

Molecular basis and fitness implications of the interplay between light and the regulation of iron homeostasis in photosynthetic organisms



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ABSTRACT

Photosynthetic organisms respond to changes in the external environment, including responses to changes in light color, light intensity and nutrient availability. Iron is one of the nutrients that is critical for the function of photosynthetic organisms, primarily due to the high demand for iron in the photosynthetic photosystems, electron transport chains of plastids and mitochondria, and the structural and functional roles for iron in many critical proteins. Given the connection between iron demands and light-dependent processes such as photosynthesis, as well as the interplay between light and iron, there is a need for finely tuned co-regulation of light and iron acclimation responses to optimize photosynthesis and minimize potential dangerous interactions between iron and light. Such regulation is critical for balancing light and nutrient availability in the coordination of light-dependent aspects of organismal fitness. To accomplish this regulation, there is molecular crosstalk and/or common effectors in light signaling and iron acclimation control. We explore known paradigms that are central to light–iron interactions and the associated regulation of fitness in photosynthetic organisms.

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1. Introduction

1.1. Iron and physiological responses in photosynthetic organisms

Iron (Fe) is a key element that has both structural and functional roles required for the growth of organisms from microbes (Hantke, 2001) to eukaryotes (Castagna et al., 2009; Connolly and Guerinot, 2002; de Silva et al., 1996; Walker and Connolly, 2008). In a variety of organisms, iron is required for a number of critical cellular functions ranging from the synthesis of heme and heme-dependent oxygen transport, to functions in redox and iron-dependent enzymatic reactions, to ribonucleotide synthesis, photosynthesis, and nitrogen fixation (Straus, 1994). In fact, Fe is an essential nutrient for plants and other photosynthetic organisms. The regulation of iron homeostasis and availability is central to optimal growth and productivity in these organisms as iron is essential for respiration and the activity of photosynthetic light-harvesting systems in many organisms capable of

oxygenic photosynthesis, including cyanobacteria. Iron serves as a component of iron–sulfur (Fe–S) clusters, heme-containing cytochromes, and nonheme iron cofactors in photosynthetic protein complexes (reviewed by Shcolnick and Keren, 2006). Iron is also important as a cofactor in enzymes and a component of key substrates that are required for the production of phytochromes. Photosensory phytochromes are light-sensitive photoreceptors that impact plant growth and development beyond photosynthesis, including seed germination, cotyledon and leaf development, stem elongation and the photoperiodic induction of flowering, among others (e.g., Li et al., 2011a). Thus, apart from direct roles in the process of photosynthesis, in which light energy is converted to chemical energy, iron also impacts organismal fitness through impacting the production of components of photosynthetic organisms such as phytochromes needed for light-dependent regulation of growth, development and mitigation of damage.

1.2. Light–iron metabolism crosstalk

Photosynthetic organisms sense changes in and adapt to environmental fluctuations of light and nutrient availability. Whereas both light and iron reduce fitness when limited, in excess both iron and light can also limit fitness by resulting in the generation of reactive oxygen species (ROS). Superoxide, hydrogen peroxide and

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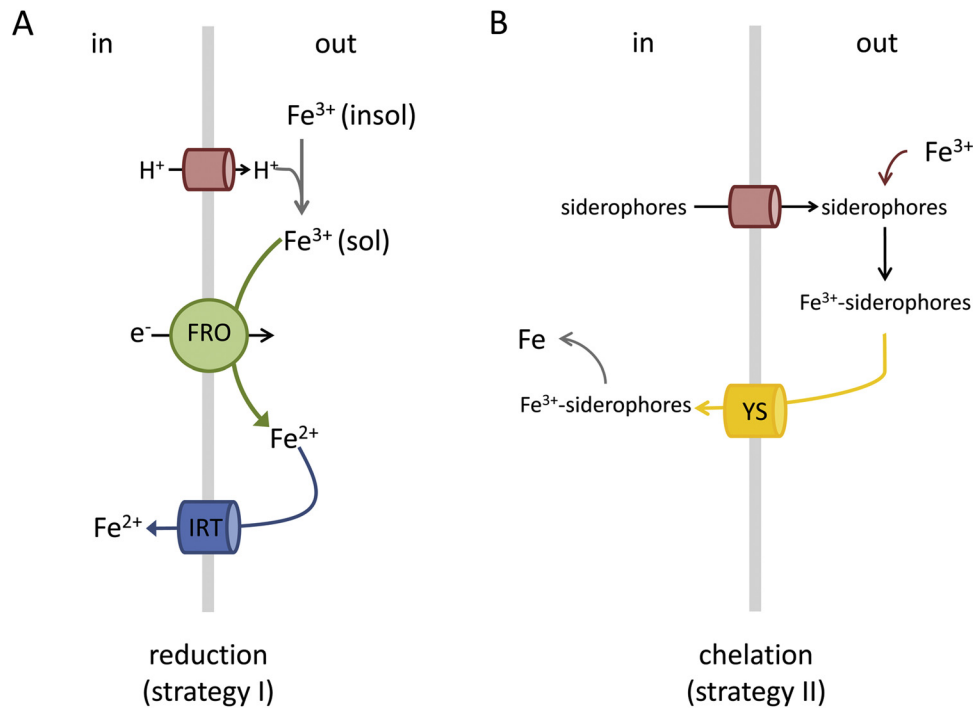


