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MANGANESE AND SILICON INTERACTION IN THE GRAMINEAE

by JAMES VLAMIS and D. EMERTON WILLIAMS

Department of Soils and Plant Nutrition, University of California, Berkeley, California

Silicon is generally not considered to be an essential element for higher plants. It has been assumed to perform one or more vital functions in grasses and it has been reported, first by Sommer [5] for rice and later by Lipman [2] for barley and sunflower, that silicon meets the criteria for essentiality. One function assigned to silicon in grasses relates to resistance against disease [1 10].

A significant response to silicon was obtained by Wagner [6] for a wide variety of plants but these results are vitiated by the excessive amounts of copper used in the solutions. Deficiency symptoms for silicon also are described by Raleigh [4] for beets. Woolley [9] conducted a very careful investigation of the essentiality of silicon for tomato plants but his results were negative.

In barley, silicon has been shown to undergo an interesting interaction with manganese. When barley is grown in standard nutrient solutions which do not include silicon, a necrotic spotting pattern develops. This necrosis increases in severity if the manganese concentration is raised and decreases if it is lowered. Another way of overcoming the symptoms is by the addition of silicon. Using Mn^{54} it was found that silicon did not appreciably alter the uptake of manganese, but rather affected the microdistribution of manganese in the leaves [8].

Barley has been found to be more sensitive to Mn-toxicity in Hoagland's solution than lettuce and tomato [7]. This phenomenon suggested the present investigation to compare the response of other members of the grass family to a range of Mn concentrations in culture solutions and the interaction between Mn and Si.

METHODS

Six members of the gramineae were used in these experiments: Atlas barley (*Hordeum vulgare*), California red oats (*Avena sativa*), wheat (*Triticum aestivum*), common rye (*Secale cereale*), ryegrass (*Lolium multiflorum*), and caloro rice (*Oryza sativa*). Seeds were germinated on cheesecloth suspended over tap water and transferred five days later to one-hole cork stoppers previously dipped in shellac. The seedlings were placed in five-gallon cans painted with Amercoat and containing 20 liters of fifth strength Hoagland's solution [8]. As a supply of iron 3 pieces of piano wire about 8 inches long were added to each tank. This has been found to be a very simple but effective source of iron at the pH of these solutions, about 5.5. Micro-nutrients except manganese were provided as in the earlier investigations with barley [8]. One half the tanks received 10 ppm silicon as sodium silicate. The addition of silicate raised the pH of these solutions and, therefore, sulfuric acid was added to adjust the reaction to 5.5. Manganese was added as the sulfate to give a range of 0, 0.05, 0.1, 0.2, 0.5, 2 and 5 ppm Mn. Gentle aeration was provided.

The plants were grown in a greenhouse from April 2 to May 6. At harvest time the shoots were divided into 3 catagories; young, mature, and old. The tops and roots were dried in a ventilated oven at 70°C, for 48 hours, then weighed and ground in a Wiley Mill for analysis.

The tissues were analyzed for manganese using periodate to develop the permanganate color which was measured in a colorimeter.

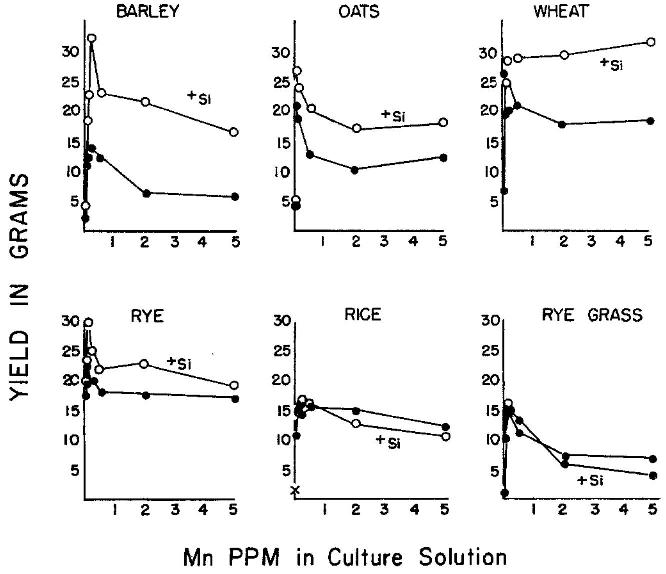

Fig. 1. Dry weight of shoots plotted against Mn in solution.

