SOME PHYSIOLOGICAL STUDIES OF IRON UTILIZATION BY *PENNISETUM AMERICANUM* (L.) K. SCHUM AND *SORGHUM BICOLOR* (L.) MOENCH

by

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Approved by:

Major Professor

Major Professor

This work is dedicated to my brother,

MR. SAMUEL OYENUHI OGUNGBAMIWA

who sent me to school in the first place.

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INTRODUCTION

Iron chlorosis in plants has been associated with genetic susceptibility to Fe deficiency and antagonistic interactions between this element and P, Ca, Ni, Cu, Mn and Zn. Other factors that cause Fe chlorosis either singly or in combination are low Fe supply, extreme temperatures, high light intensity, high levels of nitrate nitrogen and damage to roots by nematodes or other organisms.

Much research has been done in countries like Nigeria and India to improve the yields of sorghum and millet by breeding and fertilizer application but Fe deficiency and toxicity problems have not received much attention. Sorghum is produced extensively in the U.S.A. and used mainly for livestock feed. Millet is an important warm-season forage and a potential grain crop. Sorghum and millet have similar edaphic and climatic requirements, but sorghum is markedly more susceptible to Fe-deficiency chlorosis. Studies on the difference in Fe nutrition between millet and sorghum were conducted with the following objectives:

1. To investigate the effect of P levels on the growth and nutrient composition of sorghum and millet.

2. To study the distribution pattern of radioactive Fe, (^{55}Fe) in sorghum and millet by the use of autoradiography.

3. To evaluate the effect of root pruning on the absorption of Fe, P, Mn, Cu and Zn.

4. To evaluate the effect of Fe chelate on field performance of sorghum and millet and their flagleaf-nutrient composition.

5. To determine the effect of soil-applied Fe on growth,

chlorophyll content, and leaf blade Fe and P concentrations.

REVIEW OF LITERATURE

Essentiality and functions of iron in plants

Gris (1844) demonstrated that plants require Fe. He painted solutions of iron salts on chlorotic grape leaves and restored the natural color of the leaves. This demonstration implied that Fe is necessary for the maintenance of chlorophyll in plants and, therefore, posed the question of the essentiality of this element. The essentiality of Fe to plants has, however, been established. Experiments of Agarwala et al., (1965) indicated that the chlorophyll content of Zea mays and Beta vulgaris increased with increasing Fe supply. Davis (1973), however, noted that the specific mechanism by which Fe functions in the synthesis and degradation of chlorophyll is still uncertain.

It is generally accepted that Fe does not function in the enzymatic synthesis of porphyrins in plants (Carrel and Price, 1965). However, Fe is at the center of the porphyrin ring analogous to Mg in the chlorophyll molecule and presumably acts by shifting from ferric to ferrous in oxidation-reduction reactions (Mitchell, 1972).

According to Davis (1973), Fe has been identified as a component of metalloflavoproteins which are active as enzymes, e.g. the cytochromes. Iron is a constituent of catalase and peroxidase (Gauch, 1972). Iron has also been shown to be capable of partly replacing molybdenum as the metal cofactor necessary for nitrate reductase (Mitchell, 1972). Iron, a component of ferredoxin (Burris, 1966), was shown to be an electron transferring protein by Mortensen et al., (1963) and associated with chloroplasts (Smillie, 1963). Iron also functions in photosynthesis and nitrate

and nitrite reductions (Losada et al., 1965; Betts and Hewitt, 1966; Joy and Hageman, 1966).

Sorghum is one of the most sensitive plants to Fe deficiency. Krantz et al., (1962) reported that in areas where forage or grain sorghum was harvested and allowed to re-grow for a second crop, the re-growth showed Fe chlorosis more severely than the first growth. Sprague (1964) described the chlorosis in sorghum and related crops as interveinal or striping over the full length of the leaves. Chlorosis was most severe on upper leaves since Fe is relatively immobile. In cases of severe Fe deficiency, plants become white and eventually die. Although Fe is said to be the most abundant element in this planet (Mortvedt, Giordano and Lindsay, 1972), interaction with other elements, soil pH, weather, genetic and other factors greatly affect the availability of this essential element to plants.

Effect of Phosphorus on Fe chlorosis of plants

Dekock and Wallace (1965) indicated that high concentrations of phosphates in plants cause typical Fe-deficiency chlorosis. Their studies showed that organic acids in leaves are involved in absorption and distribution of minerals and the behavior of these minerals is controlled by an Fe-PO_4 balance. Khruslova (1965) also found that high concentrations of P caused chlorosis in wheat plants supplied with ionic Fe in water culture of pH 6.6.

Several workers (Biddulph, 1947; Biddulph and Woodridge, 1952; Brown et al., 1955; Franco and Loomis, 1947) found that some plants absorb less Fe and even develop Fe chlorosis when relatively high concentrations of P are present in the growth medium. Watanabe et al.

(1965) observed stunted and extremely Fe-deficient plants when P levels in a nutrient solution were increased from 0.2 to 0.6mM. The nutrient solution contained 40uM Fe as iron chelate (Fe EDDHA).

Adriano, Paulsen, and Murphy (1971) investigated P-Fe and P-Zn relationships in corn (Zea mays L.) seedlings as affected by their mineral nutrition. They reported that high P decreased Fe concentrations in the root and slightly depressed Fe concentration in the shoot.

The mechanism of P-Fe interaction in plants is not clear, but it is thought that chlorosis is caused by inability of plants to take up sufficient Fe from the growth medium or by difficulties in internal translocation. Iron might be precipitated in the veins and unable to reach the leaf mesophyll as shown in corn by Olsen (1935) and corroborated by Rediski and Biddulph (1953) in their experiments with beans (Phaseolus vulgaris).

Interaction of Fe with other metals

Uptake of Fe by plants is also sensitive to high levels of Ca (Brown, 1956; Brown, et al., 1959) and Zn (Tiffin, 1967; Watanabe et al., 1965). Excessive amounts of these nutrients in the growth medium or in the plants often cause deficiency of Fe. Watanabe et al. (1965) associated Zn-induced Fe chlorosis with decreased Fe/Zn ratios. Studies by Vretta-Kouskoleka and Kallinis (1968) on cotton (Gossypium Sp.) and by Tiffin (1967) on tomato (Lycopersicon Sp.) suggested a somewhat antagonistic relationship between Fe and Mn. Earlier work by Sommer and Shive (1942) on soybeans (Glycine Sp) indicated that Fe and Mn are interrelated in their metabolic functions with the effectiveness of each nutrient determined by the proportionate presence of the other. In nutrient solutions, soybeans developed typical Fe-deficiency chlorosis on substrates with high

Mn concentrations. Similar effects of high Mn concentrations were observed on red clover by Hanger (1965). Stunted growth and apical chlorosis were prevented by increasing the Fe concentration in the substrate.

Tiffin and Brown (1962) found that most of the Fe translocated to the shoot of soybeans was in the form of ferric malate or ferric malonate. They proposed that metabolism interfered with Fe translocation in plants by displacement of the Fe in the malic or malonic acid complexes by interfering ions such as Mn, Cu, Zn or Ca. Lingle et al. (1963) determined the effect of interfering ions Mn, Cu, Zn, Ca, Mg, K and Rb on uptake-transport of Fe by Fe-deficient soybean plants. They measured the disappearance of ^{59}Fe from the nutrient solution, the concentration of ^{59}Fe in the stem exudate of decapitated plants and Fe distribution in intact plants. Zinc was the strongest interfering ion in the decapitated plants and it also interfered with the uptake-transport of Fe by intact plants. Zinc both decreased uptake of Fe by the roots and interfered with translocation of Fe to the shoots.

Iron-molybdenum interactions have been observed frequently in plants but results have been somewhat variable (Olsen, 1972). Gerloff et al. (1959) found that increasing Mo in solution culture from 0.067 to 6.70 ppm produced a marked intensification of Fe chlorosis in tomato but Fe content of tops remained constant however. They suggested that Mo accentuated Fe deficiency due to formation of an Fe-molybdate precipitate in the roots. Excess Mo also caused Fe chlorosis in red clover (Hanger, 1965). Plants were normal when concentrations of Fe and Mo were increased proportionately. Hanger (1965), suggested that Mo interfered with a metabolic function of Fe. Berry and Reisenauer (1967) showed

that Fe accumulation by tomato shoots depended on the level of Mo in the nutrient solution. They demonstrated a greater reductive capacity of the roots as the Mo level increased.

Iron reduction by plants

Iron absorption is related to the ability of the root to reduce ferric Fe to ferrous Fe (Brown et al., 1961; Ambler et al., 1970). Chaney et al., (1970) suggested that reduction is obligatory before Fe can be absorbed. They further proposed that reduction occurs at the outer surface of the plasmalemma and suggested the source of electrons is from inside the cell via a cytochrome or flavin. Reductive capacity of the roots was greatly increased by Fe stress of the plants. According to Ambler et al., (1970), the region of the soybean root system with the greatest reductive capacity is between the zone of root elongation and maturation. This region coincides with the area of the root system with the greatest activity in absorption and translocation.

Differential Fe efficiency among lines of the same species has been reported for sorghum (Harmet, 1969; Muhsi, 1965), tomato (Brown et al., 1971), corn (Bell et al., 1958; Brown, 1967; Brown and Ambler, 1970; Brown and Bell, 1969), and soybeans (Ambler et al., 1970; Brown and Jones, 1962; Brown and Tiffin, 1960; Brown, Tiffin, Holmes, Specht and Resnicky, 1959; and Brown, Weber and Caldwell, 1967). Differential Fe efficiency is also attributable to genetic differences which might be used to improve nutrient-use efficiency of field crops (Mikesell et al., 1973). According to Brown et al., (1972), ability to absorb and translocate Fe is a regulated adaptive process that responds to Fe deficiency. An Fe-efficient plant adapts more to Fe stress than an Fe-inefficient

plant but how Fe regulates the individual reactions (or biochemical pathways) as affected by Fe stress is not understood.

Several factors are associated with efficient uptake and utilization of Fe by plants and Brown et al., (1972) has summarized some of the physiological responses characteristic of Fe-efficient plants as:

i. Hydrogen ions are excreted from the roots.

ii. Reducing compounds are excreted from the roots of some plants.

iii. Ferric reduction ($Fe^{+++} \longrightarrow Fe^{++}$) increases at the root.

iv. Organic acids (particularly citrate) increase in the root sap.

v. The plant remains tolerant of relatively high P in the growth medium.

Distribution and translocation pattern of Fe in plants

Little explicit information about the translocation of some micronutrients (including Fe) is available (Tiffin, 1972). Data summarized by Tiffin (1972) indicate that foliar-applied Fe moves from leaves into roots or from seeds into the seedling, but this movement has not been thoroughly investigated. Rediske and Biddulph (1953) reported that Fe was uniformly distributed in healthy bean plants with slightly greater concentrations in the growing points. They suggested that heavy application of Fe in the roots from a nutrient solution may account for a large percentage of that originally added to the solution. A major portion of the total Fe of leaves is in the chloroplasts (Price, 1968). This result is not surprising as Fe is essential for chlorophyll synthesis (Bogorad, 1966).

Effect of root pruning on Fe nutrition of plants

Tanaka et al. (1966), working on the effect of root pruning on rice, showed that Fe content of shoots was not affected by root pruning at 2 ppm Fe. However, at 200 or 400 ppm Fe, root cutting increased Fe content markedly. The implication was that when roots are cut, the power to deposit Fe at the root is impaired and Fe can then freely enter the plant thereby rendering plants which are root pruned more susceptible to Fe toxicity. Jungk and Barber (1974) indicated that P must be supplied to a large proportion of roots in order to adequately meet the requirements of the plant. Further information on the effects of root pruning on the nutritional status of annual plants is scarce.

