



# ROLE OF IRON IN PLANT IMMUNITY

**Abhinav Tiwari, Ramesh Chand, Vivek Singh**

Acharya Narendra University of Agriculture & Technology Kumarganj  
Ayodhya



## INTRODUCTION

Iron is an essential element for most organisms and is abundantly present in the Earth's crust. Its bioavailability is limited because iron is mainly present as ferric oxide, which is poorly soluble at neutral and high pH. Iron ions exist in both the ferric ( $\text{Fe}^{3+}$ ) and the ferrous ( $\text{Fe}^{2+}$ ) form, allowing them to function as the catalytic component of enzymes that mediate redox reactions in key cellular processes, such as DNA replication and energy production. Iron scarcity hampers the growth of many organisms; its overload can also be harmful. Excess  $\text{Fe}^{2+}$  inside a cell leads to the formation of hydroxyl radicals via the so-called **Fenton reaction**, which can cause damage to proteins, DNA, and lipids.

Metabolism of iron and the plant immune system are both essential for plant vigor in natural ecosystems and for reliable agricultural productivity. Iron plays a critical role in the generation of reactive oxygen intermediates during immunity and has been recently implicated as a critical factor for immune-initiated cell death *via* **ferroptosis**. Plant iron stress triggers immune activation, suggesting that sensing of iron depletion is a mechanism by which plants recognize a pathogen threat. In plants, iron is also essential for chlorophyll and hormone synthesis and photosynthesis.

### Role of Iron in Plant Immunity

Iron functions as a catalyst in the presence of hydrogen peroxide via the Fenton reaction, generating reactive oxygen species (ROS) such as the highly reactive hydroxide ion. These oxidants can damage lipids, proteins, and nucleic acids, leading to cellular damage that, if severe enough, results in programmed cell death. In plant defense mechanisms, immune responses are triggered upon detection of specific signals indicative of pathogen invasion. For instance, plants recognize various pathogen-associated molecular patterns (PAMPs), which initiate pattern-triggered immunity.

Research from the 1980s demonstrated that adding external iron to soils that suppress diseases could negate this suppressiveness, particularly in soils resistant to Fusarium wilt and



*Gaeumannomyces graminis* var. *tritici*, the fungus responsible for take-all disease in wheat. The prevailing hypothesis was that competition for iron between soil-borne pathogens and beneficial microorganisms underpins disease suppression. This highlighted iron's pivotal role in the complex interactions among beneficial microbes, pathogens, and plants. Under iron-limited conditions, plant growth-promoting rhizobacteria produce siderophores in the rhizosphere, which are crucial in this process. These siderophores inhibit soil-borne pathogens by sequestering iron, thus limiting its availability to the pathogens.

Pathogenic bacteria such as *Erwinia chrysanthemi* and *Erwinia amylovora* produce siderophores as virulence factors. These molecules assist in iron acquisition from the host or protect the bacteria from plant-produced toxic hydroxyl radicals at infection sites. Recent studies have revealed that the pathways controlling plant iron uptake are directly linked to the plant's immune signaling network. For example, defense hormones like salicylic acid, jasmonic acid, and ethylene influence key steps in the iron absorption process within plant roots.

### Siderophore

Siderophores are low-molecular-weight molecules that chelate iron with a very high and specific affinity. Many bacteria, both Gram positive and Gram negative, produce and secrete siderophores to scavenge iron from the extracellular environment. Siderophore-iron complexes are transported into the cell through receptors in the membrane. In Gram positive bacterial species, a putative cell surface lipoprotein receptor anchored in the cytoplasmic membrane through its N-terminal lipid moiety and an ABC-type transporter are required for the transport of the siderophore-iron complex.

Siderophores, along with other iron acquisition systems, are virulence factors in many bacterial pathogens. Siderophores are produced by different organisms in order to scavenge iron from their surrounding environment making this essential element available to the cell. Presenting high affinity for ferric iron, siderophores are secreted out to form **soluble ferric complexes** that can be taken up by the organisms.

### Role Of Iron In Pathogen Virulence And Host Defense

Siderophore-mediated iron acquisition is essential for full virulence of many plant pathogens. Pathogens that reside in the soil first need to compete with other members of the soil microbial community for the scarce available iron necessary for growth before a host plant can be infected. Microbial siderophores play a key role in this underground warfare for iron. The outcome of siderophore-mediated competition for iron depends on the iron affinity of the siderophores, the quantity of siderophores produced, and the species specificity of the siderophores. Highly specific siderophores are recognized only by the receptors of the



producing organism, whereas heterologous siderophores are recognized and taken up by different microorganisms. Plant growth– promoting rhizobacteria that produce, high-affinity siderophores can effectively deprive soil-borne pathogens of iron and thereby suppress plant disease.

The capacity to acquire iron from the host is also an important pathogenicity factor of foliar pathogens. Virulence of diverse plant-pathogenic ascomycete fungi, with host ranges varying from wheat, barley, and maize to rice and Arabidopsis, was shown to depend on the pathogen's capacity to secrete siderophores. An exogenous supply of iron relieved this siderophore dependency, highlighting the iron-scavenging function of siderophores as an important virulence factor in plant-pathogen interactions.

