Iodine biofortification in tomato

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Abstract

Iodine is an essential element in the human diet, and iodine deficiency is a significant health problem. No attempts to increase iodine content in plant-derived food (biofortification) have so far been particularly effective. We studied iodine uptake in tomato (*Solanum lycopersicum* L.) to evaluate whether it is possible to increase the iodine concentration in its fruits. Iodine translocation and storage inside tomato tissues were studied using radioactive iodine. Potassium iodide was also supplied at different concentrations to tomato plants to evaluate the resulting iodide concentration both in the vegetative tissues and the fruits. The results indicate that iodine was taken up better when supplied to the roots using hydroponically grown plants. However, a considerable amount of iodine was also stored after leaf treatment, suggesting that iodine transport through phloem also occurred. We found that tomato plants can tolerate high levels of iodine, stored both in the vegetative tissues and fruits at concentrations that are more than sufficient for the human diet. We conclude that tomato is an excellent crop for iodine-biofortification programs.

Key words: biofortification / iodine deficiency / phytotoxicity / *Solanum lycopersicum*

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1 Introduction

Iodine is an essential element for human physiology (*Andersson* et al., 2005), being involved in the synthesis of thyroid hormones. The recommended dietary allowance (RDA) for adults amounts to 150 μg iodine per day (*Pearce* et al., 2004). Chronic iodine deficiency, called hypothyroidism, can trigger goiter, growth impairment, reproductive failure, hearing loss, cretinism, and several kinds of brain damage (*Andersson* et al., 2005; *Delange*, 2000; *Dillon* and *Milliez*, 2000; *Haddow* et al., 1999). Although iodine deficiency can be treated, it is still a public health problem for almost 35% of the world's population (*Pearce* et al., 2004; *Winger* et al., 2008), and the population at risk is more than one billion (*Winger* et al., 2008; *World Health Organization*, 2004). Iodized salt is the most common approach for dietary iodine supplementation (*Andersson* et al., 2005; *Delange* and *Lecomte*, 2000). However, since iodine supplementation may cause problems during food processing, it is difficult to control its loss during transport, storage, and food cooking (*Winger* et al., 2008). Therefore, enhancing iodine content in vegetables represents a cost-effective way to control its deficiency, since iodine in food is readily bioavailable (up to 99%) and assimilated (*Dai* et al., 2004; *Weng* et al., 2009; *White* and *Broadley*, 2009).

Despite its importance for human nutrition, iodine relevance has not yet been established for plants. Vegetables can accumulate iodine, and increasing iodine application to the soil results in enhancing iodine accumulation in plants (*Dai* et al., 2004; *Whitehead*, 1973; *Zhu* et al., 2003), as it was demonstrated for pakchoi, celery, pepper, radish (*Hong* et al., 2008), cabbage (*Weng* et al., 2008a), and spinach (*Zhu* et al., 2003). However, results are largely affected by the iodine concentration and the chemical form supplied (*Blasco* et al., 2008; *Dai* et al., 2004; *Mackowiak* and *Grossl*, 1999) and by the growth substrate used (*Weng* et al., 2008c). Iodide, rather than iodate, has the greatest bioavailability for plants (*Umaly* and *Poel*, 1971; *Whitehead*, 1973), and very low concentrations of iodine, regardless to the form, are beneficial to several crops (*Borst-Pauwels*, 1961). In tomato plants, a very low amount of iodide can stimulate the tangential growth and, to some extent, improve the yield (*Lehr* et al., 1958). However, at higher concentrations, iodine can be toxic, leading to leaf damages, stunted growth, and death (*Lehr* et al., 1958). Once inside the plant, a xylem flux of iodine seems to be largely predominant (*Lewis* and *Powers*, 1941; *Shinonaga* et al., 2001; *Weng* et al., 2008c, 2009; *Whitehead*, 1973), but, generally, the absorbed iodine is not uniformly distributed among plant tissues, ranking as follows: root > leaf > stem (*Weng* et al., 2008a). Finally, a further aspect, which needs explanation, is whether iodine uptake could be affected by other nutrients. A negative correlation between nitrate and halogens has been speculated for radish, lettuce, and cabbage (*Roorda van Eysinga* and *Spaan*, 1985; *Sheppard* and *Evenden*, 1992; *Weng* et al., 2008b).

Recent studies demonstrated that leafy vegetables such as spinach (*Zhu* et al., 2003; *Dai* et al., 2006) or lettuce (*Blasco* et al., 2008; *Voogt* et al., 2010) can store iodine in their edible tissues, making them good candidates for iodine biofortification programs. The aim of the present work is to evaluate the ability of tomato plants to absorb and store iodine in vegetative tissues and fruits. Due to its widespread distribution and

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its easy growth on a commercial scale, tomato would represent a preferred crop in biofortification programs. Moreover, the possibility of fresh consumption of its fruits prevents the risk of iodine loss with certain cooking methods. To achieve our goals, radioactive iodine (^{125}I as NaI) was used for visualizing iodine distribution and storage inside plant tissues, while potassium iodide (KI) was supplied to study iodine toxicity and the overall amount stored in tomato fruits. Different kinds of treatments as well as different growth substrates were compared to set up the best experimental conditions for enhancing iodine concentration in fruits of this species.

