PHOTOSYNTHETICA
International Journal for Photosynthesis Research

DOI 10.32615/ps.2021.032 PHOTOSYNTHETICA 59 (2): 349-360, 2021

REVIEW

Role of beneficial elements in plants: implications for the photosynthetic process

E. LO PICCOLO[*], C. CECCANTI[*], L. GUIDI[*,**,+], and M. LANDI[*,**]

Department of Agriculture, Food and Environment, University of Pisa, Via del Borghetto 80, 56124 Pisa, Italy[*]
CIRSEC, Centre for Climate Change Impact, University of Pisa, Via del Borghetto 80, 56124 Pisa, Italy[**]

Abstract

Essential macro- and microelements availability strictly influences photosynthetic process as well as the overall plant status. Besides essential macro- and micronutrients, a group of other elements described as 'beneficial' has been proposed to ameliorate plant performances under optimal and/or stressful conditions. The first explanation of the term 'essential', as suggested by Arnon and Stout in 1939, defined beneficial elements as not essential since they are not necessary for plants to complete their life cycle. However, at low amounts, they can exert promoting effects on plant performances, including photosynthesis. In this review, we summarize the positive effect of seven beneficial elements (Se, Si, Na, I, Ti, Ce, and La) on plant photosynthetic processes to depict a clear picture of the influences of these beneficial elements on photosynthesis.

Keywords: ameliorative role; nonessential elements; nutrients; plant nutrition; stress condition.

Introduction

The term 'essential element' for plant nutrition was proposed by Arnon and Stout (1939), and successively modified by Epstein (1965), as an element necessary to complete the plant life cycle. However, to date, essential elements are still an open question remaining an intricate and dynamic research topic (Marschner 2012). If macroelements (Ca, K, Mg, N, S, and P) are well defined, being usually present in plant tissues at concentrations > 1,000 mg kg^{-1}(dry mass, DM), in contrast, micronutrients remain an open topic, due to their lower concentrations in tissues [usually ≤ 100 mg kg^{-1}(DM)]. There is a fine line between the microelements and 'beneficial' elements. The latter are not necessary to a plant life cycle but they can improve plant performances under optimal or stressful conditions (Vatansever *et al.* 2017). This has led several authors to consider some microelements as essential or beneficial (Broadley *et al.* 2012, Vatansever *et al.* 2017). So, no wonder that some controversial element will be included/excluded in the list of essential plant microelements in the future through further molecular and physiological studies.

Photosynthesis is the process that fuels our biosphere and some microelements, such as Cu, Fe, and Mn, are necessary for the correct functioning of photosynthetic process as they are constituents or cofactors of many

Highlights

- Beneficial elements (BE) have been proposed to ameliorate plant performances
- Se, Si, Na, I, Ti, Ce, and La were reported to improve photosynthetic traits
- Bases of photosynthesis improvement by BE are far from being fully elucidated

Received 21 April 2021
Accepted 16 June 2021

[+]Corresponding author
phone: +39 050 2216613
e-mail: lucia.guidi@unipi.it

Abbreviations: Car – carotenoids; Chl – chlorophylls; C_i – intercellular CO_2 concentration; Cyt b_6/f – cytochrome b_6f complex; E – transpiration rate; ETR – electron transport rate; F_m – maximum chlorophyll fluorescence yield; F_v/F_m – maximum photochemical efficiency of PSII; g_m – mesophyll conductance; g_s – stomatal conductance; J_{max} – maximum rate of electron transport; NP_S – nanoparticles; OEC – oxygen-evolving complex; P_N – net assimilation of photosynthesis; q_P – photochemical quenching coefficient; ROS – reactive oxygen species; V_{cmax} – maximum carboxylation rate; WUE – water-use efficiency; Φ_{PSII} – effective quantum yield of PSII.
Conflict of interest: The authors declare that they have no conflict of interest.

proteins and enzymes (Aggarwal *et al.* 2012). However, also elements called 'beneficial', administered at low doses in plants, can effectively stimulate the photosynthetic activity, probably due to nonspecific reactions in plants leading to the eustress phenomenon (Nyitrai *et al.* 2003). Moreover, beneficial elements, such as Se, Si, Na, I, Ti, Ce, and La, can additionally exert peculiar features, becoming constituents of cellular structures and proteins involved in photosynthesis or having photo-electromagnetic effects on photosynthesis (Brownell and Bielig 1996, Hong *et al.* 2002, Yamamoto *et al.* 2012, Andrade *et al.* 2018, Kiferle *et al.* 2021).

Previous literature surveys described the role of these beneficial elements *in planta* (Pilon-Smits *et al.* 2009, Broadley *et al.* 2012, Vatansever *et al.* 2017, Lyu *et al.* 2017, Gómez-Merino and Trejo-Téllez 2018) while this review aims to describe the specific effects of Se, Si, Na, I, Ti, Ce, and La on plant photosynthetic traits under both optimal and stressful conditions. However, we are aware that from the works presented in this review, the influence of a specific beneficial element on photosynthesis could both be ascribable to the ion form and also to the plant species. In addition, for certain particular plant taxa, some of these elements are essential (*e.g.*, sodium for halophytes), which, conversely, might become beneficial for plants belonging to most of the other taxa. This review attempts to provide a starting point to stimulate further molecular and physiological studies to clarify the promoting effects of these beneficial elements to the photosynthetic process.

Selenium

Selenium is one of the most studied beneficial elements in plants and often used in plant biofortification programs, due to its positive effects on the human health (Malagoli *et al.* 2015). Selenate and selenite are the two major chemical forms of Se bioavailable in the soil. Selenate is transported in plants through sulphate transporters since both ions showed molecular similarity, while selenite is taken up by phosphate transporters (White 2018, Trippe and Pilon-Smits 2021).

In plants, Se plays a positive role in photosynthesis, chloroplast and cell membrane development, and it is also involved in antioxidant and ROS regulation (Pilon-Smits 2015). Indeed, Se can improve the growth and plant performance at lower concentrations reducing the possible detrimental effects of abiotic stressors (Amirabad *et al.* 2020).

In plants subjected to drought stress, it was reported that Se, either added to the soil or sprayed on leaves, improved the photosynthetic rate (*e.g.*, Germ *et al.* 2007, Andrade *et al.* 2018); however, a positive effect on gas-exchange parameters was also observed during heat (Haghighi *et al.* 2019), salinity (Jiang *et al.* 2017), and Cd stresses (Filek *et al.* 2010, Amirabad *et al.* 2020). Under these stressful conditions, higher levels of g_s, E, P_N, WUE, and better maintenance of PSII performances (higher F_v/F_m and Φ_{PSII}) were observed with respect to control (*see* references in Table 1).

Similar effects of Se were observed in *Triticum aestivum* (Nawaz *et al.* 2015) and *Olea europaea* (Proietti *et al.* 2013) subjected to drought conditions. Under salinity, Habibi (2017a) found that higher F_v/F_m values in *Petroselinum crispum* plants treated with Se as compared to the controls were attributable to lower damage to PSII.

The positive impact of Se on g_s, E, P_N, and WUE could be very useful for plants growing in arid, semiarid, or salty areas. This protective effect of Se on photosynthetic processes consisted in minimizing damages to the chloroplast structure and enhancing the electron transport rate (Andrade *et al.* 2018). Indeed, Djanaguiraman *et al.* (2010), reported that Se application in sorghum plants grown under high temperature stress conditions increased the antioxidant defence and, in this way, increased the photosynthetic rate and grain yield. Plants cultivated with Se have a strengthened antioxidative capacity due to increased antioxidant enzyme activity and decreased ROS content (Xue *et al.* 2001). This concept is reinforced by Alves *et al.* (2020) reporting that Se can alleviate the negative effects of Cd-stress conditions and also enhance the tolerance of tomato plants against this trace element by improving the nutritional status, the proline content, and increasing the activity of antioxidant enzymes.

