differences by DMRT at P ≤ 0.05.

Maejo Int. J. Sci. Technol. **2021**, *15*(01), 1-12

Table 9. Effects of Mn on nutrient concentration in stem of rubber saplings (RRIT 251 and RRIM 600 clonal varieties)

Mn (mM)	Stem nutrient								
	N	P	K	Ca	Mg	Mn	Fe	Zn	Cu
	(g kg^{-1})					(mg kg^{-1})			
RRIT 251									
0	17	2.2b	16a	10a	2.8	225b	44a	36a	7.9a
0.01	19	3.4a	13ab	9.5a	3.0	299b	29ab	26b	4.1c
15	13	1.8b	15a	6.5b	2.6	1,146a	18b	26b	6.1b
30	13	1.5b	9.6b	8.8ab	2.8	1,094a	17b	21b	3.7c
F-test	NS	*	*	*	NS	*	*	*	*
C.V. (%)	30.58	18.56	18.52	16.05	23.99	58.36	48.29	16.03	14.61
RRIM 600									
0	13	2.6ab	15a	10	1.8ab	332b	14	29	3.1ab
0.01	14	3.3a	15a	9.9	2.1ab	382b	24	28	3.7a
15	15	2.1b	11ab	13	1.4b	2,075a	19	34	2.4b
30	17	1.7b	7.8b	14	2.5a	1,891a	19	28	3.4a
F-test	NS	*	*	NS	*	*	NS	NS	*
C.V. (%)	25.05	19.96	21.62	23.24	21.55	24.97	28.57	13.21	11.37

Note: * = significantly different at P ≤ 0.05; NS = not significantly different at P > 0.05. Different letters in the same column indicate significant differences by DMRT at P ≤ 0.05.

Table 10. Effects of Mn on nutrient concentration in lateral root of rubber saplings (RRIT 251 and RRIM 600 clonal varieties)

Mn (mM)	Lateral root nutrient								
	N	P	K	Ca	Mg	Mn	Fe	Zn	Cu
	(g kg^{-1})					(mg kg^{-1})			
RRIT 251									
0	29a	3.5	20a	6.1a	1.1a	300c	1,864b	87a	46a
0.01	26b	4.2	23a	3.7b	1.5a	383c	1,921b	71a	25b
15	22b	3.9	13b	1.8c	0.4b	14,743b	3,932a	35b	41a
30	20c	4.0	1.9c	1.7c	0.4b	27,715a	4,294a	71a	52b
F-test	*	NS	*	*	*	*	*	*	*
C.V. (%)	2.22	11.2	16.32	25.68	26.59	30.89	16.90	17.89	13.09
RRIM 600									
0	26	3.8	13a	6.1a	1.4a	251c	1,535b	92a	40
0.01	25	4.4	17a	4.5b	1.4a	178c	2,048b	49b	30
15	25	4.0	12a	2.1c	0.6b	8,786b	3,491b	38b	41
30	22	4.4	5.2b	1.8c	0.4b	31,130a	4,166a	50b	49
F-test	NS	NS	*	*	*	*	*	*	NS
C.V. (%)	14.18	14.81	22.44	16.02	28.83	7.34	27.22	12.5	28.34

Note: * = significantly different at P ≤ 0.05; NS = not significantly different at P > 0.05. Different letters in the same column indicate significant differences by DMRT at P ≤ 0.05.

Maejo Int. J. Sci. Technol. **2021**, *15*(01), 1-12

Toxicity of Mn to Rubber Tree Saplings

In contrast to 0.01 mM Mn which did not affect the dark green colour of the rubber tree leaves, exposure to 15 mM and 30 mM Mn causes leaf colour to change to light green and yellow (Figure 2). In particular, RRIT 251 after exposure to 30 mM Mn has yellow and small leaves. Rubber tree roots that receive 30 mM Mn experience root rot and the root colour changes to dark brown (Figure 3). Excessive Mn application decreases the rate of plant growth and leads to lateral root rot. Moreover, the primary root of RRIT 251 breaks and latex seeps out from the root (Figure 3).

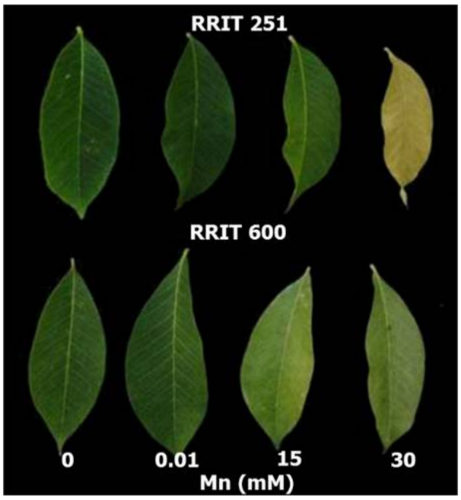

Figure 2. Effects of Mn exposure on leaves of rubber saplings (RRIT 251 and RRIM 600 clonal varieties)