MATERIALS AND METHODS

General Methods

Seeds of two hybrid species, millet (Pennisetum americanum (L.) K. Schum Var. 'Tift 23 DA X Tift 18 DB') and sorghum Sorghum bicolor (L.) Moench var. 'RS-702'), were germinated in vermiculite in a germination chamber at 29 C. After 7 days, 6 seedlings per pot were transplanted to 0.2-strength Hoagland solution (Hoagland and Arnon, 1950) in 2-liter polyethylene containers. The above conditions applied to all experiments in which plants were grown in nutrient solution media in the growth chamber. The growth chamber had a day-night temperature of 30-20 C, 16-hr photoperiod and 30,000 lux of light at plant height. All solutions were changed weekly and maintained at pH 5.0. All treatments were replicated 3 times and pots were completely randomized in the growth chamber. Plants in Experiments 1a, 1b and 2 were harvested 24 days after transplanting, but plants in experiment 3 were harvested 32 days after transplanting.

Experiment 1a - Effect of P levels on growth, iron uptake and translocation

Chelated Fe /1.8mM Fe as Fe DTPA (Diethylene triamine penta acetic acid)/ was supplied twice a week in addition to the 0.2-Hoagland solution. Four levels of NaH_2Po_4 were used: 0mM; 0.1mM; 1.0mM; and 2.5mM. The pH of all solutions was adjusted to 5.

Experiment 1b

Experiment 1a was repeated but the source of Fe was 2.2mM

Ferrous Sulphate tartrate solution (0.6% $FeSo_4 \cdot 7H_2O$ and 0.4% tartaric acid).

Experiment 2 - Distribution pattern of radioactive ^{55}Fe as affected by P levels

Eight plants were reserved from Experiment 1b. These plants were rinsed 4 times in de-ionized water. De-ionized water (250ml) was measured into 4, 800-ml thoroughly cleaned beakers and P was added as follows:

Beaker	ml stock solution	Total volume of both H_2O and P	Final P concentration
1	0	250	0mM
2	0.025	250	0.1mM
3	0.25	250	1.0mM
4	0.625	250	2.5mM

Radioactive ^{55}Fe 0.31 µci/ml water was mixed with the solution in each beaker. The 8 plants were then introduced into the beakers containing each respective level of P. The beakers were transferred to the growth chamber and left for 3 hours. Plants were then carefully removed, roots were washed once in 0.1N HCl and then rinsed 3 times in de-ionized water to remove excess ^{55}Fe. Plants were dried between filter papers, secured on chromatography paper with cellotape and covered with a second sheet of chromatography paper. The paper and the plants were placed between foam cushion to minimize friction and easy escape of radioactivity from one layer to the next. The materials were stacked and covered with weights for a period of 4 months. Plants were later exposed to Kodak x-ray films in the darkroom for 7 days. Exposed films were developed in Kodak liquid

x-ray developer and fixer. Each film was immersed with agitation for 3 minutes in developer solution and 10 minutes in fixer solution. The films were left in running cold tap water overnight and then dried.

Experiment 3 - Effect of root-pruning on Fe absorption and translocation

The 0.2-Hoagland solution was modified by using 0.1mM NaH_2Po_4. This P level produced maximum growth in Experiment 1. Iron (2.2mM) was supplied twice a week as ferrous sulphate - tartrate solution. Roots were pruned 7 days after transplanting as follows, using a stainless steel blade:

Treatment	Amount of root pruned
1	(Control) No pruning
2	1/4 length of the roots was removed
3	1/2 length of the roots was removed
4	3/4 length of the roots was removed

Experiment 4 - Effect of soil-applied iron on yield and leaf Fe concentration

'T239 x Serere 3A' millet and 'RS-702' sorghum were planted at the Garden City Branch Experiment Station May 17, 1973. The soil was classified as a Richfield silt loam. It had a pH of 7.8 and contained 60 ppm extractable phosphorus and 0.5 ppm available iron. The soil was fertilized with 90 kg/ha of nitrogen as ammonium nitrate before planting. Propazine was applied at the rate of 3.4 kg/ha to control weeds.

Two iron treatments were studied: 1) no addition of Fe and 2) addition of 2.24 kg/ha of Fe as NaFeDETPA chelate. The millet and

sorghum were planted in 4-row plots 3 m wide and 6.7 m long. A randomized complete block design with four replications was used. Iron was applied as a broadcast spray of a 10% (w/v) solution of the chelate immediately after planting. Plots were irrigated as needed throughout the growing season and harvested at maturity on October 12, 1973. Foliage samples, consisting of the flag leaf, were taken for chemical analysis, described below.

Experiment 5 - Effect of soil-applied on chlorophyll content, growth Fe, P, M, Zn and Cu concentrations

Iron-deficient soil (2.75 ppm DTPA extractable Fe) was passed through 0.5-mm aluminum screen. Nitrogen (100 ppm as NH_4No_3) and P (50 ppm as triple superphosphate) fertilizers were mixed thoroughly with the screened soil. Iron (10 ppm as Fe DTPA) was mixed with half of the soil while the other half received no additional Fe. Plastic containers (14.5-cm) were each filled with 2.5 kilos of the soil. Seeds were sown at 2-cm depth to yield six plants per pot and the soil was covered with about 1-cm layer of fine quartz sand to minimize evaporation. The containers were left in the growth chamber and soil was watered as required with de-ionized water. Plants were sampled with 3 replications 10, 20 and 30 days after emergence.

Chemical analysis

Plants from Experiments 1a, 1b and 3 were separated into roots and shoots at the mesocotyl, but only flag leaves and all leaves were used in Experiments 4 and 5, respectively. Roots were washed once in 0.1N HCl to remove surface-adsorbed mineral nutrients and rinsed twice

in de-ionized water. Shoots were rinsed twice with de-ionized water only. All plant materials were dried to constant weight at 70 C and ground to 20-mesh size in a Wiley mill with nickel plated parts. Samples of 0.5 g or less (weights were variable due to insufficient plant material in Experiment 1a and 1b) were wet-ashed using a slightly modified wet oxidation procedure of Jackson (1965) as follows: 1) A ternary mixture was prepared by mixing 70% $HClO_4$, conc. HNO_3 and de-ionized water in a 1:1:1 ratio; 2) Twenty-five milliliters of this mixture were added to each of the samples in 150-ml beakers; 3) The beakers were then put on the hot plate and the contents digested at 200 C for 1 hr and then at 400-450 C for 2-3 hours; 4) After drying, the ash was dissolved in 0.1N HCl and filtered through Whatman 42 filter paper which had been previously wetted with the HCl solution; 5) The filtrate was diluted to 25 ml (or less according to the weight of the material used) with 0.1N HCl.

The solutions were assayed for Fe, Mn, Zn, and Cu by atomic absorption spectrophotometer using a Perkin-Elmer 303 Model instrument. The instrument was set at the following values:

	Setting for respective metals			
Parameter	Fe	Mn	Zn	Cu
Slit	3	4	5	4
Source (amps)	30	15	10	15
Wave length (mu)	249	280	214	326

Phosphorus was analyzed by Jackson's Vanado-molybdophosphoric yellow color method (Jackson, 1970). Two mls each of the phosphorus standards (2 ppm, 4 ppm, 6 ppm, 8 ppm and 10 ppm) were measured into appropriately labelled tubes using an autodispenser. Two mls of each

sample were similarly measured. The standards and the samples were each diluted to 10 mls with vanadomolybdate reagent and shaken. Absorbance was read at 470 mμ on a Beckman DB spectrophotometer after 20-30 minutes.

Quantitative determination of radioactivity

Samples (0.1 g each) of shoot and root were weighed out from plants of each treatment used for radioautography in Experiment 2. These samples were dry ashed at 200 C for 1 hr and 500 C for 3 hr. The ash was dissolved in 5 ml of 2N HCl and evaporated to near dryness at 100 C. The concentrated solution was taken up in 0.1N HCl, filtered into 10-ml flasks, and made to volume. A 0.1-ml aliquot of the filtrate was added to 10 ml of aquasol scintillation liquid and the radio-activity was counted in a liquid scintillation counter (Beckman LS-200B).

Growth analysis and total chlorophyll determination

The growth parameters studied were plant height, leaf area (using a Leaf Area meter, type AAM5), specific leaf weight, dry matter and dry matter. Total chlorophyll extraction and determination were done by the method of Arnon (1949) as modified by Witham et al. (1973). The acetone used was diluted to 80% with de-ionized water. Amount of acetone used was such that 1 ml of acetone extracted 10 mg plant material.

Statistical analysis

Analysis of variance was carried out for each experiment. Fisher's LSD was computed for comparison of means wherever F ratios proved significant. The probability level chosen was $\alpha = 0.05$.

RESULTS

Experiment 1a and 1b - Effect of P levels on growth and nutrient composition

Growth of sorghum and millet varied significantly among P levels (Table 1). Growth of the plants in Experiments 1a and 1b was best for sorghum at 0.1mM P and at 1.0mM P for millet (Figure 1). However, millet plants were slightly chlorotic at this level (Table 2). The least growth for both species in Experiments 1a and 1b was at 0mM P (Tables 1 and 2; Figure 1). At this level, the plants were stunted and had narrow leaves, although millet was more stunted than sorghum. Both species, at 0mM P, exhibited purple coloration typical of P deficiency. Sorghum and millet were chlorotic at 1.0 and 2.5 mM P but chlorosis was more pronounced in sorghum (Table 2). Differences in growth between the two species were statistically significant ($\alpha = 0.05$) (Table 2).

Table 1: Dry weight of sorghum and millet as affected by P level (Experiment 1)

	S H O O T S		R O O T S	
P level	sorghum	millet	sorghum	millet
mM	----------	g/plant	----------	
0.0	0.06	0.02	0.06	0.01
0.1	0.47	0.14	0.21	0.04
1.0	0.25	0.15	0.10	0.04
2.5	0.20	0.10	0.08	0.04
$LSD_{(0.05)}$	Treatment	0.03		
	species	0.02		
species X treatment		0.05		

