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INTERACTION OF HYDROGEN (H^+) AND MANGANESE (Mn^{2+}) CONCENTRATIONS ON THE SHOOT GROWTH OF SORGHUM CULTIVARS

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ABSTRACT: Sorghum [*Sorghum bicolor* (L.) Moench] seedling (14-day) shoot length, fresh weight, and dry weight were determined in plants grown in 'white quartz flintshot' sand and watered with 0.01 M sodium acetate at pH 6.0, 5.5, 5.0, 4.5, or 4.0 to which Mn^{2+} (0, 1.4, 14.0, or 140.0 mg/Kg) was added. Cultivars evaluated were 38M, 58M, GP-140, SC283, SC574, TAM428, and Funk G522DR. Numbers of plants visible above the ground line were influenced by excess H^+ and Mn^{2+} but the influences on germination and emergence were small. Leaf length, fresh weight, and dry weight were markedly influenced by H^+ and excess Mn^{2+}; and these responses in shoots were explicable as interacting influences on gibberellic acid biosyntheses and translocation.

Abbreviations: GA = gibberellic acid.

INTRODUCTION

Acid-soils present multiple stresses to plants. These stresses include excess H^+, Mn^{2+}, and Al^{3+} as well as deficiencies of Ca^{2+}, Mg^{2+}, and PO_4^{3-} (2,5,6). Study of plant responses to these individual stresses has shown excess H^+ to inhibit sorghum seedling shoot growth by modifying GA translocation from sites of biosynthesls to sites of action by decreased partitioning from lipid membranes to water as the external H^+ concentration increased (20). Excess Mn^{2+} influenced sorghum shoot growth by modifying isoprenoid biosynthesis (21, 22). Interaction of excess H^+ and Mn^{2+} on growth of sorghum shoots has not been reported. Therefore, evaluations of these factors on sorghum shoot growth were undertaken.

METHODS

Plant Growth: Within a single cultivar, twenty-five seeds were planted 1 cm deep in 8 cm x 8 cm x 8 cm pots filled with 'white quartz flintshot' sand. The pots were watered on alternate days with 100 mL 0.01 sodium acetate whose pH was adjusted with conc. HCl to pH 6.0, 5.5, 5.0, 4.5, or 4.0. Manganese chloride was added to the water at concentrations of 0, 1.4, 14.0, or 140.0 mg Mn^{2+}/Kg. After 14 days, the number of visible plants, shoot fresh weight, and shoot dry weights were recorded. Cultivars tested included two high GA producing cultivars (38M, 58M), three acid soil tolerant cultivars (GP-140, SC283, SC574), and an intermediate tolerant and two susceptible cultivars (SC599, TAM428, and Funk G522DR). Data were subjected to analysis of variance on a five replicate, randomized complete block design for individual cultivars. Means were separated by the LSD multiple means method.

Correlation of ent-Kaurene Synthesis at 10 mM Mn^{2+} versus Response to Acid-Soil-Stress: Data from a previous report on five sorghum cultivars (21) on ent-kaurene biosynthesis as influenced by Mn^{2+} concentration were correlated with acid-soil-stress resistance. The analyses showed a > 99% correlation.

Gibberellin Reversal of H^+ Concentration Influences: Twenty five seed of Funk G522DR per pot were planted as described above. Treatments were pH 6.0 (0 GA_3), pH 4.5 (0, 0.1, 1.0, and 10.0 µM GA_3 incorporated into the sand). Data from the five replications were analyzed as described above.

