

# 1 **Iodine: An Emerging Biostimulant of Growth and Stress Responses** 2 **in Plants**

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28 **Keywords:** Iodine; ROS; Antioxidants; Hormones; Stress; Iodination

29

30 **Abstract**

31 *Background:* The growth and productivity of plants are largely dependent on the availability of  
32 various mineral nutrients, of which some are required at relatively higher concentrations and  
33 are termed as macronutrients, while others are required in low amounts and are termed as  
34 micronutrients. Both macro- and micro-nutrients are considered as essential elements as their  
35 deficiency can result in severe growth defects in plants. Moreover, some of the recent studies  
36 have highlighted the role of even non-essential elements in plants. Iodine is one such non-  
37 essential element that, at low concentrations, exhibits positive effects on plant growth.

38 *Scope:* In this review, we discuss the effects of iodine on plants including its uptake and  
39 transportation, and the current understanding of the pathways responsible for its functioning in  
40 plants as a biostimulant. Moreover, we provide evidence that supports the role of iodine as a  
41 biostimulant of growth and stress responses in plants.

42 *Conclusions:* Iodine, in the range of 0.20 to 10  $\mu\text{M}$ , has been documented to regulate the (1)  
43 expression of various genes, and (2) activities and structure of various proteins by protein  
44 iodination to improve biomass production and defense responses in plants. Further, a growing  
45 body of evidence also suggests the role of iodine in the maintenance of ROS homeostasis in  
46 plants under normal as well as challenging environmental conditions.

## 47 **Introduction**

48 Iodine as an element was isolated and recognized in the early 19<sup>th</sup> century, however, reports on  
49 its use in traditional medicines date long back around 3000 BC (Küpper et al. 2011). In humans,  
50 iodine regulates the biosynthesis of thyroid hormones, triiodothyronine, and thyroxine, and thus  
51 plays a vital role in maintaining normal metabolism and growth in humans (Charlton and Skeaff  
52 2011). Moreover, iodine also exhibits antioxidant properties and protective effects against  
53 cancer and inflammatory diseases in humans (Aceves et al. 2013). Therefore, iodine is  
54 considered as an essential element in humans, and its role in regulating normal metabolism and  
55 growth is well established. In contrast, the role of iodine in plants is currently poorly understood  
56 and the reports on its role in plant metabolism have been scarcely reported thus far (Nascimento  
57 et al. 2022). Nevertheless, some of the recent studies have shown the existence of iodine-  
58 containing plant-derived thyroid hormone analogs (PDTHA) in plants that are homologous to  
59 human transthyretin protein, which acts as T3 or T4 transporters. However, additional research  
60 is required to thoroughly understand the physiological mechanism of PDTHA in plants (Smolen  
61 et al 2021).

62 To be able to optimize the soil iodine content and harness its benefits while avoiding its  
63 deleterious effects, extensive and detailed studies are required to better understand iodine-  
64 mediated plant growth regulation. In this review, we discuss the role of iodine as a micro-  
65 nutrient and its interaction with phytohormones during the regulation of growth, development,  
66 and environmental stress tolerance in plants.

67

## 68 **Uptake, transport, and metabolism of iodine in plants**

69 The oceans are the biggest reservoir of iodine from which it spreads into the atmosphere and  
70 lands. From oceans, iodine evaporates to the atmosphere in the form of volatile methyl iodide  
71 (CH<sub>3</sub>I) at the level of 5–20 ng.m<sup>-3</sup> and as particulate iodine carried by winds at 1–5 ng.m<sup>-3</sup>  
72 (Moyers and Duce 1972). Rains deliver iodine to the soil surface mainly as I<sup>-</sup> and IO<sub>3</sub><sup>-</sup> that are  
73 available for uptake by plants. As per a study, the concentration of iodine in the rainwater is  
74 estimated as 2 µg.L<sup>-1</sup> (Bowley 2013). In soil, a major part of iodine is associated with the solid  
75 phase *i.e.*, organic matter, clay minerals, and Fe- and Al-oxides while a small portion is  
76 available in free form in the soil solution. The amount of iodine in soils depends on the  
77 geographical location, for example, the amount of iodine near the coastal areas was reported as

78 150 mg.kg<sup>-1</sup> while in the more continental plane areas soil contains only 3 mg.kg<sup>-1</sup> of total  
79 iodine (Johnson 2003; Mohiuddin et al. 2019).

