Plant and Soil **37**, 577–588 (1972) Ms. 1890

MANGANESE-SILICON INTERACTION AND ITS EFFECT ON GROWTH OF SUDAN GRASS*

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SUMMARY

Growth of sudan grass was studied for response to Mn concentrations in the culture solutions ranging from deficient to toxic and in the presence and absence of Si. In the absence of Si, the optimum Mn level was 0.25 to 0.50 mg/l. One mg/l Mn was toxic and reduced plant growth. The addition of 5 mg/l Si to the nutrient solutions decreased accumulation of Mn, Cu, Fe, and Zn in the plant tissues, and in fact induced Mn deficiency in those plants receiving 0.5 mg/l Mn or less. One function of Si under these experimental conditions was the amelioration of Mn toxicity as manifested by increased dry matter accumulation by the Mn-toxic plants when Si was added. It is doubtful that Si satisfies the criteria for essentiality in sudan grass, however, and if so, the required Si concentration must be less than 0.025 mg/l.

INTRODUCTION

Manganese (Mn) has long been recognized as an essential micronutrient for the growth and reproduction of higher plants, but it is usually accepted that silicon (Si) does not satisfy the criteria for essentiality [19]. Under some conditions, however, Si did significantly increase growth of sugarcane [1 2 3], sudan grass [8 15], barley [16], wheat [16], and rye [16]. Although Lipman [7], Sommer [13], and Raleigh [11] considered Si to be essential for barley and sunflower, rice, and beets, respectively, most modern plant nutritionists consider the stimulatory effect of Si on plant growth to be of a secondary nature. One function that has been proposed for Si is that of alleviating toxicities of micronutrients, particularly Mn [16 17 18]. Manganese

* Journal Series No. 1422 of the Hawaii Agricultural Experiment Station.

toxicity in barley [18] and sugarcane [2] is manifested as a necrotic spotting pattern on the leaf blades. In the case of barley, formation of these necrotic areas could be prevented by adding Si to the nutrient solution, increasing the macronutrient concentrations, or decreasing the Mn supply [17 18]. It was subsequently suggested that a correct balance between Mn and Si may be prerequisite for optimum growth [4 9], a proposal that has been furthered by Clements [2] in his work with sugarcane. Fox *et al.* [3] have recently noted, however, that the necrotic spotting, or 'freckle', appeared on sugarcane in locations where the plant Mn levels were low in comparison to Clements' [2] standards. It thus seemed likely that Mn toxicity or an unbalanced Mn/Si ratio was not the sole explanation for the necrotic spotting at that location.

The present work was conducted in an effort to further elucidate the nature of the interaction between Mn and Si in sudan grass, and to ascertain some of the cultural conditions under which a positive growth response to the addition of Si might be expected. Earlier work on plant responses to silicate applications and the possible mechanisms of these responses has been reviewed recently by Silva [12] and Plucknett [10].

MATERIALS AND METHODS

Seeds of sudan grass, *Sorghum sudanense* (Piper) Stapf, were allowed to germinate overnight in the dark in 1 l of aerated water at 23°C. The seeds were then spread on a layer of cheese cloth which had been washed thoroughly with water. The cheesecloth was stretched 0.5 cm above the surface of 10 l of nutrient solution in a polyethylene container. A second cheesecloth was placed over the seeds, and the corners of both cloths dipped into the nutrient solution. The entire apparatus was covered with aluminum foil which was removed after four days.

All solutions were prepared with water from snow collected at the summit of 13,680 ft Mauna Loa on the Island of Hawaii. Particulate contamination of the atmosphere is very low at this altitude, and the water thus collected contained less than 0.01 μg Si/l. The composition of the base nutrient solution was, in millimoles/l $Ca(NO_3)_2.4H_2O$, 3.0; $CaSO_4$, 4.5; KNO_3, 3.0; KH_2PO_4, 1.0; and $MgSO_4.7H_2O$, 2.0. In addition, to each solution was added 3 mg/l Fe and 0.25 mg/l each of Cu and Zn, provided as salts of EDTA. Manganese was added as $MnSO_4.H_2O$, and Si as sodium silicate. The pH was adjusted to 5.5 with 4*N* HCl, and all solutions were aerated continuously. Analyses were run every three days on aliquots of each nutrient solution and, if the con-

centration of any nutrient decreased by 10% or more, an amount of stock solution calculated to restore the original concentrations was added.