It is evident that low concentrations of Se (*e.g.*, 15 µM $Na_2SeO_3 \cdot 5H_2O$) can enhance the activity of some antioxidant enzymes, such as ascorbate peroxidase, glutathione reductase, dehydroascorbate reductase, and monodehydroascorbate reductase in *Zea mays* (Yildiztugay *et al.* 2017), glutathione reductase and glutathione peroxidase in *T. aestivum* (Balakhnina and Nadezhkina 2017), and superoxide dismutase and glutathione peroxidase in *Solanum lycopersicum* (Castillo-Godina *et al.* 2016). Also, under heat stress, in *Sorghum bicolor* plants, Djanaguiraman *et al.* (2010) demonstrated that the ameliorative effect of Se on photosynthesis resulted from lower ROS accumulation in mesophyll achieved by enhancing antioxidant enzyme activities.

In conclusion, even though the exact way by which selenium promotes benefits in plants remains until unknown, certainly Se can restore the photosynthetic capacity, improve antioxidant system and enhance crop production in plants subjected to environmental stresses (Feng *et al.* 2013, Alyemeni *et al.* 2018).

Silicon

In the Earth's crust, Si represents the second most abundant element; therefore, it can be present at relevant concentrations in the rhizosphere (Broadley *et al.* 2012, Vatansever *et al.* 2017, Sheik *et al.* 2018). Among Si accumulator plants, monocotyledons (*e.g.*, *Poaceae*) usually accounted for higher Si contents than that of dicotyledons (*e.g.*, *Cucurbitales* and *Urticales*) (Raven 2003, Kaur *et al.* 2016). Silicon is transported in plants as $Si(OH)_4$, then converted and stored to hydrated amorphous silica on cell walls (Vatansever *et al.* 2017). Silicon enhances the strength and the rigidity of cell wall due to a positive interaction with pectin and polyphenols (Zhang

Table 1. Effect of selenium (Se) on plant photosynthetic traits.

Beneficial element	Administration method	Chemical form and concentration	Species	Stress type	Observation	Concentration in plant tissues	Reference
Selenium	Leaf	1 g(Na_2SeO_4) m^{-3}	*Fagopyrum esculentum* (Moench) cv. Darja and *Fagopyrum tataricum* (L.) Gaertn.	UV-B	Higher Φ_{PSII}	-	Breznik *et al.* (2005)
	Leaf	10 mg(Na_2SeO_4) L^{-1}	*Solanum tuberosum* L.	Drought	Higher Φ_{PSII}	258–730 ng g^{-1}(leafDM)	Germ *et al.* (2007)
	Leaf	1 g(Na_2SeO_4) m^{-3}	*Fagopyrum esculentum* Moench.	Drought	Higher g_s and Φ_{PSII}	-	Tadina *et al.* (2007)
	Leaf	75 mg(Na_2SeO_4) L^{-1}	*Sorghum bicolor* (L.) Moench	Heat	Higher P_N, g_s, and E	20–30 µg g^{-1}(leaf DM)	Djanaguiraman *et al.* (2010)
	Nutrient solution	2 µM Na_2SeO_4	*Brassica napus* L.	Cadmium	Higher F_v/F_m, Φ_{PSII}, and q_P	-	Filek *et al.* (2010)
	Leaf	30 g(Na_2SeO_4) ha^{-1}	*Hordeum vulgare* L.	Drought	Higher F_v/F_m and g_s	-	Habibi (2013)
	Leaf	50–150 mg(Na_2SeO_4) L^{-1}	*Olea europaea* L.	Drought	Higher E, P_N, and g_s	26–36 µg g^{-1}(leaf FM)	Proietti *et al.* (2013)
	Substrate	10, 20, 50 g(Na_2SeO_3) ha^{-1}	*Oryza sativa* L.	No stress	Higher P_N, C_i, E, F_v, F_m, F_v/F_m, and F_v/F_0	0.9–5.5 mg kg^{-1}(shoot DM), 0.2–1.2 mg kg^{-1}(root DM), 40–70 µg kg^{-1}(grain DM)	Zhang *et al.* (2014)
	Leaf	0.017 g(Se) L^{-1}	*Pyrus* × *bretschneideri* Rehder, *Vitis vinifera* L., and *Prunus persica* (L.) Batsch	No stress	Higher P_N, g_s, E, and C_i	0.0041 µg g^{-1}(FM) in pear, 0.0092 µg g^{-1}(FM) in grape, 0.0038 µg g^{-1}(FM) in peach	Feng *et al.* (2015)
	Substrate	3–24 mg(Na_2SeO_3) kg^{-1}	*Nicotiana tabacum* L.	No stress	Higher P_N, g_s, and C_i	4.13–31.36 mg kg^{-1}(root DM), 0.53–3.66 mg kg^{-1}(stem DM), 1.17–7.52 mg kg^{-1}(leaf DM)	Jiang *et al.* (2015)
	Leaf	40 mg(Na_2SeO_4) L^{-1}	*Triticum aestivum* L.	Drought	Higher E, P_N, and g_s	2–6 µg g^{-1}(shoot)	Nawaz *et al.* (2015)
	Substrate	20, 40, 80 µM Na_2SeO_4	*Brassica juncea* L.	Epibrassinolide	Higher P_N, g_s, C_i, WUE	-	Naz *et al.* (2015)
	Nutrient solution	0.1–0.3 mg(Na_2SeO_3 or Na_2SeO_4) L^{-1}	*Helianthus annuus* L.	No stress	Higher P_N, E, F_v/F_m, and F_v/F_0	-	Garousi *et al.* (2016)
	Leaf	10, 50 and 100 µg(Na_2SeO_4) ml^{-1}	*Brassica oleracea* L.	No stress	Higher F_m	0.28–1.41 mg kg^{-1}(leaf DM)	Ghasemi *et al.* (2016)
	Substrate	5 mg(Na_2SeO_4) kg^{-1}	*Helianthus annuus* L.	Salt	Higher F_v/F_0	2.40–2.58 mg kg^{-1}(DM) in shoots and roots, respectively	Habibi (2017a)
	Nutrient solution	1 mg(Na_2SeO_4) L^{-1}	*Petroselinum crispum* L.	Salt	Higher F_v/F_m	-	Habibi (2017b)
	Nutrient solution	1 µM Na_2SeO_3	*Zea mays* L.	Salt	Higher P_N, g_s, and E	-	Jiang *et al.* (2017)
	Nutrient solution	1.5, 6 µM Na_2SeO_3	*Vicia faba* L.	Lead	Higher Chl	4.69–4.67 mg kg^{-1}(shoot DM)	Mroczek-Zdyrska *et al.* (2017)

Substrate	0.5, 1, and 2 mg(Se) kg^{-1}	*Oryza sativa* L.	Drought	Higher P_N and E	0.5–2.25 mg pot^{-1} in aerial part	Andrade *et al.* (2018)
Leaf	40 mg(Na_2SeO_3) L^{-1}	*Oryza sativa* L.	No stress	Higher g_s and E	-	Gao *et al.* (2018)
Leaf	20, 40 mg(Na_2SeO_4) L^{-1}	*Zea mays* L.	Salt	Higher Chl	-	Ashraf *et al.* (2018)
Nutrient solution	10 µM $Na_2SeO_3 \cdot 5H_2O$	*Solanum lycopersicum* L.	Cadmium	Higher Chl, Car, P_N, g_s, E, F_v/F_m, Φ_{PSII}, and q_P	0.15–0.49 µmol g^{-1}(shoot DM), 0.14–0.30 µmol g^{-1}(root DM), and 1.12–2.41 µmol g^{-1}(leaf DM)	Alyemeni *et al.* (2018)
Nutrient solution	5 ppm Na_2SeO_4	*Allium sativum* L.	Cadmium	Higher P_N, E, and g_s	-	Sepehri and Gharehbaghli (2019)
Nutrient solution	4, 6, 8 mg($SeCl_2$) L^{-1}	*Caspicum annum* L.	Heat	Higher F_v/F_m, E, g_s, and C_i	1.78–3.51 mg kg^{-1}(leaf DM), 0.98–1.18 mg kg^{-1}(root DM), 0.15–1.85 mg kg^{-1}(fruit DM)	Haghighi *et al.* (2019)
Leaf	10, 20, 30, 40, and 50 µM Na_2SeO_4	*Oryza sativa* L.	No stress	Higher P_N and g_s	20–50 ng g^{-1}(grain DM), 20–70 ng g^{-1}(leaf DM), 12 ng g^{-1}(stem DM)	Luo *et al.* (2019)
Substrate	2, 4, 6 µM(Na_2SeO_4) kg^{-1}	*Brassica juncea* L.	Chromium	Higher Chl, Car, P_N, g_s, C_i, E	-	Handa *et al.* (2019)
Nutrient solution	2, 4, 8 mg($Na_2SeO_3 \cdot 5H_2O$) L^{-1}	*Raphanus sativus* L.	Cadmium	Higher Φ_{PSII} and F_v/F_m	49.3–124.5 mg g^{-1}(root DM), 127.83–443.93 mg g^{-1}(leaf DM)	Amirabad *et al.* (2020)
Nutrient solution	1 µM Na_2SeO_3 or Na_2SeO_4	*Solanum lycopersicum* L.	Cadmium	Higher E, g_s, and P_N	-	Alves *et al.* (2020)

et al. 2015, Hussain *et al.* 2021). Table 2 shows that one of the most frequent consequence induced by foliar and substrate treatments with Si is the improvement of g_s with the parallel enhancement of P_N in both optimal and stressful conditions.