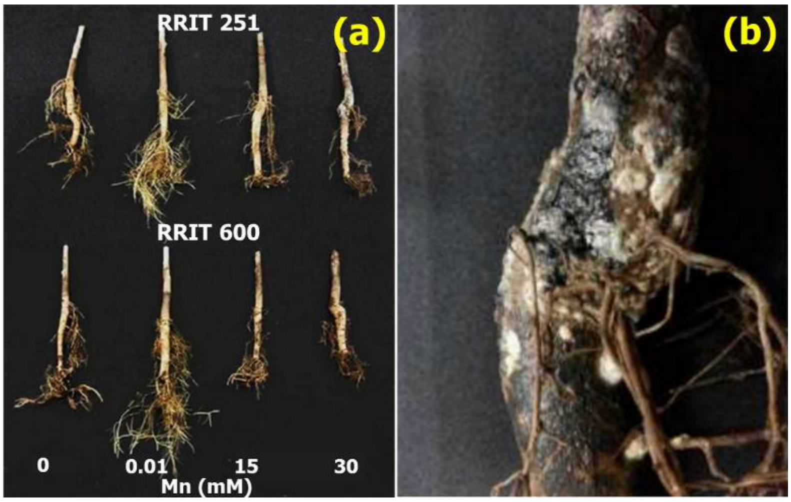

Figure 3. (a) Effects of Mn on root growth; (b) root break symptoms of rubber tree saplings (RRIT 251) on exposure to 30 mM Mn

The highest Mn concentrations found in the lateral root (Table 10) may cause root rot in the 30-mM Mn application case (Figure 3). However, according to this study, the highest growth of rubber saplings is associated with rubber leaf Mn concentrations of 169 and 217 mg kg^{-1} in RRIT 251 and RRIM 600 respectively (Table 7), which shows that leaf Mn concentrations higher than the standard leaf Mn (150 mg kg^{-1}) recommended by the Rubber Authority of Thailand [15] may not yet have any toxic effects on the growth of rubber trees. This is similar to recently reported results which suggest that the optimal leaf Mn level in immature rubber trees in Thailand is 300-500 mg kg^{-1} [8]. These results seem to indicate that a special mechanism in rubber roots reduces Mn toxicity in the plant. Mn^{2+} enters root cells through the plasmalemma with the help of a specific transporter protein that establishes an electrical gradient from the cell wall to the cell interior [1].

Excessive Mn application affects the growth of stem and height (Tables 1 and 2) and tends to decrease total chlorophyll and total non-structural carbohydrate content in rubber sapling leaves (Table 3). Therefore, photosynthesis activity is below that with optimal Mn application. Similar findings of positive correlations between chlorophyll content and Mn uptake have been observed in shoot (r = 0.70**) and in root (r = 0.74**) [16]. Increasing Mn exposure also causes loss of plant dry weight (Table 4). These results are similar to the findings for the shoot and root of grape [17], chamomile [18], cucumber [19, 20], chinese cabbage [21] and watermelon [22].

Mn concentration in a plant generally ranges between 20-500 mg kg^{-1} [1] but can approach 1,000-1,800 mg kg^{-1} in some plants growing in acidic soil [18, 19]. Some plants have a high Mn tolerance; the leaf Mn toxicity levels for rice, barley and soybean are 2020, 656 and 806 mg kg^{-1} respectively [20]. Excessive Mn not only leads to a low content of IAA needed for the growth of plant cells [21], but also reduces plant growth and inhibits Ca and Mg uptake [22].

Excess Mn causes nutrient imbalance and decreases uptake of macro- and micronutrients by rubber tree saplings (Tables 7-10), particularly the uptake of nitrogen that is a component in chlorophyll. When the soil has a high Mn content, RRIM 600 is the recommended variety for cultivation because its growth rate is higher (Tables 1 and 2) and it appears more resistant to Mn toxicity than RRIT 251 variety. It has been reported that silicon application can be used to reduce Mn toxicity in plants [23]. Further study on Si application in acidic soil, as well as the combination of lime and soil management, is required to gain control over the complex processes in rubber trees cultivated in acidic soils.

CONCLUSIONS

Optimal Mn application results in favourable growth of rubber trees. However, excess Mn application inhibits growth of rubber saplings and reduces N, P, K, Ca and Mg uptake by the plants, while enhancing Mn accumulation in plant tissues. Excessive exposure to Mn decreases height, total chlorophyll and total non-structural carbohydrate content of rubber tree saplings. Moreover, the saplings experience root rot, lateral root rot, root colour change to dark brown and latex rubber seepage from the root when exposed to 30 mM Mn. Therefore, the management of Mn level should be undertaken, especially for rubber trees grown in acidic soil. Those grown in soils high in Mn should be compensated with elevated doses of N, K, Ca and Mg.

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Maejo Int. J. Sci. Technol. **2021**, *15*(01), 1-12

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