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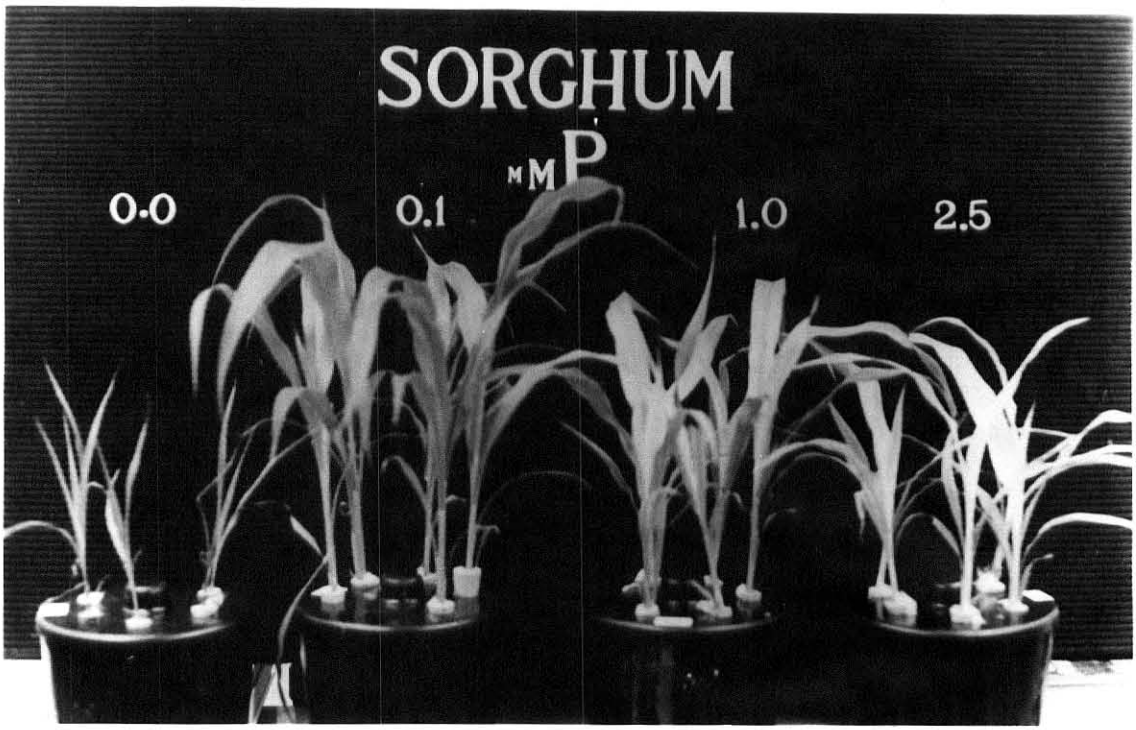
Fig. 1. Growth of sorghum and millet as affected by P levels


SORGHUM
mM P
0.0
0.1
1.0
2.5

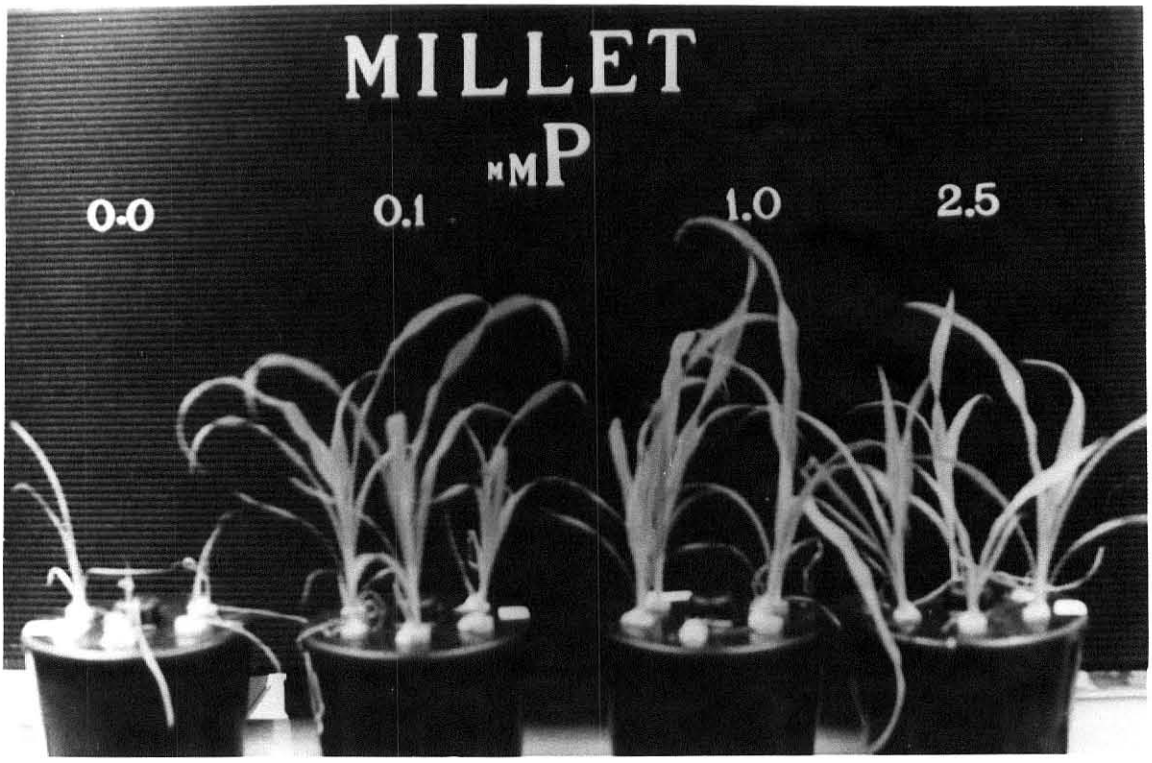

MILLET
mM P
0.0
0.1
1.0
2.5

Table 2: Degrees of chlorosis as affected by P levels in Experiment 1

P level	Sorghum	Millet
mM		
0.0	0	0
0.1	0	0
1.0	2	1
2.5	3	2

0 = no chlorosis
1 = slight chlorosis
2 = moderate chlorosis
3 = severe chlorosis

Generally root and shoot Fe concentrations decreased with increasing levels of P in both millet and sorghum in Experiments 1a and 1b (Figure 2). This trend was significant, however (Table 4), only in Experiment 1b. Shoot Fe concentrations at each P level, were consistently higher in millet than in sorghum (Tables 3 and 4, Figure 2).

Phosphorus concentration in shoots and roots of both species significantly increased with increasing P levels in growth medium in Experiments 1a and 1b (Tables 3 and 4, Figure 2). The P concentrations at the P level where sorghum grew best (0.1m*M*P) were 2219 ppm and 2539 ppm (Table 4) in the shoots and roots, respectively. Millet, in contrast, which grew best at 1.0m*M*P, had shoot and root P concentrations of 5,734 and 7,125 ppm, respectively, at that P level (Table 4). The P concentrations of millet at 1.0 and 2.5m*M*P did not differ significantly.

Mn concentration in the shoots of sorghum and millet and in root of sorghum tended to increase with increasing rates of applied P (Tables 3 and 4). Species differences shown by combined analysis were not significant, but the interaction between species and P level was

Fig. 2. Effect of P levels on shoot and root Fe and P concentrations.

Root Fe and P concentrations were multiplied by 10^{-2}

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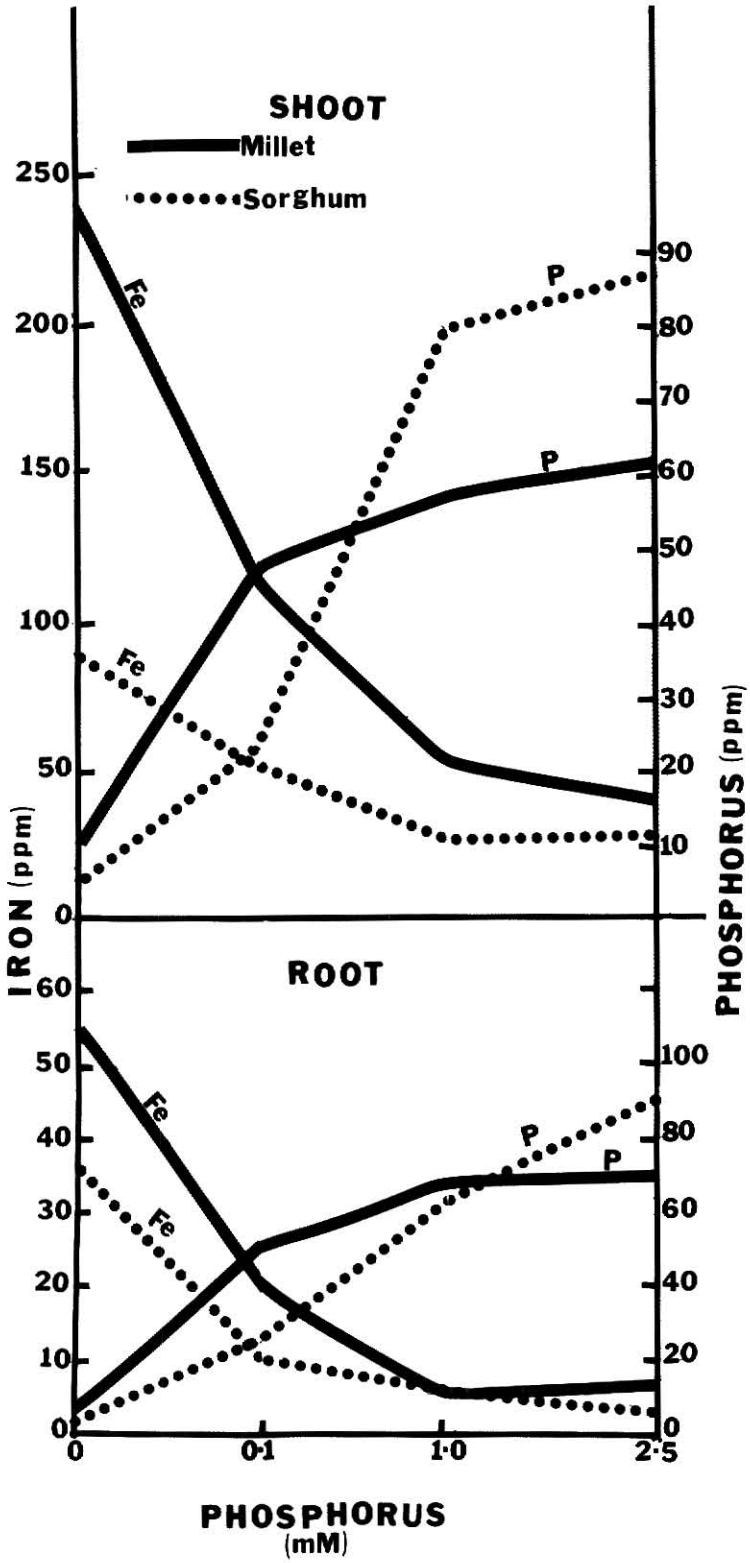

SHOOT
Millet
Sorghum
Fe
P
Fe
P
ROOT
Fe
P
Fe
P
IRON (ppm)
PHOSPHORUS (ppm)
250
200
150
100
50
0
90
80
70
60
50
40
30
20
10
60
50
40
30
20
10
0
100
80
60
40
20
0
0
0·1
1·0
2·5
PHOSPHORUS
(mM)

Table 3: Tissue nutrient concentrations as affected by P level (Experiment 1a)

Species	P level	Fe	P	Mn	Cu	Zn
	mM	PPM				
		SHOOTS				
Sorghum	0.0	32.6	397.7	113.3	10.3	112.2
	0.1	24.2	4,444.9	296.1	10.3	133.5
	1.0	22.5	6,104.2	260.2	10.0	88.1
	2.5	21.4	7,619.0	298.9	9.7	86.6
Millet	0.0	72.6	24.4	168.7	15.2	169.9
	0.1	41.8	4,175.3	256.0	10.6	101.3
	1.0	29.3	5,274.0	387.5	12.6	65.9
	2.5	25.9	3,809.0	195.4	9.7	40.3
$LSD_{(0.05)}$	(Treatment)	ns	231.6	73.0	ns	40.3
	species	ns	163.6	ns	1.54	ns
species X level		ns	327.2	103.2	ns	ns
		ROOTS				
Sorghum	0.0	134.9	363.5	309.6	15.00	145.5
	0.1	192.9	2,685.9	533.5	23.5	89.5
	1.0	197.3	4,364.3	302.4	17.9	50.0
	2.5	118.0	5,046.1	253.2	19.7	49.6
Millet	0.0	223.0	534.9	178.4	74.4	128.7
	0.1	200.1	2,974.8	349.9	62.3	113.9
	1.0	141.5	5,263.2	265.1	45.5	60.2
	2.5	85.4	5,457.1	105.2	47.5	37.3
$LSD_{(0.05)}$	Treatment	ns	247.8	134.0	ns	40.3
	species	ns	ns	94.7	8.2	ns
species X treatment		ns	ns	ns	16.3	ns