Hussain *et al.* (2021) found that Si, even in low amounts, increased P_N, g_s, and E in *Glycine max* subjected to low light conditions, reducing C_i and increasing chlorophyll (Chl) content. These effects of Si are reported in plants grown in shade conditions and the authors related the enhanced photosynthetic rate to the reduction in the leaf area, the increase in fresh mass (FM) and leaf thickness. Similar ameliorative effects on photosynthesis were observed by Tripathi *et al.* (2021) in *G. max*. However, in this case, the increase in photosynthetic rate was related to an improved root system suggesting that Si enhanced water and mineral uptake from the soil. Furthermore, in Si hyperaccumulators, such as *Oryza sativa*, some authors found that Si had a positive effect on photosynthesis by enhancing the g_m (Detmann *et al.* 2012, Pereira *et al.* 2020). The g_m reflects the entire diffusive CO_2 pathway in the leaf, from the substomatal air spaces to the carboxylation sites localised in the chloroplast stroma. Obviously, from stomata to chloroplast, CO_2 crosses different biophysical barriers such as intercellular air spaces and cell wall (Gago *et al.* 2020). Although there is evidence that Si might modify the cell wall thickening (Yamamoto *et al.* 2012), how Si contributes to both anatomical and biochemical components of g_m remains far to be clear. Future studies related to this aspect might help understand Si–photosynthesis interactions.

Sodium

As it emerges from the literature, Na can be beneficial or even essential mainly for C_4/CAM, halophyte, and natrophilic species (Pilon-Smits *et al.* 2009, Broadley *et al.* 2012, Maathuis 2014, Kaur *et al.* 2016). Martínez *et al.* (2005) reported higher values in P_N and increase in WUE levels in Na-treated plants (with respect to controls) of *Atriplex halimus* (C_4 xerohalophyte species) under water stress (Table 3). Moreover, in *Panicum antidotale*, Hussain *et al.* (2020) observed an alleviation of the negative impact of drought on gas-exchange parameters in Na plants (100 mM NaCl) by maintaining higher values in P_N, g_s, E, V_{cmax}, and J_{max} with respect to drought Na-untreated plants. These beneficial effects are related to a positive impact of the low Na concentration on photochemical reactions and, in particular, stimulating photosynthetic pigments and photochemical PSII efficiency. This could

Table 2. Effect of silicon (Si) on plant photosynthetic traits.

Beneficial element	Administration method	Chemical form and concentration	Species	Stress type	Observation	Concentration in plant tissues	Reference
Silicon	Nutrient solution	2 mM Si	*Oryza sativa* L.	No stress	Higher P_N and g_m	47–51 g kg^{-1}(leaf DM)	Detmann *et al.* (2012)
	Nutrient solution	1.5 mM added as K_2SiO_3	*Oryza sativa* L.	Zinc	Increase of expression of genes associated with photosynthesis	-	Song *et al.* (2014)
	Leaf	6 mM Na_2SiO_7	*Triticum aestivum* L.	Drought	Higher P_N and g_s	-	Maghsoudi *et al.* (2016)
	Substrate	100–500 mg($CaO \cdot SiO_2$) L^{-1}	*Saccharum officinarum* L.	Drought	Higher P_N and g_s	1–4 mg g^{-1}(leaf DM)	Verma *et al.* (2020)
	Substrate	2 mM Si added as SiO_2	*Sorghum bicolor* (L.) Moench	Drought	Higher P_N, g_s, and P_N/C_i	382–417 mg kg^{-1}(leaf DM)	Avila *et al.* (2020)
	Nutrient solution	2 mM Si	*Oryza sativa* L.	Biotic	Higher P_N and g_m	18–20 g kg^{-1}(leaf DM)	Pereira *et al.* (2020)
	Substrate	1g($CaO \cdot SiO_2$) kg^{-1}(soil)	*Piper nigrum* L.	Biotic	Higher P_N, g_s, and WUE	-	D'Addazio *et al.* (2020)
	Substrate and leaf	Substrate: 0.08 kg m^{-2} of fertilizer with 25% of SiO_2 Leaf: 2 mM Na_2SiO_3	*Glycine max* (L.) Merr.	No stress	Higher P_N and g_s	-	Tripathi *et al.* (2021)
	Leaf	200 mg(Na_2SiO_3) kg^{-1}	*Glycine max* (L.) Merr.	Low light	Higher P_N and g_s	0.17 mg g^{-1}(stem FM)	Hussain *et al.* (2021)

Table 3. Effect of sodium (Na) on plant photosynthetic traits.

Beneficial element	Administration method	Chemical form and concentration	Species	Stress type	Observation	Concentration in tissues	Reference
Sodium	Nutrient solution	50 mM NaCl	*Atriplex halimus* L.	Drought	Higher P_N	400–800 µmol g^{-1}(leaf DM)	Martínez *et al.* (2005)
	Nutrient solution	510 mM NaCl	*Arthrocnemum macrostachyum* (Moric) C. Koch	No stress	Higher P_N, g_s, and midday F_v/F_m	0.1–9 mmol g^{-1}(root DM), 0.5–5 mmol g^{-1}(shoot DM)	Redondo-Gómez *et al.* (2010)
	Leaf	50 mM NaCl	*Zygophyllum xanthoxylum* (Bunge) Engl.	Drought	Higher Chl, P_N, g_s, WUE, and Φ_{PSII}	2.13 mmol g^{-1}(leaf DM)	Ma *et al.* (2012)
	Nutrient solution	100 mM NaCl	*Panicum antidotale* Retz.	Drought	Higher P_N, g_s, C_i, E, V_{cmax}, and J_{max}	-	Hussain *et al.* (2020)
	Nutrient solution	100–200 mM NaCl	*Beta vulgaris* subsp. *maritima* L.	No stress	Higher P_N	190–400 mM in leaves	Rasouli *et al.* (2021)

be explained by the fact that, in C_4 plants, Na acts as an essential element for the conversion of pyruvate to phospho*enol*pyruvate in mesophyll cells, and it is also involved in the transport of pyruvate into mesophyll cell chloroplasts by sodium-dependent pyruvate transporters (Furumoto *et al.* 2011). Indeed, Furumoto *et al.* (2011) proposed that sodium-dependent pyruvate transport in some C_4 species is regulated by a two-translocator system as follows. Pyruvate enters the chloroplast with Na by a sodium/pyruvate cotransporter (BASS2). On the other hand, a sodium/H^+ antiporter (NHD1) exchanges protons (required for the conversion of phospho*enol*pyruvate) with sodium cations. Pyruvate is an essential molecule for many plastid-localized metabolic pathways of plants, including the C_4 photosynthetic CO_2-concentrating mechanism (Ohnishi *et al.* 1990, Furumoto *et al.* 2011). Sodium, maintaining the granal stacking, also provides a suitable environment for the energy transfer between PSII and PSI (Brownell and Bielig 1996); however, further studies need to be conducted to elucidate the effects of low salinity on photochemical reactions.

