Sustainable Plant Nutrition in a Changing World

Mohammad Anwar Hossain
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Zsuzsanna Kolbert · Hassan El-Ramady
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Sustainable Plant Nutrition in a Changing World

This book series aims to provide new insight and improve understanding of plant nutrition, a crucial component in plant production and food security. Plant nutrition encompasses the study of plant growth and metabolism, external supply of necessary chemical compounds and the biochemistry of various nutrients in plants. This field of study has grown in light of recent scientific advances and climate change and has expanded to include the impact of climate change, pollution, nanomaterials, biofortification and genomics on the nutrition of plants.

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Selenium and Nano-Selenium in Environmental Stress Management and Crop Quality Improvement

Springer

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ISSN 2662-2394 ISSN 2662-2408 (electronic)
Sustainable Plant Nutrition in a Changing World
ISBN 978-3-031-07062-4 ISBN 978-3-031-07063-1 (eBook)
https://doi.org/10.1007/978-3-031-07063-1

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Preface

Climate change provokes a plethora of environmental stresses in plants. These environmental stresses are the major limiting factors for constraining crop yield and quality of produce. In order to achieve sustainable development in agriculture and to increase agricultural production for feeding an increasing global population, it is necessary to use ecologically compatible and environmentally friendly strategies to decrease the adverse effects of stresses on the plant. Selenium is one of the critical elements from the biological contexts because it is essential for human health; however, it becomes toxic at high concentrations. It has been widely reported that selenium can promote plant growth and alleviate various stresses as well as increase the quantity and quality of the yield of many plant species. Nonetheless, at high concentrations, selenium causes phytotoxicity. In the last decade, nanotechnology has emerged as a prominent tool for enhancing agricultural productivity. The production and applications of nanoparticles (NPs) have greatly increased in many industries, such as energy production, healthcare, agriculture, and environmental protection. The application of NPs has attracted interest for their potential to alleviate abiotic and biotic stresses in a more rapid, cost-effective, and more sustainable way than conventional treatment technologies. Recently, research related to selenium-NPs-mediated abiotic stresses and nutritional improvements in plants has received considerable interest by the scientific community. While significant progress was made in selenium biochemistry in relation to stress tolerance, an in-depth understanding of the molecular mechanisms associated with the selenium- and nano-selenium-mediated stress tolerance and bio-fortification in plants is still lacking. Gaining a better knowledge of the regulatory and molecular mechanisms that control selenium uptake, assimilation, and environmental stress tolerance in plants is therefore essential to develop modern crop varieties that are more resilient to environmental stresses.

In this book, *Selenium and Nano-Selenium in Environmental Stress Management and Crop Quality Improvement*, we present a collection of 20 chapters written by leading experts engaged with selenium- and nano-selenium mediated environmental stress management and crop quality improvement. This book aims to provide a comprehensive overview of the latest understanding of the physiological, biochemical, and molecular basis of selenium- and nano-selenium-mediated environmental stress tolerance and crop quality improvements in plants. This endeavor would help researchers to develop strategies to enhance crop productivity under stressful conditions and to better utilize natural resources to ensure future food security and to reduce environmental pollution. We are extremely grateful to all the learned contributors and sincerely thank them for their contribution in compiling useful and updated information on different aspect of selenium- and nano-selenium-mediated stress tolerance and bio-fortification in plants. Finally, this book will serve as a unique key source of information and knowledge for graduate and postgraduate students, teachers, and frontline environmental stress researchers around the globe and would be a valuable resource for promoting future research in plant stress tolerance as well as crop quality improvement through bio-fortification and phytoremediation. We believe that the information presented in this book will make a sound contribution to this fascinating area of research.

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Tofazzal Islam is a Professor in the Institute of Biotechnology and Genetic Engineering (IBGE) at Bangabandhu Sheikh Mujibur Rahman Agricultural University, Bangladesh. He completed his PhD in applied biosciences at Hokkaido University, Japan. Dr. Tofazzal conducted postdoctoral research at Hokkaido University, the University of Goettingen, the University of Nottingham, and West Virginia University under the fellowship programs of JSPS, Alexander von Humboldt, Commonwealth, and Fulbright, respectively. He has published more than 250 research articles and chapters in international journals and book series. He is the editor-in-chief of two book series, Bacilli and Agrobiotechnology, and CRISPR-Cas Methods published by Springer Nature. He serves as an academic editor of *PLOS ONE* and associate editor of *Frontiers in Microbiology*. An elected fellow of the Bangladesh Academy of Sciences (BAS), The American Phytopathological Society (APS) and The World Academy of Sciences (TWAS), Professor Tofazzal received many awards, prizes, and medals including a Gold Medal of BAS, University Grants Commission Awards, Commonwealth Innovation Award, and Transformer Road Show Innovation Award of Islamic Development Bank, among others. Professor Tofazzal supervised a good number of postdoc, PhD, and MS fellows. His current research foci include genomics, genome editing, plant probiotics, and nanobiotechnology.

Michela Schiavon is Associate Professor of Agriculture Chemistry (2017–) at the University of Turin (Italy). She obtained her MD in biology in 2002 and a PhD in crop productivity in 2006 from the University of Padova (Italy). She was research scientist at the Colorado State University (USA) from 2015 to 2017 and is still a faculty associate member of the same university. Her expertise is in plant nutrition and physiology, crop biofortification, phytoremediation, and plant-rhizosphere interactions. Her research activity was initially focused on studying the physiological and molecular mechanisms of heavy metal tolerance and acquisition by crops, and on metal-nutrient interactions during uptake processes. Then, she developed a major interest in the beneficial element selenium and biostimulants, with focus on their mode of action in crops to enhance NUE and resistance to abiotic stress. The main projects in which she has taken responsibilities or has been involved as an investigator are the following: US National Science Foundation grant IOS-1456361, US National Science Foundation grant MCB-9982432, PRID 2018 (Unipd), and Young Researchers (Unipd). She is a member of the Scientific and Economic Committee of the TEAM-NET (Foundation for Polish Science) Grant Program No. 1/4.4/2018. She has 53 publications in peer-reviewed journals and 14 book chapters. She is the topic editor of the *International Journal of Molecular Sciences* and associate editor of *Plants*.

Chapter 1
Sources of Selenium and Nano-Selenium in Soils and Plants

Hassan El-Ramady, Alaa El-Dein Omara, Tamer El-Sakhawy, József Prokisch, and Eric C. Brevik

1.1 Introduction

Many fascinating aspects of selenium (Se) have been documented since its discovery in 1817. Studies have discussed themes such as Se geochemistry and geopedology (do Nascimento et al. 2021; Favorito et al. 2021), Se biogeochemistry (Wang et al. 2022a), Se plant ecology (Pilon-Smits 2019), Se bioavailability in soil (Xiao et al. 2020a), Se essentiality and metabolism in plants (Lanza and Reis 2021; Trippe III and Pilon-Smits 2021), Se nano-biofortification (El-Ramady et al. 2021a, b), and Se in human health, especially its use against cancer (Li and Xu 2020a, b; Hou et al. 2021) and COVID-19 (Liu et al. 2021d; Majeed et al. 2021). The name

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M. A. Hossain et al. (eds.), *Selenium and Nano-Selenium in Environmental Stress Management and Crop Quality Improvement*, Sustainable Plant Nutrition in a Changing World, https://doi.org/10.1007/978-3-031-07063-1_1

selenium originated from the Greek name “*Selene*”, which means “the goddess of the moon” (Bodnar et al. 2012). Selenium is a trace element that is only needed in very small amounts, and the difference between Se deficiency and its dietary toxicity is very narrow (40–400 μg d^{-1}; Fordyce 2013). This causes concerns in several areas worldwide regarding Se deficiency or Se toxicity (Xiao et al. 2021). The toxic cases of Se mainly depend on the Se content of the seleniferous soil (i.e., high soil content of Se); such soils are found in several locations worldwide including Punjab in India (Solovyev et al. 2018; Chawla et al. 2020), the Central Valley in California, Colorado in the United States (Ekumah et al. 2021; Favorito et al. 2021), and the Enshi region in China (Chang et al. 2019; Lyu et al. 2021). Areas with soil Se levels low enough that it causes health problems include the mountainous belt of northeast China to the Tibetan Plateau, parts of Africa, the Pacific Northwest, Great Lakes region, and east coast in the United States (Brevik 2009).

The global distribution of soils enriched in Se is generally in spots rather than sheets (Rosenfeld et al. 2018). Many factors create this heterogeneous Se distribution in soils, like microbial processes (Wells and Stolz 2020; Wang et al. 2022a), human activities, and geogenic conditions (Reynolds and Pilon-Smits 2018). Soil parent material is considered the major factor controlling soil Se. In general, the highest Se content occurs where the soil parent materials are siliceous and carbonaceous shales, whereas soils with parent materials originating from acidic rocks and Quaternary sediments have the lowest Se content (Liu et al. 2021b). Pedogenic process can also control Se release through the weathering of rocks and redistribution of minerals in soil (Imran et al. 2020; Xiao et al. 2020a). Human activities such as the application of Se fertilizers, smelting of metals, combustion of fossil fuels, and discharge of Se-containing wastewaters can affect Se distribution in soil (Lei et al. 2021). Furthermore, the soil microbial community can impact Se solubility and its release in soil by changing Se forms and valence in the soil (Wang et al. 2022a). Soil matter organic and pH are dominant factors influencing soil Se bioavailability (Liu et al. 2021b). Several studies have been published about global soil Se distribution (e.g., Ekumah et al. 2021), including countries like Brazil (do Nascimento et al. 2021), China (Lei et al. 2021; Liu et al. 2021a; Lyu et al. 2021; Zhong et al. 2021), Pakistan (Imran et al. 2020), the United States (Favorito et al. 2021), and France (Pisarek et al. 2021), whereas the global distribution of nano-Se in soils and plants need more investigation.

Therefore, the main objective of this chapter is to discuss different sources of both selenium and nano-selenium in soils and cultivated plants. Bioavailability of Se and nano-Se in soil, the factors that influence it, their microbial transformations, and their potential impacts on human health are also highlighted.

1.2 Sources of Selenium and Nano-Se in Soils and Plants

Selenium (Se) is widespread across all compartments of the Earth including the atmosphere, hydrosphere, lithosphere, and biosphere (Hossain et al. 2021). Selenium ranks as the 67th most abundant element, 145th among hazardous and toxic ingredients, and 125th as a priority pollutant (Hasanuzzaman et al. 2020). The main source of Se in soils are Se-containing minerals, which represent more than 50 types including berzelianite ($Cu_{2-x}Se$), clausthalite (PbSe), crookesite ($(Cu,Tl,Ag)_2Se$), klockmanite (CuSe), tiemannite (HgSe), and ferroselenite ($FeSe_2$). The mean Se content in the Earth's crust is estimated as 0.05 mg kg^{-1}, whereas the mean global Se content in soil is 0.44 mg kg^{-1} (Kabata-Pendias 2011). Selenium content in soil varies from place to place based on the parent material, with higher values in soils formed in argillaceous sediments (0.3–0.6 mg kg^{-1}) as compared to sandstones and limestones (0.01–0.1 mg kg^{-1}). Cretaceous rocks are often an enriched Se source (>100 mg kg^{-1}) because many of them were derived from volcanic dust and gases brought down by rain into the Cretaceous Sea (Kabata-Pendias and Mukherjee 2007). In general, there are two main sources of Se in the environment, natural sources and artificial or man-made sources (El-Ramady et al. 2015). Natural sources of Se include volcanic activity (Floor and Román-Ross 2012), weathering of rocks (Tian et al. 2020), sea spray, atmospheric flux (Roulier et al. 2021), volatilization, and recycling from biota and aerial deposition (Fordyce 2013; do Nascimento et al. 2021). Volatile Se compounds in the atmosphere include hydrogen selenide (H_2Se) and selenium oxide (SeO_2) as inorganic gaseous Se forms and dimethyl di-selenide (DMDSe), dimethyl seleno-sulfide (DMSeS), dimethyl selenone ($DMSeO_2$), and dimethyl selenide (DMSe) as organic Se gaseous forms (Hossain et al. 2021; Ye et al. 2021).

Selenium mining districts are widely distributed based on geogenic origin. There are many natural ores of Se, and mining depends on the composition of these ores, the tectonic setting, and the stratigraphic position of ore minerals (Funari et al. 2021). The main Se ore minerals are associated with igneous rocks like volcanogenic sulfides (i.e., volcanogenic massive sulfides and native sulfur) and sedimentary sources (e.g., polymetallic nodules, phosphorites, shales, and marine seafloor sediments) (Funari et al. 2021). The total content of soil Se can be divided into five levels based on Se abundance and its environmental risk: deficient, low, medium, high, and excessive ($<$ 0.125, 0.125–0.175, 0.175–0.40, 0.40–3.0, and $>$ 3.0 mg kg^{-1}), respectively (Lyu et al. 2021). Several spots of high Se content soils (seleniferous soils) have been observed in countries like China, the United States, Russia, Australia, Canada, and Ireland (Table 1.1), whereas more than 70% of countries have soils that are considered Se deficient including wide portions of Europe and New Zealand (Hossain et al. 2021). Selenium availability to cultivated plants depends on many soil chemical and biochemical characteristics, including sorption, soil pH, presence of other nutrients like S and P, and methylation process (Hossain et al. 2021). The total Se content in soils is not a reliable parameter for measuring plant-found Se or the amount of Se available to humans and animals through plants (Hossain et al. 2021). Humans may control the Se content in soil through many activities such as metal smelting, combustion of fossil fuels, and the over-use of mineral fertilizers (Hossain et al. 2021). In general, most cultivated plants have a low Se content (around 25 μg kg^{-1}), whereas high Se content (exceeding 100 μg kg^{-1}) is rare, but could be found in Se-accumulating plants. These plants may accumulate Se to extremely high levels of over 1000 mg kg^{-1}, which may cause toxicity to

Table 1.1 Se abundance in many different soils around the globe

Studied location (the country)	Number of sampling sites	Total Se content (mg kg^{-1}) in soil	Soil type or Se category	Reference
Pine ridge Fort Collins, Colorado (USA)	–	8.20	Seleniferous soils	Yasin et al. (2015)
Punjab (India)	–	0.024–3.06 (0.449)	Seleniferous soils	Dhillon and Dhillon (2016)
Australia	1315	< 0.01–2.0 (0.06)	Australian soils	Reimann and de Caritat (2017)
The east bank of Dianchi Lake (China)	130	0.10–0.35 (0.20)	Greenhouse soils	Jia et al. (2019)
The USA	4857	< 0.2–8.3 (0.20)	U.S. soils	Smith et al. (2019)
Pothwar uplands (Pakistan)	45	0.27–7.05 (0.74)	Soils from different parent materials	Imran et al. (2020)
Hechi, Guangxi (China)	60	0.288–1.673 (0.705)	Cropland and woodland soils	Xiao et al. (2020a)
Karst area, Guangxi Zhuang, (Southwest China)	125	0.22–1.820 (0.676)	Soil of cropland, grassland, shrubland, and secondary forest	Xiao et al. (2020b)
Western phosphate resource area (the USA)	–	2.7–435	Seleniferous soils	Favorito et al. (2021)
Enshi, Hubei Province (China)	92	0.12–20.62 (2.01)	Seleniferous soils	Lyu et al. (2021)
Aksu, Xinjiang (China)	183	0.22–1.90 (0.56)	Oasis farmland soils	Lei et al. (2021)
Southwest China	3382	0.010–16.24 (0.171)	Mainland soils	Liu et al. (2021a)
Forest sites from the French RENECOFOR network (France)	51	25–1222	Forest soils	Pisarek et al. (2021)
Heilongjiang Province (China)	160	0.045–0.444 (0.228)	Black soil region	Zhong et al. (2021)
Rio Grande do Norte and Paraíba, northeastern (Brazil)	198	0.02–1.7 (0.30)	Se-deficient soils in the semi-arid regions	do Nascimento et al. (2021)
Southern Songnen plain (China)	20,929	0.01–1.14 (0.29)	Cropland soils	Yang eta l. (2021)
Naore Village, Ziyang County, Shaanxi Province (China)	14	1.99–8.54	Natural seleniferous soils	Zhou et al. (2021c)
Western Jinhua City, Zhejiang Province (China)	53	0.1789–0.5738 (0.40)	Farming pattern in Se-enriched soils	Wang et al. (2022a)

Values in parentheses show the mean value humans and animals (El-Ramady et al. 2015). The main source of Se to cultivated plants is applied through Se fertilizers; plants can uptake this nutrient in selenite ($SeO_3{}^{2-}$) and selenate ($SeO_4{}^{2-}$) forms (Trippe III and Pilon-Smits 2021). The uptake of Se and its bioavailability will be discussed in the next section. Elemental Se can be precipitated as Se homo-spheres during the biological preparing method of bio-nano-Se. Red elemental nano-Se spheres in water may produce H_2Se and H_2SeO_3 in small amounts as shown in Eq. 1.1:

$$3Se + 3H_2O \leftrightarrow 2H_2Se + H_2SeO_3 \quad (1.1)$$

H_2Se and H_2SeO_3 are formed in solution. When the solution dries, the H_2Se and H_2SeO_3 react with each other and elemental selenium is precipitated, forming crystals (El-Ramady et al. 2015).

1.3 Bioavailability of Se and Nano-Se in Soil and Controlling Factors

Selenium occurs in multiple valence states (i.e., −2, 0, +2, +4, and + 6), which include the metal selenide (Se^-, Se^{2-}), elemental Se or nano-Se (Se^0), thio-selenate ($SSeO_3{}^{2-}$), selenite ($SeO_3{}^{2-}$), and selenate ($SeO_4{}^2$). Several natural soil factors control the bioavailability of Se and nano-Se (i.e., Se that can be taken up by plants), including physical (e.g., sorption impacts of soils and sediments), chemical (soil pH, organic matter content, redox potential, Fe/Al oxides content [Jones et al. 2017; Fan et al. 2018; Xu et al. 2018; Deng et al. 2021; Wang et al. 2018a, b], and competitive ions [Lyu et al. 2021]) and biological (reduction and methylation) factors (Hasanuzzaman et al. 2020; Xu et al. 2020). Other factors that influence Se and nano-Se bioavailability include exogenous applied Se or Se fertilizer type (Li et al. 2021) and the kind of cultivated plants like wheat (El-Saadony et al. 2021; Liu et al. 2021b), rice (Lyu et al. 2021), soybean (Deng et al. 2021), and maize (Wang et al. 2019a). This is explored in more detail in Table 1.2.

1.3.1 Soil pH and Redox Potential (Eh)

The total Se content in soils is not an accurate indicator for Se bioavailability, whereas the fractionation of Se in the soil is the main factor controlling the transformation of Se, migration, and its bioavailability in soil (Fordyce 2013). The speciation of Se and its fractionation in soil can be regulated through processes such as dissolution/precipitation, adsorption/desorption, and oxidation/reduction. The classical method for Se sequential extraction is widely applied to determine soil Se fractions, and the results can be used to predict Se uptake by plants (Wang et al.

Table 1.2 Some recent published articles that explore Se fertilizers for different crops, the bioavailability of Se in soil, and controlling factors

Se fertilizer type (soil properties)	Applied dose of Se fertilizer (mg kg^{-1})	Target crop	Main aim of study	Reference
Pots filled with peatmoss and perlite at 2:1	Foliar applied nano-Se (50–150 nm) at 5, 10, 15, 20 mg l^{-1}	Korean ginseng (*Panax ginseng* C. A. Meyer)	Oxidative stress resulted from 20 mg l^{-1}, which accumulated high ginsenoside and increasing quality of ginseng roots.	Abid et al. (2021)
Field experiment: Soil pH 5.9; total Se 0.4 mg kg^{-1}; SOM 18.0 g kg^{-1}	Foliar se-doses (Na_2SeO_4) at 5, 10 and 20 g ha^{-1}	Wheat (*Triticum* spp.) var. IAC 385	Under lower Se doses (5 g ha^{-1}), highest absorption efficiency with supply up to 75% of the recommended daily intake	Delaqua et al. (2021)
Pot experiments (soil pH 5.68 & 7.87; SOM 15.32 & 16.28 g kg^{-1}; total Se 0.14 & 0.16 mg kg^{-1})	Soil applied Na_2SeO_4 at 2 mg kg^{-1}) with or without S-fertilizer (100 mg kg^{-1})	Soybean (*Glycine max* L.)	Se bioavailability in calcareous alluvial soil was higher compared to yellow–brown soil, whereas S application inhibited Se uptake in both soil types, without any impact on Se speciation in seeds.	Deng et al. (2021)
Bio- and chemical Se-NPs; pots filled with soil (50% sand and 50% clay)	Each Se-NP applied at 50, 75, 100, 125, and 150 μg ml^{-1}	Wheat (*Triticum asetivum* L.) cv. Masr1	Applied Bio-Se-NPs at 100 μg ml^{-1} reduced root rot disease incidence in wheat; enhanced plant tolerance to drought and heat stress by increasing the growth and productivity of wheat.	El-Saadony et al. (2021)
Mineral Se (soil pH 5.5; SOM 18 g kg^{-1})	Selenate/selenite foliar applied at 0.075–0.15 kg ha^{-1}	Apple (*Malus domestica*)	Improved protein content in different varieties of apple by foliar Se fertilizer, which enhanced tolerant apple to stress.	Groth et al. (2021)
Field experiment: Soil pH 4.6; total and available Se 45 and 3.0 μg kg^{-1}	Foliar Se at 10, 25, 50, 100, and 150 g ha^{-1} as sodium selenate	Cowpea (*Vigna unguiculata* L.)	Optimal foliar Se was 50 g Se ha^{-1} to increase the yield and higher rates caused oxidative stress, which may be linked to stress attenuation caused by Se.	Lanza et al. (2021)

(continued)

Table 1.2 (continued)

Se fertilizer type (soil properties)	Applied dose of Se fertilizer (mg kg^{-1})	Target crop	Main aim of study	Reference
Organic Se fertilizer (soil pH 8.68; total Se 0.086 mg kg^{-1})	Se-IV at 36.4 mg kg^{-1}; NPK ≥ 5%; organic matter ≥45%	Naked oat (*Avena nuda* L.)	The grain yield and its quality were increased by combined foliar and soil Se fertilizer, as well as the total se, and organic Se content.	Li et al. (2021)
Hydroponics	Spray 20 ml of se, as Na_2SeO_3 at 2 mg L^{-1} every day for 5 consecutive days	Tea (*Camellia sinensis*) cv. Longjing 43	Under low temperature (4 °C), applied Se increased sugar accumulation, promoted the synthesis of amino acids and improved tea quality.	Liu et al. (2021c)
Field experiment (soil pH 6.8, SOM 23.3 g kg^{-1}, total Se 0.031 mg kg^{-1})	Foliar and root applied Na_2SeO_3 at 50, 75 and 100 g ha^{-1}	Peanut (*Arachis hypogaea* L.)	Se-fertilizer can enhance both inorganic and organic Se content in peanut kernels by foliar spraying as an effective bio-transformation of se.	Luo et al. (2021)
Greenhouse pots; pH 5.32; SOM 44.66 g kg^{-1}; total Se 0.66 mg kg^{-1}	–	Rice (*Oryza sativa* L.) cv. Minfengyou 3301	Se-bioavailability is controlled by SOM and pH; predominant Se fraction is OM-Se and has low mobility; exploring Se bioavailability in naturally seleniferous soils is crucial to the stable production of Se-enriched agricultural products.	Lyu et al. (2021)
Soilless system (nutrient solution, EC 3.6 mS cm^{-1} and the pH 5.6)	Fertigation was used for Se in the nutrient solution (1.0, 2.0, 4.0 µmol·L^{-1})	Cherry tomato (*Solanum lycopersicum* L)	Se applied at 2.0 µmol L^{-1} improved total fruit yield and N use efficiency by 31.4 and 31.5% in grafted plants, respt. With similar trend for 4.0 µmol L^{-1}.	Sabatino et al. (2021)
Biological nano-Se (soil EC 4.49 dS m^{-1}, pH 8.66)	Foliar application at 25 mg L^{-1}	Cucumber (*Cucumis sativus* L.)	Under combined salinity and heat stress, boi-nano-Se increased the growth and productivity of cucumber in net house.	Shalaby et al. (2021)

(continued)

Table 1.2 (continued)

Se fertilizer type (soil properties)	Applied dose of Se fertilizer (mg kg^{-1})	Target crop	Main aim of study	Reference
Field experiment (SOM 126 g kg^{-1}, available Se 0.21 mg kg^{-1})	Foliar applied sodium selenite at rate of 1.2 kg ha^{-1}	Alfalfa (*Medicago sativa* L.) cv. Kangsai	Proteomics level is an important tool to assist in a more detailed elucidation of Se enrichment in alfalfa for the future.	Wang et al. (2021a)
Pot experiment (soil pH 7.89; total Se 0.058 mg kg^{-1}, SOM 14.44 g kg^{-1})	Se fertilizers as selenate and selenite were applied at 1 and 10 mg Se kg^{-1}	Wheat (*Triticum aestivum* L.) eight cultivars	Applied Se at rate of 10 mg kg^{-1} decreased grain yield; Se selenite was almost accumulated in grain and roots, whereas in leaves and straw for Se selenate.	Wang et al. (2021b)
Field experiment (soil pH 4.71, total Se 0.38 mg kg^{-1}, SOM 41.26 g kg^{-1})	Foliar spray sodium selenite at rate of 12.5, 25, 50 and 100 mg L^{-1}	*Atractylodes macrocephala* Koidz	Optimal foliar Se fertilizer was at 25–50 mg L^{-1} Se on these medicinal plants to enhance plant growth, soil nutrients in the rhizosphere, and soil microbial community composition.	Zhou et al. (2021b)
Pot experiment (soil pH = 5.93; total Se 0.61 mg kg^{-1})	Se-fertilizer as Na_2SeO_4 or selenite applied to soil at 0.5 mg kg – 1	Rice (*Oryza sativa* L. cv. Xinliangyou 6)	Organic Se content of the rice grain enhanced by combined soil applied arbuscular mycorrhizal fungus and mineral Se fertilizer.	Chen et al. (2020)
Field experiment (soil pH 7.5, total Se 0.11 mg kg^{-1}, SOM 8.6 g kg^{-1}	Spraying Na_2SeO_4 at levels of 1.5 and 3 mg L^{-1}	Canola (*Brassica napus* L.)	High yield of canola could be achieved by Se spraying at 1.5 mg L^{-1} Se under sub-tropical dryland conditions.	Mohtashami et al. (2020)
Pot experiment (soil silty loam; pH 7.02)	Foliar applied 15 and 30 ppm Se as sodium selenate	Garlic (*Allium sativum* L.)	The simultaneous application of gypsum (20 and 40 mg S kg^{-1} soil) and Se foliar spraying improved the nutritional value of garlic plants.	Sohrabi et al. (2020)

SOM = soil organic matter

2019b). However, Se uptake by plants is a dynamic process, and the results of sequential extraction do not fully reflect Se fractionation and its dynamics in soil (Lyu et al. 2021).

Soil pH and redox potential (Eh) are considered important factors controlling Se bioavailability for plants (Natasha et al. 2018). The selenate form of Se is dominant in alkaline and oxidizing soils (with electron activity pE + pH > 15), whereas under acidic and neutral conditions, selenite will be present as $7.5 < pE + pH < 15$ (Elrashidi et al. 1987). Many studies confirm that Se bioavailability may vary across such distinct soil types with varying pH levels (e.g., Deng et al. 2021; Lyu et al. 2021). Xiao et al. (2020a) reported that Se bioavailability in soil generally declines with decreasing soil pH. Under low soil pH (acidic soil), total Se content tends to be low compared to alkaline or neutral soils (Table 1.3). In general, Se bioavailability decreases when the soil contains high levels of SOM, clay, and Fe-oxides. In acidic soils (low pH), SeO_3^{2-} is the dominant Se form, but in alkaline soils (high pH) the dominant form is SeO_4^{2-}.

Table 1.3 Impact of soil pH and organic matter content on total Se content in some Chinese soils

Sample no.	Chinese location	Soil pH	Soil organic matter (g kg^{-1})	Total Se in soil (mg kg^{-1})
3	Ertaihuang	5.21	36.33	0.50
1	Huangjintang	5.32	44.66	0.66
4	Longtan	5.72	25.56	1.76
10	Tongluo	5.78	15.82	0.55
9	Xiaomaotian	6.04	32.02	0.59
17	Hongyansi	6.15	32.35	0.27
20	Shenjiahuang	6.18	32.42	0.19
6	Menghualing	6.32	28.34	0.68
12	Guihuashu	6.52	26.63	0.75
7	Lanhongcao	6.53	54.51	3.32
21	Xinchang	6.54	26.79	0.12
13	Yujingba	6.65	27.19	0.47
2	Weijiaya	6.78	79.66	2.59
15	Juweihui	6.84	38.70	0.80
22	Heixiba	6.91	28.40	0.13
23	Yaoziping	6.96	64.15	20.37
64	Cheyun	7.01	27.54	1.53
36	Sunjiaba	7.16	36.73	0.44
53	Xiaqipeng	7.28	97.13	4.03
86	Fengchunba	7.35	19.59	1.31
38	Qiyangba	7.43	67.35	5.55
5	Chahouzi	7.46	21.43	0.19
42	Huangyan	7.65	53.53	0.99
44	Leijia	7.70	51.16	2.64
11	Huolong	7.72	34.33	1.49
30	Fenghuangguan	7.78	36.84	0.36
14	Yangjiaoshan	7.84	43.31	3.94

Source: extracted from Lyu et al. (2021)

1.3.2 Soil Organic Matter

Soil organic matter (SOM) is an important soil factor controlling Se bioavailability, which links to many human issues like Se risk environmental assessment and Se biofortification for human health (Li et al. 2017a). The interaction between SOM and soil Se content under soil–plant systems is a dual effect through two dimensions: enhancing or reducing Se bioavailability in soil (Wang et al. 2017). In other words, SOM can immobilize Se in soil through abiotic and biotic mechanisms and/or release of SOM-immobilized Se via the mineralization process (Li et al. 2017a). In general, selenite is less bioavailable in soil due to its easy adsorption and immobilization through Fe/Al-oxides or their hydroxides in soils (Francisco et al. 2018), whereas selenate is unlikely to be immobilized and/or adsorbed in soils leading to relatively high Se bioavailability (Deng et al. 2021). Soil organic acids may interact with Se in soil through many processes like adsorption, reduction, and complexation. These acids may lead to Se mobilization and immobilization in soil, which control Se bioavailability. Fulvic acid Se is considered a latent source of available Se in soil and humic acid Se is a sink of Se under some conditions (Dinh et al. 2017).

Therefore, the composition of SOM can play a crucial role in Se bioavailability or its binding speciation with Se (Li et al. 2017a). Moreover, based on the strong adsorption capacity of SOM and its large specific surface area, soil Fe/Al oxides and minerals may play decisive roles in Se adsorption and fixation in soil, which directly affect Se bioavailability (Liu et al. 2021b). Thus, the main dominant influential factors for soil Se bioavailability should be clarified as well as establishing a proper prediction model for Se bioavailability, and Se bioavailability can be regulated by different agronomic parameters for the proper utilization of the soil Se resource to produce natural Se biofortified foods (Dinh et al. 2018, 2019; Liu et al. 2021b). Many studies have investigated the bioavailability of Se in soil and the role of SOM in this context, such as Li et al. (2017a), Cheng et al. (2020), Lyu et al. (2021), and Liu et al. (2021b). There are few published materials on SOM and nano-Se, but Wang et al. (2019c, d) reported that particulate organic matter (at a level of 60 mg L^{-1}) can impact the fate of Se-NPs in the environment by inhibiting their homo-aggregation and hetero-aggregation as well as enhancing the stability of Se-NPs. More investigations are needed to focus on the bioavailability of nano-Se in soils and its transformation under cultivated plant conditions.

1.3.3 Parent Materials

Parent materials play a crucial role in Se bioavailability because the soils are mainly derived from these materials, and the chemical composition of soils is largely determined by their parent materials. Selenium content in soils also depends on pedogenic processes (i.e., additions like OM, losses by processes, such as erosion and leaching, transformations by weathering, and translocations within the profile

[Simonson 1959]). Thus, soil Se level could be determined based on the parent materials as main sources (Reynolds and Pilon-Smits 2018, Jia et al. 2019). Parent materials also can exert a strong control on many soil physicochemical properties, further impacting the behavior of Se in soils (Carvalho et al. 2019). The total Se in soil could be used in general to assess potential Se uptake and its utilization by plants, however, based on the selectivity of plants and the bioavailability of Se, the Se content of plants grown in seleniferous soils may not achieve Se-enriched standards (Li et al. 2017a; Wang et al. 2019a, b). Therefore, identifying the bioavailable Se or soil Se supply capacity is important for predicting the Se content in plants (Liu et al. 2021b). Many studies have investigated the role of parent materials in determining Se bioavailability in soil such as Jia et al. (2019), Xiao et al. (2020a), and Liu et al. (2021b).

1.3.4 Land Use

Changes in land use or land cover are an important aspect of global change, which is accompanied by changes in the communities of plants which strongly influences the properties of soil, particularly SOM. This change can be linked to the biogeochemical cycles of many essential nutrients like N, P, K, S, Ca, Mg, Cu, Mn, Mo, etc. (Li et al. 2018). Recently, several studies confirmed that land use influences many soil properties and processes (Wang et al. 2018b). Local geology may greatly influence the effects of land use on different biogeochemical cycles of nutrients, including selenium (Xiao et al. 2020b). Land use change has a direct relationship with many soil attributes like pH, soil organic carbon, and metal oxides contents (Lizaga et al. 2019), which are closely related to the behavior of Se in the environment (Li et al. 2017b). Thus, it could logically be assumed that the cycling of soil Se might be substantially changed by land use conversions. Therefore, there is an urgent need for precise understanding of the fate and behavior of soil Se as well as factors controlling the magnitude and direction of land use effects to manage soil Se resources and improve Se status in human populations under future land use change scenarios (Xiao et al. 2020a).

In addition, the climate and its changes are also important factors controlling Se biogeochemistry in soil, which can impact soil Se abundance directly through atmospheric Se deposition (Sun et al. 2016) or indirectly by influencing the uptake of Se by plants, which climatic elements including temperature and moisture control this uptake. Depending on climatic conditions and soil type, the previous factors (climate and soil factors) may act alone, or in combination with each other, to mediate soil Se abundance and its bioavailability (Xiao et al. 2020b). There are limited studies on Se variations in soil under various land use or land cover types (Plak and Bartminski 2017), and there is no general consensus yet on the magnitude and direction of land use change effects on Se abundance and its bioavailability in soil. Some authors, such as Xing et al. (2015), reported that Se is more enriched in forest soils compared to agricultural soils, but Shang et al. (2015) reported the opposite.

Therefore, there is a need for more information on Se dynamics in soil under different scenarios of global change, particularly changes in global land use/land cover (Xiao et al. 2020b).

1.3.5 Soil Amendments

Any material added to improve soil properties (e.g., permeability, aeration, drainage, water retention, infiltration, nutrient status, biome changes) is called a soil amendment. This amending action could be achieved by applying organic (e.g., mulching, green manure, compost, peat, biochar) and/or inorganic or mineral amendments (e.g., gypsum, fly ash, lime, vermiculite, fertilizers). Organic or mineral amendments could improve Se bioavailability in soil (Table 1.4). Several studies have been published that investigate Se bioavailability under different soil amendments such as zinc sulfate (Xue et al. 2020), chicken manure (Dinh et al. 2021), vermicompost (Liu et al. 2020), biochar (Wang et al. 2019d; Mandal et al. 2020; Wei et al. 2021), and nanomaterials like nano-biochar (Mandal et al. 2020).

1.4 Microbial Transformation of Se and Nano-Se in Soils

Selenium and nano-Se have distinct chemical reactions and transformations in soil. These include oxidation, reduction, methylation, and demethylation (Nancharaiah and Lens 2015). Microbial Se oxidation did not receive a significant amount of attention during the last decades due to the low oxidation rate of Se, which increased the difficulty of researching this element (Wells and Stolz 2020). Due to its essentiality for microorganisms, Se microbial transformations in soils have received increasing attention recently including Se dissimilatory reduction under aerobic and anaerobic conditions and its bioremediation applications (Wang et al. 2022b). Many studies on the transformations and applications of Se have been published recently focusing on topics such as Se bioremediation (Paul and Saha 2019; Huang et al. 2021a), Se biogeochemistry and its ecophysiology (Wells and Stolz 2020; Wang et al. 2022a), assimilatory genomes (Davy and Castellano 2018), Se biosynthesized nanoparticles (Mulla et al. 2020; Borah et al. 2021; El-Saadony et al. 2021; Sun et al. 2021), Se applications (Ojeda et al. 2020; Huang et al. 2021b), reducing plant uptake of heavy metals from soil by Se (Handa et al. 2019; Niu et al. 2020; Feng et al. 2021a, b), effects of Se nanoparticles on plant biology (Zsiros et al. 2019; Zhou et al. 2021d) and their tolerance against stress (Joshi et al. 2021; Qi et al. 2021; Shalaby et al. 2021), Se volatilization from soils (Ye et al. 2021; Zhou et al. 2021a), and Se microbial reduction and its resistance (Lusa et al. 2019; Zhou et al. 2021a; Wang et al. 2022b).

Selenium is characterized by its ability to volatilize some Se forms into the atmosphere such as H_2Se, DMSe, DMDSe, DMSeS, and $DMSeO_2$, where “DMSe” is the

Table 1.4 Impact of some soil amendments on the bioavailability of Se in soil

Experimentation and soil properties	Applied Se dose (mg kg^{-1})	Applied soil amendment	Main effects of applied soil amendments on Se availability.	References
Pot experiment (soil pH 7.75, 55.0 g kg^{-1} $CaCO_3$; total Se 0.1 mg kg^{-1}; SOM 16.3 g kg^{-1})	Applied selenite at 1.0 and 2.5 mg se·kg^{-1} soil	Applied cow or chicken manure at 2, 4 and 6%	Simultaneously applied chicken or cow manure with Se as selenite could lead to decreased Se availability to Chinese mustard.	Dinh et al. (2021)
Pot experiment (soil pH 5.42; available cd 2.96 mg kg^{-1})	Total Se content in soil was 0.31 mg kg^{-1}	Lime at 0.03–0.12%, bentonite at 6 and 12 g kg^{-1}; biochar at 0.3, 0.9, 1.8 g kg^{-1}	Applied agricultural lime, ca − bentonite, and rape straw biochar or lime and biochar increased soil pH values and SOC to remediate high Se soil polluted by cd.	Xu et al. (2021)
Batch experiments (pH 6.3)	Applied Se (VI) at 2 mg L^{-1}	Biochar added at 3 g L^{-1} soil	Biochar supporting iron-based nano-particles had high removal rate of SeO_4^{2-} by highly reversible adsorption.	Wei et al. (2021)
Batch experiments (pH 6.36, total Se 0.093 mg kg^{-1})	Applied Se (VI) at 150 mg kg^{-1}	Biochar added at 10 g kg^{-1} soil	Biochar-supported nanoscale zero-valent iron and polysulfide decreased Se availability by 77.3% after 30 days.	Mandal et al. (2020)
Rhizobox experiment (pH 5.0, SOM 41.1 g kg^{-1}; total Se 0.34 mg kg^{-1})	Applied Se at 0.5 and 5.0 mg kg^{-1} soil as Na_2SeO_3	Root secretion of organic acids (indigenous)	High Se rice cultivar could activate Se by increasing soil pH and regulate rice root secretion of organic acids compared to the low-Se rice cultivar.	Zhang et al. (2019)
Pot experiment (soil pH 7.75; SOM 16.3 g kg^{-1}; total Se 0.1 mg kg^{-1})	Selenate as fertilizer applied at 1.0 mg kg^{-1}	Wheat straw & pak choi-Se enriched at 21.35 & 47.48 mg kg^{-1}, respectively	Exchangeable Se and fulvic acid-bound Se-fraction could better reflect availability of Se in organic materials amended soils, where Se-enriched pak choi was better in Se-utilization efficiency than wheat straw.	Wang et al. (2018a)

main dominant volatile Se species (Ye et al. 2021). Se volatilization due to biological methylation into the atmosphere is considered an important process of Se biogeochemical cycling in agroecosystems. About 50–70% of total global emission is the gaseous emission of Se from natural sources into the atmosphere (Ye et al.