80 Plants absorb iodine both from soil and the atmosphere through their roots and leaves,  
81 respectively. Iodine species available for absorption by plants from the soil include organic-  
82 iodine, IO<sub>3</sub><sup>-</sup>, and I<sup>-</sup> ions while gaseous iodine molecules, available as molecular iodine (I<sub>2</sub>) and  
83 methyl iodide (CH<sub>3</sub>I), are absorbed from the atmosphere. The mobility of iodine in soil depends  
84 upon several factors including soil composition, pH, texture, and redox conditions. Specific  
85 reductases such as nitrate reductases in plant roots can convert iodate to iodide by using it as an  
86 alternative substrate (Smolen et al. 2011; Medrano-Macías et al. 2016a). Once absorbed via  
87 roots, iodine is generally transported through xylem vessels, however, phloem-mediated  
88 transport of iodine has also been observed in some plants including tomato and lettuce (Landini  
89 et al. 2011; Caffagni et al. 2012; Smoleń et al. 2014). The mobility of iodine inside the plants  
90 is low and therefore, its levels decrease from roots to leaves followed by stem and fruits  
91 (Gonzali et al. 2017). On foliar application of iodine, leaves absorb and retain the majority of  
92 iodine by fixing it in the cuticular wax as reported in spinach (Zhu et al. 2003). In addition,  
93 some plants such as *Arabidopsis thaliana*, rice, wheat, and daikon radish are also capable to  
94 release excess iodine from their aerial parts in the form of volatile methyl iodide which is  
95 produced by the activity of either S-adenosyl-L-methionine (SAM)-dependent halide  
96 methyltransferase (HMT) or by SAM-dependent halide/thiol methyltransferase (HTMT)  
97 enzymes utilizing iodide as substrate (Itoh et al. 2009; Lawson et al. 2015; Gonzali et al. 2017).  
98 This release of excess iodine in the form of methyl iodide is dependent on several factors  
99 including plant growth stage, soil organic content, and environmental conditions such as  
100 temperature fluctuations, soil salinity, and flooding stress (Redeker et al. 2000, 2004).  
101 Therefore, the *in planta* levels and the consequent physiological influences of iodine are largely  
102 dependent on its intake and release mechanisms (Humphrey et al. 2019).

103 Phytohormone salicylic acid (SA) seems to control the absorption of iodine by plants (Smoleń  
104 et al. 2015a). For instance, co-treatment of KIO<sub>3</sub> and SA enhanced iodine uptake into the tomato  
105 fruits by 157% as compared to KIO<sub>3</sub> treatment only. Likewise, when KI was the source of  
106 iodine, its accumulation was increased by 37% in the presence of SA, supporting the role of SA  
107 in iodine absorption by tomato independently of the type of iodine salt applied. In addition to  
108 SA, selenium (Se) and vanadium have also been shown to promote iodine uptake by plants  
109 (Smoleń et al. 2021). Application of SA together with Se led to enhanced accumulation of  
110 iodine in peels of tubers, petioles, and leaves in potatoes (Smoleń et al. 2018). Moreover, it's

111 worth noting that absorption of iodine in the presence of Se was affected by the SA dose applied.  
112 The highest iodine accumulation was noted in potato tubers at the dose of 1.0 mg SA.dm<sup>-3</sup> out  
113 of the three doses of 0.1, 1.0, and 10.0 mg SA.dm<sup>-3</sup> in nutrient solution (Smoleń et al. 2018).  
114 Similar results of SA concentration-dependent iodine uptake in the presence of Se were also  
115 reported in the case of lettuce cultivar ‘Zimująca’ (Smoleń et al. 2016). In the leaves, the highest  
116 iodine accumulation was reported at 30 µg.dm<sup>-3</sup> iodine+8.5 µg.dm<sup>-3</sup>+0.1 mg.dm<sup>-3</sup> SA while  
117 increasing the SA concentration to 1.0 mg.dm<sup>-3</sup> led to a significant decrease in iodine uptake  
118 by the plants. A similar increase in the iodine concentration was also observed in the roots at  
119 30 µg.dm<sup>-3</sup> iodine+8.5 µg.dm<sup>-3</sup>+0.1 mg.dm<sup>-3</sup> SA, however, increasing SA concentration to 1.0  
120 mg.dm<sup>-3</sup> did not result in any significant difference in iodine uptake (Smoleń et al. 2016). A  
121 recent study investigated the differences in iodine uptake on six lettuce varieties (Cud  
122 Voorburgu, Zimuja,ca, Maugli, Królowa lata, Lollo rossa, and Redin) at different SA  
123 concentrations (Smoleń et al. 2019). The effective SA dose elevating iodine uptake ranged  
124 between 0.1-10 mg.dm<sup>-3</sup> SA depending on the variety, however, three varieties, Cud  
125 Voorburgu, Maugli, and Redin, showed a significant decrease in iodine concentration in leaves  
126 upon SA application even at the lowest SA concentration of 0.1 mg.dm<sup>-3</sup>. These results suggest  
127 a dose-dependent effect of SA on iodine accumulation in plants with great differences among  
128 not only various species but different varieties.

129

### 130 **The effect of iodine on plant growth**

131 In the early 19<sup>th</sup> century, several studies highlighted the potential role of iodine in plant growth  
132 regulation and those studies laid a foundation stone for subsequent iodine research in plants. At  
133 first, Lehr and co-workers reported that treatment of iodine induce early flowering, higher fruit  
134 yields, and improved growth in tomato (Lehr et al. 1958). Similar observations were also  
135 reported in the case of other plants such as spinach, white clover, fodder beet, perennial  
136 ryegrass, turnips, barley, flax, wheat, and mustard, among others, where exogenous iodine  
137 treatment in the form of either potassium iodide (KI) or potassium iodate (KIO<sub>3</sub>) improved the  
138 plant growth (Pauwels 1961). However, subsequent studies showed that these beneficial effects  
139 of iodine on plant growth and productivity could only be observed at low concentrations ranging  
140 from 10<sup>2</sup>–10<sup>4</sup> nM while its higher concentrations evoked phytotoxic effects (Voogt et al. 2010;  
141 Medrano-Macías et al. 2016a; Gonzali et al. 2017; Incrocci et al. 2019; Kiferle et al. 2021). For  
142 instance, Landini et al. (2012) reported that treatment of 900 µM sodium iodide (NaI) resulted  
143 in the reduction of rosette diameter and plant growth in Arabidopsis. Likewise, a higher