RESULTS

Plant Emergence: Excess H^+ concentration (0 mg Mn^{2+}/L) did not alter plant emergence between ptt 6.0 and 4.5 for any cultivar (Table 1). When grown at pH 4.0, significant decreases in plant emergence were noted for SC283, SC574, SC599, TAM428, and Funk G522DR (Table 1). These significant differences were variable between pH 5.0, 4.5, and 4.0. For example: a) SC283 had a significantly different plant emergence between 0 mg Mn^{2+}/Kg at pH 4.5 and 4.0; b) plant emergence was low at pH 5.0 in SC574; and c) the significant differences were between pH 5.0 and pH 4.0 in SC599, TAM428, and Funk G522DR, (Table 1). Over all, these data show a small influence of excess H^+ concentration on plant emergence from pH 6 to 4.5. Combination of excess H^+ and Mn^{2+} showed a significantly decreased plant emergnce at pH 4.0. Yet, even these general combinations of interactions were variable.

Shoot Length: Leaf length (cm) was, generally, inhibited as the watering solution was decreased from pH 6.0 to pH 4.0 (0 mg Mn^{2+}/kg) (Table 2). These data corroborate previous reports (20). In some cultivars (*i.e.*, SC283), low Mn^{2+} concentrations (*i.e.*, 1.4 mg Mn^{2+}/kg - pH 6.0) induced Increased leaf length (Table 2). This was a general response in several cultivars even though this response was not statistically significant. Increased leaf growth appeared at Mn^{2+} concentrations below 14.0 mg Mn^{2+}/kg. At high Mn^{2+} concentrations (*i.e.*, 1, 140 mg/kg) growth decreased at pH 6.0 (Table 2). As the general decrease in leaf length due to excess H^+ became more evident at pH 4.5 or 4.0, the influence of excess Mn^{2+} disappeared (Table 2). These data show that both H^+ and Mn^{2+} influence plant growth independently. When stress (pH 4.0) became sufficiently severe to decrease leaf elongation to a subsistence level; the addition of a second stress (140 ppmw Mn^{2+}) significantly decreased the capacity of the plant to grow, and the interaction of the two stresses tended to become indistinguishable from either stress individually.

Correlation of ent-Kaurene Biosynthesis with Acid-Soil-Stress Resistance: Excess Mn^{2+} altered the capacity of the sorghum cultivars to produce GA precursors; and the response was dependent upon Mn^{2+} concentration and the sorghum cultivar (21). Nearly all of the cultivars showed high GA precursor biosynthesis at 1 mM Mn^{2+}. However, the ability of individual cultivars to produce the GA precursor ent-kaurene at 10 mM Mn^{2+} varied widely (21). When the quantity of ent-kaurene produced at 10 mM Mn^{2+} by the individual cultivars was correlated with the relative resistance of five cultivars to survive acid-soil-stress, the correlation was a near perfect line (Fig. 1). Impact phase (germination and emergence) SC283 was highly resistant while TAM428 was

TABLE 1. Average Numbers of Plants Emerging after 14-Days of Sorghum Cultivars Watered with Solutions of Different pH Containing Mn^{2+} at Different Concentrations. Each Number is the Average of Five Replications.

Cultivar	Mn^{2+}	pH					
	(ppmw)	6.0	5.5	5.0	4.5	4.0	pH
		----------	----------	----#----	----------	----------	
38M	0	22.6abc[1]	23.8ab	23.8ab	22.6abc	21.8abc	
	1.4	21.8abc	21.2a	22.6abc	24.0a	22.8abc	
	14.0	23.0abc	23.4abc	23.6ab	23.2abc	21.0c	*
	140.0	23.0abc	23.4abc	23.8ab	22.4abc	21.4bc	
58M	0	24.8a	24.6ab	24.4ab	24.2abc	24.2abc	
	1.4	24.4ab	23.4b-e	24.0a-d	23.0cde	24.0a-d	*
	14.0	24.6ab	23.6a-e	24.2abc	23.8a-d	22.4e	*
	140.0	23.6a-e	23.6a-e	24.4ab	23.4b-e	22.8de	*
						*	
GP-140	0	18.8ab	19.5ab	19.5ab	20.0a	17.8ab	
	1.4	19.5ab	20.0a	19.5ab	20.8a	14.2c	*
	14.0	19.0ab	18.8ab	18.5ab	18.0ab	16.2abc	
						*	
SC283	0	17.8a-e	19.8ab	19.8ab	20.8a	16.2b-e	*
	1.4	19.0abc	19.8ab	19.8ab	17.5a-e	14.5de	*
	140.0	19.5ab	18.8a-d	17.8a-e	14.8cde	13.8e	*
					*		
SC574	0	16.2bcd	18.0bcd	15.5d	17.0bcd	19.5ab	*
	1.4	18.5a-d	16.8bcd	18.0bcd	19.0abc	21.5a	*
	140.0	16.8bcd	15.8cd	17.5bcd	17.2bcd	15.5d	*
						*	

