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A Proteomic Perspective on Plant Iron Insufficiency and Advanced Technologies

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ABSTRACT

Inadequate iron (Fe) intake causes chlorosis is a serious nutrient deficiency that affects crops grown on calcareous soils. It leads to stunted vegetative development, decreased yield, and compromised quality. Thanks to developments in mass spectrometry, a wealth of information about how iron shortage alters the protein profiles of various plant parts and compartments has emerged. Medicago truncatula, cucumber, sugar beetroot, tomato, and a Prunus rootstock root proteome profile changes have all been studied using gel-based two-dimensional electrophoresis methods. Researchers have also used thylakoids and roots of Arabidopsis thaliana plants that are low in iron to conduct high-throughput proteomic research. The review emphasizes future research objectives in this subject and summarizes the primary results reached from various "-omic" techniques with regard to metabolic alterations happening with Fe shortage. Our capacity to improve agronomically important plants' responses to Fe-deficiency tolerance might be improved via a deeper understanding of the procedures involved in root Fe homeostasis.

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1. Introduction

Among the elements found in the cosmos and on Earth, iron (Fe) ranks sixth in abundance (Remick et al., 2023; Scott et al., 2015). A vast majority of Earth's living creatures rely on iron as an important element. In oxygenated settings, nevertheless, its chemical characteristics severely restrict its availability. Therefore, Fe shortage is evident in many plant and animal species. More than 2 billion individuals around the globe suffer from anaemia, including iron deficient anaemia, as reported by the World Health Organization (WHO). A significant nutritional issue in crops, particularly those cultivated on calcareous soils, is iron deficiency, which results in stunted vegetative development, along with noticeable declines in yield and quality. Molecular features of plant iron acquisition processes produced by low iron availability have been the subject of a great deal of research in the genomic era (Hindt and Guerinot, 2012). According to Kermeur et al. (2023), all plants, with the exception of grasses, adjust to Fe restriction by increasing the reducing capacity of root plasma membrane Fe reductase and the energy available to the PM H^+ ATPase. To better understand the broad metabolic reprogramming required to meet these demands, proteomic methods are a great resource. Gaining a deeper understanding of the proteome responses to Fe restriction in plants may provide light on the mechanisms involved in Fe homeostasis, which in turn can help mitigate the impact of Fe shortage on crops. This study provides a thorough summary of the key findings about metabolic changes in roots and thylakoids of various plant species in response to Fe shortage, and it also points the way for future research in the area. A common example of abiotic stress in crops is examined in the paper, along with an overview of the limits of the many proteomic methods now available.

1.1.Root proteome alterations caused by iron deficiency

Using Strategy, I, plants adapt morphologically and biochemically to increase their capacity to absorb Fe in the face of a deficiency. Some examples of morphological changes include hairs on the root, enlarged tips, new lateral roots, and transfer cells. Increased iron absorption can be attributed to metabolic modifications such as plasma membrane induction (Abadía et al., 2011).

Root proteome changes in response to Fe deficiency have been studied using a gel-based technique that uses two-dimensional electrophoresis as the gold standard. Research on the proteome in plants using Strategy II has so far only been carried out on the maize root plasma membrane (Hopff et al., 2013); in contrast, all studies reviewed here have used Strategy I plant root extracts during their investigations. More recently, smaller gels were used in research involving Prunus dulcis × Prunus persica, Medicago truncatula, and Beta vulgaris (Rellán-Álvarez et al., 2010). Lin et al. (2011) identified 101 proteins in this pool whose abundance changed in response to iron deficiency.

Proteome comparison between several plant species is a challenging task. This is because treating interspecies homology can be difficult,

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particularly in cases where B. vulgaris is discovered and public genomic data sets are lacking or insufficient. Furthermore, the accuracy of findings obtained from database comparisons for protein identification is directly related to the stringency of the positive identification criteria, which include sequence coverage and the number of matching peptides. As such, there is always a margin for doubt. In addition, as a proteomic profile is only a moment in time, differences in the developmental stage of the plant and the method of applying Fe restriction may provide highly diverse final protein profile images. Proteomic studies are more difficult to interpret since post-translational modifications could be linked to variations in spot intensity. We examined the proteins found to change in each plant species and compared them to those found in A. thaliana in order to identify a happy medium. A BLAST search was conducted for every protein species in the various studies; matches with E-values less than e-30 were considered positive Arabidopsis orthologs. The same plant species had multiple entries eliminated, leaving only one representative entry. To further reduce treatment-related heterogeneity, the proteomes of M. truncatula and B. vulgaris plants grown without Fe but with CaCO3 were hypothetically excluded from the comparison.