2021). The volatile Se fractions can be produced in natural environments through the biological methylation of organic and inorganic Se species by microorganisms, plants, and animals. There are many precursors or intermediates in the Se methylation process including inorganic (i.e., selenate and selenite) and organic Se fractions such as methyl-seleninic acid (CH_3SeO_3H), seleno-methionine (SeMet), selenocystine, and dimethyl-selenoniopropionate (Moreno-Martin et al. 2021). There are limited studies on Se volatilization, particularly as regards Se-enriched plants/soils and Se-polluted environments (Ye et al. 2021). The great role of microorganisms in the Se cycle is to biosynthesize nano-Se. Bacteria can biosynthesize spherical Se-nanoparticles (11–700 nm in diameter), whereas fungi can biosynthesize smaller Se-NPs that range from 17 to 150 nm (Wang et al. 2022b).

1.5 Selenium and Nano-Se for Human Health

Humans need Se as an essential element (Brevik 2009). Therefore, Se supplementations can be important to improve human immunity and fertility, as well resistance to problems like tumors and pathogens (Fig. 1.1). However, excessive Se supplementation can cause toxic impacts due to Se duality, and may in severe cases lead to death (Lv et al. 2021). Several years ago, Se was thought to be poisonous, but in 1957, its essentiality and importance in small amounts were established. Now, Se is

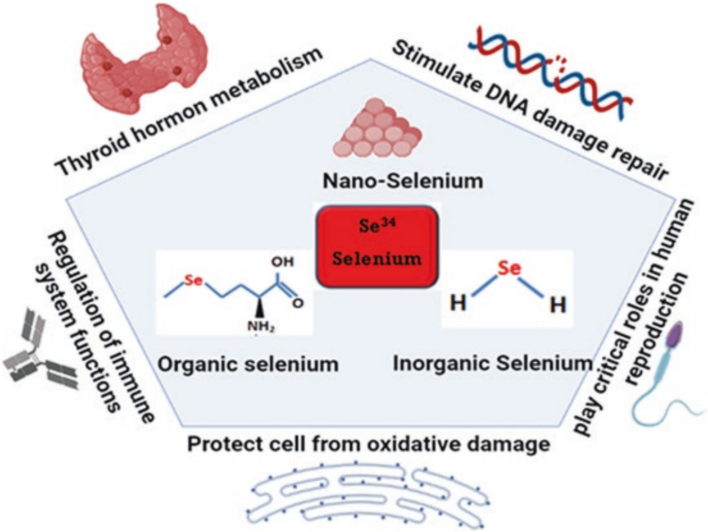

Fig. 1.1 Forms of selenium in the human diet and its physiological effects on body functions, which include the role of Se in protecting human cells from oxidative damage, its crucial role in human reproduction, repairing DNA damage, importance for metabolism of thyroid hormone, and regulation of immune system functions. (This figure was created at BioRender.com)

recognized as an essential micronutrient for the proper functioning of several physiological processes, such as its antioxidative properties, synthesis of thyroid hormone, and its support for metabolic functions (Pappas et al. 2019; Ryant et al. 2020). The antioxidative properties of Se are linked to its significance as a component of certain proteins, which are referred to as selenoenzymes and selenoproteins (Santesmasses et al. 2020; Ekumah et al. 2021). Selenium deficiency in humans can result in “Kashin–Beck disease” and “Keshan disease”, whereas Se toxicity leads to nail and hair loss, nervous system disorders, and other symptoms in humans (Liu et al. 2021a).

Biofortification can be used to increase available Se content in soil and, through that, in crops raised for human consumption. Several studies have investigated the production of crops biofortified with Se (e.g., Shalaby et al. 2017; Schiavon et al. 2020; Sarwar et al. 2020; Zagrodzki et al. 2020; Kleine-Kalmer et al. 2021; Izydorczyk et al. 2021; and Tiozon et al. 2021). Biofortification with nano-Se still needs more investigation (El-Ramady et al. 2020, 2021a, b; Ranjitha and Rai 2021). Considering the health benefits of nano-Se and its applications, Kumar and Prasad (2021) reported that these applications may include (1) using nano-Se as antioxidant agents to prevent cellular damages caused by free radicals (Qamar et al. 2021), (2) Se-NPs as anticancer agents (Li and Xu 2020b), (3) nano-Se to control the growth of various pathogenic microbes (Rajagopal et al. 2021), (4) nano-Se to control diabetes (Abdulmalek and Balbaa 2019), (5) nano-Se for bioremediation and wastewater treatment (Chauhan et al. 2021), and (6) Se-NPs for the fabrication of nano-biosensors that could be used to diagnose diseases, test drugs, and monitor and detection environmental pollutants (Huang et al. 2021b).

1.6 Conclusions

Selenium is an essential nutrient for human health but still needs to be confirmed as essential for higher plants. A great amount of recent attention has been paid to the use of nano-Se to enhance human health, particularly against diseases like COVID-19. The main sources of Se in soils include parent materials, which depends on their mineralogic composition. Several recent studies confirmed that Se applied at a low concentration shows positive impacts on the growth of cultivated plants, including their development and yield. Therefore, Se is a vital nutrient through the way it changes many physiological and biochemical processes in plants (e.g., antioxidant defense, tolerance against many abiotic stresses like drought, salinity, extreme temperature, and toxic element stress). Many factors control the bioavailability of Se such as soil pH, redox potential (Eh), soil organic matter, clay content (soil texture), parent materials, land use or cover, and soil amendments.

The main forms of Se include selenite, selenate, and selenide, as well as nano-selenium. Soil microorganisms have roles in several reactions that influence the species of Se found in soils. Selenium bioavailability in soil depends heavily on Se speciation and how that affects binding to different soil fractions. Available soil Se fractions (i.e., exchangeable Se and its water-soluble fraction) are a more critical indicator of Se deficiency or Se excess than total content. Cultivated plants have the ability to uptake Se from soil and alter Se bioavailability and mobility via many processes such as excreting organic acids (e.g., citrate, oxalate, and malate), which lead to complexation, adsorption, and reduction of soil Se. The fate and behavior of Se in soil is important for crops and of consequence to human health. Selenium may be either detrimental or beneficial to human health, and the range between deficient and toxic is small. Therefore, understanding soil Se and the processes that influence its bioavailability as well as its association with human health are of great concern for both policy makers and the scientific community. There are still many open questions about Se in soils.

Acknowledgments This work was financialized and supported by the Central Department of Mission, Egyptian Ministry of Higher Education (Mission 19/2020) for H. El-Ramady and also by the Hungarian Tempus Public Foundation (TPF), grant no. AK-00152-002/2021.

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Chapter 2
Synthesis and Characterization of Nano-Selenium Using Plant Biomolecules and Their Potential Applications

Mohd Ahmar Rauf, Jolly Jolly, and Zeeshan Ahmad

2.1 Introduction

Nanotechnology has become one of the most promising interdisciplinary technologies, connecting physics, chemistry, biology, materials science, electronics, and medicine (Marjorie et al. 2021). The quantity of engineered nanoparticles (NPs) is expected to increase significantly in the years to come as they receive growing global attention due to their attractive properties, multi functionalities, unique characteristics, and innovative applications in different industrial and scientific domes (Marjorie et al. 2021). Nanomaterials are of great interest due to their unique physical, chemical, optical, electronic, and thermal properties (Manna et al. 2000). Among various types of nanomaterials, semiconductor NPs are widely explored because they have excellent nonlinear properties, saturable absorption, and optical biostability (Manna et al. 2000). Nanomaterials (NMs) fabrication can be achieved involving different physical and chemical techniques; apart from this, biogenic synthesis was also employed (Devanesan et al. 2018). The physical and chemical synthesis methods may produce high radiation, and toxic reductants can affect both humans and other living organisms (Devanesan et al. 2018). In distinction, green synthesis route is a single step to synthesizing NPs with low cost and eco-friendliness

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M. A. Hossain et al. (eds.), *Selenium and Nano-Selenium in Environmental Stress Management and Crop Quality Improvement*, Sustainable Plant Nutrition in a Changing World, https://doi.org/10.1007/978-3-031-07063-1_2

(Elechiguerra et al. 2005; Blackman 2009; Khan et al. 2015). In addition, biomolecule reductants are found to be more noteworthy than chemical reductants (Elechiguerra et al. 2005). Undeniably, bio nanoscience concept was developed to design novel nanomaterials which are environmentally and biocompatible to human beings benign (Anu et al. 2020). Such formulated NPs have antifungal, antibacterial, anti-insecticidal effect, and antimicrobial activity (Anu et al. 2020).

Selenium (Se) is a trace element, which plays a crucial role in biological systems and has antioxidant, antibacterial, and anticarcinogenic properties (Rayman 2000). Se is available as selenate and selenite oxo-anions. Reducing soluble Se^{4+} and Se^{6+} by microbes to insoluble non-toxic elemental Se is an effective way to remove it from contaminated soil, water, and drainage (Dungan and Frankenberger 1999). Biogenic synthesis of Se NPs is frequently achieved by reduction of selenate/selenite in the presence of bacterial proteins or plant extracts containing phenols, flavonoids, amines, alcohols, proteins, and aldehydes (Tapiero et al. 2003). The deficiency of Se is known to be associated with over 40 diseases in man (Tapiero et al. 2003; Cox and Bastiaans 2007). At low dosage, it can stimulate the plant's growth, whereas at high dosages it can cause damage to it (Turakainen et al. 2004; Hartikainen et al. 2000; Lyons et al. 2009). Se has also been shown to be effective against cancer. Their compounds in the form of selenocysteine and Selenomethionine are metabolized in biological systems (IpC et al. 2000; Miller et al. 2001). Selenium nanoparticles (SeNPs) are accepted by many enthusiastic researchers and recommended for use in various scientific disciplines due to their less toxicity and high stability (Gunti et al. 2019). Also, it can be synthesized by different approaches like physical, chemical, and biological. According to Wadhwani et al. (2016) statement, biologically mediated SeNPs are safer, environmental friendly, and economically viable when compared with other approaches (chemically and physical). At the same time, reports are available on the biological approach to produce SeNPs via plants such as dried leaf, seed, flowers, and bark (Zhang et al. 2018; Alam et al. 2019). Biological methods of synthesis can be achieved by using plant extracts and microorganisms. Using plants to synthesize NPs is advantageous over microorganisms-based synthesis as it eliminates the elaborate process of maintaining the cell in culture (Ren et al. 2012). Synthesis of SeNPs using various plants, such as *Citrus limon* (lemon) (Prasad et al. 2013), *Capsicum annum* (Li et al. 2007), *Terminalia arjuna* (Prasad and Selvaraj 2014), *Vitis vinifera* (Sharma et al. 2014), *Trigonellafoenum-graecum* (Fenugreek) seed extract (Ramamurthy et al. 2013), *Clausena dentata* (Sowndarya et al. 2016), and *Allium sativum* (Anu et al. 2017) have been reported in the literature. Moreover, 16 different species of bacteria and Arechaea have been found to reduce colorless selenite and selenite to red elemental Se of different shape and size (Stolz and Oremland 1999; Oremland and Stolz 2000). Many bacterial strains have been found to reduce selenate/selenite to SeNPs in different environment (Narasingarao and Häggblom 2007) even in sewage and sludge under both aerobic and anaerobic conditions (Lortie et al. 1992; Oremland et al. 1994). It has been suggested that a substantial quantity of soluble toxic selenate/selenite is reduced by bacterial strain to produce non-toxic insoluble SeNPs, although in doing so many such microbes would die (Sabaty et al. 2001).

Use of plants as a source of medicine has been an ancient practice and is an essential component of the healthcare system (Ekor 2014). The use of herbal medicines is growing with approximately 40% of the population reporting medicinal plants to treat medical disease within the past year. Currently available antibacterial therapy is limited due to various complications, such as toxicity and adverse effects of drug interactions and resistance to antibacterial agents as they can survive and multiply in the presence of antibiotics. Kim et al. (2011) have shown that the lethal doses of bactericidal antibiotics may lead to genetic and biochemical changes and induce the formation of highly detrimental oxidative radical species. Therefore, there is an inevitable need to develop effective antibacterial therapies to avoid the above-mentioned adverse effects. Hariharan et al. (2012) reported that bacterial cell-mediated SeNPs can inhibit the growth of both gram-positive and gram-negative bacteria.

2.2 Plants-Mediated Synthesis of the Selenium Nanoparticles

Several papers have reported the plant-derived biosynthesis of SeNPs with varying sizes and morphologies (Table 2.1). For instance, *Hibiscus sabdariffa* fabricated spherical, triangular, and hexagonal SeNPs with a size of 20–50 nm (Fan et al. 2020), whereas *Azadirachta indica* has been used as a rapid and efficient biosystem to produce crystalline and spherical SeNPs with a smooth surface (Fig. 2.1) (Mulla et al. 2020). *Withania somnifera* was the best adaptogen herb active with anolide and flavonoids, used as a bio reductant system to fabricate SeNPs of 40–90 nm (Alagesan and Venugopal 2019). Although plants offer the most suitable green synthesis protocols, the mode of action of plant-produced SeNPs against bacteria remains unknown; it is suggested that the nanoparticles interact with the peptidoglycan layer and break up the bacterial cell wall (Alam et al. 2019). Besides, SeNPs are able to induce apoptosis or programmed cell death (Sonkusre et al. 2014). Anu et al. (2017) reported spherical SeNPs produced by a cheap aqueous extract of garlic cloves, *Allium sativum* that acted as both the reducing and capping agent. These biogenic SeNPs showed lower cytotoxicity against the Vero cell line than those chemically synthesized. The same group took advantage of the medicinal properties of *Cassia auriculata* to synthesize functional SeNPs that displayed interesting anticancer and antiproliferative characteristics (Anu et al. 2017). Similar studies have reported the use of *Vitis vinifera* (Sharma et al. 2014), *Broccoli extract* (Kapur et al. 2017), and *Capsicum annum* to fabricate Se nanorods and nanoballs. Importantly, Ramamurthy et al. (2013) presented a combination of SeNPs, made using fenugreek seed extract and doxorubicin to form a chemoprotective agent against cancer; Vennila et al. (2018) studied the antibacterial, anticancer, and anti-inflammatory activity of SeNPs biofabricated by *Spermacoce hispida* and functionalized with apigenin, quinoline, quinazoline, and synaptojanin B. Kokila et al. (2017) reported on SeNPs using the leaves of *Diospyros montana* as a biocidal agent against both Gram positive *S. aureus* and Gram– *E. coli* and the fungus *A. niger* (Kokila et al. 2017).

Table 2.1 Different species of plants used for the biosynthesis of SeNPs

Plant	Species part	Metabolites	Shape	Size (nm)	Activity/ application	References
Withania somnifera	Leaves	Flavonoids Phenolics Tannins	Spherical	40–90	Antibacterial Antioxidant Anticancer	Alagesan and Venugopal (2019)
Brassica oleracea var. italica	N/A	Carotenes Glucosinolates Polyphenols	Spherical	50–150	Antioxidant Anticancer	Kapur et al. (2017)
Allium sativum	Cloves	N/A	Spherical	40–100	Cytotoxicity	Anu et al. (2017)
Hibiscus sabdariffa	Leaves	Phenols Alcohols	Spherical Triangular Hexagonal	20–50	Antioxidant	Fan et al. (2020)
Azadirachta indica	Leaves	Polyphenols Flavonoids Proteins	Spherical	142–168 221–328	Antibacterial	Mulla et al. (2020)
Cassia auriculata	Leaves	N/A	Amorphous	10–20	Antileukemia	Anu et al. (2017)
Vitis vinifera	N/A	Lignin	Spherical	3–18	N/A	Sharma et al. (2014)
Fenugreek	Seeds	Phenol Flavonol	Oval	50–150	Anticancer	Ramamurthy et al. (2013)
Aloe vera	Leaves	Hydroxyls Amides	Spherical	121–3243	Antibacterial Antifungal	Fardsadegh and Jafarizadeh-Malmiri (2019)
Diospyros montana	Leaves	Phenolics Flavonoids	Spherical	4–16	Antibacterial Anticancer	Kokila et al. (2017)
Spermacoce hispida	Leaves	Polyols Saponins	Rod-shaped	120 ± 15	Anti-inflammatory Antibacterial Anticancer	Vennila et al. (2018)

The application of SeNPs in toxicological studies is relevant due to their association with DNA cytosine methylation, chromatin structure, and transcription processes. It is advantageous for manipulating and studying cellular division, tissue differentiation, metabolism, and transcription programs (Rajaee Behbahani et al. 2020). Cui et al. (2018) reported on the production of monodispersed and stable SeNPs from hawthorn fruit extract (HE-SeNPs) whose antitumor activity was evidenced by the apoptosis induced in HepG2 cells through the overproduction of intracellular ROS and mitochondrial membrane potential (MMP) loss or disruption. Additionally, HE-SeNPs induced the upregulation of caspase-9 and downregulation of Bcl-2. Fardsadegh and Jafarizadeh-Malmiri (2019) detailed the hydrothermal synthesis of SeNPs using *Aloe vera* leaf extract and determined a prediction model and optimal conditions using response surface methodology (RSM).

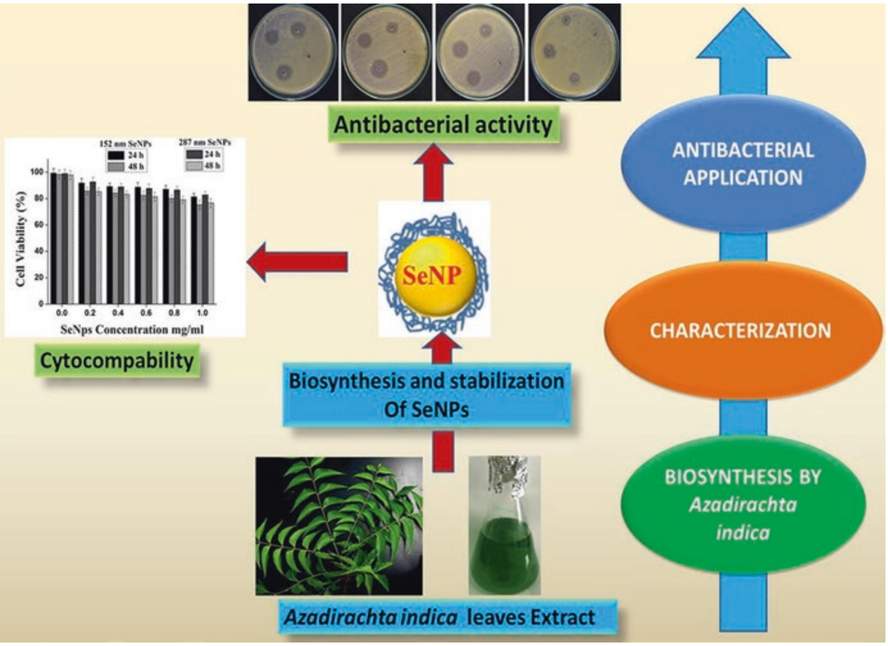
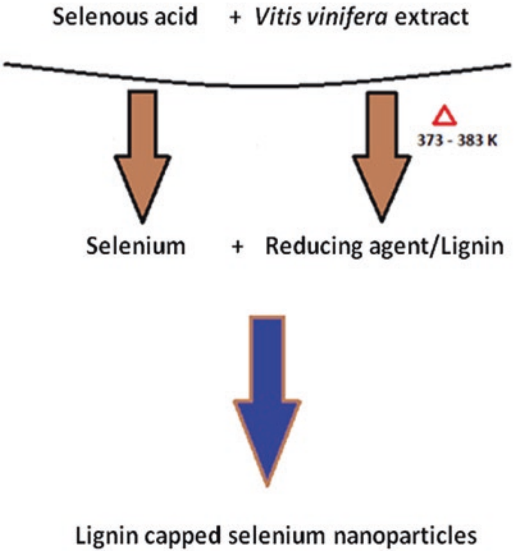


Fig. 2.1 Biosynthesis of SeNPs employing plants-based approach. (Figure adapted from Mulla et al. 2020 with permission)

2.3 Mechanism of the Synthesis of the Selenium Nanoparticles

There is a fine line between optimum limit/or deficiency and excess of Se in living system, which may cause toxicity. It is known that the Se nanoparticles prepared from biological material are less toxic than the bulk Se nanoparticles prepared from chemicals. The biomolecules present in the extract act both as reducing agent and stabilizer of Se nanoparticles. Bacteria, algae, dry fruits, and plant extracts are used to produce nanoparticles. Green synthesis of selenium nanoparticles from selenious acid was achieved by dried extract of raisin (*Vitis vinifera*) (Fig. 2.2) (Sharma et al. 2014). Like other biological materials, raisin also contains sugar, flavonoids, and phenols in addition to minerals such as iron, potassium, and calcium (Li et al. 2007). A change from colorless to deeply brick-red color indicated the formation of nanoparticles. The formation of Se-nanoballs was examined at different interval of time. It took nearly 6 min to start conversion of Se ion to Se nanoparticles which was indicated by a decrease in Se ion concentration in the solution. Transmission electron microscopy (TEM) images analyzed the nature of nanoparticles and showed that the diameter of nanoballs ranges between 3 and 18 nm. They were found to be encapsulated with a thin polymorphic layer (Fesharaki et al. 2010). The formation of Se nanoparticles was confirmed from the energy-dispersive x-ray

Fig. 2.2 Synthesis of SeNPs from *Vitis vinifera* extract. (Image adapted from Sharma et al. 2014 with permission)



spectroscopy. The Se nanoballs were identified from their characteristic absorption peaks at 1.37KeV, 11.22KeV, and 12.49KeV (Dhanjal and Cameotra 2010). The morphology of Se nanoparticles can be analyzed by x-ray diffraction (XRD) analysis. The broad diffraction peak suggests the presence of amorphous nature of Se nanoparticles (Ingole et al. 2010). Their particle size has been found to be of the order of 12 nm and has characterized Se nanoballs fabricated from *V. vinifera* by FTIR spectral studies (Sharma et al. 2014). The spectrum exhibited two sharp absorption peaks at 3420 cm^{-1} attributed to OH and the second peak at 1620 cm^{-1} to C-H vibration of the organic molecules. A distinct peak at 1375 cm^{-1} has been assigned to phenolic OH. The other peaks of medium intensity are due to – CH3 and OCH3 groups associated with the biopolymers, present in the *V. vinifera* extract acting as reducing agent and stabilizer for the Se nanoballs. Since lignin is a component of all vegetables, fruits, and cell walls, it can be extracted from them, and the compounds present in them may be identified. In this work, a phenolic group has been identified which generally acts as a reducing agent and it is oxidized to ketone during the redox process. However, the extract also contains a substantial amount of reducing sugars, and therefore they also help in the reduction and formation of Se nanoballs (Klug and Alexander 1967).

2.4 Applications of Selenium Nanoparticles in Medicine

Application field of SeNPs has been growing dramatically during recent years owing to its essential role in cellular metabolism. Based on the improved properties of SeNPs over Se, they have been explored in various disease conditions. SeNPs offer improved bioavailability with the added advantage of decreased toxicity. The prooxidant and the antioxidant effects provide different avenues for exploration in a variety of pathological conditions. Today, targeted drug delivery, anticancer therapy, biocidal activities, and antioxidant actions represent the major biomedical applications of SeNPs.

2.4.1 Anticancer Activity

Anticancer activity of SeNPs derived from diverse mechanisms of actions including modification of thiol compounds, binding of chromatin (Maiyo and Singh 2017), and triggering of apoptosis by depletion of mitochondrial membrane potential and overproduction of reactive oxygen species (ROS) (Wei et al. 2011). Accumulation of ROS inside the cells is caused by interaction of SeNPs with intracellular proteins and enzymes that have cysteine in their active site such as glutathione peroxidase, superoxide dismutase, or catalase (Yang et al. 2012). Cancer cells are characterized by higher level of these enzymes due to their increased metabolic activity and mitochondrial respiration. This may explain higher toxicity of SeNPs for cancer cells compared to normal cells. Selenium by itself is well known for cancer-protective action in breast, lung, prostate, and colon cancers (Weekley and Harris 2013; Sanmartín et al. 2012). Small size of SeNPs allows their efficient internalization into tumor cells which is ideal for passive targeting (Emerich and Thanos 2003). In some cases, differences in tumor porosity may reduce drug accumulation and activity, while nano-formulations enhance the permeability and retention of drugs at the tumor site. In addition, attachment of different moieties and active molecules, including antibodies, aptamers, or peptides that will be recognized by specific receptors of the tumor cells, enable active targeting (Emerich and Thanos 2003; Maiyo and Singh 2017). SeNPs are increasingly being employed as nanocarriers due to their biocompatibility, simple preparation procedures, low toxicity, in vivo degradability, and good antioxidant activity (Liu et al. 2012; Huang et al. 2013).

2.4.2 Drug/Gene Delivery

Preclinical studies showed that SeNPs reduced systemic toxicities of conventional chemotherapeutic drugs when used as carriers for these drugs while working synergistically to improve their efficacy (Maiyo and Singh 2017). The drug can be physically dispersed in SeNPs colloidal solution or even chemically bound to the SeNPs surface. Use of Se-nano delivery system may enhance drug solubility and availability while providing concomitant protection from degradation and systemic toxicities (Nicolas et al. 2013). For example, efficient deliveries of doxorubicin, cisplatin, and 5-fluorouracil using SeNPs to cancer cells were described (Huang et al. 2013). Polymeric nano formulation of selenium has also been described in a controlled drug- or gene-release system employing responsive stimuli such as temperature, pH, light, and redox state (Xu et al. 2016; Zhou et al. 2017). In such nano-Se systems, Se–Se bonds are weaker and more cleavable in an oxidative environment than S–S, C–C, and C–Se bonds, leading to more favorable drug/gene release (Xu et al. 2013). Synergistic effects and fewer side effects were also shown for SeNPs conjugated with transferrin and loaded with doxorubicin (Wei et al. 2011) or for hyaluronic acid attached to the SeNPs (Yang et al. 2012).

Furthermore, multifunctional properties of SeNPs are useful for dual drug delivery or codelivery by binding and transporting different therapeutic cargoes to various destinations in the body (Maiyo and Singh 2017). Such systems have been shown as an innovative strategy in targeted therapy and imaging, diagnosis, and combating multidrug resistance (MDR). Causes of MDR may be both cellular and noncellular mechanisms and may involve acquired and multiple multidrug-resistant mechanisms. Usually, MDR results from the expression of drug efflux pumps, upregulation of antiapoptotic proteins, and increase in regulators of drug metabolism (Liu et al. 2015). To prevent drug resistance and adaptation ability of the cancer cells, different chemotherapeutic agents are usually combined in cancer patients, but MDR is often inevitable (Gottesman 2002; Jabr-Milane et al. 2008). Targeted delivery systems are employed to improve stimuli-triggered drug release and minimize drug side effects if released to normal cells (Liu et al. 2015). One of the very promising strategies to combat MDR is activating MDR-associated genes through siRNA targeting (Kapse-Mistry et al. 2014). Although the potential of SeNPs is still not fully exploited, SeNPs have been successfully employed for codelivery of chemotherapeutic agents and siRNA to reverse MDR (Kapse-Mistry et al. 2014). The use of Se is still a novel and essentially new biomedical field, especially for gene delivery. Most studies described the development of SeNPs based multifunctional therapeutic vehicles for siRNA delivery as a powerful gene-silencing tool (Liu et al. 2015; Zheng et al. 2015).

2.4.3 Drug Resistance

Another significant biomedical application of SeNPs is associated with developing novel biocidal agents due to the emergence of antimicrobial resistance (AMR). AMR is a consequence of the overuse of antibiotics for human use or extensive agricultural usage of antibiotics in livestock as a growth supplement. Such practice inevitably leads to AMR and increases the threat of bacterial and biofilm-associated infections (Ahonen et al. 2017). Multidrug-resistant bacteria are one of the critical factors for mortality increase and costs in the healthcare sector. It has been estimated that AMR-derived infections are responsible for 25,000 deaths every year only in the European Union (Renwick et al. 2016). The most serious concerns are related to the methicillin-resistant Staphylococcus aureus (MRSA), vancomycin-resistant Enterococcus faecium (VRE), drug-resistant Streptococcus pneumoniae, multidrug-resistant Acinetobacter baumannii (MRAB), carbapenem-resistant

Enterobacteriaceae (CRE), and Pseudomonas aeruginosa (Tor et al. 2014). Another huge problem in the healthcare sector comprising up to 80% of all human bacterial infections is represented by biofilm-related infections including chronic wounds, urinary tract infections, and infections related to the use of medical devices (Michael et al. 2014; Ahonen et al. 2017; Bjarnsholt 2013). Nanotechnology can provide innovative solutions to fight against AMR microorganisms. Nanoparticles can be designed as targeted and combinatorial delivery systems for antibiotics; they may provide biocidal activity by themselves or be used as adjuvants and delivery vehicles in vaccines (Gao et al. 2014a, b). The commonly accepted mechanism of biocidal activity of SeNPs is the release of the Se ions into the bacterial cell after close interaction of SeNPs with the bacterial surface, similar as has been ascribed to the biocidal activity of silver NPs (Grant and Hung 2013; Cremonini et al. 2016). Internalization of ionic Se induces a cascade of damaging pathways for bacterial cells, including oxidative stress, inhibition of protein synthesis, or DNA mutation (Sondi and Salopek-Sondi 2004). In addition to the antibacterial mode of action, SeNPs have also been shown as effective antifungal agents (Eswarapriya and Jegatheesan 2015).

2.4.4 Diabetes and Associated Complications

SeNPs exhibited biological activity in streptozotocin-induced diabetic nephropathy by reducing oxidative stress and increasing the activity of cytoprotective protein Hsp-70, longevity protein Sirt1. They modulated the expression of apoptotic protein Bax and antiapoptotic protein Bcl-2 in apoptotic kidneys. However, the effects were not correlated either with selenoprotein concentration or a common inorganic Se source (Kumar et al. 2014). BAY 55–9837 is a long peptide with 27 amino acids found to be beneficial for type 2 diabetes mellitus (T2DM). To increase the plasma half-life and decrease the renal clearance rate, this protein was conjugated with chitosan stabilized SeNPs. Conjugation increases the apparent size of the protein, thereby enhancing the t1/2. Conjugation of small molecules with nanocarriers increases the t1/2 of therapeutics. SeNPs were found to reduce the apoptosis of pancreatic β-cells by its antioxidant activity. Stable BAY 55-9837 SeNPs with 200 nm size were found to stimulate insulin release from pancreatic cells (Rao et al. 2014). Vasoactive intestinal peptide receptor 2 (VPAC2) agonist peptide conjugated chitosan modified SeNPs were found to show selective activity against type-2 diabetes. The NPs were reported to enhance proliferation, glucose uptake, insulin uptake, and reduce intracellular oxidative stress (Zhao et al. 2017). In a recent breakthrough, SeNPs were proposed as a plausible vehicle for oral delivery of insulin. The NPs were reported to have synergistic antidiabetic activity with good antioxidants, improved pancreatic islet function, and promoted glucose utilization (Dang et al. 2017).

2.4.5 SeNPs in Inflammatory Diseases

Inflammation is one of the most critical initial steps in the pathobiology of a plethora of diseases. Combating inflammation by using novel strategies is one of the fertile areas, and many research groups worldwide are exploring the utility of such interventions. One study reported that a combination of silymarin and SeNPs at low concentrations (120 mg/kg silymarin+2μg/kg SeNPs) is a good candidate for reducing experimental trinitrobenzene sulphonic acid (TNBS) induced colitis in rats (Miroliaee et al. 2011). The combination showed superior benefits compared to SeNPs alone at 2 mg/Kg. SeNPs were found to inhibit the MAP kinase, NFκB, and reduced TNF-α levels. The combination exhibited excellent antioxidant and anti-inflammatory properties. However, clinical studies are warranted for the safety and efficacy of the new intervention (Miroliaee et al. 2011). SeNPs decorated with Ulva lactuca polysaccharide with enhanced stability and prolonged residence time effectively reduced dextran sodium sulfate induced colitis via inhibiting proinflammatory cytokines (IL-6 and TNF-α) and NFκB signaling (Zhu et al. 2017). In another study, SeNPs were reported as anti-inflammatory agents in multiple models, including carrageenan-induced paw edema with and without irradiation using 6 Gy gamma radiation. SeNPs (0.5, 1, and 2.55 mg/kg) could effectively alleviate paw oedema of non-irradiated and irradiated rats in a dose-dependent manner (El-Ghazaly et al. 2017).

2.4.6 Cerebral Protection

Since Se is also present in higher concentrations in gray matter regions and the glandular sections (Roman et al. 2014) participating in several neurotransmission and dopaminergic pathways (Vicente-Zurdo et al. 2020), this element has been studied as a biomarker for several neurological diseases, such as epilepsy, Alzheimer disease, and Parkinson's disease (Roman et al. 2014). Se antioxidant, neuroprotective function, impact on the regulation of cytoskeleton assembly, as well as the ability to bind to several neurotoxic metals and attenuate Aβ deposition and tau proteins hyperphosphorylation (Vicente-Zurdo et al. 2020; Solovyev et al. 2021) constitute some of the factors that have been identified as possible causes for the role of Se in Alzheimer disease development. Vicento Zurdo group more recently studied the metal-chelating potential of several Se species, such as SeMet, Sec, Se-methyl selenocysteine, and Se(VI), concluding that although Cu(II) and Fe(II) interacted with all Se species, Zn(II) only interacted with SeMet (Vicente-Zurdo et al. 2020). However, these Se species have shown to increase the Aβ fibrils width to the same degree as the neurotoxic metals studied (Vicente-Zurdo et al. 2020). In addition, several selenoproteins were shown to protect dopaminergic neurons, reinforcing the beneficial property of Se against Parkinson's disease (Ellwanger et al. 2016). Se levels have also been correlated with mood alterations, depression, and aggressive behavior (Rayman 2000). However, since brain Se levels are rarely low, and excessive Se levels may also be prejudicial, its application in neuronal disorders may only be advantageous for patients with severe Se deficiency and with mutations in genes related to Se delivery selenoproteins production (Zhang et al. 2019).

2.4.7 Reproductive System Protection

Se involvement in pregnancy (Zachara 2018) and reproduction (Qazi et al. 2018) as well as male fertility (Qazi et al. 2019) has recently been discovered. Low plasmatic Se levels have been linked to miscarriage and other pregnancy-related problems such as preeclampsia, preterm labor, and gestational diabetes (Zachara 2018). Se has also been shown to act as an intracellular antioxidant in Leydig cells (Qazi et al. 2019; Burk and Hill 2009) and to neutralize H_2O_2 generated during testosterone production (Micke et al. 2009). Se supplementation appears to have a crucial role in spermatogenesis, as it has been demonstrated to reduce the amount of defective sperm in mice, as well as to improve the vitality of Sertoli cells and the expression of crucial protein components, thanks to its antioxidant characteristics (Qazi et al. 2019; Asadpour et al. 2020).

2.4.8 Thyroid Protection and Cardiovascular Protection

Because the thyroid is the organ in the human body with the highest concentration of selenium (Winther et al. 2020; Valea and Georgescu 2018), Se supplementation has also been proven effective in treating autoimmune thyroiditis and other thyroid disorders, including Graves hyperthyroidism and chronic autoimmune Hashimoto's thyroiditis. Se has been related to thyroid protection against oxidative stress, mainly due to GPx3 activity, thyroid hormone metabolism control, and enhanced IDI efficiency (Roman et al. 2014), all of which contribute to the conversion of T4 to T3. Se supplementation has also been demonstrated to aid the therapy of hyperthyroidism-related pathologies, such as moderate Graves' orbitopathy, by increasing the patient's quality of life and slowing the course of the disease in patients treated with levothyroxine (Rayman 2019).

Numerous studies have demonstrated that selenium and selenoproteins may protect the cardiovascular system from oxidative stress and excessive platelet aggregation, preventing several cardiovascular pathologies such as atherosclerosis, hypertension, heart hypertrophy, and subsequent congestive failure (Rayman 2000; Roman et al. 2014; Ingles et al. 2020).

2.5 Conclusion

Bioreduction of selenate or selenite from microorganisms such as bacteria, fungi, and plant extract has become the favorite pursuit of biologists, chemists, and engineers. It is expected that in the future the metal would be extracted by biomineralization because they produce the purest form of the element. Many raw materials like waste vegetables, fruit peels, and leather cuttings may be utilized to produce elemental metal/metalloid from their oxide, halide, nitrate, sulfide, and carbonates. Generally, protein, phenol, alcohol, flavonoid, or sugar are required for the reduction of SeO3–2, SeO4–2 and at least one of the above organic molecules is present in microbes and plant extracts. They may, therefore, be exploited for the biotransformation of selenate and selenite to elemental Se of various shapes and sizes. Since the reduced metals or metalloids are insoluble in aqueous medium, they can be quickly sequestered. The benefits of using plant biomolecules for the synthesis of SeNPs were cost-effective, energy-efficient, environment and human health-friendly, plus is the safest product. This eco-friendly method could be used as a potential biomedical and environmental mode of the application soon.

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Chapter 3
Selenium and Nano-Selenium as a New Frontier of Plant Biostimulant

Julia Medrano-Macías and Willian Alfredo Narvaéz-Ortiz

3.1 Introduction

The exponential growth of the world population will impose a greater demand in the agricultural sector, requesting better products and yields with fewer resources. So far, these demands have been achieved through the wide use of chemical fertilizers and/or pesticides, improving the aforementioned factors, as well as biotic and abiotic stress (Alix and Capri 2018). However, the indiscriminate use of agrochemicals has long-lasting consequences on environmental pollution and loss of production quality (Mola et al. 2019).

Searching for more sustainable alternatives, without depending completely on the use of fertilizers and pesticides (Mannino et al. 2020), biostimulants are increasingly integrated into production systems, offering a potentially novel approach for regulation/modification of physiological processes in plants to stimulate growth, mitigate stress-induced limitations, and increase performance (Yakhin et al. 2017). Initially, the biostimulants application was aimed at the management of plants under abiotic stress and their tolerance mechanism (Dal Cortivo et al. 2017; Pereira et al. 2019; Campobenedetto et al. 2020; El Boukhari et al. 2020; Hoffmann et al. 2020). However, a limited number of works is directed to fruit quality (size, weight, and color) and production (Bajpai et al. 2019; Francesca et al. 2020). Consequently, the biostimulant effects on nutritional and nutraceutical attributes were and still are largely unexplored (Mannino et al. 2020).

Biostimulants have been classified into completely divergent groups and categories of function, use, and type of activity. Authors like du Jardin (2015) and La Torre

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M. A. Hossain et al. (eds.), *Selenium and Nano-Selenium in Environmental Stress Management and Crop Quality Improvement*, Sustainable Plant Nutrition in a Changing World, https://doi.org/10.1007/978-3-031-07063-1_3

et al. (2016) classify them as humic substances, plant and algae extracts, hydrolyzed proteins, and other compounds that contain N, microorganisms (beneficial fungi and bacteria), biopolymers, and inorganic compounds.

