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Review

Producing more with less: Strategies and novel technologies for plant-based food biofortification

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ABSTRACT

About half of the world population suffers from the malnutrition of iron, zinc, calcium, iodine and selenium. Most of the major staple crops of the world, such as rice, wheat, cassava, beans, sweet potato, pearl millet or maize are often deficient in some of these mineral elements. Hence, increasing the concentration of bioavailable micronutrients in edible crop tissues (biofortification) has become a promising strategy in modern agriculture, allowing the access of more nutritious foods, to more people, with the use of fewer resources. Traditional agricultural practices can partly enhance the nutritional value of plant foods, but the advances in the 'omics' technologies are rapidly being exploited to engineer crops with enhanced key nutrients. Ionomics, or the study of the ionome (which can be defined as the mineral trace element composition of a particular organism), is a modern functional genomics tool that can provide high throughput information about the broad spectrum nutrient composition of a given plant food. In alliance with other 'omics' technologies, such as genomics, transcriptomics and proteomics it can be used to identify numerous genes with important roles in the uptake, transport and accumulation of mineral nutrients in plant foods, in particular in their edible parts. This review provides a critical comparison of the strategies that have been developed to diminish nutrient deficiencies in plant-based foods (SWOT analysis) and a summary of the gene families involved in the mineral nutrient pathways. Finally, it also discusses how 'omics' techniques can be used in genetic engineering programs to increase mineral levels and bioavailability in the most important staple food crops and the socioeconomic implications of plant-based biofortified foods.

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1. Introduction

Humans and other animals require a multitude of nutrients in order to have a properly functioning body, in terms of growth, development and metabolism. Plant based foods constitute one of the most important nutrient sources in human diet since the beginning of mankind. From a health perspective, plant nutrients of dietary interest can be divided into five main categories, the first three to be enhanced and the latter two to be limited or removed: macronutrients, micronutrients, 'promoters', anti-nutrients, and allergens (Newell-McGloughlin, 2008). There is a strong evidence that the consumption of plant-based foods is associated with reduced risk of many chronic diseases (McEvoy, Temple, & Woodside, 2012; Sabaté, 2003), cardiovascular disease (Tomé-Carneiro et al., 2012), and certain types of cancer (Magee, Owusu-Apenten, McCann, Gill, & Rowland, 2012; Olsen, Grimmer, Aaby, Saha, & Borge, 2012). Therefore, there is a strong recommendation for increasing the amount of vegetable, fruits and cereals intake.

The Food and Agriculture Organization (FAO) estimates that by 2050 the world's population will reach 9.1 billion (FAO, 2009). Most of this population growth will occur in developing countries and will be accompanied with an increasing rural flight. In order to feed this larger, more urban population, food production must increase by 70% (FAO, 2009). However, the amount of arable land is being reduced and much of the natural resources already in use show signs of degradation. Moreover, staple crops (i.e. plants that constitute the major food item in the diets of people in developing countries; e.g. rice, wheat, cassava and maize) regrettably contain low levels of micronutrients, making them insufficient to meet the minimum daily requirements. Deficiencies in mineral micronutrients, including iron (Fe), zinc (Zn), selenium (Se), and iodine (I), are affecting more than half of the world population (Zhao & McGrath, 2009). For instance, Fe deficiency is the most serious nutritional problem in the world today, affecting approximately 2.7 billion people (Hirschi, 2009). Other minerals, such as calcium (Ca), magnesium (Mg), and copper (Cu), can also be deficient in the diets of some populations (White & Broadley, 2005). Widespread micronutrient malnutrition (MNM) results in an enormous negative socio-economic impact at the individual, community, and national levels (Darnton-Hill et al., 2005). This problem – also known as hidden hunger – is considered as one of the most serious global challenges of the humankind (Copenhagen Consensus 2004; http://www.copenhagenconsensus.com). MNM has been significantly mitigated in some countries thanks to the programs that fortify processed foods. Nevertheless, fortification efforts had only a partial success in countries with limited industrial agriculture, food processing and distribution networks (Pfeiffer & McClafferty, 2007). In this scenario, it is vital to develop strategies that allow us to produce plant foods more efficiently, and with higher micronutrient concentration and bioavailability in their edible tissues. The major goal of the plant-based foods biofortification programs is to provide a continuous supply of nutrient-dense plant foods to large numbers of people (for guarantying 'nutrient security') with making use of few resources (cost-effective strategies with one-off cost and reduced logistics).