1.2.Common variations in plant species

1.2.1. Defending against oxidative stress

Five unique proteins that underwent alterations in response to iron deficiency in different plant species were included in the category of oxidative stress. A few of the changes were an increase in monodehydroascorbate reductase (MDAR1), a decrease in catalase (CAT-2), and an upregulation of superoxide dismutases (CuZnSOD and MnSOD). These data suggest that redox equilibrium is substantially impacted by Fe shortage since numerous proteins involved in oxidative stress, including as catalase and peroxidases, contain iron, and free iron ions cause the generation of reactive oxygen species (ROS) via Fenton reactions. The decrease in Fe availability is likely connected to the observed changes, which include the SOD isoenzyme compensatory mechanism in P. dulcis × P. persica, M. truncatula, and Arabidopsis, as well as the decrease in catalase in S. lycopersicum and P. dulcis × P. persica. Both increases and decreases in different peroxidase species in different plant species demonstrate the complex link between Fe and redox homeostasis processes. Fe has been included in PER12, PER3, PER53, and PER21, all of which have increased and decreased, respectively. The glutathione-ascorbate cycle is increased in response to iron shortage, as evidenced by increases in MDAR in Arabidopsis and ascorbate peroxidase (APX) in S. lycopersicum.

According to Dixon and Edwards (2010), the tau subclass of GST is linked to fatty acid derivative binding, the lambda family to oxidoreductase activity, and the phi class to tolerance to oxidative stress. While the precise functions of these GSTs are still unknown, proteomic data indicates that glutathionylation could be a common detoxification process in iron-deficient roots.

1.3.Alteration dependent on species or treatment

1.3.1. The cellular skeleton

Since most of the proteins involved in the metabolism of glycosyl compounds are found in the apoplast, it is likely that deficiencies in iron cause modifications to the structure and metabolism of cell walls. M. truncatula is the only tested species of plant that is not affected by Fe. Except for one, the remaining species are S. lycopersicum, C. sativus, P. dulcis × P. persica, and Arabidopsis. It appears that these responses to Fe deficiency are species-specific, albeit additional biochemical studies are needed to elucidate these modifications. In C. sativus, there was a decrease in both 1,4-β-xylosidase and an invertase, two enzymes involved in the hydrolysis of O-glycosyl compounds; in P. dulcis × P. persica, there was only a decrease in 1,4-β-xylosidase. Not only did proteins related to hydrolysis, lignin catabolism, and glycosyl group transfer decrease in Arabidopsis, but five additional proteins—including four proteins involved in lignin or cellulose production and a β-glucosidase implicated in cellulose degradation—saw increases throughout the same period. In S. lycopersicum, two cell wall-related proteins increased and two decreased, resembling the previously mentioned situation. According to Donnini et al. (2010), the authors of the study on C. sativus proposed that these alterations might be caused by a change in carbon flux away from cell wall biosynthesis and towards other metabolic processes including glycolysis. However, the proteins discovered might suggest that another mechanism for obtaining carbon skeletons is through the hydrolysis of the cell wall. After Fe limitation, cell wall remodelling takes place.

1.3.2. Metabolic byproducts

An interesting discovery about species-specific changes in secondary metabolism proteins is illuminated by our comparison. Roots of Arabidopsis plants grown in $CaCO_3$ showed an increase in proteins involved in the riboflavin synthesis pathway, while P. dulcis and P. persica plants exhibited increases in isoprenoid and flavonoid synthesis, and M. truncatula and B. vulgaris plants showed an increase in proteins involved in the riboflavin synthesis pathway. Interestingly, there were no overlaps among the proteins whose abundance changed in response to Fe deficiency in these different plant species. Consistent with earlier biochemical and transcriptomic studies (Lan et al., 2011), our proteomic work found that roots produce a variety of secondary metabolites in reaction to iron deprivation; further research into the involvement of roots in this response is needed.