Plants were grown in an environmental growth chamber at 28°C, 80±5% relative humidity, and 2000 foot-candle light on a 12-h light, 12-h dark diurnal cycle. The air in the growth chamber was not filtered which thus accounted for some degree of Si contamination as discussed below. Air bubbled into the nutrient solutions was filtered through fiberglass to remove macroscopic particles and a paper filter to remove microscopic particles down to 1 μ.

After 6 weeks, the plants were harvested and separated into roots and tops. The tissues were dried for 24 h at 80°C and the dry weights ascertained. The dried tissue was ground to pass a 20-mesh screen and, after thorough mixing, a portion of the ground tissue was stored in polyethylene bottles until analyzed. Sub-samples (0.2 g) of the tissue were ashed at 450°C overnight, and the ash was dissolved in 5 ml of 0.1 *N* HCl. This preparation was used for analysis of Mn, Fe, Cu, and Zn by atomic absorption spectrophotometry. For Si determinations on the plant material, a sub-sample was dried at 100°C for 12 h, transferred to a nickel crucible and placed in a muffle furnace at 200°C. The furnace temperature was raised slowly to 500°C over a 6-hr period and then held at 500°C for 10 h. The ash was fused with anhydrous Na_2CO_3, cooled, dissoved in water and brought up to a standard volume. An aliquot of this solution was analyzed for Si by the reduced silicomolybdate method [5 6 14]. The silicon concentrations of the nutrient solutions were also determined by this method after the solutions had been concentrated by evaporation under a partial vacuum.

RESULTS AND DISCUSSION

Plant growth as a function of Mn supply

In this experimental series the nutrient solutions contained no added Si (0-Si) while the Mn concentration was varied from 0 to 5 mg/l. Actually, those solutions designated as 0-Mn and 0-Si contained initially less than 0.015 mg/l Mn or Si, respectively. After 6 weeks, the 0-Mn plants manifested severe symptoms of Mn deficiency, a conclusion confirmed by the observation that addition of 0.25 mg/l Mn to the nutrient solution prevented the appearance of such symptoms. Growth, as measured by the dry weight of the plant tops, was increased almost 2-fold over the 0-Mn treatment by the presence of 0.25 mg/l Mn (Fig. 1). There was apparently a very narrow optimum range for Mn in sudan grass, however; *i.e.*, 0.25 to 0.50 mg/l. When the external Mn concentration was increased to 1 mg/l, growth of the plant tops was reduced by 16 per cent as compared to growth obtained with 0.25 mg/l Mn. Further increases in the Mn level of the nutrient solutions to 3 and 5 mg/l were increasingly