2 Materials and methods

2.1 Plant material

All the experiments were carried out using tomato (*Solanum lycopersicum* L. cv. MicroTom). Tomato seeds were sown on wet filter paper under continuous light until germination. When the cotyledons were well expanded, the plants were transplanted into soil or transferred into a hydroponic system. This latter was based on thick gravel (3–5 mm in diameter) and a nutrient solution whose composition was as follows (in mM): NO_3-N 12; NH_4-N 0.5; P 1.30; K 8; Ca 4; Mg 1.19; Na 9; SO_4-S 1.59; Cl 9.87; (in μM): Fe 19.5; B 28.6; Cu 3.6; Zn 4.5; Mn 10.9; Mo 0.2. Electrical conductivity (EC) was 2.84 dS m^{-1}, and pH 5.8. Fresh solution was added weekly. Plants grown in soil (Hawita Flor, Vechta, Germany) were watered twice a week. All plants were grown in plastic pots (diameter 5 cm) in a growth chamber, with 80 μmol m^{-2} s^{-1} PAR (Gro-Lux, Sylvania, OH, USA), 12 h light photoperiod, 24°C temperature, 55% relative humidity.

2.2 Reagents and chemicals

Potassium iodide was purchased from Sigma-Aldrich (St Louis, MO, USA), while the radioactive iodine (^{125}I as NaI) from Perkin Elmer (Waltham, MA, USA).

2.3 Iodine-uptake experiments

Tomato plants, grown in hydroponics or soil, were treated with radioactive iodine starting at the age of: (1) 2 weeks, (2) 1 month, or (3) 2 months after germination. Iodine was supplied as root or leaf treatment, and in both the experiments, a total of three iodine-feeding treatments were performed, at 2-day intervals. In the root-treatment experiments, the iodine stock solution (Na^{125}I, 10 μCi mL^{-1}) was diluted to the final activity of 0.25 μCi mL^{-1}, and 1 mL was supplied directly to the gravel of the hydroponic system or to the soil of each treated plant. At the end of the experiment, after the three feeding treatments, a total amount of 0.75 μCi iodine was supplied per plant. In the leaf-treatment experiments, 25 μL of radioactive iodine (Na^{125}I, 10 μCi mL^{-1}) were spotted on a leaf blade. The first true leaf or a well expanded leaf at the second branch was treated in 2-week-old or 1-/2-month-old plants, respectively. Also in this case, three iodine-feeding treatments were performed, for a total amount of iodine supplied per plant equal to 0.75 μCi. Each experiment was replicated three times.

2.4 Nitrate experiment

Two groups of 2-week- and 2-month-old tomato plants grown in hydroponics were treated with radioactive iodine (Na^{125}I, 0.25 μCi mL^{-1}). Starting from the beginning of the iodine treatment, one set of both 2-week- and 2-month-old plants was maintained in the usual complete hydroponic solution, while another identical set was grown in a modified nutrient solution in which the nitrate concentration was diluted 1:10 (reaching a final concentration of 1.2 mM nitrate). Three root iodine feeding treatments (1 mL for each treatment) were carried out, at 2-day intervals, for a total amount of iodine supplied per plant equal to 0.75 μCi. Each experiment was replicated three times.

2.5 Visualization of radioactive-iodine uptake

At the end of each experiment, both leaf- and root-treated plants were cut at the hypocotyl level, gently washed, blotted onto filter paper, and then exposed for 2 d to a multipurpose phosphor storage screen (Cyclone Storage Phosphor System, Packard, CT, USA) in order to obtain a digital image of the radioactivity distribution. For the leaf treatment, each Na^{125}I-treated leaf was removed from the original plant and exposed on a separate screen. When possible, sepals and fruits from each treatment were collected at the end of the experiment. Fruits were cut into several longitudinal sections in order to display where iodine was stored. All the digital images were obtained and analyzed using a phosphoimager (Cyclone Storage Phosphor System, Packard). Data are presented as DLUs (digital light units), and the scanned images are shown using false colors, where red and blue indicate a high or low level of radioactivity, respectively.

2.6 Iodine toxicity

To investigate the effects of iodine on tomato plant physiology and fruit production, a dose-response experiment was carried out. Plants at the flowering stage (about 45 d old) and grown in hydroponics were treated. Different concentrations of KI (0, 5, 10, 20 mM), added to the hydroponic solution, were tested, and three treatments (once a week) were carried out. During this period, the plants were observed and photographed. Twenty-four days after the beginning of the treatment, all the plants were collected to analyze the iodine content. Fruits were sampled at the mature green stage for all the iodine treatments and also at the red ripe stage for the 5 mM KI treatment, and analyzed separately. Three replicates were analyzed for each treatment.

