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IRON DEFICIENCY IN SOILS AND ASSOCIATED BIOCHEMICAL CHANGES IN FORAGE CROPS - A REVIEW

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SUMMARY

Iron (Fe) is an important micronutrient for plant growth and it has several functions. A large portion of agricultural soils around the world has low Fe-availability to plants due to its unavailable forms or varying nature of soils including calcareous soils. The deficiency of Fe led to adverse effects on plant growth and agricultural productivity. It has got recent attention and molecular, biochemical, physiological responses of plants under Fe deficiency is being reported in some crops. To understand the mechanism of Fe deficiency tolerance, this review provides an overview of such studies.

Keywords: Fe-deficiency, calcareous soils, phytosiderophores, Superoxide dismutase

One of the most important micronutrients that plants need for a variety of metabolic processes is Fe (Gupta *et al.*, 2021). As a necessary redox active metal involved in physiological and metabolic processes, such as photosynthesis, respiration, nitrogen assimilation, sulphur metabolism, hormone biosynthesis, production and scavenging of reactive oxygen species, osmoprotection, and pathogen defense, Fe is regarded as a kingpin for plant growth and development (Hänsch & Mendel, 2009). Due to the gaining of high yield and multiple benefits, the micronutrient deficiency is increasing in the soil day to day (Patel *et al.,* 2015). For optimal growth plants need to maintain the concentration of Fe in the range of 10^{-9}-10^{-4} M, but due to the low solubility of Fe in the soil solution Fe acquisition was challenging. Fe is not readily available to plants although it is the fourth most abundant element in the earth's crust. The concentrations of free Fe^{3+} and Fe^{2+} are less than 10^{-15} M, in well-aerated soil at the physiological pH this value is far below than the required value for optimal growth of plant (Kim and Guerinot, 2007). Despite the fact that Fe makes up around 5% of the earth's crust and is the fourth most plentiful element in the lithosphere, Fe deficiency is one of the key yield-limiting issues for crop development in many agricultural locations across the world, particularly in calcareous soils (Awad and Elsokkary, 2020). The deficiency of Fe in crop is one of the most difficult micronutrient problems to manage as the Fe applied to soil through inorganic Fe carrier is susceptible to rapid transformation into unavailable forms. Screening of genotypes for Fe deficiency tolerance is scarcely available. In this review article, an overview of Fe status of soils and plant responses to Fe deficiency is given in following sections.

IRON STATUS OF SOILS

Calcareous soils make up about 30% of all agricultural soils worldwide (Mori, 1999). In the hill soils of the Indian state of Uttar Pradesh (UP), the total and accessible amounts of Fe, copper, zinc, manganese, molybdenum, and boron were determined. According to examinations of the entire sample, the soils were deficient in 17.3% of Fe, 20% of Cu, 74.6% of Zn, 20% of Mn, 24% of Mo, and 18.6% of B (Rawat and Mathpal, 1981). Haryana is the second most important state in India contributing to central food grain pool. According to Shukla *et al.* (2015), the amount of accessible Fe in the soils of

Haryana ranges from 0.12 to 81.43%, depending on the district. In Haryana's soil, Fe is regarded as the micronutrient that is most deficient, followed by Zn, Mn, B, and Cu. Numerous studies have shown that the soil in India lacks Zn in 49% of cases, Mn in 5%, Fe in 12%, and Cu in 3% of cases. A case study was done on the mining of micronutrients from soils from the two agro-climatic zones of the state: the one southwestern (SW) zone and the other is northeastern (NE) zone. The maximum imbalance in both the zones was of Fe, among the micronutrients, followed by Mn, Cu, and Zn. In the SW-zone the deficiency of Fe in the soils ranged from 12 to 57%, and in NE zone Fe deficiency ranged from 7 to 29% (Narwal *et al.,* 2005).

IRON AVAILABILITY TO PLANTS

As a result of its low solubility, Fe is frequently unavailable to plants even if it is far more abundant in soil than what plants need in the form of oxidised (ferric) Fe^{3+} (Kobayashi & Nishizawa, 2012). High soil pH and high bicarbonate concentrations are blamed for the limited solubility. In conclusion, it causes the limited uptake by plant roots since the root cells are unable to quickly absorb it (Lucena, 2006).