144 concentration of iodine KI (>50  $\mu\text{M}$ ) and  $\text{KIO}_3$  (>400  $\mu\text{M}$ ) proved to be toxic in two cultivars  
145 of *Ocimum basilicum* i.e Tigullio and Red Rubin, resulting in reduced leaf area, total plant dry  
146 matter, and plant height (Incrocci et al. 2019). However, these possible phytotoxic effects of  
147 iodine salts (NaI, KI, and  $\text{KIO}_3$ ) could be because of the counter ions like  $\text{K}^+$  and  $\text{Na}^+$  that might  
148 mimic salinity stress in plants. Similarly,  $\geq 10$   $\mu\text{M}$  concentration of both iodate ( $\text{IO}_3^-$ ) and iodide  
149 ( $\text{I}^-$ ) were reported to exhibit deleterious effects on growth and biomass in hydroponically grown  
150 spinach, however, iodate had not as serious effects as iodide as it has to be first reduced to  
151 iodide before its uptake which limits and possibly delays its absorption by plants (Zhu et al.  
152 2003). Furthermore, 10 and 100  $\mu\text{M}$  concentrations of  $\text{IO}_3^-$  and  $\text{I}^-$  both showed a negative  
153 impact on yield and reduced the overall plant growth in hydroponically grown rice (Mackowiak  
154 and Grossl 1999). In the case of radish, pakchoi, celery, and pepper, chlorosis in young leaves,  
155 brown and stunted roots as well as growth inhibition were observed at doses of iodine greater  
156 than 50  $\text{mg}\cdot\text{kg}^{-1}$  (Hong et al. 2009). Similar phytotoxicity symptoms such as chlorosis of older  
157 leaves and necrosis of leaf tips were also reported in other crops such as *Triticum aestivum*, *Zea*  
158 *mays*, *Hordeum vulgare*, *Solanum tuberosum*, and *Solanum lycopersicum* at either 2.34 mM  
159  $\text{KIO}_3$  or 3.01 mM KI concentrations (Caffagni et al. 2011). The phytotoxic effects of iodine at  
160 high concentrations seem to be species-specific and dependent on the type of iodine salt applied.  
161 For instance, 80  $\mu\text{M}$   $\text{IO}_3^-$  treatment improved biomass and N uptake in lettuce while 80  $\mu\text{M}$   $\text{I}^-$   
162 reduced N uptake, decreased nitrate reductase (NR) and glutamate dehydrogenase activities,  
163 and biomass production (Blasco et al. 2010). In contrast, lower concentrations of  $\text{IO}_3^-$  (20 or  
164 40  $\mu\text{M}$ ) positively regulated the activity of NR, and glutamine synthetase/glutamate synthase  
165 and optimized the process of photorespiration while  $\text{I}^-$ , at the same concentrations, evoked  
166 opposite effects (Blasco et al., 2010). These results altogether suggest that the effect of iodine  
167 on plants is determined by multiple factors including the applied concentration, the type of  
168 iodine salt applied, and the plant species.

169

## 170 **The effect of iodine on photosynthesis**

171 The nutritional role of iodine in promoting plant growth is a topic of research interest for many  
172 scientists around the globe, however, iodine research in plants is still in its infancy. The reports  
173 published so far indicate a beneficial effect of iodine in plants depending on its concentration,  
174 exposure duration, plant species, and type of iodine salt used for the treatment as discussed in  
175 the previous section. Determining its concrete functions in plants needs further extensive  
176 investigation. Iodine, at present, is categorized as a non-essential but beneficial element for

177 plants (Şahin 2020; Medrano Macías et al. 2021; Nascimento et al. 2022). Concurrent evidence  
178 hints that iodine can be used as a biostimulant similar to silicon, iron, magnesium, selenium,  
179 and sodium, among others (Nascimento et al. 2022).

180 Iodine, besides being a micro-nutrient, affects plant growth and development depending on the  
181 concentration applied. For instance, the application of iodine at the 1000 mg.L<sup>-1</sup> enhanced  
182 chlorophyll-a concentration along with moderate changes in the photochemical efficiency of  
183 photosystem II (*F<sub>v</sub>/F<sub>m</sub>* ratio) in the leaves of buckwheat microgreens (Germ et al. 2019).  
184 Similarly, hydroponically grown lettuce showed a higher leaf chlorophyll-a content under  
185 iodate treatments while iodide treatment had no significant effect (Blasco et al. 2011). Iodine  
186 can affect the activities of various proteins by protein iodination and recently, the first detailed  
187 report on protein iodination was reported in *A. thaliana* (Kiferle et al. 2021). In this study, 31  
188 iodinated proteins were identified that were related to the photosynthetic apparatus including  
189 Psb(A, B, C, D), Psa(B, E, F, H), Psb(O, P, Q, R), CAB3, LHCB2.1, LHCB1B1, LHCB3,  
190 LHCB5, and Pet(A, C), are components of PSII, PSI, OEC, LHCII, and Cyt b6/f complexes.  
191 Several other identified iodinated proteins are associated with the degradation of the  
192 photodamaged D1 reaction center or the maintenance or protection of both PSI and PSII (Psb27,  
193 Psb29, Psb31, Psb33, MPH1) (Kiferle et al. 2021). Iodine can also be attached to the  
194 plastocyanin electron carrier (PETE2), the ferredoxin–NADP(+)-oxidoreductase (FNR1)  
195 enzyme, and proteins involved in the Calvin cycle (RBCL, ORF110A, RBCS1A) (Kiferle et al.  
196 2021). These results suggest that iodine contributes to the formation and maintenance of  
197 functional photosynthetic machinery in plants by improving the chlorophyll-a concentrations  
198 and by directly regulating the activities of photosynthetic enzymes by protein iodination.