### Effects Of Iron Availability on Pathogenic Microorganisms

In soil, bacteria and fungi compete for available iron (grey circles) by secreting iron-chelating siderophores. Siderophores (SID) can be taken up upon recognition by specific receptors once they have bound iron. By producing siderophores with high iron affinity, beneficial microbes can outcompete pathogenic microbes that produce siderophores with a lower iron affinity, resulting in suppression of disease. Increased production of toxic compounds by iron-starved pathogens also contribute to the enhanced susceptibility phenotype of iron-deficient plants.

### Iron As A Tool In Plant Immunity

- ▶ Iron act as a powerful weapon for the plant, when wielded against pathogens.
- ▶ **Recruitment of iron to infection sites**, to exploit its redox chemistry, is a critical immune response for many plants, particularly the Poaceae. E.g. Irondeficient maize is unable to produce reactive oxygen species at Colletotrichum infection sites, and this correlates with increased susceptibility to this hemibiotrophic fungal pathogen.
- ▶ **ROS (reactive oxygen species)** are crucial components of plant immunity with multiple roles. They can **act as second messengers**, transmitting perception of a pathogen to nearby cells, they can **promote oxidative cross-linking of cell wall components**, and they can also act as direct weapons against microbes.
- ▶ The plant cell membrane is impermeable to superoxide, but superoxide can be converted to membrane-permeable hydrogen peroxide (H<sub>2</sub>O<sub>2</sub>) by superoxide dismutase, some of which contain iron as a cofactor.

### Affect Of Beneficial Microbes in Plant Resistance *Via* Iron

Plant iron homeostasis is affected not only upon pathogen infection but also root colonization by specific beneficial soil microbiota. Among these are plant growth–promoting rhizobacteria



and fungi that are known to trigger ISR (Induced Systemic Response). ISR by beneficial rhizosphere microbes is a plant-mediated systemic immune response that primes plant tissues for enhanced defense against a broad spectrum of pathogens.

A connection between iron homeostasis and ISR was found in 1996 when Leeman and co-workers reported that the elicitation of ISR against Fusarium wilt in radish by beneficial *Pseudomonas* spp. was more effective under low-iron conditions. Siderophores secreted by *Pseudomonas* spp. under such low-iron conditions were subsequently shown to act as elicitors of ISR in tomato and rice.

### **Effects Of Plant Hormones on Iron-Uptake Responses**

In plants, the iron-deficiency response is regulated at both the transcriptional and the post translational levels. The plant hormones auxin, ethylene, nitric oxide, cytokinin, and gibberellic acid emerged as important players in the regulation of this process. In *Arabidopsis*, ethylene and gibberellic acid increase *FRO2* and *IRT1* expression in the root epidermis, leading to increased iron uptake. Furthermore, ethylene and auxin stimulate the accumulation of nitric oxide production in iron-deficient roots. Both ethylene and the accumulated nitric oxide result in stabilization of *FIT* and enhanced iron uptake. In addition, auxin stimulates formation and elongation of lateral roots, enabling the plant to take up more iron. Cytokinin, in contrast, decreases root growth and suppresses genes involved in the iron-deficiency response. The major defense hormones salicylic acid and jasmonic acid also influence plant iron acquisition. Salicylic acid, jasmonic acid, ethylene, and auxin play key roles in the regulation of the plant immune signaling network. Hence, the fact that these hormones also affect iron uptake responses in plant roots pinpoints a potentially important link between iron availability and immunity.

### **Causes of iron deficiency in plants**

#### **1. High pH (Alkaline Soil)**

If the pH of soil is too high, then plants can end up with an iron deficiency – even if there is plenty of iron in the soil already. For every nutrient that a plant needs, including iron there is an ideal pH range for the soil. Within this range, the nutrient is highly available, and the plant can easily absorb the nutrient through its roots. Outside of this range, the nutrient is not available, and so the plant cannot absorb enough of the nutrient, even if it is present in the soil. As a general rule, you have to keep your soil pH between 5.5 and 6.5 (slightly acidic) for most plants. More specifically, iron is highly available in acidic soil (pH below 7). However, as pH rises to 8 or higher, iron becomes less available in the soil. Plants that like acidic soil, such as raspberries, blueberries, pears, and azaleas, are more likely to get iron chlorosis.



## Nutrient Imbalance

Improper balance of nutrient can cause iron deficiency in plants. In addition to having enough of each nutrient in the soil, we need to have the proper ratios for each nutrient. Too much of one nutrient can block a plant from absorbing another. For example, excessive amounts of phosphorus can prevent iron uptake in a plant. This can occur if we use a garden fertilizer with high phosphorus content. The label NPK on fertilizers represent the ratio in which nitrogen, phosphorus and potassium are present. If you think phosphorus is too high, find a fertilizer with lower (or zero) phosphorus content.