Selenium (Se) has been classified as an inorganic plant biostimulant, because it has shown an improvement in nutrient absorption, increases the tolerance of plants to stress and improves the quality of crop yield (Dima et al. 2020). Compared to most elements, there is a very small range between beneficial effects and toxicity: problems present all over the world. Therefore, Se application in plants as a biostimulant requires a more detailed study due to its harmful effects (high doses); however, it cannot be ignored that its application induces a great variety of beneficial effects.

Therefore, a new approach has been taken to use of this biostimulant: selenium nanoparticles (nSe), which have physicochemical characteristics that have added value compared to bulk material; a small size (<100 nm diameter), low weigh and high surface/volume ratio that interacts with the surface charges found on cell walls and membranes (Juárez-Maldonado et al. 2018). All these characteristics give rise to the differences presented by the bulk material of the same composition (Judy and Bertsch 2014).

3.2 Biochemical Process of Ionic Selenium and Nano-Selenium as Plant Biostimulants

Exogenous selenium applications in plants stimulates the metabolism; increasing molecule synthesis involved in defense (Wrobel et al. 2020), enhancing the growth (Xia et al. 2020) and increasing the stress tolerance (D'Amato et al. 2020). The current state of the art indicates that the main form of application are via foliage, via soil, via nutrient solution, or via seeds imbibition. However, the accurate mechanics under which these processes occur is still unclear. The principal pathways of impact to date elucidated will be indicated below, in both ionic and nanoparticulated forms.

3.2.1 Ionic Selenium

Several investigations have been carried out to demonstrate the selenium effect, being selenite (SeO_3^-) and selenate (SeO_4^-) main chemical sources, and the most favorable results in bioestimulation and biofortification have been evidenced with SeO_4 applied via foliage and via soil. The results are probably due to the fact that SeO_4 is easier to take up and translocation from the root to the shoot, as well as better incorporation into organic compounds, while selenite applied directly to the soil forms inorganic compounds, as well as transportation is limited (Gali 2021).

Biostimulation and biofortification have been evaluated more specifically by measuring the balance of primary and secondary metabolites and essential elements. Although the results have been quite varied, it is difficult to establish with precision the concentration intervals that need to be applied to each crop to achieve the same benefits. The following tolerance pattern has been concluded: seed imbibition> hydroponics> foliar> soil (García Márquez et al. 2020). These authors also reviewed and grouped ranges and frequencies in which Se can be applied as shown in Fig. 3.1.

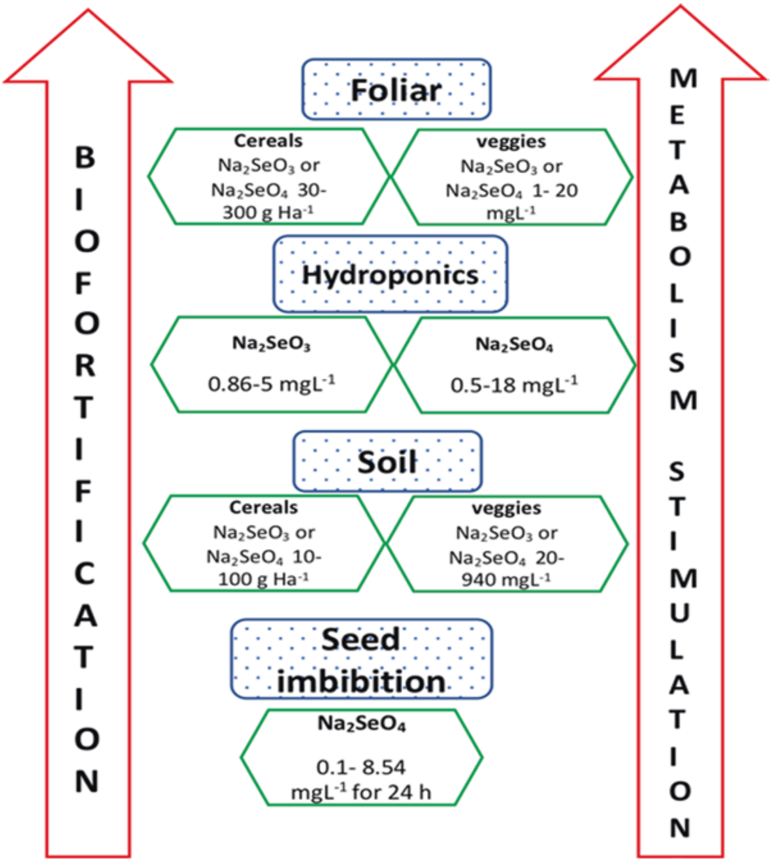

Fig. 3.1 Ranges of selenium application in several crops, applications form to achieve benefits such as biofortification and stimulation

3.2.1.1 Effect of Ionic Selenium in Primary Metabolites

It has been found that ionic selenium applications in plants give advantages from a biochemical and physiological perspective and may be the best known pathway that is related to selenoproteins synthesis, which act as antioxidants (Steinbrenner et al. 2016), and within this group, the most widely studied is the glutathione peroxidase (GPX) mechanism.

GPX catalysis involves acid selenium in its catalytic cycle, which reacts with glutathione (GSH), a tripeptide that functions as a coenzyme and contains a sulfhydryl functional group (-SH), to form a sulfide–selenium complex. At this point, a second GSH molecule intervenes, and selenol (PSeOH) is formed at the active site (Battin and Brumaghim 2009). Furthermore, the selenium application has been reported to promote an increase in activity of other enzymes with antioxidant capacity, such as ascorbate peroxidase (APX), catalase (CAT), superoxide dismutase (SOD), dehydroascorbate reductase (DHAR), glutathione reductase (GSHR), and monodehydroascorbate reductase (MDHR) (Schiavon et al. 2017).

Although it has not been studied as thoroughly, it has also been related to an increase in other non-catalytic antioxidant proteins, such as thioredoxin (TrxR) and protein P, the latter with more than 10 Se atoms (Pyrzynska and Sentkowska 2020).

In a study carried out in *Brassica napus*, effects of Se on primary metabolism were determined, and it was found in higher concentration of glucose and production of ATP; increased activity of SOD in mitochondria and enhancement in the pentose phosphate pathway, which supplies large amounts of non-enzymatic antioxidants; as well as a reduction in the tricarboxylic acid (TCA) cycle (Dimkovikj and Van Hoewyk 2014).

Also, there is an increase in synthesis of sulfur amino acids cysteine (Cys) and methionine (Met) as well as selenoamino acids such as seleno-cysteine (SeCys) and seleno-methionine (SeMet), which are incorporated into proteins. However, there is evidence that other non-protein amino acids are synthesized, such as glutamyl methyl selenocysteine (gluMetSeCys), methyl-SeCys, and methyl-SeMet, mainly in families of sulfur accumulators, such as *Brassica* and *Allium* (Lima et al. 2018). Furthermore, these metabolites have shown powerful anticancer activities (Brummell et al. 2011; Ávila et al. 2014). In hyperaccumulators species, volatile species such as dimethyldisulfide (DMDSe) are produced, which takes part in control of selenium accumulation. In non-hyperaccumulator plant species (those that accumulate <100 mg of Se per kg of dry weight), the methylated species of selenium as dimethyl selenide (DMSe) is synthesized (Pilon-Smits and Quinn 2018).

It is known that Se increases the sulfur transporters, SULTR1 and 2, as well as ATP sulfurylase at the transcriptomic level, which leads to major absorption of sulfur, and therefore to the synthesis of both primary and secondary metabolites that contain these elements. However, it is important to highlight the balance between the concentrations of Se and S. It has been found that high concentrations of Se and low concentrations of S promote competition, preventing adequate absorption of sulfur and, in this case, a reduction in the synthesis of the mentioned metabolites (Schiavon et al. 2015).

3.2.1.2 Effect of Selenium in Secondary Metabolites

Regarding sulfur secondary metabolites, both positive and negative effects have been reported after selenium applications, such as glutathione and glucosinolates. For the first case, examples of increased concentrations were observed in radish (*Raphanus sativum L.*) (Schiavon et al. 2016), plum trees (*Prunus domestica*) (Sun et al. 2020), and the accumulator species (*Brassica oleracea*) (Tian et al. 2018). However, the reduction of GSH found in strawberry plants was associated with an increase in concentration of its oxidized form: glutathione disulfide (GSSH) (Huang et al. 2018). This could be related to the aforementioned, where the selenium presence increases sulfur receptors, and, consequently, major absorption of both elements, favoring the synthesis of secondary metabolites. Additionally, it is hypothesized that selenium modifies the phenylpropanoid pathway, increasing the enzymatic activity of phenylalanine ammonium lyase (PAL), which is a possible reason for positive correlation with phenolic compounds (Mimmo et al. 2017). Likewise, an increase in synthesis of ascorbic acid has been found as the effect of Se, which functions as a direct scavenger of reactive oxygen species (ROS) and a cofactor of enzymes with antioxidant activity, such as APX (Tavakoli et al. 2020).

In recent investigations, an impact over secondary metabolites not directly related with Se or S has been reported. For example, the increase in photosynthetic pigments in coffee plants (Mateus et al. 2021) and cowpea, such as chlorophyll a, b, total and carotenoids, as well as an increased stomatal conductance and other gas exchange parameters have been observed as the effect of Se (Silva et al. 2020). The conclusion in these studies was that selenium's participation as a facilitator in electron transport chain of respiration leads to a greater chlorophyll biosynthesis. This effect is also attributed to selenium, which provides protection to chloroplast enzymes. In a study carried out on rice (*Oryza sativa*), a three-fold increase in fatty acids (oleic, linoleic, and linolenic) was found after the selenite and selenate applications; however, the metabolic pathway is unclear (Lidon et al. 2018).

In summary, selenium stimulates metabolism in two ways: (1) through antioxidants, where it participates in the catalytic cycling of enzymes like GPX and (2) through pro-oxidants, where selenite and selenate probably mimic moderate stress, synthetizing reactive species will activate signaling to achieve the formation of entire antioxidant machinery (Tamaoki and Mayurama 2017).

3.2.2 Nano-Selenium (nSe)

Unlike the information available about the effects and mechanisms of Se action in its ionic form, the corresponding nanoparticles (nSe) are much more recent; therefore it remains unclear. But some findings have shown favorable results from the nutritional value point of view, production of primary and secondary metabolites, as well as an increase in adverse conditions in plants, even more than those observed after the exogenous application of this element as bulk material. This is probably due to better uptake and transportation, which leads to greater bioavailability, bioactivity, and release of selenium (Kumar and Prasad 2021), even so there is still a long way to go regarding the elucidation of the mechanisms of action. In general, it is known that nSe could be first related to their redox balance as well as the physicochemical reactivity, which are the principal inducing factors, and those stimuli are captured by the plant cell initiating an orchestrated process of signaling and transduction that will culminate into physiological and biochemical changes. Some biochemical modifications have been reported through methylation of cytokinin in DNA and expressed to epigenomic level; an example was the results obtained in bitter melon plants; an increase in the synthesis of transcription factors such as WRKY1, which regulates the transcription process of stress-related genes, as well as the transcription of PAL and CoA ligase (Behbahani et al. 2020). In wheat plants, it was found after nSe applications at 10 ppm induced modifications in gene expression of the heat shock factor A (HSFA4), which acts as a substrate of MPK3/MPK6, the greatest signaling pathway in control of plant immunity, it was also documented that HSFA4 triggers the synthesis of second messengers such as ROS, mainly H_2O_2 (Safari et al. 2018).

The phenomenon of overproduction of reactive oxygen species function as a second signaling event (Wu et al. 2016) is known as oxidative stress. However, at low doses of nSe application, this stress does not cause negative effects on biomass, but it leads to changes in the synthesis of antioxidants and other secondary defense metabolites, such as major content of total phenolic compounds, ascorbate, lycopene, carotenoids, and as a consequence, an increased antioxidant capacity (Babajani et al. 2019; Morales-Espinoza et al. 2019).

In a study carried out in celery plants, nSe was applied in foliar form and an increase in concentration of α-linoleic acid was obtained, which led to greater production of jasmonic acid, acting as regulator and trigger synthesis of defense proteins (PR) (Li et al. 2020a).

Also, application of nSe evidenced greater activity in enzymes with antioxidant properties, such as GPX and CAT, which maintain ROS balance, and they are a predominant contributor to tolerance to stress, so a significant reduction in cell membrane damage has been observed (Hussein et al. 2019). In strawberry plants subjected to saline, stress was found in higher concentration of secondary defense metabolites, as proline and thiolic compounds (Solymanzadeh et al. 2020).

Additionally, it was found that nSe gives protection to photosynthetic pigments as chlorophyll a, b and less lipoperoxidation during stress conditions, probably due to storage of nSe in thylakoids membranes, because they provide stability to some enzymes (Ahmed et al. 2018), and thus achieve an improvement in photosynthetic rate, homeostasis, and growth (Broadley et al. 2010).

Due to the above, the use of nSe to cope stress has been successfully tested. This has been reported in species such as winter wheat (*Triticum aestivum*), sorghum (S*orghum bicolor*), radish (*Raphanus sativus var. Sativum*), arugula (*Eruca sativa*), eggplant (*Solanum melongena*), pumpkin (*Cucumis sativus*)*,* tomato (*Solanum lycopersicum*)*,* and chili (*Capsicum annuum*) under high temperatures (Hawrylak-Nowak 2009; Broadley et al. 2010; Djanaguiraman et al. 2018; Morales-Espinoza et al. 2019; Gudkov et al. 2020; Li et al. 2020b) and in strawberry plants, tomato, coriander, basil, and barley (*Hordeum vulgare*) subjected to salinity stress (Hasegawa et al. 2000; Ghazi 2018; Oprica et al. 2018; Morales-Espinoza et al. 2019). A particularly explored topic is the nSe triggered increase in tolerance to stress caused by pathogens such as *Alternaria solani* (Skalickova et al. 2017), *Meloidogyne incognita* (Udalova et al. 2018), *Phytophthora infestans* (Joshi et al. 2021), and *Botrytis cinearea* (Liu et al. 2020). The reasons why selenium NPs trigger an antipathogenic effect, in addition to the possible mechanisms already mentioned, could be the synthesis of enzymes such as ß1,3-glucanase, lipoxygenase, and phenylalanine lyase (PAL). The first two attack directly the fungal cell wall of pathogens (Balasubramanian et al. 2012) while the PAL promotes the depositions of phenolic compounds and lignification in plant cell wall (Hörger et al. 2013; Wu et al. 2016; Joshi et al. 2021). The plethora of actions has been quite wide; however, another series of studies have warned about toxicity both in plant species and in the environment via its passage through the different trophic chains (El-Ramady et al. 2020) which increases the necessity for more scientific research on this topic.

3.3 3 Ionomic Process of Ionic Selenium and Nano-Selenium as Plant Biostimulants

3.3.1 Ionic Selenium

As has been widely reported, the selenium uptake via root occurs in the form of SeO_4 by the sulfur transporters: SULTR 1 and 2 (Schiavon et al. 2015), so it has been concluded that Se presence affects S assimilation, and the selenium impact on other essential macroelements is linked to this phenomenon. However, there is no universal trend; the results that have been found are ambiguous, both synergy and competition have been revealed, depending on the concentration balance of both elements, plant species, organs studied, forms of application among others (Cheng et al. 2016). Examples of this were the experiments carried out in monocotyledonous plants exposed to cadmium, the insight was an improvement in sulfur absorption, after the application of SeO4 *via* roots but a reduction in phosphorus (P) assimilation; on the other hand, in turnip plants, the Se application via foliage showed a greater absorption of P (Li et al. 2018).

Likewise, Na_2SeO_4 application, both foliar and by fertirrigation, caused an increase in S absorption in curly endive plants at concentrations of 4 and 8 μM, but a reduction in nitrogen concentration (Sabatino et al. 2019). Lei et al. (2018) found that Se promotes the NO_3 uptake *via* root, due to stimulation in nitrate reductase, nitrite reductase, glutamine, and glutamate synthase, but the nitrogen concentration in aerial parts was reduced, probably due to saturation in transporter enzymes, so it remained stored only in the root. On the other hand, in barley grains, a reduction in sulfur concentration and nitrogen was found after the application of direct selenium to the soil in the form of Na_2SeO_3 at concentrations greater than 12.5 g ha^{-1}(Ilbas et al. 2012). Possibly such phenomenon is due to the close relationship that exists between the sulfur and nitrogen metabolism, the variation in concentration of one of these elements leads to an imbalance in other.

Regarding the microelements, a higher concentration of Mn and Zn has been reported in the aerial part of monocots treated with Se under cadmium stress; the authors demonstrated that the selenate-treated plants improved root length, active surface, and total surface, probably achieving a major microelements absorption (Qin et al. 2018).

The above statements are in accordance with Zhou et al.(2020), who concluded that it is necessary to carry out more research on the physiological and molecular impact of the uptake and transport of selenium, emphasizing the gene expression or repression made with each chemical species of selenium (selenite, selenate, selenide, selenium in organic form) in order to elucidate the interactions with essential macro and microelements. Also it is necessary to study the changes in pH and redox potential (*Eh*) in the surrounding environment, especially in those that occur in soil, where the interactions are extremely complex.

3.3.2 Nano-Selenium (nSe)

This section is incorporated into this chapter to highlight the information gap that exists about the impact selenium nanoparticles have on plant metabolism from ionomic perspective. Some authors have previously emphasized the lack of knowledge, such as El-Ramady et al. (2016) and Gudkov et al. (2020).

Only one research was found; Neysanian et al. (2020) reported that application of low concentrations of nSe (3 mgL^{-1}) caused an increase in nutritional quality of tomato fruit, due to increase in elements such as Fe, Zn, and Mg; however, the only hypothesis was a possible modification in vascular conducting tissues: xylem and phloem. The mechanism by which nSe impacted or modified other elements remain frankly unclear due to lack of research. Other authors have pointed out that, in general, nanomaterials interact with other elements by indirect impacts, such as change in pH, *Eh*, soil microbiota, of course, as has already been mentioned in another section, due to the particularities of the nano size (Wang et al. 2020). Everything previously mentioned is schematized in Fig. 3.2.

3.4 Conclusion

Analyzing in parallel the existing information on ionic and nano-selenium effects on plant metabolism, it can be seen that there is a need to increase the data in order to more precisely understand the uptake, transportation, and assimilation of both selenium forms.

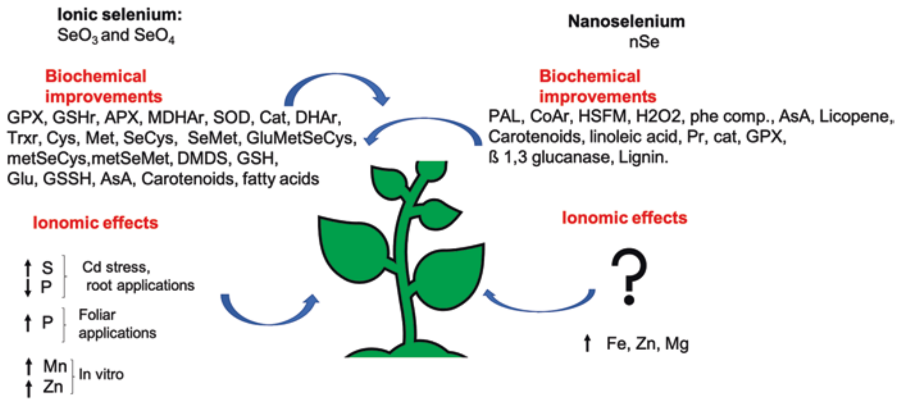

Fig. 3.2 Summary of the known biochemical and ionomic effects of selenium and nanoselenium application. *GPX* glutathione peroxidase, *GSHR* glutathione reductase, *APX* ascorbate peroxidase, *MDHAR* monodehydro ascorbate reductase, *SOD* superoxide reductase, *CAT* catalase, *DHAR* dehydroascorbate reductase, *TRXR* thioredoxin, *Cys-cysteine* Selenium CystemylCys-selenium cysteine methyl selenocysteine, *metSeCys* methyl selenocysteine, *metSeMet* methyl selenium methionine, *DMDS* dimethyl disulfide, *GSH* Glutathione, *Glu* glucosinolates, *GSSH* glutathione sulfide, *AsA* ascorbate, *PAL* phenylalanineammonium lyase, *HSFA4* Shock transcription factor thermal, phe comp.-total phenolic compounds, *PR* defense proteins

It is necessary to test particularly the Se nanoparticle application more extensively, especially in vegetables, as well as the consequences between trophic levels and over time.

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Chapter 4
Selenium and Nano-Selenium for Plant Nutrition and Crop Quality

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4.1 Introduction

Selenium (Se) is an essential nutrient for humans, animals, and lower plants, but its need for higher plants still needs more research. Selenium is a key component of many selenoenzymes in humans including thioredoxin reductase, glutathione peroxidase, and iodothyronine deiodinase, which protect human cell membranes from oxidative damage such as those involved in the breakdown process of hydrogen peroxide (H_2O_2) and lipid hydroperoxide (Zhang et al. 2021b). The story of Se for plant nutrition is amazing and several workers have contributed to it (e.g., El-Ramady et al. 2016; Lanza and Reis 2021; Trippe III and Pilon-Smits 2021). Higher plants

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M. A. Hossain et al. (eds.), *Selenium and Nano-Selenium in Environmental Stress Management and Crop Quality Improvement*, Sustainable Plant Nutrition in a Changing World, https://doi.org/10.1007/978-3-031-07063-1_4

have the ability for root uptake of both selenate (SeO_4^{2-}) and selenite (SeO_3^{2-}) ions through Se-specific transporters including sulfate transporters (SULTRs) for selenate and phosphate transporters for selenite (Schiavon and Pilon-Smits 2017; Lima et al. 2018; White 2018). Selenite ions are quickly metabolized upon uptake, whereas selenate ions can be found throughout plants (Trippe III and Pilon-Smits 2021). Selenium has several physiological and biochemical roles in plants, particularly the mitigation of different types of abiotic stresses such as drought (Rady et al. 2020; Nawaz et al. 2021), salinity (Habibi 2017; Astaneh et al. 2019; Bañuelos et al. 2020; Regni et al. 2021; Xu et al. 2021a), heavy metals (Shekari et al. 2019; Feng et al. 2021a, b) like arsenic (Lv et al. 2020; Pokhrel et al. 2020), cadmium (Huang et al. 2019, 2021a, b; Zhang et al. 2021a), fluoride (Niu et al. 2020), lead (Wang et al. 2020a), and mercury (Li et al. 2019; Kavčič et al. 2020); excess light (Jaiswal et al. 2018), high temperature or heat stress (Seliem et al. 2020), and low temperature (Liu et al. 2021a). Great attention has been paid to different applications of nano-Se for crop production under stress as reported by many workers (Abid et al. 2021; El-Ramady et al. 2021a, b; El-Saadony et al. 2021a, b; Huang et al. 2021a, b; Qi et al. 2021; Shalaby et al. 2021).

Selenium has distinguished functions in plants that increase production and quality, particularly under stress as reported by several studies on Se and plant nutrition (e.g., El-Ramady et al. 2014, 2016; Hasanuzzaman et al. 2020; Ryant et al. 2020; Lanza and Reis 2021; Wen 2021). These functions may include (1) increasing crop growth and its yield (Li et al. 2021a), (2) promoting crop ripening, senescence, and shelf-life (Wen 2021), (3) enhancing Se-containing compounds related to human health (El-Ramady et al. 2020; Chen et al. 2021; Groth et al. 2020, 2021), (4) increasing crop resistance and/or tolerance to abiotic and biotic stresses (Hossain and Islam 2021), (5) enhancing photosynthesis and its rate (Yin et al. 2019; Amirabad et al. 2020), accumulation of osmo-protectants (Rady et al. 2020), and secondary metabolites (Hasanuzzaman et al. 2020), and (6) increasing the activity of enzymatic antioxidants like SOD, CAT, and APX (Rady et al. 2020; Nawaz et al. 2021) and non-enzymatic antioxidants like ascorbic acid (Sabatino et al. 2021), flavonoids (Sohrabi et al. 2020), proline (Lima et al. 2019), and tocopherols, which act as a scavenging system (Mateus et al. 2021) and promote cell detoxification (Lanza and Reis 2021; Riaz et al. 2021). Recently, many studies have confirmed that using nano-Se as nanofertilizers provide several benefits, especially production of crops under stresses such as soil salinity and heat stress (Shalaby et al. 2021), drought and heat stress (El-Saadony et al. 2021a, b), heavy metal stress (Wang et al. 2021a), and Se-nano-biofortification (El-Ramady et al. 2021a, b).

Therefore, this chapter discusses the use of Se and nano-Se to produce high-quality crops, particularly under different stresses. The crucial role of Se and nano-Se in removing pollutants from soil and water environments will also be discussed in this chapter.

4.2 Selenium and Nano-Se for Plant Nutrition

Selenium and nano-selenium have been investigated by several researchers over more than 200 years, since Se was discovered by Jöns Jacob Berzelius in 1817. The field of plant nutrition was one of the most important fields to investigate Se, which discussed the biological role of Se and nano-Se from their essentiality for plants to their uptake, metabolism in plants, speciation, accumulation, and toxicity, as well as their biofortification and phytoremediation. Several studies about the previous themes have been published, with some examples summarized in Table 4.1 and Fig. 4.1.

Many workers have studied Se and nano-Se topics that can be summarized as follows:

Table 4.1 The main biological functions of selenium and nano-Se in plants and suggested mechanisms

Biological functions of Se and nano-Se	Suggested mechanism or clarification	References
(1) Increases crop growth and yield	Applied Se or nano-Se in proper dose enhances plant growth and yield	Neysanian et al. (2020) and Li et al. (2021a)
(2) Promotes crop ripening, senescence and shelf-life	Increasing Se content in fruits lead to reduce fruit-softening rates, thus increasing the shelf-life of fruit products	Wen (2021)
(3) Enhances Se-containing compounds related to human health	These compounds may include the 30 known selenoproteins (e.g., selenocysteine) and other organic Se like seleno-amino acids, seleno-proteins, Se-polysaccharides, etc.	El-Ramady et al. (2020), Chen et al. (2021) and Groth et al. (2020, 2021)
(4) Increases crop resistance and/or tolerance to abiotic and biotic stresses	By regulating the antioxidant system *via* stimulating photosynthesis; repairing damaged cell structures and their functions; and rebalancing of essential nutrients in plant tissues	Feng et al. (2021b) and Hossain and Islam (2021)
(5) Enhances the photosynthesis process (photosynthetic pigments including chlorophyll and carotenoids) and its rate	Regulates photosynthesis system; Se impacts on PSII and their electron transfer processes; Bio-Se-NPs increases content of photosynthetic pigments because Bio-Se-NPs surface is surrounded with active phytochemicals	Yin et al. (2019), Hernández-Hernández et al. (2019), Amirabad et al. (2020) and Borbély et al. (2021)
(6) Increasing activity of enzymatic antioxidants like superoxide dismutase (SOD), catalase (CAT), and peroxidase (APX)	Selenium can increase plant tolerance to oxidative stress because it is the main component of many enzymatic antioxidants like glutathione peroxidase and SOD, which reduce lipids content	Rady et al. (2020), Hasanuzzaman et al. (2020) and Nawaz et al. (2021)
(7) Increases accumulation of non-enzymatic antioxidants, e.g., ascorbic acid, flavonoids, proline and tocopherol	Accumulation of osmo-protectants, and secondary metabolites, which act as a scavenging system and promote cell detoxification	Sabatino et al. (2021), Lanza and Reis (2021) and Mateus et al. (2021)

(continued)

Table 4.1 (continued)

Biological functions of Se and nano-Se	Suggested mechanism or clarification	References
(8) Reduces the toxicity of metals/metalloids like Cd, Hg, Pb, and Se itself	By regulating gene expression, sequestering HMs in the root cell walls and organelles, and reducing HM transfer from roots to the shoots	Huang et al. (2021a, b) and Riaz et al. (2021)
(9) Metal detoxification in soil–plant systems	May reduce HM bioavailability in soil by forming HM-Se-containing complexes in the roots and/or rhizosphere; reducing the uptake of HMs by plant roots and their translocation	Tran et al. (2018, 2021) and Yang et al. (2021)
(10) Restricts the uptake and translocation of heavy metals (As, Cd, Cu, Mn, Zn, etc.) in plants	Through changing root hair morphology by regulating hormones and increasing thickness of cell wall by enhancing contents of cell wall components (e.g., lignin, pectin, hemicelluloses) Se regulates accumulation of HMs in cell wall	Feng et al. (2021a), Riaz et al. (2021) and Wang et al. (2021a)
(11) Reduces accumulation and toxicity of heavy metals (As, Cr, Cd, Hg, Pb, etc.) in plants	Reducing the bioavailability of HMs in soils and then uptake by plants; Se impacts on uptake/the sequestration of HMs; Se combines with HMs and then sequesters them in plant cells	Ding et al. (2020), Hussain et al. (2020) and Feng et al. (2021b)

1. The major Se-forms; plants can uptake inorganic Se as selenate (SeO_4^{2-}), selenite (SeO_3^{2-}), selenide (Se^{2-}), elemental Se (Se°) or nano-Se, while the most important organic forms include seleno-amino acids, selenocysteine (SeCys), and selenomethionine (SeMet) (Gupta and Gupta 2017; Wiesner-Reinhold et al. 2017). Plants can uptake Se via sulfur transporters (SULTRs) for selenate in the plasma membrane of roots, whereas phosphate transporters for selenite could metabolize via the S-assimilatory pathway, and then volatilize into the atmosphere (Schiavon and Pilon-Smits 2017; Lima et al. 2018; White 2018). The aquaporin inhibitor $AgNO_3$ is the main inhibitor that prevents nano-Se uptake by rice plants. $AgNO_3$ is a potential inhibitor that can react with the sulfhydryl group (-SH) of the amino acids cysteine and histidine, resulting in a 60.4% decrease in rice root Se-NPs uptake (Wang et al. 2020b). The uptake of Bio-Se-NPs could be inhibited by aquaporins inhibiters at higher rates compared to chemical Se-NPs (Hu et al. 2018). In general, the uptake rate of selenite and selenate was equal, but both were much higher than nano-Se. The influx rate for selenite was 2.5-fold higher than for nano-Se (Hu et al. 2018). Selenite can be rapidly assimilated in wheat roots into organic forms (e.g., SeMet), whereas nano-Se appeared stable in solution and did not oxidize to selenite (Hu et al. 2018). Se-NPs can be successfully transported into the aerial parts of rice roots and the dominant Se species was SeMet under different Se-NPs treatment (Wang et al. 2020b).

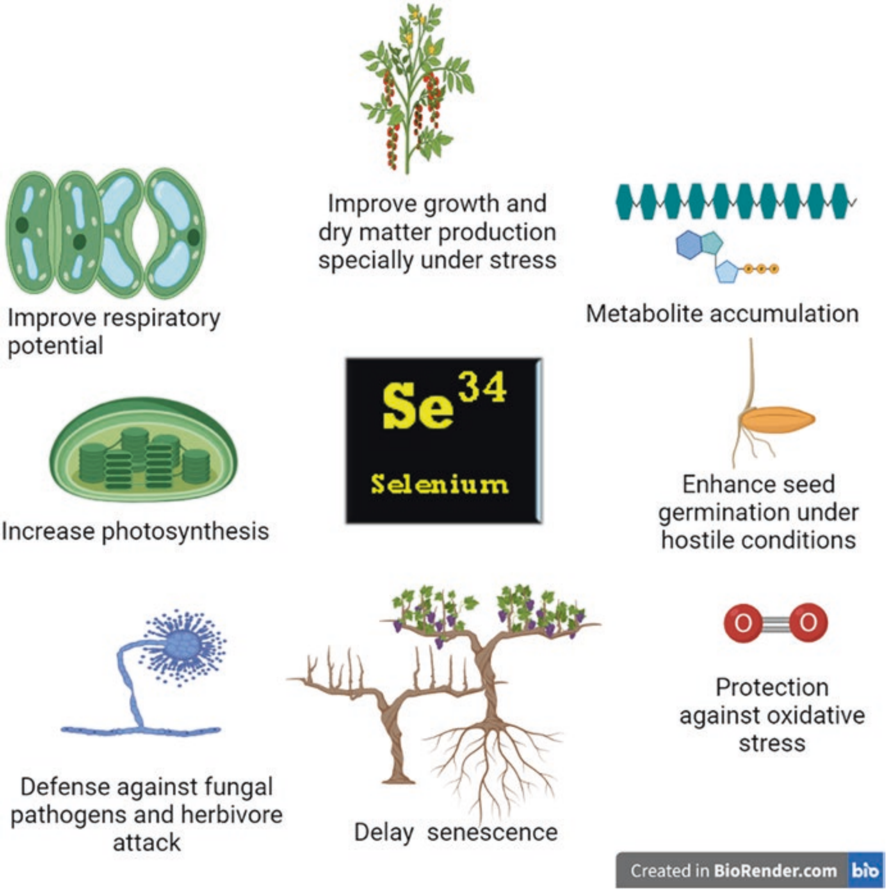

Fig. 4.1 The role of selenium in plants: Se increases the photosynthetic rate, enhances the plant defense system against microbial pathogens and herbivore attacks, delays the senescence of plants, protects plants against oxidative stress, and improves plant growth and dry matter production, especially under stresses

2. Many recent studies have reported on the uptake, transportation, and accumulation of different forms of Se in various plant species like lettuce (Ferreira et al. 2020), wild peach (Sun et al. 2020), *Cardamine violifolia* (Wu et al. 2020b), rice seedlings (Wang et al. 2020b), maize (Wang et al. 2020c), and wheat (Ahmad et al. 2021; Wang et al. 2020d, 2021c). These studies confirmed that the source of applied Se and its dose to cultivated plants control the uptake and toxicity of Se in plants.
3. Some studies reported that combined foliar and soil Se-fertilizer improved the uptake and transport of this nutrient, antioxidant activity, yield, and nutritional quality, including studies on lettuce (Shalaby et al. 2017), oats (Li et al. 2021a, b), and wheat (Zhou et al. 2021).

4. The biofortification and phytoremediation of Se and nano-Se are still an important theme because the Se processes in plants have a strong link to human health, particularly in the era of COVID-19, as discussed in many studies such as D'Amato et al. (2020), Sarwar et al. (2020), Schiavon et al. (2020), Zhou et al. (2020), Groth et al. (2020, 2021), Hossain et al. (2021), Trippe III and Pilon-Smits (2021), and Mateus et al. (2021). Other studies focused on the nano-biofortification with Se, such as El-Ramady et al. (2021a, b).
5. Many co-relation between Se and other elements (e.g., N, P, K, Ca, Mg, Cd, Cr, Hg, etc.) have been recognized, like (*i*) the antagonism between Se (at high concentration) and Ca, Mg, and Zn contents, but this relation is positive when Se is optimum; (*ii*) Se has a synergistic relationship with N because Se can increase N-metabolism through its impact on the activities of glutamine synthetase and nitrate reductase (Zhan et al. 2021); (*iii*) Se has the ability to alleviate salinity stress by regulating the homeostasis of Na^+ and K^+ (Lanza and Reis 2021; Yaldiz and Camlica 2021); (*iv*) excess applied P or S inhibit the transport of Se from root to shoot, where applied Se increases S uptake and its accumulation and vice versa (Deng et al. 2021); and (*v*) Se has a special relationship with Si, where Se can alleviate some heavy metal stresses like Cd (Huang et al. 2021a, b; Riaz et al. 2021; Wen 2021).

4.3 Selenium and Nano-Se for Improving Crop Quality

As stated in the previous section, Se and nano-Se have very important biological functions, which include the growth of cultivated plants, their yield, and quality. These benefits of applied Se and/or nano-Se can be achieved under the proper or optimum applied Se dose, which depends on the growth period of different agricultural crops for safe and better yield (Wen 2021). Crop quality has a strong connection with different sources and doses of Se on cultivated plants, which reflect the potential of Se to improve ripening, senescence and shelf-life, high Se-containing health-related compounds, and increasing the tolerance of stressed plants (Wen 2021; Zhu et al. 2017, 2018; Puccinelli et al. 2017, 2019). The yield and quality of many crops like tomato have been improved by Se application by inhibiting uptake metals like Cd (Xie et al. 2021). Nano-Se can improve the growth and flowering of chicory by Se-seed priming (Abedi et al. 2020, 2021). Nano-Se at 100 $mg \cdot L^{-1}$ can promote photosynthetic functions in tobacco (Zsiros et al. 2019). Nano-Se applied (2 μM) to pomegranate fruit had beneficial impacts on yield and quality in arid regions by increasing fruit antioxidants, total sugars, content of phenols and anthocyanins, and decreasing fruit cracking (Zahedi et al. 2019).

Selenium and nano-Se have the ability to improve the productivity and fruit quality of many crops, especially under stresses such as drought (Zahedi et al. 2020;

El-Saadony et al. 2021a, b), salinity (Morales-Espinoza et al. 2019; Badawy et al. 2021; Shalaby et al. 2021), and heavy metals (Riaz et al. 2021). Heavy metals are considered serious stressors on crop production and quality, as they can cause cell oxidative damage that can be alleviated by applying Se and nano-Se to offset arsenic (As) exposure in rice (Camara et al. 2019; Ding et al. 2020), cadmium (Cd) in tomato (Xie et al. 2021) or tobacco (Luo et al. 2019), Cd and As in potato (Shahid et al. 2019), and Cd and Pb in rice (Hussain et al. 2020; Wang et al. 2021a). Cadmium detoxification through Se application occurs by reducing the uptake of Cd from the soil, regulating the plant antioxidative defense system and preventing Cd distribution by cell wall and phytochelatin sequestration (Riaz et al. 2021). On the other hand, Se has adverse effects on plants at toxic concentrations (Gupta and Gupta 2017; Schiavon and Pilon-Smits 2017), which leads to over-generation of methylglyoxal and reactive oxygen species (ROS) causing oxidative damage that can be mitigated using salicylic acid (Mostofa et al. 2020). The problem of Se phytotoxicity has been discussed by many researches such as Kolbert et al. (2019), Ulhassan et al. (2019), Hasanuzzaman et al. (2020), Gouveia et al. (2020), Mostofa et al. (2017, 2020), Liu et al. (2021b), and Yang et al. (2021).

4.4 Selenium and Nano-Se for Mitigating Stress in Plants

Abiotic stresses are the main factors that reduce the productivity of crops (Canter 2018; Zörb et al. 2019). These include salinity, drought, high or low temperatures, flooding, nutrient deficiencies, and heavy metals (Vaughan et al. 2018; Zafar et al. 2018) which cause serious problems for cultivated plants including damages to photosynthesis, enzymatic activities, and metabolism (Haghighi et al. 2014; Du et al. 2018). About 90% of arable land is subject to one or more of these stressors (dos Reis et al. 2017), which causes yield losses of up to 70% (Mantri et al. 2012). This can have serious consequences for food security (Tigchelaar et al. 2018).

Several chemical compounds, known as plant growth regulators (PGRs), modify plant responses to biotic and abiotic stresses, especially at the cellular, tissue, and organ levels. Among these compounds, different forms of Se (selenite, selenate, nano-selenium, and selenoproteins) may be essential for higher plants (Chauhan et al. 2019; dos Reis et al. 2020). Selenium has been reported to ameliorate stress in plants due to its ability to stimulate the synthesis of S- and N compounds, in addition to stimulating the activity of antioxidant enzymes and metabolites. Also, under both stressful and non-stressful environments, selenium can alter the absorption of some microelements such as molybdenum, which acts as a cofactor for the nitrate reductase enzyme (Schiavon and Pilon-Smits 2017), promotion of growth (White and Broadley 2009), and productivity (Jiang et al. 2015; Kaur and Nayyar 2015).