TABLE 1. (cont'd)

Cultivar	Mn^{2+} (ppmw)	pH 6.0	5.5	5.0	4.5	4.0	pH
		-------------------- # --------------------					
SC599	0	19.2ab	20.8ab	21.5a	20.2ab	16.0bc	*
	1.4	19.8ab	20.2ab	18.8ab	18.8ab	13.5c	*
	140.0	20.0ab	19.2ab	19.5ab	20.8ab	12. c	*
TAM428	0	20.5ab	21.5a	19.5abc	21.5a	14.5d	*
	1.4	20.2ab	21.5a	20.0abc	19.5abc	15.5cc	*
	140.0	21.2a	20.8ab	20.5abc	20.0ab	16.8bcd	*
Funk G522DR	0	22.5a	20.5a	21.5a	21.2a	15.5b	*
	1.4	20.8a	19.8ab	20.2a	20.8a	15.2b	*
	140.0	21.5a	22.0a	21.8a	22.0a	21.8a	
						*	

[1]Values within a genotype followed by the same letter are not significantly different at the 5% level.

*Indicates a significant difference in a line or column.

extremely sensitive to acid-soil-stress (3,24). Therefore, in the multiple factored acid-soil-stress phenomena, excess Mn^{2+} may be a major factor in the seedling establishment of TAM428.

Gibberellin Reversal of H^+ ***Concentration Influence:*** Water at pH 4.5 induced a significantly decreased shoot length when compared to pH 6.0 (Fig. 2). Addition of 1 or 10 µM GA_3 to the sand reversed the growth inhibition induced by excess H^+ concentration (Fig. 2) while GA_3 concentrations at 0.1 and 100 µM did

TABLE 2. Average Shoot Length (cm) of Sorghum Cultivars at 14-Days Growth after Watering with Various Mn^{2+} Concentrations at Different pH. Each Number is the Average of Five Replications.

Cultivar	Mn^{2+} (ppmw)	pH 6.0	5.5	5.0	4.5	4.0	pH
		---cm---					
38M	0	18.4a[1]	15.8ef	18.3ab	11.5g	8.0i	*
	1.4	17.1cd	16.4def	19.0a	12.2g	7.6i	*
	14.0	18.1abc	16.8de	18.4a	11.5g	7.2i	*
	140.0	17.2bcd	15.6f	16.7def	10.0h	5.5j	*
58M	0	17.5bc	16.7d	15.3ef	11.9i	9.1j	*
	1.4	18.0ab	17.4bcd	15.8e	12.8h	9.0j	*
	14.0	18.7a	17.6bc	15.3ef	13.6g	7.9k	*
	140.0	17.2cd	15.9e	14.9f	13.1gh	7.5k	*
		*	*	*	*	*	
GP-140	0	25.0ab	28.8a	26.2bc	21.2bc	16.2cd	*
	1.4	25.0ab	21.2cd	21.2bc	11.2de	12.5de	*
	14.0	16.2cd	11.2de	10.0de	8.8e	7.5e	*
		*	*	*	*	*	
SC283	0	20.0c	22.5bc	20.0c	20.0c	7.5d	*
	1.4	27.5ab	23.8abc	28.8a	18.8c	10.0d	*
	140.0	11.2d	10.0d	12.5d	8.8d	8.8d	
		*	*	*	*		
SC574	0	16.2abc	15.0a-d	12.5b-e	16.2abc	7.5ef	*
	1.4	20.0a	17.5ab	17.5ab	11.2cf	7.5ef	*
	140.0	6.2f	10.0def	8.8ef	7.5ef	6.2f	
						*	