Similar ameliorative effects of Na supplementation under drought stress were also observed in *Zygophyllum xanthoxylum*, a succulent xerophyte woody C_3 species (Ma *et al.* 2012). The authors suggested that this species showed similar properties to salt-accumulating halophytes as the increase in P_N values was strongly related to g_s, probably enhanced through Na-mediated osmotic adjustments (Redondo-Gómez *et al.* 2010, Hedrich and Shabala 2018).

In conclusion, Na is not only beneficial but essential for some C_4 or CAM species but it is beneficial even for some halophytic species that accumulate this element in the salt-resistance mechanism and in natrophilic species or in drought conditions.

Iodine

Although I biofortification in plants was deeply investigated (Cheng 1981, Blasco *et al.* 2011, Kiferle *et al.* 2021, Izydorczyk *et al.* 2021), there is a lack of information about the ameliorative effects on photosynthesis related to I if compared to other elements used in plant biofortification such as Se (Table 4). This was probably due to the high I toxicity for plants and to the difficulty to find the concentration at which this element can be useful for plant growth. Once inside the plant, I is transported predominantly through the xylem; however, a transport through phloem was also reported suggesting that I is relatively mobile to sink organs (Herrett *et al.* 1962, Landini *et al.* 2011, Smoleń *et al.* 2014).

In an experiment conducted by Blasco *et al.* (2011), by using low (20 and 40 μM) and high doses (80 μM) of I as KI (I^-) or KIO_3 (IO_3^-), it was observed that the administration of very low doses of I^- or IO_3^- promoted g_s and E, that, in turn, enhanced P_N in lettuce plants. However, only plants treated with IO_3^- (at 80 μM) maintained an elevated P_N in respect to controls, whereas I^- induced a decrease in gas-exchange parameters, highlighting the phytotoxic effect of high doses of this I form (Blasco *et al.* 2011).

To date, a detailed report of Kiferle *et al.* (2021) using *Arabidopsis* plants, revealed the existence of several iodinated proteins involved in photosynthesis, such as constituents of PSII (PsbA, PsbB, PsbC, and PsbD), OEC (PsbO, PsbP, PsbQ, and PsbR), LHCII (CAB3, LHCB2.1, LHCB1B1, LHCB3, LHCB5), PSI (PsaB, PsaE, PsaF, and PsaH), Cyt b_6/f (PetA and PetC), plastocyanin electron carrier (PETE2), and ferredoxin–NADP(+)-oxidoreductase (FNR1). Moreover, other iodinated proteins were involved in the development/maintenance of both photosystems (Psb27, Psb29, Psb31, and Psb33), in PSII photoprotection (MPH1) or in the degradation of the photodamaged D1 reaction centre. Since I can be a structural component of several different proteins involved in photosynthesis, the authors proposed that I could have a potential nutritional role in plants. However, the capability to generate iodinated proteins represents one of the main reasons of the high toxicity exerted by this element and explain why the range of concentrations between positive and negative effects in plants is extremely narrow.

Titanium

Ti, after Fe, is the most abundant transition metal, and its abundance on Earth's crust is about five times lower than that of Fe and 100 times greater than that of Cu. Ti, usually administrated on leaves as ionic Ti or TiO_2 nanoparticles (NPs), was successfully used as beneficial element to improve crop production (Ercoli *et al.* 2008, Lyu *et al.* 2017).

In plants, there is a lack of knowledge about the transport of Ti and TiO_2 NP_S; it is conceivable that they can be absorbed by roots or leaf stomata and actively/passively transported through plant tissues following a similar transport of Fe (Lyu *et al.* 2017).

About the beneficial effects of this element in the photosynthetic process, it was observed that Ti application stimulated the Chl content in *Vigna radiata* (Raliya *et al.* 2015), *Fragaria* × *ananassa* (Choi *et al.* 2015), *Cucumis sativus* (Servin *et al.* 2013), *G. max* (Hussain *et al.* 2019a), and *Dracocephalum moldavica* (Gohari *et al.* 2020) (Table 5). However, the way in which Ti induces an accumulation in Chl is still an open question. Nonetheless, Ze *et al.* (2011) observed an increase in *PSII LHCII-b* gene expression resulting in an enhancement of the energy transport between Chl *b* and carotenoid and in this way promoting the distribution of light energy from PSI to PSII by increasing LHCII in *Arabidopsis* plants treated with a solution of 0.25% Ti NPs.

It was observed that Ti and TiO_2 NP_S promoted P_N and g_s under nonlimiting or stressful conditions (Gao *et al.*

Table 4. Effect of iodine (I) on plant photosynthetic traits.

Beneficial element	Administration method	Chemical form and concentration	Species	Stress type	Observation	Concentration in plant tissues	Reference
Iodine	Nutrient solution	20, 40 μmol(KI) L^{-1}, and 20, 40, 80 μmol(KIO_3) L^{-1}	*Lactuca sativa* L.	No stress	Higher P_N, g_s, E	-	Blasco *et al.* (2011)
	Nutrient solution	0.20 or 10 μM KIO_3	*Arabidopsis thaliana* (L.) Heynh.	No stress	Presence of 31 iodinated proteins involved in photosynthesis (constituents of PSII, PSI, OEC, LHCII, Cyt b_6/f)	-	Kiferle *et al.* (2021)

Table 5. Effect of titanium (Ti) on plant photosynthetic traits.

Beneficial element	Administration method	Chemical form and concentration	Species	Stress type	Observation	Concentration in plant tissues	Reference
Titanium	Nutrient solution Leaf	Solution with 0.03% TiO_2 NPs	*Spinacia oleracea* L.	No stress	Higher P_N, higher Rubisco carboxylase and activase activity	-	Gao *et al.* (2008)
	Leaf	Solution with 0.25% TiO_2 NPs	*Arabidopsis thaliana* (L.) Heynh.	No stress	Increase of LHCII *b* gene expression and LHCII content	-	Ze *et al.* (2011)
	Leaf	720 ppm TiO_2 NPs	*Cucumis sativus* L.	No stress	Increase in Chl index (SPAD)	-	Servin *et al.* (2013)
	Leaf	50–100 mg(TiO_2) kg^{-1}	*Fragaria* × *ananassa* Duch.	No stress	Increase in Chl content	-	Choi *et al.* (2015)
	Leaf	10 mg(TiO_2 NPs) L^{-1}	*Vigna radiata* L.	No stress	Increase in Chl content	-	Raliya *et al.* (2015)
	Leaf	12.5–25 mg(ionic Ti) L^{-1}	*Glycine max* (L.) Merr.	Low light	Higher Chl, Φ_{PSII}, q_P, P_N, g_s, and E	25–40 mg kg^{-1}(leaf DM), 12.5–35 mg kg^{-1}(stem DM), 12.5–150 mg kg^{-1}(root DM)	Hussain *et al.* (2019a)
	Leaf	2.5 mg(ionic Ti) $plant^{-1}$	*Glycine max* (L.) Merr.	Low light	Higher ETR, F_v/F_m, Chl, Rubisco activase activity	35–100 mg kg^{-1}(root DM), 2–12 mg kg^{-1}(stem DM), and 20–80 mg kg^{-1}(leaf DM)	Hussain *et al.* (2019b)
	Nutrient solution	50–100 mg(TiO_2 NPs) L^{-1}	*Dracocephalum moldavica* L.	No stress	Higher Chl, F_v/F_m, and Φ_{PSII}	-	Gohari *et al.* (2020)
	Leaf	10–1500 mg(TiO_2 NPs and µPs) L^{-1}	*Raphanus sativus* L.	No stress	Transient increase of P_N and g_s	10–80 mg kg^{-1}(DM) in leaves treated with NPs and 10–225 mg kg^{-1}(DM) in leaves treated with µPs	Tighe-Neira *et al.* (2020)

2008, Hussain *et al.* 2019a, Tighe-Neira *et al.* 2020). In addition, other positive effects of Ti or TiO_2 NP_S on photosynthetic traits, such as a higher F_v/F_m, Φ_{PSII}, ETR, and q_P, have been reported in *Dracocephalum moldavica* and *G. max* (Hussain *et al.* 2019a,b; Gohari *et al.* 2020). The increase of photosynthetic rate is likely linked to the capability of Ti-treated plants to increase the rate of Rubisco activase and the carboxylation activity of Rubisco (Gao *et al.* 2008, Hussain *et al.* 2019b). The promising beneficial roles exerted by Ti on leaf photosynthesis could open up new research lines in plant nutrition, fertilization, and biofortification.