RESULTS

The yields of the six species as a function of Mn in solution show similar trends for the most part. There is a sharp increase in top dry weight going from zero to 0.1 or 0.2 ppm Mn followed by a decline of varying magnitude at the higher concentrations (Fig. 1). The effect of silicon in most of the range of Mn-values is to increase yields by more than 100 per cent in the case of barley, about 50 per cent for oats and wheat, about 25 per cent for rye, with no significant differences appearing for rice and ryegrass. A decline in yield with increasing Mn at the high range, with or without Si, was obtained generally except in the wheat plus silicon treatment. In the latter the dry weight production was sustained up to the highest rate of 5 ppm Mn in solution. The smallest yield depression due to high Mn was registered by the rice plants both in the presence and in the absence of silicon. Similar curves were obtained for the roots (Fig. 2).

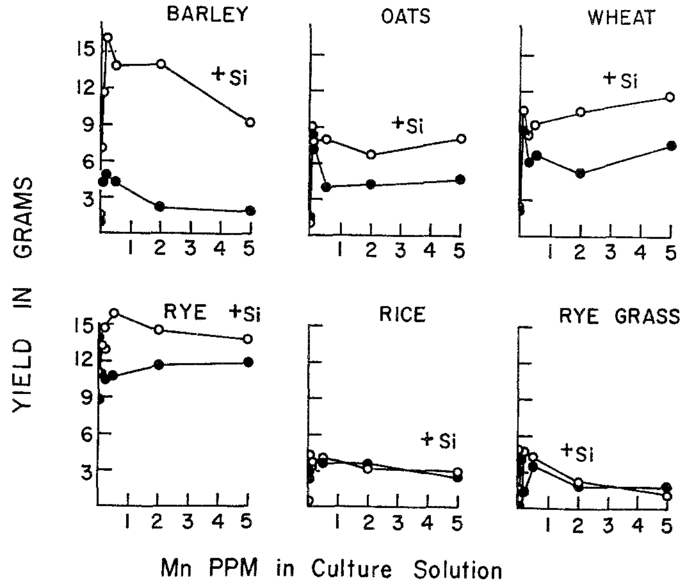

Fig. 2. Dry weight of roots plotted against Mn in solution.

In Figure 3 are shown the Mn-contents of the old leaf tissues. There is an apparent tendency of the plus silicon plants to contain less Mn, but this is felt to be a dilution effect and is discussed further

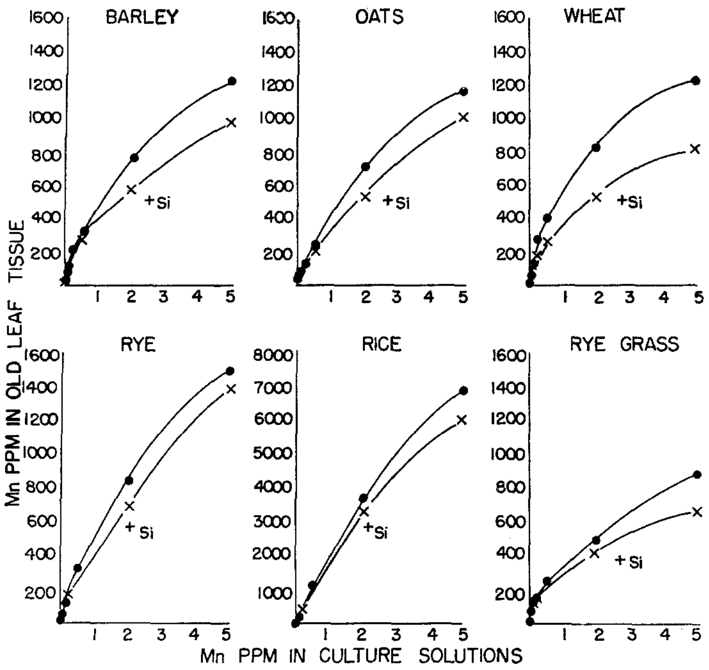

Fig. 3. Mn-content of old leaves versus Mn in solution, plus or minus silicon.

