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DIFFERENTIAL RESPONSES OF SORGHUM (SORGHUM BICOLOR (L.)
MOENCH) GENOTYPES TO IRON NUTRITION

The University of Nebraska - Lincoln

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PREVIEW

DIFFERENTIAL RESPONSES OF SORGHUM [SORGHUM BICOLOR (L.)
MOENCH] GENOTYPES TO IRON NUTRITION

by

Yunusa Yusuf

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TITLE

DIFFERENTIAL RESPONSES OF SORGHUM (SORGHUM BICOLOR (L.) MOENCH)

GENOTYPES TO IRON NUTRITION

BY

YUNUSA YUSUF

APPROVED

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INTRODUCTION

The supply, absorption, movement, and use of chemical compounds needed for growth and metabolism may be defined as nutrition, and the chemical compounds required by an organism are termed nutrients. Iron is one of 19 nutrient elements essential for the growth and development of higher plants. The essentiality of Fe for higher plants was established about 140 years ago when Gris (1844) noted that low Fe caused a chlorosis in the leaves of vine and that specific cell inclusions now known as chloroplasts became abnormal in color and shape.

In the plant, Fe is a constituent of cytochrome a, b, and their function in the electron transport chain reactions of metabolism is vital. Iron is also a constituent of non-haem proteins such as ferredoxin which participates in the electron transport processes of photosynthesis, nitrite reduction, sulfate reduction, and N_2 assimilation. Besides photosynthetic processes, non-haem iron proteins are also associated with N_2 fixing and anaerobic bacteria reactions and in the hydrogenase systems.

Iron has also been found to be involved in the oxidation step from coproporphyrinogen to photoporphyrinogen in chlorophyll synthesis (Brown et al., 1980). Iron has been given a possible involvement in protein metabolism. Iron is also involved in nucleic acid metabolism, cell division, and chromosome structure. Recent evidence suggests that high amounts of Fe are located in leaf chloroplasts and plastids as phytoferritin (Seckbach, 1968, 1972).

From the above information on the importance of iron in plants, this nutrient element plays a significant role in the growth and metabolic processes of plants.

Sorghum [Sorghum bicolor (L.) Moench] is one of the most important cereals grown for food in many developing countries (especially in Africa, where it originated) and is also the third most widely grown cereal in the United States. Sorghum is grown to some extent in nearly all countries of the world, except those in the cool northwestern part of Europe. According to a 1975 Crop Census, the countries producing the most sorghum were the United States, India, Nigeria, Argentina, Mexico, and Sudan. In the U.S., the leading states in grain sorghum production are Texas, Kansas, Nebraska, Missouri, and Oklahoma (Agric. Stat., 1977).

Sorghum is well known for its susceptibility to Fe deficiency compared to other plant species (Brown and Jones, 1973, 1976, 1977). The soils where large amounts of sorghum are grown are often calcareous and high in pH, and the sorghum usually develops some degree of Fe chlorosis which limits productivity. These soils contain high amounts of Fe, but the Fe is not available for plant use. This is because the Fe in calcareous or alkaline soils is usually in the inactive ferric (Fe^{3+}) form. This form of Fe must be converted to the ferrous (Fe^{2+}) form before it becomes available for plant use (Chaney et al., 1972).

Since sorghum is the third most widely grown cereal in the U.S. and the fourth most widely grown cereal in the world, the need to identify sorghum genotypes that have greater ability to cope with Fe deficiencies becomes a matter of urgency.

With this urgency in mind, a series of experiments were conducted in nutrient solutions and in soils to provide information on this subject. The research was conducted with the following objectives in mind:

1. To develop a rapid and relatively simple method for growing large numbers of plants in nutrient solutions to determine Fe efficiency;
2. To screen sorghum genotypes for Fe efficiency using this method;
3. To correlate genotype responses to Fe in nutrient solutions to those in soil; and
4. To determine the effect of varied levels of Fe on certain physiological and chemical properties of 'Fe-efficient' and 'Fe-inefficient' sorghum genotypes.

LITERATURE REVIEW

Chlorosis is a general term which denotes leaf yellowing and a lack of chlorophyll in leaves. This condition is related to a large number of abnormalities or maladies. Iron chlorosis refers to the leaf yellowing that can be overcome by providing sufficient iron to plants. As such, these plants are said to be iron deficient.

Iron deficient plants can be found on both acid and alkaline soils in some plant species. Iron deficiency is more prevalent in plants grown on calcareous and alkaline soils where Fe is easily converted and maintained in unavailable forms (ferric compounds).

Many factors affect Fe availability or balance. Such factors as bicarbonate concentration, pH, macro- and micro-nutrient imbalances, level of soil organic matter, oxygen tension, and extreme moisture regimes have been associated with the severity of Fe deficiencies. Plants also have different capacities to make Fe available from the soil.