Table 4: Tissue nutrient concentrations as affected by P levels (Experiment 1b)

Species	P level	Fe	P	Mn	Cu	Zn
	mM	----------P P M----------				
			S H O O T S			
Sorghum	0.0	89.1	558.5	78.5	20.3	128.8
	0.1	49.6	2,219.2	120.4	14.4	140.0
	1.0	27.6	8,064.9	234.8	12.9	132.2
	2.5	27.5	8,526.6	296.3	17.9	138.6
Millet	0.0	242.8	622.4	88.0	14.3	88.7
	0.1	114.8	4,899.6	285.5	14.7	218.8
	1.0	52.3	5,734.1	277.3	14.8	143.9
	2.5	41.1	6,111.2	289.9	18.8	158.4
			R O O T S			
Sorghum	0.0	3,608.3	503.3	251.6	52.5	104.8
	0.1	977.9	2,539.4	255.5	40.1	97.7
	1.0	585.6	7,037.3	261.7	33.5	94.6
	2.5	411.6	9,537.0	342.3	47.3	89.4
Millet	0.0	5,426.8	521.3	70.6	112.6	231.3
	0.1	1,995.4	5,039.3	459.2	119.3	344.5
	1.0	628.9	7,125.3	402.9	87.7	150.7
	2.5	671.6	6,301.8	248.3	97.4	142.1
$LSD_{(0.05)}$	Treatment	241.6	558.2	66.2	7.8	31.6
	Species	170.8	ns	ns	5.5	22.3
Species X treatment		341.6	789.4	93.6	ns	44.7

not significant, but the interaction between species and P level was significant at the 5% level in Experiment 1b. Copper concentration in the shoot and root of both species progressively decreased as P level increased in the two experiments. However, differences were significant at the 5% level only in Experiment 1b (Table 4). Species differences were significant in both experiments, with millet having higher Cu concentration. Increasing P levels in the growth medium consistently decreased Zn

concentration in shoots and roots of both millet and sorghum in Experiment 1a (Table 3) but not in Experiment 1b (Table 4). Effect of P level was, however, significant in both experiments ($LSD_{0.05}$ = 40.3 and 31.6, Tables 3 and 4). Significant F ratios were obtained in Experiment 1b (Table 4) for species, plant part (root or shoot) X species and species X P levels interactions.

Experiment 2 - Distribution pattern of Fe^{55} in sorghum and millet as affected by P levels

Regardless of P levels, ^{55}Fe accumulation was higher in the roots than in the shoots of the two species (Table 5). The distribution may be summarized as follows: roots > leaf-sheats > vascular tissues > leaf blades. In the leaves, ^{55}Fe accumulated more in the vascular tissues (veins). At 0.0mMP, millet translocated more ^{55}Fe than sorghum to the leaves (Table 5). Sorghum, however, translocated more ^{55}Fe to the leaves than millet at 0.1, 1.0 and 2.5mMP. Sorghum had a higher ^{55}Fe concentration in the younger leaves than in the older leaves, particularly at 1.0mMP (Figures 3a and 3b). In both species, more ^{55}Fe was translocated to the shoot at 1.0mMP than at 2.5mMP (Figures 3a, b, 4a, b and Table 5).

Table 5: Counts for Fe^{55} absorption and translocation as affected by P level (Experiment 2)

P level	S H O O T S		R O O T S	
	sorghum	millet	sorghum	millet
mM	----------C P M/g of dry weight X 10^{-6}----------			
0.0	0.04	0.90	14.61	15.08
0.1	0.47	0.48	36.80	9.85
1.0	3.99	2.60	77.87	46.89
2.5	0.85	0.42	21.66	13.94

Fig. 3a. Distribution pattern of ^{55}Fe in sorghum as affected by 1.0m<u>M</u> P in the growth medium.

Fig. 3b. Distribution pattern of ^{55}Fe in millet as affected by 1.0mM P in the growth medium.

Fig. 4a. Distribution pattern of ^{55}Fe in sorghum as affected by 2.5m$\underline{M}$P in the growth medium.

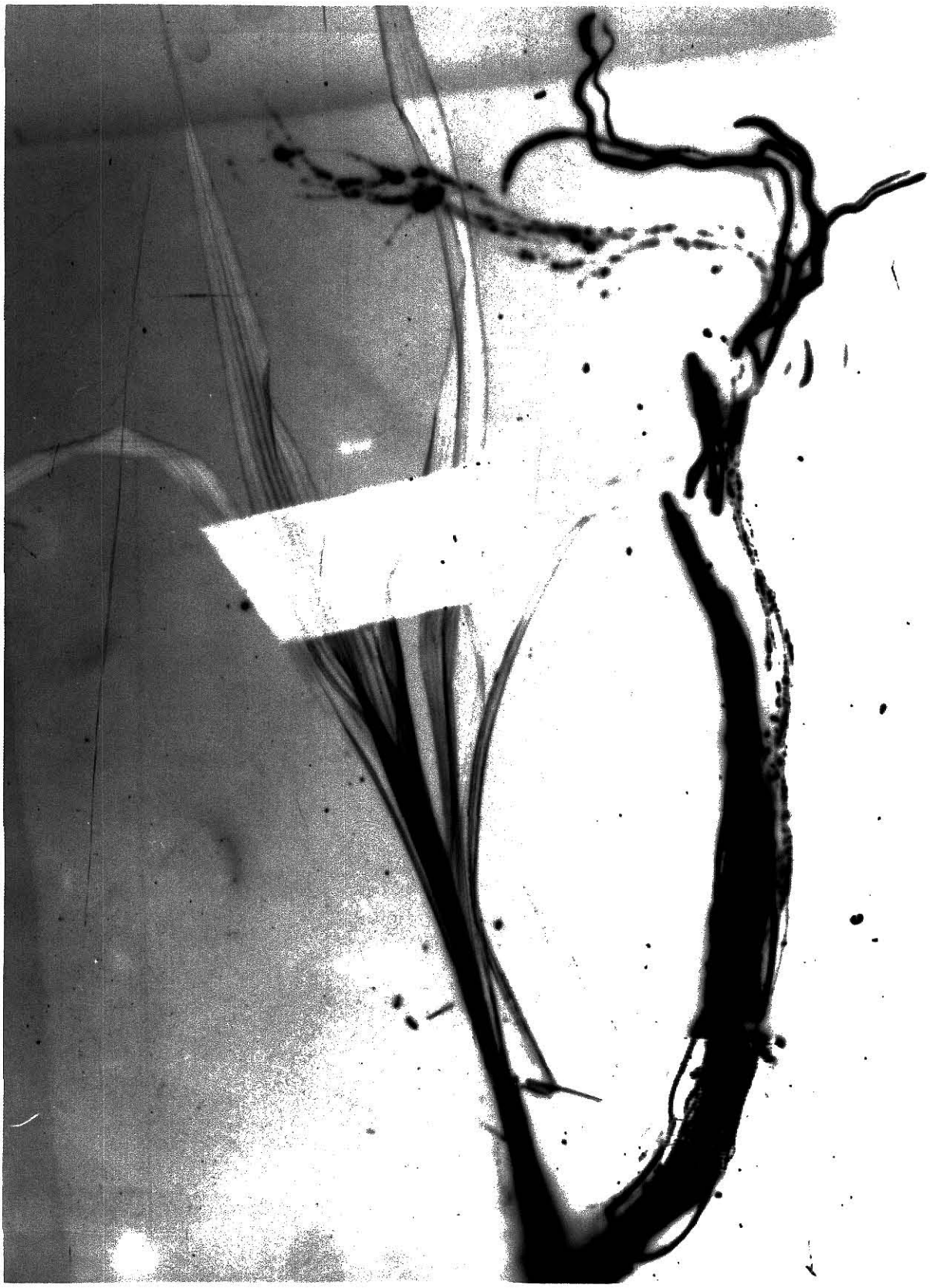
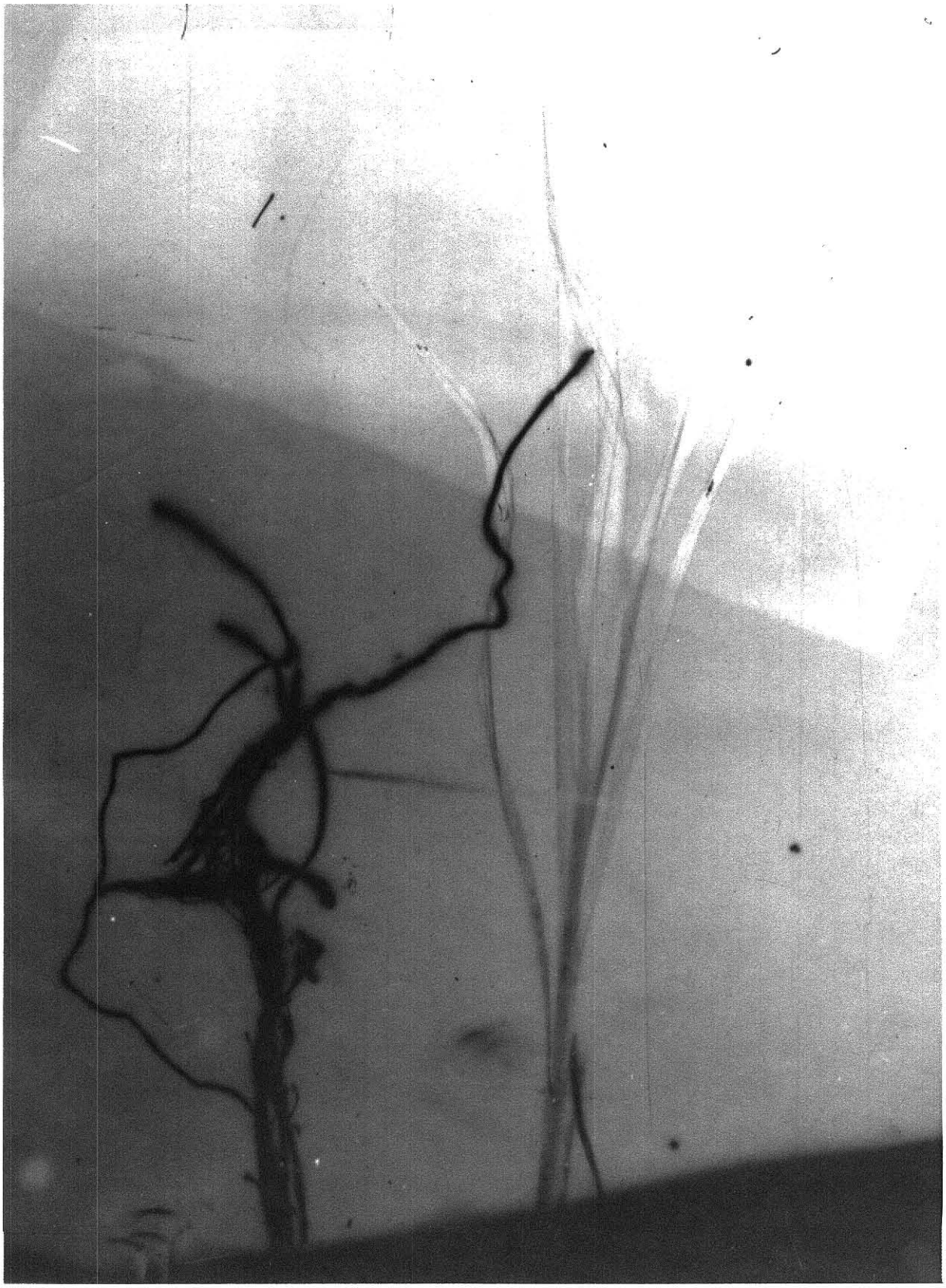


Fig. 4b. Distribution pattern of ^{55}Fe in millet as affected by 2.5m<u>M</u>P in the growth medium.