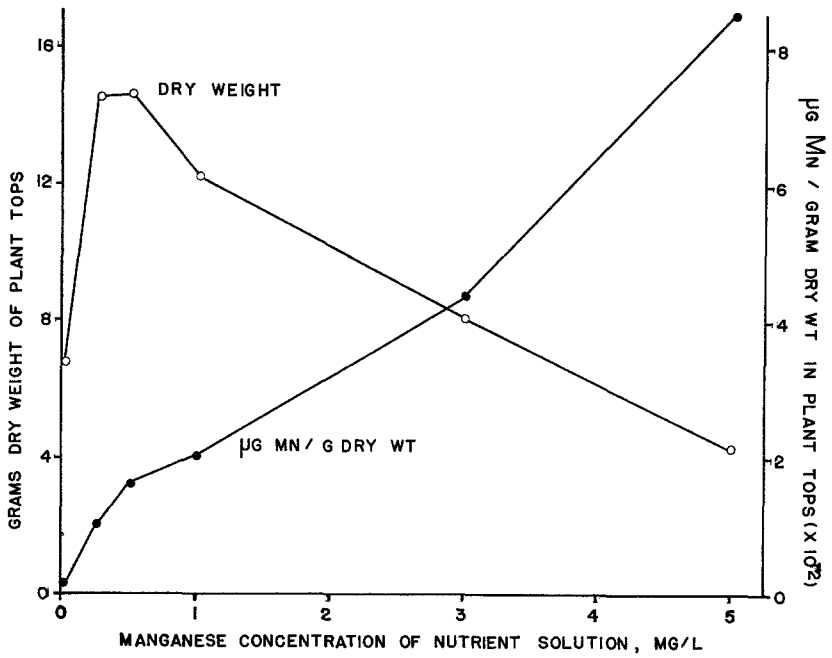

Fig. 1. Growth (grams dry weight of plant tops) and manganese accumulation (μg Mn/g dry wt of plant tops) in 6-week-old hydroponically cultured sudan grass as a function of the manganese concentration of the nutrient solutions.

toxic, with 5 mg/l Mn causing a 70 per cent decrease in the dry weight of the plant tops (Fig. 1).

The Mn concentration of the tops of the 0-Mn plants was 8 μg/g dry wt, and increased in an approximately linear manner to 850 μg/g dry wt when the external Mn concentration was 5 mg/l. In the range of optimum growth – 0.25 to 0.50 mg/l Mn – the Mn concentration of the plant tops was 100 to 160 μg/g dry wt. Mn levels in the plant tops in excess of 200μg/g dry wt were associated with decreased dry matter accumulation and thus were apparently toxic. Based upon these findings, all subsequent experiments were conducted in nutrient solutions containing 0.25 mg/l Mn, unless Mn was the variable.

Plant growth as a function of the external Si and Mn concentrations

The first experiment in which the Si concentration of the nutrient solution was the variable was designed to determine the effect of Si

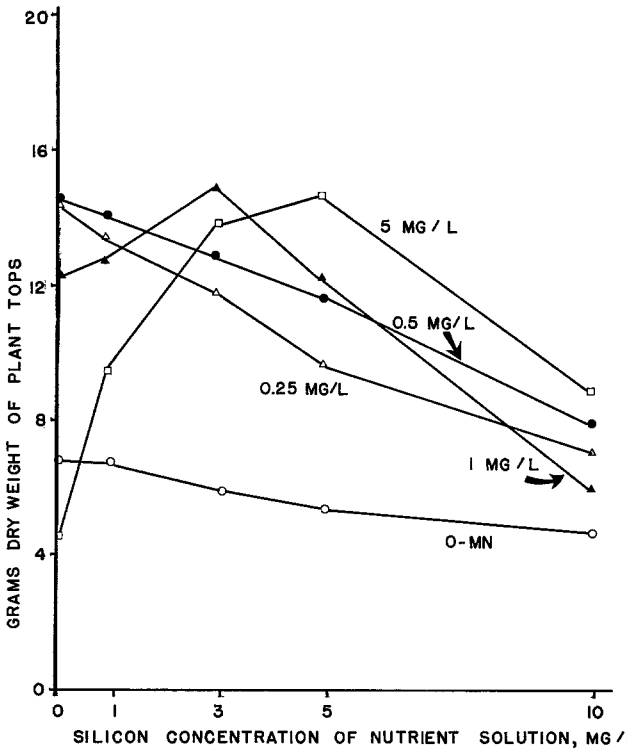

Fig. 2. Growth (grams dry weight of plants top) of 6-week-old sudan grass as a function of the manganese and silicon concentrations of the nutrient solutions. (Mn concentrations indicated for each curve; Si concentration shown on the abscissa.)

on plant growth when the Mn supply was optimal; *i.e.* 0.25 mg Mn/l. Although several authors have reported the growth of various plant species to be increased by Si [2 8 9 14 15 16], such was *not* the case in the present study when Mn availability was optimal (Fig. 2). When the Mn concentration of the nutrient solution was maintained at 0.25 mg/l and the Si concentration varied from 0 to 10 mg/l, growth of the plant tops decreased linearly with increasing Si supply from 14.4 g dry wt to 7.0 g dry wt, a 51 per cent reduction in dry matter accumulation. In addition, the leaves of plants in the 5 and 10 mg/l Si solutions developed a necrotic spotting pattern typical of Mn deficiency in grasses, suggesting that the decreased growth in the cultures receiving 5 and 10 mg/l Si may have been due to an induced

Mn deficiency. There is a well-known interaction between Mn and Si in higher plants, especially grasses, but it is debatable whether Si actually decreases Mn accumulation in the leaves [2] or merely alters the distribution of Mn in the leaf tissue [18]. The present data appear to favor the former alternative, but this will be examined in detail in a later section of this paper.

