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Iodine biofortification of crops: agronomic biofortification, metabolic engineering and iodine bioavailability

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lodine deficiency is a widespread micronutrient malnutrition problem, and the addition of iodine to table salt represents the most common prophylaxis tool. The biofortification of crops with iodine is a recent strategy to further enrich the human diet with a potentially cost-effective, well accepted and bioavailable iodine source. Understanding how iodine functions in higher plants is key to establishing suitable biofortification approaches. This review describes the current knowledge regarding iodine physiology in higher plants, and provides updates on recent agronomic and metabolic engineering strategies of biofortification. Whereas the direct administration of iodine is effective to increase the iodine content in many plant species, a more sophisticated genetic engineering approach seems to be necessary for the iodine biofortification of some important staple crops.

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Introduction

Iodine is an essential element for the human body as it is involved in the synthesis of thyroid hormones [1]. The intake of iodine is through the diet, and a daily amount in the range of $90-250 \mu g$ is recommended [2] (Figure 1a).

The geochemical cycle of iodine concentrates this element in the oceans thereby reducing its levels in mainland soils and groundwater $[3^{\bullet,}4^{\bullet,}]$. Therefore, whereas seafood (fish, shellfish, edible seaweeds) is generally rich of iodine, vegetables and fruits from plants grown on inland soils are low and the content in most food sources is thus low as well $[3^{\bullet,},5]$. Inadequate iodine intake is one of the main micronutrient deficiencies worldwide (Figure 1b), leading to a spectrum of clinical and social issues called 'Iodine deficiency disorders' (IDDs). These are the result of an insufficient secretion of thyroid hormones, whose classic sign is goiter, the enlargement of the thyroid gland [1]. IDDs can affect all age groups leading to increased pregnancy loss, infant mortality, growth impairment and cognitive and neuro-psychological deficits [1], with effects on the quality of life and the economic productivity of a community. A significant reduction in the number of countries suffering iodine deficiency has been registered in the last two decades (Figure 1c) [2]; nevertheless, it is still a public health problem for almost one-third of the human population [3^{••}].

Dietary iodine supplementation is widely practised and 'universal salt iodization', which is the most common iodine deficiency prophylaxis, has been successfully implemented in several countries [1,2]. However, the use of iodized salt in food processing is still extensively inadequate [2] and the volatilization of iodine during food storage, transport or cooking is high [6]. Furthermore, the policies adopted by many countries are aimed at reducing salt intake in order to prevent hypertension and cardiovascular diseases [2,7].

Complementary approaches are thus necessary. The diversification of the diet with increasing seafood consumption can be effective, but not always possible, especially in inland regions [3^{••},8] or in poor countries. On the other hand, the production of iodine-enriched plants through 'biofortification' [9] could represent an effective way to control iodine deficiency.

lodine in plants

Although essential for animals and strongly accumulated in marine algae $[1,3^{\bullet\bullet},4^{\bullet\bullet}]$, iodine is not considered a micronutrient for higher plants, but an increasing number of studies shows that it is involved in plant physiological and biochemical processes.

Plants can take up iodine from the soil $[10-22,23^{\circ}]$, but the iodine behaviour in a soil-plant system is very complex due to the high number of factors involved $[3^{\circ\circ},4^{\circ\circ}]$. Iodine in soil can be present in inorganic [iodide (I⁻) and iodate (IO₃⁻) ions] and organic forms. The soil composition, texture, pH and redox conditions $[4^{\circ\circ}]$ control iodine





lodine human requirements, geographical deficiency and progress. (a) Recommended iodine daily dietary intakes by population groups [1]. (b) Global iodine scorecard map updated at 2015 (adapted from: Global Map of Iodine Nutrition 2014–2015, The Iodine Global Network; URL: http://www.ign.org/scorecard.htm). The iodine status is based on median urinary iodine concentrations (UIC) of school-age children. Reference values in the figure legend: moderate iodine deficiency (UIC 20–49 μ g/L); mild iodine deficiency (UIC 50–99 μ g/L); adequate iodine nutrition (UIC 100–299 μ g/L); excess iodine intake (UIC > 300 μ g/L) [1]. (c) Global Iodine deficiency restraint during the past two decades. The total number of countries interested by iodine deficiency from 1993 to 2014 is reported (adapted from: Global Iodine Scorecard 2014: Number of iodine-deficient countries more than halved in the past decade, IDD Newsletter 1/2015, The Iodine Global Network; URL: http://www.ign.org/scorecard.htm).

speciation and mobility in the soil, thus affecting the uptake by roots.

Very low amounts of iodine can be beneficial for plant growth: positive effects have been described in barley, ryegrass, tomato [24], cabbage [14], and strawberry [25]. On the other hand, high concentrations may inhibit its absorption by roots [14] and over a certain threshold it becomes toxic [14,18,19,22,26–28]: actually iodine is registered as a herbicide for agricultural use [27].

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