Experiment 3 - Effect of root pruning on Fe uptake and translocation

Dry weight of sorghum was greatest when one-fourth of the root length was pruned (Table 6). Millet dry weight, on the other hand, was greatest when roots were not pruned. Sorghum shoot Fe concentrations decreased significantly with increasing severity of root pruning. This was contrary to millet shoot Fe concentrations, which increased significantly with each level of pruning. Root Fe concentrations increased in both species up to the removal of one-half the length of the roots. Root Fe concentrations decreased in both species, however, when three-fourths the length of the roots were removed (Table 7).

Table 6: Dry weight of sorghum and millet as affected by levels of root-pruning (Experiment 3)

Pruning level	SHOOTS		ROOTS	
	sorghum	millet	sorghum	millet
	g/plant			
0 (control)	1.9	1.2	0.56	0.41
1/4 of root length pruned	2.1	1.1	0.92	0.34
1/2 of root length pruned	1.8	1.1	0.82	0.39
3/4 of root length pruned	1.8	0.8	0.84	0.27
$LSD_{(0.05)}$ Level of pruning		ns		
species		0.15		
Species X level of pruning		ns		

Table 7: Iron content and nutrient concentrations as affected by levels of root length pruning (Experiment 3)

Species	Length of root pruned	Fe content	Fe	P	Mn	Cu	Zn
		µg/plant	----------P P M----------				
			S H O O T S				
Sorghum	0	94.3	50.7	1,294.9	48.7	8.6	65.6
	1/4	88.4	41.9	1,195.3	42.3	9.5	59.5
	1/2	70.9	39.6	1,334.7	41.1	9.8	52.6
	3/4	69.5	38.9	1,334.7	38.3	9.5	63.9
Millet	0	62.2	52.3	1,613.6	55.8	11.0	57.8
	1/4	69.3	62.1	1,494.1	64.6	11.9	73.9
	1/2	73.4	63.9	1,673.3	54.2	12.1	65.0
	3/4	75.4	96.9	2,071.8	119.9	16.3	90.8
Sorghum	0	363.9	440.5	1,095.7	82.5	16.5	50.2
	1/4	683.5	740.1	1,093.7	102.2	15.4	52.7
	1/2	664.0	809.6	1,135.5	96.1	13.7	42.9
	3/4	506.1	602.3	1,135.5	115.8	13.0	57.5
Millet	0	800.3	2,034.0	2,749.1	126.6	38.0	86.6
	1/4	857.8	2,537.4	2,250.6	117.6	38.0	109.2
	1/2	967.4	2,517.2	2,988.1	128.7	54.4	114.4
	3/4	564.2	2,108.2	2,616.9		47.0	
$LSD_{(0.05)}$	Level of pruning	ns	138.6	ns	12.6	3.3	7.2
	Species	ns	98.0	32.0	8.9	2.4	5.1
Species X level of pruning		ns	ns	ns	17.8	4.7	10.2

Overall P concentrations differed significantly in the two species. Overall P concentrations were 239.95 ppm and 436.45 ppm for sorghum and millet, respectively. Pruning tended to increase P concentrations but the effect was not significant (Table 7). Sorghum shoot Mn concentrations decreased while root Mn concentrations increased as severity of pruning increased (Table 7). In millet, however, Mn

concentrations increased in both shoots and roots. Root pruning significantly decreased shoot Zn concentrations and increased root Zn concentrations in sorghum (Table 7). Both millet shoot and root Zn concentrations, on the other hand, increased significantly as the severity of root pruning increased. Sorghum root Cu concentrations decreased with increasing levels of root-pruning but millet root Cu concentrations increased up to where one-half the length of the roots were pruned (Table 7). Shoot Cu concentrations increased with severity of pruning in both millet and sorghum. All differences above were significant at the 5% level.

Experiment 4 - Effect of iron chelate on field performance and flag leaf mineral composition of sorghum and millet

Sorghum grown on soil fertilized with additional Fe headed earlier (Figure 5) than sorghum grown on soil with no additional Fe. Application of Fe did not, however, affect the heading time of millet. Applied Fe significantly increased the grain yield of sorghum ($LSD_{0.05}$ = 604). Millet grain yield, however, increased only slightly from 2562 kg/ha to 2742 kg/ha at 0 and 2.24 kg/ha applied Fe, respectively (Table 8). Test weight and percent protein content of the two species were not affected by the application of 2.24 kg/ha Fe (Table 8). Millet maintained higher concentrations of P, Mn, Cu and Zn than sorghum at 2.24 kg/ha soil applied Fe (Table 9). Sorghum, however, had a higher concentration of Fe than millet at both 0 and 2.24 kg/ha Fe.

Fig. 5. Effect of soil-applied Fe at 0 and 2.24 kg/ha on the field performance of sorghum and millet.

Sorghum was chlorotic and maturity was delayed at 0 Fe but millet was not affected.

Table 8: Millet and sorghum field performance as affected by Fe supplied as Fe DTPA (Experiment 4).

Species	Fe level	Yield	Test weight
	Kg/ha	Kg/ha	Kg/HL
Sorghum	0	7,482	73.3
	2.24	8,588	73.7
	$LSD_{(0.05)}$	604	ns
Millet	0	2,256.2	68.6
	2.24	2,742	67.2
	$LSD_{(0.05)}$	ns	ns

Table 9: Flag-leaf nutrient concentrations as affected by chelated Fe supplied as Fe DTPA (Experiment 4).

Species	Fe level	Fe	P	Mn	Cu	Zn
	kg/ha	----------P P M----------				
Sorghum	0.0	163.4	1,106.0	180.2	8.7	13.0
	2.24	170.8	1,049.0	177.2	7.7	14.4
Millet	0.0	121.7	1,383.6	366.2	12.0	12.1
	2.24	115.5	1,325.2	370.3	11.3	12.3
$LSD_{(0.05)}$	Treatment	ns	ns	ns	0.44	ns
	Species	17.0	39.5	31.9	0.44	ns
Species X treatment		ns	ns	ns	ns	ns

Experiment 5 - Effect of soil-applied Fe on some growth parameters, total chlorophyll content, and Fe, P, Mn, Zn and Cu concentrations of millet and sorghum

Millet plants were much more chlorotic than sorghum on soil with no additional Fe 10 days after emergence (Table 10). Sorghum plants,

however, became more chlorotic than millet on soil with 0 ppm added Fe by 20 days after emergence. The youngest millet leaves appeared green at this Fe level and the plants appeared only mildly chlorotic. Millet almost completely recovered from Fe chlorosis 30 days after emergence, while sorghum was still highly chlorotic at 0 ppm Fe (Table 10).

At first sampling date, both species slightly increased in height at 10 ppm Fe compared with 0 ppm Fe. Sorghum, however, was twice the height of millet at both Fe levels. Millet was taller than sorghum on soil with 10 ppm added Fe 20 and 30 days after emergence. Sorghum however was taller than millet on soil with no additional Fe (Table 10 and Figure 6).

Ten days after emergence, sorghum and millet plants growing on soil with 10 ppm Fe increased 2.90 cm^2 and 0.72 cm^2, respectively, in leaf area (LA) over control plants (Table 10). Twenty days after emergence the increase in leaf area was 10.87 cm^2 and 34.94 cm^2 for sorghum and millet, respectively. Millet now had more La than sorghum at 10 ppm but sorghum had more LA at 0 ppm Fe (Table 10). Millet had much greater LA than sorghum at both Fe levels 30 days after emergence.

Average specific leaf weight (SLW) was much higher for sorghum than for millet on soil with no additional Fe at 10 days after emergence (Table 10). The SLW of both species, however, was almost the same on soil with added Fe. Twenty days after emergence, millet SLW was slightly higher than that of sorghum at both Fe levels (Table 10). SLW decreased in both species on soil with no additional Fe 30 days after emergence. Millet SLW was, however, slightly more than that of sorghum at 10 ppm Fe.

Sorghum produced a greater percentage dry weight than millet both on soil with and without additional Fe 10 and 20 days after emergence

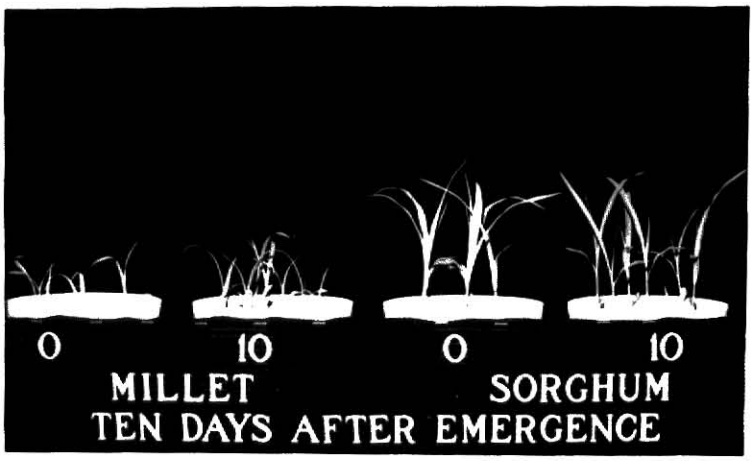
Table 10: Effect of soil-applied Fe on growth, total chlorophyll content, and some nutrient concentrations of leaf-blade (Experiment 5).

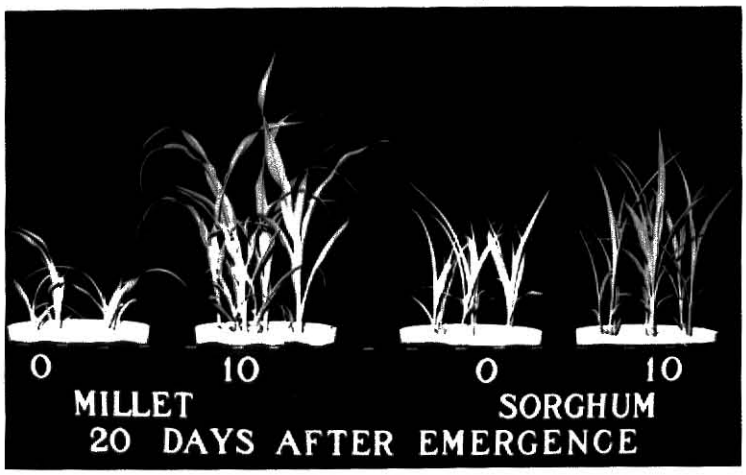
Species	Fe level	Chlorosis	Plant height	LA	Dry weight	% Dry weight
	ppm		Cm/plant	Cm^2/plant	mg/plant	
Sorghum	0	3	16.8	10.9	25.5	19.0
	10	1	17.9	13.8	33.5	18.1
Millet	0	4	8.0	3.7	6.5	11.4
	10	1	9.2	4.4	10.4	13.4
Sorghum	0	3.6	18.3	13.8	41.9	20.9
	10	1	23.4	24.6	83.3	22.8
Millet	0	2.3	12.7	9.0	25.0	16.3
	10	1	25.9	44.0	141.3	13.4
Sorghum	0	4.3	20.0	20.9	57.0	21.0
	10	1	34.6	56.4	190.0	23.8
Millet	0	2	31.7	65.9	118.3	11.1
	10	1	39.2	86.3	299.8	15.1
OVERALL:						
$LSD_{(0.05)}$						
a) Sampling date		ns	2.33	14.0	25.4	1.9
b) Species		0.3	ns	11.4	20.7	1.5
c) Treatment		0.3	1.9	11.4	20.7	17.5
d) Sampling date X species		0.4	3.3	19.8	35.9	ns
e) Species X treatment		0.4	ns	ns	ns	ns
f) Sampling date X treatment		ns	3.3	ns	35.9	ns