In subsequent experiments the effects of variable Si concentrations upon plant growth were examined when the external Mn supply was stabilized at a sub- or supra-optimal level (Fig. 2). When Mn was withheld from the nutrient solutions or when 0.5 mg/l Mn was added, the plant growth responses to increasing Si concentrations up to 10 mg/l were similar to that noted at 0.25 mg/l Mn. When the Mn concentration of the nutrient solution was high enough to be toxic, however, the growth response was quite different. With 1

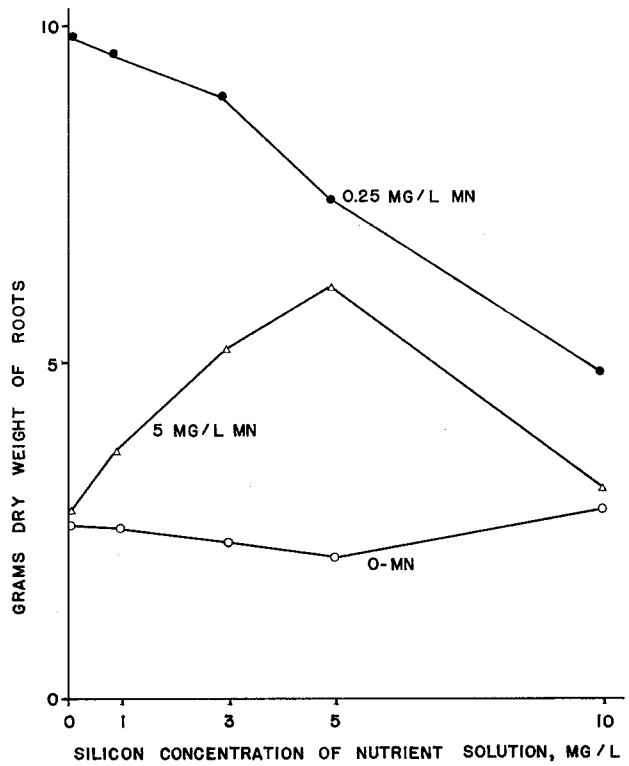

Fig. 3. Growth (grams dry weight) of sudan grass roots as a function of the manganese and silicon concentrations of the nutrient solutions..

mg/l Mn in the external solution, the addition of 3 mg/l Si *increased* growth of the plant tops by 21 per cent as compared to the 1 mg/l Mn, 0-Si control. The growth response to the addition of Si to the nutrient solution was most marked when the Mn concentration was 5 mg/l, a highly toxic Mn level. Under this condition, maximum growth was obtained upon addition of 5 mg/l Si to the solutions, the increased growth being 3-fold greater than that in the 5 mg/l Mn, 0-Si treatment.

The Mn-Si interaction as evaluated in terms of root growth was generally similar to that of top growth (Fig. 3). Under conditions of Mn deficiency (0-Mn), root growth was not significantly affected by Si additions over the 0 to 10 mg/l range. When the Mn concentration of the nutrient solution was optimum; *i.e.* 0.25 mg/l, root growth was decreased by 51 per cent in the presence of 10 mg/l Si, as compared to the 0-Si control. Manganese toxicity was considerably alleviated, although not totally eliminated, by 5 mg/l Si in the nutrient solution. Silicon concentrations above 5 mg/l added to the Mn-toxic (5 mg/l) cultures resulted in a decrease in root growth as compared to the maximum growth obtained in the 5 mg/l Mn, 5 ml Si cultures.