2.7 Iodine measurements

The iodine content inside plant vegetative tissues and fruits was measured using the inductively coupled plasma–mass spectrometry (ICP-MS) technique (*Yoshida* et al., 2007). Iodine was determined using an isotope dilution with ^{127}I. The iodine concentration in the samples was evaluated using a calibration curve obtained with the standard additions method. Three replicates were analyzed for each treatment. Analyses were carried out by Neotron Spa (Modena, Italy).

3 Results

3.1 Iodine uptake in tomato plants: storage and distribution

Plants at different developmental stages were root- or leaf-treated with radioactive iodine. After the treatment, iodine was clearly detectable in all the treated plants (Fig. 1a). Regardless of the plant age, the amount of iodine accumulated after the root treatment was higher than that stored in leaf-treated plants (Fig. 1). Two-week-old plants accumulated more iodine than the older ones, both after root and leaf treatment (Fig. 1). In the youngest plants, especially in the root-treated ones, iodine was widely distributed in the aerial parts, being strongly accumulated both in the stem and in the leaves (Fig. 1a). In adult plants, iodine was prevalently stored in the stem and in the main veins of the leaves (Fig. 1a). In 2-month-old plants, iodine was accumulated not only in vegetative organs but also, although at lower levels, in fruits (Fig. 1a).

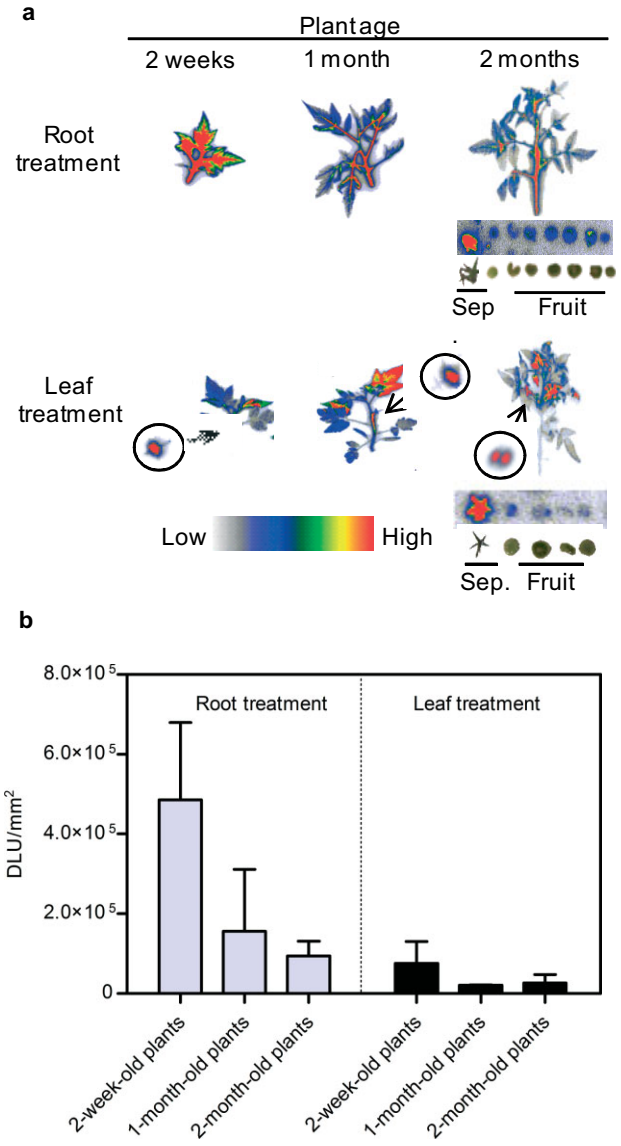

Figure 1: (a) Iodine root and leaf treatment on 2-week-, 1-month-, and 2-month-old MicroTom hydroponically grown tomato plants. Iodine was supplied as $Na^{125}I$, and three treatments were performed at 2-day intervals. A representative plant for each condition is shown. In the leaf treatment, each single treated leaf is shown besides the corresponding plant. Arrows indicate the position of the treated leaf that was removed from the plant after the treatment. In 2-month-old plants, sepals (referred as Sep.) and fruits were exposed separately. Blue/red colors indicate low/high iodine content, respectively. (b) Histograms showing the iodine amount taken up by tomato plants at the different developmental stages after being root- or leaf-treated. Values are expressed as DLU (Digital Light Unit) mm^{-2}. Data are means of three replicates ± SD.

When plants were grown in soil, the amount of radioactive iodine accumulated after a root treatment was dramatically lower, both in young and adult plants (Fig. 2a, b).