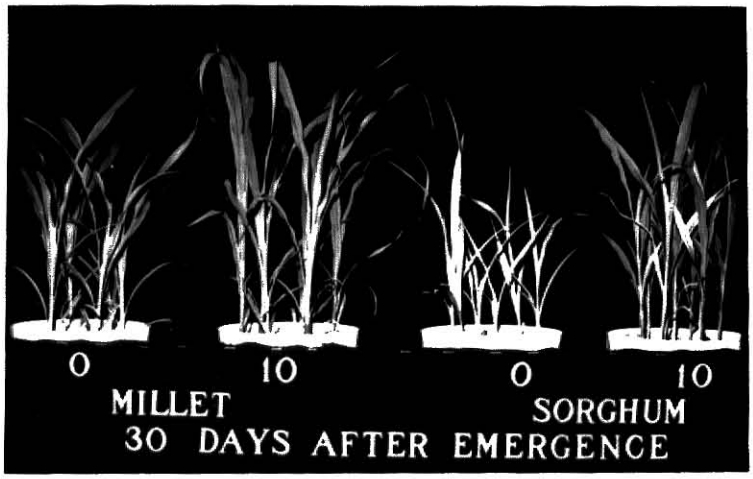
Table 10--Continued

SLW	Chlorophyll content	Fe content	Fe	P	Mn	Cu	Zn
mg/dm^2	mg/g leaf	$\mu g/dm^2$	----------P P M----------				
10 days after emergence----------							
236.5	1.1	19.8	83.6	8,626.8	129.4	7.8	22.4
246.7	1.28	33.6	136.3	12,611.8	41.9	7.3	28.3
184.8	1.0	10.3	54.9	14,733.8	83.9	12.3	31.5
240.3	1.2	75.4	313.7	18,684.2	21.0	14.6	26.4
20 days after emergence----------							
309.3	2.1	33.8	109.2	4,804.5	59.8	6.9	15.7
338.4	3.6	24.1	71.3	3,116.5	34.1	9.7	19.2
315.0	1.1	45.9	145.7	6,765.8	133.5	14.7	27.1
340.0	3.4	28.5	83.7	7,516.5	74.8	17.1	17.4
30 days after emergence----------							
274.6	1.4	9.5	34.6	2,771.2	83.8	9.7	14.2
338.5	3.8	29.9	88.4	1,537.4	63.2	9.9	9.0
230.3	2.1	18.4	79.8	5,633.6	179.4	12.2	32.8
346.6	3.0	23.6	68.2	2,968.1	84.8	9.6	18.9
31.8	0.4	4.9	6.6	676.8	12.0	1.3	1.5
ns	ns	4.0	5.4	552.6	9.8	1.1	1.2
26.0	0.3	4.0	5.4	ns	9.8	ns	1.2
ns	ns	6.9	9.4	957.2	17.0	1.9	2.1
ns	ns	5.7	7.7	ns	13.9	ns	1.7
ns	0.6	6.9	9.4	957.2	17.0	1.9	2.1

Fig. 6. Growth of sorghum and millet as affected by soil-applied Fe at the rate of 0 and 10 ppm; in the growth chamber.


0
10
0
10
MILLET
SORGHUM
TEN DAYS AFTER EMERGENCE


0
10
0
10
MILLET
SORGHUM
20 DAYS AFTER EMERGENCE


0
10
0
10
MILLET
SORGHUM
30 DAYS AFTER EMERGENCE

(Table 10 and Figure 7). Percentage dry weight for both species dropped slightly on soil with no additional Fe at 30 days after emergence. Sorghum, however, had a higher percentage dry weight at both Fe levels.

Sorghum had a higher chlorophyll content than millet on soil with no additional Fe at 10 days after emergence (Table 10 and Figure 8). On soil supplied with 10 ppm Fe, however, there was little difference between species (Table 10). Chlorophyll content increased in both species on soil with and without added Fe 20 days after emergence. Sorghum, however, maintained a higher chlorophyll content (Figure 8) on both soils.

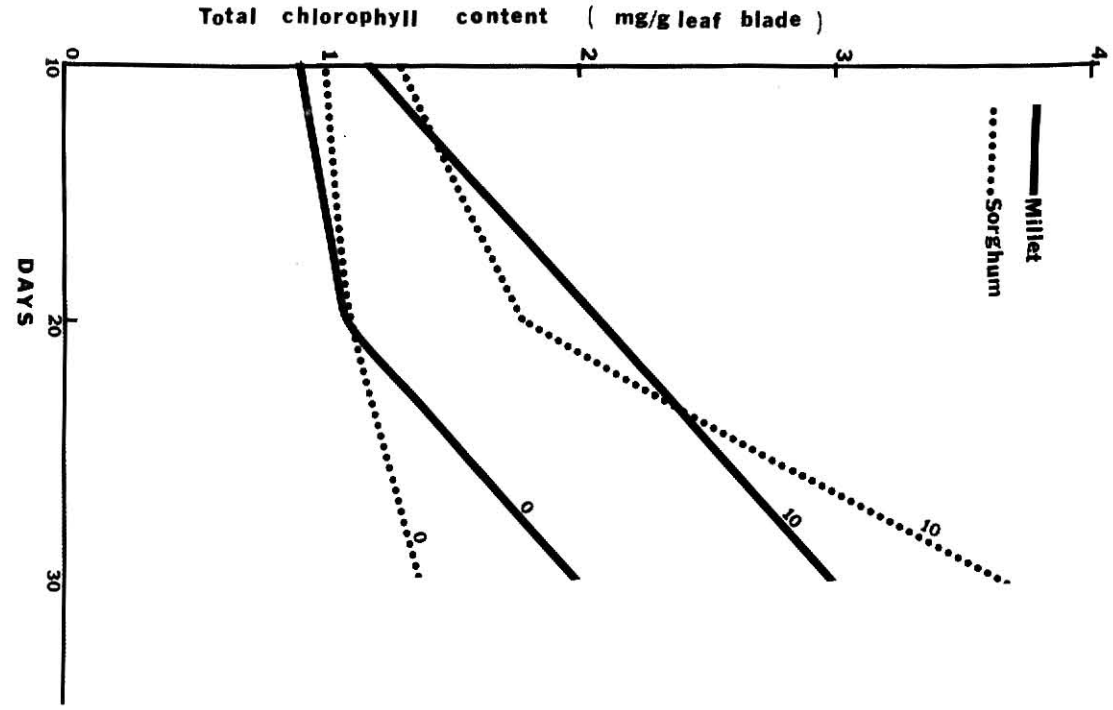
Chlorophyll content of millet increased over that of sorghum on soil with no additional Fe 30 days after emergence. Sorghum had a slightly greater chlorophyll content than millet on soil supplied with 10 ppm Fe. Applied Fe significantly increased Fe concentrations in millet and sorghum 10 and 30 days after emergence, respectively. Iron concentration decreased with applied Fe in both species 20 days after emergence. The highest Fe in both species occurred on soil with additional Fe 10 days after emergence. Millet tended to maintain a higher Fe concentration than sorghum on both soils except at the first sampling on soil with no added Fe (Table 10 and Figure 9).

Phosphorus concentrations differed significantly for both species (Table 10). Phosphorus accumulation was highest for both species and on both soils 10 days after emergence. Thereafter, P concentration decreased with each sampling period. Applied Fe also tended to decrease P accumulation in the leaf blades of both species, but this effect was not statistically significant. Mn concentration significantly decreased with applied Fe for both species at each sampling date. With applied Fe,

Fig. 8. Total chlorophyll content of sorghum and millet as affected by soil-applied Fe at the rate of 0 and 10 ppm, in the growth chamber.

Fig. 7. Leaf-blade dry weight of millet and sorghum as affected by soil-applied Fe at the rate of 0 and 10 ppm; in the growth chamber.

Measurements in both Figs. 7 and 8 were taken at 10, 20 and 30 days after emergence.


Total chlorophyll content (mg/g leaf blade)
0
1
2
3
4
10
20
30
DAYS
Millet
Sorghum
0
10
0
10