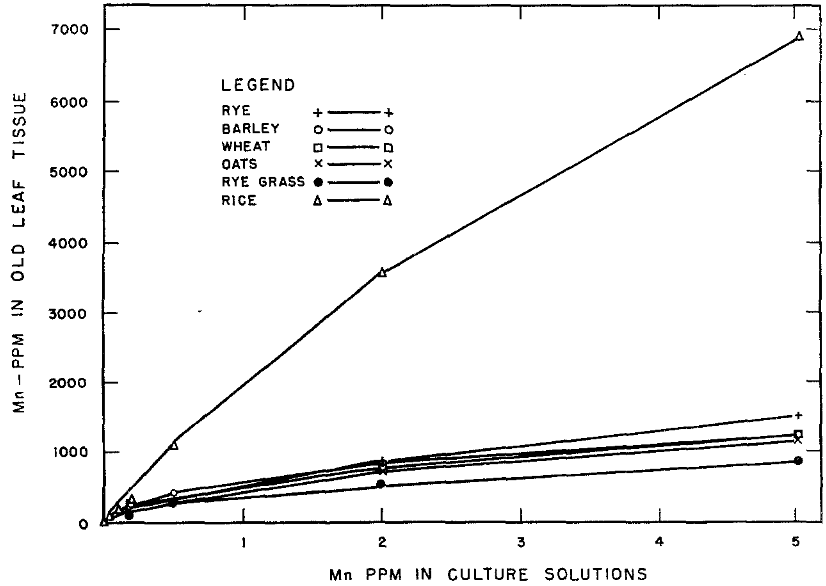

Fig. 4. Mn-content of old leaves of plants grown without Si plotted on a common scale to show disparity between rice and all other grasses.

on. In Figure 4 are plotted the data to compare the Mn-uptake (in the absence of Si) of each species plotted against a common scale on the y-axis. This brings out the enormous concentration of Mn in rice leaves relative to the five other species. The analyses of the young and mature leaves show the same relationships but on a smaller scale, the young leaves having the lowest Mn-content and the mature leaves intermediate between the young and the old. Only the old tissue analyses are given here.

The Mn content of the root tissues is shown in Figure 5. All curves are plotted on common scales and are directly comparable. Again there appears to be a depression of Mn-content in the presence of silicon and especially for oats, barley, and wheat. In rice this difference is reversed but is sufficiently small as to be considered negligible. It should also be noted that where rice had by far the highest Mn-content in the leaves, in the roots it ranked only fourth. Ryegrass roots with or without Si failed to show the steep increase in Mn-content at the highest or 5 ppm Mn level that was shown by the

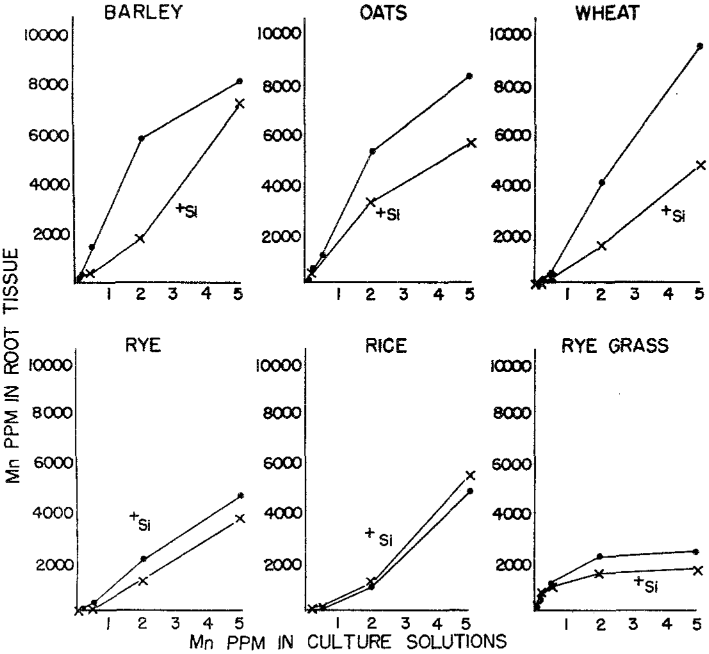

Fig. 5. Mn-content of roots versus Mn in solution, plus or minus silicon.