Fig. 1. Distinct strategies for iron uptake in plants. (A) Strategy I plants extrude protons into the extracellular environment to promote solubilization of insoluble ferric iron (Fe^{3+} insolub) to more soluble forms (Fe^{3+} solub) at low pH values, which are reduced to ferrous iron (Fe^{2+}) by ferric chelate reductases (FRO) at the surface of roots. Fe^{2+} is then taken into the cell by iron regulated transporters (IRT). (B) Strategy II plants chelate iron through synthesizing and excreting siderophores into the extracellular environment. Siderophores function as strong Fe^{3+} chelators and thus iron–siderophore complexes form, which are transported into cells via the Yellow Stripe (YS) family of transporters.

other ROS molecules are generated and accumulate under stressful conditions in plants, including in response to excess light (Li et al., 2009) and when the overaccumulation of iron can result in the formation of highly reactive and potentially damaging hydroxyl radicals (Halliwell and Gutteridge, 1992). Thus, interplay between light absorption, excitation pressure, oxidative damage and iron homeostasis are critical for photosynthetic organisms to properly acclimate to variable environments. Light and iron are specifically linked as the ability to convert photons to chemical energy during photosynthesis requires iron-rich photosystems and other iron-dependent components (Kolber et al., 1994). Levels of ROS can increase when light excitation exceeds the photosynthetic capacity of cells, and iron limitation is one stress that can contribute to such an imbalance (for review see Latifi et al., 2009). In this sense, light can become co-limiting at low iron concentrations due to limitation of Fe-containing photosynthetic proteins in some cases (Thamatrakoln et al., 2013). Iron-dependent enzymes, such as catalases, peroxidases, and some superoxide dismutases, also contribute to mitigating damage that can occur when ROS are generated and accumulate in cells (Michel and Pistorius, 2004). Thus, iron limitation can indirectly support ROS accumulation due to reduced cellular ROS-mitigating capacity. Given the requirement of iron for light-dependent process such as photosynthesis, together with the potential for the generation of damaging products when iron and light are coordinately in excess, the need for finely-tuned regulation of plant responses to light and iron availability are tightly linked. Thus, balancing iron homeostasis with changes in the external photoenvironment and organismal iron demands is critical for fitness of plants and other photosynthetic organisms. Together, these observations suggest potential strong connections and/or overlap in the regulation of organismal responses to light and iron availability. Here, we discuss general mechanisms for iron uptake and transport in photosynthetic organisms, the interplay between iron homeostasis and light responses, and compare strategies used by plants and cyanobacteria for regulating light–iron interactions.

2. Iron transport strategies in photosynthetic organisms

Fe is abundant in soil; however, due to its low solubility, it is either assimilated by plants that exude protons which contribute to acidifying the soil and thereby lead to reduction of iron to a form competent for uptake and conversion by roots (common in dicots such as *Arabidopsis*) or iron is chelated and taken up as iron–chelator complexes by roots (common in monocots) (Kim and Guerinet, 2007; Olsen et al., 1981) (Fig. 1). The widely studied model plant *Arabidopsis thaliana* (hereafter *Arabidopsis*) uses a reduction-based strategy, known as Strategy I, for iron uptake in response to iron-deficiency. Central to this strategy is a family of Fe-reductase enzymes encoded by the *Ferric Reductase Oxidase* (FRO) gene family and iron transporters encoded by the *Iron Regulated Transporter* (IRT) gene family (Jeong and Connolly, 2009). When the rhizosphere is acidified by secreting protons into the soil, the ferric to ferrous iron reduction is catalyzed by Fe(III)-chelate reductase (FROs) at the surface of roots before transfer into the plant (Fig. 1). Reductive iron uptake also has been reported in a cyanobacterial system (Kranzler et al., 2014). Other organisms, including grasses and many cyanobacteria, use a chelation-based strategy, i.e., Strategy II, for responding to iron deficiency (e.g. Abadía et al., 2011). In this strategy, organisms synthesize and secrete Fe-chelating siderophores under Fe-deficient conditions, followed by uptake of iron–siderophore complexes into the cell (Abadía et al., 2011). Siderophores are Fe(III) chelators with high binding affinity for iron (Kranzler et al., 2013). Yellow Stripe (YS) transporters contribute to this Strategy II iron acquisition response through the transport of siderophore–iron complexes which function to increase iron uptake (Jeong and Connolly, 2009).

2.1. IRT- and FRO-based iron reduction and uptake in plants

There are 8 FROs in *Arabidopsis* which are expressed at different levels and in different parts of the plant (Jain et al., 2014; Wu et al.,

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