199

## 200 **Iodine as a modulator of antioxidants**

201 It is a fact that the coordinated action of environmental conditions and genetic regulation  
202 controls the growth and development of plants. Reactive oxygen species (ROS), such as  
203 hydrogen peroxide (H<sub>2</sub>O<sub>2</sub>), superoxide (O<sub>2</sub><sup>-</sup>), and hydroxyl radicals (·OH), are produced as by-  
204 products in various plant metabolic processes in different cellular organelles such as  
205 chloroplasts, peroxisomes, and mitochondria (Sandalio and Romero-Puertas 2015; Dietz et al.  
206 2016; Huang et al. 2016). A transient increase in ROS concentration exhibits a signaling role  
207 and is required for the modulation of normal growth, development, and defense responses of a  
208 plant (Gupta et al. 2018; Meng et al. 2019). However, ROS accumulation for a prolonged period

209 can damage the cell membrane, proteins, lipids, and DNA ultimately leading to plant cell death  
210 (Miller et al. 2009; Riyazuddin et al. 2021). Therefore, plants are equipped with different  
211 enzymatic and non-enzymatic antioxidants that participate in ROS detoxification and the  
212 maintenance of ROS homeostasis. Enzymatic antioxidants include superoxide dismutase  
213 (SOD), peroxidase (POD), catalase (CAT), ascorbate peroxidase (APX), glutathione peroxidase  
214 (GPX), dehydroascorbate reductase (DHAR), and monodehydroascorbate reductase  
215 (MDHAR), while non-enzymatic antioxidants include glutathione (GSH), ascorbic acid (AsA),  
216 phenols, flavonoids, and anthocyanin that play a fundamental role in scavenging these harmful  
217 and toxic ROS to reduce the negative effects and damages of environmental stress conditions  
218 (Apel and Hirt 2004; Mittler 2017; Riyazuddin et al. 2020; Riyazuddin and Gupta 2021).

219 Recent studies have shown that iodine application activates enzymatic and non-enzymatic  
220 antioxidants to facilitate the detoxification of stress-induced ROS (Consentino et al. 2022;  
221 Fuentes et al. 2022). For instance, foliar application of 100  $\mu\text{M}$   $\text{KIO}_3$  significantly increased the  
222 antioxidant capacity and the level of AsA in tomato under salt stress conditions (Fuentes et al.  
223 2022). In lettuce, the enzymatic activities of APX, DHAR, SOD, GR, and the levels of GSH  
224 and AsA were augmented in 20-80  $\mu\text{M}$  iodate-treated plants growing in the presence of 100  
225 mM NaCl (Leyva et al. 2011). In another study, biweekly foliar application of 100  $\mu\text{M}$   
226 potassium iodate enhanced GSH content while daily iodine treatment (1  $\mu\text{M}$ ) increased GSH  
227 and AsA in tomato seedlings (Medrano-Macías et al. 2016b). Halka and co-workers used  
228 iodosalicylic acids (5-iodosalicylic & 3,5-diiodosalicylic acids) and iodobenzoates (2-  
229 iodobenzoic acid, 2,3,5-triiodobenzoic acid, and 4-iodobenzoic acid) for treatment of tomato  
230 seedlings and compared their efficacies with that of KI (Halka et al. 2020; Halka. et al. 2020).  
231 All iodine compounds affected AsA and dehydroascorbic acids (DHA) levels in a  
232 concentration-dependent manner, however, the effects were different. High KI concentration  
233 (25 or 50  $\mu\text{M}$ ) increased APX and DHAR activities due to the strong effect of free I while the  
234 organic compounds either slightly increased or slightly or strongly decreased their activities  
235 probably because of the different number and location of iodine atoms in the aromatic ring of  
236 the organic compounds (Halka et al. 2020b). The uptake of KI by roots was higher as compared  
237 to the organic iodine compounds which also exhibited reduced mobility in the plant and  
238 accumulated in the root (Halka. et al. 2020b). The CAT and POD activities were unaffected or  
239 decreased by KI in a concentration-dependent manner but were decreased by most of the tested  
240 organic iodine-containing compounds at all used concentrations (Halka. et al. 2020a, b).