Effect of Si on micronutrient accumulation

Plants were grown in nutrient solutions containing a full complement of micronutrients, one-half of the solutions receiving no Si (0-Si) and the other half being supplemented with 5 mg/l Si. At harvest, the 6-week-old plants were separated into roots and tops and each tissue was analyzed for Mn, Cu, Zn, Fe, and Si. Accumulation of each micronutrient cation in both roots and tops was decreased by 50 to 70 per cent by the presence of 5 mg/l Si in the culture solution, as compared to the 0-Si controls (Table 1). The differences were highly significant (1% confidence level) in each case. The Si concentration of the roots and tops of the 0-Si plants was 16 and 121 μg/g dry weight, respectively. Roots of plants receiving 5 mg/l Si contained 1720 μg Si g dry wt, and the plant tops, 2620 μg Si/g dry wt. The Si levels of the 0-Si plants were considerably higher than could be accounted for by the Si known to be present in the nutrient solution, a point to be discussed in a later section of this paper.

The data in Tables 1 and 2 show unequivocally that Mn accumulation in the leaves was decreased by the presence of Si in the nu-

TABLE 1

Effect of silicon on micronutrient composition of 6-week-old sudan grass plants

Nutrient*	Conc. in nutrient solution mg/l	Roots		Plant tops	
		0-Si	+5 mg/l Si	0-Si	+5 mg/l Si
Mn (μg/g)	0.25	122	40	101	49
Cu (μg/g)	0.25	30	14	28	7
Fe (μg/g)	5	1134	342	220	82
Zn (μg/g)	0.25	43	21	17	11
Si (μg/g)	—	16	1720	121	2620

* Nutrient concentrations in tissues expressed on a dry-weight basis.

trient solutions. In this respect sudan grass differs from some other grasses in which Si causes a re-distribution of Mn in the leaves but does not reduce total Mn accumulation [16 18].

Another question that arose from these data was whether Si could ameliorate Cu and Zn toxicities also since, like Mn, these levels of Cu and Zn in the plant tissues were decreased in the 5 mg/l Si plants. This possibility will be examined in the following paragraph.

Alleviation of copper and zinc toxicities by silicon

Control plants in this series were grown with the normal complement of micronutrients in the nutrient solution (see Materials and Methods). Copper toxicity was induced by increasing the external Cu concentration to 2 and 5 mg/l, whereas Zn toxicity was achieved by adding Zn to the nutrient solutions to final concentrations of 5 and 10 mg/l of Zn. Toxicity of both Cu and Zn at these concentrations was evidenced by the statistically significant (1% level) reduction in growth of the plants (Table 3).

The addition of 5 mg/l Si to the culture solutions almost completely eliminated the toxic effects of 2 mg/l Cu and 5 mg/l Zn (Table 3). In the 2 mg/l Cu + 5 mg/l Si treatment, growth of both the plant tops and roots equaled that in the 0.25 mg/l Cu control plants, whereas growth of the plant tops was reduced by 24 per cent in solutions containing 2 mg/l Cu but no Si. When the Cu concentration was raised to 5 mg/l in the absence of Si, the dry weight of the plant tops was decreased by 82 per cent, as compared to the 0.25 mg/l Cu + 0-Si control plants. When 5 mg/L Si was added to the 5 mg/l

TABLE 2

Effect of 5 mg/l Si on Mn accumulation in sudan grass

Nutrient concentration in culture solution, mg/l		μg Mn/g dry wt	
Mn	Si	Roots	Plant tops
0.25*	0	122	101
0.25	5	40	28
1**	0	377	213
1	5	194	140
3**	0	908	448
3	5	517	208
5**	0	1371	850
5	5	720	363

* Optimum Mn concentration.
** Toxic Mn concentrations.

TABLE 3

Alleviation of copper and zinc toxicities in 6-week-old sudan grass plants by 5 mg/l silicon

Treatment	Grams dry wt		μg Cu/g dry wt		μg Zn/g dry wt	
	Roots	Plant tops	Roots	Plant tops	Roots	Plant tops
0.25 mg/l Cu	10.9	14.8	33	27	—	—
2 mg/l Cu	6.1	11.2	47[illegible]	254	—	—
2 mg/l Cu + 5 mg/l Si	10.4	15.3	156	44	—	—
5 mg/l Cu	3.0	2.7	840	395	—	—
5 mg/l Cu + 5 mg/l Si	9.7	13.0	387	114	—	—
0.25 mg/l Zn	10.0	15.2	—	—	40	21
5 mg/l Zn	5.8	9.4	—	—	517	209
5 mg/l Zn + 5 mg/l Si	10.6	14.2	—	—	104	57
10 mg/l Zn	2.3	1.6	—	—	1270	563
10 mg/l Zn + 5 mg/l Si	8.8	12.7	—	—	306	131

Cu nutrient solution, resultant plant growth was 88 per cent of that of the 0.25 mg/l Cu + 0-Si control, however (Table 3).