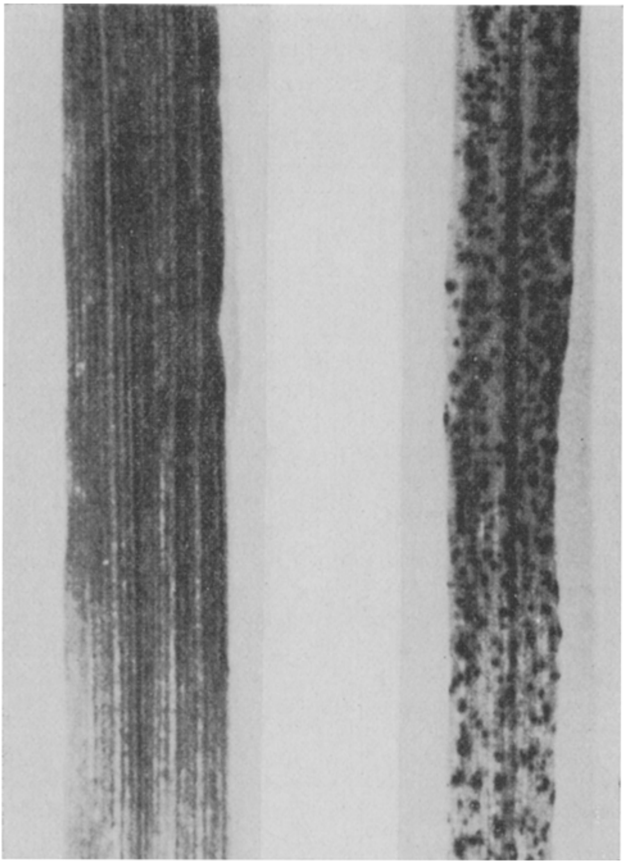

Fig. 6. Photograph of barley leaves, showing small, brown, necrotic spots on a leaf of a plant grown in solution containing 5 ppm Mn without silicon contrasted with a symptom-free leaf from a plant grown with silicon, same Mn-concentration.

other plants. In the case of rye roots, the effect of Si on Mn-content is too small to be considered significant.

Of further interest in this study is the relation of Mn and Si to the appearance of the small, necrotic, brown spots on the older leaves that has been described for barley [7]. Barley, rye, rice, and ryegrass, in that order, were the only plants to show the brown spotting characterized as Mn-toxicity. In all four of these species silicon prevented the appearance of spotting. Figure 6 shows the characteristic brown spots on a barley leaf and the healthy appearance of another which had been grown with silicon in a culture solution having the same Mn concentration. The substitution of sodium sulfate in amounts equivalent to the sodium silicate used in this work failed to eliminate the necrotic systems. This eliminates sodium as an alternative source of the results reported.

DISCUSSION

In earlier experiments it has been shown that barley plants grown in Hoagland's solution developed necrotic brown spots on the old leaves and that this was related to the Mn-content. It was further demonstrated that silicon prevented the symptoms and resulted in much higher yields. It was also concluded from those studies that barley had a very narrow range of tolerance between deficiency and toxicity of Mn.

In the present investigation of six grasses, barley emerged as the most sensitive species to Mn-toxicity and gave the largest percent increase in yield from the addition of silicon to the nutrient solution. A smaller order of magnitude of response was shown by oats and wheat. One anomaly appeared in that wheat plus silicon was the only combination which maintained optimum yields right up to the highest concentration of Mn in solution. This could be explained on the grounds that only with wheat was the Si added sufficient to completely overcome the effects of Mn.

The next highest response to Si was given by rye. Rice and ryegrass showed insignificant differences. Rice also gave the smallest depression in yield as a result of high Mn in solution. All other species showed a very sharp peaking of yield at low concentrations of Mn followed by a rapid drop, with the exception noted above of wheat grown with silicon.

The Mn content of the shoots as exemplified by the old leaves is a function of the Mn supplied in solution. In addition to this the effect of silicon is to decrease the Mn-content of the tissues. While this decrease seems to be substantial in some of the plants it is still within the bounds of what is called the dilution effect. That is, the much greater growth of the plants with silicon can account for the lower Mn content in these plants. Support for this point of view comes from an earlier experiment where larger volumes of solution per plant were used to minimize the growth dilution effect. It was found with barley that silicon eliminated Mn toxicity symptoms with no significant alteration of the Mn-content [8].