Cerium and lanthanum

Cerium and lanthanum belong to the group of rare earth elements and possess unique photo-electromagnetic effects on photosynthesis (Liu *et al.* 2009). Ce NP_S can be absorbed by the leaves through stomatal apertures or by roots but are difficult to be translocated within the plant (Birbaum *et al.* 2010, Zhang *et al.* 2011). Nonetheless, Ma *et al.* (2015) demonstrated Ce NP_S were translocated to aerial parts in the form of CeO_3 (~ 30%) or combined with carboxyl group (~ 70%). Once transported into the mesophyll cell, Ce enters the chloroplast *via* nonendocytic pathways, influenced by the electrochemical gradient of the plasma membrane potential (Wu *et al.* 2017). Ma *et al.* (2015) also observed that, in plant roots, about 80% of La NP_S were transformed into La carboxylates and phosphates, and only these two forms were found in leaves at similar abundances. In general, the supply of Ce or La to plants, grown with or without stress, improves the P_N values, in some cases due to an increase in g_s, as it was reported in La-treated plants of *Amorphophallus sinensis* (Li *et al.* 2020), Ce-treated plants of *Phaseolus vulgaris* and *S. bicolor* (Djanaguiraman *et al.* 2018, Salgado *et al.* 2020), or in La-treated *Z. mays* plants (Cui *et al.* 2019) (Table 6). Moreover, Wu *et al.* (2017) reported that

Table 6. Effect of lanthanum (La) and cerium (Ce) on plant photosynthetic traits.

Beneficial element	Administration method	Chemical form and concentration	Species	Stress type	Observation	Concentrations in plant tissues	Reference
Lanthanum	Nutrient solution Leaf	500 μmol($CeCl_3$) L^{-1}	*Spinacia oleracea* L.	No stress	Promotes the energy transfer from LHCII to PSII and accelerates water photolysis and O_2 evolution	-	Liu *et al.* (2007b)
	Leaf	100 mg(La) L^{-1}	*Pseudostellaria heterophylla* (Miquel) Pax	No stress	Higher P_N, g_s, F_v/F_m, and Φ_{PSII}	-	Ma *et al.* (2017)
	Nutrient solution	400–800 μmol($LaCl_3$) L^{-1}	*Zea mays* L.	No stress	Higher Chl, Car, P_N, g_s, F_v/F_m, and Φ_{PSII}	-	Cui *et al.* (2019)
	Leaf	160 mg($LaCl_3$) L^{-1}	*Amorphophallus sinensis* Belval	No stress	Higher Chl, Car, P_N, and g_s	-	Li *et al.* (2020)
Cerium	Nutrient solution Leaf	20 μmol($CeCl_3$) L^{-1}	*Spinacia oleracea* L.	No stress	Promotes the energy transfer from LHCII to PSII and accelerates water photolysis and O_2 evolution	-	Liu *et al.* (2007b)
	Nutrient solution Leaf	20 μmol($CeCl_3$) L^{-1}	*Arabidopsis thaliana* (L.) Heynh.	No stress	Higher Chl, increase of LHCII *b* gene expression and LHCII content	-	Liu *et al.* (2009)
	Leaf	CeO_2 NPs with low Ce^{3+}/Ce^{4+} ratio	*Arabidopsis thaliana* (L.) Heynh.	Heat High light Chilling	Higher P_N, V_{cmax}, F_v/F_m, and Φ_{PSII}	-	Wu *et al.* (2017)
	Leaf	10 mg(CeO_2 NPs) L^{-1}	*Sorghum bicolor* (L.) Moench	Drought	Higher Chl index (SPAD), P_N, g_s, and F_v/F_m	5.1–10 mg kg^{-1}(root FM) and 4–4.5 mg kg^{-1}(shoot FM)	Djanaguiraman *et al.* (2018)
	Nutrient solution	0.1 μmol($Ce(NO_3)_3 \cdot 6H_2O$) L^{-1}	*Phaseolus vulgaris* L.	Drought	Higher Chl, P_N, and g_s	-	Salgado *et al.* (2020)

in *Arabidopsis* plants treated with a low Ce^{3+}/Ce^{4+} ratio photosynthetic performance improved under stress conditions (excess light, continuous excess light, heat, and dark chilling). The authors also observed that the lower Ce^{3+}/Ce^{4+} ratio was able to scavenge ROS, including hydrogen peroxide, superoxide anion, and hydroxyl radicals. The capability of Ce to reduce oxidative stress was also suggested in plants subjected to drought (Djanaguiraman *et al.* 2018, Salgado *et al.* 2020).

Besides their capability to increase the Chl content improving the light-harvesting complex (Liu *et al.* 2007a, Liu *et al.* 2009, Li *et al.* 2020), Ce increases light absorption as well as the energy transfer within LHCII and from tyrosine residues on the oxidizing side of PSII II to Chl *a* in the PSII reaction centres (Liu *et al.* 2007b). This is probably explained by the results of Hong *et al.* (2002) in *Spinacia oleracea*, where they found that La or Ce can replace Mg in the Chl assembling and promote the formation of PSII more significantly than that of PSI.

Conclusion: More attention was focused on the toxic effects of some elements whereas it is evident that some elements are beneficial in plant photosynthetic process (Fig. 1). As previously reported, the mechanisms through which these beneficial elements exert their promoting effects on leaf photosynthesis are far to be fully elucidated. Moreover, in some works, there are no explanations of the physiological/biochemical mechanisms underlying these ameliorative effects.

The regulatory mechanisms in which those elements are involved need to be clarified in condition of plant stress, too; this, in order to establish their possible ameliorative role under abiotic stresses. Only further investigations focused on the physiological and biochemical mechanisms of action of beneficial elements will make possible to fully exploit those elements to promote plant growth, resilience, and productivity.