3.2 Iodine uptake and nitrate

Nitrate may interfere with iodine uptake (*Roorda van Eysinga* and *Spaan*, 1985). For this reason, an experiment was performed to compare iodine uptake and accumulation in plants in the presence of different nitrate concentrations. Young and adult tomato plants, previously grown in a full-strength hydroponic solution, were treated with iodine in the presence of a high (12 mM) or low (1.2 mM) nitrate concentration. The latter was modified only at the beginning of the iodine treatment to avoid that plant root architecture and growth were influenced by different nitrate levels. The results show that when plants were maintained in the presence of low nitrate, iodine uptake and accumulation were negatively affected (Fig. 3a–c). This was particularly evident in 2-week-old plants (Fig. 3a, c), but also in plants at the reproductive stage the final iodine levels detected in the presence of low nitrate were lower (Fig. 3b, c). The reduction in iodine accumulation of plants treated with low nitrate concentration was more evident in the vegetative rather than reproductive organs (Fig. 3a, b).

3.3 Phytotoxic effects of iodine

In order to detect possible phytotoxic effects and consequences for fruit production, an iodine dose–response experiment was carried out supplying KI at increasing concentrations (0, 5, 10, 20 mM) to plants at the flowering stage. After 3 weeks of iodine treatments, all the plants survived and produced fruits (data not shown), but those treated with iodine showed symptoms of phytotoxicity (Fig. 4). The main physiological effects observed were leaf chlorosis and burns, mainly located at the tips of the leaves and becoming more evident when the iodine concentration increased (Fig. 4a). Toxicity symptoms initially appeared on the lower leaves and moved gradually towards the upper parts of the plant. Generally, the lowest branches were those mostly injured and discolored quickly, becoming brownish and, finally, turning necrotic. At the highest iodine concentrations (10–20 mM), tomato branches showed a strong epinasty in comparison to the control plants and the leaf edges were down-curved (Fig. 4b). Another effect was the presence of small white spots on the adaxial leaf surface (Fig. 4c). This was also observed for the lowest iodide concentration applied (5 mM) and generally increased with the iodide concentration, gradually moving

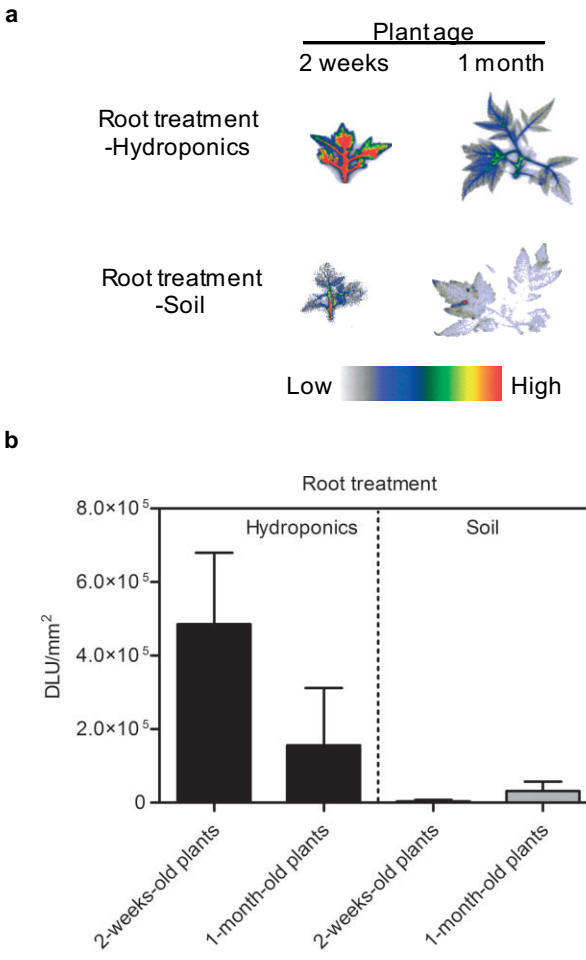

Figure 2: (a) Iodine root treatment of 2-week- and 1-month-old tomato plants grown in solution culture or in soil. Iodine was supplied as $Na^{125}I$, and three treatments were performed at 2 d intervals. A representative plant for each condition is shown. Blue/red colors indicate low/high iodine content, respectively. (b) Histograms showing the iodine amount taken up by tomato plants at the two different developmental stages and grown on the two different substrates. Values are expressed as DLU (Digital Light Unit) mm^{-2}. Data are means of three replicates ± SD.