4.4.1 Salinity and Drought Stress

Salt and drought stress causes the production of reactive oxygen species in plants. Therefore, the protective role of Se against these stresses has been reported in different plant species and occurs by suppressing ROS accumulation by regulating the level of enzymatic and non-enzymatic antioxidants (Yao et al. 2012; Durán et al. 2015; Elsheery et al. 2020; Shalaby et al. 2021). Yao et al. (2011) showed that optimal concentrations of Se could help wheat seedlings maintain high growth performance under drought stress by increasing the activities of peroxidase and CAT that lower the level of ROS. The decrease in ROS levels by Se in plants exposed to salinity and drought stress was also observed in other plant species such as rapeseed seedlings (Hasanuzzaman and Fujita 2011), *Trifolium repens* (Wang 2011), wheat (Nawaz et al. 2015; Elkelish et al. 2019), lettuce (Shalaby et al. 2017), rice (Subramanyam et al. 2019), and grapevine (Karimi et al. 2020).

4.4.2 Stress from Temperatures

Similar to salinity and drought stress, high and low temperatures (heat and chilling stress) can increase the production of reactive oxygen species in plants, particularly in species that possess a low antioxidant capacity for detoxification of reactive oxygen species (Wang et al. 2009; Djanaguiraman et al. 2010). Selenium and nano-Se have been observed to protect plants from oxidation under these stresses. In wheat, for example, application of Se has been reported to relieve symptoms related to cold stress by reducing MDA content and increasing production of antioxidant metabolites, such as anthocyanins, flavonoids, and phenolic compounds (Chu et al. 2010). Similar results were attained for potato (Seppänen et al. 2003), cucumber (Hawrylak-Nowak 2009; Shalaby et al. 2021), sorghum (Abbas 2013), and chrysanthemum (Seliem et al. 2020) at low temperatures when treated with Se.

4.4.3 Stress from Heavy Metals

High concentrations of heavy metals in soil can reduce plant's ability to accumulate these and other nutrients and affect the synthesis of molecules such as chlorophyll, carotenoids, proteins, and antioxidant enzymes, which contain one or more of these nutrient minerals in their active sites to act as catalysts (Cuypers et al. 2010; Hasanuzzaman et al. 2012). As mentioned above, Se can stimulate the antioxidant capacity of cells in plants grown in the presence of heavy metals through the enhanced activity of antioxidant enzymes and the synthesis of non-enzymatic metabolites, i.e., GSH and PC, as well as stimulate spontaneous superoxide radicals into H_2O_2 (Feng et al. 2013).

Recent studies have reported a positive effect of Se on the activity of antioxidant enzymes in response to Cd stress. Lin et al. (2012) showed that the application of 3 μM Se to rice plants can increase the activity of SOD and POX enzymes in roots and leaves. Similarly, 5 μM Se has been reported to reduce absorption in mung bean (*Phaseolus aureus*) and reduce oxidation by enhancing the activity of SOD, POD, and APX enzymes (Malik et al. 2012). Similar results were found in tobacco plants (*Nicotiana tabacum*) treated with 0.1 mg L^{-1} selenite (Han et al. 2015). The beneficial effects of Se have been described by several authors recently for plant exposed to Pb, with the benefits related to ROS scavenging in cells (Mroczek-Zdyrska and Wojcik 2012; Yuan et al. 2013; Hu et al. 2014). For example, a supply of 1.5 μM selenite reduced the production and concentration of superoxide (O_2) in the apical part of the rootstock of *Vicia faba* (Mroczek-Zdyrska and Wojcik 2012). Also, 1 μM selenite improved the leaf biomass of coleus (*Coleus blumei*) and decreased the rate of lipid peroxidation in the roots (Yuan et al. 2013). Furthermore, Hu et al. (2014) suggested that 0.5 mg kg^{-1} selenite could decrease Pb accumulation in rice shoot and husk tissues. Several studies have been published concerning the role of nano-Se in mitigating abiotic stresses on cultivated crops as presented in Table 4.2.

4.5 Se and Nano-Se for Efficient Removal of Pollutants

Environmental pollution is a complicated problem, and several organic and inorganic pollutants can be found in various wastewaters. These pollutants are easy to diffuse with surface runoff and can reach groundwater. The use of Se to mitigate the effects of pollutants has received considerable attention (Table 4.3). The most important inorganic pollutants in soil that Se and nano-Se can mitigate include arsenic (As), cadmium (Cd), chromium (Cr), fluoride (F), lead (Pb), mercury (Hg), and Se itself.

Many studies have investigated the role of Se and/or nano-Se using pot and hydroponic systems (water system) (Table 4.3). The distinguished role of Se and its synergistic effect on cultivated plants using hydroponic cultures under pollution by heavy metals, such as arsenic (Wang et al. 2021b), cadmium (Huang et al. 2021a, b; Zhang et al. 2021a), fluoride (Niu et al. 2020), lead (Mateus et al. 2020), and mercury (Liu et al. 2021b) show the ability of Se to ameliorate metal toxicity, inhibit metal-translocation from roots to shoots, and have antagonistic effects with the pollutants (Alam et al. 2020; Guo et al. 2020; Liu et al. (2020). Other factors can control the bioavailability of heavy metals in soils such as soil pH (Xu et al. 2021a, b), The combined application both of Se and Si during the tillering to booting stage of rice reduced Cd and Pb uptake, translocation to grains, mitigated oxidative damage, and promoted photosynthesis (Wang et al. 2020a). More studies are needed to investigate the combined effects of jointly applied Se and Si, as well as nano-Se and nano-Si, on cultivated crops under different stresses.

Table 4.2 The role of Se-nanoparticles in mitigating abiotic stresses on some cultivated crops

Crop and its scientific name	Stress type and its details	Se-nanofertilizer and its applied dose details	Role of Se-nanoparticles	Reference
Chicory: *Cichorium intybus* L.	Stress from foliar Se at 4 and 40 mg l^{-1} SeO_2 as bulk Se	Chemical nano-Se at 4 and 40 mg l^{-1} (particle size 10-45 nm)	Nano-Se-triggered signaling, which associates with tolerance or regulatory roles of transcription factors, like *DREB1A*.	Abedi et al. (2021)
Moldavian balm: *Dracocephalum moldavica* L.	Applied Cd in form of $CdCl_2$, at 2.5 and 5 mg kg^{-1}	Chitosan-selenium-NPs at 5 and 10 mg l^{-1}	Chitosan-Se NPs (5 mg l^{-1}) mitigated Cd stress by enhancing antioxidant enzymes; proline.	Azimi et al. (2021)
Bitter melon: *Momordica charantia* L.	Applied salinity levels were 50 and 100 mM NaCl	Foliar applied chitosan–Se-NPs at 10, and 20 mg l^{-1} (75 nm)	Applied Cs–Se NPs (20 mg l^{-1}) recorded best antioxidant enzyme activities; decreased oxidative damage under salinity.	Sheikhalipour et al. (2021)
Wheat: *Triticum asetivum* L.; cv. Masr1	Drought and heat stress	Chemical and bio-Se-NPs at 50, 75, and 100 mg l^{-1} (size 46 nm)	Bio-Se-NPs scavenged 88 and 92% of DPPH$^+$ and ABTS$^+$ radicals; enhanced quantity and quality of wheat grains by 5–40%.	El-Saadony et al. (2021a, b)
Lemon balm: *Melissa officinalis* L.	Salinity in nutrient solution 50, 100, and 150 mM NaCl	Foliar spray chemical Se-NPs at 50, and 100 mg l^{-1} and 10–45 nm	Se-NPs (up to 100 mg l^{-1}) decreased lipid peroxidation due to high SOD, CAT, and POX activities.	Ghasemian et al. (2021)
Coffee: *Coffea arabica* L. red Itucaí cultivar	Stress from foliar Se at 10, 20, 40, 80, 120, and 160 mg l^{-1} as Na_2SeO_4	Microbial nano-Se and nano-Se at 10, 20, 40, 80, 120, and 160 mg l^{-1}	Foliar Se increased yield by 38 and 42% for 20 mg Se l^{-1} (at selenate) and for 160 mg Se l^{-1} in the form of nano-Se.	Mateus et al. (2021)
Common bean: *Phaseolus vulgaris* L.	Soil salinity stress (EC 7.55–7.61 dS m^{-1})	Foliar applied Se-NPs at 0.5, 1.0, and 1.5 mM (size 10–45 nm)	Foliar 1.0 mM was the best for growth and yield; osmo-protectant (soluble sugars and free proline), K^+/Na^+ ratio; all enzyme activities	Rady et al. (2021)
Cucumber: *Cucumis sativus* L.	Soil salinity (EC 4.49 dS m^{-1}) and heat stress (41 °C)	Biological nano-Se (50–200 nm; 25 mg l^{-1})	Improved productivity and growth under combined heat and salinity stress.	Shalaby et al. (2021)

(continued)

Table 4.2 (continued)

Crop and its scientific name	Stress type and its details	Se-nanofertilizer and its applied dose details	Role of Se-nanoparticles	Reference
Paddy rice: *Oryza sativa* L.	Cd and Pb stress (3.0 and 300 mg kg^{-1}, resp.)	Chemical nano-Se (160 nm; 25–100 µmol l^{-1})	A dose of 50 µmol L^{-1} Se-NPs is the best, which decreased Cd accumulation, and improved photosynthesis.	Wang et al. (2021a)
Bitter melon: *Momordica charantia* L.	*In vitro* applied Se stress at 1, 4, 10, 30, and 50 mg L^{-1} as selenate	Nano-Se at 1, 4, 10, 30, and 50 mg L^{-1} (size 10–45 nm)	Based on high phytotoxicity due to bulk-Se, nano-Se mediated real variations in DNA cytosine methylation.	Behbahani et al. (2020)
Paddy rice: *Oryza sativa* L.	Cd and Pb stress (3.0 and 300 mg kg^{-1}, resp.)	Chemical nano-Se (50 nm; 4, 6, 12 mg l^{-1})	Combined nano-silica & nano-Se reduced Cd and Pb accumulation; mitigated oxidative stress damage.	Wang et al. (2020a)
Strawberry: *Fragaria* × *ananassa* Duch.	Drought stress (30, 60, and 100 % field capacity)	Chemical Se-NPs (25 mg l^{-1}, 60 nm)	Applied Se/SiO_2-NPs at 100 mg l^{-1} managed drought stress by higher level of osmolytes like carbohydrate and proline.	Zahedi et al. (2020)

Abbreviations: *SOD* super oxide dismutase, *CAT* catalase, *POX* peroxidase, *DREB1A* dehydration response element B1A gene, *DPPH* 1,1-diphenyl-2-picryl hydrazyl, *ABTS* 2,2′-azino-bis(3-ethylbenzothiazoline-6-sulfonic acid

4.6 Conclusions

Selenium and nano-Se have a wide range of beneficial effects on different crops including field and horticultural plants. These impacts mainly depend on crop varieties, growth stages, applied Se-doses, and its form. A good strategy for cultivated crops could include (*i*) not applying any excess Se through fertilizers or foliar spray, (*ii*) Se-bio-nanofertilizer is the best choice, followed by organic Se, (*iii*) applying Se-fertilizers derived from methyl sources may be safe for human health, and (*iv*) Se-nano biofortification is a promising approach. Selenium and nano-Se fertilization for plant nutrition will be the cornerstone for any human nutrition program enriched in Se. Following a fertilizer program containing Se and/or nano-Se may enhance crop production quality, especially for plants under stress (e.g., salinity, drought, stress from temperature extremes, and stress from heavy metals). In the coming years, new approaches for Se and nano-Se will be discovered in the field of plant nano-nutrition and crop nano-quality.

Table 4.3 Some published studies on the role of Se or nano-Se under polluted soils and waters

Crop and its scientific name	Pollutant type and its details	Applied Se/ nano-Se and its dose	Main findings of study and experimental conditions	Reference
Pot experiments				
Rice (*Oryza sativa* L.) var. Gangyou 198	Soil Pb, Cr, As and Cd at 30.23, 65.92, 7.11 and 0.46 mg kg^{-1}, resp.	Soil Se content was 0.45 mg kg^{-1}	The availability of Se and Cd was totally controlled by soil pH; increased pH decreased available Cd and increased Se; applied soil amendment was effective for medium-high Se soil contaminated by Cd.	Xu et al. (2021a, b)
Pea (*Pisum sativum* L.), 3 varieties	Initial soil As was 5.06 mg kg^{-1} increased to 30 mg kg^{-1}	Se metal powder at 20 or 30 mg kg^{-1}	Se as soil amendment has great potential in improving pea yield grown in As-polluted soil and reducing its transfer into humans through the food chain.	Alam et al. (2020)
Water spinach (*Ipomoea aquatica* L.) genotypes	Foliar 50 mg kg^{-1} as $K_2Cr_2O_7$; soil total Cr was 67.54 mg kg^{-1}	Foliar Se as Na_2SeO_3 solution (3 mg L^{-1})	Simultaneously applied Se and biochar increased the biomass; increased soluble protein content and soluble sugar in leaves; reduced Cr content in roots and shoots.	Guo et al. (2020)
Lettuce (*Lactuca sativa* L.)	Spiked soil with 100 mg kg^{-1} mercury as $HgCl_2$	Foliar Se at 5 μM as K_2SeO_4	Foliar Se increased Se content in the lettuce without any toxic effects, whereas Hg decreased biomass, photosynthetic efficiency, and total chlorophyll content.	Kavčič et al. (2020)
Rice (*Oryza sativa* L.), 2 cv. CLY & YZX low-and high Cd accumulation, res.	Original soil had 0.22 mg kg^{-1} Cd; spiked with 5.0 mg Cd kg^{-1} soil	Added 0.8 mg Se kg^{-1} soil as Na_2SeO_3	Combined Se and organic amendments (vermicompost and biochar) increased grain Se content and reduced grain Cd levels by 5.8–20.8%, compared to organic amendments only.	Liu et al. (2020)
Rice (*Oryza sativa* L.), cv. Yang-Dao No 6	Soil total As and Cd 282 & 8.10 mg kg^{-1} resp.	Selenite (Na_2SeO_3) at 1 and 5 mg kg^{-1}	Applied selenite stimulated yield of rice exposed to As and Cd; reduced their content in grains for some combined treatments.	Lv et al. (2020)

(continued)

Table 4.3 (continued)

Crop and its scientific name	Pollutant type and its details	Applied Se/ nano-Se and its dose	Main findings of study and experimental conditions	Reference
Rice (*Oryza sativa* L.), cv. Ming Hui 63	Soil total As 3.63 mg kg^{-1}; spiked 50 mg As(III) or As(V) per kg soil	Spiked 4.0 mg Se(IV) or Se(VI) in per kg soil	Selenite or selenate decreased arsenate content in pore water of soils; inhibited arsenate uptake by rice roots and reduced their accumulation in shoots.	Pokhrel et al. (2020)
Rice (*Oryza sativa* L. subsp. Indica)	Spiked soil 3.0 and 300 mg kg^{-1} Cd and Pb, resp.	Foliar applied at 4, 6 and 12 µg mL^{-1} Se combined with Si (15, 22, 44 µg mL^{-1})	Foliar applied Si and Se during tillering to booting stage reduced Cd and Pb uptake, translocation to grains; mitigated oxidative damage; and promoted photosynthesis.	Wang et al. (2020a)
Rice (*Oryza sativa* L.)	Hg-polluted soils with methyl-mercury (MeHg) at 2.95 mg kg^{-1}	Applied Se levels of 20, 40, 60, 100, 300, 500 mg kg^{-1}	Applied Se reduced inorganic Hg by > 48%, 18%, and 80% in root, stem, and grain, respectively (not leaf); reduced MeHg in grain and root (not stem and leaf)	Xu et al. (2019)
Wheat (*Triticum aestivum* L.)	Soil Cd was 1.12 mg kg^{-1}; soil pH 8.13	Original soil Se was 0.16 mg kg^{-1}; foliar Se 10, 20, and 40 mg L^{-1}	Foliar Se and Zn application (10, 20, 40 mg L^{-1}) decreased malondialdehyde and Cd concentrations in wheat grains, leaves, hulks, stalks, and roots in a dose-additive manner.	Wu et al. (2020a)
Hydroponic culture				
Halophyte of *Suaeda salsa* L.	Mercury as $HgCl_2$ at 20 µg L^{-1}	Selenium as Na_2SeO_3 at 2 µg L^{-1}	Se could induce synergistic effects in *S. salsa* under mercury pollution and help evaluation of the toxicity and interaction of marine pollutants.	Liu et al. (2021b)
Rice (*Oryza sativa* L.) var. EZhong 5	Soil amended Cd using 100 µM of $CdCl_2{\cdot}2H_2O$	Added Se at 3 µM (Na_2SeO_3)	Synergistic impact of combined Si (1.5 mM $Na_2SiO_3{\cdot}9H_2O$) and Se to ameliorate Cd toxicity and promote rice growth under this metal stress.	Huang et al. (2021a, b)

(continued)

Table 4.3 (continued)

Crop and its scientific name	Pollutant type and its details	Applied Se/nano-Se and its dose	Main findings of study and experimental conditions	Reference
Rice (*Oryza sativa* L.), cv. Zhunliangyou 608	Added As at 10 mM of arsenite or arsenate to solution	Added Se at 30 mM of Se-NPs or selenite into the solution	Selenite had a stronger inhibiting impact on As translocation compared to Se-NPs; selenite also reduced As in rice shoots by altering its localization and its speciation.	Wang et al. (2021b)
Rice (*Oryza sativa* L.), var. Ezhong 5	Added Cd to the solution at 1.0 mg L^{-1} as $CdCl_2{\cdot}2.5H_2O$	Applied Se at 1.0 mg L^{-1}; selenite or selenate	Combined added Se and Fe (60 mg L^{-1}) inhibited Cd adsorption onto the iron plaque and its uptake by roots and its translocation from rice roots to shoots.	Zhang et al. (2021a)
Arabian coffee (*Coffea arabica* L.) 5 genotypes	Selenium itself as a pollutant	Applied Se at 1.0 mmol L^{-1}	Under Se stress, coffee seedlings had negative impact, led to decreased P, S, and Fe in leaves as the antagonistic effect.	Mateus et al. (2020)
Tea plants (*Camellia sinensis* L.) O. Kuntze	Fluoride at 5 or 20 mg L^{-1} and F as NaF	Applied Se at 0.25, 0.5, or 1.0 mg L^{-1} as Na_2SeO_3	Exogenous Se reduced the accumulation of F in tea leaves under hydroponic culture, which could be used at high natural F levels in the soils.	Niu et al. (2020)

Acknowledgments This work was financed and supported by the Central Department of Mission, Egyptian Ministry of Higher Education (Mission 19/2020) for H. El-Ramady and also by the Hungarian Tempus Public Foundation (TPF), grant no. AK-00152-002/2021.

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Chapter 5
Uptake and Metabolism of Selenium in Plants: Recent Progress and Future Perspectives

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5.1 Introduction

Plants fulfill their requirement for essential minerals by absorbing nutrients from the soil solution. Through pathways of essential nutrient absorption, plants take up also non-essential elements from the soil. One of these elements is selenium (Se), a metalloid that can be found in soils in both inorganic and organic forms. The dominant types of inorganic forms are selenate (SeO_4^{2-}) and selenite (SeO_3^{2-}), while selenide (Se^{2-}) and elemental Se (Se^0) can also be found in soils as minor components. In well-aerated soils, selenate is dominant, while in anoxic soils, selenite is present in higher quantities (White 2018). Additionally, certain soils contain small concentrations of organic selenium species (e.g., selenocysteine, SeCys; selenomethionine, SeMet; volatile methylselenides) resulting from biological activities and degradation of organic material. Beyond soil oxygen levels, the phytoavailability of Se forms is influenced also by soil pH and salinity. In the case of high salinity and high pH, selenite adsorbs more strongly onto the surface of clays and metal oxides than selenate, thus selenate is the major form for plant uptake. Some soil anions, such as phosphate and sulfate influence selenium uptake by plant roots due to ionic competitions, while other anions, such as chloride, actually enhance Se uptake by affecting plant metabolism (Mayland et al. 1991).

Selenium is interesting in several ways considering its relationship with plants. Within the plant kingdom, there is a difference in selenium essentiality. Higher plants do not require selenium as an essential element, while for 33 primitive microalgae species, the presence of Se in the environment proved to be essential (Araie and Shiraiwa 2009). The evolutionarily lost ability of higher plants to utilize Se as

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M. A. Hossain et al. (eds.), *Selenium and Nano-Selenium in Environmental Stress Management and Crop Quality Improvement*, Sustainable Plant Nutrition in a Changing World, https://doi.org/10.1007/978-3-031-07063-1_5

an essential element can be explained by the fact that the availability of Se on the land is lower than in the aquatic environment (Pilon-Smits and Quinn 2010; Schiavon and Pilon-Smits 2017).

Given that plants can absorb and accumulate Se to a certain extent without toxic symptoms and Se is an essential component in 25 human selenoproteins (Rayman 2012), it is a desirable goal to enrich food plants with Se in order to prevent diseases associated with human Se deficiency. This process became known as biofortification and is continuously improved due to the novel trends of genetic and metabolic engineering (Van Der Straeten et al. 2020). In the past decades, multiple laboratory and field experiments have demonstrated the applicability of biofortification in the case of Se in several plant species (recently reviewed by D'Amato et al. 2020). Another practical aspect related to plant Se uptake and accumulation is phytoremediation. In many parts of the world, areas rich in Se can be found (Yang et al. 2022), which are habitats of special plant species capable of hyperaccumulating Se. Selenium-hyperaccumulator (Se-HA) plants (e.g. *Astragalus bisulcatus, Stanleya pinnata, Cardamine violifolia, Pulcinella distans,* Galeas et al. 2007; Freeman et al. 2012; Yuan et al. 2013; Kök et al. 2020) can have tissue Se concentrations reaching 1.5% of their dry matter and have larger Se:sulfur (S) ratio than non-hyperaccumulator species (Cappa et al. 2014). Due to the high accumulation capability and good Se tolerance, Se-HA species can be used as models in research related to Se phytoremediation.

Due to these practical applications, researches on plant Se uptake and metabolism are timely and have high importance. This chapter discusses the available scientific literature and provides a state-of-the-art overview regarding our knowledge about Se uptake and metabolism in higher plants.

5.2 Uptake and *in planta* Transport of Se in Higher Plants

The major Se forms taken up from the soil solution by plant roots are selenate anion, selenite anion, SeMet, and SeCys. The transport mechanisms that plants use to absorb Se forms are different, therefore the next part of this chapter will discuss the root-level uptake of selenate, selenite, and organic Se forms.

5.2.1 Selenate Uptake Routes

Selenate can enter plant roots via H^+/sulfate symporters (Gigolashvili and Kopriva 2014). Of the four groups of sulfate transporters, Group 1 SULTR1;1 and SULTR1;2 have been reported to transport selenate (Yoshimoto et al. 2002). In *A. thaliana*, SULTR1;2 proved to be the main selenate transporter (Barberon et al. 2008). Due to the competition between sulfate and selenate at the level of transporters, it is possible that selenate treatment can inhibit sulfur uptake by causing S starvation

(Takahashi et al. 2000; Van Hoewyk et al. 2008). S deficiency increases the expressions of SULTR1;1 and SULTR1;2 (Rouached et al. 2008) which may contribute to enhanced selenate uptake when Se in this form was applied to plants. Furthermore, it has been hypothesized that selenate treatment also directly influences the expression of sulfate transporters; however, reported data in this matter remained still unclear (Rouached et al. 2008; Takahashi et al. 2000; Zhang et al. 2006).

5.2.2 Selenite Uptake Routes

Compared to selenate, selenite has been reported to be taken up *via* inorganic phosphate (P_i) transporters and aquaporins (Schiavon and Pilon-Smits 2017; White 2018). Overexpression of P_i transporters significantly increased selenite uptake in rice (*Oryza sativa*) and tobacco (*Nicotiana tabacum*) (Song et al. 2017; Zhang et al. 2014). From the aquaporin family, NIP2;1 protein has been reported to be able to transport selenite in rice (Zhao et al. 2010). These studies require further investigations, especially considering that rice is grown on anoxic soil, in which selenium is the most available in the form of selenite.

5.2.3 Absorption of Organic Selenium Forms

Beyond selenate and selenite, plants are able to utilize organic selenium forms, especially SeMet and SeCys (Kikkert and Berkelaar 2013). In *A. thaliana,* it has been proposed that amino acid permease (AAP) 1 and its homolog LHT1 are transporters involved in absorbing S-containing amino acids (Cys, Met) (Boorer et al. 1996; Hirner et al. 2006), but the Se transporting capacity of these permeases has not been experimentally verified yet.

5.2.4 **In planta** *Transport of Se Forms*

Following the uptake into the root cells, most of the selenate is translocated into the shoot, as has been shown in rice and wheat (Li et al. 2008; Huang et al. 2017; Wang et al. 2015). SULTR2;1 and SULTR3;5 S transporters may play a role in loading Se into the xylem (Fig. 5.1). Expression of SULTR2;1 is induced by high Se concentration (Takahashi et al. 2000), which suggests the role of the transporter in Se translocation, although this is not supported by direct evidence (Trippe and Pilon-Smits 2021). Se remobilization *via* phloem may be realized by the function of SULTR1;3 (Fig. 5.1), whose expression is upregulated by selenate in wheat (Boldrin et al. 2016).

Regarding intracellular Se transport, our knowledge is even more limited. SULTR4;1 and SULTR4;2 function as sulfate exporters in the tonoplast (Kataoka

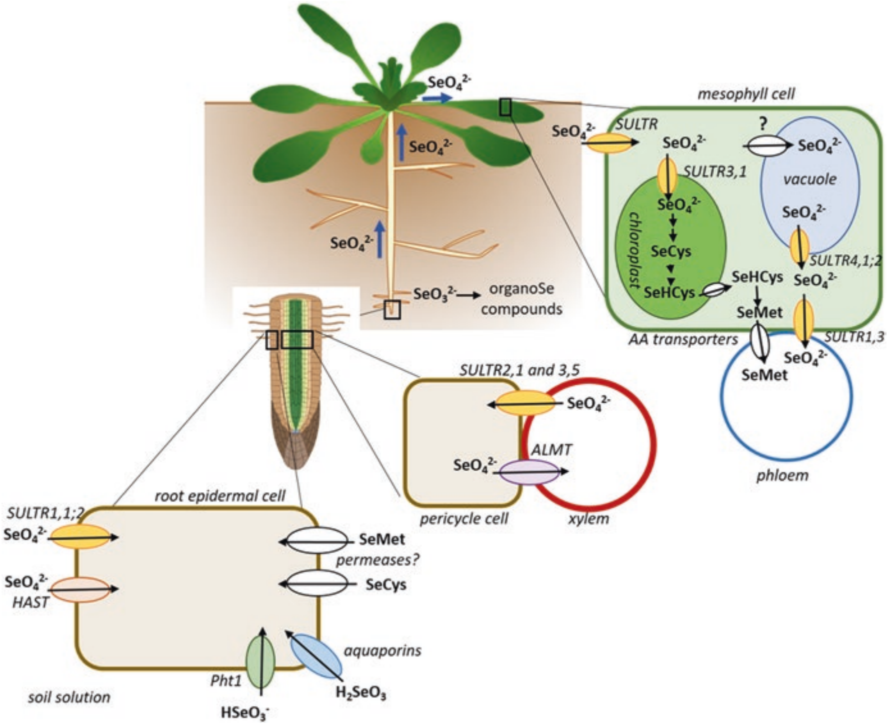

Fig. 5.1 Schematic model of uptake and primary metabolism of Se in higher plants. *SeO_4^{2-}* selenate, *SeO_3^{2-}* selenite, *$HSeO_3^-$* hydrogen selenite, *H_2SeO_3* selenous acid, *HAST* high-affinity sulfate transporter, *Pht1* high-affinity phosphate transporter, *SULTR* sulfate transporter, *ALMT* aluminum-activated malate transporters, *AA transporters* amino acid transporters, *SeMet* selenomethionine, *SeCys* selenocysteine, *SeHCys* seleno-homocysteine. (Modified after Guignardi and Schiavon 2017; White 2017; Hasanuzzaman et al. 2020)

et al. 2004, Fig. 5.1) and are upregulated by high doses of Se (Zhang et al. 2006) indicating that these transporters may catalyze Se export from the vacuoles. Additionally, Se may be imported into the vacuoles by P_i transporters, but the evidence is poor (Trippe and Pilon-Smits 2021).

Chloroplast is an important organelle in both S and Se metabolism. It is known that sulfate is taken up into the chloroplasts by Group 3 SULTRs (SULTR 3;1-3;5) and these five transporters are likely to be involved also in chloroplastic Se import (Trippe and Pilon-Smits 2021, Fig. 5.1). At present, we have no knowledge about chloroplast S exporters and it is possible that the electrochemical potential gradient makes possible the passive movement of selenate and sulfate out from the chloroplast. Since sulfate and selenate are assimilated in the chloroplasts, the export of organic forms can be more physiologically relevant (Gigolashvili and Kopriva 2014).

Collectively, our knowledge is limited about the movement of selenate within the plant body. The few available evidence indicates that sulfate transporters may be involved in selenate translocation between organs and also in intracellular selenate movement.

5.3 Pathways of Se Metabolism in Plants

Due to its chemical similarity to S, beyond Se uptake its metabolism is also accomplished *via* S-associated mechanisms. Being more toxic, selenite can get transformed to less harmful organic Se, like SeMet or selenomethionine Se-oxide (SeOMet), and remains in the root, while selenate reaches the vascular cylinder via symplastic transport (White 2018; Fig. 5.1). Then selenate moves from the pericycle into the xylem and participates in xylem-associated translocation to the shoot. Within the mesophyll cells, there are two pathways for selenate: it is transported into the chloroplast, which is the scene of primary Se metabolism, or move to the vacuole for sequestration (Fig. 5.1). If selenite is translocated to the shoot, it can enter the mesophyll cells, too but *via* P_i transporters again (Guignardi and Schiavon 2017).

As a result of the multistep process of the primary Se metabolism, SeCys and SeMet are synthetized. In the chloroplast, first selenate is converted to adenosine 5′-phosphoselenate (APSe) by an ATP sulfurylase (APS), then to selenite by an APR (adenosine 5′-phosphosulfate reductase) (Guignardi and Schiavon 2017; White 2018; Kolbert et al. 2019). Selenite can be reduced to selenide (Se^{2-}) by sulphite reductase (SiR) enzyme, which is able to produce a gasotransmitter molecule, hydrogen sulfide (H_2S), as well (Corpas et al. 2019). The conversion of selenite to selenide might happen in the presence of glutathione (GSH). The formation of SeCys from selenide and O-acetylserine (OAS) is catalyzed by cysteine synthase (CS) and dominantly happens in the chloroplast (White 2018).

The other seleno-amino acid, SeMet derives from SeCys, which is first enzymatically converted to selenocystathione (SeCysta), then to selenohomocysteine (SeHCys). In the cytosol, SeMet is generated from SeHCys by methionine synthase (MTR) (White 2018; Kolbert et al. 2019).

The production of further metabolites from SeCys or SeMet, i.e., secondary Se metabolism seems to be similar to secondary S metabolism. From SeCys, selenoglutathione or Se-allyl-L-cysteine sulfoxide can be synthetized in alliums, while in *Brassica* genus Se-containing glucosinolates might arise derived from SeMet (summarized by White 2018; Hasanuzzaman et al. 2020).

According to the former and recent publications, it seems that from Se uptake through the formation of SeCys and SeMet to Se-containing secondary metabolites, the above-mentioned process are general, namely in all plant species regardless of their ability to tolerate and/or accumulate Se. At the same time, the expression levels of genes (and homologs) encoding Se transporters involved in Se uptake, delivery and primary metabolism are different in various ecotypes: non-accumulators, Se-indicators, and Se-(hyper) accumulators (reviewed by Gupta and Gupta 2017; White 2017). Moreover, to avoid the incorporation of SeCys and SeMet into proteins resulting in mal/dysfunction, distinct Se detoxification mechanisms have been evolved in these groups. Henceforth, in the following subsections, we focus on these differences.

5.3.1 Se Metabolism in Non-accumulators

Although numerous reviews dealt with Se tolerance and accumulation of plants, the categories of non-accumulators, accumulators, and hyperaccumulators are not always clear. Gupta and Gupta (2017) classified plants into three groups based on Se accumulation: non-accumulators, which contain <100 mg/kg Se dry weight (DW), with, e.g., *Arabidopsis thaliana* or species from Poaceae; secondary accumulators, accumulating 100–1000 mg/kg Se (DW), e.g., rapeseed, Indian mustard, sunflower, alfalfa, and also hyperaccumulators, which can accumulate >1000 mg/kg Se (DW), with species like *Stanleya pinnata* from Brassicaceae and *Astragalus bicultatus* from Fabaceae. White (2017, 2018) gave a finer assortment: most of the angiosperms can be regarded as non-accumulators (leaf Se content <10–100 mg/g DW); Se indicators like several members of Fabaceae or Asteraceae (leaf Se content <1 mg/g DW); and Se accumulators (leaf Se content >1 mg/g DW). The subtypes of Se-accumulators are the so-called hyperaccumulators containing almost 60 species which typically grow on seleniferous soils (detailed by White 2016).

Non-accumulators commonly grow in non-seleniferous soils that are found in Se-deficient or Se-low regions of the world (detailed in Gupta and Gupta 2017). Nevertheless, Se indicators can be discussed together with non-accumulators due to the similar biochemical and physiological characteristics (White 2017). Reports have assessed that generally they take up Se in the case of S deficiency. In non-accumulator species, such as *Arabidopsis,* it has been determined that the expression of the genes (and homologs) encoding SULTR1,1 and 1,2 is upregulated when S is absent or Se is abundant (Fig. 5.1, Schiavon et al. 2015; White 2018). Similarly, in the leaf, other transporters such as SULTR3,1 located in plastid membrane to take up selenate or SULTR4,1 and 4,2 realizing selenate efflux from the vacuole also showed higher expression level in case of S absence or Se supply (Kataoka et al. 2004; Shinmachi et al. 2010; White 2018).

The key enzymes which catalyze the biosynthesis of SeMet and SeCys from selenate are APS, APR, SiR, CS, and MTR. The expression of the genes encoding these showed to be increased by Se application in non-accumulator species (reviewed by White 2016).

Since the incorporation of Se-amino acids instead of Cys and Met can lead to dysfunctional proteins and consequently to toxicity, non-accumulator plants have some strategies to avoid it. In the case of excess Se, first, non-accumulators can sequester selenate in the vacuoles of the mesophyll cells or the vascular parenchyma cells; second, if Seamino acids are produced, plants can transform SeCys to SeMet in the mesophyll cells. Then SeMet is converted to Se-methylselenomethionine (SeMSeMet) by cytosolic S-adenosyl-methionine: methionine methyl transferase (MMT). SeMSeMet is metabolized to dimethylselenide (DMSe) which can be volatilized (Pilon-Smits and Quinn 2010).

5.3.2 *Se Metabolism in Accumulators and Hyperaccumulators*

Se-(hyper)accumulators show relatively high taxonomic diversity, since they can be found not only in Asteraceae, Fabaceae, and Brassicaceae but also in Amaranthaceae, Rubiaceae, and Orobanchaceae (White 2016). The common feature is that they colonize seleniferous soils. The main alterations compared to non-accumulators are the followings: (1) the form of absorbed Se is dominantly selenate, (2) the genes of the transporters (e.g., SULTR) are expressed constitutively, therefore the uptake and transport of selenate show high rate, (3) the enzymes involved in primary Se metabolism show higher activity (detailed by White 2017, 2018). Moreover, in case of excess Se, they can sequester Se in the reproductive organs (seeds, caryopsis), as it was demonstrated in rice (summary by Chauhan et al. 2019).

Not surprisingly, (hyper)accumulator species have also evolved a detoxification strategy to avoid potential Se toxicity, but using another enzyme that does not exist in non-accumulators, namely, selenocysteine methyltransferase (SMT). It can convert SeCys to selenomethylselenocysteine (SeMSeCys) which later turns to volatile dimethyl diselenide (DMDSe) (Kolbert et al. 2019). Naturally, SMT genes show high expression in these plant species (White 2018).

5.4 Selenium Speciation in Plants

Plant tissues contain inorganic forms of selenate and selenite taken up from the soil. In addition, organic seleno-amino acids such as SeMet, SeCys, Me-SeCys formed through metabolism can also be found in plant tissues (Galinha et al. 2015; Schiavon and Pilon-Smits 2017). Plant species show difference in the quality and quantitative distribution of Se forms, since, e.g. in rice, SeMet was detected in the highest amount (Carey et al. 2012), while in broccoli and onions, seleno-methylselenocysteine (Se-MeSeCys) proved to be the dominant Se specie (Wu et al. 2015; Zhu et al. 2009). The specification also depends on the form of selenium used, which can be supported by the early work of Zayed et al. (1998). In SeMet-exposed *Brassica* plants, Se-MeSeCys proved to be predominant, followed by SeHCys and Se-cystathionine, while in the case of selenate-treated *Brassica* plants, shoot mostly contains selenate, Se-MeSeCys, and SeMet, whereas root contains selenate, selenite, and SeMet. Furthermore, in selenite-enriched Brassica plants, shoot extracts contained SeMetSeOxide hydrates as the dominant organic Se species followed by selenite and SeMet, while root extracts showed the presence of SeMet and Se-MeSeCys (Zayed et al. 1998; Dumont et al. 2006). Recently, the application of nano-selenium (nSe) has become popular in both basic and applied plant science, since the nanoform of this metalloid proved to have several more beneficial effects on plants compared to the bulk material (GarcíaMárquez et al. 2020). In the work of Wang et al. (2020), the Se speciation has been compared in nanoSe (nSe)- and selenate/selenite-treated rice. In the shoot, only organic Se forms (MeSeCys, SeMet) were present as the effect of nSe treatment, while selenate or selenite supplementation resulted in the enhanced quantities of inorganic Se species (Wang et al. 2020).

According to a recent study, the mode of application also influences Se speciation. The effect of soil and foliar Se application was examined in purple grain wheat and common wheat in a 2-year-long field study, and it was found that the foliar application of Se more efficiently increased SeMet and SeCys concentrations in the grain than the soil application (Xia et al. 2020). Se speciation is also influenced by the hyperaccumulation capacity of the plant species. In general, Se-HA species contain less inorganic Se forms compared to non-accumulators. For example, in selenium hyperaccumulator *Astragalus bisulcatus*, Se-MeSeCys is the main Se compound and *Stanleya pinnata* accumulated high amount of MeSeCys in its tissues (Freeman et al. 2006). Recently, the Se forms in another hyperaccumulator, *Cardamine violifolia*, have been examined in detail (Both et al. 2020). Interestingly, the Se hyperaccumulating *Cardamine* species showed some differences from other hyperaccumulators, since its growth was not induced by selenium and phosphate didn’t inhibit selenite uptake in either of the *Cardamine* species. More importantly, Se-HA *Cardamine violifolia* accumulates selenolanthionine but doesn’t contain selenocystine (Both et al. 2020).