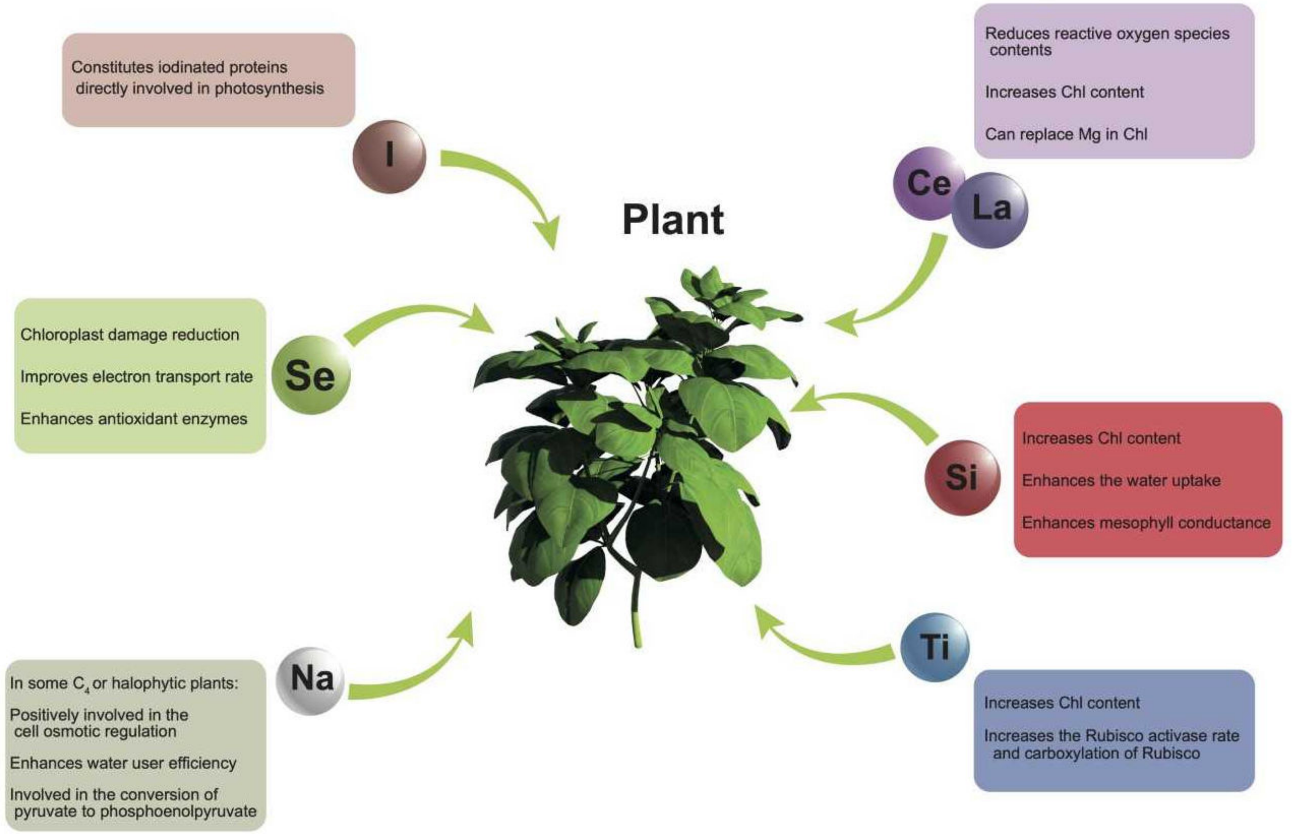

Fig. 1. Potential promoting roles of beneficial elements on plant photosynthetic traits.

References

Aggarwal A., Sharma I., Tripati B.N. *et al.*: Metal toxicity and photosynthesis. – In: Ithoh S., Mohanty P., Guruprasad K.N. (ed.): Photosynthesis: Overviews on Recent Progress & Future Perspectives. Pp. 229-236. IK International Publishing House, New Delhi 2012.

Alves L.R., Rossatto D.R., Rossi M.L. *et al.*: Selenium improves photosynthesis and induces ultrastructural changes but does not alleviate cadmium-stress damages in tomato plants. – Protoplasma **257**: 597-605, 2020.

Alyemeni M.N., Ahanger M.A., Wijaya L. *et al.*: Selenium mitigates cadmium-induced oxidative stress in tomato (*Solanum lycopersicum* L.) plants by modulating chlorophyll fluorescence, osmolyte accumulation, and antioxidant system. – Protoplasma **255**: 459-469, 2018.

Amirabad S.A., Behtash F., Vafaee Y.: Selenium mitigates cadmium toxicity by preventing oxidative stress and enhancing photosynthesis and micronutrient availability on radish (*Raphanus sativus* L.) cv. Cherry Belle. – Environ. Sci. Pollut. R. **27**: 12476-12490, 2020.

Andrade F.R., da Silva G.N., Guimarães K.C. *et al.*: Selenium protects rice plants from water deficit stress. – Ecotox. Environ. Safe. **164**: 562-570, 2018.

Arnon D.I., Stout P.R.: The essentiality of certain elements in minute quantity for plants with special reference to copper. – Plant Physiol. **14**: 371-375, 1939.

Ashraf M.A., Akbar A., Parveen A. *et al.*: Phenological application of selenium differentially improves growth, oxidative defense and ion homeostasis in maize under salinity stress. – Plant Physiol. Bioch. **123**: 268-280, 2018.

Avila R.G., Magalhães P.C., da Silva E.M. *et al.*: Silicon supplementation improves tolerance to water deficiency in sorghum plants by increasing root system growth and improving photosynthesis. – Silicon **12**: 2545-2554, 2020.

Balakhnina T.I., Nadezhkina E.S.: Effect of selenium on growth and antioxidant capacity of *Triticum aestivum* L. during development of lead-induced oxidative stress. – Russ. J. Plant Physiol. **64**: 215-223, 2017.

Birbaum K., Brogioli R., Schellenberg M. *et al.*: No evidence for cerium dioxide nanoparticle translocation in maize plants. – Environ. Sci. Technol. **44**: 8718-8723, 2010.

Blasco B., Rios J.J., Leyva R. *et al.*: Photosynthesis and metabolism of sugars from lettuce plants (*Lactuca sativa* L. var. *longifolia*) subjected to biofortification with iodine. – Plant Growth Regul. **65**: 137-143, 2011.

Breznik B., Germ M., Gaberscik A., Kreft I.: Combined effects of elevated UV-B radiation and the addition of selenium on common (*Fagopyrum esculentum* Moench) and tartary [*Fagopyrum tataricum* (L.) Gaertn.] buckwheat. – Photosynthetica **43**: 583-589, 2005.

Broadley M., Brown P., Cakmak I. *et al.*: Beneficial Elements. – In: Marschner P. (ed.): Marschner's Mineral Nutrition of Higher Plants. Pp. 249-269. Academic Press, Amsterdam 2012.

Brownell P.F., Bielig L.M.: The role of sodium in the conversion of pyruvate to phosphoenolpyruvate in mesophyll chloroplasts of C_4 plants. – Funct. Plant Biol. **23**: 171-177, 1996.

Castillo-Godina R.G., Foroughbakhch-Pournavab R., Benavides-Mendoza A.: Effect of selenium on elemental concentration and antioxidant enzymatic activity of tomato plants. – J. Agr. Sci. Tech. **18**: 233-244, 2016.

Cheng B.T.: The role of iodine, silicon and titanium on manganese toxicity in an acid soil [in the cultivation of tomatoes and cucumber]. – Agrochimica **25**: 268-277, 1981.

Choi H.G., Moon B.Y., Bekhzod K. *et al.*: Effects of foliar fertilization containing titanium dioxide on growth, yield and quality of strawberries during cultivation. – Hortic. Environ. Biote. **56**: 575-581, 2015.

Cui W., Kamran M., Song Q. *et al.*: Lanthanum chloride improves maize grain yield by promoting photosynthetic characteristics, antioxidants enzymes and endogenous hormone at reproductive stages. – J. Rare Earth. **37**: 781-790, 2019.

Detmann K.C., Araújo W.L., Martins S.C.V. *et al.*: Silicon nutrition increases grain yield, which, in turn, exerts a feed-forward stimulation of photosynthetic rates via enhanced mesophyll conductance and alters primary metabolism in rice. – New Phytol. **196**: 752-762, 2012.

Djanaguiraman M., Nair R., Giraldo J.P. *et al.*: Cerium oxide nanoparticles decrease drought-induced oxidative damage in *Sorghum* leading to higher photosynthesis and grain yield. – ACS Omega **3**: 14406-14416, 2018.

Djanaguiraman M., Prasad P.V.V., Seppanen M.: Selenium protects sorghum leaves from oxidative damage under high temperature stress by enhancing antioxidant defense system. – Plant Physiol. Bioch. **48**: 999-1007, 2010.

D'Addazio V., Silva J.V.G., Jardim A.S. *et al.*: Silicon improves the photosynthetic performance of black pepper plants inoculated with *Fusarium solani* f. sp. *piperis*. – Photosynthetica **58**: 692-701, 2020.

Epstein E.: Mineral metabolism. – In: Bonner J., Varner J.E. (ed.): Plant Biochemistry. Pp. 438-466. Academic Press, New York 1965.

Ercoli L., Mariotti M., Niccolai L. *et al.*: The use of titanium shavings as a fertilizer alternative for maize production. – Agrochimica **52**: 360-376, 2008.

Feng R., Wei C., Tu S.: The roles of selenium in protecting plants against abiotic stresses. – Environ. Exp. Bot. **87**: 58-68, 2013.

Feng T., Chen S.S., Gao D.Q. *et al.*: Selenium improves photosynthesis and protects photosystem II in pear (*Pyrus bretschneideri*), grape (*Vitis vinifera*), and peach (*Prunus persica*). – Photosynthetica **53**: 609-612, 2015.

Filek M., Kościelniak J., Łabanowska M. *et al.*: Selenium-induced protection of photosynthesis activity in rape (*Brassica napus*) seedlings subjected to cadmium stress. Fluorescence and EPR measurements. – Photosynth. Res. **105**: 27-37, 2010.

Furumoto T., Yamaguchi T., Ohshima-Ichie Y. *et al.*: A plastidial sodium-dependent pyruvate transporter. – Nature **476**: 472-475, 2011.