1.3.3. Power and ATP-dependent transportation mechanisms

There has been contradictory evidence on energy-related proteins in root proteomes. Fe shortage resulted in an increase in the number of mitochondrial transport chain proteins, including several complex I subunits, in Arabidopsis, but a decrease in the abundance of a complex I subunit and mitochondrial ATPase subunit B in M. truncatula and C. sativus. In addition, while two of these enzymes were less prevalent in Fe-deficient Arabidopsis, one vacuolar ATPase was discovered to be more abundant in Fe-deficient S. lycopersicum. Complex I level also decreased in C. sativus, according to Vigani et al. (2009). Distinct species or growing conditions could account for these variations; for instance, Arabidopsis was cultured on agar in a controlled environment with constant sunlight, which altered electron transfer mechanisms.

1.3.4. Biochemistry of proteins

Overall, it is more difficult to determine how an iron deficiency affects protein metabolism systems. When iron levels dropped in Arabidopsis, some ribosomal components became less abundant while others became more abundant in elements involved in translation elongation and initiation (Lan et al., 2011). In a study involving P. dulcis x P. persica, researchers found an increase in the quantity of a translation initiation factor. However, no such changes were observed in other species. Based on measures of increased activity in particular proteases and changes in the structure of the proteasome, proteolysis may

increase in two species, M. truncatula and S. lycopersicum, in response to Fe-deficiency. C. sativus revealed no change in proteolytic enzyme levels but decreased amounts of structural proteins such globulins and actin. Donnini et al. (2010) hypothesised that these proteins may be utilised as a nitrogen and carbon source in the case of iron deficiency resulting in macronutrient deprivation.

1.3.5. The proteome of shooting

Herbik et al. (1996) found that only S. lycopersicum showed changes in the shoot proteome caused by Fe deprivation. Due to the fact that the objective of that study was to identify differences between a mutant wild type and a S. lycopersicum genotype, protein identification was not investigated. This was the case despite the fact that variances in the protein profiles of Fe-sufficient and Fe-deficient leaves were readily apparent.

1.3.6. The proteome of thylakoids

The reaction centres that transform the energy of light into chemical bond energy are among the numerous components of the multiprotein photosynthetic complexes that are present in thylakoid membranes. Other components of these complexes include cytochrome b6/f and ATPase complexes. Iron shortage causes plants to have a decrease in the amount of granal and stromal lamellae per chloroplast, as well as a decrease in the amount of thylakoid membrane components (proteins, electron transporters, and lipids). This results in a decrease in the rate at which plants produce photosynthetic energy.

1.4. Advancement in technology to treat iron deficiency

The most direct and easy way to cure the signs of iron shortage in plants is to use iron fertiliser. An example would be injecting the tree's trunk, then mixing the chemical with soil and spraying it on the leaves. As an example, kiwifruit that has been treated with iron amino acid complex and iron citrate improves in quality and increases the amount of chlorophyll, vitamin C, soluble solids, and iron overall. Ferric citrate applied foliarly to grapes increased their anthocyanin, flavanol, and flavonol content while balancing their sugar-acid ratio. Research by Liu et al. (2016) indicated that iron fertiliser complexes combining EDDHA-Fe and iron citrate Fe increased the iron content of peanuts throughout their life cycle, from the ripening stage to the blooming hypocotyl and beyond, and into their leaves and kernels.