TABLE 2. (cont'd)

Cultivar	Mn^{2+} (ppmw)	pH 6.0	5.5	5.0	4.5	4.0	pH
		--------------------cm--------------------					
SC599	0	12.5ab	10.0a-d	8.8a-d	8.8a-d	5.0d	*
	1.4	13.8a	11.2abc	11.2abc	7.5bcd	6.2cd	*
	140.0	8.8a-d	6.2cd	7.5bcd	7.5bcd	5.0d	
TAM428	0	21.2abc	22.5ab	18.8bcd	13.8d-g	8.8g	*
	1.4	26.2a	21.2abc	22.5ab	15.0def	8.8g	*
	140.0	16.2cde	12.5efg	10.0fg	11.2efg	8.8g	*
		*	*	*			
Funk G522DR	0	28.8a	21.2b-e	21.2be	20.0bf	13.8f	*
	1.4	25.0ab	23.8abc	22.5a-d	25.0ab	16.2def	*
	140.0	13.8f	15.0ef	20.0f	17.5c-f	15.0ef	
		*	*		*		

[1]Values within a genotype followed by the same letter are not significantly different at the 5% level.
*Indicates a significant difference in a line or column.

not reverse the H^+ concentration influence (Fig. 2). Thus, GA at a specific concentration range is requisite for sorghum leaf growth.

Fresh Weight: Total fresh weight (g/pot) (Table 3) was roughly equivalent to leaf length for genotypes 38M and 58M (Table 2). Leaf length of 38M showed Mn^{2+} responses at pH 6.0, 5.5, and 5.0 while total fresh weight showed significant differences at pH 5.0 and 4.5 (Table 3). Total fresh weight of 58M was responsive to excess H^+ and Mn^{2+} concentrations.

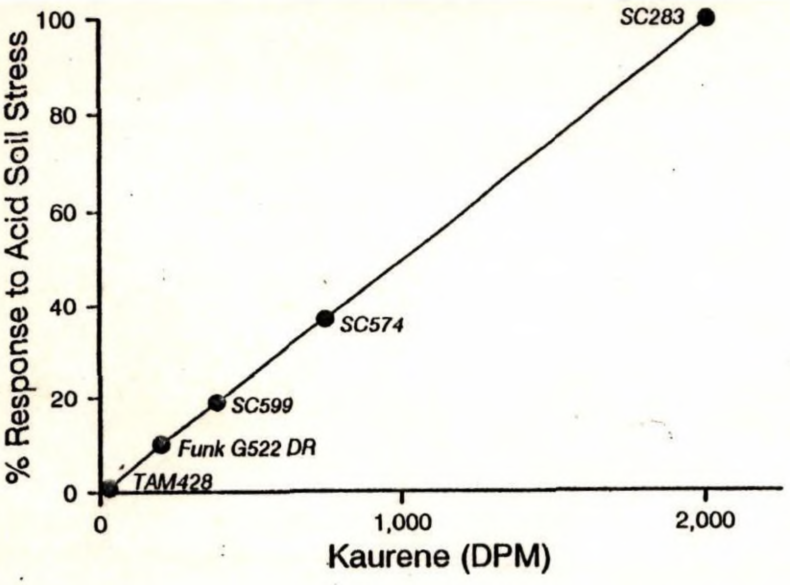

FIGURE 1. Response to acid-soil-stress in five sorghum cultivars as explained by ent-kaurene biosynthesis at 10 mM Mn^{2+}. Each point is the average of five determinations. Regression was significant at 1%.