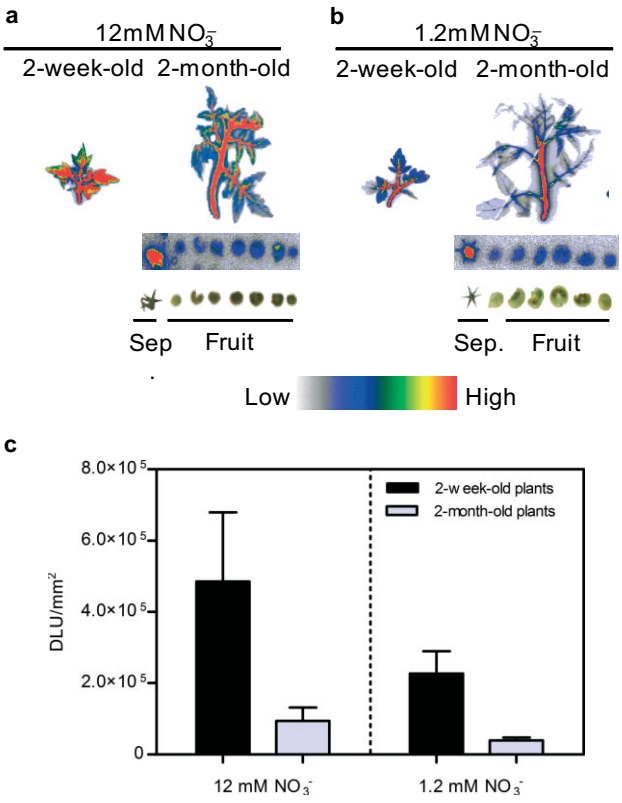

Figure 3: Iodine root treatment of 2-week- or 2-month-old plants concomitantly fed with high (12 mM, a) or low (1.2 mM, b) nitrate. Iodine was supplied as $Na^{125}I$ directly in the growth medium, and three treatments were performed at 2 d intervals. A representative plant for each condition is shown. In 2-month-old plants, sepals (referred as Sep.) and fruits were exposed separately. Blue/red colors refer to low/high iodine content, respectively. (c) Histograms showing the amount of iodine taken up by 2-week- or 2-month-old plants after iodide treatment in the presence of the two different nitrate concentrations. Values are expressed as DLU (Digital Light Unit) mm^{-2}. Data are means of three replicates ± SD.

towards the upper leaves. A difference in color was observed between the iodide-treated plants and the control ones, the former leaves being darker green (Fig. 4d). This effect was evident particularly for the lowest concentrations used (5–10 mM). A slight anthocyanin accumulation was observed in the stem and along the main veins of the iodine-treated leaves (data not shown). However, no phytotoxic effects were observed in fruits and flowers (Fig. 4e, f), apart from some white spots on a few fruits treated with 10 mM KI, similar to those observed on leaves (Fig. 4e). Regardless to the iodine concentration supplied, flowers and fruits grew and developed normally (Fig. 4e, f).

3.4 Iodide concentration in tomato vegetative tissues and fruits

Plants treated with KI in the dose-response experiment were collected at the end of the treatment and analyzed for their iodine concentration in vegetative tissues and fruits. High concentrations of iodine were found in leaves and stems (Fig. 5a). The iodine concentration increased in proportion to its concentration in the hydroponic medium (Fig. 5a). The highest value (approximately 9000 mg $[kg\ FW]^{-1}$) was observed in plants treated with 20 mM iodide (Fig. 5a). However, also at concentrations of 5 and 10 mM, the iodine concentration was very high, approximately 3000 and 5000 mg $(kg\ FW)^{-1}$, respectively (Fig. 5a). Green fruits contained lower levels of iodine, reaching the maximum concentration (30 mg $[kg\ FW]^{-1}$) in plants treated with 20 mM KI (Fig. 5b). At the lowest concentration supplied (5 mM), the iodine content in fruits was still high enough (10 mg $[kg\ FW]^{-1}$) to fulfill the goal of a biofortification program (Fig. 5b). Tomato fruits treated with 5 mM KI were also collected at the red ripe stage and analyzed. Red fruits showed the same iodine concentration as green fruits (Fig. 5b).

4 Discussion

Most of the attempts to develop iodine biofortification of crops have failed, particularly those aimed at increasing iodine con-