The Harvest Plus Challenge Program is a large biofortification platform that was launched in 2004 with the goal of reducing micronutrient malnutrition in Asia and Africa. The program has focused on seven staple food crops (rice, beans, cassava, maize, sweet potatoes, pearl millet and wheat) and targeted three major nutrients: Fe, Zn and vitamin A. However, enrichment of these three micronutrients only scratches the surface of what is currently being done in biofortification programs worldwide. Research also includes other nutrients and secondary metabolites such as antioxidants, anthocyanins, lycopene, vitamin E, essential amino acids, essential and very long chain fatty acids or folate. Biofortification programs have also been diversified to other crops such as apple (Szankowski et al., 2003), canola (Roesler, Shintani, Savage, Boddupalli, & Ohlrogge, 1997; Shewmaker, Sheehy, Daley, Colburn, & Ke, 1999), carrots (Morris, Hawthorne, Hotze, Abrams, & Hirschi, 2008), lettuce (Goto, Yoshihara, & Saiki, 2000), potato (Diretto et al., 2006), amongst many others.

In order to accomplish the biofortification challenges, novel technologies have started to provide valuable information: the so-called 'omics' era. Genomics has given researchers the complete genome from an increasing number of plant foods, and has provided single nucleotide polymorphims (SNPs) information of important nutrient-related genes. The field of transcriptomics has delivered holistic, non-targeted identification of genes that are expressed by the plant in response to nutritional changes. Proteomics has helped in identifying which transcripts will actually be utilized for protein synthesis, whereas metabolomics has gone a step forward and provided information on the metabolites produced by the plant that may be involved in plant nutrition. Finally, the field of ionomics has integrated the nutrient profiles of a given plant food, incorporating information from the previous 'omic' sciences, and accounting for plant tissue, environmental, and developmental factors.

This review will comprehensively describe the challenges, limitations, and potentials of biofortified crops. It will also explain the different types of biofortification strategies and the principal gene families involved in plant nutrition. Finally, it will focus on how the different 'omics' fields can be important tools to achieve the goal of producing plant foods that are nutritionally richer and environmentally sound.

2. Strategies for biofortification of food crops

There are three main strategies currently in practice which have been successfully adopted for improving the nutritional content of plant-based foods: agronomic biofortification, conventional plant breeding and genetic engineering. The agronomical approach is mainly focused on optimizing of the application of mineral fertilizers and/or the improvement of the solubilization and mobilization of mineral elements in the soil (White & Broadley, 2009). The other two approaches aim at improving plant varieties for a higher capacity to accumulate micronutrients in the edible plant tissues and to increase their bioavailability to humans (through higher concentrations of 'promoter' substances and lower concentrations of 'antinutrients'). The choices of conventional breeding or of the use of genetically modified crops are two possible approaches when breeding for this type of biofortified crops. Table 1 summarizes the strengths, weaknesses, opportunities and threats (SWOT analysis) of each biofortification strategy allowing a critical comparison between them.

2.1. Agronomic biofortification

Mineral elements in the soil can be present as free ions, as surface-adsorbed ions, as dissolved compounds or precipitates, as part of lattice structures or contained within the soil biota (White & Broadley, 2009). A common limitation for biofortification is the generally low phytoavailability of mineral micronutrients in the soil. Thus, the agronomic efforts have been directed toward the application of mineral fertilizers and the improvement of the solubilization and mobilization of mineral elements in the soil.

Although relatively simple and with immediate results, this strategy can only be used for fortifying plants with mineral elements and not with organic nutrients (e.g. vitamins) which must be synthesized by the plant itself. Moreover, the viability of this biofortification strategy depends on several factors, including soil composition, mineral mobility in the soil and in the plant, and its accumulation site (Hirschi, 2009; Zhu et al., 2007). Therefore, the application of fertilizers containing essential mineral micronutrients cannot be seen as an universal approach for enhancing the micronutrient levels in edible crop tissues. In general, mineral elements with a good mobility in the soil and in the plant are good candidates for a successful agronomic biofortification (reviewed by White & Broadley, 2009). This is

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