241 In the case of radish, the KI treatment of 0.15-1.5 mg.g<sup>-1</sup> of seeds elevated the levels of iodine,  
242 total phenols, AsA, and the total antioxidant capacity in two cultivars in a concentration-  
243 dependent manner (Krzepiłko et al. 2021). Likewise, iodine at 300 or 600 mg.L<sup>-1</sup> concentration  
244 enhanced the growth, yield, and functional quality traits of eggplants in parallel with improving  
245 the production of AsA, anthocyanins, and chlorogenic acid (Consentino et al. 2022). Exogenous  
246 treatment of potassium iodate (20-80 μM) enhanced the enzymatic activities of SOD and APX  
247 in soybean (Gupta et al. 2015) while IO<sub>3</sub><sup>-</sup> treatment (7.88 μM) enhanced the contents of non-  
248 enzymatic antioxidants such as AsA and phenolic compounds in tomato (Smoleń et al. 2015).  
249 A similar increase in the AsA content was also reported in *Opuntia ficus-indica* following  
250 treatment of 100 μM potassium iodate (Osuna et al. 2014). Further, I<sup>-</sup> application was shown  
251 to stimulate higher production of AsA while IO<sub>3</sub><sup>-</sup> treatment in the form of iodoacetic acid  
252 reduced the AsA level in *Ipomoea aquatica* (Weng et al. 2008). In lettuce, the application of  
253 iodine (20, 40, and 80 μM) increased the activities of antioxidant enzymes such as CAT, SOD,  
254 and L-galactono dehydrogenase and induced the accumulation of non-enzymatic antioxidants  
255 such as AsA, GSH, flavonoids, anthocyanins, and phenol in a concentration dependant manner  
256 (Blasco et al. 2008, 2010). Both KI and KIO<sub>3</sub> applications resulted in higher contents of AsA  
257 and other activities of enzymatic antioxidants such as CAT. However, SOD and GSH levels  
258 were reduced significantly in the lettuce plants after the application of 80 μM I<sup>-</sup> and all the  
259 tested concentrations of IO<sub>3</sub><sup>-</sup> (20, 40 80 μM). Further, KIO<sub>3</sub> induced a higher APX level than  
260 KI, indicating that iodate exhibit a higher potential in terms of increasing the antioxidants as  
261 compared to iodide (Blasco et al. 2011). Similar findings were also reported for *Ocimum*  
262 *basilicum* where a higher amount of total phenols and increased antioxidant capacity (DPPH  
263 assay) were reported in the mature leaves following KI and KIO<sub>3</sub> treatments (Incrocchi et al.  
264 2019). However, iodine, IO<sub>3</sub><sup>-</sup>, and Se treatments did not alter GSH levels in the leaves of *Pisum*  
265 *sativum*, but the combination of I<sup>-</sup> with SeO<sub>4</sub><sup>-2</sup> reduced the anthocyanin content in leaves in  
266 contrast to that of the seeds (Jerše et al. 2018). KIO<sub>3</sub> treatment increased the activity of APX  
267 and GSH content along with higher concentrations of AsA and phenolic compounds (Macías et  
268 al., 2021).

269 KI (100 mg.L<sup>-1</sup>) and sodium selenate (50 mg.L<sup>-1</sup>) were applied separately and together to check  
270 their interactions in *Brassica juncea*, a selenium (Se) hyperaccumulator plant. KI treatment  
271 increased Se concentrations in plants while sodium selenate treatment increased that of iodine.  
272 In contrast to their separate biostimulating effects, their co-application did not promote plant  
273 growth. In addition, while the separate application of Se and iodine improved the AsA levels in

274 leaves, their co-application did not show any such impact. However, both the separate and  
275 combined application of Se and iodine inhibited nitrate deposition, activated flavonoids  
276 synthesis, promoted the accumulation of aluminum and boron, and the reduction of strontium  
277 (Sr) and cadmium (Cd) concentrations, indicating the potential of iodine in reducing heavy  
278 metal uptake by plants (Golubkina et al. 2018, 2021). These results, taken together, clearly  
279 suggest that iodine treatments interfere with the antioxidant defense response under normal as  
280 well as challenging environmental conditions.

281

### 282 **Iodine in the alleviation of stress conditions**

283 Abiotic stressors significantly affect crop productivity and thus research on biostimulants  
284 improving abiotic stress tolerance has gained momentum in the last few decades (Dey(née  
285 Pathak) and Mukherjee 1984; Medrano-Macías et al. 2016a). A growing body of evidence  
286 suggests that iodine treatment can promote abiotic stress tolerance in plants majorly by inducing  
287 ROS-detoxification via activating the antioxidant defense (Kiferle et al. 2022). For instance,  
288 exogenous application of 20-80  $\mu\text{M IO}_3^-$  mitigated the negative effects of salt stress (100 mM  
289 NaCl) on biomass production in lettuce plants. The iodate treatment reduced the concentrations  
290 of both  $\text{Na}^+$  and  $\text{Cl}^-$  ions but increased that of the osmoprotectant soluble sugars as well as the  
291 level and activity of various ROS scavengers (Leyva et al. 2011). Iodine was found to be active  
292 in boosting the antioxidant response in plants exposed not only to salinity but heavy metal stress  
293 (Leyva et al. 2011; Gupta et al. 2015). A subsequent study revealed that iodine treatment  
294 improved salt stress tolerance in lettuce by inducing the accumulation of hydroxycinnamic acids  
295 and derivatives along with total phenols that play a protective role against salt stress (Blasco et  
296 al. 2013). It has been shown that the application of  $\text{KIO}_3$  or an iodine-based biostimulant  
297 product improved the yield and quality (high K and P content) of strawberry fruits under salt  
298 stress (Medrano Macías et al. 2021). Similarly, foliar application of 100  $\mu\text{M KIO}_3$  increased the  
299 fruit yield, nitrogen level in leaves, and level of AsA in tomato (Fuentes et al. 2022). However,  
300 a decrease in the biomass was reported in these 100  $\mu\text{M KIO}_3$ -treated tomato plants probably  
301 due to the pro-oxidant activity of iodine enhancing antioxidant capacity at the expense of  
302 biomass production (Fuentes et al. 2022).