Genotypes of the same plant species when grown under Fe stress conditions differ in their susceptibility to Fe chlorosis. In some Fe uptake studies with PI-54619-5-1 soybeans (Glycine max L. Merr.), Thatcher Spring wheat (Triticum aestivum L.), Minnesota No. 800 hybrid corn [Zea mays (L.)], and Hawkeye soybean, only PI-54619-5-1 soybean failed to absorb sufficient Fe from the calcareous Millville (pH 7.8, coarse silty, Typic Ustochrept) soil to maintain growth. This led Brown et al. (1959) to conclude that the availability to plants of any Fe supply in the growth medium is dependent upon both the plant species and the growth medium.

Availability of Fe is directly dependent upon the solubility of the Fe compound applied, and this is dependent on soil pH. Lindsay (1974) estimated that in order for mass flow to transport sufficient Fe to the roots, the total solubility of Fe would have to be at least 10^{-6} M. This soluble inorganic Fe level is only achieved at pH 3. By raising the pH to just over 4, only 1% of the Fe demand would be met. At normal soil pH values (pH 5 to 7), Fe levels would be far below those required by plants. This would also be the case if the amount of diffused Fe is considered. It appears, therefore, that for plants growing in soil, the formation of soluble organic complexes (mainly chelates) will be important in the Fe supply. These compounds may originate from root exudates, soil organic matter, metabolic products of microorganisms, or as Fe chelate fertilizers added to the soil. Soluble Fe organic complexes are known to occur in soils. For example, Webley and Duff (1965) showed that α -ketogluconic acid excreted from the rhizosphere solubilized Fe which could then be taken up by plants. The significance of root exudates in the availability of Fe had been demonstrated by Raju and Marschner (1972). These workers observed a release of riboflavin from the roots of sunflower plants growing in culture solution under Fe deficiency. Conditions followed by the precipitation of Fe^{3+} -phosphate in the solution. The release of riboflavin was accompanied by a decrease in solution pH. The decrease in pH and the reducing effect of riboflavin mobilized precipitated Fe by reducing it to Fe^{2+} . Thus, Fe availability was improved and the plants became green again.

As mentioned earlier, crop cultivars differ considerably in their susceptibility to Fe deficiency. For example, in soybeans, the cultivar

Hawkeye (HA) is 'Fe-efficient' (i.e., capable of inducing some biochemical reactions to make Fe more available under Fe stress conditions), and PI-54619-5-1 (PI) is 'Fe-inefficient' (not capable of inducing biochemical reactions to make Fe more available under Fe stress conditions). Similarly, 'Fe efficient' and 'Fe-inefficient' cultivars of corn (Brown, 1967; Clark and Brown, 1974), tomatoes (Lycopersicum esculentum) (Brown et al., 1974), grapes (Vitis vinifera) (Sarlio, 1969), oat [Avena sativa (L.)] (Brown, 1979; MacDaniel and Dunphy, 1978), peanut (Arachis hypogea) (Hartzook et al., 1974), sorghum [Sorghum bicolor (L.) Moench] (Mikesell et al., 1973), pineapple [Ananas comosus (L.) Merr.] (Sideris and Young, 1956), and many other horticultural plants (Wallace and Lunt, 1960) have been identified. A tree species Eucalyptus viminalis was also reported to be 'Fe-inefficient' (Ladiges, 1977). By reciprocal grafting between efficient and inefficient cultivars of soybeans, Brown (1961) showed that rootstocks were responsible for differences in Fe efficiency. It has also been established that 'Fe-efficient' plants can respond or adapt to Fe deficiency by increasing the efficiency of Fe utilization. This is achieved by enhancing the solubility and the rate of reduction of Fe^{3+} to Fe^{2+} by compounds ('reductants') such as riboflavin or phenols in the nutrient medium and by increasing citrate in the roots.

Iron efficiency factors have been reported to be genetically controlled. In soybeans, Weiss (1943) reported that differences in iron utilization of certain new introductions of soybeans were conditioned by a single dominant gene. Thus, the inefficiency factor was governed by a recessive gene. Performance of F_1 plants from crosses between efficient and inefficient cultivars indicated complete dominance of the Fe (efficient) allele over the Fe (inefficient) allele. However, in corn, Gorsline et al. (1963) observed additive gene actions for ear, leaf, and

grain concentrations for not only Fe, but also for P, K, Mg, Ca, Zn, Mn, and Al. These same workers also reported that the concentrations of Ca, Sr, Mg, and K were heritable.