A similar situation was observed in the case of Zn toxicity. Five and 10 mg/l Zn in the nutrient solution, in the absence of Si, resulted

in reductions in dry matter accumulation in the plant tops of 38 and 89 per cent, respectively. When 5 mg/l Si was added to the Zn-toxic (5 and 10 mg/l Zn) cultures, the decrease in dry weight was 7 and 16 per cent in the 5 and 10 mg/l Zn cultures, respectively (Table 3). It is thus obvious that Si at a low concentration (5 mg/l) can almost completely overcome the effects of highly toxic Cu and Zn concentrations in the nutrient solutions.

Further examination of the data in Table 3 will show that Si ameliorated Cu and Zn toxicity by decreasing the accumulation of these nutrients in the plant tissues, as is also the case with Mn toxicity (Table 2; Figs. 2 and 3).

Observations on the question of essentiality of silicon for growth of sudan grass

Silicon is usually considered as a non-essential element for the growth and reproduction of higher plants [19]. There are exceptions to this generality, however, and at least three authors have reported that Si satisfies the criteria for essentiality in rice [13], barley and sunflower [7], and beets [11]. In addition, there are numerous reports in the literature that plant growth is increased by Si under various conditions, but these effects were thought to be secondary in nature.

One facet of the present study was an attempt to resolve the question of a possible Si essentiality in sudan grass. Although an unequivocal answer was not possible for the reasons discussed below, the following observations are offered for consideration. As in all other cases reported herein, the plants were grown in an environmental growth chamber under the conditions described above. Sources and amounts of known Si contamination were as follows, expressed as μg Si per 10 l culture solution: Salts added initially, 4.0; supplementary salts added, 20.0; initial 10 l of water, 0.10; water subsequently added, 0.03; seeds, 0.12; polyethylene culture vessel, 5.34; and contamination from the air bubbled into the culture, 37.0 The total known Si present in the 'Si-0' cultures was thus 67 μg, or 0.007 mg/l. Woolley [19] had 0.016 mg/l of Si in his '0-Si' cultures in the study which resulted in the conclusion that Si was non-essential for tomato plants.

At harvest, about 7 μg Si remained in the '0-Si' nutrient solution and about 1900 μg Si were recovered from the sudan grass plants. Thus, despite the precautions taken, Si contamination in the nu-

rient solutions from unknown sources was very great. The Si requirement of sudan grass, if any, could have been met conceivably by the Si contamination in the cultures. Although the initial Si level in the solution was 0.007 mg/l, the highest Si concentration recorded during the 6-week experiment was 0.022 mg/l. These concentrations are by no means too low to satisfy a micronutrient requirement of plants. A case in point is molybdenum which is usually added to nutrient solutions at a final concentration of 0.01 to 0.10 mg/l.

With the knowledge that the cultures designated as 0-Si actually contained as much as 0.022 mg/l of Si, the growth of sudan grass plants was studied when the Si supply was minimal; *i.e.*, 0.022 mg/l Si, and with 0.1 mg/l Si. Higher Si levels decreased growth by reducing micronutrient cation accumulation (Figs. 1 and 2; Tables 1, 2, and 3). Otherwise, the composition of the nutrient solution was the same as reported under Materials and Methods and contained 0.25 mg/ Mn. The dry weights of the sudan grass roots in the 0.022 and 0.10 mg/l Si cultures was 9.9 ± 0.8 g and 9.4 ± 1.1 g, respectively. The dry weight of the plant tops was 14.8 ± 1.3 g in the low-Si cultures, and 15.2 ± 0.9 g in the 0.1 mg/l Si cultures. The difference between the dry weights in the 0.022 mg/l and 0.10 mg/l Si cultures was not statistically significant for either roots or plant tops. Therefore, it can only be concluded that if Si is essential for sudan grass, the required concentration is very low, being on the order of 0.025 mg/l or less.

Received January 31, 1972.

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