Recently, several studies have examined the effect of exogenous treatments on alterations in Se speciation. For example, Dai et al. (2020) observed that nitric oxide (NO) donor (sodium nitroprusside) decreased the accumulation of inorganic Se speciation in rice roots and shoots, and it caused no notable changes in the amount of organic Se forms (SeCys, SeMet). Besides other parameters, these changes also contributed to the improving effect of NO on rice selenium tolerance. In a recent study, the effects of the combined application of selenite/SeMet and salicylic acid (SA) enhanced, especially organic Se uptake of lettuce. Plants treated with SeMet alone or together with SA accumulated mainly SeMet and MeSeCys in their leaves, while lettuce treated with selenite or selenite+SA accumulated MeSeCys and selenite. Furthermore, lettuce roots showed no expression of SMT gene, while the expression of two MMT genes was independent of either Se or SA (Kowalska et al. 2020).

Collectively, the amount and ratio of Se forms in the plant tissues is influenced by the species of the plant, the Se hyperaccumulating capacity of the plant, the method and form of Se application, and also by exogenous treatments (Fig. 5.2).

5.5 Conclusions and Future Perspectives

Although selenium is not essential for higher plants, they absorb and accumulate it in their organs in connection with sulfate and phosphate transport. In past decades, many steps in Se uptake and metabolism have been explored in non-hyperaccumulator species. However, a number of questionable points remained unanswered, e.g. the clarification of the sulfate-selenate competition, the elucidation of the uptake mechanism of selenite, etc. Additionally, a more detailed study of the transporters

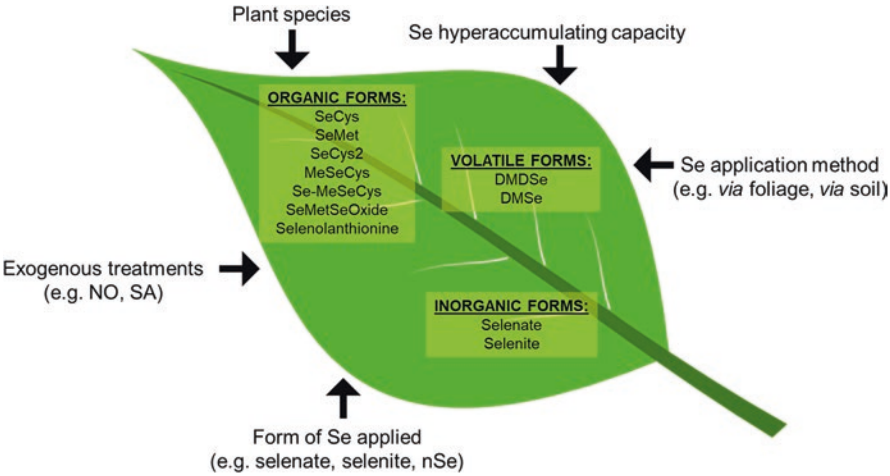

Fig 5.2 Schematic representations of the factors that influence the amount and ratio of Se forms (organic, inorganic, volatile) in the plant tissues. Abbreviations: *NO* nitric oxide, *SA* salicylic acid, *SeCys* selenocysteine, *SeMet* selenomethionine, *SeCys2* selenocystatione, *MeSeCys* methylselenocysteine, *Se-MeSeCys* selenium-methylselenocysteine, *SeMetSeOxide* selenium-selenomethionine oxide, *DMDSe* dimethyl diselenide, *DMSe* dimethyl selenide, *nSe* nano-selenium

involved in seleno-amino acid absorption will also be needed in the future. Currently, Se-specific transporters are not known in hyperaccumulators, although their discovery could represent a major advance in two practical areas: during the development of biofortification and phytoremediation technologies.

Acknowledgements This work was supported by The National Research, Development and Innovation Office (Grant no. K135303).

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Chapter 6
Selenium- and Se-Nanoparticle-Induced Improvements of Salt Stress Tolerance in Plants

Barbara Hawrylak-Nowak

6.1 Introduction

Excessive soil salinity is one of the widespread soil degradation processes and an important factor limiting crop productivity. It is believed that, on a global scale, no other toxic substance limits the yield of plants as drastically as salt stress (Aslam et al. 2011). However, there are no recent and precise statistics of the global extent of salt-affected soils (Shahid et al. 2018a). Salinization is characterized by the presence of high concentrations of easily soluble salts in the soil solution, and its causes are divided into natural and anthropogenic sources. Recent reports indicate that 80% of salinity is related to natural factors and 20% to anthropogenic sources (Mbarki et al. 2018). It is estimated that about 20% of agricultural land in the world is exposed to high salt concentrations, mainly Na^+ and Cl^- ions, and the problem continues to grow as a result of anthropogenic activities along with climate change (Gupta and Huang 2014; Roy and Chowdhury 2021). The salt-induced reduction of crop productivity is predicted to have affected up to 50% of arable land by the mid-twenty-first century (Kamran et al. 2020). The majority of salt-affected soils occur in the semiarid and arid areas of South America, Australia, and Asia. Although salinity is a serious problem for agriculture, it is mainly aggravated by the intensification of agriculture and improper fertilizer management (Roy and Chowdhury 2021).

Plants exposed to saline conditions suffer from three different interrelated stresses: 'osmotic', 'salt-specific', and 'oxidative'. Osmotic stress and ion toxicity cause secondary oxidative stress, which in turn contributes to the disturbance in physiological processes (Singh and Sharma 2018). Furthermore, the excessive

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M. A. Hossain et al. (eds.), *Selenium and Nano-Selenium in Environmental Stress Management and Crop Quality Improvement*, Sustainable Plant Nutrition in a Changing World, https://doi.org/10.1007/978-3-031-07063-1_6

uptake of inorganic ions such as Na^+ and Cl^-, contributes to nutritional imbalances and reduction of the uptake of macronutrients, leading to their deficiencies (Roy and Chowdhury 2021). All of these factors exert adverse pleiotropic effects on plants at physiological, biochemical, and molecular levels.

Although many efforts have been made to solve the problem of soil salinity, no simple and effective methods have been found. Where excessive salt accumulation in the soil is caused by irrigation or by land cleaning, altered agronomic procedures (e.g. drainage or crop rotation) can be used. However, if a large amount of salt is naturally present in the soil or such global processes as climate warming intensify and accelerate soil salinization, more advanced steps need to be taken to ensure production of stable crops in this type of farmland (Shabala and Munns 2017). Currently, scientists' efforts are focused mainly on the cultivation of plant varieties that are more resistant to salinity and the use of various types of biostimulants, osmoprotectants, antioxidants, and mineral fertilizers to prevent the toxic effects of salt stress in plants (Van Oosten et al. 2017; Hawrylak-Nowak et al. 2018).

In recent years, many articles have been published confirming the beneficial effect of Se on plant growth and development in conditions of excessive salinity (Kamran et al. 2020 and references therein). These studies focus on many taxonomically distant plant species, mainly crop plants. The results clearly indicate the high potential of Se compounds in reducing the harmful effects of salt stress and in maintaining the productivity of crops in saline areas. However, there is still much to be clarified regarding the detailed mechanisms of the biological action of Se in salt-exposed plants to transfer these positive Se effects from laboratory to field conditions.

6.2 Effects of Salinity on Plant Growth and Physiology

Soil salinization can occur due to both anthropogenic and natural events, including global warming, sea-level rise, drought, changing water demands, storm surge, and groundwater pumping (Tully et al. 2019). In general, soil with the electrical conductivity (EC) of the saturation paste extract (EC_e) higher than 4 dSm^{-1} (about 40 mM NaCl) and exchangeable Na^+ of 15% is considered a saline soil (Shrivastava and Kumar 2015). Nevertheless, soils are rarely saturated, and the salt concentration in the rhizosphere can be higher than in the saturation extract. It is believed that a soil with EC_e of 4 dS m^{-1} may have NaCl concentrations in the range of 80–100 mM most of the time, which has a very negative impact on the yield of most crops (Shabala and Munns 2017). From the point of view of plant physiology, it is very difficult to unequivocally and generally determine a salt concentration that induces salt stress, because its limit value depends on many factors, e.g. plant species, variety, and development stage, as well as other environmental factors (Negrão et al. 2017). NaCl is the predominant salt-inducing salinity in natural conditions. During evolution, plants have evolved complex regulatory mechanisms regulating its uptake and accumulation, which allow plants to survive and colonize saline soils (Munns and Tester 2008).

The harmfulness of salt stress depends primarily on the concentration and type of salt in the soil solution and the length of plant exposure to stress. The intensity of the stress factor plays a decisive role in the plant response to salinity and the possibility of reversible or irreversible changes in its metabolism and functioning (Gupta and Huang 2014). However, there is no doubt that excessive salt concentrations in the soil solution inhibit plant growth and limit their yield. Salt-affected soils are the most important factor limiting plant production for every staple crop. The damaging effects of salinity on plants are complicated and result from multifaceted interactions between biochemical, physiological, and morphological processes, e.g. water and nutrient uptake, photosynthesis, ion homeostasis, seed germination, and plant development (Shrivastava and Kumar 2015). Since salinity directly reduces the plant water uptake and root hydraulic conductivity, a decrease in the growth rate of individual cells and then entire plant organs is the main effect of these disorders (Negrão et al. 2017).

Nevertheless, moderate salt stress can also have a positive influence on some plant parameters. A process causing increased concentration of desired biologically active compounds to improve the health-promoting quality of plants is called elicitation (Baenas et al. 2014), and NaCl can be a simple, cheap, and efficient abiotic elicitor (Hawrylak-Nowak et al. 2021). One of the vast numbers of such examples may be the enhanced accumulation of phenolic secondary metabolites, especially anthocyanins, in lemon balm (*Melissa officinalis*) under NaCl exposure (Hawrylak-Nowak et al. 2021). A similar phenomenon was found in *Thymus* species, where a positive correlation between salt stress, concentrations of phenolic compounds, and antioxidant activity of plant extracts was noted (Bistgani et al. 2019). In turn, garlic (*Allium sativum*) exposed to 30 mM NaCl in hydroponic cultivation showed a considerable increase in root and bulb biomass, bulb diameter, and bulb height in comparison to the control (Astaneh at al. 2019). Thus, critically referring to scientific reports, it can be claimed that salinity may have some positive effects, but these are incomparably less important compared to the global decline in the yield of staple crops growing on saline-affected soils.

6.2.1 Osmotic Stress

The negative effect of salt stress results mainly from the limitation of water availability for plants as a result of its interaction with inorganic ions and an increase in the osmotic forces keeping water in the soil solution and preventing effective water uptake by plants (Shabala and Munns 2017). A decrease in cell turgor, as a result of impairment in water uptake by roots, is generally considered a possible mechanism to distinguish osmotic stress, but the osmosensing is not solely related to changes in turgor (Zhu et al. 1997).

The growth of the plant cell is regulated mainly by turgor pressure, which is the physical force acting on the cell wall, and is preserved by osmotically active substances inside cells such as K^+, soluble sugars, and free amino acids. Therefore, the decrease in cell turgor and cell volume, although transient, reduces the rate of cell elongation and division. Osmotic stress also affects the degree of opening of the stomatal aperture, which reduces the penetration of CO_2 into leaves, and thus lowers the net photosynthetic rate and flow of photoassimilates. An ion-independent reduction of plant growth provokes inhibition of cell expansion mainly in the shoot and leads to slower leaf appearance and a smaller final size (Negrão et al. 2017; Shabala and Munns 2017; Isayenkov and Maathuis 2019). Although roots, unlike leaves, are directly exposed to salinity, their control of ion uptake and ability to trigger efflux of ion excess allows them to control salt accumulation more precisely to avoid its toxicity (Shabala and Munns 2017). Moreover, most studies indicate that osmotic stress plays a larger role in overall salinity toxicity than salt-specific stress (Isayenkov and Maathuis 2019).

6.2.2 Salt-Specific Stress

While salt-induced osmotic stress occurs when inorganic ions are still outside the plant, the salt-specific stress begin with the ions enter the plant cells (Singh and Sharma 2018). A recent detailed evaluation of the ion toxicity mechanisms suggests that the toxicity affects the cytosol to a small extent and may be more dominant in the vacuole (Isayenkov and Maathuis 2019). Osmotic stress occurs fairly, quickly (within minutes to days), while the salt-specific toxicity is slower (days to weeks). As a result of excessive inorganic ion accumulation in the cells, ion homeostasis and thus cellular processes are disturbed, which may induce premature leaf senescence (Hasanuzzaman et al. 2021) associated with changes in the plant hormonal balance (Ghanem et al. 2008).

Under salinity, there is a rapid influx of Na^+ ions from the soil solution into the cortical cytoplasm of roots across non-selective cation channels (NSCCs) and then via the high-affinity K^+ transporters (HKT1). As cells cannot tolerate high concentrations of Na^+ in the cytoplasm, due to diminished enzyme activities and ion-specific cytotoxicity, they eliminate Na^+ ions from the cytosol and sequester them in the vacuole. To reduce further the influx of Na^+, NSCCs are quickly deactivated (Ismail et al. 2014). Contrary to Na, Cl is an essential plant micronutrient and Cl^- ions are taken up with the participation of the H^+/Cl^- symporter. However, under high salinity, the external Cl^- concentration may be high enough for a fraction of the Cl^- ion pool to enter passively via anion channels, causing toxicity and ion imbalance. Moreover, the high levels of Na^+ and Cl^- in the cell can directly affect water structure through chaotropic and kosmotropic effects and inhibit enzyme activities (Isayenkov and Maathuis 2019).

Plants need large amounts of K^+ for proper growth and development. Many physiological processes such as growth, photosynthesis, osmoregulation, enzyme activation, stomatal movement, water and nutrient transport via the xylem, and protein synthesis are regulated by K^+. This macronutrient may also play a significant role in cell signalling under salinity. Plant tolerance to salinity is related to the ability to maintain sufficiently high K^+ uptake despite the competitive influence of Na^+

(Houmani and Corpas 2016; Isayenkov and Maathuis 2019). Furthermore, it has been found that Na^+-induced membrane depolarization results in more difficult uptake of K^+ through inward-rectifying channels (KIRs) and promotes K^+ leakage by activating K^+ outward-rectifying channels (KORs) (Wakeel 2013). Membrane depolarization also disrupts the passive uptake of other necessary cations, making it thermodynamically unfavourable (Shabala and Munns 2017). The combination of a high salt concentration and a low K^+ level can cause even over 10^3-fold elevation in the Na/K ratio, which significantly exceeds the K/Na selectivity of many K^+ channels (Isayenkov and Maathuis 2019).

The *de novo* biosynthesis of osmoprotectants taking place under the influence of salt-induced osmotic stress reduces the availability of the ATP pool, making the high-affinity uptake of essential cations more difficult. The uptake of NO_3^- or PO_4^{3-} anions may be reduced because their active transport across plasma membrane requires a proton gradient generated by H^+-ATPase (Shabala and Munns 2017).

6.2.3 Oxidative Stress

It is well recognized that reactive oxygen species (ROS), i.e. derivatives of molecular oxygen that are normally formed during aerobic processes, act as universal signalling agents at low physiological concentrations (Sies and Jones 2020 and references therein). However, under exposure to adverse environmental factors, the balance between the production and neutralization of ROS by the antioxidant machinery is disturbed and oxidative stress appears as a result of overaccumulation of highly reactive ROS. Oxidative stress has toxic effects on all major plant cell biomolecules and biological structures, resulting in their dysfunction (Demidchik 2015; Hasanuzzaman et al. 2021). In salinity conditions, the osmotic stress and osmotically induced closure of stomata as well as the accumulation of toxic ions (especially Na^+) disrupt photosynthesis, thus preventing the plant from full utilization of light absorbed by photosynthetic pigments. This phenomenon causes overproduction of ROS and provokes ROS-induced damage (Shabala and Munns 2017). It has been shown that ROS are generated in both leaves and roots of salt-exposed plants (Lodeyro et al. 2016; Saini et al. 2018).

6.3 Efficiency of Selenium Supplementation in Mitigation of Salt Stress

6.3.1 Selenite, Selenate, and Selenide

Selenium is an essential trace element for animals, including humans, and also for some microorganisms, but it is not categorized as an essential element for vascular plants. Nevertheless, recent studies have indicated that low concentrations of Se (most often a few micromoles) are beneficial and can enhance plant resistance to some biotic and abiotic stress factors. Thus, Se may act as a beneficial element for plants by altering several metabolic processes (Hawrylak-Nowak et al. 2018; Hasanuzzaman et al. 2020).

The first significant and comprehensive scientific report on the positive effect of Se supplementation under salt stress was presented by Kong et al. (2005). They studied the impact of Se on NaCl-stressed sorrel (*Rumex patientia* × *R. tianshanicus*) and showed that low concentrations of Se (1–5 μM) improved salt stress resistance in this species. Enhanced activity of antioxidant enzymes (superoxide dismutase – (SOD) and peroxidase (POX)), a simultaneous increase in the level of soluble sugars, and improved integrity of membrane systems and ultrastructure of chloroplasts and mitochondria have been recorded. Consequently, the biomass of the salt-exposed plants supplemented with 5 μM Se was about two-fold higher than that of plants treated with NaCl alone (Kong et al. 2005).

Later experiments confirmed these observations and provided a lot of important information about the influence of Se on plants subjected to salt stress. Experiments conducted by Hawrylak-Nowak (2009) on cucumber (*Cucumis sativus*) have shown that Se promoted growth in NaCl-exposed plants protecting the cell membrane against lipid peroxidation, increasing accumulation of free proline in the leaves, and decreasing the concentration of Cl^- in aboveground organs. Since assimilation of inorganic Se compounds takes place predominantly in plastids (Pilon-Smits 2012), an intense influence of this element would be expected also in these organelles. This hypothesis is well supported by the results reported by Diao et al. (2014), who demonstrated that exogenously applied Se induced many antioxidative responses in the chloroplasts of salt-stressed tomato (*Solanum lycopersicum*). In these conditions, increased activity of most antioxidant enzymes (mainly related to the ascorbate–glutathione cycle) and increased content of key non-enzymatic antioxidants were noted. Further studies with maize (*Zea mays*) showed that Se supplementation also prevented unfavourable ultrastructural damage to chloroplasts induced by salinity (Jiang et al. 2017). More integrated internal lamellae, thicker grana lamellae, and a more regular shape of the thylakoids were observed in the presence of Se in comparison to plants exposed to NaCl alone. The increase in the content of photosynthetic pigments, which is very often noted during Se supplementation in salinity conditions (e.g. Hawrylak-Nowak 2009; Hashem et al. 2013; Lan et al. 2019), may be a result of the preserved ultrastructure of chloroplasts that are less damaged by ROS. Additionally, α-tocopherol treatment can reinforce the efficacy of Se in prevention of the photosynthetic pigment damage induced by salt stress in maize (Khalil et al. 2022).

Sustenance of the function of chloroplasts under salt stress was associated with maintenance of better photosynthesis parameters in Se-supplemented plants (Diao et al. 2014, Habibi 2017a, b; Jawad Hassan et al. 2020). It was found that application of Se enhanced the excitation energy trapping and electron transport in PSII, thus the harmful effect of salinity on PSII functioning was reduced (Habibi 2017b). In a study conducted by Diao et al. (2014), supplementation of salt-exposed plants with 50 μM of selenite increased the net photosynthetic rate (P_n), maximum quantum yield of PSII (F_v/F_m), actual photochemical efficiency of PSII (Φ_{PSII}), photochemical quenching coefficient (q_P), and non-photochemical quenching coefficient (q_N). A similar effect was also achieved in field conditions, where the chlorophyll fluorescence parameters, i.e. the maximum quantum yield of PSII (F_v/F_m) and the activity of PSII reaction centres (F_v/F_0), were increased, thus the photosynthetic performance index (P_I) was improved in response to foliar selenate spraying (Semida et al. 2021).

The NaCl-induced oxidative stress can be reduced in the presence of Se because this element may be involved in upregulating the activity of enzymatic antioxidants and the accumulation of a number of compounds from the group of non-enzymatic antioxidants, e.g. L-ascorbate, reduced glutathione (GSH), and phenolic compounds, both in isolated chloroplasts as indicated by Diao et al. (2014) and in whole leaves (Hasanuzzaman et al. 2011; Elkelish et al. 2019; Lan et al. 2019). A study reported by Hasanuzzaman et al. (2011) demonstrated the high effectiveness of Se supplementation in improving the functioning of the antioxidant machinery in salt-exposed rapeseed (*Brassica napus*) seedlings. Almost all of the plant antioxidant defence components (L-ascorbate and GSH contents, GSH/GSSG ratio, activities of ascorbate peroxidase (APX), catalase (CAT), glutathione peroxidase – (GPX), monodehydroascorbate reductase – (MDHAR), dehydroascorbate reductase– (DHAR), glutathione reductase – (GR), glutathione S-transferase – (GST), glyoxalase I (Gly I), and glyoxalase II (Gly II) enzymes) were improved when Se was added to the nutrient solution. They first showed that Se could be involved in activation of the methylglyoxal (MG) detoxification system, which includes two glyoxalase enzymes (Gly I and Gly II). Increased activity of these enzymes contributes to detoxification of the reactive and cytotoxic compound MG and maintaining GSH homeostasis (Hasanuzzaman et al. 2011; Li 2016). KeLing et al. (2013) reported boosted SOD and POX activities in melon (*Cucumis melo*) subjected to salt stress, while CAT activity was generally not enhanced. On the other hand, the enhanced resistance of tomato (*S. lycopersicum*) to salinity was rather not associated with the elevated level of phenolic compounds in the leaves although the activity of CAT was upregulated in the presence of Se (Mozafariyan et al. 2016). When Se was supplied to salt-stressed wheat (*Triticum aestivum*), enzymes related to the ascorbate–glutathione cycle were upregulated. Therefore, increased concentrations of L-ascorbate and GSH may protect the photosynthetic electron transport chain by maintaining the $NADP^+$ pool and neutralizing toxic ROS (Elkelish et al. 2019). In addition, other compounds with confirmed antioxidant activity accumulated under Se supplementation. An increase in the level of polyphenols (Astaneh et al. 2019; Lan et al. 2019; Karimi et al. 2020), α-tocopherol (Desoky et al. 2021), or carotenoids (Habibi 2017b; Lan et al. 2019; Desoky et al. 2021) has been reported. As a result of the activation of enzymatic and non-enzymatic antioxidant systems, the oxidative stress parameters decreased. Reduction of H_2O_2 and/or superoxide accumulation, as well as inhibition of lipid peroxidation, was demonstrated in most studies on different species (Hawrylak-Nowak 2009; Hasanuzzaman et al. 2011; KeLing et al. 2013;

Diao et al. 2014; Hawrylak-Nowak 2015; Astaneh et al. 2019; Subramanyam et al. 2019; Jawad Hassan et al. 2020; Desoky et al. 2021).

Onion (*Allium cepa*) cultivated in salt-affected soil (5.25 dS m^{-1}) under field and foliar spraying with selenate grew better than plants that were non-supplemented with Se (Semida et al. 2021). The osmotic adjustment of the Se-treated plants was more efficient due to the accumulation of larger amounts of osmoprotectants (total soluble sugar, free proline, choline, and glycine betaine) in leaves and bulbs. The relative water content (RWC) in leaves, water use efficiency (WUE), and photosynthetic efficiency were increased in such conditions. Like in many other studies, the performance of the antioxidant defence system was also significantly enhanced. Another field experiment with onion (*A. cepa*) treated with a mixture of zeolite, Se, and Si demonstrated that the yield of onion in the conditions of higher soil salinity (8 dS m^{-1}) than in the previous study was effectively enhanced (Bybordi et al. 2018). However, it should be taken into account that the authors used relatively high doses of the individual components of the applied mixture (8 tons ha^{-1} zeolite along with 1 kg ha^{-1} Se and 400 kg ha^{-1} Si), which were found to have the greatest growth-promoting effect on plants. In practice, the application of such a mixture containing up to 1 kg ha^{-1} Se can be too high and potentially uneconomical. It was found that foliar application of Se under salt stress also improved the quality of canola oil (Hashem et al. 2013). The linoleic, linolenic, and oleic acid contents were elevated in oil from seeds produced by Se-supplemented plants. Additionally, the addition of Se induced reduction in the erucic acid level, which makes such oil better in quality and safer for consumers.

The ion antagonism between Na^+ and K^+ (described in Sect. 6.2.2) is one of the main sources of ion imbalance in plants growing under salinity. In salt stress conditions, the maintenance of a sufficiently high K/Na ratio in cells becomes decisive for plant survival (Isayenkov and Maathuis 2019). The results of studies on the effect of Se supplementation on the ability of plants to preserve this ratio are not clear. Hawrylak-Nowak (2009) found that, under Se treatment, the accumulation of Na^+ was not reduced and the content of K^+ was not increased, thus the K/Na ratio in shoots was comparable in plants exposed to NaCl alone and those supplemented with Se (Hawrylak-Nowak 2009). Similarly, the K/Na ratio was not affected by Se treatment in experiments conducted by Jiang et al. (2017). In turn, Kong et al. (2005) found that, under a growth-promoting concentration of Se (i.e. 5 μM), the K^+ and Na^+ concentrations increased in shoots, while the opposite tendency was observed in the roots. This proves the influence of Se on changes in the translocation of these elements between the root and aboveground organs. Moreover, the generation of additional osmotic potential in aboveground organs can allow photosynthetic organs to absorb more water by lowering their water potential. There is evidence that Na^+ can act as an osmotic regulator (Zhang et al. 2010). However, many subsequent studies (Habibi 2017a, b; Elkelish et al. 2019; Subramanyam et al. 2019; Karimi et al. 2020; Desoky et al. 2021) showed that the K/Na ratio increased in Se-treated plants subjected to salt stress, compared to NaCl-stressed plants not supplemented with Se. It was found that Se increased the K^+ concentration in the shoots, simultaneously decreasing the Na^+ accumulation in the roots of salt-stressed maize

(*Z. mays*). The *ZmNHX1* gene expression, which may be involved in Na^+ compartmentalization in salinity stress, was upregulated in root cells under Se treatment (Jiang et al. 2017). Also, increased transcript levels for OsNHX1, which is considered an important Na^+/H^+ antiporter that catalyses the sequestration of Na^+ in the vacuole, were demonstrated in rice (*Oryza sativa*) treated with selenate prior to salinity stress (Subramanyam et al. 2019). In addition to keeping the K/Na ratio more appropriate, the Ca/Na ratio was also more favourable when Se was used in alleviation of the adverse effect of salinity in parsley (*Petroselinum crispum*) (Habibi 2017b). Moreover, in most of the experiments, no significant effect of Se on the accumulation of Cl^- ions in plants under high salt exposure was found (Hawrylak-Nowak 2015; Jiang et al. 2017; Jawad Hassan et al. 2020; Karimi et al. 2020). A significant decrease in the Cl level in the shoots was demonstrated as an effect of selenate treatment only in cucumber (*C. sativus*) (Hawrylak-Nowak 2009).

Not only K homeostasis was improved as a result of the beneficial effects of Se supplementation. In salt-stressed rapeseed (*B. napus*), the amounts of Mg and P, but not Ca, increased in the leaves of plants treated with Se compared to Se-untreated objects (Hashem et al. 2013). A study reported by Elkelish et al. (2019) on wheat (*T. aestivum*) demonstrated that N and Ca uptake and accumulation were more favourable after the application of Se. Similarly, in NaCl-stressed grapevine (*Vitis vinifera*), the N, Ca, and Mg contents increased in response to the Se supply (Karimi et al. 2020). In turn, in olive (*Olea europaea*) grown under salinity, the supplementation with Se promoted the release of Ca^{2+} ions from the roots, which contributed to the rebuilding of plant ion homeostasis, as claimed by the authors (Regni et al. 2021). Amidst micronutrients, increased accumulation of shoot Fe, but not Zn, has been found in similar research conducted on wheat (Atarodi et al. 2018).

When plants are grown in a saline environment, the synthesis of substances with osmoprotective properties is crucial in addition to the ionic balance. In terms of the chemical structure, three groups of osmoprotectants can be distinguished: (i) those containing ammonium groups (glycinebetaine, ß-alanine betaine, polyamines), (ii) amino acids (proline, ectoine), and (iii) sugars and sugar alcohols (trehalose, fructan, mannitol, sorbitol) (Singh et al. 2015). Fluctuations in the level of these groups of compounds were noted under both salinity and Se supplementation. In general, treatment of plants with Se under salt stress increased the accumulation of soluble sugars (Kong et al. 2005; Elkelish et al. 2019; Jawad Hassan et al. 2020; Karimi et al. 2020; Desoky et al. 2021; Semida et al. 2021), glycinebetaine (Shah et al. 2020; Semida et al. 2021), and free proline (Hawrylak-Nowak 2009; Hashem et al. 2013; Atarodi et al. 2018; Elkelish et al. 2019; Subramanyam et al. 2019; Karimi et al. 2020; Desoky et al. 2021; Semida et al. 2021). The role of endogenous proline seems to be very important in terms of plant resistance to different stresses, because it is assigned the functions of an excellent osmolyte, a low-molecular weight chaperon, and an antioxidative and signalling molecule (Kishor et al. 2005; Hayat et al. 2012). Although, as mentioned earlier, an increase in the content of free proline in leaves of salt-exposed plants was observed under the influence of Se in most studies, the growth-promoting effect of this element was not always associated with such a relationship (Hawrylak-Nowak 2015; Mozafariyan et al. 2016). Moreover, the mechanisms by which Se can improve proline accumulation have not been studied in detail. In addition to the antioxidant and metal chelating function, an osmoprotective role is assigned to anthocyanins, which can be involved in reduction of the leaf osmotic potential and improvement of plant water status in osmotic stress conditions (Chalker-Scott 2002). A Se-induced increase in the content of these compounds was demonstrated in wheat (*T. aestivum*) subjected to different levels of salinity (Lan et al. 2019).

Amongst the inorganic Se forms, selenate or selenite was used most frequently in experiments on the effect of this element on plant resistance to salinity. Recently, Desoky et al. (2021) conducted studies using a selenide ($SeCl_2$) solution that was sprayed onto salt-exposed wheat (*T. aestivum*). Their results showing beneficial effects of Se supplementation were similar to those obtained with the use of selenate or selenite. Selenide was found to stimulate plant growth, photosynthetic efficiency, and thus grain yield. The higher accumulation of osmoprotectans (free proline, total soluble sugars) contributed to an increase in RWC and better leaf water retention. The Mg, P, and K concentrations were improved as a result of the Se supplementation. Additionally, enhanced antioxidative plant defence caused a decrease in H_2O_2 and superoxide accumulation. Thus, these studies have shown that selenide is effective in reducing all negative effects related to salinity, i.e. osmotic, salt-specific, and oxidative stresses. The question is whether this compound would be as effective in field conditions as in plants and cultures grown in a greenhouse. Currently, there are no studies on the use of selenide in saline field conditions.

It has been established that not only edible plants can benefit from such Se supplementation but also ornamental plants, i.e. *Plectranthus scutellarioides*, can be more resistant to a moderate level of salinity, and their decorative value can be maintained in these conditions (Hawrylak-Nowak et al. 2019). This may be of particular importance in urban areas, where the threat of excessive accumulation of salts in soils is significantly elevated.

Table 6.1 summarizes the results of research on the use of inorganic forms of Se in alleviating the harmful effects of salt stress in different plant species grown in various experimental conditions (growth-chamber, greenhouse, field).

6.3.2 Nano-selenium

Nanotechnology is a new field exerting an impact on an increasing number of areas of everyday life. It has also provided promising results in agriculture, giving an opportunity to improve the use of essential and beneficial elements and enhance food quality and safety (Prasad et al. 2017). As low-toxic (Shakibaie et al. 2013) environmentally friendly substances (Hussein et al. 2019) with high bioavailability and efficiency (El-Ramady et al. 2020), Se nanoparticles (Se-NPs) can be used for enhancement of the yield and quality of various crop plants. For example, in three groundnut (*Arachis hypogaea*) cultivars grown in sandy soil conditions, supplementation with 20 and 40 ppm Se-NPs applied as foliar spray during the vegetative stage

Table 6.1 Effects of exogenous application of selenium in the form of selenate, selenite, or selenide on metabolic changes in selected plant species exposed to salt stress

Plant species	Plant growth conditions	Salt stress induction	Form, dose, and method of Se application	Effects of Se ions on the physiology and biochemistry of salt-stressed plants	References
Allium sativum	Greenhouse; perlite and hydroponic solution	30, 60, or 90 mM NaCl	Selenate; 4, 8, or 16 mg L^{-1} Se applied to the nutrient solution	Increased chlorophyll concentration; reduced lipid peroxidation and electrolyte leakage; enhanced accumulation of total phenolics; higher activity of SOD, CAT, APX; reduced antioxidant activity	Astaneh et al. (2019)
A. cepa	Field conditions; sandy loam soil	Soil salinity of $EC_e = 5.27$ dS m^{-1}	Selenate; 25 or 50 mg L^{-1} Se applied foliar three times	Improved photosynthetic efficiency; increased membrane stability index and RWC; better osmotic adjustment by accumulation of larger amounts of osmoprotectants (free proline, glycine betaine, choline, soluble sugars); increased enzymatic (SOD, APX, CAT) and non-enzymatic (L-ascorbic acid and GSH) antioxidant defence	Semida et al. (2021)
Brassica napus	Laboratory conditions; semi-hydroponic cultivation	100 or 200 mM NaCl	Selenate; 25 μM applied to the nutrient solution	Increased L-ascorbate and GSH contents; improved GSH/GSSG ratio; enhanced activities of APX, MDHAR, DHAR, GR, GST, GPX, CAT, Gly I, and Gly II enzymes; reduced H_2O_2 accumulation and lipid peroxidation	Hasanuzzaman et al. (2011)

(continued)

Table 6.1 (continued)

Plant species	Plant growth conditions	Salt stress induction	Form, dose, and method of Se application	Effects of Se ions on the physiology and biochemistry of salt-stressed plants	References
B. napus	Greenhouse; soil substrate	2000, 4000, or 6000 mg L^{-1} of salt mixture	Selenate; 2.5, 5, or 10 mg Se L^{-1} applied foliar	Improved photosynthetic pigment contents; increased free proline accumulation; enhanced CAT activity; increased Mg and P contents; improved quality of canola oil	Hashem et al. (2013)
Cucumis melo	Greenhouse; hydroponic cultivation	100 mM NaCl	Selenite; 2, 4, 8, or 16 μM Se applied to the nutrient solution	Inhibited lipid peroxidation; increased activity of SOD and POX, but not CAT; decreased leaf electrolyte leakage	KeLing et al. (2013)
C. sativus	Climate chamber; hydroponic cultivation	50 mM NaCl	Selenate; 5, 10, or 100 μM Se applied to the nutrient solution	Increased concentrations of photosynthetic pigments and free proline; lowered lipid peroxidation; decreased Cl^- accumulation in the shoots	Hawrylak-Nowak (2009)
Helianthus annuus	Greenhouse; soil substrate	Soil substrate salinity of EC = 15 dS m^{-1}	Selenate; 5 mg kg^{-1} applied to the soil substrate	Improved photochemical efficiency of PSII; lowered lipid peroxidation; limited root-to-shoot translocation of Na^+; increased K/Na ratio in the leaves	Habibi (2017a)
Lactuca sativa	Climate chamber; hydroponic cultivation	40 mM NaCl	Selenite or selenate; 2 or 6 μM Se applied to the nutrient solution	Increased photosynthetic pigment content; reduced H_2O_2 accumulation and lipid peroxidation; greater efficiency of selenite than selenate in alleviation of salt stress	Hawrylak-Nowak (2015)

(continued)

Table 6.1 (continued)

Plant species	Plant growth conditions	Salt stress induction	Form, dose, and method of Se application	Effects of Se ions on the physiology and biochemistry of salt-stressed plants	References
Solanum lycopersicum	Greenhouse; hydroponic cultivation	100 mM NaCl	Selenite; 50 µM Se applied to the nutrient solution	Improved photochemical efficiency of PSII; decreased H_2O_2 and lipid peroxidation levels; increased SOD, GR, DHAR, MDAR, GPX, thioredoxin reductase – TRXR activities; enhanced L-ascorbate, GSH, and NADPH contents in the chloroplasts	Diao et al. (2014)
S. lycopersicum	Greenhouse; perlite/peat moss substrate irrigated with the nutrient solution	25 or 50 mM NaCl	Selenite; 5 or 10 µM Se applied to the nutrient solution	Increased photosynthetic pigment content; elevated CAT activity; increased leaf RWC; lowered electrolyte leakage; enhanced antioxidant activity	Mozafariyan et al. (2016)
Olea europaea	Climate chamber; hydroponic cultivation	200 mM NaCl	Selenate; 10 or 30 mg L^{-1} Se applied to the nutrient solution	Improved photosynthetic efficiency; increased leaf RWC and gas exchange; stabilization of free proline accumulation in leaves and reduced loss thereof from the roots; promotion of the release of Ca^{2+} from the roots	Regni et al. (2021)

(continued)

Table 6.1 (continued)

Plant species	Plant growth conditions	Salt stress induction	Form, dose, and method of Se application	Effects of Se ions on the physiology and biochemistry of salt-stressed plants	References
Oryza sativa	Phytotron room; sand/polymer mixture irrigated with the nutrient solution	150 mM NaCl	Selenate; 6 mg L^{-1} Se applied as foliar spray, seed priming, and a combination of seed priming and foliar spray	Enhanced activity of antioxidant enzymes (SOD, APX, CAT, GPX); increased free proline accumulation; decreased H_2O_2 accumulation and lipid peroxidation; increased leaf RWC; increased transcript levels for OsNHX1 – an important vacuolar Na^+/H^+ antiporter; reduced Na^+ accumulation and higher K/Na ratio	Subramanyam et al. (2019)
Petroselinum crispum	Greenhouse; hydroponic cultivation	80 mM NaCl	Selenate; 1 mg L^{-1} applied to the nutrient solution	Higher levels of carotenoids; improved excitation energy trapping and electron transport of PSII; enhanced PSII function; decreased shoot Na^+ accumulation; reduced root-to-shoot translocation of Na^+; exclusion of Na^+ from cell sap; maintenance of K/Na and Ca/Na ratios	Habibi (2017b)
Rumex patientia × *R. tianshanicus*	Greenhouse; sand cultures	100 mM NaCl	Selenite; 1, 3, 5, 10, or 30 μM applied with the nutrient solution to sand cultures	Enhanced activities of SOD and POX; increased accumulation of soluble sugars; lowered electrolyte leakage; increased K^+ and Na^+ in leaves and reduced in roots; improved integrity of membranes in chloroplasts and mitochondria	Kong et al. (2005)

(continued)

Table 6.1 (continued)

Plant species	Plant growth conditions	Salt stress induction	Form, dose, and method of Se application	Effects of Se ions on the physiology and biochemistry of salt-stressed plants	References
Triticum aestivum	Climate chamber; hydroponic cultivation	100, 200, 300, or 400 mM NaCl	Selenite; 22 µM Se applied to the nutrient solution	Improved photochemical efficiency of PSII; increased chlorophyll and carotenoid concentrations; enhanced accumulation of total phenols, flavonoids, and anthocyanins; elevated CAT activity	Lan et al. (2019)
T. aestivum	Greenhouse; soil substrate	Salinity of irrigation water 0.12, 0.30, or 0.60 S m^{-1}	Selenite; 0.5, 1, or 4 mg kg^{-1} Se applied to the soil substrate	Improved chlorophyll and free proline concentrations; increased accumulation of shoot Fe; enhanced CAT activity	Atarodi et al. (2018)
T. aestivum	Greenhouse; soil substrate	100 mM NaCl	Selenate; 5 or 10 µM Se applied with the nutrient solution to the soil substrate	Upregulated activity of antioxidant enzymes; increased concentration of ascorbate and GSH; enhanced accumulation of free proline and soluble sugars; increased leaf RWC; lowered Na/K ratio and improved N and Ca ions uptake	Elkelish et al. (2019)

(continued)

Table 6.1 (continued)

Plant species	Plant growth conditions	Salt stress induction	Form, dose, and method of Se application	Effects of Se ions on the physiology and biochemistry of salt-stressed plants	References
T. aestivum	Greenhouse; sand cultures	200 or 250 mM NaCl	Selenide; 2, 4, or 8 μM foliar application three times	Increased chlorophyll and carotenoid contents; improved stomatal conductance, net photosynthesis, and transpiration rate; elevated RWC and better leaf water retention; increased accumulation of free proline and total soluble sugars; enhanced antioxidant enzyme activities and content of non-enzymatic antioxidants; decreased H_2O_2 and superoxide levels; decreased Na, but elevated Ca and K concentrations	Desoky et al. (2021)
Vigna mungo	Greenhouse; soil substrate	100 mM NaCl	Selenate; 1.5, 3, or 4.5 ppm Se applied to the soil substrate	Improved chlorophyll content and photosynthesis parameters; improved antioxidative enzyme activities (SOD, CAT, APX, GR, GPX); higher concentrations of osmoprotectants (sucrose, reducing sugars); decreased H_2O_2 and lipid peroxidation; reduced Na^+ uptake, but not Cl^-	Jawad Hassan et al. (2020)

(continued)

Table 6.1 (continued)

Plant species	Plant growth conditions	Salt stress induction	Form, dose, and method of Se application	Effects of Se ions on the physiology and biochemistry of salt-stressed plants	References
Vitis vinifera	Greenhouse; soil substrate	75 mM NaCl	Selenate; 5, 10, or 20 mg L^{-1} Se in foliar application	Enhanced integrity of cell membranes (reduced electrolyte leakage and lipid peroxidation); increased accumulation of non-enzymatic antioxidants and osmotically active substances (total phenols, flavonoids, soluble sugars, free proline); higher activity of CAT, APX, GPX; improved balance of essential elements	Karimi et al. (2020)
Zea mays	Climate chamber; hydroponic cultivation	100 mM NaCl	Selenite; 1, 5, or 25 µM Se applied to the nutrient solution	Enhanced net photosynthetic rate; prevention of damage to chloroplast ultrastructure; enhanced SOD and APX activities; increased K^+ level in the shoots and decreased Na^+ in the roots; modulation of Na^+ homeostasis and compartmentalization	Jiang et al. (2017)

induced positive physiological and biochemical changes depending on the Se-NP concentration and groundnut cultivar (Hussein et al. 2019). However, like every compound, Se-NPs can be toxic, and this toxicity in pepper (*Capsicum annuum*) was associated with anomalies in the structure of the stem apical meristem and inhibition in the differentiation of xylem cells. These abnormalities in the development of plant organs may have been induced by epigenetic hypermethylation of DNA (Sotoodehnia-Korani et al. 2020).