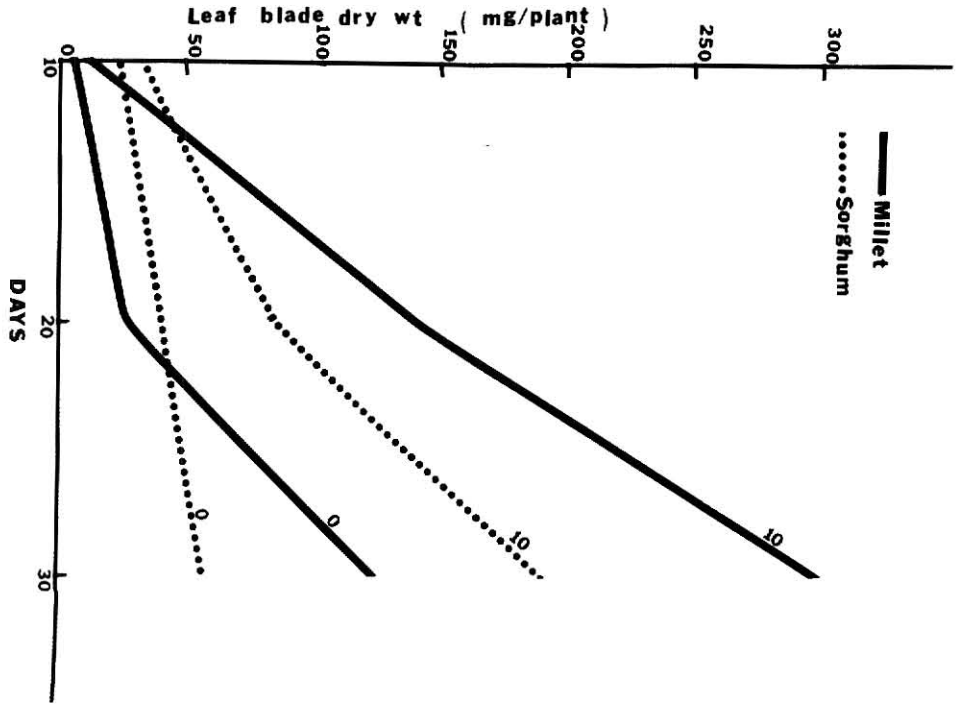
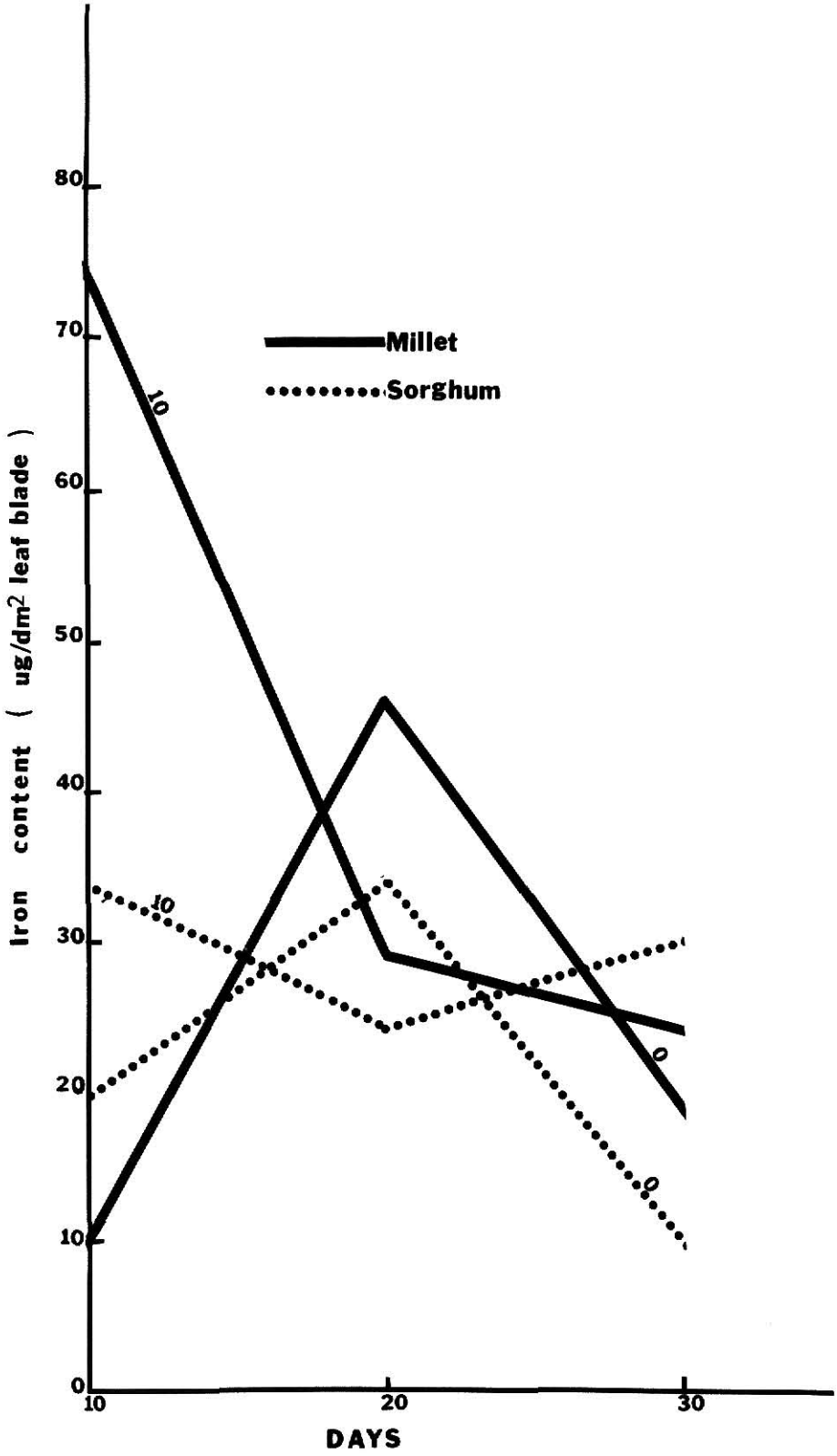

Leaf blade dry wt (mg/plant)
0
50
100
150
200
250
300
10
20
30
DAYS
Millet
Sorghum
0
10
0
10

Fig. 9. Leaf-blade Fe content as affected by soil-applied Fe and days after emergence.


Millet
Sorghum
10
10
0
0
Iron content (ug/dm2 leaf blade)
80
70
60
50
40
30
20
10
0
10
20
30
DAYS

Zn concentration significantly increased in both species on the first sampling date and decreased on sorghum and was constant in millet on the second sampling date (Table 10). Zinc concentration decreased in both species at the third sampling date. Applied Fe did not significantly affect Cu concentration in either species.

DISCUSSION

The P level for optimum growth was higher for millet than for sorghum, but both species become chlorotic at high P levels (Biddulph, 1947; Biddulph and Woodbridge, 1952; Brown et al., 1955; Franco and Loomis, 1947; Khruslova, 1965). The chlorosis rating was lower in millet than in sorghum, however. Apparently, millet is more tolerant of high P in the growth medium. Millet also maintained a consistently higher shoot Fe concentration than sorghum. This might mean that millet absorbed and translocated more Fe to its shoot. This species difference may help explain why sorghum is more susceptible to P-indiced Fe chlorosis. Similar observations were reported in soybean (Olsen, 1935) and in corn (Brown, 1965).

The shoot and root Fe concentrations of both species decreased as P levels increased. Similar changes were previously observed in corn (Adriano et al., 1969). The considerably lower Fe concentration in the chlorotic leaves of millet and sorghum contradicted earlier reports that chlorotic leaves contained as much or even more Fe than their green counterparts (Bennett, 1945; Davis, 1973). There are two possible explanations for the findings reported here in this thesis: 1) High P in the growth medium prevented plants from taking up and translocating sufficient Fe from the nutrient solutions, 2) Since the plants also had difficulty in interveinal translocation at 2.5mMP (Figure 4a), perhaps Fe was inactivated or precipitated in the veins and was not translocated to the mesophyll. Apparently millet had a threshold value for P absorption and accumulation. This probably explains why sorghum, which contained much higher P at 1.0 and 2.5mMP, was more susceptible to P-induced chlorosis. The incidence of higher P concentrations in chlorotic leaves

than in green leaves as observed in this experiment is consistent with results reported by Bennett, 1945.

The increase in Mn concentration in sorghum shoots and roots and in millet shoots is contrary to the trend for Fe concentrations. This result suggests an inverse relationship between Fe and Mn concentrations in plants supporting the existence of an Fe-Mn antagonistic relationship as proposed by Tiffin (1967) and Sommer and Shive (1942). The significant differences in Mn concentration of the two species may contribute to the differential ability of the species to translocate Fe to their shoots under varying P levels.

Millet maintained a significantly higher Cu concentration than sorghum, Copper in both species decreased with increasing P levels in the medium. Similar observations were reported in sour orange (Bingham, 1963). Phosphorus concentrations, however, were reported as having no effect on Cu concentrations of red kidney beans, sweet corn and tomatoes (Bingham, 1963).

Species response to root pruning as shown by shoot dry weight was significantly different. Sorghum shoots increased in dry weight while millet shoot dry weight decreased. Economically, therefore, it would appear that root damage in row cultivation or insect damage to roots would be less detrimental to sorghum than to millet. The general decrease in dry matter of roots in both species may be attributed to decreased absorption capacity of the roots as a result of reduction in root volume by pruning. Root pruning evidently stimulated root growth in sorghum and had the opposite effect in millet (Table 6). The slight increase in sorghum shoot dry matter when one-fourth length of the roots were removed is not readily explainable. It might reflect an adequate

root absorption capacity on the one hand and a decreased competition of the root with the shoot on the other hand.

Concentrations of Fe, P, Mn, Cu and Zn in the shoots of the two species differed significantly. These elements tended to decrease in sorghum shoots but increased in millet shoots. The concentrations of the elements might have been diluted out in sorghum due to increased growth. Also, probably more and more of the Fe absorbing site of sorghum roots were removed with each pruning level. Hence the decrease in sorghum Fe concentration with increase in severity of pruning. Perhaps root pruning resulted in certain metabolic disturbances in millet and this led to decreased dry matter accumulation hence increased concentrations of these elements in millet.

Apparently, very severe pruning may produce Fe-toxicity in millet (Tanaka et al., 1966). However, the increase in P concentrations of both roots and shoots of the two species as a result of pruning is contrary to the report of Jungk and Barber (1974) which suggests that P must be supplied to a large proportion of roots in order to adequately supply the plant when roots are pruned. The ease of entry of P to the roots through the cut surfaces might explain the increase in P concentrations.

The differences in heading and yield responses to Fe by sorghum and millet (Table 8, Figure 6) confirm species differential response to Fe (Gavrilenko et al. 1966). The increase in sorghum grain yield and decrease in test weight as a result of the applied Fe suggest that increase in grain number per head rather than increase in individual grain weight is responsible for the increase in sorghum grain yield. The practical implications of the data reported here, would seem to be twofold: 1) It is not economical to apply Fe fertilizers to millet but it

could be beneficial for sorghum because of the significant yield response of the latter to added Fe. 2) Perhaps it is advisable to apply Fe to sorghum to prevent delayed maturity but this needs further investigation for validity.

High accumulation of ^{55}Fe in roots is not surprising since roots are the absorbing organs in which mineral elements accumulate temporarily before being translocated to the aerial parts. Concentrations of ^{55}Fe were higher in leaf sheaths than in blades probably since the former have more veins than the latter. Absorption and translocation of mineral elements is said to be controlled by Fe-PO_4 balance (DeKock and Wallace, 1965). Perhaps lack of P in the growth medium at 0.0mMP caused negligible Fe^{55} translocation to sorghum aerial parts, whereas, millet was affected less; so, some ^{55}Fe was translocated to its shoots. This suggests that P deficiency was less detrimental to the translocation mechanism of millet. The considerable decrease in the amount of ^{55}Fe translocated to the shoots of both species at 2.5mMP may also be explained by the Fe-PO_4 balance mechanism. The concentration of P in the medium at this level was probably too high to enhance Fe^{55} absorption and translocation.

Iron deficiency (chlorosis) might be related to Fe/P ratio rather than to the quantity of Fe present in the tissue. The very high P concentration in the medium and tissues of both species at 2.5mMP might also explain the considerable decrease in ^{55}Fe concentration of millet and sorghum at this P level (Khadr and Wallace, 1964). The highest ^{55}Fe concentration occurred at 1.0mMP in both species; sorghum had more Fe^{55} in the shoot than millet (Table 10, Figure 3a and b). Greater precipitation of ^{55}Fe in the tissues of chlorosis susceptible sorghum variety was

demonstrated earlier by Muhsi, 1965. Occurrence of precipitation may explain why sorghum, which is more susceptible to Fe chlorosis (Table 2), contained a higher Fe^{55} concentration than millet. The lower ^{55}Fe concentration at 0.1mMP in both species, however, was probably related to lack of chlorosis in either species at this level. Iron uptake was not particularly desirable at this level since the tissues of both species contained sufficient Fe.

Retardation of millet and sorghum growth by low Fe supply was similar to that reported on strawberry and radish (Webb and Hallas, 1966; Agarwala et al., 1965). Increased SLW and dry matter and the high plant LA on soil with additional Fe implies that photosynthetic activity increased. The dependence of dry matter production on leaf surface is well established (Shibles and Webber, 1965). Applied Fe significantly increased total chlorophyll content in both plants. This is consistent with the findings of Agarwala et al. (1965) and Bennett (1943). Although the chemical role of Fe is still uncertain (Davis, 1973), results of Experiment 5 here support the observation that Fe is necessary for the maintenance of chlorophyll in plants (Gris, 1884).

The lower Fe concentration in millet at the first sampling period on soil with additional Fe may explain the higher chlorosis rating at this time. The more severe chlorosis may also have been caused by inadequate root development in millet during this early growth stage. During subsequent sampling dates, millet recovered from Fe chlorosis while sorghum became more progressively chlorotic on soil with 0 ppm Fe. This may mean that millet developed a larger root system for greater Fe absorption. This is also reflected in the higher Fe concentration in millet. In any case, millet tolerated Fe-deficiency stress better than sorghum.