Likewise, excess calcium can prevent iron uptake in a plant. This can occur in soil with high lime content (lime is just another word for certain calcium compounds). Be careful about adding lime to your garden as a supplement if you suspect iron deficiency in your plants.

## Poor Soil

The physical condition of the soil plays a vital role in determining the availability and absorption of iron by plants. One of the key requirements for efficient iron uptake is the presence of adequate oxygen in the root zone, which is essential for proper root respiration and nutrient transport mechanisms. Waterlogged or poorly drained soils often become compacted and oxygen-deficient, leading to a condition known as anaerobic stress. In such environments, root function is impaired, and the redox conditions in the soil may shift in ways that convert soluble iron into insoluble forms, further limiting its availability. This issue is common in heavy clay soils or in areas where the ground remains saturated due to poor drainage or over-irrigation.

Another factor that limits aeration and iron uptake is the use of plastic mulches or impermeable covers around plants. While plastic sheeting is commonly used to suppress weeds and conserve moisture, it can also trap heat and prevent air exchange, creating conditions that inhibit root oxygenation and microbial activity. This, in turn, can reduce the bioavailability of iron and other micronutrients. Cold soil temperatures can restrict iron uptake. At lower temperatures, root metabolic activity slows down, reducing both the energy available for nutrient transport and the solubility of certain minerals, including iron. This is particularly relevant during early spring planting or in high-altitude regions where soils warm up slowly.

To eliminate these issues, it is advisable to improve soil structure by incorporating organic matter, such as compost, peat moss, well-rotted manure, or plant residues (like banana peels, coffee grounds, grass clippings, or leaf mold). Organic amendments enhance soil porosity, promote microbial activity, improve moisture retention and drainage, and contribute to the natural cycling of nutrients, including iron. In clay-heavy soils, such amendments can break up



compacted layers, increasing aeration and making the root environment more favorable for iron uptake.

### Extreme Conditions

Environmental stressors, particularly **high temperatures** and **intense sunlight**, can significantly interfere with a plant's ability to absorb and utilize iron efficiently. Just like soil pH, plants require **an optimal temperature range** for proper nutrient uptake. When temperatures rise above this ideal range, several physiological processes within the plant are affected. High heat can impair root function, reduce transpiration efficiency, and alter enzyme activities involved in iron transport. As a result, even if iron is present in the soil, plants may not be able to absorb or mobilize it effectively, leading to symptoms of iron deficiency such as **interveinal chlorosis** (yellowing between leaf veins).

Similarly, **excessive sunlight**, particularly high-intensity light for extended periods, can exacerbate iron stress. While light is essential for photosynthesis, too much light—especially when coupled with high temperatures—can accelerate plant metabolism and create an imbalance between the demand for and supply of iron within plant tissues. This imbalance often results in oxidative stress, further hindering the plant's ability to maintain iron homeostasis.

Moreover, extreme heat and sunlight can cause **soil moisture loss**, making the root environment drier and more compact. This dry, hot soil condition negatively impacts the solubility and mobility of iron, particularly ferric iron ( $\text{Fe}^{3+}$ ), making it less available for root uptake.

### Insufficient Iron in Soil

Iron deficiency in plants can result from several factors, but one of the most overlooked yet critical reasons is the **long-term depletion of iron in the soil**. This depletion may occur for two primary reasons:

- The soil might have been naturally deficient in iron from the beginning. This condition is often found in sandy, highly weathered, or alkaline soils where iron exists in forms that are not readily available to plants. Even though total iron content may seem sufficient, much of it can be locked in insoluble forms, especially in soils with high pH.
- iron that was initially present in adequate amounts may gradually become depleted over time. Continuous cultivation of the same crop—especially iron-demanding crops like spinach, legumes, maize, or soybean—on the same piece of land without replenishment can exhaust available iron. This is particularly



true in monoculture systems where soil management practices do not include nutrient recycling or replenishment. Over time, repeated cropping without proper rotation or fertilization can lead to significant nutrient imbalance, including reduced iron availability.

To prevent such depletion, it is essential to adopt **crop rotation strategies**. Crop rotation involves growing of alternate crops in the same field across different growing seasons. This practice not only helps in managing soil fertility and minimizing pest and disease build-up but also reduces the specific nutrient demand from any one plant species. For example, following an iron-intensive crop with one that has a lower iron requirement allows the soil to partially recover and maintain a better nutrient balance.

However, visual symptoms like yellowing of leaves (iron chlorosis) are often not enough to confirm iron deficiency. This is why conducting a **soil test** is crucial for accurate diagnosis. **Soil test kits**, available at most garden centers or online, allow farmers and gardeners to assess not only iron levels but also pH, organic matter content, and other macro- and micronutrients such as nitrogen, phosphorus, potassium, magnesium, and calcium. Regular soil testing helps in understanding the root cause of nutrient deficiencies and facilitates appropriate corrective measures, such as soil amendments, pH adjustment, or iron fertilization.

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