Plants have evolved practical methods for absorbing Fe from sources that aren't very soluble. There have been reports of two different techniques (Römheld, 1987). Conversely, Strategy II is exclusively established in graminaceous plant species. Strategy I is present in dicotyledons and non-graminaceous monocotyledons species. The process by which they solubilize and transfer Fe varies. By secreting protons and reductants or chelators, such as organic and phenolic compounds, into the rhizosphere, Strategy I plant species increase soil Fe solubility, whereas Strategy II plant species are distinguished by the secretion of ferric chelating substances (known as phytosiderophores) in conjunction with a specific Fe^{3+} ion chelate uptake system (Ma, 2005).

The identification of important genes needed for Fe absorption, translocation, homeostasis, circulation, etc. has made considerable strides in recent years. The most significant instances are the discovery of the genes FRO2 and IRT1, which correspond to the Fe^{3+} chelate reductase and the Fe^{2+} transporter, respectively, in the Arabidopsis thaliana (Ma, 2009). Low-molecular-weight secondary amino acids (mugineic acids), also referred to as "phytosiderophores," are extruded as part of the chelation process in order to form complexes with sparingly soluble Fe. A transporter called yellow stripe1 (ys1) at the root surface then takes up the complex that has generated (Curie *et al.*, 2001). There are several genes known to reduce ferric chelate. As a result of them, FRO2 in Arabidopsis thaliana functions as a significant reductase that is engaged in the reduction of ferric chelate in roots. In comparison to wild type plants, the transgenic plants demonstrated greater growth when FRO2 was overexpressed under low Fe conditions. One of the eight members of the FRO family, FRO genes are expressed differently depending on the tissue they are expressed in (Jeong and Guerinot, 2009). For instance, the FRO2 gene is specific to roots, whereas FRO6 and FRO7 are particular to shoots. Ferrous-Fe (Fe^{2+}) transfer across the plasma membrane requires Fe-regulated transporters (IRT). Many IRT genes have been discovered in a variety of plants, including IRT1 and IRT2 from Arabidopsis and LeIRT1 and LeIRT2 from tomatoes (Yuan *et al.*, 2008).

PLANTS RESPONSE UNDER IRON DEFICIENCY

MORPHO-PHYSIOLOGICAL RESPONSES OF PLANTS TO FE DEFICIENCY

Most of the plants show signs of Fe-deficiency symptoms, such as leaf interveinal chlorosis without acquiring active mechanisms for extracting Fe from the soil (Briat and Lobréaux, 1997). Plants with visual symptoms of injury and interrupted growth were characterized by increased content of dry substance in a unit of fresh weight and by some peculiarities in ^{14}C metabolism as compared to plants, subjected to a strong Fe deficiency (Nenova and Stoyanov, 1993). The fruits of Fe-deficient plant were small and pale yellow in colour with low Iycopene and free (titrable) acidity in tomatoes compared to Fe sufficient plants (Bisht *et al.,* 2002). Under partial Fe deficiency, at 4^{th} day, the amount of dry biomass decreased by almost 20%, and in the complete Fe deficiency, decrease by about 35% in maize. But there is no difference in plant height at this age. In the roots of the control plants, the dry biomass was about 28% of total biomass, at the 14^{th} day whereas in the Fe-deficient plants, that biomass percentage difference was in between 30-35% (Nenova and Stoyanov, 1993). Mikami *et al.* (2011) have reported study on contrasting iron responsive crops, Barley and sorghum, which are tolerant and susceptible to Fe

deficiency, respectively. According to study, they had similar Fe and chlorophyll contents in their leaves, however, the Fe-deficient barley photosynthetic apparatus was functional while that of sorghum was not. In contrast to the Fe-efficient barley, where iron was allocated preferentially to the thylakoid membranes during Fe deficiency, in the Fe-deficient sorghum, the photosynthetic apparatus was seriously damaged, and the proportion of leaf Fe allocated to the thylakoids was not altered.