It is currently unclear whether the key biological action of Se-NPs is related to enhanced biosynthesis of Se-proteins, direct antioxidant/pro-oxidant effects, or both (Surai and Kochish 2020). Although several experiments on the effective impact of Se-NPs on animals in stress conditions, including salt stress (Sarkar et al. 2015), have been published (e.g. Qin et al. 2016; Safdari-Rostamabad et al. 2017), there are fewer similar reports on plants. For the last 3 years (Table 6.2), Se-NPs have attracted increasing attention in terms of their characteristics and potential use in the enhancement of plant resistance to salinity. A recent study conducted by Soleymanzadeh et al. (2020) indicates that Se-NPs in foliar application can be absorbed by leaves and translocated to roots. The authors also demonstrated that, in addition to relieving oxidative stress and improving plant macronutrient status, the foliar spray with Se-NPs increased the accumulation of phenylpropanoid derivatives (salicylic acid, caffeic acid, and catechin) in strawberry (*Fragaria* × *ananassa*) grown under salinity (EC = 5 dS m^{-1}). A similar increase in the concentration of bioactive compounds (flavonoids, β-carotene, xanthophyll) was found in fruits of pepper (*Capsicum annuum*) (González-García et al. 2021). Moreover, the observed growth-promoting effect of Se-NPs noted under salinity exposure was connected with improvement of the mitotic index and a reduced percentage of chromosomal abnormalities in root tip meristems of salt-exposed pea (*Pisum sativum*) (El-Araby et al. 2020).

A similar beneficial effect of Se-NPs was noted by Shalaby et al. (2021) in their research on cucumber (*Cucumis sativus*). They applied a 25 mg L^{-1} Se-NP solution onto leaves under combined salinity and heat stresses, as a dominant and negative influence of these factors on plant production is expected due to climate changes. The applied Se-NPs stimulated the vegetative growth of cucumber, improved the K/Na ratio, RWC, and CAT activity in the leaves, but did not cause significant improvement in fruit yield. These studies were carried out reliably in conditions very similar to commercial cucumber cultivation, taking into account physiological and biochemical changes as well as the marketable yield and quality of fruits. This indicates that the positive changes recorded in the vegetative growth phase in plants subjected to stress do not always translate into their later higher yield. Therefore, careful and critical conclusions should be drawn from experiments with plants at very early stages of development for which the actual yield has not been taken into account.

Under salt stress, tomato (*S. lycopersicum*) supplied with 1–20 mg L^{-1} Se-NPs exhibited an increase in the growth and yielding parameters and concentration of phenolic compounds in the leaves and in the majority of compounds with antioxidant properties (lycopene, ß-carotene, polyphenols, flavonoids) in the fruits. Moreover, NaCl-stressed plants enriched with Se-NPs in general showed increased activity of antioxidant enzymes, particularly in fruits (Morales-Espinoza et al. 2019). In turn, in salinity-exposed lemon balm (*M. officinalis*) supplied with Se-NPs, increased abundance of phenylalanine ammonia-lyase (PAL) and rosmarinic acid synthase (RAS) transcript levels was found in addition to the improved plant antioxidant status and yield. The activity of these enzymes involved in the biosynthesis of polyphenols and rosmarinic acid also contributed to the elevated concentration of rosmarinic acid in the aboveground organs. The most effective concentration to mitigate the effects of salinity was 50 mg L^{-1} Se-NPs (Ghasemian et al. 2021). In turn, the use of chitosan-functionalized Se-NPs (Cs–Se–NPs) in stevia (*Stevia rebaudiana*) was most effective at a lower concentration of 20 mg L^{-1}. Under salt stress, the foliar application of Cs–Se–NPs additionally increased the accumulation

Table 6.2 Effects of exogenous application of selenium in the form of Se-NPs on physiological and biochemical changes in selected plant species exposed to salt stress

Plant species	Plant growth conditions	Salt stress induction	Dose, method, and number of Se-NPs application	Effects of Se ions on the physiology and biochemistry of salt-stressed plants	References
Brassica napus	Laboratory conditions; germination box	150 mM NaCl	150 μmol L^{-1} Se-NPs; seed priming	Augmented germination percentage and rate; increased activity of CAT and decreased activity of SOD, APX, and POX; improved seed microstructure; modulated expression of abscisic and gibberellic acid genes	El-Badri et al. (2021)
Capsicum annuum	Greenhouse; peat/perlite substrate irrigated with the nutrient solution	25 or 50 mM NaCl	10 or 50 mg L^{-1} Se-NPs; five applications of Se-NPs by drenching of the substrate	Increased chlorophyll content; enhanced activity of GPX in leaves; increased activity of APX, GPX, CAT, PAL in fruits; elevated concentrations of flavonoids, GSH, β-carotene, xanthophyll in fruits	González-García et al. (2021)
Cucumis sativus	Greenhouse; soil	soil salinity EC = 4.49 dS m^{-1} combined with heat stress	25 mg L^{-1} Se-NPs; single foliar application	Increased level of chlorophyll and photosynthetic efficiency; higher leaf RWC; increased activity of POX; improved N accumulation and K/Na ratio	Shalaby et al. (2021)
Fragaria × *ananassa*	Greenhouse; soil substrate	Soil substrate salinity of EC = 5 dS m^{-1}	10 or 100 μM Se-NPs; double foliar application	Improved PSII functioning by preservation of the water-splitting complex; increased CAT and PAL activity; enhanced accumulation of total phenolics, salicylic acid, caffeic acid, and catechin; increased foliar Ca and K level, and decreased Na accumulation	Soleymanzadeh et al. (2020)

(continued)

Table 6.2 (continued)

Plant species	Plant growth conditions	Salt stress induction	Dose, method, and number of Se-NPs application	Effects of Se ions on the physiology and biochemistry of salt-stressed plants	References
Fragaria × *ananassa*	Greenhouse; perlite/coco peat/sand substrate irrigated with the nutrient solution	25, 50, or 75 mM NaCl	10 or 20 mg L^{-1} Se-NPs; five foliar applications of Se-NPs	Improved osmoprotection (increased soluble sugars and free proline); reduced oxidative stress (lipid peroxidation and H_2O_2 accumulation); increased SOD and POX activities; increased accumulation of organic acids and sugars in fruits; enhanced accumulation of indole-3-acetic acid and abscisic acid	Zahedi et al. (2019)
Melissa officinalis	Greenhouse; perlite/coco peat/sand substrate irrigated with the nutrient solution	50, 100, or 150 mM NaCl	50 or 100 mg L^{-1} Se-NPs; fourfold foliar application	Reduced lipid peroxidation; increased activity of SOD, CAT, POX; enhanced accumulation of photosynthetic pigments and free proline; increased abundance of phenylalanine ammonia-lyase and rosmarinic acid synthase transcript levels; elevated level of rosmarinic acid	Ghasemian et al. (2021)
Phaseolus vulgaris	Field conditions; soil	Soil salinity EC = 7.55–7.61 dS m^{-1}	0.5, 1.0, or 1.5 mM Se-NPs; triple foliar application	Increased level of photosynthetic pigments and photosynthetic efficiency; enhanced accumulation of free proline and soluble sugars; improved nutrient status and K/Na ratio; better stability of biomembranes; increased activity of antioxidant enzymes; lowered markers of oxidative stress; improvement in leaf anatomy	Rady et al. (2021)

Plant species	Plant growth conditions	Salt stress induction	Dose, method, and number of Se-NPs application	Effects of Se ions on the physiology and biochemistry of salt-stressed plants	References
Pisum sativum	Greenhouse; hydroponic cultivation	60 or 120 mM salt mixture	10 or 20 ppm Se-NPs; double foliar application	Improved cytological parameters (increased mitotic index in root tip meristems and reduced percentage of chromosomal abnormalities)	El-Araby et al. (2020)
Solanum lycopersicum	Greenhouse; peat moss/perlite substrate irrigated with the nutrient solution	50 mM NaCl	1, 5, 10, or 20 mg L^{-1} Se-NPs; five applications of Se-NPs directly to the growth substrate	Increased level of photosynthetic pigments; increased activity of antioxidant enzymes (CAT, APX, GPX, SOD) in leaves and fruits; enhanced accumulation of non-enzymatic antioxidants in fruits (lycopene, ß-carotene, total phenols, flavonoids); lowering the pH of fruits	Morales-Espinoza et al. (2019)
Stevia rebaudiana	Greenhouse; coco peat/perlite substrate irrigated with the nutrient solution	50 or 100 mM NaCl	10 or 20 mg L^{-1} Se-NPs; triple foliar application	Improved photosynthetic pigment concentration and photosynthesis-related parameters; decreased oxidative stress and membrane injury markers (H_2O_2, lipid peroxidation, electrolyte leakage); increased essential oil content; enhanced stevioside and rebaudioside A accumulation; enhanced antioxidant activity	Sheikhalipour et al. (2021)

of essential oil, stevioside, and rebaudioside A (Sheikhalipour et al. 2021). In herbal plants, the use of Se-NPs may therefore have an additional beneficial eliciting effect by increasing the content of bioactive compounds with nutraceutical properties. Nevertheless, the mechanism underlying the capability of Se-NPs to increase the biosynthesis and accumulation of secondary metabolites in plants remains unexplained. Li et al. (2020) proposed that stimulation of the α-linolenic acid pathway and increased jasmonic acid biosynthesis may play a role in this regard.

The influence of Se-NPs on seed germination in a saline medium is equally interesting. This type of research using the seed-priming technique was conducted by El-Badri et al. (2021). They used Se-NPs for nanopriming of rape (*B. napus*) seeds and examined their germination percentage and selected physiological parameters under salinity (150 mM NaCl). In addition to the effect on the seed germination, seed microstructure, and activity of antioxidant enzymes, the authors also focused on some aspects related to the hormonal regulation. It was found that the improvement in the germination percentage and seedling growth parameters under stress in seeds primed with Se-NPs can be attributed to the modulated expression of abscisic acid (ABA) and gibberellic acid (GA) related genes. These phytohormones play crucial roles in mediating plant defence under stress factors, and an appropriate GA/ABA ratio is necessary for initiation of germination (Diaz-Vivancos et al. 2013). Their differentiated expression under the influence of nanopriming may be related to the increased resistance of plants to salinity (El-Badri et al. 2021). Previously, a very similar phenomenon in the conditions of Se-NPs/salinity interaction was reported by Zahedi et al. (2019) in strawberry (*Fragaria* × *ananassa*). Se-NP-inducement enhanced accumulation of indole-3-acetic acid (IAA), and ABA in leaves was observed both in saline and non-saline conditions. Therefore, it seems that Se-NPs influence the hormonal homeostasis and balance in plants at the stage of both seed germination and later plant development.

In terms of practical use, interesting and valuable open field experiments have been carried out recently by Rady et al. (2021). They studied salt-sensitive common bean (*Phaseolus vulgaris*) growing in salt-affected soil (EC = 7.55–7.61 dS m^{-1}) and subjected three times to foliar spraying with Se-NPs at concentrations of 0.5, 1.0, or 1.5 mM. Very promising results were obtained in these conditions. Salt-exposed common bean supplemented with Se-NPs showed an improvement in almost all analysed parameters: growth and productivity, photosynthetic pigment content and photosynthesis-related indicators, antioxidant enzyme activities, oxidative stress parameters, cell membrane stability, osmoprotective indicators, essential nutrient status, and leaf anatomy. The best effects were obtained using 1.0 mM Se-NPs. These results suggest a real chance of using Se-NPs in open field conditions as a stress-relieving agent. However, it is still necessary to consider the limitations of this method related to weather conditions (including heavy rainfall, thermal conditions), different levels of soil salinity, or species-specific sensitivity of plants to salt stress and/or Se-NPs.

6.4 Importance of the Chemical Form of Selenium and the Application Method in Amelioration of Plant Salt Stress

When using Se to mitigate the effects of various abiotic stresses in plants, it is necessary to take into account the chemical form of this element in addition to its concentration. Most experiments focused only on comparison of the influence of particular forms of this element on the growth, metabolism, and Se transformations in plants (e.g. Hawrylak-Nowak et al. 2015; Longchamp et al. 2015; Neysanian et al. 2020). However, insufficient attention has been paid to comparison of the effectiveness of various chemical forms of Se in preventing the negative effects of abiotic stresses, which is extremely important considering the possibility of using Se supplementation of plants on a wider scale.

Comparative studies of tobacco (*Nicotiana tabacum*) on the effects of two inorganic Se forms in mitigating the deleterious effects of drought, which generates osmotic stress in plants, have shown that selenate was markedly superior to selenite (Han et al. 2022). The application of selenate induced a higher level of expression of stress-responsive genes (*NtP5CS* and *NtAREB*) and much more effectively stimulated photosynthesis and lowered the level of oxidative stress markers (H_2O_2, lipid peroxidation) than selenite. On the other hand, an opposite relationship was shown by Hawrylak-Nowak (2015) analysing the influence of these forms of Se on NaCl-stressed lettuce. Low concentration of selenite (2 μM) was more effective than the same concentration selenate in root system growth stimulation, reduction of salt-induced oxidative stress, and maintenance of the level of photosynthetic pigments. This report also indicated that the beneficial biological activity of Se under salinity was not associated with increased free proline accumulation or decreased Na^+ or Cl^- concentrations in aboveground organs.

The application of 50 μM selenite under NaCl-induced salinity improved the growth of tomato (*S. lycopersicum*), while no significant effect of this Se concentration was observed in plants grown without salinity (Diao et al. 2014). This concentration of selenite, however, was relatively high, compared to other studies in which this chemical form of Se was introduced into hydroponic cultures. The selenite concentrations that stimulated the growth of NaCl-stressed plants were mostly in the range of 1–10 μM (Kong et al. 2005; Hawrylak-Nowak 2015; Mozafariyan et al. 2016; Jiang et al. 2017). Since selenite is more toxic to plants than selenate (Hawrylak-Nowak 2013; Hawrylak-Nowak et al. 2015), in conditions of high bioavailability of selenite in the hydroponic solution, such concentration may be severely phytotoxic to other species. For example, the growth of NaCl-stressed maize (*Z. mays*) was suppressed when selenite was applied at a concentration of 25 μM (Jiang et al. 2017). In turn, 22 μM of selenite still had a growth-stimulating effect on wheat (*T.aestivum*) (Lan et al. 2019). Certainly, unlike in hydroponic cultivation, the bioavailability of inorganic Se forms in soil cultivation is much more complicated and significantly modified by the influence of soil physicochemical properties, i.e. pH, Eh, Fe/Al/Mn oxides, organic matter, or clay (Fan et al. 2015;

Dinh et al. 2019). In general, the bioavailability and mobility of selenate in the soil-plant system are greater than those of selenite (Fan et al. 2015). This probably results from the strong adsorption capacity of selenite versus selenate to soil components. It has been found that selenate is adsorbed via outer-sphere complexation on soil particles, whereas selenite is capable of inner-sphere adsorption, which is much stronger and causes the lower mobility and availability of selenite in the soil (Dinh et al. 2019). This differentiated biogeochemical behaviour of Se in the soil-plant system determined by Se speciation should be given special attention when using Se fertilization (Shahid et al. 2018b), and this behaviour can be even more complicated in saline soils.

The problem of the complicated behaviour of individual Se compounds in the soil can be solved by applying foliar fertilization with this element. This method seems to be as effective as introducing Se into the root environment (soil, soil substrate, nutrient solution). Many experiments have reported a high efficiency of foliar fertilization with selenate (Hashem et al. 2013; Subramanyam et al. 2019; Karimi et al. 2020; Semida et al. 2021), selenide (Desoky et al. 2021), or Se-NPs (e.g. Zahedi et al. 2019; Ghasemian et al. 2021; Shalaby et al. 2021) in alleviating the effects of salinity. The Se-NPs seem to have some advantage amongst the chemical forms of Se used as foliar spray. Namely, they are less toxic to plants and other organisms than the inorganic forms of this element (Domokos-Szabolcsy et al. 2012; Shakibaie et al. 2013). On the other hand, the potential long-term effects of nanoparticles, including Se-NPs, on organisms and their metabolism is still insufficiently understood, which limits their wide-scale application.

6.5 Conclusion and Future Perspectives

The boundary between the beneficial and toxic effects of Se supplementation under salinity is narrow and highly depends on the Se concentration, its chemical form, the application method, salinity level, and plant genotype. Additionally, in natural conditions, the environmental factors, e.g. soil pH, soil S/Se ratio, rainfall intensity, and air temperature, can influence the uptake and accumulation of this element and modify its biological action in salt-exposed plants. However, by generalizing the collected bibliographic data, it can be stated that the protective effects of Se under salt stress could be attributed to several mechanisms including (i) protection of cell membranes and organelles from oxidative injury, (ii) regulation of ion homeostasis by modulation of Na^+ and Cl^- compartmentalization and translocation, (iii) enhanced accumulation of osmoprotectants, (iv) regulation of the free proline metabolism, and (v) influence on hormonal balance. Figure 6.1 is a schematic diagram explaining the biological activity of Se in mitigation of the adverse impacts of salt stress on plants.

Foliar application of Se, especially in the form of low-toxic Se-NPs, seems to be a particularly promising strategy to prevent the destructive effects of salinity on crops. This method is easier and more effective than soil application and does not

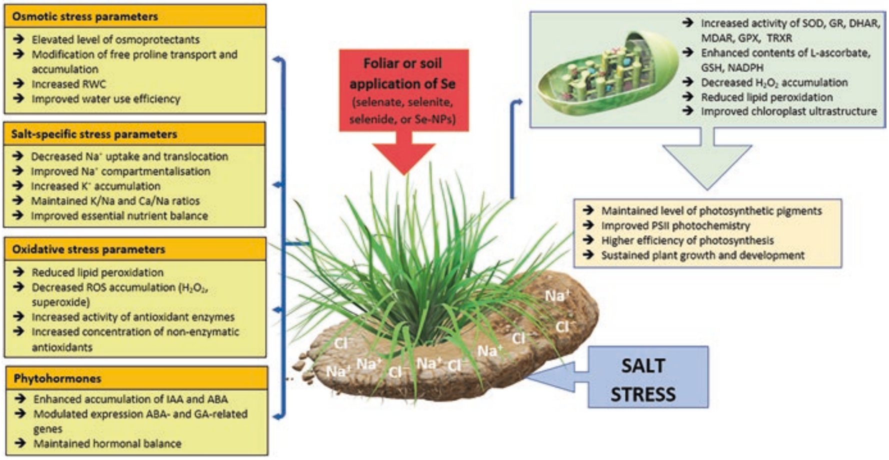

Fig. 6.1 Schematic diagram explaining the beneficial effects of Se in amelioration of the adverse impacts of salt stress on plants

carry a risk-binding Se ions by soil components, causing its limited phytoavailability. In addition, microorganisms that are present in the soil and are able to transform and assimilate Se compounds may thus limit its pool available to plants in the rhizosphere. This will not occur under foliar fertilization. When Se is applied as foliar spray, the problem of soil contamination with this element can also be avoided: when used correctly, Se should be assimilated by plants and immobilized in their biomass.

The comprehensive analysis of available scientific information on salinity and its mitigation with Se fertilization indicates the need for more extensive field research. Most of the experiments on the effects of Se on salt-affected plants have been carried out in hydroponic conditions, which do not reflect the full complexity of the soil system. In hydroponic cultivation and sand cultures, a much easier and higher uptake of various substances (including inorganic ions) is observed, compared to field conditions. Therefore, thorough knowledge of the uptake and transport of particular chemical forms of Se for each specific crop and set of salinity as well as other environmental conditions is necessary to facilitate the use of this element on a large scale.

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Chapter 7
Selenium and Nano-Selenium-Mediated Drought Stress Tolerance in Plants

Akanksha Sharma, Sanchi Gupta, Neelam Prabha Negi, Devangi Pritesh Patel, Meenakshi Raina, and Deepak Kumar

Abbreviations

ABA	Abscisic acid
ADH	Alcohol dehydrogenase
APSR	APS reductase
APX	Ascorbate peroxidase
ATPS	
ATP sulphurylase	
AsA	Ascorbate/Ascorbic acid
Car	Carotenoid
CAS	CRISPR associated proteins

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M. A. Hossain et al. (eds.), *Selenium and Nano-Selenium in Environmental Stress Management and Crop Quality Improvement*, Sustainable Plant Nutrition in a Changing World, https://doi.org/10.1007/978-3-031-07063-1_7

CAT	Catalase
CGR	Crop growth rate
GPX	Glutathione peroxidase
GR	Glutathione reductase
GSH	Glutathione
LAI	Leaf area index
MDA	Malondialdehyde
NPs	Nanoparticles
PEG	Polyethylene glycol
POD	Peroxidase
PSY	Phytoene synthase
PTs	Phosphate transporters
RGR	Relative growth rate
RO$^{\bullet}$	Alkoxyl radicals
ROO$^{\bullet-}$	Peroxyl radicals
ROS	Reactive Oxygen Species
RWC	Relative water content
SDH	Sorbitol dehydrogenase
Se	Selenium
SeCys	Selenocysteine
SeMet	Selenomethionine
SiR	Sulphite reductase
SOD	Superoxide dismutase
STs	Sulphate transporters
TDW	Total dry weight
UV	Ultra violet

7.1 Introduction

Agriculture around the world is severely affected by water scarcity due to global weather fluctuations. This has resulted in a serious decline in global agricultural productivity in developing countries of South Asia like India (Waraich et al. 2011; Ahmad et al. 2020). Dry spells eventually cause a substantial risk of crop failures giving rise to food scarcity (Wang et al. 2012; Hao and Singh 2015; Zhang et al. 2015). Furthermore, water stress has a negative impact on both the biochemical and physiological processes of plants, such as osmotic potential, rate of photosynthesis, turgor pressure, and cell membrane integrity (Miao et al. 2015; Sharma et al. 2021). Assessing and alleviating the adverse effects of water stress on crops can help to maximize agricultural yields (Madadgar et al. 2017). The adverse effects of drought include cellular and oxidative damage to the plant which can be defended via various techniques which can further be used to regulate the activities of enzymes produced in the crops during water stress conditions (Filgueiras et al. 2020; Ahmad et al. 2021). During drought, the plants usually get lower amounts of soil water for their growth and development (Chaves et al. 2002; Zia et al. 2021). Moreover, the biophysical affinities of crop plants are also altered due to recurring drought and temperature changes, which eventually change their cultivation periods, irrigation water requirements, soil characteristics and cropping season routine, further, increasing the risk of drought stress. The drought stress progresses slowly with time and becomes more intense, thereby causing more damage (Kumar et al. 2012). The major damages include premature plant death (Tian and Lei 2006; Xu et al. 2007), debilitated germination and seedling growth, ultimately causing a decrease in the harvestable yield of plants (Nawaz et al. 2012). Various studies have been conducted reporting the adverse effects of drought stress on various plants like sugar beet (Sadeghian and Yavari 2004), sunflower (Sajjan et al. 1999; El-Midaoui et al. 2001), kochia (Masoumi et al. 2010), maize (Moussa and Abdel-Aziz 2008), and sorghum (Gill et al. 2002). A better understanding of plant responses to drought stress can be achieved by focusing on three key factors: the severity, timing, and duration of water stress (Plaut 2003). According to Siddique et al. (2000), leaf water potential is considered a reliable and efficacious method to enumerate a plant's response to drought stress. Variable plant relationships are crucial in determining whether a plant species is drought resistant or sensitive (Waraich et al. 2011a). When the water conditions are restricted, the accumulation of solutes causes a drop in the leaf water potential. It has been observed that different cultivars show variation in water potential in normal as well as drought conditions (Nawaz et al. 2012). Reduced yield and water potential of wheat were observed by Sairam et al. (1990) at both the budding and tillering stages of wheat, although the budding stages were found to be more perceptive to water stress than the latter stage. Similarly, Aneja et al. (2021) conducted studies on *Brassicajuncea* and observed a decrease in various physiological processes like water potential, photosynthesis, osmotic potential, and chlorophyll content when affected by water scarcity (Aneja et al. 2021). Various active oxygen species generated in response to drought stress annihilate several cellular components like lipids, nucleic acids, carbohydrates, and proteins, which ultimately cause decreased growth, photosynthesis, and respiration. On the other hand, during water scarcity in plants, the synthesis of starch is also prohibited, while the concentration of soluble salt is persistent or can even slightly rise during stress (Chaves et al. 2002). Plants rely on a variety of several enzymatic and non-enzymatic systems to reduce reactive oxygen species (ROS) production caused by water stress (Khushboo et al. 2018). The various effects and responses of drought stress on plants are depicted in Fig. 7.1.

7.2 Selenium: A Promoter of Plant Growth and Development

Selenium (Se) is known to be a potential mineral nutrient in higher plants (Lyons et al. 2009, Pilon-Smits et al. 2009). Hamilton (2004) classified selenium's biotic activity into three categories based on its concentration: (a) microscopic concentrations for improved plant growth and development, (b) moderate concentrations for

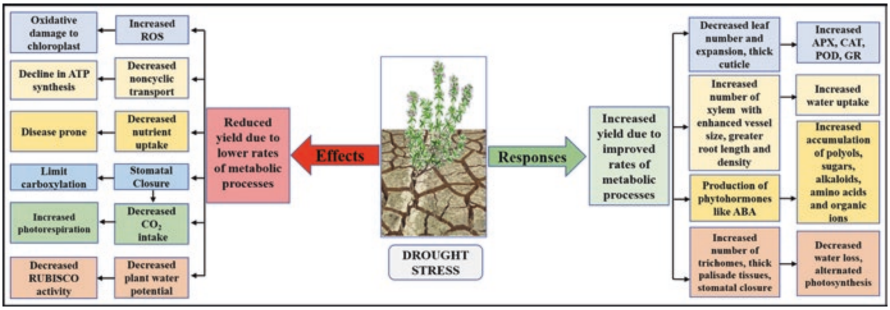

Fig. 7.1 The various effects and responses of drought stress in plants

balanced homeostatic functioning, and (c) higher concentrations that can harm plants. Selenium plays a substantial role in the mitigation of both biotic (pathogens and herbivory) and abiotic (oxidative) stresses in plants (Pilon-Smits et al. 2009, White and Brown 2010, El Mehdawi and Pilon-Smits 2012, Feng et al. 2013, Gupta and Gupta 2017; Quinn et al. 2007; El-Ramady et al. 2016).

The absorption and transfer of selenium in plants takes place via the sulphate and phosphate transporters (STs and PTs, respectively). Upon uptake by the plant, the inorganic Se transfigures into other organic forms such as selenomethionine (SeMet) and selenocysteine (SeCys) (Zhang et al. 2003). An assumption that STs localized in the cell membranes of roots help in selenate uptake although PTs are involved in the translocation of selenite has been put forth by Hopper and Parker (1999). The conversion of selenate and selenite into selenocysteine (SeCys) and selenomethionine (SeMet) involves a number of enzymes, namely ATP sulphurylase (ATPS), APS reductase (APSR), and sulphite reductase (SiR) (Rotte and Leustek, 2000). Genetic factors can also play an important role in controlling the translocation of selenium (Eurola et al. 2004).

Selenium is an integral part of about 30 selenoenzymes. Selenoenzymes play a crucial role in protecting the cell from the damage caused by free radicals while mitigating oxidative damage in plants. It also plays an important role in controlling the amount of water in the cell and preventing the cell membrane from the adverse effects of ROS, and thereby acting as a stress buster for the plants. Se detoxifies peroxyl ($ROO^{\bullet -}$) and alkoxyl ($RO^{\bullet -}$) radicals, systemizing the antioxidant protecting mechanisms. Apart from these, Se is also known to trigger the maturation of senescent seedlings (Hartikainen and Xue 1999; Xue et al. 2001). It acts as a positive regulatory element required for plant germination, and due to its antioxidant properties, it also plays a crucial role in delaying senescence. Chen and Sung (2001) observed that selenite-treated seeds showed greater rates of germination in *Momordica charantia* L. Also, decreasing rates of germination have also been observed in radish, tomato, and lettuce when Se treatments were increased up to 29 mg Kg^{-1} (Carvalho et al. 2003; Mozafariyan et al. 2017).

7.3 Different Modes of Se Administration in Plants

Se treatments are generally given via foliar application since, it is the most preferred and contamination-free method (Toor et al. 2020). During foliar application, the Se ions easily diffuse across the epidermal cells and can be transported easily via. xylem and phloem, therefore integrating in the plant system and leads to significant improvements in the yield of agricultural crops (Plaut, 2003).

Application of Se to foliage is known to increase the seed contents (MacLeod et al. 1998), improve chlorophyll synthesis, boost higher concentrations of starch in chloroplasts (Pennanen et al. 2002), improve plant–water relations, control cell contents, and trigger the effect of antioxidants (Xue et al. 2001). Selenate fertilizers, when applied directly to soil or on foliage, are found to be more efficient in increasing the Se concentration in plants than the selenite fertilizers (Gissel-Nielsen et al. 1984). Therefore, we can say that selenate is the principal form of selenite absorbed by plants (Broadley et al. 2007). The chemical form of Se, soil attributes, foliar time, and method of application play an important role in the relative efficacy of Se fertilizers (Lyons et al. 2009).

Selenate and selenite treatment of soil (0–10 mg kg^{-1}) has been found to increase Se concentration in ryegrass seedlings (Cartes et al. 2005). An important correlation between shoot Se concentration and glutathione peroxidase (GPX) activity in ryegrass has been highlighted by Cartes et al.(2010). When Se concentrations were found to be higher in shoots, the GPX activity was later correlated with the chemical form of Se used. The highest Se content was observed in grain (0.732 mg kg^{-1}) followed by straw (0.227 mg kg^{-1}) and lastly roots (1.375 mg kg^{-1}) on an application of 0.2 mg Se kg^{-1} whereas the minimum application of Se (0.05 mg Se kg^{-1} of soil) yielded 0.155 mg Se kg^{-1} in grain. Therefore, from these results, an interpretation can be made stating that Se concentration was highest in grain while it was lowest in straw dry matter. Another application of Se was given by Djujic et al. (2000a) in Serbia when the Se application on wheat foliage correspondingly increased the Se concentrations in the blood plasma (53% increase after 6 weeks). This led to an increase in glutathione peroxidise activity in the blood and reduced oxidative stress framework (Djujic et al. (2000a). The levels of iron, copper, and zinc also increased when Se-enriched wheat was consumed (Djujic et al. (2000b). Selenium, when applied exogenously, aids abiotic stress alleviation in plants.

7.4 Selenium Toxicity and Its Role in Combating Various Abiotic Stresses in Plants

Selenium, a unique element, was earlier not contemplated to be a major element involved in mitigation of plant abiotic stresses. It was not until the middle of the twentieth century that its importance was recognized (Schwarz and Foltz 1957; Hasanuzzaman et al. 2010). Several studies on human and animal health, particularly diseases caused by Se deficiency, such as cancer, cataract, Kashin–Beck disease, liver and cardiovascular diseases, have enumerated the role of Se in plants (Tapiero et al. 2003; Cox and Bastiaans 2007; Huang et al. 2018). Selenium, being a rare element, is found very sparsely in a few parts of the world, therefore being least uptaken through plant-based diets. This fact led the researchers to unravel the various aspects of selenium biofortification and its toxicity. Recently, additional studies on the biofortification of Se in crops have been conducted, and it has been concluded that higher concentrations of Se are detrimental and can even cause toxicity. Concentrations greater than 1 ppm are assumed to be toxic to plants and can cause severe damage to the plant cell. The importance of Se to plants remains in doubt. The role of Se in mitigating plant abiotic stress was initially studied under conditions of heavy metal stress by Kumar et al. (2012). However, several researches were conducted by various scientists highlighting the role of Se in combating various other plant stresses like drought (Hasanuzzaman and Fujita 2011), high temperature (Djanaguiraman et al. 2010), cold (Chu et al. 2009), heavy metals (Kumar et al. 2012; Hasanuzzaman et al. 2012), UV (Yao et al. 2010a, b), senescence (Hartikainen et al. 2000), desiccation (Pukacka et al. 2011), excess water (Wang 2011), and salt stress (Hasanuzzaman et al. 2011) with many new details being unravelled with each passing day. Amongst all these researches, Se-mediated drought stress alleviation has been an active topic of research. However, the studies on reports on Se and its role in water stress management are still inadequate.

7.5 Role of Selenium and Nano-Selenium in Mitigating Drought Stress

Amongst all of these abiotic factors, drought stress is the most significant factor limiting agricultural crop productivity. The drought condition can significantly reduce the quality and quantity plants yields, specifically crops (Sourour et al. 2017; Adnan, 2020). It can influence many plant aspects, anatomical and morphological. Leaf anatomy and its structure are mostly significantly influenced due to severe drought conditions (Kapoor et al. 2020). Photosynthesis reduction and inhibition is one of the most important effects of drought in plants. In addition to this decrease in the leaves, chlorophyll contents are another most important factor that reduces the rate of photosynthesis under drought conditions (Demireviska et al. 2009). In the following section, the effect of drought on agricultural crop output and the role of selenium in boosting crop productivity under drought conditions are explained as follows:

7.5.1 ROS Generation and Signaling under Drought Stress

Drought is a multi-dimensional stress influencing the plant's physiological and biochemical responses (Dhanda et al. 2000; Wang et al. 2003; Verhagen et al. 2004). The pre-requisite response to drought stress results in the ROS production in plant (Feng et al. 2013; Mittler 2002, Ahanger et al. 2017; Ahanger and Agarwal 2017). ROS production can be harmful to plants; however, ROS are also thought to act as signals for the activation of stress response and defence pathways when present in small amounts (Mittler, 2002). Reactive oxygen species (ROS) includes H_2O_2, AOH, O_2^{-}, and ${}^1O_2$ (Mittler 2002; Shigeoka et al. 2002; Apel and Hirt 2004; Khushboo et al. 2018). Plants can utilize the level of steady-state cellular ROS to monitor their intracellular level of stress, which regulate to prevent an oxidative burst by over-accumulation of ROS, which would ultimately result in cell damage and death. Various enzymes such as glutathione reductase (GR), ascorbate peroxidase (APX), catalase (CAT), peroxidase (POD), superoxide dismutase (SOD) and non-enzymatic antioxidants like ascorbate (AsA), carotenoid (Car),glutathione (GSH), α-tocopherol, β-carotene, flavonoids, and hydroquinones are used by plants to mitigate various cytotoxic effects produced by these active radicals (Foyer et al. 1997; Foyer and Noctor 2000; Li et al. 2009; Negi et al. 2016; Kumar et al. 2013; Shekhar et al. 2019; Chandra and Roychoudhury 2020; Raina et al. 2021a). Altogether, the production of antioxidant enzymes in plants is an adaptive response to drought stress. Symptoms of oxidative damage (like lipid peroxidation) have been used to assess the increase in ROS production under drought stress (Kumar et al. 2013a). ROS production is being enhanced due to stomatal closure and the concomitant limitation on CO_2 fixation. This rise in ROS production is likely to be beneficial to the plant. Enhanced cellular ROS production is sensed by the plant as an alarm signal that triggers defense pathways and acclimatory responses, enabling the plant to adapt to the changing environment (Kumar et al. 2013; Kumar et al. 2013a). ROS induces an increase in $[Ca^{2+}]_{cyt}$ by the activation of hyper polarization-dependent Ca^{2+}-permeable channels in the plasma membrane of *Arabidopsis* guard cells. This ROS-induced increase in $[Ca^{2+}]_{cyt}$ has also been detected in other cell types which suggests that the activation of Ca^{2+} channels could be a key step in many ROS-mediated processes (Mazars et al. 2010). On the other hand, several reports have shown that H_2O_2 induces mitogen-activated protein kinases (MAPKs), which are in turn implicated in several signal transduction cascades that modulate gene expression (Mazars et al. 2010).

7.5.2 Effect of Antioxidant on ROS Reduction

Plants develop various defensive mechanisms that allow for ROS removal and minimize and prevent progressive damage to cellular components. The antioxidant system includes the action of small molecule antioxidants and the induction of antioxidant enzymes. A crucial enzyme in sequestering ROS for protecting the plant cells is ascorbate peroxidase (APX; Gill and Tuteja 2010). APX is a part of the water–water as well as the ASH–GSH (ascorbate-glutathione) cycles that quench H_2O_2 produced in the chloroplasts during stress conditions (Asada 2006; Gill and Tuteja 2010). The plant water transport mechanisms aid in the activation and modulation of the antioxidant defence system leading to the production of APX under conditions of water scarcity (Srivalli et al. 2003; Selote and Khanna-Chopra 2004). In the case of rice seedlings as observed by Sharma and Dubey (2005), the APX activity is proclaimed to increase when administered with low stress conditions and decrease in case of elevated stress (Sharma and Dubey 2005; Seleiman et al. 2021). Several oxidant enzymes like catalase (CAT) and peroxidase (POD) act simultaneously in a stepwise manner for enduring plants in a dynamic environment. H_2O_2 is majorly scavenged by antioxidant enzymes like CAT and POD by converting it into water and oxygen (Apel and Hirt 2004; Singh et al. 2016). Many accessible reductants are used by peroxidases for the reduction of H_2O_2 into plants undergoing stress treatments (Mittler 2002). The alleviated POD activity has been observed by Turkan et al.(2005) in bean cultivars. A potential stress enhancer is a pre-requisite for obtaining maximum agricultural yield when stress conditions are prevalent (Nawaz et al. 2014).