With the exception of rice, the Mn contents in the roots were substantially higher than those found in the shoots. At the high Mn levels the root tissues ranged from 2,000 ppm Mn in the case of ryegrass to over 8,000 ppm for wheat, barley, and oats. These values were from 2 to 8 times higher than found in the shoots. The Mn-content of rice shoots was slightly higher than in the roots.

Of considerable interest is the unusually large amount of Mn in the leaves of the rice plant. This was from five to ten times as much as was found in the other grasses. Also, in spite of this huge accumulation of Mn, the rice plants showed the smallest yield depression at the high Mn-levels in solution. It is speculated that rice, adapted as it is to growing under anaerobic soil conditions, may have evolved a mechanism for tolerating the high Mn which appears on soil submersion [3].

From an ecological point of view the sharp responses of the grasses, rice excepted, to high Mn in the external medium are not likely to be very critical. Plants growing in soil with a high-Mn environment, i.e., acid or manganiferous soils, will also be exposed to a supply of Si. This should tend to soften the effects of high Mn situations both as to yield, and the characteristic Mn necrotic spotting in those species where this symptom occurs.

This experiment was not designed to test the essentiality of Si for the six plants studied. Substantial increases in yield were obtained from the addition of Si to the solutions in the case of barley, oats, wheat, and rye. Some of this increase could be based on the effect of Si in preventing Mn-toxicity. On the other hand, the fact that the Si increases in yield extended to some of the deficiency levels suggests a function for Si beyond that of preventing Mn-toxicity.

In four of the six grasses Si overcame only a part of the Mn-toxicity measured by yield depression. The question remains – if a continuous supply of Si were maintained at a sufficiently high level, would the protective action of Si be extended. In oats and wheat, no toxicity symptoms were apparent yet there was a substantial increase in growth due to Si. This may be regarded as growth stimulation per se or as still another case of overcoming toxic amounts of Mn, even though the necrotic, brown spots do not appear. Ryegrass showed a steep drop in growth at high Mn-levels, yet Si failed to overcome this at any point. And finally, in the case of shoots of rice, with the highest Mn content of all, the depression in yield due to high Mn was minimal and Si had no beneficial effect.

These are some of the apparent anomalies that seem to require further exploration.

SUMMARY

Six species of grasses were tested for response to Mn covering a range from deficiency to toxicity in nutrient solutions in the presence or absence of silicon. The growth curve of all plants peaked sharply in the deficiency range up to 0.1 or 0.2 ppm Mn in solution, then fell away abruptly for oats, barley, rye, wheat, and ryegrass in the toxicity range up to 5 ppm. In the presence of silicon the peaks were higher for barley, oats, wheat, and rye, but not for rice or ryegrass. The silicon treatment produced an increased yield percentagewise over the no silicon in the following order from most to least; barley, wheat, oats, and rye. Rice and ryegrass showed no significant yield response from the addition of silicon. Where the other grasses showed a sharp yield decline in the toxicity range, the growth of rice decreased slightly up to 5 ppm Mn.

The Mn content of the shoots increased with the age of the leaves. The old leaves of rice had a Mn-content of 6,000 to 7,000 ppm of Mn at the 5 ppm treatment, while oats, wheat, and barley ranged from 800 to 1200 ppm. Rye leaves contained 1400 to 1500 ppm Mn in the same treatment while ryegrass was lowest at 600 to 900 ppm. In all grasses the effect of silicon was to lower the Mn-content slightly, but it was concluded that this could be explained for the most part as a dilution effect due to the increased growth where silicon was added.

The Mn-content of the roots was higher than that of the shoots in all plants except rice where the situation was reversed. Ryegrass stood apart from the other grasses in that the Mn-content of the roots plus or minus Si tapered off at the 5 ppm level instead of increasing rapidly as did the others.

Toxicity symptoms of necrotic, brown spots on the old leaves appeared in barley, rye, rice, and ryegrass at the high Mn-levels. The addition of Si to the solutions prevented the appearance of symptoms. The oats and wheat were free of symptoms.

A few observations were made on the ecological implications of the Mn–Si interaction reported. The functional role of Si in overcoming Mn toxicity and its effect in increasing growth were discussed in relation to its possible essentiality for grasses.

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