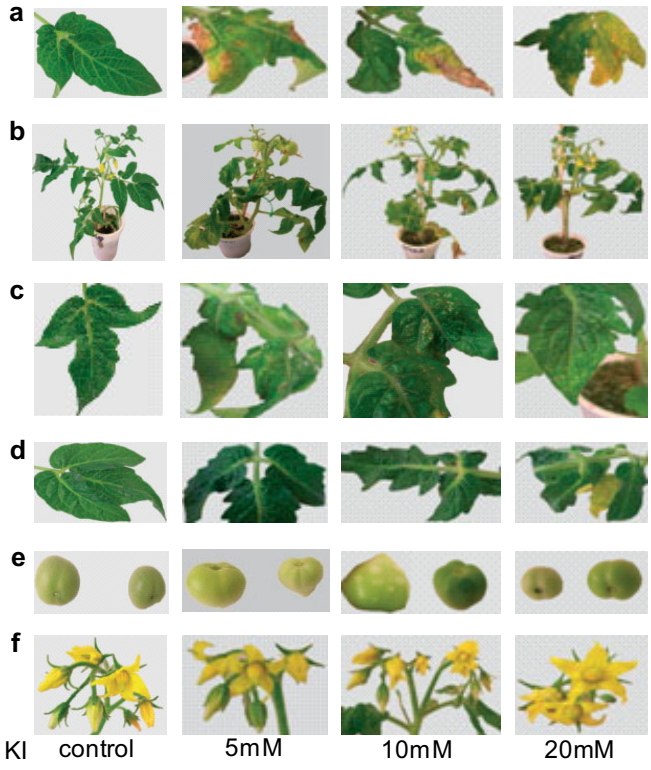

Figure 4: Effects of iodine on tomato plants after treatment with different KI concentrations. For each concentration, three different treatments (once a week) were applied. Pictures in the first column show the absence of phytotoxicity symptoms in untreated plants, in comparison with the main effects observed on the leaves in KI-treated plants, which are, respectively: (a) chlorosis and burns; (b) epinasty; (c) presence of white spots; (d) dark-green color. Fruits (e) and flowers (f) sampled from iodine-treated plants are not different from their relative controls.

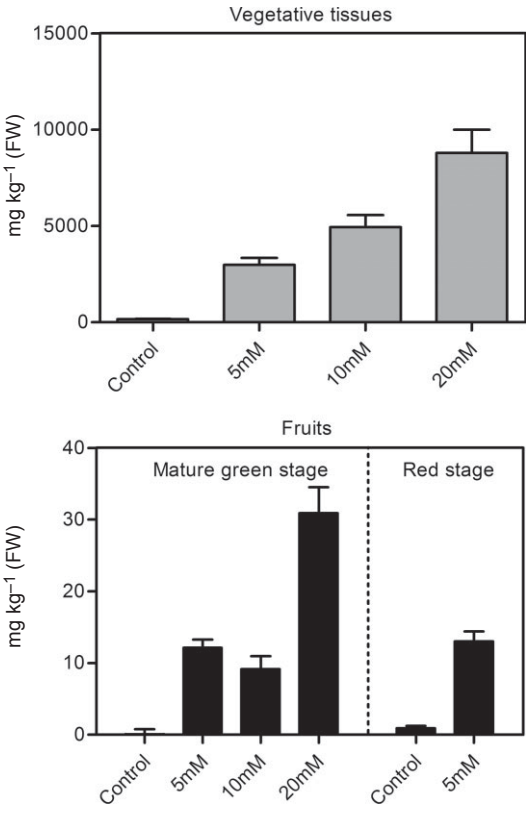

Figure 5: Iodine concentrations in vegetative tissues (a) and fruits (b) of plants treated with various iodine (KI) concentrations. For each concentration, three different treatments (once a week) were applied. Plant tissues and fruits were collected 24 d after the beginning of the iodine treatment. Control refers to vegetative tissues or fruits sampled from KI-untreated plants. Iodine was measured using the ICP-MS technique. Values are expressed as mg kg^{-1} on the basis of fresh weight (FW). Data are means of three replicates ± SD.

centration in fruits (*Mackowiak* and *Grossl*, 1999). Our results obtained for tomato showed that when iodine was supplied in the growth medium, root uptake and xylem transport were highly efficient, as the element was found widely distributed in the shoot. Iodine was accumulated in the stem and in the main veins of the leaves, but in many cases, particularly in young plants, it also spread to cover the entire leaf blade (Fig. 1a). Previous results obtained in cabbage indicated that also in this species iodine distribution in the shoot was not uniform and iodine was stored predominantly in the main leaf veins (*Weng* et al., 2008a). Hydroponics was more effective than soil in promoting iodine absorption (Fig. 2a, b), probably because in soil iodine can be retained by organic matter, being therefore less available for plant uptake. The overall amount of iodine taken up by tomato plants was generally higher when iodine was supplied to the roots rather than onto the leaf blade (Fig. 1a, b). These results imply that root treatment is most effective in terms of iodine uptake and storage. Hydroponic culture, with iodine added to the nutrient solution, thus, gives excellent possibility for tomato biofortification.

A possible inhibitory effect of nitrate on halide, particularly bromide, uptake, as a consequence of a competition during plant uptake, has been described (*Roorda van Eysinga* and *Spaan*, 1985), although results are controversial (*Sheppard* and *Evenden*, 1992). Our results show that nitrate did not inhibit iodine uptake (Fig. 3). On the contrary, plants concomitantly fed with iodine and 12 mM nitrate showed a higher iodine accumulation than plants fed with iodine and 1.2 mM nitrate (Fig. 3). The iodine content in fruits was less negatively affected by low nitrate (1.2 mM) than in vegetative organs (Fig. 3a, b). This may suggest that low nitrate could negatively affect the xylem transport of iodine with a limited effect on iodide content of fruits, which largely depends on the phloem transport (*Ho* et al., 1987).