BIOCHEMICAL RESPONSES OF PLANTS TO FE DEFICIENCY

In contrast to Fe sufficient plants, the leaves of the Fe-deficient maize plant displayed lower chlorophyll concentrations, higher phenolase activity, lower catalase activity, and higher activities of acid phosphatase, alanine aminotransferase, ribonuclease, and aspartate aminotransferase. Depending on the degree of Fe shortage in the maize, different amounts of Fe were supplied for a week, and the activity of total catalase reduced by 20 to 70%. Peroxidase activity under Fe deprivation changed similarly to catalase activity, however the initial decline was less pronounced. The activity of total peroxidase decreased by 20 to 55% and also the specific activity decreases by 10-20%, on the 14th day (Nenova and Stoyano, 1995). As a result of Fe deficiency, a sharply decrease in activity of the antioxidant enzymes, catalase and superoxide dismutase was observed. When bicarbonate was present or Fe was absent, the activity of SOD was significantly decreased both at 20 days and 10 days. At 10 days, it decreased by 62% for FC and 78% for FA, whereas, at 20 days, it was 5% for FC and 46% for FA. The same trend was observed for catalase activities: 81% and 70%, respectively, for FA and FC at 10 days and 67% and 56%, respectively, for FA and FC at 20 days (Lombardi *et al.,* 2003).

Proline content

Under drought conditions increased proline content maintains the cell water level (Choudhary *et al.,* 2021). Arias *et al.* (2015) investigated the leaves and roots of six barley varieties under the Fe deficiency, and found that the amount of proline accumulated was higher in the leaves as compared to roots. In the varieties Pewter and Belgrano, the proline of shoot increase with Fe deficiency, whereas there is no effect on the variety Henley and Scarlett, while in the Quench and Shakira, there was decrease in the proline content with decrease in the amount of Fe.

Malondialdehyde content

Malondialdehyde (MDA) is considered a good indicator of the oxidative damage. According Teixeira *et al.* (2020), 31.1% decrease in MDA content under Fe deficiency with silicon application, as compared to 61.1% decrease in MDA under Fe deficiency without silicon application was reported in sorghum leaves. There were variations in MDA content under the oxidative damage during Fe deficiency. For instance, in the leaves of Balta4, which is a sensitive variety, had eight-fold higher content of MDA under Fe deficiency treatments than in the control plant, whereas, in the tolerant varieties Khamri and 140Ru, MDA content was maintained at similar levels. When the Fe availability decreased in the culture medium, there was slight increase in the root MDA content (Ksouri *et al.,* 2006).

Superoxide dismutase activity

Superoxide dismutase (SOD) is an antioxidant enzyme and a variation in SOD activity was obtained in different plants under the Fe deficiency (Table 1). Nikolic *et al.* (2019) reported that in Barley plants, activity of enzyme ascorbate decreased under Fe deficiency as it a heme containing enzyme, whereas, no significant effect was observed on SOD enzyme because it has three isoforms *i.e.,* Fe, Mn, Cu-Zn isoforms and works on the base of availability of isoform. However, in cauliflower, maize and mulberry plants under the Fe deficiency, increasedactivity of SOD was observed (particularly non-Fe-SOD isoforms) (Tewari *et al.,* 2005). In strawberry, a significant increase in SOD activity and decrease in activity of other antioxidant enzymes was reported under Fe deficient conditions (Kaya *et al.,* 2019). In wheat, the activity of enzyme SOD significantly decreased under Fe-deficiency conditions as compared to Fe-sufficiency (Esfandiari and Sabaghnia, 2012). According to Sun *et al.* (2007), SOD activity increased by about 17.6% under Fe deficiency in the *Zea mays*.

Catalase activity

According to Lombardi *et al.* (2003), the catalase activity in peach rootstock was decreased by

TABLE 1
Activity of superoxide dismutase enzyme in different crops under Fe deficiency

Crop	Plant sample	Effect of Fe-deficiency on SOD Activity	Reference
Peach	Root	Decrease	Lombardi *et al.* (2003)
Barley	Leaf	No change	Nikolic *et al.* (2019)
Maize	Leaves	Increase	Tewari *et al.* (2005)
Strawberry	Leaf	Increase	Kaya *et al.* (2019)
Wheat	Leaf	Decrease	(Esfandiari and Sabaghnia, 2012)
Maize	Leaf	Increase	Sun *et al.* (2007)
Bean	Nodule	Decrease	Abdelmajid *et al.* (2008)
Sorghum	Root	Decrease	Prity *et al.* (2021)