303 Intriguingly, the application of dry iodine with a calcium carbonate carrier alleviated the  
304 negative effects of humidity and heat stress on soybean and sunflower seeds during postharvest  
305 storage (Dey(née Pathak) and Mukherjee 1984). It has been suggested that iodine can act as a

306 free radical scavenger preventing membrane damage and can interact with carbon-carbon  
307 double bonds of unsaturated lipids stabilizing the membranes (Dey(née Pathak) and Mukherjee  
308 1984). Rapeseed seeds pre-treated with iodine for short period exhibited increased survival  
309 under oxidative stress conditions (Powell et al. 2005). These results, although preliminary,  
310 suggest that iodine can be promoted to the commercial agriculture sector as a biostimulant to  
311 reduce the impact of abiotic stress conditions (Medrano-Macías et al. 2016a).

312 The role of iodine in biotic stress tolerance has not been investigated so far, however, it has  
313 been used in water purification as an agent with antifungal activity. The role of iodine as a  
314 fungicide can be exemplified by its use in the recirculated water of soil-less tomato cultures  
315 where iodine at 0.7 mg.L<sup>-1</sup> or higher concentrations completely kills the conidia of *Fusarium*  
316 *oxysporum* f. *Lycopersici* (Runia 1993). However, high concentrations of iodine can be toxic  
317 even to plants, and thus to minimize its toxicity at a concentration that still exhibits microbicidal  
318 properties, co-treatment with humic acid was suggested (Mackowiak et al. 2005). It was shown  
319 that the application of 0.5 mM humic acid facilitated the conversion of I<sub>2</sub> to I<sup>-</sup> which minimized  
320 the iodine uptake and thus the iodine toxicity response in rice (Mackowiak et al. 2005;  
321 Yamagami and Yanai 2022).

322 Although there is no direct evidence of iodine involvement in the alleviation of biotic stress in  
323 plants, a recent study showed iodine-induced expression of pathogenesis-related genes such as  
324 *pathogenesis-related 1*, *PR3*, *PR5*, Class III peroxidase *Perx33*, *lectin receptor kinase a4.1*,  
325 *DMR6-LIKE OXYGENASE 1*, *Glucan endo-1,3-beta-D-glucosidase*, *BASIC CHITINASE*, and  
326 *cytochrome P450 family 71 polypeptide* in *Arabidopsis* (Kiferle et al. 2021). These preliminary  
327 data suggest the potential use of iodine in the activation of plant defense response against biotic  
328 stress agents via upregulation of defense-related genes.

329

### 330 **Iodine-induced molecular changes in plants**

331 A substantial number of investigations now confirm that the application of iodine alters the  
332 growth and stress tolerance in plants and thus iodine-induced changes in gene expression and  
333 activity of various proteins can be expected. However, the molecular mechanism of iodine-  
334 mediated growth alteration has been poorly investigated so far. *In vitro* experiments have shown  
335 that iodine can react with the tyrosine and histidine residues of the proteins under alkaline  
336 conditions, a process which is known as protein iodination. In order to better understand the  
337 iodine-induced changes in plants, an integrated transcriptomic and proteomic analysis was

338 performed in Arabidopsis under the treatment of 10  $\mu$ M KI, NaI, or potassium bromide (KBr)  
339 for 2 days (Kiferle et al. 2021). Transcriptomic data showed that many iodine-regulated genes  
340 were associated with stress and defense responses including the activation of genes coding for  
341 proteins with antioxidant or oxidoreductase activities especially in the root but to a lesser extent  
342 in the shoot as well. Besides, iodine also regulated the expression of genes related to cellular  
343 signaling (e.g. calcium signaling, receptor kinases, protein modification/degradation,  
344 transcription factors, and redox components) in the Arabidopsis roots. In addition, iodine also  
345 regulated various genes related to plant development including some that might cause early  
346 blooming of the iodine-treated Arabidopsis plants (Kiferle et al. 2021). Interestingly, the iodine-  
347 treated changes in gene expression were found to be similar to the changes observed under  
348 biotic stress, SA, or SA analogs treatments, highlighting a relationship between SA and iodine  
349 (Kouzai et al. 2018). It is also supported by the observation that the exogenous application of  
350 iodine regulated the expression of several genes associated with the SA pathway such as *halide*  
351 *ion methyltransferase (HMT)*, *SA methylation (SAMT) responsible gene*, and *salicylic acid 3-*  
352 *hydroxylase (S3H)* in tomato (Halka et al. 2018, 2019). Another similar transcriptomics study  
353 showed genes responsible for the synthesis of enzymes having HMT- or HTMT-like function,  
354 accountable for iodine methylation such as S-adenosylmethionine synthase, lysine-specific  
355 demethylase REF6 methyltransferase, probable methyltransferase, and histone-lysine N-  
356 methyltransferase, were altered in lettuce plants following iodine treatment (Smoleń et al.  
357 2021). The combined application of 10  $\mu$ M iodine and 10  $\mu$ M SA efficiently enhanced the  
358 expression of the *peroxidase 12-like, S-adenosyl-L-methionine-dependent methyltransferase*  
359 *(samdmt)*, *CBL-interacting serine/threonine-protein kinase 6*, and *S-adenosylmethionine*  
360 *synthase 5 (msams5)* genes in the roots of lettuce plants (Smoleń et al. 2021). An 8.5-fold  
361 higher expression of *msams5* was observed in roots, suggesting that the *msams5*-encoded  
362 enzyme, which is likely involved in iodine methylation, has its main role in the roots of lettuce  
363 plants. Besides, a higher expression of *samdmt* gene, which is involved in SA esterification and  
364 volatilization during stress responses, was observed in the leaves (Smoleń et al. 2021). In  
365 addition, treatment of 5-ISA induced the PDTHA and augmented the protein level of the *CBL-*  
366 *interacting protein kinases 6 (cipk6)* gene that likely acts as triiodothyronine (T3) and/or  
367 thyroxine (T4) receptor in lettuce roots (Smoleń et al. 2021).