The possible role of phloem in iodine transport was ruled out by *Herrett* et al. (1962) and *Mackowiak* and *Grossl* (1999). In contrast, we found that a phloem route for iodine transport is present in tomato plants. Spotting radioactive iodide on a single leaf resulted in a widespread distribution of iodine in all the surrounding tissues of the shoot (Fig. 1a, b). Tomato fruits are relatively isolated from the xylem stream, and therefore, they accumulate little amount of mineral elements that are mainly translocated along the transpiration stream (*Ho* et al., 1987; *Mingo* et al., 2003). Therefore, an adequate accumulation of iodine inside fruits depends on phloem transport. The fact that in tomato a moderate phloem flux of iodine was ob-

served is particularly noteworthy because, in order to obtain an effective biofortification strategy in this species, it is crucial to ensure an adequate concentration of iodine inside fruits. Iodine treatments to plants at the reproductive stage demonstrated that iodine could be transported into fruits (Fig. 1a).

Plants treated with iodine often show toxicity symptoms, with crop-specific effects. Our data indicate that tomato plants, despite the presence of some phytotoxicity symptoms, tolerate relatively high concentrations of KI (20 mM) without severe injuries (Fig. 4). Plants treated with the lowest iodide concentrations were darker green (Fig. 4d), suggesting a slight production of antioxidant compounds, such as anthocyanins, in response to iodine. In lettuce, iodine can increase the amount of antioxidant compounds, probably interfering with the oxidative state of the plant (*Blasco* et al., 2008). It is noteworthy, in the framework of iodine-biofortification programs, that iodine application up to 20 mM, starting from the beginning of the reproductive stage, did not importantly affect tomato vegetative and reproductive growth and development.

During tomato ripening, the translocation of nutrients from roots to fruits is higher at the green stage and falls down in later phases (*Srivastava* and *Handa*, 2005). It is reasonable to assume that iodine could be more easily translocated during the early fast growth of the fruits. The quantitative data obtained by ICP-MS showed that a huge amount of iodine was stored in both vegetative tissues and in green fruits, reaching the maximum concentration of about 9000 mg kg^{-1} and 30 mg $(kg\ FW)^{-1}$, respectively (Fig. 5a, b). Even at the lowest concentration of KI supplied (5 mM), the iodine concentration in tomato fruits was high (about 10 mg $[kg\ FW]^{-1}$). The iodine concentration did not change when fruits reached the mature red stage (Fig. 5b), suggesting that, once inside the fruit, iodine concentration was stable.

5 Conclusion

Our results indicate that iodine uptake and translocation in tomato plants are efficient and lead to considerable iodine accumulation in fruits. The fruit concentration of iodine detected in 5 mM iodide–treated plants was more than enough to cover a daily human intake of 150 μg. Nitrate, at least in the range which is commonly used in hydroponics, had no negative effect on iodine uptake, and thus modifications of the usual nutrient solution used to grow tomato commercial varieties are not required.

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References

Andersson, M., Takkouche, B., Egli, I., Allen, H. E., de Benoist, B. (2005): Current global iodine status and progress over the last decade towards the elimination of iodine deficiency. *Bull. World Health Organ.* 83, 518–525.

Blasco, B., Rios, J. J., Cervilla, L. M., Sánchez-Rodrigez, E., Ruiz, J. M., Romero, L. (2008): Iodine biofortification and antioxidant capacity of lettuce: potential benefits for cultivation and human health. *Ann. Appl. Biol.* 152, 289–299.

Borst-Pauwels, G. F. W. H. (1961): Iodine as micronutrient for plants. *Plant Soil* 14, 377–392.

Dai, J. L., Zhu, Y. G., Zhang, M., Huang, Y. Z. (2004): Selecting iodine-enriched vegetables and the residual effect of iodate application to soil. *Biol. Trace Elem. Res.* 101, 265–276.

Dai, J. L., Zhu, Y. G., Huang, Y. Z., Zhang, M., Song, J. (2006): Availability of iodide and iodate to spinach (*Spinacia oleracea* L.) in relation to total iodine in soil solution. *Plant Soil* 289, 301–308.

Delange, F. (2000): The role of iodine in brain development. *Proc. Nutr. Soc.* 59, 75–79.

Delange, F., Lecomte, P. (2000): Iodine supplementation: Benefits outweight risks. *Drug Saf.* 22, 89–95.

Dillon, J. C., Milliez, J. (2000): Reproductive failure in women living in iodine deficient areas of West Africa. *Br. J. Obstet. Gynaecol.* 107, 631–636.

Haddow, J. E., Palomaki, G. E., Allan, W. C., Williams, J. R., Knight, G. J., Gagnon, J., O'Heir, C. E., Mitchell, M. L., Hermos, R. J., Waisbren, S. E., Faix, J. D., Klein, R. Z. (1999): Maternal thyroid deficiency during pregnancy and subsequent neuropsychological development of the child. *New Engl. J. Med.* 341, 549–555.

Herrett, R. A., Hatfield, Jr. H. H., Crosby, D. G., Vlitos, A. J. (1962): Leaf abscission induced by the iodide ion. *Plant Physiol.* 37, 358–363.

Ho, L. C., Grange, R. I., Picken, A. J. (1987): An analysis of the accumulation of water and dry matter in tomato fruit. *Plant, Cell Environ.* 10, 157–162.