The beneficial antioxidant activity of Se has been observed under stress conditions when increased amounts of ROS are generated. Se can affect the formation and quenching of ROS either directly or indirectly through the regulation of antioxidants. Se′s positive antioxidant action has been shown during stress settings when high levels of ROS are produced. The mechanism of Se′s antioxidant activity in plants is yet to be fully understood (Mittler 2002).

As mentioned above, Se is an effective stress ameliorant and plays a crucial role in mitigating plant stress via various means (Hartikainen and Xue 1999). It reduces the detrimental effects of UV-induced damage (Valkama et al. 2003; Nawaz et al. 2014), improves chlorophyll contents under conditions of extreme light stress (Seppänen et al. 2003), and eventually triggers the plant to enhance plant tolerance by producing antioxidants and maintaining water availability (Kuznetsov et al. 2003; Djanaguiraman et al. 2005; Ekelund and Danilov 2001). The SOD (superoxide dismutase) and GPX (glutathione peroxidase) activities when increased lead to the activation of defense mechanisms in response to oxidative stresses. Ding et al. (2014) demonstrated that Se-mediated superoxide radical dismutation to H_2O_2 reduced Al toxicity in rye grass. However, at high levels, Se behaves as a prooxidant, causing oxidative stress in plants, such as the Pb-stressed roots of *Vicia faba*. 1.5 M Se reduced ROS, whereas 6 M increased ROS accumulation and cell survival (Mroczek-Zdyrska and Wójcik, 2012). Diao et al. (2014) discovered improved photosynthesis in rice seedlings at low Se concentrations but reported impaired photosynthetic machinery at high Se concentrations.

The enhanced activity of glutathione peroxidase (GPX) is found to be closely connected with the antioxidative effect produced by Se (Xue et al. 2001). This was demonstrated by Kuznetsov et al. (2003) where Se was used as a stress ameliorant on spring wheat cultivar. Se concentrations up to 1.0 mg kg^{-1} remarkably show higher GPX activity in rye grass (*Lolium perenne*) which causes a concurrent decline in lipid peroxidation. Hartikainen et al. (2000) further highlighted the positive relationship between GPX activity and Se concentrations in plants. SOD is also known to affect the antioxidants by lowering the concentrations of the ROS produced intracellularly by triggering proline and peroxidase synthesis (Kuznetsov et al. 2003). Several reports about the Se application in drought conditions have been stated that Se has aided the plants like maize (Sajedi et al. 2009) and rapeseed Valadabadi et al. 2010) to tolerate drought and alleviate its negative effects on leaf area index (LAI), total dry weight, (TDW), crop growth rate (CGR), and relative growth rate (RGR). Selenium having various physiological and antioxidant properties has driven many biologists to study the same lately. Nevertheless, Se has no major role in important metabolic processes of the plant but can mitigate the damages caused during stress conditions (Plaut 2003; Seppänen et al. 2003; Raina et al. 2021b). The range of oxidants produced by the plant on the application of Se that aids in quenching ROS along with the harmful effects of ROS on plants and the mechanism of action of Se treated stressed plants in quenching ROS and alleviating drought stress have been collectively illustrated in Fig. 7.2.

Researchers have demonstrated that Se is not only able to promote growth and development of plants but also increases resistance and antioxidant capacity of plants subjected to various stresses (Djanaguiraman et al. 2005). The beneficial effect of Se in plants subjected to stress conditions has in most cases been attributed to increased antioxidant activity. Research work conducted by Xue et al. (2001) and afterwards by Djanaguiraman et al. (2005) and Ramos et al. (2010) showed the effect of Se application in the form of selenate on senescence in lettuce and soy, confirming that the decline in antioxidant enzyme activity was milder in plants treated with this element, which offsets oxidative damage by boosting growth in plants treated with Se.

Rios et al. (2009) showed the effects of different concentrations (5, 10, 20, 40, 60, 80, and 120 μM) of selenite or selenate on the production and detoxification of H_2O_2 in lettuce plants in non-stressed conditions. The results show that the selenate form of Se is less toxic than selenite. On the contrary, the application of selenite triggered a higher foliar concentration of H_2O_2 and a higher induction of lipid peroxidation (MDA content and LOX activity) in comparison to that observed after the selenate application. Also, the plants treated with selenate induced higher increases in enzymes that detoxify H_2O_2, especially ascorbate peroxidase (APX) and glutathione peroxidase (GPX), as well as an increase in the foliar concentration of antioxidant compounds such as ascorbate (AsA) and glutathione (GSH). These indicate that an application of selenate at low rates can be used to promote the induction in plants of the antioxidant system, thereby improving stress resistance.

As discussed above, it is applied basally or on foliage to mitigate drought stress. Amongst the isoforms discussed above, selenite (IV, VI) are the most prominent species found in soil (Raina et al. 2021b). Se was discovered to have an antioxidant effect by controlling the intracellular ROS produced by the synthesis of proline and peroxidises (Kuznetsov et al. 2003; Lanza and Dos Reis 2021). However, this did not have any impact on the plant's water absorption capacity as well as plant

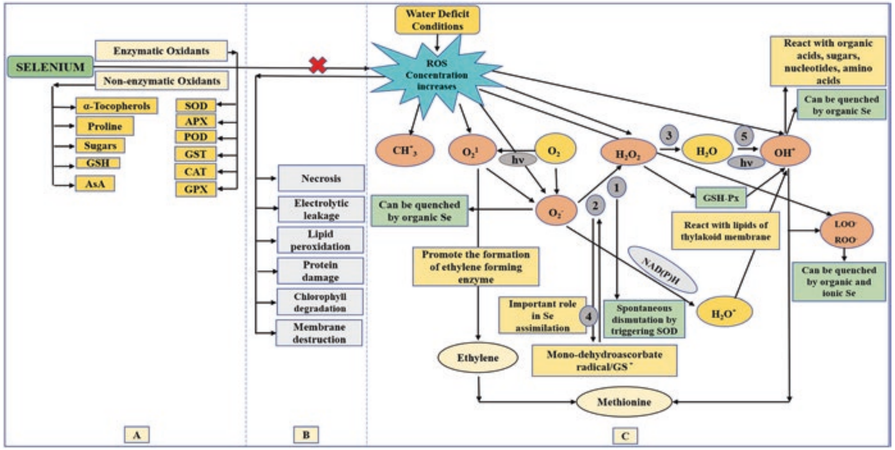

Fig. 7.2 Selenium treatment activates the antioxidant defence system in plants under stress. Figure (**a**) depicts the range of oxidants produced by the plant on Se application which quench ROS generated; (**b**) Some of the harmful effects of ROS on plants; (C) mechanism by which Se ameliorates the drought stress in plants. Se modulates the antioxidant defense system in plants with the help of various antioxidant enzymes.(1) SOD/Dismutation; (2) ASA/GSH; (3) ASA/GSH system, POD/CAT; (4) Ferredoxin, GSH; (5) Harber–Weiss reaction, Fenton Reaction)

biomass under the conditions of drought stress (Nawaz et al. 2012; Sharma et al. 2022).

Harris et al. (2014), in their experiments on *Stanleya pinnata* and *Brassica juncea* seedlings examined a notable increase in the biomass of about 22.3% and 30%, respectively, when exogenous Se was administered in normal as well as mild drought stress conditions but eventually found no major difference under severe drought conditions. Additionally, the Fv/Fm ratio was observed to be lower in Se-treated stressed plants, indicating that it is a probable antagonist of photosynthesis. Contrary to this, Nawaz et al. (2015a, b) reported a synergistic effect of Se on the rate of photosynthesis. Table 7.1 enlists the effects of exogenously applied selenium on plants under conditions of drought stress.

By activating the antioxidant machinery of plants encountering water stress, Se can manage the status of water (Yao et al. 2009) and considerably improve biomass production (Martiniano et al. 2020).

7.6 Plant Hormones Under Drought Stress

Plant hormones play an important role in perception, signalling, and downstream response of plants to stresses. Controlling and coordinating cell division, development, and differentiation are the most significant tasks of plant hormones (Hooley, 1994). Plant hormones can influence a variety of plant functions, such as seed dormancy, flowering, fruiting, senescence, etc. (Graeber et al. 2012). Plant hormones, which include Abscisic acid (ABA), brassino steroids, ethylene, auxins, gibberlins, and cytokinins, are biological molecules that regulate various biochemical and physiological processes in plants (Santner et al. 2009). It is possible that the role of plant growth regulators in overcoming the negative effects of drought on growth is due to a shift in endogenous growth regulators that alters plant water balance (Santner et al. 2009).

Plants ability to adapt to abiotic stressors is mediated by phytohormones, which mediate a wide range of adaptive responses. Drought stress is dealt with in different ways by cytokinin and ABA (Fernández-Lizarazo and Moreno-Fonseca 2016). Oelmüller et al. (2009) on similar lines demonstrated an increase in the concentration of plant stress hormones in Chinese cabbage upon treatment with polyethylene glycol (PEG), an inducer of drought stress.

Table 7.1 Effect of exogenously applied selenium and nanoselenium on plants under conditions of drought stress

Crop name	Plant class	Plant family	Drought-inducing agent	Mode of application of Se/nano-selenium		Dosage	Effect on plants after Se application	References
Buckwheat (*Fagopyrum esculentum* Moench)	Dicotyledonae	Polygonaceae	Water-deficit conditions	Foliar application	Se treatment	1 g M^{-3}	Increased stomatal conductance and PSII functioning	Tadina et al. (2007)
Chinese Mustard (*Brassica juncea* L.)	Dicotyledonae	Brassicaceae	Water-deficit conditions	Foliar application	Se treatment	30 g/l Na_2SeO_3	Increased total dry weight, leaf area index (LAI), relative growth rate (RGR), and crop growth rate (CGR)	Valadabadi et al. (2010)
False Flax (*Camelina sativa* L.)	Dicotyledonae	Brassicaceae	Water-deficit conditions	Foliar application and seed priming	Se treatment	75 μM, 7.06 μM Na_2SeO_3	Enhanced chlorophyll production and plant growth	Ahmad et al. (2021)
French Marigold (*Tagetes patula* L.)	Dicotyledonae	Solanaceae	Water-deficit conditions	Foliar application	Se treatment	0.4–0.8 mg dm^{-3}	Increased tolerance to drought stress conditions	Kleiber et al. (2020)
Groundnut (*Arachis hypogaea* L.)	Dicotyledonae	Fabaceae	Water-deficit conditions	Foliar application	NanoSelenium treatment	0–40 ppm	Improved yield components and seeds oil with altered protein signatures as well as fatty acids composition.	Hussein et al. (2019)
Ladyfinger (*Abelmoschus esculentus* L.)	Dicotyledonae	Malvaceae	Water-deficit conditions	Foliar application	Se treatment	1^{-3} mg L^{-1}	Improved vegetative attributes and yield	Ali et al. (2020)

Maize (*Zea mays* L.)	Monocotyledonae	Poaceae	Water-deficit conditions	Seed priming	Se treatment	0.075 mM Se	Improved seed germination with enhanced antioxidant activity	Nawaz et al. (2021)
Maize (*Zea mays* L.)	Monocotyledonae	Poaceae	Water-deficit conditions	Foliar application	Se treatment	150 mg Na_2SeO_3	Increased content of proline, N and K in plants along with enhanced activity of SDH, PSY, and ADH genes	Bocchini et al. (2018)
Maize (*Zea mays* L.)	Monocotyledonae	Poaceae	Water-deficit conditions	Foliar application	Se treatment	20 g ha^{-1}	Improved yield and water uptake	Sajedi et al. (2009)
Mung Bean (*Vigna radiata* (L.) R. Wilczek)	Dicotyledonae	Fabaceae	Water-deficit conditions	Foliar application	Se treatment	2–4 μM Se L^{-1} in the form of Na_2SeO_4	Improved nutritional quality of grains with enhanced antioxidative machinery	Aqib et al. (2021)
Olive (*Olea europaea* L.)	Dicotyledonae	Lamiaceae	Water-deficit conditions	Foliar application	Se treatment	50 and 150 mg Se L^{-1}	Improved leaf water content, photosynthesis, and fruit yield	Proiettia et al. (2013)
Potato (*Solanum tuberosum* L.)	Dicotyledonae	Solanaceae	Water-deficit conditions	Seed priming	Se treatment	16.2–1.7 ng g^{-1}	Increased respiration and photosynthesis along with enhanced growth of aging seedling	Germ et al. (2007); Germ (2008)
Rapeseed (*Brassica napus* L.)	Dicotyledonae	Brassicaceae	Water-deficit conditions	Foliar application and seed priming	Se treatment	75 μM, 7.06 μM Na_2SeO_3	Enhanced drought stress tolerance by increased activity of antioxidant enzymes	Ahmad et al. (2021)

(continued)

Table 7.1 (continued)

Crop name	Plant class	Plant family	Drought-inducing agent	Mode of application of Se/nano-selenium		Dosage	Effect on plants after Se application	References
Rice (*Oryza sativa* L.)	Monocotyledonae	Poaceae	Water-deficit conditions	Foliar application	Se treatment	40% WHC + 0.5–1.5 mM Se	Improved water loss and improved chlorophyll content	Ghouri et al. (2021)
Sesame (*Sesamum indicum* L.)	Dicotyledonae	Brassicaceae	Water-deficit conditions	Foliar application	Se treatment	5–40 mgL^{-1}	Increased plant weight and proline content	Thuc et al. (2021)
Soybean (*Glycine max* (L.) Merr)	Dicotyledonae	Fabaceae	Water-deficit conditions	Foliar application	Se treatment	75 mgL^{-1} in the form of Na_2SeO_4	Enhanced plant growth during senescence	Djanaguiraman et al. (2010)
Strawberry (*Fragaria* × *ananassa Duchesne*)	Dicotyledonae	Rosaceae	Water-deficit conditions	Foliar application	Se treatment	50–100 mg L^{-1}	Increased proline content and enhanced activity of CAT, SOD, GPX, APX enzymes. Decreased H_2O_2 content and lipid peroxidation	Zahedi et al. (2020)
Sweet Basil (*Ocimum basilicum* L.)	Dicotyledonae	Lamiaceae	Water-deficit conditions	Foliar application	Nanoselenium treatment	0–120 mgL^{-1}	Improved proline contents with enhanced effects on plant metabolism ultimately leading to improved nutrition and increased against drought stress conditions	Ardebili et al. (2015)
Tobacco (*Nicotiana tobacum*L.)	Dicotyledonae	Solanaceae	PEG induced	Foliar application	Se treatment	200 µg L^{-1} Na_2SeO_3 and Na_2SeO_4	Reduced MDA and H_2O_2 content along with an increased activity of antioxidant enzymes	Han et al. (2021)

Tobacco (*Nicotiana tobacum*L.)	Dicotyledonae	Solanaceae	Water-deficit conditions	Foliar application	Nanoselenium treatment	0-24 mg kg^{-1}	Increased stomatal conductance, photosynthesis, Rubisco content and carboxylation efficiency	Jiang et al. (2015)
Wheat *Triticum aestivum*L.	Monocotyledonae	Poaceae	Water-deficit conditions	Foliar application	Se treatment	40% WHC with 40 mM Se	Enhanced plant growth, chlorophyll content, water potential, rate of photosynthesis, and transpiration	Sattar et al. (2019)
Wheat (*Triticum aestivum*L.)	Monocotyledonae	Poaceae	Water-deficit conditions	Nanoparticle treatment	Se treatment	100 mg mL^{-1}	Increased tolerance against drought stress conditions and *Fusarium* species	El-Saadony et al. (2021)
Wheat (*Triticum aestivum*L.)	Monocotyledonae	Poaceae	Water-deficit conditions	Foliar spray	Se treatment	1–3 mg Se kg^{-1}	Decrease in concentration of MDA along with a subsequent increase in levels of proline content, root activity, POD and CAT activities, chlorophyll, and carotenoid content	Yao et al. (2009)

(continued)

Table 7.1 (continued)

Crop name	Plant class	Plant family	Drought-inducing agent	Mode of application of Se/ nano-selenium		Dosage	Effect on plants after Se application	References
Wheat (*Triticum aestivum*L.)	Monocotyledonae	Poaceae	Water-deficit conditions	Foliar application	Se treatment	7.06 µM (0.48 mg L^{-1})	Improved yield, osmotic potential, transpiration rate, turgor and accumulation of soluble sugars and amino acids. Enhanced Fe and Na uptake	Nawaz et al. (2015a)
Wheat (*Triticum aestivum*L.)	Monocotyledonae	Poaceae	Water-deficit conditions	Foliar application, seed priming	Se treatment	40 mg Se L^{-1}	Improved quality of grain and enhanced yield	Nawaz et al. (2015b)
Wheat (*Triticum aestivum*L.)	Monocotyledonae	Poaceae	Water-deficit conditions	Foliar application	Se treatment	1.0 mg Se/kg	Improved biomass, recovery of MDA and increased production of CAT and soluble protein	Yao et al. (2011)
White Clover (*Trifolium repens*L.)	Dicotyledonae	Fabaceae	PEG induced	Foliar application	Se treatment	5 µM Na_2SeO_4	Activation of APOX, SOD, GR, and alleviation of lipid peroxidation	Wang et al. (2011)
Wild mustard (*Brassica rapa*)	Dicotyledonae	Brassicaceae	Water-deficit conditions	Foliar application	Nanoselenium treatment	10 µg kg^{-1}	Enhanced metabolism in leaves and flowers.	Lyons et al. (2009)

7.6.1 Selenium Regulates Response of ABA in Guard Cells Under Drought Stress

Abscisic acid (ABA) is considered the main hormone which intensifies drought tolerance in plants through various morpho-physiological and molecular processes including stomata regulation, root development, and initiation of ABA-dependent pathway (Ullah et al. 2018). Drought causes the root to produce the primary stress hormone ABA, which is then transported to the shoot and causes stomatal closure. ABA-responsive elements (ABREs) are cis-regulatory elements that bind to transcription factors that change the transcription of related proteins. Selenium belongs to a class of antioxidant metabolites which reduce the accumulation of ROS in guard cells to regulate stomatal closure (Watkins et al. 2017). Under drought condition, exogenous ABA is stimulated by the proteins which can regulate the process of energy metabolism; increase enzymatic and non-enzymatic antioxidant regulation systems; relative water content of plants to promote plant growth including maize, wheat, sweet potato, pearl millet, potato, and other plants (Germ et al. 2007; Zhang et al. 2012; Wei et al. 2015; Awan et al. 2020; Huan et al. 2020). Some studies have shown that treatment with ABA and jasmonate simultaneously is more effective in promoting plant drought resistance (Awan et al. 2020; Huan et al. 2020). ABA regulates the expression of various stress-responsive genes and in the synthesis of LEA proteins, dehydrins, and other protective proteins.

Se plays a role in the regulation of moisture-stressed seedlings water status as well as the activation of plant hormones responsible for cell expansion and enlargement. The maximum PHSI (Plant height of stressed plant) observed by Se fertigation treatment and Se foliar application might be attributed to the Se-regulated decrease in the osmotic potential that increases the water relations of water-stressed and actively growing plant parts such as young leaves and seed (Nawaz et al. 2013, 2014).

7.7 Genetic Control of Selenium-Mediated Drought Stress Alleviation in Plants

Seki et al. (2002) have broadly classified the drought-tolerant genes under two main classes, i.e., directly and indirectly affecting proteins. While the former directly participate in the process of drought stress alleviation, the latter do so by modulating the functioning and signalling cascade of secondary stress-responsive genes (Shinozaki et al. 2003). Secondary messengers, such as Ca^{2+}, ROS, hormones, such as ABA, and phospholipids carry early signals. They use kinase relays and target a wide range of drought-responsive genes. The latter often encode functional proteins, such as chaperones, which protect soluble proteins and maintain membrane integrity. Xu et al. (2018), while working on drought-affected and AMF-associated *Solanum lycopersicum* reported the upregulation of 14-3-3 genes (TFT1-TFT12) actively associated with the ABA signalling pathway. Drought-affected plants have increased the activity of antioxidant enzymes like CAT, POD, and SOD as well as drought-responsive genes like Dehydration-responsive element-binding protein 2A (DREB2A), Response-to-Dehydration 29A(RD29A), Calcineurin B-like protein 1 (CBL1), and *Arabidopsis*NAC domain containing protein 72 (ANAC072) (Sharma et al. 2021). Increased levels of CRISPR-associated proteins (CAS) and mRNA for Ca^{2+} monitoring associated with the thylakoid membrane have also been reported.

Amongst different Se species, the effects and mechanisms of drought stress on mitigation are not well understood till date. According to Han et al. (2021), drought stress can notably stop growth processes in plants, although sodium selenate (Na_2SeO_4) and sodium selenite (Na_2SeO_3) were found to promote the growth of *Nicotiana tabacum* under drought conditions. Nevertheless, in comparison, the application of Se as sodium selenate induces a magnificent number of root tips and bifurcations when drought conditions are provided. Additionally, both forms show inflated levels of photosynthetic pigments, antioxidant enzymes, concentrations of osmotic substances, and expression of stress-responsive genes (NtCDPK2, NtP5CS, NtAREB, and NtLEA5) relative to drought stress alone. Interestingly, sodium selenate application showed maximum expression levels in the case of NtP5CS and NtAREB genes. Both the isoforms of selenium are known to mitigate the various detrimental effects of drought stress on leaves. They were analysed by experimentally reducing MDA and H_2O_2 content and enhancing the antioxidant enzyme activity, wherein Na_2SeO_4 when applied reduced both H_2O_2 and MDA content.

7.8 Role of Nano-Selenium in Alleviating Drought Stress

Modern and advanced techniques such as hybridization, genetic engineering and locus mapping are now being used to mitigate the damage caused by water scarcity. Unfortunately, these advanced and modern techniques have some negative effects (Zhao et al. 2008). These advanced techniques require skilled workers for operation and are not as cost-efficient. Pertaining to the current situation and demands, the emergence of reasonable, cheaper, and practical techniques can help us overcome these difficulties (Sharma et al. 2021a). The agriculture sector and its employment of varied nano-techniques have enhanced the eminent role of nanotechnology in current times (Ahmad et al. 2020; Zahedi et al. 2020). Nowadays, nanotechnology finds a wide range of applications in the fields of agriculture, climate change, and food security. Moreover, this emerging technology can also be used to design various chemicals and tools like nano-herbicides, nano-pesticides, nano-fertilizers, and nano-machines (Chhipa 2017; Elizabeth et al. 2019; Gudkov et al. 2020).

Se, as an essential plant nutrient, affects the processes of senescence, agronomy, biochemistry, and water supply in water-stressed conditions (Hasanuzzaman and Fujita 2011; Bocchini et al. 2018; Ahmad et al. 2020). The plants-based approach for the synthesis of nanoparticles (NPs) being harmless can be used as an alternative to mitigate water stress complications in plants (Ikram et al. 2020, 2021). Pertaining

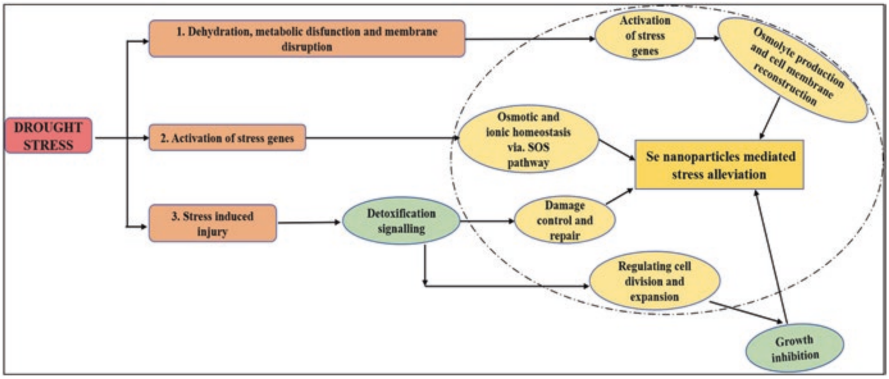

Fig. 7.3 Detrimental effects of drought stress on plants and the associated stress amelioration by Se nanoparticle treatment (the highlighted circle represents the various physiological responses initiated by the stressed plant on the application of Se nanoparticles)

to these observations, plant-based Se nanoparticles (SeNPs) are considered to be an efficient approach to alleviating drought stress in plants. They are biocompatible in nature and require no stabilizing or capping agents to be added during their synthesis (Tariq et al. 2021). The role of selenium nanoparticles in mitigating drought stress is highlighted in Fig. 7.3. Unfortunately, the current research in this area is very preliminary, and the field is yet to be explored since the investigations carried out are very few in number. Nevertheless, a latest study has reported the synthesis of SeNPs from *Allium sativum* L. The effect of these synthesized SeNPs was studied on wheat plants in water-scarce conditions. Amazingly, it was observed that a concentration of about 30 mg/L of these plant-mediated SeNPs has augmented the various characteristics of wheat plant, for instance, shoot length, root length, plant height, and number of leaves per plant (Ikram et al. 2020). The reason for this change is presumed to be the SeNPs augmentation of the enzymatic activities in stress conditions. Furthermore, the antioxidant defense in plants in water stress conditions is ameliorated by these biogenic nanoparticles (Jozwiak and Politycka 2019). Additionally, some reports about the role of plant-based SeNPs in quenching malondialdehyde (MDA) and ROS levels have also been described (Djanaguiraman et al. 2018). Another study has also reported the enhanced photosynthetic pigments in stressed strawberry fruits by the use of selenium and silicon dioxide nanoparticles. The Se/SiO_2 NPs enhance various plant attributes like relative water content (RWC), membrane stability index, and water use efficacy at 100 mg/L concentration. Also, these Se/SiO_2 NPs are known to promote drought tolerance in stressed plants by increasing the activity of antioxidant enzymes like GPX, SOD, APX, and CAT along with reduced lipid peroxidation and H_2O_2 concentrations (Morales-Espinoza et al. 2019; Zahedi et al. 2019, 2021; Abedi et al. 2021). Further, a recent study has revealed that foliar application of SeNPs at 10 nm is exceptionally effective in mitigating the detrimental effects of water scarcity in the stressed pomegranate plants, eventually improving their yield. SeNPs are also reported to improve the nutrient status and total phenolic contents in the stressed plants (Zahedi et al. 2021). Thus, by contemplating the exemplary biocompatibility of green SeNPs, it can be said that plant-based SeNPs can be a comprehensive and prognosticating means to alleviate drought stress in agronomics.

7.9 Conclusion

Plants in response to water deficit display structural changes in stomata, ROS scavenging, and metabolic and biochemical changes including lipid peroxidation, eventually resulting in reduced plant growth, photosynthesis, and respiration. Se application reduces these damages by producing organic solutes which accumulate and sequester the ROS and protect the stressed plant by enhancing water use efficiency and photosynthetic rate through stomatal movement inside the cell. Another way in which selenium protects the plant from stress is via. the production of ROS scavenging enzymes. The majority of the antioxidative stress response has been intensively researched as a mechanism for Se-mediated detoxification. Therefore, we can say that the application of Se and nano-Se improves drought tolerance by ameliorating antioxidant enzyme activity and reducing membrane damage. Nevertheless, this is a comparatively naïve area of research with an insufficient amount of literature available to completely understand and support the role of Se as an ameliorant of stress. Future research should consider the interactions between antioxidants (SOD, APX, CAT, GSH), various Se isoforms, and the uptake and redistribution of co-factors for some of the enzymes such as Cu, Zn, Mn, and Fe.

Acknowledgement DK acknowledges Science and Engineering Research Board (Grant No-EEQ/2016/000487), India, and Institution of Eminence Seed Grant (Dev. No. 6031 (B), Banaras Hindu University, Varanasi, India, for providing financial support to the laboratory. DK also acknowledges the Centre of Advanced study in Botany, Institute of Science, Banaras Hindu University,Varanasi, India, for providing necessary facilities and infrastructural support.

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Chapter 8
Selenium and Nano-Selenium-Mediated Heat Stress Tolerance in Plants

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8.1 Introduction

Considering the effect of heat stress (HS) on plants is of vital importance due to the continually increasing temperature as a result of global warming. The temperature above the optimum is termed HS and is harmful to all organisms, particularly plants, because of their sessile nature. HS disturbs cellular homeostasis, pollen development, and various other functions and thus is a severe threat to crop productivity (Serrano et al. 2019). To combat the hazardous effects of increasing temperature, plants usually modify different morphological traits and restructure metabolic networks by regulating *ad hoc* physiological and molecular mechanisms (Krishna 2004). These responses of plants are called adaptations to high-temperature stress and help the plant to maintain growth (Wang et al. 2003; Peverelli and Rogers 2013). Furthermore, the activation of the antioxidative defence system, stabilization of membranes and enzymes by heat shock proteins (HSPs), accumulation of osmoprotectants, and ethylene production increase thermotolerance in plants (Serrano et al. 2019).

The selenium (Se) is a naturally occurring metalloid present inside the earth's crust at concentrations ranging from 0.1 to 10 μg g^{-1}, although seleniferous rocks-derived soils may contain higher levels up to 1000 μg g^{-1} (Olfield 1999; Bagriantseva et al. 2012; Lindblom et al. 2012). It exhibits multiple oxidation states such as selenide (−2), Se (0; elemental form), selenite (+4), and selenate (+6) (Eiche et al. 2015). The physical and chemical properties of Se overlap with sulphur (S) and

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M. A. Hossain et al. (eds.), *Selenium and Nano-Selenium in Environmental Stress Management and Crop Quality Improvement*, Sustainable Plant Nutrition in a Changing World, https://doi.org/10.1007/978-3-031-07063-1_8

tellurium (Te) in terms of electron affinities, ionization, and bonding energies. The essentiality of Se for humans was first established in 1973 when it was identified as the component of glutathione peroxidase (GSHx) and its role in protection against oxidative stress (Garousi 2017). At present, the dietary recommendation of Se for humans is 55 µg day^{-1} (Hu et al. 2018), and its functions are mainly reliant upon selenoproteins (Kopsell and Kopsell 2007).

For higher plants, Se is considered a beneficial element (Pilon-Smits et al. 2009) and is required for the synthesis of several essential amino acids like selenomethionine (SeMet), selenocysteine (SeCys), and Se-methylselenocysteine, respectively (Kabata-Pendias 2011; Yang et al. 2012). Involvement of the seleno-amino acids is substantial in the regulation of cellular redox status (Labunskyy et al. 2014; Rayman et al. 2008). Other Se-derived compounds naturally found in plants include selenobetaine, selenoecholine, selenotaurine, trimethylselenium, dimethyl selenide, and dimethyldiselenide (Pyrzynska 1995). Cereal crops, legumes, and lentils contain Se-methionine (SeMet) as the dominant organic Se form (up to 90% of total Se), while some vegetables contain selenomethyl selenocysteine (SeMSC) (Djujic et al. 2001). Therefore, Se in trace quantities is widely accepted as beneficial for plant development and can also contribute to homeostatic functions (Hamilton 2004; Quiterio-Gutiérrez et al. 2019), promoting plant growth and antioxidant capacity (Astaneh et al. 2018). This chapter focuses on the involvement of Se in the regulation of a plethora of cellular, biochemical and molecular processes to induce HS tolerance in plants. Further, an in-depth analysis of Se and nano-selenium (nSe) involvement in different physiological functions in relation to HS tolerance in crops has been discussed in detail.

8.2 Influence of Se and nSe on Plant Adaptability and Quality Traits

Plants respond to HS by a series of biochemical and physiological changes at the metabolomic, epigenomic, transcriptomic, and proteomic levels (Serrano et al. 2019). At the morphological level, plants respond to HS by altering the shoot, root, and leaves growth, and thus life cycle (Handayani and Watanabe 2020). The heat-tolerant plants have thicker leaves, fewer and smaller organs, and shortened life cycle duration (Natarajan and Kuehny 2008). The plants could acquire thermotolerance by maintaining a healthier canopy cover with higher eaves to intercept light and fix CO_2 linked with higher transpiration cooling, and synthesis and translocation of abundant photoassimilates to the reproductive tissues and roots (Natarajan and Kuehny 2008). The HS also induces changes in physiological traits of plants by affecting photosynthesis, respiration, and assimilate partitioning and mobilization of reserves to different organs. The effect on reserve mobilization is due to the altered activities of enzymes involved in the starch breakdown. The thermotolerant plants maintain lower tissue temperature by increasing the stomatal conductance and transpiration rate (Li et al. 2020a, b). At the cellular level, HS damages the cell membranes with disorganized thylakoid structures, reduces cell size, alters the function of stomatal guard cells and relative water content, and promotes programmed cell death. At the same time, the higher stomatal frequency is related to HS tolerance in plants (Handayani and Watanabe 2020).

Different Se-forms have been shown to promote plant growth and adaptability under both normal and stressed conditions. Positive effects of bulk Se and different ionic forms (Se^{2-}, O_3Se^{-2}, and O_4Se^{-2}) and nSe have been reported for various crops growing under different environmental conditions. On a comparative basis, almost all the forms of Se could regulate plant growth. In this context, lower concentrations of bulk Se (1 and 2 mg L^{-1}) improved biomass, pigments, and decreased oxidative stress-induced damage via up-regulation of antioxidant enzymes in drought-stressed wheat (Yao et al. 2009; Xiaoqin et al. 2009). Likewise, the ameliorative effect of Se on heat-stressed cucumber plants has been reported (Balal et al. 2016). Similarly, seed pre-treatment with selenite improved the germination percentage of *Momordica charantia* exposed to high-temperature stress (Chen and Sung 2001). Selenate also imparted beneficial effects as the exogenous application of sodium selenate induced HS tolerance in wheat at a very low dose (Iqbal et al. 2015). Apart from the effects of bulk forms, nSe has also been proven to enhance plant growth under diverse environmental conditions. A literature review suggested that nSe improved stress tolerance among different organisms, including plants (El-Ramady et al. 2018). The ability of nSe to modulate antioxidant capacity and improve growth under nutrient deficiency has been recently reported in peanut (Hussein et al. 2019a, b). Similarly, the exogenous application of bulk and nSe improved fruit quality in cucumber; however, nSe was much more effective, which also improved vegetative growth and total yield (Shalaby et al. 2021). Tomato plants treated with nSe exhibited higher photosynthetic pigments, antioxidant capacity, and concentrations of primary and secondary metabolites (Quiterio-Gutierrez et al. 2019). The bioactive and antioxidant properties of nSe are ascribed to its smaller diameter due to more surface-to-volume ratio (Zhang et al. 2001; Peng et al. 2007). Above all, both the bulk and nSe forms showed potential stimulatory and ameliorative effects that contributed to the plant adaptability under higher temperature regimes. An in-depth analysis is presented to explain the involvement of different Se forms in HS tolerance in plants (Table 8.1).

8.3 Induction of Heat Stress Tolerance by Se- and nSe-Mechanistic Insights

The HS primarily impairs photosynthetic activity and interferes with vital physiological processes at multiple levels. Loss of photosynthetic pigments, necrosis and growth inhibition, and flower sterility are the primary causes of HS-induced global losses in crop production (Thuy and Kenji 2015; Ding et al. 2016). In addition, the

Table 8.1 Improvements in plant quality traits by exogenous application of different selenium (Se) sources

Se source	Application method	Se concentration	Plant species	Plant responses	References
Potassium selenate (K_2O_4Se) and selenite (K_2SeO_3)	Soil and foliar	10, 20, or 30 kg ha^{-1}	*Lens culinaris* Medik	Increased biomass and grain yield	Thavarajah et al. (2015)
Selenium		30 mg L^{-1}	*Solanumtuberosum* L.	Higher plant height, number of stems, leaf area, chlorophyll, proline content, and tuber weight	Ali et al. (2021)
Selenium dioxide (SiO_2)as nSe	Foliar	50 mg L^{-1}			
Sodium selenate (Na_2SeO_4)	Foliar	40 mg Se L^{-1}	*Triticum aestivum* L.	Enhanced transpiration rate, total soluble sugars, free amino acids, activity of antioxidants, and increased grain yield	Nawaz et al. (2015)
nSe, sodium selenite (Na_2SeO_3) and sodium selenate (Na_2SeO_4)	Nutrient solution	10 µM	*Oryza sativa* L.	nSe uptake rate was much lower than that of selenite or selenate	Wang et al. (2020)
Selenium nanoparticles (nSe)	Foliar	10, 20, 30, and 40 mg L^{-1}	*Triticum aestivum* L.	Growth parameters were enhanced at 30 mg L^{-1}	Ikram et al. (2020)
Selenium nanoparticles (nSe)	Nutrient solution	10 and 100 µM	*Fragaria* × *ananassa* Duch.	Increased CAT activity,photosynthesis, ion homeostasis and secondary metabolites	Soleymanzadeh et al. (2020)
Bio-nSe	Nutrient solution	100 ppm	*Hordeum vulgare* L.	Enhanced biomass and total phenolics; reduced MDA content	Habibi and Aleyasin (2020)
Sodium selenate (Na_2SeO_4)	Fertigation	100 g ha^{-1}	*Zea mays* L.	Improved calcium homeostasis and pollen fertility	Del Pino et al. (2019)

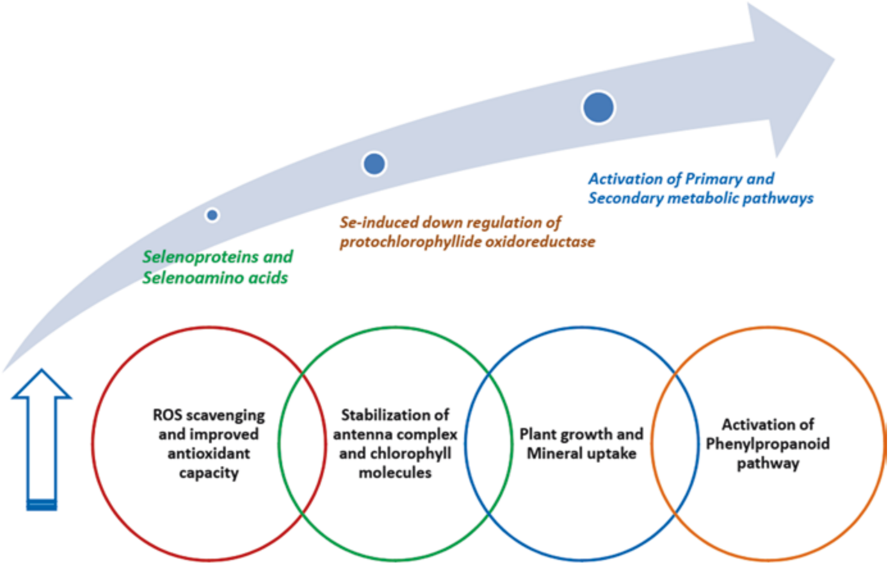

Fig. 8.1 (Left to Right) Mechanistic insights into Se-mediated heat stress tolerance in plants through (**a**) re-enforcement of antioxidant capacity through mediating the synthesis of enzymatic and non-enzymatic antioxidants (possibility of direct involvement of Se and nSe in the redox reactions through synthesis of selenoproteins and/or selenoamino acids is also suggested), and induction of heat shock proteins, (**b**) inhibition of chlorophyll degradation and improving its stability, (**c**) improvements in nutrients uptake and transport, photosynthetic activity, and photoassimilates transport, and (**d**) activation of primary metabolism and induction of secondary metabolism. ⇧, show beneficial effects of exogenous Se and nSe on different attributes under heat stress

application of soil amendment with nSe contributed to HS tolerance in eggplant and tomato (Gudkov et al. 2020). The results from another study depicted that the exogenous application of nSe particles (40 nm diameter) mitigated the adverse effects of HS (Djanaguiraman et al. 2018). A detailed analysis of the involvement of different Se forms in mitigating the adverse effects of HS is proposed (Fig. 8.1).