Gago J., Daloso D.M., Carriquí M. *et al.*: Mesophyll conductance: the leaf corridors for photosynthesis. – Biochem. Soc. T. **48**: 429-439, 2020.

Gao F., Liu C., Qu C. *et al.*: Was improvement of spinach growth by nano-TiO_2 treatment related to the changes of Rubisco activase? – BioMetals **21**: 211-217, 2008.

Gao M., Zhou J., Liu H. *et al.*: Foliar spraying with silicon and selenium reduces cadmium uptake and mitigates cadmium toxicity in rice. – Sci. Total Environ. **631–632**: 1100-1108, 2018.

Garousi F., Kovács B., Veres S.: Investigation of photosynthesis status of sunflower plants up-taking different forms of selenium. – Adv. Plants Agric. Res. **3**: 00083, 2016.

Germ M., Kreft I., Stibilj V., Urbanc-Berčič O.: Combined effects of selenium and drought on photosynthesis and mitochondrial respiration in potato. – Plant Physiol. Bioch. **45**: 162-167, 2007.

Ghasemi Y., Ghasemi K., Pirdashti H., Asgharzadeh R.: Effect of selenium enrichment on the growth, photosynthesis and mineral nutrition of broccoli. – Not. Sci. Biol. **8**: 199-203, 2016.

Gohari G., Mohammadi A., Akbari A. *et al.*: Titanium dioxide nanoparticles (TiO_2 NPs) promote growth and ameliorate salinity stress effects on essential oil profile and biochemical attributes of *Dracocephalum moldavica*. – Sci. Rep.-UK **10**: 912, 2020.

Gómez-Merino F.C., Trejo-Téllez L.I.: The role of beneficial elements in triggering adaptive responses to environmental stressors and improving plant performance. – In: Vats S. (ed.): Biotic and Abiotic Stress Tolerance in Plants. Pp. 137-172. Springer, Singapore 2018.

Habibi G.: Effect of drought stress and selenium spraying on photosynthesis and antioxidant activity of spring barley. – Acta Agr. Slov. **101**: 31-39, 2013.

Habibi G.: Selenium ameliorates salinity stress in *Petroselinum crispum* by modulation of photosynthesis and by reducing shoot Na accumulation. – Russ. J. Plant Physiol. **64**: 368-374, 2017a.

Habibi G.: Physiological, photochemical and ionic responses of sunflower seedlings to exogenous selenium supply under salt stress. – Acta Physiol. Plant. **39**: 213, 2017b.

Haghighi M., Ramezani M.R., Rajaii N.: Improving oxidative damage, photosynthesis traits, growth and flower dropping of pepper under high temperature stress by selenium. – Mol. Biol. Rep. **46**: 497-503, 2019.

Handa N., Kohli S.K., Sharma A. *et al.*: Selenium modulates dynamics of antioxidative defence expression, photosynthetic attributes and secondary metabolites to mitigate chromium toxicity in *Brassica juncea* L. plants. – Environ. Exp. Bot. **161**: 180-192, 2019.

Hedrich R., Shabala S.: Stomata in a saline world. – Curr. Opin. Plant Biol. **46**: 87-95, 2018.

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

Hong F., Wang L., Meng X. *et al.*: The effect of cerium (III) on the chlorophyll formation in spinach. – Biol. Trace Elem. Res. **89**: 263-276, 2002.

Hussain S., Iqbal N., Brestic M. *et al.*: Changes in morphology, chlorophyll fluorescence performance and Rubisco activity of soybean in response to foliar application of ionic titanium under normal light and shade environment. – Sci. Total Environ. **658**: 626-637, 2019b.

Hussain S., Iqbal N., Raza M.A. *et al.*: Distribution and effects of ionic titanium application on energy partitioning and quantum yield of soybean under different light conditions. – Photosynthetica **57**: 572-580, 2019a.

Hussain S., Li S.X., Mumtaz M. *et al.*: Foliar application of silicon improves stem strength under low light stress by regulating lignin biosynthesis genes in soybean (*Glycine max* (L.) Merr.). – J. Hazard. Mater. **401**: 123256, 2021.

Hussain T., Koyro H.-W., Zhang W. *et al.*: Low salinity improves photosynthetic performance in *Panicum antidotale* under drought stress. – Front. Plant Sci. **11**: 481, 2020.

Izydorczyk G., Ligas B., Mikula K. *et al.*: Biofortification of edible plants with selenium and iodine – A systematic literature review. – Sci. Total Environ. **754**: 141983, 2021.

Jiang C., Zu C., Lu D. *et al.*: Effect of exogenous selenium supply on photosynthesis, Na^+ accumulation and antioxidative capacity of maize (*Zea mays* L.) under salinity stress. – Sci.

Rep.-UK **7**: 42039, 2017.

Jiang C., Zu C., Shen J. *et al.*: Effects of selenium on the growth and photosynthetic characteristics of flue-cured tobacco (*Nicotiana tabacum* L.). – Acta Soc. Bot. Pol. **84**: 71-77, 2015.

Kaur S., Kaur N., Siddique K.H.M., Nayyar H.: Beneficial elements for agricultural crops and their functional relevance in defence against stresses. – Arch. Agron. Soil Sci. **62**: 905-920, 2016.

Kiferle C., Martinelli M., Salzano A.M. *et al.*: Evidences for a nutritional role of iodine in plants. – Front. Plant Sci. **12**: 616868, 2021.

Landini M., Gonzali S., Perata P.: Iodine biofortification in tomato. – J. Plant Nutr. Soil Sc. **174**: 480-486, 2011.

Li X.X., Yu B., Dong Y.Y. *et al.*: Lanthanum chloride enhances the photosynthetic characteristics and increases konjac glucomannan contents in *Amorphophallus sinensis* Belval. – Photosynthetica **58**: 165-173, 2020.

Liu X.Q., Huang H., Liu C. *et al.*: Physico-chemical property of rare earths. Effects on the energy regulation of photosystem II in *Arabidopsis thaliana*. – Biol. Trace Elem. Res. **130**: 141-151, 2009.

Liu X.Q., Su M.Y., Liu C. *et al.*: Effect of 4f electron characteristics and alternation valence of rare earths on photosynthesis: Regulating distribution of energy and activities of spinach chloroplast. – J. Rare Earth. **25**: 495-501, 2007a.

Liu X.Q., Su M.Y., Liu C. *et al.*: Effects of $CeCl_3$ on energy transfer and oxygen evolution in spinach photosystem II. – J. Rare Earth. **25**: 624-630, 2007b.

Luo H.W., He L.X., Du B. *et al.*: Foliar application of selenium (Se) at heading stage induces regulation of photosynthesis, yield formation, and quality characteristics in fragrant rice. – Photosynthetica **57**: 1007-1014, 2019.

Lyu S., Wei X., Chen J. *et al.*: Titanium as a beneficial element for crop production. – Front. Plant Sci. **8**: 597, 2017.

Ma Q., Yue L.J., Zhang J.L. *et al.*: Sodium chloride improves photosynthesis and water status in the succulent xerophyte *Zygophyllum xanthoxylum*. – Tree Physiol. **32**: 4-13, 2012.

Ma Y., Zhang P., Zhang Z. *et al.*: Origin of the different phytotoxicity and biotransformation of cerium and lanthanum oxide nanoparticles in cucumber. – Nanotoxicology **9**: 262-270, 2015.

Ma Y., Zou H., Gu H. *et al.*: Stimulatory effect of lanthanum nitrate on the root tuber yield of *Pseudostellaria heterophylla* via improved photosynthetic characteristics. – J. Rare Earth. **35**: 610-620, 2017.

Maathuis F.J.M.: Sodium in plants: perception, signalling, and regulation of sodium fluxes. – J. Exp. Bot. **65**: 849-858, 2014.

Maghsoudi K., Emam Y., Pessarakli M.: Effect of silicon on photosynthetic gas exchange, photosynthetic pigments, cell membrane stability and relative water content of different wheat cultivars under drought stress conditions. – J. Plant Nutr. **39**: 1001-1015, 2016.