Hong, C. L., Weng, H. X., Qin, Y. C., Yan, A. L., Xie, L. L. (2008): Transfer of iodine from soil to vegetables by applying exogenous iodine. *Agron. Sustain. Dev.* 28, 575–583.

Lehr, J. J., Wybenga, J. M., Rosanow, M. (1958): Iodine as micronutrient for tomatoes. *Plant Physiol.* 33, 421–427.

Lewis, J. C., Powers, W. L. (1941): Iodine in relation to plant nutrion. *J. Agric. Res.* 63, 623–637.

Mackowiak, C. L., Grossl, P. R. (1999): Iodate and iodide effects on iodine uptake and partitioning in rice (*Oryza sativa* L.) grown in solution culture. *Plant Soil* 212, 135–143.

Mingo, D. M., Bacon, M. A., Davies, W. J. (2003): Non-hydraulic regulation of fruit growth in tomato plants (*Lycopersicon esculentum* cv. Solairo) growing in drying soil. *J. Exp. Bot.* 54, 1205–1212.

Pearce, E. N., Pino, S., He, X., Bazrafshan, H. R., Lee, S. L., Braverman, L. E. (2004): Sources of dietary iodine: Bread, cow's milk and infant formula in Boston area. *J. Clin. Endocrinol. Metabol.* 89, 3421–3424.

Roorda van Eysinga, J. P. N. L. R., Spaans, L. (1985): Nitrate and bromide contents of glasshouse radish as affected by soil content and global radiation. *Commun. Soil Sci. Plant Anal.* 16, 1307–1318.

Sheppard, S. C., Evenden, W. G. (1992): Response of some vegetable crops to soil-applied halides. *Can. J. Soil Sci.* 72, 555–567.

Shinonaga, T., Gerzabek, M. H., Strebl, F., Muramatsu, Y. (2001): Transfer of iodine from soil to cereal grains in agricultural areas of Austria. *Sci. Total Environ.* 267, 33–40.

Srivastava, A., Handa, A. K. (2005): Hormonal regulation of tomato fruit development: A molecular perspective. *J. Plant Growth Regul.* 24, 67–82.

Umaly, R. C., Poel, L. W. (1971): Effects of iodine in various formulations on the growth of barley and pea plants in nutrient solution culture. *Ann. Bot.* 35, 127–131.

Voogt, W., Holwerda, H. T., Khodabaks, R. (2010): Biofortification of lettuce (*Lactuca sativa* L.) with iodine: The effect of iodine form and concentration in the nutrient solution on growth, development and iodine uptake of lettuce grown in water culture. *J. Sci. Food Agric.* 90, 906–913.

Weng, H. X., Hong, C. L., Yan, A. L., Pan, L. H., Qin, Y. C., Bao, L. T., Xie, L. L. (2008a): Mechanism of iodine uptake by cabbage: effects of iodine species and where it is stored. *Biol. Trace Elem. Res.* 125, 59–71.

Weng, H. X., Yan, A. L., Hong, C. L., Xie, L. L., Qin, Y. C., Cheng, C. Q. (2008b): Uptake of different species of iodine by water spinach and its effect to growth. *Biol. Trace Elem. Res.* 124, 184–194.

Weng, H. X., Weng, J. K., Yan, A. L., Hong, C. L., Yong, W. B., Qin, Y. C. (2008c): Increment of iodine content in vegetable plants by applying iodized fertilizer and the residual characteristics of iodine in soil. *Biol. Trace Elem. Res.* 123, 218–228.

Weng, H. X., Yan, A. L., Hong, C. L., Qin, Y. C., Pan, L., Xie, L. L. (2009): Biogeochemical transfer and dynamics of iodine in a soil-plant system. *Environ. Geochim. Health* 31, 401–411.

White, P. J., Broadley, M. R. (2009): Biofortification of crops with seven mineral elements often lacking in human diets -iron, zinc, copper, calcium, magnesium, selenium and iodine. *New Phytol.* 182, 49–84.

Whitehead, D. C. (1973): Uptake and distribution of iodine in grass and clover plants grown in solution culture. *J. Sci. Food Agric.* 24, 43–50.

Winger, R. J., Konig, J., House, D. A. (2008): Technological issues associated with iodine fortification of foods. *Trends Food Sci. Technol.* 19, 94–101.

World Health Organization (2004): Iodine status worldwide. WHO global database on iodine deficiency. Geneva.

Yoshida, S., Muramatsu, Y., Katou, S., Sekimoto, H. (2007): Determination of the chemical forms of iodine with IC-ICP-MS and its application to environmental samples. *J. Radioanal. Nuclear Chem.* 273, 211–214.

Zhu, Y. G., Huang, Y. Z., Hu, Y., Liu, Y. X. (2003): Iodine uptake by spinach (*Spinacia oleracea* L.) plants grown in solution culture: Effects of iodine species and solution concentrations. *Environ. Int.* 29, 33–37.