368 Kiferle et al. (2021) analyzed the *in vivo* iodination of proteins in the shoots and roots of  
369 hydroponically grown Arabidopsis plants by using radio-labeled <sup>125</sup>Iodine. Similar iodinated  
370 proteins were also reported in both shoots and roots of the maize, tomato, and wheat plants

371 (Kiferle et al. 2021). The analysis showed that tyrosine exhibits a higher affinity for iodination  
372 as compared to histidine, tryptophan, or cysteine, and iodinated proteins showed altered activity  
373 as compared to non-iodinated proteins. The iodinated proteins of shoots were mainly associated  
374 with the photosynthesis machinery and were related to chlorophyll-binding (GO:0016168),  
375 protein domain-specific binding (GO:0019904), tetrapyrrole binding (GO:0046906), and  
376 electron transfer activity (GO:0009055). In roots, the iodinated proteins included class III  
377 peroxidases, copper amine oxidase, beta-galactosidase 5, glycosyl hydrolases family 32 protein  
378 (ATBFRUCT1), Pole Ole1 allergen/extension domain (IPR006041)-containing proline-rich  
379 protein-like 1 (PRPL1-MOP10), root hair specific 13 protein (RHS13), D-mannose binding  
380 lectin protein (MBL1), and glyceraldehyde-3-phosphate dehydrogenase C sub 1 (GAPC1).  
381 These enzymes have various activities/functions such as primary amine oxidase activity,  
382 modification of cell wall polysaccharides, acting as cell wall invertase, cell-wall components,  
383 or key enzyme components of glycolysis. Of these iodinated proteins identified in roots,  
384 peroxidases were of key importance as these regulate the redox status, plant growth and  
385 development, cell differentiation as well as tolerance against biotic/abiotic stresses (Hiraga et  
386 al. 2001). However, further experiments are required to uncover the effect of iodine on the  
387 catalytic and/or regulatory function of the plant proteins at the biochemical level. It can be  
388 nevertheless concluded that iodination is a tissue-dependent process that regulates the function  
389 of specific proteins associated with biological processes in the shoots and roots differently.

390 In summary, iodine regulates several physiological and biochemical processes in a specific way  
391 at both transcriptional and post-translational levels via the regulation of the expression of genes  
392 and the activity of proteins associated with stress tolerance, redox regulation, photosynthesis  
393 machinery, and plant development. Thus, iodine not only plays an important role in terms of  
394 nutrition but it is also involved in plant adaptation to unfavorable conditions by regulating  
395 various genes/enzymes mainly related to oxidative stress tolerance and defense.

396

## 397 **Conclusions and future perspectives**

398 A substantial number of investigations have shown that a low concentration of iodine is  
399 involved in the regulation of plant growth and productivity during normal as well as challenging  
400 environmental conditions possibly by two mechanisms (1) through maintenance of  
401 photosynthesis, and (2) by maintaining ROS homeostasis (Table 1). Exogenous application of  
402 iodine in the form of iodide, iodate, or organic conjugated compounds has been shown to induce

403 the activities of enzymatic antioxidants and biosynthesis of non-enzymatic ones. Additionally,  
404 there seems to be an intricate relationship between iodine and SA. The application of SA is  
405 known to elevate the uptake of iodine by plants while the effects of iodine at molecular levels  
406 are like those induced by SA, for example, the expression of defense proteins (Fig. 2). The fact  
407 that iodine treatment induces SA-like responses and early flowering indicates that iodine may  
408 possibly be perceived as a stressor by the plants. However, if this could be the case, a rise in  
409 other stress-related parameters such as the decline in photosynthesis, reduced growth, and  
410 accumulation of ROS, among others, should be observed following iodine treatment, however,  
411 no such deleterious effects of the iodine treatment were reported at a concentration (0.2 – 12  
412  $\mu\text{M}$ ) that induced early flowering. These results indicate that this flowering-promoting role of  
413 iodine is a beneficial effect and is not associated with the activation of any stress response in  
414 plants.