81% and 67% at the 10th day and 20th day, respectively, under Fe deficiency. In barley leaves, a huge decrease in the activity of heme containing enzymes catalase and ascorbate peroxidase was observed (Nikolic *et al.,* 2019). Tewari *et al.* (2005) also observed adecreased activity of catalase in the maize, cauliflower and mulberry, with decrease in supply of Fe. Decrease in the catalase activity observed also in strawberry (Kaya *et al.,* 2019). In wheat leaves, decrease in the catalase activity was observed under Fe deficiency (Esfandiari and Sabaghnia, 2012). According to Sun *et al.* (2007), catalase activity was decreased approximately 60% in response to Fe deficiency in maize. In bean, 27% decreased catalase activity was noticed in genotype Coco blanc, whereas, in genotype ARA14, catalase activity remains almost on same level as compared to control, indicating possible role of genotypes also (Abdelmajid *et al.,* 2008). Accroding to Prity *et al.* (2021), the CAT and SOD activities showed a substantial decline in the root but not in the shoot in Fe-deprived plants relative to controls sorghum plants.

Phytosiderophores content

Shen *et al.* (2002) compared two genotypes of wheat for phytosiderophores (PS) release under varying Fe supply. The genotype N85021 showed large amount of PS release as compared to genotypes Z181 in response to 0 µM Fe supply. The high level of PS leading to mobilization of Fe for easily uptake was attributed to less chlorosis under calcareous soil in genotype N85021 as compared to genotypes Z181. Among different wheat genotypes studied, durum wheat, HD-2967 was reported with maximum PS content release under Fe deficient conditions (Divte *et al.,* 2019). In the Fe deficient conditions, the phytosiderophores content release was almost ten folds higher than the Fe sufficient condition. According to Yousfi *et al.* (2007), the PS content was up to 1.654 mmol h^{-1} g^{-1} root DW, under Fe-deficient conditions. Bocchini *et al.* (2015) observed the PS release in the barley plants grown hydroponically in Fe deficient conditions. After 8 days of treatments, the plants having Fe deficient conditions released PSs in higher concentration and remains constant level up to 12 days. From the 13 days onwards, the PS release content sharply increased specially at the 13, 15 and 19 days, in Fe deficient conditions. Sorghum plants produce only low amounts of deoxymugineic acid (DMA), making it highly vulnerable to Fe deficiency (Dey *et al.*, 2020). PS release from the roots remarkably decreased (more than 50% reduction) in Fe-starved sorghum in contrast to Fe-adequate plants (Prity *et al.*, 2021).

IRON CONTENT UNDER IRON DEFICIENCY

In the Fe sufficient condition, the durum wheat genotype showed more amount of Fe content than the bread wheat but in the Fe deficient conditions it showed the six folds decrease in the Fe content of shoot (Divte *et al.,* 2019). According to Yousfi *et al.* (2007), during the salt treated conditions (NaCl), the plants showed declined in the Fe content and quantity in leaves and roots. The comparison of all treatments showed the concentration of Fe was higher in roots than shoots. In barley, Fe content and its distribution in roots and shoots is strongly affected by Fe deprivation (Bocchini *et al.* 2015). The ratio of root to shoot of Fe content increased in Fe fed barley plants. Wang *et al.* (2019) analyzed the samples collected at 25–28 DPA (days post anthesis) and concentration of Fe in grain and flag leaves was observed lower under Fe deficient plants of wheat. According to Divte *et al.* (2019), Fe sufficient condition in Durum wheat cultivars showed high Fe concentration in roots when compared to the bread wheat. However, decline in Fe

content in root was more than ten folds. The root and shoot Fe concentration of sorghum plants decreased considerably under low Fe supplement compared to plants cultivated with sufficient Fe in the hydroponic culture (Prity *et al.*, 2021).

CONCLUSION

In conclusion, Fe deficiency in soils is a prevailing situation, which is more aggravated in calcareous soils. The high soil pH and high bicarbonate concentration limits Fe bioavailability to plants. The deficiency of Fe adversely affected the plant growth and metabolism, and reflects leaf Interveinal chlorosis as most common Fe deficiency symptom. In response, the biochemical changes including altered activity of antioxidant enzymes (CAT, SOD), decreased MDA content, increased phyotosiderophores, and decreased Fe uptake are noticed in plants. It is suggested that plants with of high Fe uptake potential could mitigate its deficiency response and more such studies should be conducted with an insight of molecular aspects for a better understanding and action.

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