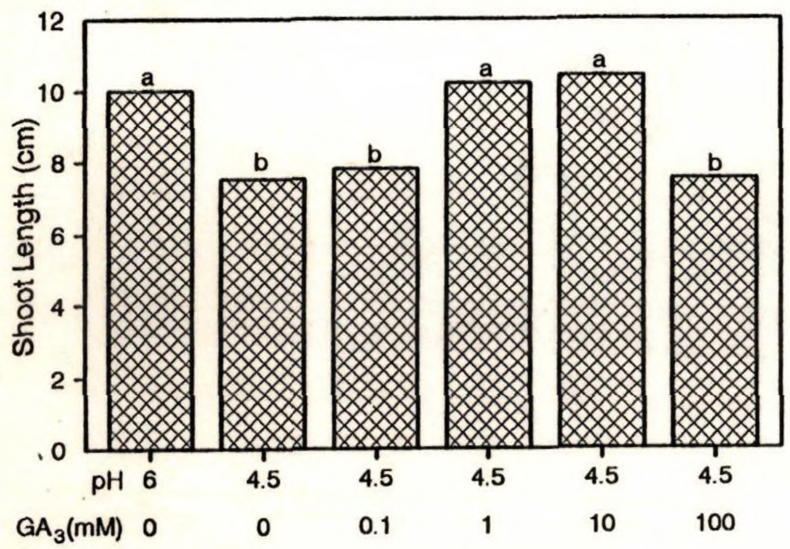

FIGURE 2. Influence of sand incorporated gibberellic acid GA_3) on the growth of Funk G522DR sorghum shoots watered with pH 4.5 (0.01 mM sodium acetate). Bars with the same letter are not significantly different at the 5% level.

Table 3. Shoot Fresh Weight (gm/pot) of Sorghum Cultivars Grown for 14 Days and Watered with Solutions of Different pH and Mn^{2+} Concentrations. Each Value is the Average of Five Replications.

Cultivar	Mn^{2+} (ppmw)	pH 6.0	5.5	5.0	4.5	4.0	pH'
		gm/pot					
38M	0	2.50cde[1]	2.59b-e	2.91a	1.57f	1.03gh	*
	1.4	2.39de	2.55b-e	2.74abc	1.75f	1.12gh	*
	14.0	2.60bcd	2.56b-e	2.84ab	1.72f	1.05gh	*
	140.0	2.30e	2.34de	2.47cde	1.26g	0.89gh	*
		*		*	*	*	
58M	0	2.57b	2.40bcd	2.03gh	1.52k	1.19lm	*
	1.4	2.59ab	2.52bc	2.34cde	1.61jk	1.24l	*
	14.0	2.77a	2.29def	2.20efg	1.75ij	1.04m	*
	140.0	2.29def	1.91hi	2.13fg	1.58jk	1.00m	*
		*	*	*	*	*	

[1]Values followed by the same letter are not significantly different at the 5% level.

*Indicates a significant difference in a line or column.

Because differences in the number of plants emerged/pot appeared, plant fresh weights (mg/plant) were calculated (Table 4). Responses of 38M and 58M to combinations of excess H^+ and Mn^{2+} were found at all levels of each stress except that 38M did not show a response to excess Mn^{2+} at pH 4.0 (Table 4).

Fresh weight per unit leaf length (mg/cm) showed a composite of the leaf length (cm) and total fresh weight (g/pot) responses (Table 5). These data further

Table 4. Shoot Fresh Weight (mg/plant) of Sorghum Cultivars Grown for 14 Days and Watered with Solutions of Different pH and Mn^{2+} Concentrations. Each Value is the Average of Five Replications.

