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Iron biofortification in the 21st century: setting realistic targets, overcoming obstacles, and new strategies for healthy nutrition

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Plant-based foods offer a wide range of nutrients that are essential for human and animal health. Among these nutrients, iron stands out as one of the most important micronutrients. Increasing the iron content in many staple and non-staple plant foods continues to be a goal of many scientists around the world. However, the success of such initiatives has sometimes fallen short of their expected targets. In this review we highlight the most recent and promising results that have contributed to increasing the iron content in different crops. We also discuss methods that to date have been used to reach iron biofortification goals and new strategies that we believe are most promising for crop biofortification in the future. Plant anatomical, physiological and metabolic hurdles still need to be tackled for making progress on further increasing currently reached levels of micronutrient improvements. New strategies need to take into account growing environmental challenges that may constrain biofortification efforts.

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Iron deficiency severely affects human health

Deficiencies of essential micronutrients often have longterm negative and irreversible impact on human health. Iron deficiency anemia (IDA) affects around two billion people globally. Children, pregnant women, and nonpregnant women in particular are more vulnerable [1]. IDA can decrease cognitive and physical development, as well as reduce immunity. It often affects work performance in all age groups and enhances the risk of maternal and perinatal mortality [1]. The recommended daily intake of iron varies between 8–18 mg/day according to age, body weight and gender, and 30 mg/day are recommended for pregnant women [2].

Dietary diversification, industrial food fortification and pharmaceutical supplementation are among different intervention strategies aimed at tackling IDA. These interventions, however, are often constrained by various socioeconomic circumstances, including lack of access to diverse diets, insufficient income to afford commercial fortified food products, lack of agricultural infrastructure, and long-term governmental policies and food distribution networks [3,4]. Fortified food products often have low public acceptance because of color and/or flavor changes resulting from added micronutrients [5]. Given these challenges, biofortification of staple crops, that is, the intrinsic enhancement of nutritional content in the edible plant parts, is a recommended strategy that is also sustainable and cost effective. The HarvestPlus Challenge Program of the Consultative Group for International Agricultural Research (CGIAR) focuses on the biofortification of major food crops, including rice, wheat, maize, beans, sweet potato, cassava and pearl millet [6]. For successful biofortification strategies, knowledge of the molecular mechanisms controlling iron uptake and translocation is essential (Figure 1).

Iron biofortification of food crops

To date, conventional breeding and genetic engineering strategies have the potential of effectively delivering nutritious iron-rich food to malnourished populations (Figure 2). To breed high micronutrient-containing varieties, natural genetic variation for the trait of interest must exist in the germplasm available to breeders. Bean and Pearl millet varieties with a high iron content have been developed and were shown to improve the physiological iron status in affected young women in Rwanda [7^{••}] and of school children in India [8[•]]. In several cases, however, conventional breeding approaches alone cannot increase the micronutrient content in crops to nutritionally relevant levels (Table 1) because of lacking natural genetic variation and/or negative correlations between grain yield and micronutrient content [9]. In rice, for



Figure 1

The parameters affecting the success of iron biofortification strategies are represented. Effective iron uptake by the roots is one of the primary requisites. Iron acquisition from the soil is generally categorized into two distinct strategies: a reduction-based strategy (Strategy I) and a chelation-based strategy (Strategy II) [45]. In Strategy I, ATPases are released into the soil to acidify the rhizosphere in order to increase the solubility of Fe³⁺. NADPH-dependent ferric chelate reductases then reduce Fe³⁺ to Fe²⁺ and ZINC-REGULATED TRANSPORTER/IRON-REGULATED TRANSPORTER-RELATED PROTEIN (ZIP) family transporters, including IRT1, transfer Fe²⁺ across the epidermal plasma membrane [46]. Iron uptake in grass species mainly involves the chelation strategy (Strategy II), which comprises of four main steps involving (1) biosynthesis of mugineic acid family phytosiderophores, (2) release of phytosiderophores (PS) to the rhizosphere, (3) iron solubilization and chelation to PS and (4) Fe(III)-PS transport to the plant. Rice is a unique grass species which can use both strategies for iron uptake, that is, uptake of iron in the form of Fe(III)-PS complexes, as well as in the form of Fe(II). However, rice is not capable of reducing Fe(III) to Fe(II) form, as other non-grass species can do (Strategy I). FRO2: FERRIC REDUCTASE OXIDASE 2; TOM1: TRANSPORTER OF MUGINEIC ACID 1; YS1: YELLOW STRIPE 1; IRT1: IRON-REGULATED TRANSPORTER 1.

example, long-term breeding efforts to achieve the recommended iron content of $14 \mu g/gDW$ in polished grains have failed [10], but this target has now been achieved using genetic engineering strategies $[11,12^{\bullet\bullet},13^{\bullet\bullet}]$.

Different processes — root uptake, transport, remobilization, storage and enhanced iron bioavailability — can be modulated in order to produce plant foods with higher iron content [14]. In cereals, including rice and wheat, engineering of iron transport and storage in the endosperm has been an important goal. To achieve this, plants have been transformed with *FERRITIN* expressed under the control of endosperm-specific promoters, resulting in considerable increases in iron content in polished rice grains and in wheat flour [15–18] (Table 2). However, expressing *FER-RITIN* alone could not achieve the recommended target iron levels in either rice or wheat. In parallel, rice transformed with genes related to phytosiderophore synthesis (Figure 2) or encoding iron transporters has also met with varied degrees of success in increasing iron in rice grains [11,19–21]. More recently, iron biofortification of rice has

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