Malagoli M., Schiavon M., dall'Acqua S., Pilon-Smits E.A.H.: Effects of selenium biofortification on crop nutritional quality. – Front. Plant Sci. **6**: 280, 2015.

Marschner P.: Marschner's mineral nutrition of higher plants. Pp. 651. Academic Press, Amsterdam 2012.

Martínez J.-P., Kinet J.-M., Bajji M., Lutts S.: NaCl alleviates polyethylene glycol-induced water stress in the halophyte species *Atriplex halimus* L. – J. Exp. Bot. **56**: 2421-2431, 2005.

Mroczek-Zdyrska M., Strubińska J., Hanaka A.: Selenium improves physiological parameters and alleviates oxidative stress in shoots of lead-exposed *Vicia faba* L. minor plants grown under phosphorus-deficient conditions. – J. Plant Growth Regul. **36**: 186-199, 2017.

Nawaz F., Ahmad R., Ashraf M.Y. *et al.*: Effect of selenium foliar spray on physiological and biochemical processes and chemical constituents of wheat under drought stress. – Ecotox. Environ. Safe. **113**: 191-200, 2015.

Naz F.S., Yusuf M., Khan T.A. *et al.*: Low level of selenium increases the efficacy of 24-epibrassinolide through altered physiological and biochemical traits of *Brassica juncea* plants. – Food Chem. **185**: 441-448, 2015.

Nyitrai P., Bóka K., Gáspár L. *et al.*: Characterization of the stimulating effect of low-dose stressors in maize and bean seedlings. – J. Plant Physiol. **160**: 1175-1183, 2003.

Ohnishi J., Flügge U.-I., Heldt H.W., Kanai R.: Involvement of Na^+ in active uptake of pyruvate in mesophyll chloroplasts of some C_4 plants: Na^+/pyruvate cotransport. – Plant Physiol. **94**: 950-959, 1990.

Pereira L.F., Martins S.C.V., Aucique-Pérez C.E. *et al.*: Silicon alleviates mesophyll limitations of photosynthesis on rice leaves infected by *Monographella albescens*. – Theor. Exp. Plant Phys. **32**: 163-174, 2020.

Pilon-Smits E.A.H.: Selenium in plants. – In: Lüttge U., Beyschlag W. (ed.): Progress in Botany. Pp. 93-107. Springer, Cham 2015.

Pilon-Smits E.A.H., Quinn C.F., Tapken W. *et al.*: Physiological functions of beneficial elements. – Curr. Opin. Plant Biol. **12**: 267-274, 2009.

Proietti P., Nasini L., Del Buono D. *et al.*: Selenium protects olive (*Olea europaea* L.) from drought stress. – Sci. Hortic.-Amsterdam **164**: 165-171, 2013.

Raliya R., Biswas P., Tarafdar J.C.: TiO_2 nanoparticle biosynthesis and its physiological effect on mung bean (*Vigna radiata* L.). – Biotechnol. Rep. **5**: 22-26, 2015.

Rasouli F., Kiani-Pouya A., Tahir A. *et al.*: A comparative analysis of stomatal traits and photosynthetic responses in closely related halophytic and glycophytic species under saline conditions. – Environ. Exp. Bot. **181**: 104300, 2021.

Raven J.A.: Cycling silicon – the role of accumulation in plants. – New Phytol. **158**: 419-421, 2003.

Redondo-Gómez S., Mateos-Naranjo E., Figueroa M.E., Davy A.J.: Salt stimulation of growth and photosynthesis in an extreme halophyte, *Arthrocnemum macrostachyum*. – Plant Biol. **12**: 79-87, 2010.

Salgado O.G.G., Teodoro J.C., Alvarenga J.P. *et al.*: Cerium alleviates drought-induced stress in *Phaseolus vulgaris*. – J. Rare Earth. **38**: 324-331, 2020.

Sepehri A., Gharehbaghli N.: Selenium alleviate cadmium toxicity by improving nutrient uptake, antioxidative and photosynthetic responses of garlic. – Russ. J. Plant Physiol. **66**: 152-159, 2019.

Servin A.D., Morales M.I., Castillo-Michel H. *et al.*: Synchrotron verification of TiO_2 accumulation in cucumber fruit: A possible pathway of TiO_2 nanoparticle transfer from soil into the food chain. – Environ. Sci. Technol. **47**: 11592-11598, 2013.

Sheik M.A., Hameed A., Farooq T., Ibrahim M.: Evaluation of sodium silicate as antioxidant activator and growth enhancer in wheat. – Agrochimica **62**: 113-125, 2018.

Smoleń S., Kowalska I., Sady W.: Assessment of biofortification with iodine and selenium of lettuce cultivated in the NFT hydroponic system. – Sci. Hortic.-Amsterdam **166**: 9-16, 2014.

Song A., Li P., Fan F. *et al.*: The effect of silicon on photosynthesis and expression of its relevant genes in rice (*Oryza sativa* L.) under high-zinc stress. – PLoS ONE **9**: e113782, 2014.

Tadina N., Germ M., Kreft I. *et al.*: Effects of water deficit and selenium on common buckwheat (*Fagopyrum esculentum* Moench.) plants. – Photosynthetica **45**: 472-476, 2007.

Tighe-Neira R., Reyes-Díaz M., Nunes-Nesi A. *et al.*: Titanium dioxide nanoparticles provoke transient increase in photosynthetic performance and differential response in antioxidant system in *Raphanus sativus* L. – Sci. Hortic.-Amsterdam **269**: 109418, 2020.

Tripathi P., Na C.-I., Kim Y.: Effect of silicon fertilizer treatment on nodule formation and yield in soybean (*Glycine max* L.). – Eur. J. Agron. **122**: 126172, 2021.

Trippe R.C., Pilon-Smits E.A.H.: Selenium transport and metabolism in plants: Phytoremediation and biofortification implications. – J. Hazard. Mater. **404**: 124178, 2021.

Vatansever R., Ozyigit I.I., Filiz E.: Essential and beneficial trace elements in plants, and their transport in roots: a review. – Appl. Biochem. Biotech. **181**: 464-482, 2017.

Verma K.K., Wu K.-C., Verma C.L. *et al.*: Developing mathematical model for diurnal dynamics of photosynthesis in *Saccharum officinarum* responsive to different irrigation and silicon application. – PeerJ **8**: e10154, 2020.

White P.J.: Selenium metabolism in plants. – BBA-Gen. Subjects **1862**: 2333-2342, 2018.

Wu H., Tito N., Giraldo J.P.: Anionic cerium oxide nanoparticles protect plant photosynthesis from abiotic stress by scavenging reactive oxygen species. – ACS Nano **11**: 11283-11297, 2017.

Xue T., Hartikainen H., Piironen V.: Antioxidative and growth-promoting effect of selenium on senescing lettuce. – Plant Soil **237**: 55-61, 2001.

Yamamoto T., Nakamura A., Iwai H. *et al.*: Effect of silicon deficiency on secondary cell wall synthesis in rice leaf. – J. Plant Res. **125**: 771-779, 2012.

Yildiztugay E., Ozfidan-Konakci C., Kucukoduk M., Tekis S.A.: The impact of selenium application on enzymatic and non-enzymatic antioxidant systems in *Zea mays* roots treated with combined osmotic and heat stress. – Arch. Agron. Soil Sci. **63**: 261-275, 2017.

Ze Y., Liu C., Wang L. *et al.*: The regulation of TiO_2 nanoparticles on the expression of light-harvesting complex II and photosynthesis of chloroplasts of *Arabidopsis thaliana*. – Biol. Trace Elem. Res. **143**: 1131-1141, 2011.

Zhang J., Zou W., Li Y. *et al.*: Silica distinctively affects cell wall features and lignocellulosic saccharification with large enhancement on biomass production in rice. – Plant Sci. **239**: 84-91, 2015.

Zhang M., Tang S., Huang X. *et al.*: Selenium uptake, dynamic changes in selenium content and its influence on photosynthesis and chlorophyll fluorescence in rice (*Oryza sativa* L.). – Environ. Exp. Bot. **107**: 39-45, 2014.

Zhang Z., He X., Zhang H. *et al.*: Uptake and distribution of ceria nanoparticles in cucumber plants. – Metallomics **3**: 816-822, 2011.