Cultivar	Mn^{2+}	pH					
	(ppmw)	6.0	5.5	5.0	4.5	4.0	pH
		Fresh Wt (mg/plant)					
38M	0	110cd[1]	108cd	122a	70f	47gh	*
	1.4	110cd	105cd	122a	73f	49gh	*
	14.0	113bc	110cd	120ab	74f	50gh	*
	140.0	100e	100e	103de	56g	42h	*
		*	*	*	*		
58M	0	104bc	97cd	83f	63i	49jk	*
	1.4	106ab	108ab	98cd	70hi	52j	*
	14.0	113a	97cd	91de	74gh	47jk	*
	140.0	97cd	81fg	88ef	68hi	44k	*
		*	*	*	*	*	

[1]Values followed by the same letter are not significantly different at the 5% level.

*Indicates a significant difference in a line or column.

document the concept that decreases in length due to reduced GA biosynthesis were not entirely equivalent to an inhibition of cell size. Excess H^+ and Mn^{2+} induced greater fresh weight/cm leaf length (38M at pH 4.0) when increases in leaf length were inhibited more than increases in cell size. Thus, the very short leaves of 38M plants grown at pH 4.0 and 140 mg Mn^{2+}/kg had greater weight/cm length values than leaves of plants grown with 0 Mn^{2+} (Table 5).

Table 5. Shoot Fresh Weight (mg/cm) of Sorghum Cultivars Grown for 14 Days and Watered with Solutions of Different pH and Mn^{2+} Concentrations. Each Value is the Average of Five Replications.

Cultivar	Mn^{2+} (ppmw)	pH 6.0	5.5	5.0	4.5	4.0	pH
		(mg/cm)					
38M	0	136cde[1]	163a	159ab	136cde	130de	*
	1.4	139be	155abc	145a-e	146a-e	148a-d	
	14.0	143a-e	153abc	155abc	149a-d	146a-e	
	140.0	134cde	150a-d	148a-d	125e	163a	*
					*		
58M	0	147a	144ab	133b-e	128def	130cf	*
	1.4	144ab	145ab	148a	126def	138a-d	*
	14.0	148a	130def	144ab	129def	132b-f	*
	140.0	134b-e	120f	143abc	121ef	133b-e	*
		*	*	*			

[1]Values followed by the same letter are not significantly different at the 5% level.

*Indicates a significant difference in a line or column.

Dry Weight: Total shoot dry weight change (mg/pot) (Table 6) were similar to fresh weight/pot changes (Table 3). Because cytosol pH is normally heavily buffered and pH changes of approximately 0.1 pH unit for each 1.0 pH unit of the external medium (4), these responses might possibly be due to changes in the absorption of ions through the plasma membrane (23). Responses at high Mn^{2+} concentration are a reflection of altered metabolism due to the excess Mn^{2+} concentration. Excess Mn^{2+} is known to induce decreased activity of mevalonic

Table 6. Shoot Dry Weight (mg/pot) of Sorghum Cultivars Grown for 14 Days and Watered with Solutions of Different pH and Mn^{2+} Concentrations. Each Value is the Average of Five Replications.

Cultivar	Mn^{2+} (ppmw)	pH 6.0	5.5	5.0	4.5	4.0	pH
		(mg/pot)					
38M	0	248cd[1]	282abc	202efg	170gh	174fg	*
	1.4	254bcd	290ab	232de	194efg	132hi	*
	14.0	280abc	302a	200efg	214def	126i	*
	140.0	254bcd	292ab	186fg	176fg	116i	*
					*		
58M	0	204bcd	176de	212abc	136f	44gf	*
	1.4	202bcd	214abc	242a	140f	60g	*
	14.0	222ab	184cde	228ab	158ef	72g	*
	140.0	160ef	180de	240a	136f	46g	*
		*	*				

[1]Values followed by the same letter are not significantly different at the 5% level.

*Indicates a significant difference in a line or column.

kinase (17) phytoene synthetase (14), ent-kaurene synthesis (12), and isocitrate lyase activity (7,8,18). In the latter enzyme, Mn^{2+} is active, but the normal activity usually utilizes Mg^{2+} (7,8). Because Mn^{2+} is dissociated from the enzyme at rates $<10^4$ *less* than what occurs for Mg^{2+}, Mn^{2+} might be considered an inhibitor of isocitrate lyase (7). ent-Kaurene synthetase was most active at specific ratios of Mg^{2+}/Mn^{2+} (12). Either ion served as an electron carrier for the enzyme; but, specific mixtures were more active (12).