415 Future efforts should be focused on the identification of direct molecular targets of iodine in  
416 plants and the functional role of protein iodination to understand the mechanisms of iodine-  
417 mediated growth regulation in plants. Besides, an in-depth understanding of iodine functions  
418 inside the plants and its interaction with different proteins and metabolites is also required on a  
419 global scale with the help of high-throughput proteomics and metabolomics approaches. As  
420 emerging evidence suggests that iodine responses vary drastically with the iodine  
421 concentration, type of salt used, plant species, and plant growth stage, it is crucial to have a  
422 more precise understanding of iodine uptake, translocation, partitioning, and accumulation  
423 mechanisms in different tissues and growth stages of plants. Moreover, the present knowledge  
424 on iodine is confined to a limited number of plants and thus, additional studies are required on  
425 other crop and non-crop plants in order to obtain more robust results on the biostimulator  
426 activity of iodine. The threshold limit of iodine for different cash crops should also be  
427 investigated to avoid any potential deleterious effects of high iodine concentrations on yield  
428 and periodic monitoring of the areas following iodine application is required to investigate the  
429 amount of residual iodine left in the soil after every growing period. This periodic monitoring  
430 will help us to optimize the iodine application rate and to prevent environmental degradation  
431 due to high levels of iodine that could exhibit deleterious effects. In addition, the accumulation  
432 of iodine should also be studied in the grains, fruits, and other edible parts of the crops to enable  
433 the biofortification of these crops with iodine together with avoiding any potential toxicity to  
434 humans. Furthermore, the effects of iodine in the mitigation of stress conditions should also be  
435 investigated in a more systematic way. At present, the role of iodine has mainly been studied

436 under salt stress. Therefore, the potential of iodine in the mitigation of other abiotic stresses and  
437 biotic stresses should also be investigated to establish its role as a stress mitigator.

438

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656 **Statements & Declarations**

657 **Funding**

658 The authors declare that no funds, grants, or other support were received during the preparation  
659 of this manuscript.

660 **Competing Interests**

661 The authors have no relevant financial or non-financial interests to disclose.

662 **Author Contributions**

663 Conceptualization, R.R and R.G.; writing—original draft preparation, R.R., K.S., N.I., N.K.,  
664 and N.N.; writing—review and editing, R.R., A.R., M. K., M.H.S., S.T.K., A.F., and R.G.;  
665 supervision, R.G. All authors read and approved the final manuscript.

666 **Figure legends**

667 **Figure 1:** An overview of the impact of iodine on plants' performance under favorable and  
668 unfavorable environmental conditions. Plant roots absorb iodine in the form of organic iodine,  
669 iodide, and iodate which then follows a symplastic or apoplastic pathway. Moreover, exogenous  
670 application of iodine salts solely or along with in combination with Salicylic acid, selenium,  
671 and Vanadium leads to the absorption and accumulation of iodine in various plant parts, in turn,  
672 positively influencing biochemical and physiological activities such as photosynthesis,  
673 reductase activity, antioxidant level, early flowering, fruit ripening and uptake of nitrogen.  
674 Further, iodine also triggers both enzymatic and non-enzymatic antioxidants that scavenge  
675 uncontrolled ROS production.

676

677 **Figure 2:** A graphical representation of the possible mechanism of iodine uptake and iodine-  
678 induced molecular responses in plants.  $KIO_3$  is converted into  $IO_3^-$  which is metabolized into  
679  $I^-$ , HIO, and  $I_2$  in the apoplast region and is transported into the cytoplasm via different channels  
680 and transporter proteins.  $I^-$  in the cell might directly iodinate proteins or induce gene expression  
681 indirectly. The way of its action on antioxidant enzyme activities and non-enzymatic  
682 antioxidant levels is unknown at present. Nevertheless, increased cellular iodine was shown to  
683 have a role in the detoxification of stress-induced ROS and in controlling the redox status of  
684 the cell. The iodination of several proteins involved in the maintenance and stability of  
685 photosynthetic protein complexes was reported as well as that of the key enzyme of glycolysis  
686 (GAPC1), several cell-wall-related proteins, and a number of class III peroxidases involved in  
687 redox regulation. Moreover, iodine species trigger the transcription of various photosynthesis-  
688 related genes, genes involved in salicylic acid (SA) metabolism, and several stress- (especially  
689 hypoxia-induced) and defense-related genes. Many of the iodine-regulated genes overlap with  
690 those controlled by SA/ROS and therefore iodine might control stress and defense-related gene  
691 expression by affecting ROS and/or SA metabolism. The arrows indicate only regulation, which  
692 can be activation or inhibition. For more details, see the text and Kiferle et al. 2021.  
693 Abbreviations: Iodate ( $IO_3^-$ ); iodide ( $I^-$ ); potassium iodate ( $KIO_3$ ); Hypoiodous acid (HIO);  
694 Salicylic acid (SA); glyceraldehyde-3-phosphate dehydrogenase C sub 1 (GAPC1); glutathione  
695 (GSH), ascorbic acid (AsA), dehydroascorbate (DHA); superoxide dismutase (SOD), ascorbate  
696 peroxidase (APX); glutathione reductase (GR); dehydroascorbate reductase (DHAR); halide  
697 ion methyltransferase (HMT); SA methylation (SAMT) responsible gene; and salicylic acid 3-  
698 hydroxylase (S3H); pathogenesis-related protein (PR); reactive oxygen species (ROS).