SUMMARY AND CONCLUSIONS

Some physiological studies of differential Fe utilization by two crop plants (sorghum and millet) were conducted in the growth chamber and in the field. Evaluations were made of: 1) Effect of P levels on their growth and nutrient composition; 2) The distribution pattern of ^{55}Fe in the plants; 3) Effect of root pruning on growth and nutrient composition; 4) Effect of Fe chelate on field performance and flagleaf nutrient composition; 5) Effect of soil-applied Fe on growth, Chlorophyll content and leaf blade mineral composition.

Results indicated that high P in the growth medium depressed Fe but increased Mn and P concentrations in both millet and sorghum. Chlorosis developed at 1.0 and 2.5mM P in both plants but chlorosis was more severe in sorghum with millet generally maintaining higher concentrations of these elements than sorghum.

Plants grown under varying P levels in nutrient solution were exposed to ^{55}Fe and the distribution pattern in both plants as shown by radioautography was as follows: roots > leaf sheats > leaf blades. Radioactive Fe absorption and translocation was inhibited most in both plants when P level was 2.5mM in the growth medium.

Root pruning consistently decreased millet dry matter. Sorghum however had highest dry matter value when one-fourth length of roots was removed. Sorghum dry matter, however, remained constant with greater severity of pruning. While root pruning decreased concentrations of Fe, P, Mn, Cu and Zn in sorghum, it increased these elements in millet.

Soil-applied Fe significantly increased (in the field) the yield of sorghum but not of millet. Also applied Fe did not delay maturity in millet but did so in sorghum.

Soil-applied Fe in the growth chamber increased plant height, leaf area, specific leaf weight, dry matter, total chlorophyll content and Fe content 10, 20 and 30 days after emergence. Applied Fe decreased P concentrations in both sorghum and millet but millet maintained higher P, Fe and Mn concentrations than sorghum.

Conclusion

1. Millet is more Fe-efficient than sorghum and will tolerate relatively high P in the growth medium without developing severe P-induced Fe chlorosis when sorghum would.

2. Applied Fe delayed maturity of sorghum in the field but not that of millet. Perhaps Fe should be applied to sorghum to hasten maturity in the field, but further investigation is required to establish the validity of this suggestion.

3. Sorghum tolerated root-pruning better than millet. The implication of this is that mechanical cultivation must be done with more care in a field of millet than in a field of sorghum. Or, chemical weed control should be substituted in millet fields if the economics of this is sound.

4. The increase in total chlorophyll due to applied Fe in both millet and sorghum is an evidence that Fe is necessary for the maintenance, or perhaps, synthesis of chlorophyll in the plants.

5. Significant increases in plant height, LA, SLW, and dry matter on soil with additional Fe imply that photosynthetic activity was increased with applied Fe.

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APPENDICES

Note: **denotes significance at 1% level

*denotes significance at 5% level

Appendix A

Summaries of analysis of variance for effect of P levels (Experiment 1)

Table 1: Dry Weight

Source	d.f	MS	F
Plant part	1	0.1139	73.3017**
Species	1	0.1561	100.4851**
P levels	3	0.0574	36.9226**
Plant part X species	1	0.0168	10.8138**
Species X P level	3	0.0315	20.2468
Plant part X P level	3	0.0135	8.7099**
Plant part X species X P level	3	0.0052	3.3755*
Error	32	0.0016	

Table 2: Iron concentration

Source	d.f	MS	F
Plant part	1	34992975.99	416.77**
Species	1	2163125.99	25.76**
P levels	3	11176404.99	133.11**
Plant part X species	1	564400.00	18.55**
Species X P level	3	9823791.99	6.722**
Plant part X P level	3	415726.31	117.00**
Plant part X species X P level	3	83962.12	4.95**
Error	32		

Table 3: Phosphorus concentration

Source	d.f	MS	F
Plant part	1	65420.19	1.46
Species	1	1298243.99	2.90
P levels	3	128119967.99	285.79**
Plant part X species	1	353300.63	0.79
Species X P level	3	15518057.99	34.61**
Plant part X P level	3	234477.88	0.52
Plant part X species X P level	3	1521702.99	3.39*
Error	32	448306.82	

Table 4: Manganese concentration

Source	d.f	MS	F
Plant part	1	73750.44	11.70**
Species	1	14079.44	2.23
P level	3	85184.38	13.51**
Plant part X species	1	4060.48	0.64
Species X P level	3	47102.71	7.47**
Plant part X P level	3	11576.61	1.84
Plant part X species X P level	3	12182.05	1.93
Error	32	6306.15	

Table 5: Zinc concentration

Source	d.f	MS	F
Plant part	1	2364.32	1.65
Species	1	56067.38	39.04**
P level	3	13619.29	9.48**
Plant part X species	1	32629.20	22.72**
Species X P level	3	11905.83	8.29*
Plant part X P level	3	6171.000	4.30*
Plant part X species X P level	3	4326.21	3.01*
Error		1436.29	

Appendix B

Summaries of analysis of variance for effect of root pruning (Experiment 3)

Table 6: Dry weight

Source	d.f	MS	F
Plant part	1	9.1263	133.2491**
Species	1	5.5692	81.3132**
Levels of root pruning	3	0.0844	1.2319
Plant part X species	1	0.3519	5.1382*
Species X levels of root pruning	3	0.0495	0.7233
Plant part X levels of root pruning	3	0.0287	0.4193
Plant part X species X levels of root pruning	3	0.0081	0.1184
Error	32	0.0685	

Appendix C

Summaries of analysis of variance for effect of soil-applied Fe (Experiment 5)

Table 7: Plant height

Due to	DF	Mean Square	F
Sampling date	2	1030.094482422	134.361251831**
Species	1	4.417076111	0.576145113
Treatment	1	457.317138672	59.650543213**
Sampling date X species	2	218.427734375	28.490798950**
Species X treatment	1	0.386468530	0.050409354
Sampling date X treatment	2	82.527465820	10.764540672**
Sampling date X species X treatment	2	44.135284424	5.756823540**
Error	24	7.666603088	

Table 8: Leaf area

Due to	DF	Mean Square	F
Sampling date	2	8691.449218750	31.453613281**
Species	1	1763.157714844	6.380717278*
Treatment	1	2223.431152344	8.046407700**
Sampling date X species	2	2082.658203125	7.536962509**
Species X treatment	1	6.417774200	0.023225378
Sampling date X treatment	2	430.757568359	1.558874130
Sampling date X species X treatment	2	490.240722656	1.774139404
Error	24	276.325927734	

Table 9: SLW

Due to	DF	Mean Square	F
Sampling date	2	30526.828125000	21.429473877**
Species	1	1783.927734375	1.252295494
Treatment	1	22115.812500000	15.525041580*
Sampling date X species	2	775.080322266	0.544097304
Species X treatment	1	2086.298828125	1.464556694
Sampling date X treatment	2	3712.583984375	2.606189728
Sampling date X species X treatment	2	689.755371094	0.484200180
Error	24	1424.525146484	

Table 10: Dry matter

Due to	DF	Mean Square	F
Sampling date	2	68403.062500000	75.494735718**
Species	1	8141.996093750	8.986115456**
Treatment	1	56058.277343750	61.870101929**
Sampling date X species	2	9244.484375000	10.202904701**
Species X treatment	1	2948.471191406	3.254153252
Sampling date X treatment	2	16367.097656250	18.063949585**
Sampling date X species X treatment	2	1110.724609375	1.225878716
Error	24	906.063964844	

Table 11: Fe content

Due to	DF	Mean Square	F
Sampling date	2	738.092285156	21.766342163**
Species	1	689.935058594	20.346176147**
Treatment	1	1530.895507812	45.146118164**
Sampling date X species	2	160.765136719	4.740964890*
Species X treatment	1	210.830657959	6.217397690*
Sampling date X treatment	2	2082.251953125	61.405624390**
Sampling date X species X treatment	2	986.043457031	29.078414917**
Error	24	33.909790039	

Table 12: Total chlorophyll content

Due to	DF	Mean Square	F
Sampling date	2	6.497205734	25.922897339**
Species	1	0.003402785	0.013576612
Treatment	1	7.425630569	29.627166748**
Sampling date X species	2	0.046519488	0.185605943
Species X treatment	1	0.282667935	1.127802849
Sampling date X treatment	2	1.602922440	6.395425797**
Sampling date X species X treatment	2	0.643435001	2.567211151
Error	24	0.250635743	

Table 13: P concentration

Due to	DF	Mean Square	F
Sampling date	2	360291327.999999900	558.400634766**
Species	1	130342847.999999900	202.013046265**
Treatment	1	2400584.999999999	3.720567703
Sampling date X species	2	12540519.999999990	19.436035156**
Species X treatment	1	236315.562500000	0.366255820
Sampling date X treatment	2	28444655.999999990	44.085205078**
Sampling date X species X treatment	2	2880855.999999999	4.464920044*
Error	24	645219.937500000	

Table 14: Mn concentration

Due to	DF	Mean Square	F
Sampling date	2	3747.802734375	18.491653442**
Species	1	7258.984375000	35.815826416**
Treatment	1	29733.144531250	146.703338623**
Sampling date X species	2	8538.816406250	42.130523682**
Species X treatment	1	1495.109863281	7.376872068*
Sampling date X treatment	2	948.770507813	4.681233406*
Sampling date X species X treatment	2	1830.093261719	9.029680252**
Error	24	202.675292969	

SOME PHYSIOLOGICAL STUDIES OF IRON UTILIZATION BY *PENNISETUM AMERICANUM* (L.) K. SCHUM AND *SORGHUM BICOLOR* (L.) MOENCH

by

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AN ABSTRACT OF A THESIS

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Millet hybrid and sorghum hybrid were employed in growth chamber and field studies. Analysis of growth and certain nutrient concentrations of the two species at four P levels showed that growth was best at 0.1mM and 1.0mM P for sorghum and millet, respectively.

Both species developed chlorosis at 1.0 and 2.5mM P, but chlorosis was more severe in sorghum. Millet was more resistant to P-induced Fe chlorosis. Root and shoot Fe decreased but Mn and P concentrations increased in both species with increasing P levels in the growth medium. Millet usually maintained higher concentrations of these elements than sorghum.

Plants grown with the four P levels mentioned above were exposed to Fe^{55}. The distribution pattern of ^{55}Fe (radioautographs) was as follows: roots > leaf sheaths > leaf blades. Chlorotic plants absorbed and translocated Fe^{55} better than non-chlorotic plants in both species. Also, sorghum, which was more chlorotic than millet, accumulated more ^{55}Fe. Radioactive Fe absorption and translocation was inhibited most in the two species when P level was 2.5mM in the growth medium.

Response of millet and sorghum to varying levels of root pruning was tested. Millet dry matter decreased as severity of root pruning increased. Sorghum dry matter however, was highest when 1/4 length of the roots were removed. With 1/2 and 3/4 lengths of roots removed, sorghum dry matter remained constant.

Mineral concentrations (Fe, P, Mn, Cu and Zn) in roots and shoots increased in millet but decreased in sorghum with increasing levels of root pruning.

In the field, Fe deficiency delayed maturity in sorghum but not in millet. Soil-applied Fe significantly increased yield of sorghum but not of millet.

Soil-applied Fe significantly increased plant height, leaf area, specific leaf weight, dry matter, total chlorophyll content and Fe content ($\mu g/dm^2$ leaf) of growth chamber-grown plants of 10, 20 and 30 days after emergence. Both species accumulated highest P concentration 10 days after emergence. Applied Fe decreased P concentrations in both species but millet maintained higher P, Fe and Mn concentrations than sorghum. Although millet developed chlorosis earlier on Fe-deficient soil, it later recovered while sorghum became progressively more chlorotic. Millet appeared to be more Fe-efficient than sorghum.