DISCUSSION

These few examples illustrate the concept that individual enzyme systems have evolved for maximum specific activity under limited ionic environments. Activity of specific enzymes decreases when the ionic concentrations have been severely altered from the particular optimum enzyme environment. Plant foliage Mg^{2+} and Mn^{2+} ionic contents (mg/g dry weight) reflected the availability of ions in the soil solution (3,24). Under acid- soil -stress conditions, the Mg^{2+}/Mn^{2+} ratio changed markedly (3); the Mg^{2+}/Mn^{2+} ratio and ionic contents of the leaves matched what was available in the soil solution. Altered Mn^{2+} availability greatly influenced plant growth (3,24). However, under conditions of toxic Mn^{2+} concentrations the toxicity was decreased when Mg^{2+} was added (10). Growth was decreased when the Mg^{2+}/Mn^{2+} was < 20:1 (10).

Sorghum has three major growth stages (*i.e.*, impact, vegetative, and reproductive) (3,24). This progression of life stages may be controlled by external environmental factors (*i.e.* - ions, water, temperature, photoperiod, etc.) that control hormonal syntheses or activities. These, in turn, induce synthesis and/or activities of specific enzymes. The relative activities of the enzymes change the physiological state of the plant and a new stage (reproductive) ensues. Enriched GA in sorghum greatly altered the rates of development of the various growth stages (1). GA biosynthesis inhibitors altered the rates of development of the reproductive stage; and, exogenous GA reversed the inhibition by the GA biosynthesis inhibitors (1). GA biosynthesis was altered by photoperiod (9), temperature (16), and ions (14,22,23,24). The data presented herein on the response of seedling sorghum leaves to excess Mn^{2+} are understandable on the basis of an influence of Mn^{2+} on GA biosynthesis. Specific enzyme biosynthesis and/or activity as a function of GA concentration/activity need to be understood. Acid soils present conditions of excess H^+, Mn^{2+}, and Al^{3+} as well as deficiencies of Ca^{2+}, Mg^{2+}, and PO_4^{3-} to plants (2,5,6). Excess Al^{3+} is toxic (13,15). Al^{3+} replaces Mg^{2+} in Mg^{2+}-ATPase enzyme activity but dissociates from the enzyme at 10^6x less than the Mg^{2+} dissociation (13). Manganese (Mn^{2+}) replaces Mg^{2+} in isocitric lyase (7,8,18) and dissociates from the enzyme - 10^4x slower than the Mg^{2+}. Cytosol Ca^{2+} concentration is very closely regulated and maintains control of many metabolic functions (11). Altered cytosol Ca^{2+} concentration would have deleterious results. Soil solution Ca^{2+} is greatly decreased at the pH associated with acid-soil-stress (2,5,6). Magnesium deficiency could be due to: a) decreased quantities of Mg^{2+} or b) increased quantities of Mn^{2+} in the soil solution (3,21,24). Either situation would result in Mg^{2+}/Mn^{2+} ratios that have been found to be highly deleterious to plant growth (23). Even though some sorghum GA biosynthesis systems appeared to function very well at low Mg^{2+}/Mn^{2+} ratios, other sorghum cultivars were not efficient at low Mg^{2+}/Mn^{+} ratios (19). Excess H^+ induced decreased $^{45}Ca^{2+}$ absorption by sorghum roots (21) and may, possibly, decrease root absorption of other ions. Acid-soils present specific growing conditions to plants. Root response varied between cultivars (21). The data presented herein show that sorghum growth at different H^+ concentrations interacts with Mn^{2+} concentrations in the overall plant response. Thus, every factor in the soil-plant continuum must be evaluated in the study of acid-soil-stress.

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