Plant species also differ in the concentration of Fe required in the growth medium for growth processes and chlorophyll synthesis. In a study to determine Fe requirements of some plant species, Christ (1974) grew four monocotyledonous plant species (oat, wheat, rice, and corn) and three dicotyledonous species (tomato, cucumber, and soybean) in nutrient solutions. He found that the monocotyledonous plants required a substantially higher Fe concentration in the growth medium to attain maximum growth than did the dicotyledonous plants. Analyses showed that the monocotyledonous species were less efficient in Fe uptake. When the results obtained by using chelated forms of Fe were compared with results using inorganic forms of Fe, he showed that the inefficient species were equally inefficient in utilizing Fe^{3+} . However, when Fe^{2+} was used, the differences between the 'Fe-efficient' and the 'Fe-inefficient' plants disappeared. This confirmed the results of Ambler et al. (1971), Brown (1972), and Brown et al. (1961), who postulated that Fe^{3+} is reduced to Fe^{2+} before uptake of chelated Fe occurs in plant roots. Christ (1974) also reported that the efficiency of Fe uptake depended on the efficiency of the root system of a particular plant species to reduce Fe^{3+} to Fe^{2+} . The removal of Fe from the chelate complex after reduction seemed to present no difficulties in various plant species. Melsted et al. (1969) reported critical concentrations of Fe to be 25.0, 30.0, 25.0, and 30.0 mg/g in corn, soybeans, wheat, and alfalfa, respectively.

Even though Fe may be supplied to plant roots as Fe^{2+} , Fe^{3+} , or as Fe-chelates, absorption appears to be dependent on the ability of the roots to reduce Fe^{3+} to Fe^{2+} (Brown et al., 1961; Ambler et al., 1970; Ayed, 1970). According to Chaney et al. (1972), the reduction of Fe^{3+} to Fe^{2+} is essential (obligatory) before Fe can be absorbed, and they suggested that Fe^{3+} reduction at the outer plasmalemma is mediated by a source of electrons within the cell via cytochrome or flavin compounds.

Brown and Ambler (1974) and Ambler et al. (1970) reported that Fe reduction sites in tomato and soybean were predominantly in young lateral roots and between the region of root elongation and maturation in the primary root. The Fe moved through the protoxylem into the metaxylem of primary roots and then to the top of the plant as Fe-citrate (Brown and Ambler, 1974). Tiffin (1972) also observed that the major form of Fe translocated in soybean was Fe^{3+} -citrate. Rate of Fe uptake seems to be restricted to a narrow zone in the roots of barley (about 1-4 cm from the root tip).

Oliver and Barber (1966) reported that Fe diffusion in soils was the most important mechanism in which soybean roots were supplied Fe. When Fe-chelates were supplied to plant roots at the normally low Fe levels required by plants, a separation between Fe and chelate occurs prior to Fe absorption (Tiffin and Brown, 1961). However, at high levels of Fe-chelate, Jeffreys and Wallace (1968) were able to detect appreciable amounts of Fe-chelate in plant leaves. Evidence is sufficient to support the concept of active Fe uptake (Moore, 1972). Tiffin (1966) noted Fe concentrations in sunflower and soybean stem exudates to be 30 times greater than those in ambient solutions.

The uptake of Fe is influenced markedly by other cations. Thus, Fe nutrition of plants is most frequently disturbed in plants growing on calcareous soils. Chlorotic plants growing under these conditions are often referred to as having lime-induced chlorosis. The chlorosis may also be aggravated by high HCO_3^- levels in the soil solution. It may be possible that HCO_3^- raises the pH of the plant tissues and decreases the reduction of Fe^{3+} to Fe^{2+} . Calcium may also compete with Fe^{2+} for the same binding sites to reduce the availability of Fe.

Plant species show differences in their susceptibility to Fe deficiency chlorosis on calcareous soils. Iron deficiency is most commonly observed in calcifuge species such as blueberry, cranberry, and azalea. Among the important commercial crops affected by Fe deficiency are citrus, deciduous fruit trees, soybean, sorghum, ornamental shrubs, and trees and vines. Iron deficiency chlorosis has also been found in many other commercially important crop plants.

Lahar and Zipon (1978) suggested that high Ca concentrations near the root surface constituted a chemical barrier for the movement of Fe-EDTA toward roots. Singh and Sinha (1977) reported that Fe^{3+} was rapidly displaced in a calcareous soil by Ca^{2+} and Mg^{2+} . According to Burstrom (1968), high quantities of Ca in the soil solution or in the plant have a negative effect on physiologically active Fe. Calcium has been reported to interfere with Fe absorption and translocation by grain sorghum in the presence of P in calcareous soils of Texas (Onken and Walker, 1966). In a low Fe soil, Salardini and Murphy (1975) reported that Fe applications lowered Ca, Mg, Zn, and Mn concentrations in the plant.