Although chelate iron fertiliser and inorganic iron fertiliser have seen extensive usage in production, there are a number of drawbacks to this approach, including a high price tag and rapid soil deterioration. Achieving sustainable agriculture is becoming more and more dependent on microbial fertilisers, which offer hope as alternatives to chemical fertilisers. Fungal fertiliser, which is another name for biofertilization, is a mixture of microorganisms that, via their metabolic processes, enhance agricultural output and the agro-ecological setting. Plant growth-promoting rhizobacteria (PGPR) are the microbes that make up biofertilizers. These microbes may dissolve soil minerals and produce hormones and ferritic metabolites that encourage plant development, either directly or indirectly. In the presence of Bacillus or Bacillus-like organisms, PGPR significantly enhances maize growth, yield, and quality. Other research has demonstrated that microbes that promote plant growth make a variety of biomolecules, increase the concentration of all macronutrient synthesis micronutrients in EFB (empty fruit bunches) biomass, convert them from an indigestible form to an absorbable one, and control the amount of iron that plants can take in. Under acidic circumstances, the ground balloon mould may decrease the development of iron deficiency yellowing illness and increase the activity of trivalent iron reductase in the root systems of Hovenia solida seedlings. Soil fertiliser and ferrous siderophore-producing bacterium (Fe-SPBs) may increase the overall iron absorption capability of peanuts. The potential of bacterial aggregates including rhizobium and other plant growth-promoting microbes to increase the biological yield and iron content of lentil seeds.

One typical agricultural strategy that enhances nutrient uptake, particularly iron (Fe) is intercropping. When it comes to intercropping, there are typically two methods to alter the iron nutrition of crops. One is to alter the pH level of the soil. For instance, intercropping peanuts and sesame seeds can lower the pH of peanut roots and increase soil available iron, which in turn increases the amount of active iron in peanut above-ground organs and improves the yellowing effect of peanuts caused by iron deficiency. Nodule formation and root nitrogen fixation efficiency may both be improved with iron supplementation in leguminous plants. The second is to enhance soil iron absorption by secreting chelates. As an example, grass has a higher iron-absorbing capacity than dicotyledons in calcareous soil. Intercropping purple fake brome and barley with olives may help reduce iron shortage. Intercropping maize and peanuts increased the uptake and utilisation of iron by peanuts and relieved their yellowing. Wheat root acids released by maize roots chelated insoluble soil iron.

2. Conclusion and future prospects

Both plant and human life depend on iron for proper growth and development. Both the dietary iron requirements of plants and the molecular processes by which plants control their iron levels have been the subject of much research and development in recent years. Prior research has classified plant iron absorption systems into two categories: Mechanism I, which applies to dicotyledons and non-grass plants, and Mechanism II, which is exclusive to grass plants. The following investigations, however, need be improved in future study since plants cannot survive on their own.

Enhance studies focusing on processes that do not adapt. Soil microbes interact with plants to release iron into the soil. Plants are able to detect when the soil's reducing iron level is low and send a signal to the microbes in their rhizosphere, telling them to release iron carriers that plants may use. Fertiliser microorganisms have been the subject of growing interest due to the progressive expansion of studies on microbial nutrition. Biological iron fertilisers have several benefits, including a higher fertiliser utilisation rate, normal plant development with reduced fertiliser input, and environmental protection. The majority of research on the quantity of microbial fertiliser has focused on its potential environmental effect, as both its manufacturing and its application are still in their early stages. Following this, studies can investigate the production or breakdown of certain compounds involved in the physiology of iron absorption in plants by screening appropriate microbes. Lay down the theoretical groundwork for manufacturing and implementation. Raise the profile of iron deficiency mechanism studies conducted on fruit trees. Based on what we know so far, studies investigating the mechanisms of iron deficiency have been focused on rice, lentils, and other crops, with very little investigation into fruit trees. Hence, fruit tree research has to step up its game in order to improve economic efficiency, increase fruit quality, and decrease yield declines caused by soil iron shortage. One of the most important ways to combat plant tolerance to iron deficiency stress is to continuously screen genotypic variety against the stress and genotypic plants with high resistance to the stress.

Since no iTRAQ profiles have been disclosed and no whole genomes are available, this comparison can only be conducted in Arabidopsis, a plant species for which both studies have been published and whose genome is already available. Together, the two omic approaches provide a comprehensive picture, and the results demonstrate that methodological limitations and the complex regulation of stress reactions, such as iron deficiency, are to blame for the data gap. Proteomics has helped us understand the metabolic changes caused by Fe deficiency more thoroughly, as this work shows. Iron shortage drastically changes C metabolism and the architecture of the photosynthetic machinery, according to many proteomic approaches, and many of these changes are retained across plant species. The discovery of species-and treatment-specific changes, however, calls for additional research.

3. Conflict of interest

Authors declared no conflict of interest each other.

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5. Contributions

All the authors contributed equally in the current manuscript.

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