8.3.1 Oxidative Stress and Antioxidant Capacity

Of the 25 known Se-dependent proteins in different organisms other than plants, about 12 selenoproteins are antioxidants that solely work in tandem with other antioxidants (Sharapov and Novoselov 2019; Ulrich and Jakob 2019). Among Se-dependent antioxidant peptides, glutathione peroxidase, selenoprotein P, and thioredoxin reductase play a vital role in maintaining cellular redox homeostasis (Steinbrenner et al. 2016; Gudkov et al. 2020). The selenoprotein P (SePP) has been identified as an extracellular antioxidant peptide that scavenges extracellular reactive oxygen species (ROS) and acts as a barrier (Mostert 2000; Lyakhovich et al.

2006). On the other hand, the thioredoxin reductase (TrxRs) regulate cellular redox potential and participate in the redox-signalling events. Both SeMet and SeCys (selenoamino acids) are involved in the biosynthesis of Se-dependent antioxidant enzymes like GPX, TrxRs, and methionine sulfoxide reductases (MsRs) that can directly scavenge ROS due to their nucleophilic properties (Chauhan et al. 2019). By contrast, HS and other abiotic stresses cause the production of various harmful ROS. The ROS such as hydroxyl radical (OH^-), singlet oxygen species ($^1O_2$), superoxide radical (O_2^-), and hydrogen peroxide (H_2O_2) are generated and accumulated in different cell organelles due to high temperature (Liu and Huang 2000; Wahid et al. 2007). To reduce these ROS levels, plants have a natural defence system consisting of various enzymes and non-enzyme antioxidants. The enzymes include superoxide dismutase (SOD), peroxidase (POD), catalase (CAT), glutathione reductase (GR), and ascorbate peroxidase (APX) (Bowler et al. 1992). Various findings showed that the plants that exhibited higher production of these antioxidants had higher tolerance against HS (Peverelli and Rogers 2013). On the other hand, the heat-resistant plants had lower levels of H_2O_2 (Li et al. 2020a, b).

In earlier studies, the exogenous supply of Se stimulated SOD and GPX activities leading to reduced cell membrane damage (Ardebili et al. 2015). An increase in GPX and TrxRs activities was observed upon nSe supplementation (Wang et al. 2007). The exogenous application of selenate and nSe enhanced antioxidant capacity in sorghum plants and ameliorated HS (Djanaguiraman et al. 2010, 2018). Under different abiotic stress conditions, the Se supplementation resulted in the up-regulation of SOD, CAT, APX, and GR activities, although these enzymes are not directly reliant on Se-substrate (Feng et al. 2013). The application of nSe alleviated HS-induced damage in tomato plants through improved antioxidant capacity (Haghighi et al. 2014). According to Balal et al. (2016), Se application conferred HS-tolerance in cucumber through a substantial reduction in free radicals (O_2^-, H_2O_2, and LPO) by over 40% compared to the control. Not only this, significant improvements in the SOD, CAT, APX, GPX, and GR in both leaves and roots of cucumber were recorded upon Se treatment (Balal et al. 2016). Overall, Se application to plants could result in the acclimation responses leading to the tolerance via up-regulation of antioxidants. Although not yet known, the seleniferous peptides and selenoamino acids are expected to either directly neutralize ROS or through the synthesis or regulation of other antioxidants in plants.

8.3.2 Heat-Shock Proteins (HSPs)

The HS in plants causes the denaturation of native proteins and disturbs normal metabolic processes. Heat shock factors (HSFs) regulate the transcription of HSP genes. The expression of HSPs is an adaptive and conserved mechanism in plants to counter the effects and induce HS tolerance through various pathways and regulatory networks (Mittler et al. 2012; Płazek et al. 2020). Plant tolerance to HS can be directly linked with the synthesis of HSPs which act as molecular chaperones and contribute to HS tolerance. Plants respond to HS by elevated transcription and translation of HSPs. Furthermore, HSPs exhibit membrane stabilization, protein synthesis, and renaturation of heat-sensitive proteins (Tripp et al. 2009; Doyle et al. 2013; Diaz-Villanueva et al. 2015) to protect cells from injury and to assist restoration of cellular functions under HS (Al-Whaibi 2011; Basha et al. 2010; Li et al. 2014). Owing to the enormous diversity of the HSP family, these can be categorized into five different sub-families primarily based on sequence homologies and molecular weights as sHSP, HSP60, HSP70, HSP90, and HSP100 (Vierling 1991; Torok et al. 2001; Park and Seo 2015).

The 100 families of HSPs contain proteins of 100–104 kDa size, and the evidence showed their involvement in thermotolerance acquisition by plants. For instance, a mutationin HSP101 caused inability in *Arabidopsis* (Hong and Vierling 2000; Larkindale et al. 2005) and maize to acquire thermotolerance (Nieto-Sotelo et al. 1999). However, the sHSPs representing 12–42 kDa monomeric size serve as the first line of defense and prevent protein denaturation, aggregation, and initiate ATP-dependent protein renaturation of non-native proteins by HSP100 and HSP70 (Haslbeck and Vierling 2015; Nagaraju et al. 2020). The sHSPs are ubiquitous in the plant kingdom, particularly more diverse in monocots with 11 more gene families (Waters 2013). The primary function is to prevent protein denaturation and achieve proper folding of denatured proteins (Huttner and Strasser 2012). Evolutionarily, sHSPs belong to the superfamily of proteins (Kokke et al. 1998) and their expression is increased under abiotic stress conditions, most particularly under higher temperature regimes (Narberhaus 2002; Haslbeck et al. 2005). The protective role of HSPs (as molecular chaperones) could be changed under normal conditions (Timperio et al. 2008). For example, both HSP-70 and HSP-90 were involved in *PSII* repair and photoprotection (Li et al. 2016; Płazek et al. 2020). Overall, the activation of signalling cascades leads to several HSFs and subsequent HSP expression of HSPs. Very few reports are available that directly relate the induction of HSPs to Se application in plants. Only recently, it has been reported that Se application reduced endogenous levels of HSP-90, BiP, and 14-3-3s consistent with the reduction of oxidative stress and the activity of caspase-3-like proteases (Malerba and Cerana 2018). In addition, the exogenous nSe modulated *HSFA4A*gene expression in *Triticum aestivum* (Safari et al. 2018). Future studies should focus on the identification of Se interactions with HSFs as well as how different signalling cascades interlink to mediate a Se-mediated cumulative tolerance to HS in plants.

8.3.3 Growth and Mineral Nutrition

The improvement in growth and yield traits of heat-stressed spring wheat upon Se application is reported (Iqbal et al. 2015). Likewise, nSe application mitigated the adverse effects of HS via improvements in pollen germination percentage and seed yield (Djanaguiraman et al. 2018). Furthermore, in different studies, nSe promoted root growth and organogenesis (Domokos-Szabolcsy et al. 2012), plant height, and leaf area in cucumber plants (Shalaby et al. 2021). In addition to these reports, the application of nSe improved HS tolerance in cotton plants that were linked with better antioxidant capacity and growth attributes (Saleem et al. 2018). In a follow-up study, the authors demonstrated that the nSe application improved cotton fiber length and fineness under HS compared to control plants (Saleem et al. 2021). Consistent with these reports, the application of Se improved HS tolerance in cucumber plants that was evident in terms of improvements in plant vegetative and yield attributes by over 40% compared to plants to which no Se was applied (Balal et al. 2016). In addition, Se-mediated improvements in the yield of potato (Turakainen et al. 2004), mustard (Lyons et al. 2005), tobacco (Jiang et al. 2015), and basil plants (Ardebili et al. 2015) were linked with better antioxidant capacities.

In the case of nutrients, the Se application can potentially enhance the uptake of critical nutrients in plants. For example, an increase in calcium (Ca), potassium (K), magnesium (Mg), and iron (Fe) was recorded in carrots upon Se foliar application (Kikkert and Berkelaar 2013). Also, an improvement in nitrogen (N) and K in cucumber plants was recorded under HS (Shalaby et al. 2021). Moreover, higher uptake of macronutrients (N, P, K, Ca, and Mg) rather than micronutrients(Fe, Zn, and Mn)was evident in four microgreen species (coriander, green basil, purple basil, and tatsoi) in response to Se application (Pannico et al. 2020). Similarly, Se-induced improvements in N, K, and Ca contributed to the induction of salinity stress tolerance in wheat (Elkelish et al. 2019). However, in contrast, N and K concentrations in roots and pepper fruits remained unaffected; instead, a reduction in S and P contents was recorded in response to Se application (Haghighi et al. 2019). This can be explained based on the roles of transporters present on root cell membranes and their interaction with Se supplementation at root level (Feist and Parker 2001; Zhang et al. 2013; Kikkert and Berkelaar 2013).

8.3.4 Pigments and Photosynthetic Activity

Plants exposed to high temperatures exhibit chlorophyll degradation, and thus have lower levels of photosynthetic pigments. The reduced chlorophyll content is due to the impaired and reduced chlorophyll synthesis or accelerated chlorophyll degradation (Efeoglu and Terzioglu 2009; Dutta et al. 2009). The inhibition of chlorophyll synthesis is by the destruction of enzymes involved in chlorophyll synthesis (Dutta et al. 2009), such as 5-aminolevulinate dehydratase (Mohanty et al. 2006), protochlorophyllide synthesis, protochlorophyllide oxidoreductase, and porphobilinogen deaminase (Mathur et al. 2014).In addition, HS impairs photochemical efficiency, degrades antenna complex pigments and associated proteins, and alters the efficiency of photosystems (*PS-I* and *PS-II*) and electron transport (Mohanty et al. 2002; Takahashi et al. 2004).

The application of different Se-forms improved chlorophyll contents in plants (Khalid et al. 2017; Luo et al. 2019), and improved chloroplast size under stress conditions (Feng et al. 2013). This can be explained based on the involvement of Se in porphyrin synthesis through improved mineral nutrition linked to chlorophyll synthesis (Põldma et al. 2011; Dong et al. 2013; Han and Wei 2015; Andrade et al. 2018). Also, Se supplementation could assist chlorophyll stability (stay-green trait) via down-regulation of protochlorophyllide oxidoreductase (Astaneh et al. 2018). This property, in turn, contributed to the sustained biosynthesis of carbohydrates and their partitioning to other plant parts (Qin et al. 2018). In addition, the Se application can protect/ stabilize photosystem-II (*PS-II*) via effective dissipation of energy in plants under HS (Andrade et al. 2018; Saleem et al. 2021), which ultimately contributed to better photosynthetic activity under HS. Another study reported protective effects of exogenous Se on chlorophyll fluorescence parameters (Fv/Fm, Fv0/Fm0, PQ, and ETR) and *PSII* by over 40% increase in the efficiency among heat-stressed plants (Balal et al. 2016). Therefore, both chlorophyll and energy transformation reactions benefit from Se-supplementation to plants leading to improvements in photosynthesis.

Photosynthesis is crucial for determining growth and yield and is the most sensitive factor affected by HS. The HS affects photosynthesis by photoinhibition phenomenon (Gururani et al. 2015). Photosystem II (*PSII*) is the primary target of HS, and *PSII* inhibition is an opposing mechanism to protect *PSII*, resulting in limited photosynthesis (Handayani and Watanabe 2020).The oxygen-evolving complex (*OEC*) and the activity of ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) are other prominent sites for heat damages, while *PSI* is relatively more stable at higher temperatures compared to *PSII* (Peverelli and Rogers 2013).Reports suggested that the foliar application of Se could enhance the photosynthetic rate at lower concentrations (Wang et al. 2012). Similarly, the Se-application at lower concentrations promoted photosynthetic activity and CO_2 assimilation in plants exposed to HS (Haghighi et al. 2016; Alyemeni et al. 2018). The findings of Jiang et al. (2015) confirmed that the application of Se could promote leaf photochemical efficiency, stomatal conductance, and carboxylation efficiency of RUBISCO. Overall, the Se-mediated improvements in the photosynthetic parameters can effectively improve sugar production and photoassimilate transport. To an estimate, about 90% of the photoassimilates from photosynthesis are directly utilized in dry matter production (Petridis et al. 2018). Nonetheless, Se-mediated improvements in rice yield were evident (Lai et al. 2019). The application of nSe also improved fruit quality attributes in cucumber exposed to HS (Shalaby et al. 2021). Similarly, the better quality of fragrant rice in Se-treated plants was linked to the improved photoassimilate transport during the grain filling stage (Luo et al. 2019). Similar results were reported by different researchers who explained the positive effects of Se on photosynthetic activity, carbohydrate partitioning, and photoassimilates transport in different crops, which improved HS tolerance (Hajiboland and Sadeghzade 2014; Iqbal et al. 2015; Balal et al. 2016; Haghighi et al. 2019; Saleem et al. 2021).

8.3.5 Primary and Secondary Metabolism

The metabolites are the products of cellular pathways. Therefore, changes in the metabolome provide insight into the responses of plants to stress conditions. Plants mitigate various types of biotic and abiotic stresses by modulating the primary and secondary metabolites. The primary (carbohydrates, amino acids, peptides, and lipids) and secondary metabolites were found to be differentially accumulated by HS. Das et al. (2017) analysed non-targeted metabolomic of soybean under HS and showed that the metabolites involved in carbohydrate, amino acid, and peptide metabolisms, i.e., metabolites in glycolysis and tricarboxylic acid (TCA) cycle, starch biosynthesis, pentose phosphate pathway were influenced by HS.

The direct incorporation of Se into seleno-amino acids can also trigger the synthesis of some metabolites without being an essential element (Tavakoli et al. 2020; Garza-García et al. 2021). The involvement of Se in the photosynthetic process and photoassimilate transport is directly linked to plant primary and secondary metabolic profiles. The exogenous Se-induced HS tolerance in cucumber plants via up-regulation of proline, soluble sugars, and glycine betaine contents by over 35% (Balal et al. 2016). The exogenous treatment with nSe also increased soluble protein and sugar levels in *Lubia* seedlings at only a 1.18 mg/L concentration (Mohamed-Zeid et al. 2019). Moreover, Se-mediated enhanced proline accumulation in plants exposed to water stress (Shen et al. 2008) and chilling stress (Hawrylak-Nowak et al. 2010). Similarly, in wheat plants exposed to low-temperature stress, an increase in the anthocyanins, flavonoids, and phenolics was recorded (Chu et al. 2010). The application of selenate at lower concentrations promoted glutathione levels in lettuce (Rios et al. 2009). Likewise, an increase in the ascorbic acid contents and antioxidant capacity among Se-treated plants was recorded (De Los Santos-Vázquez et al. 2016; Tavakoli et al. 2020). Apart from this, the exogenous application of selenate and selenite caused a substantial increase in oleic, linoleic, and linolenic acid concentration in rice (Lidon et al. 2018). Likewise, nSe application also caused improvements in a fatty acid profile linked to better antioxidant capacity in *Arachis hypogea* (Hussein et al. 2019a, b). Not only this, exogenous Se could alter S-metabolism within plants leading to changes in glucosinolates which protect plants against multiple environmental stress factors (Dinkova-Kostova 2013; Malagoli et al. 2015).

High temperature changes the secondary metabolites by effecting resource allocation, particularly through induction of isoprene biosynthesis and shikimate pathway (Austen et al. 2019). Some reports indicated that short-term heat increased the biogenic volatile compounds (Loreto and Schnitzler 2010) and isoprene emission (Austen et al. 2019). Isoprene is an important hydrocarbon against abiotic stress, although energetically expensive and therefore tightly regulated (Sasaki et al. 2007). The phenolic compounds were reported to decrease (Paajanen et al. 2011) and metabolite intermediates in the flavonoid pathway were found suppressed (Austen et al. 2019). Similarly, the level of several metabolites involved in TCA cycle, i.e. alpha-ketoglutarate, succinate, and oxaloacetate were reduced by HS which also decreased the production of ATP (Das et al. 2017). Plants synthesize different phenolic compounds via the phenylpropanoid pathway, and these play critical roles in the protection against biotic and abiotic stress factors and act as regulatory molecules with a role in signal transduction (Wanner et al. 1995). A key enzyme named phenylalanine ammonia-lyase (PAL) synthesizes cinnamic acid from phenylalanine which serves as the regulatory point between primary and secondary metabolism (Xu et al. 2008; Junli et al. 2010). The Se-induced synthesis of various secondary metabolites (mainly phenolic compounds) under abiotic stress conditions is reported by many researchers (Ahmad et al. 2016; Mimmo et al. 2017; Skrypnik et al. 2019; Islam et al. 2020; Pannico et al. 2020). Similarly, Se-mediated regulation in the PAL activity is earlier reported (Walaa et al. 2010; Mimmo et al. 2017; Astaneh et al. 2018). The nSe application also promoted phenylpropanoid and capsaicinoid pathways which subsequently resulted in enhanced secondary metabolite synthesis in pepper plants (Li et al. 2020a, b). Consistent with these reports, twice the application of nSe as foliar spray at 50 mg L^{-1} concentration increased total phenolics in watercress (Tocai et al. 2018). Overall, the diverse integration of Se with primary and secondary metabolic pathways could confer tolerance in plants exposed to high temperature stress.

8.4 Molecular Mechanisms of Se- and nSe-Mediated HS Tolerance in Plants

Different environmental stress factors, including HS, could alter gene expression leading to changes in downstream metabolic pathways and biochemical activities. The sub-cellular involvement of bulk and nSe in the mitigation of HS via regulation of stress-responsive mechanisms is shown in Table 8.2. To elucidate the genetic and molecular basis of thermotolerance in crops, the identification of Se-induced genes involved in HS tolerance is of primary importance. In this context, the exogenous nSe caused up-regulation of the dehydration-responsive element-binding (DREB1A) transcription factor leading to downstream signalling cascades and subsequent stress tolerance mechanisms (Abedi et al. 2021). Different concentrations of nSe up-regulated the expression of the *DREB1A* gene by 43.7- and 36-fold; *PAL* gene expression by 20-fold, and *HCT1* gene expression by about 35–37-fold (Abedi et al. 2021). Transcriptomic studies in *Arabidopsis thaliana* revealed DREB transcription factors are Se-responsive (Van Hoewyk et al. 2005). Likewise, the exogenous Se led to the over-expression of transcription factors viz. DREB2A and N-acetyl cysteine (NAC5) (Khattab et al. 2014). Since the expression of *DREB* genes is linked to diverse phytohormones and stress-responsive networks (Xu et al. 2017; Kudo et al. 2017), the increased expression of these genes/transcription factors could result in plant tolerance to abiotic stresses, including HS.

Interestingly, Se-mediated increased expression of genes linked to antioxidants (SOD, CAT, POD, GR, and GST), secondary metabolism (PAL and CHS) has been

Table 8.2 Induction of heat stress tolerance by exogenous application of selenium (Se) and selenium nanoparticles (nSe)

Se source and concentration	Application method	Particle size (nm)	Plant species	Mechanisms	References
nSe (50, 100, 150, 200 mg L^{-1})	Foliar	50–200	*Chrysanthemum morifolium* Ramat	Low concentrations increased activities of antioxidant enzymes (CAT, POD) while all used concentrations decreased polyphenol oxidase and electrolyte leakage	Seliem et al. (2020)
nSe (0, 5, 10, 50 mg L^{-1})	Foliar	10-45	*Triticum aestivum* L.	Altered expression of heat shock factor A4A and high molecular weight glutenin subunit 1Bx; changed nitrate reductase activity	Safari et al. (2018)
nSe (50, 100 mg L^{-1})	Nutrient medium	10–40	*Sorghum bicolor* (L.) Moench	Improved antioxidant enzymes activity; reduced the concentration of oxidants; improved pollen germination percentage and seed yield	Djanaguiraman et al. (2018)
Sodium selenate (Na_2SeO_4) (75 mg L^{-1})	Foliar	–	*Sorghumbicolor* (L.) Moench	Decreased membrane damage; enhanced antioxidant defense; higher grain yield	Djanaguiraman et al. (2010)
nSe (25 mg L^{-1})	Foliar	–	*Cucumis sativus* L.	Improved chlorophyll and proline content; promotes biostimulant effect on plant growth; reduced electrolyte leakage; enhanced antioxidant defence system	Shalaby et al. (2021)

(continued)

Table 8.2 (continued)

Se source and concentration	Application method	Particle size (nm)	Plant species	Mechanisms	References
Bio-nSe (100 μgmL^{-1})	Foliar	46	*Triticum aestivum* L.	Scavenged DPPḢ and ABTṠ radicals; increased photosynthetic pigments and gas exchange parameters	El-Saadony et al. (2021)
Sodium selenate (Na_2SeO_4) (1 mM)	Growth media	–	*Nicotiana tabacum*L. cv Bright-Yellow 2	Reduced cell death and protease activity; lowered MDA; diminished accumulation of microsomal BiP and mitochondrial Hsp90	Malerba and Cerana (2018)
Se (2.5, 5 and 8 μM)	Nutrient medium	–	*Lycopersicum esculentum* Mill. cv. 'Halil	Enhanced photosynthetic parameters, respiration, and mesophyll conductance	Haghighi and Abolghasemi (2018)
nSe (1, 4, 8, and 12 μM)	Nutrient medium	–			
nSe (0, 3, and 10 mg L^{-1})	Nutrient medium	10–40	*Lycopersicum esculentum*	Enhanced fruit production and postharvest longevity; stimulated expression of basic leucine zipper (bZIP) and carotene isomerase	Neysanian et al. (2020)
Sodium selenate (Na_2SeO_4) (0, 3 and 10 mg L^{-1})		–			
Sodium selenate (Na_2SeO_4) (0, 2 and 4 mg L^{-1})	Foliar		*Triticum aestivum* L.	Increased enzymatic and non-enzymatic (ascorbicacid, carotenoids, anthocyanins contents) antioxidants	Iqbal et al. (2015)
Se (0, 50, 100, and 150 mg L^{-1})	Foliar		*Gossypium hirsutum* L.	Improved fibre quality and cotton yield	Saleem et al. (2021)

(continued)

Table 8.2 (continued)

Se source and concentration	Application method	Particle size (nm)	Plant species	Mechanisms	References
Sodium selenite (Na_2SeO_3) (5–15 μM)	Nutrient medium		*Zea mays*	Regulation of glutathione-ascorbate cycle by modulating glutathione reductase activity	Yildiztugay et al. (2017)
Sodium selenite (Na_2SeO_3) (0, 0.2, 0.7, and 0.8 mg L^{-1})	Foliar		*Cucumis sativus* L.	Increased biomass and leaf area	Kazmi and Hussain (2020)
Se (2–10 μM)	Foliar		*Cucumis sativus* L.	Improvement in growth, photosynthetic traits, chlorophyll, and osmolyte content; enhanced antioxidant enzyme activities	Balal et al. (2016)

reported in *Brassica juncea* (Handa et al. 2019). Another evidence suggested Se-mediated upregulation of an ethylene-responsive transcription factor (ERF96) that improved antioxidant capacity in *Arabidopsis* (Jiang et al. 2020). In response to the nSe treatments, the wheat plants synthesized a heat shock factor (HSFA4A) linked to the H_2O_2-mediated signal transduction and redox regulation (Safari et al. 2018). A positive relationship of Se on the expression of genes related to flavonoids biosynthesis (Xu et al. 2008; Li et al. 2019), and nSE-induced positive regulation of *PAL*, *COMT*, *CAD*, and *F6H* genesis reported (Deng et al. 2021). The expression of *F3H* and *F6H* genes are required for the biosynthesis of flavonoids, and the nSe application directly promoted gene expression of *FMO*, *C3'H*, and *IGS* involved in the flavonoids biosynthesis in *Ginkgo biloba* (Shen et al. 2006; Deng et al. 2021). The inorganic Se also up-regulated the expression of different genes including *CCR, HCT*, *C3'H*, *CCoAOMT*, *CYP,* and *DFR,* linked to plant secondary metabolism (Deng et al. 2021). The expression of both the *HCT1*, *HQT1,* and *PAL* genes is linked with the phenylpropanoid pathway and enhanced synthesis of secondary metabolites in Se-treated plants (Li et al. 2020a, b; Abedi et al. 2021). Consistent with these reports, the bitter melon, and pepper plants treated with nSe exhibited increased WRKY1 and bZIP transcription factor levels and subsequent regulation of secondary metabolites (Rajaee et al. 2020; Sotoodehnia-Korani et al. 2020). Likewise, Se-mediated enhanced expression of *NCDE1/NCDE2* genes has been reported which contributed to lower ROS/RNS levels, ABA synthesis, and higher proline accumulation (Li et al. 2020a, b).

8.5 Conclusions

The exogenous application of both Se and nSe has been shown to alter nutrient uptake, antioxidative potential, photosynthesis, and metabolism in different plants. Such beneficial effects of Se and nSe are reported to improve growth and productivity under both normal and stressed conditions. Overall, different Se forms regulate a plethora of molecular and physiological mechanisms and subsequently the levels of primary and secondary metabolites that could induce HS tolerance in plants. In this context, low concentrations of both Se and nSe mostly ≤ 2 mg L^{-1} have been suggested for better growth and productivity irrespective of growth conditions. However, for synthesis of secondary metabolites and improving the nutraceutical value of crops, higher concentrations of nSe ≤ 50 mg L^{-1} are suggested for various crops. Thus, the optimization of concentration coupled with the mode of exogenous application could be investigated in the future for various crops and under different environmental conditions to get consistent benefits from the exogenous application of Se and nSe, especially under HS.

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Chapter 9
Selenium- and Nano-Selenium-Mediated Cold-Stress Tolerance in Crop Plants

Huang Chongping, Huang Wenjie, and Liao Junlin

9.1 Introduction

9.1.1 Low-Temperature Stress

Low temperature is an abiotic environmental stress often encountered in plant growth that leads to plant metabolic disorders. It not only reduces plant yields, but it can also cause plant death in serious cases. Based on the different degrees of plant damage, low-temperature stress can be divided into two categories: chilling stress when the environmental temperature is above 0 °C and freezing stress when the environmental temperature is less than 0 °C (Yamamoto et al. 2012). For crops of tropical and subtropical origin, such as rice, corn, and soybean, a temperature less than 10 °C or 12 °C will cause low-temperature damage. Additionally, temperatures of less than 15 °C and 23 °C stop vegetative growth and pollen abortion, respectively, resulting in grain-filling failure and yield reduction or extinction (Keshavkant and Naithani 2001; Song et al. 2012). Even for winter crops of temperate and northern subtropical regions, such as barley, wheat, grape, and strawberry, chilling stress has adverse effects, especially at low temperatures between 0 °C and 5 °C or less than 0 °C in the spring season, sometimes causing serious losses (Huang et al. 2016). Therefore, low-temperature stress is a concerning environmental factor in agricultural production.

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M. A. Hossain et al. (eds.), *Selenium and Nano-Selenium in Environmental Stress Management and Crop Quality Improvement*, Sustainable Plant Nutrition in a Changing World, https://doi.org/10.1007/978-3-031-07063-1_9

The degree of plant damage resulting from a low temperature is affected by two factors. The degree of the low temperature (how cold the low temperature becomes) and the duration (how long the plant is exposed to the low temperature). The lower the temperature and the longer the duration, the greater the plant damage.

9.1.2 Selenium and Nano-Selenium

Selenium is located in the VIA group of the fourth cycle of the periodic table of chemical elements. It is in the same group as oxygen and sulfur, and its physical and chemical properties are similar to those of sulfur. It is an essential nutrient element for humans and animals, and it is a beneficial nutrient element for plants (Ellis and Salt 2003). Selenium can be divided into its physical and chemical forms in accordance with its nature and state. The physical form includes ordinary and nano-selenium. The chemical form is divided into inorganic and organic selenium. In nature, selenium exists in the inorganic chemical form and as plant-active selenium. Inorganic selenium refers to sodium selenite and sodium selenate; plant-active selenium is formed by combining selenium with amino acids through biological transformation. It mainly exists in the form of selenomethionine. An appropriate concentration of selenium plays an important role in plant growth, the antioxidant system, and the photosynthetic system, as well as in producing osmotic adjustment substances (Gupta and Gupta 2017).

Under low-temperature stress conditions, plant growth status and physiological and biochemical indicators are affected, as is photosynthetic respiration. In addition, cell structure damage occurs and antioxidant system activity is reduced. Appropriate amounts of selenium and nano-selenium improve plant performances under low-temperature stress conditions. The chlorophyll and proline contents increase, the malondialdehyde (MDA) content decreases, and the level of active oxygen is adjusted, thereby alleviating the damage to plants caused by low-temperature exposure (Zhang et al. 2013).

9.2 The Responses of Plants to Low-Temperature Stress

9.2.1 Impacts on Plant Morphology and Growth

9.2.1.1 Changes in Plant Morphology

Under low-temperature stress conditions, the most intuitive effect is the changes in plant biological characteristics. The external morphology of plant bodies revealed that the tissues are soft, part or all of the leaves are water-stained, and the leaf or fruit surfaces appear brown, yellow, spotted, and chlorotic. In extreme cases, withering or shedding and death occur (Gao et al. 2011; Tan et al. 2012).

9.2.1.2 Changes in Plant Growth and Development

Low-temperature stress causes adverse effects during the entire growth and development process of plants, including seed germination, seedling and plant growth, and flowering and fruiting, as well as quality-related trait formation. The degree of chilling damage to the plant body depends not only on the degree of the low temperature, but also on the length of the low-temperature exposure. The colder the low temperature and the longer the exposure, the lower the viability of cell protoplasm and the greater the inhibition of plant growth. If the low temperature lasts too long or the temperature is too cold, then it will delay plant growth and development, which will cause a decline in the yield, and may even lead to plant death in severe cases. However, rice and tomato crops undergo low-temperature acclimation after 48- or 72-h chilling treatments, which leads to increases in chilling tolerance (Kato-Noguchi 2007; Zhou et al. 2012).

9.2.2 Impacts on Plant Membrane System

The plant membrane system includes the cell membrane, cell nuclear membrane, chloroplast, and mitochondrial membrane. They work closely together during plant growth and development, cooperate with each other, and undertake various physiological functions. In addition, they complete necessary physiological and morphological processes, such as photosynthesis, respiration, cell division, flowering, and fruiting. The membrane system is the plant component most vulnerable to low temperature- and drought-related injury (Duan et al. 2012; Huang et al. 2020).

The cell membrane system is the first plant part damaged by chilling and (or) freezing stress. Low temperatures cause the breakdown of thylakoid structures in plant cells, reduce the selectivity of plant membranes and cause the intracellular solutions to extravasate. Under strong freezing-stress conditions, extracellular and intracellular freezing occurs. The intracellular water flows out through the plasma membrane, and the ice crystals formed outside the cell pierce the cell wall or cell membrane, which causes cell rupture, leading to severe cellular dehydration and to structural and functional membrane damage (Gurme et al. 2021).

Impacts on membrane components: Exposure to low-temperature conditions alters membrane lipid components. To improve cold resistance, the contents and proportions of unsaturated fatty acids must be increased. When plants are under low-temperature conditions, the numbers of carbon atoms and carbon–carbon double bonds in the lipid membrane will change, which is conducive to directly controlling the membrane’s structure and function to adapt to the low-temperature environment. As the temperature decreases, fatty acid desaturases are activated, the fatty acid composition changes greatly, and more unsaturated fatty acids are metabolized to produce more unsaturated fatty acids. Unsaturated fatty acids bind to the cell surface, preventing the permeation of water molecules and regulating the phase-transition temperature of the plasma membrane. The increase in their content increases the plant's ability to resist chilling and freezing damage (Erdal 2012).

Impacts on the membrane lipid phase: When plants encounter a low-temperature stress, a series of physiological, biochemical, and physical changes occur in the cell, which reduce the fluidity of the membrane, and the membrane lipid undergoes a phase change, changing from the original disordered state to an ordered state, and from the liquid crystal state to the gel state. Some areas in the membrane lipid bilayer enter a solid phase, separate from the membrane lipid. Thus, the structure of the membrane lipid is changed, which destroys the structural and functional unity (Sun et al. 2011). As the unsaturated fatty acid content in the lipid component of the cell membrane increases, which increases the membrane lipid unsaturation, the morphology of the protoplasts also changes accordingly to maintain the active liquid crystal state and maintain the normal life activities of the plant (Hassanein et al. 2021).

Impacts on the protective enzyme systems: Owing to low-temperature stress, the active oxygen metabolic balance in the cell is destroyed, resulting in the production of reactive oxygen species (ROS), including active oxygen and superoxide free radicals, and the reduction of antioxidant enzyme activity levels (Huang et al. 2016, 2018). The accumulation of ROS under low-temperature stress induces membrane lipid peroxidation in the plant cell membrane system, destroys the membrane structure, and causes the substances in the membrane to leak out, thereby inflicting low-temperature damage (Li et al. 2013). The penetration of the cell membrane causes a large amount of external calcium to enter the cytoplasmic matrix. The combination of calcium ions and calmodulin activates phospholipase A2, resulting in the release of unsaturated fatty acids, which are under the action of lipoxygenase. Consequently, unsaturated fatty acids form hydroxyperoxides, which can spontaneously decompose MDA. Its presence causes membrane damage and leakage, which allows more calcium ions to enter the cell, and this eventually results in phospholipid degradation. Then, the cell membrane collapses (Ruelland and Collin 2012).

9.2.3 Impacts on Photosynthesis and Respiration

9.2.3.1 Impacts on Photosynthesis

Low-temperature stress leads to a decline in the photosynthetic intensity of a plant. It has significant impacts on a series of important physiological and biochemical parameters, such as plant photosynthetic pigment content and chloroplast submicroscopic structure, and processes, such as photosynthetic energy metabolism and photosynthesis system II (PSII) activity (Zhou et al. 2012).

Under low-temperature stress conditions, the chlorophyll fluorescence and photosynthetic quantum efficiency are rapidly inhibited, and the inhibition increases with a greater degree of low-temperature stress. Analyses of weakening chloroplast fluorescence under low-temperature stress revealed that the site of low-temperature damage may be PSII in the transmission chain. Under low-temperature stress conditions, the abilities of plants to quench excitation energy are inhibited. A low-light intensity also causes an excess of excitation energy, which affects the transmission of light energy and causes peroxidation, resulting in an impaired PSII activity level (Zhou et al. 2012; Huang et al. 2016).

Low temperatures lead to plant photoinhibition and even photooxidation, which may result from the relatively high plant chloroplast-encoded D1 protein synthesis rate under normal temperature conditions, whereas under low-temperature stress, the chloroplast-encoded D1 protein synthesis rate is relatively low. Low temperatures inhibit PS repair by inhibiting protein degrading enzyme activity levels and DI protein synthesis, leading to increased photoinhibition (Huang et al. 2016). Chilling damage inhibits chlorophyll synthesis, resulting in the destruction of chloroplast structures, a reduced photosynthesis rate, and abnormal respiration.

Chen (1998) reported that the photosynthetic rate of bananas decreases rapidly under low-temperature stress. The photosynthetic rates are 27%, 16.2%, and 13.4% of the control at 2, 5, and 8 d, respectively, after a 10 °C low-temperature treatment compared with control 25 °C normal conditions. In mulberry, low-temperature treatments (10–12 °C, 3 d) significantly decrease the net photosynthetic rate by 22.1% (Liu et al. 2019). Low-temperature treatments significantly reduce the net photosynthetic rate of Wenzhou mandarin orange leaves at a saturated CO_2 concentration, implying that the ribulose 1,5-diphosphate carboxylase regeneration rate in the leaves is affected, and the decrease in the initial slope of the CO_2 concentration curve and net photosynthetic rate indicate a decrease in ribulose 1,5-diphosphate carboxylase activity. The chlorophyll fluorescence parameter Fv/Fm indicates the original light energy conversion efficiency of PSII. Under low-temperature stress, the Fv/Fm of Wenzhou mandarin orange significantly decreases (Guo et al. 1998).

9.2.3.2 Impacts on Respiration

Under low-temperature stress conditions, within a certain temperature range, plant respiration decreases along with the temperature. The respiration increases during the initial stage of low-temperature stress and then decreases. Additionally, the mitochondrial structures are damaged to varying degrees (Hu et al. 2006).

At a low temperature of 4 ± 1 °C, the breath intensity of rubber continues to decrease as the low-temperature treatment time increases (Li et al. 1994)., Microscopic observations of corn mitochondria under low-temperature stress conditions have revealed that the inner and outer double membranes are damaged. The ridge structure is blurred, the nuclear mimicking disappears, the mitochondrial profile is in a disordered state, the cytoplasmic membrane is broken or the double-layered membrane structure is blurred, the plasmodesmata are enlarged and deformed, and even the connection with the plasma membrane is broken and rough (Zhang et al. 1995). The endoplasmic reticulum curls into a hollow circle and the starch grains are broken, deformed, or fused together.

9.2.4 Impacts on Plant Endogenous Hormones

The changes in plant endogenous hormones under low-temperature stress are closely related to cold resistance and tolerance. Both ABA and GA play important roles in the cold resistance of plants. Maintaining a high ABA level and ABA/GA ratio under low-temperature stress conditions is of great significance for resisting related damage.

Higher ABA levels, lower GA levels, and higher ABA/GA ratios are the inherent reasons for the cold resistance of grafted cucumber seedlings. Additionally, the GA content is the same after exposure to different treatments. Under low-temperature and weak-light conditions, resulting in greenhouse tomatoes experiencing low-temperature stress, the ABA content increases, and the IAA and GA contents decrease. The contents undergo different changes in different varieties. Thus, the changes in some endogenous hormones are active adaptive processes in plants responding to low temperature-related adversity (Gonzalez-Villagra et al. 2021).

9.2.5 Effects on Plant Soluble Sugars

Soluble sugars accumulate and protect plants against cold damage under low-temperature stress (Chen et al. 2014). As an osmotic protective substance, soluble sugars increase the cell sap concentration and the non-icing water in the cell water-holding tissues, and they reduce the cytoplasmic water content. The increased soluble sugars decrease the freezing point and buffer the excessive dehydration of the cytoplasm, protect the cytoplasmic colloid from freezing and solidification, and generate energy and protective substances through metabolism. There is a positive correlation between the soluble sugar content and the cold resistance of plants.

As the treatment temperature decreases, the soluble sugar content in tomatoes gradually increases, and the increase in cold-tolerant varieties is greater than that of non-cold-tolerant varieties. A selenium treatment increases the soluble sugar contents of *Jatropha curcas* (Wang et al. 2018).

9.2.6 Effects on Amino Acids in Plants

Under normal conditions, the free amino acid contents in plants are very low, but under low-temperature stress conditions, the free amino acid contents rise rapidly, which increases the cell sap concentration, providing a collateral protective effect on the cells. In addition, free amino acids have a strong affinity, which affects the water retention capacity and colloidal stability of the protoplasm. Among the free amino acids, the relationship between proline and plant cold resistance has received widespread attention. Proline contains imino groups, and its hydrophobic pyrrolidine ring can bind to the hydrophobic region of the protein, whereas the hydrophilic groups are distributed on the surface. This increases the protein's hydrophilic surface and improves its solubility, thereby increasing the soluble protein content and maintaining the enzyme's conformation at a low temperature (Tan et al. 2012).

9.2.7 Effects on Plant Soluble Proteins

In plants, there is a close relationship between the soluble protein content and cold resistance. The hydrocolloids of soluble proteins are strong, which significantly enhances the cell's water-holding capacity. Under low-temperature stress, the soluble protein content of plants increases, which allows plants to retain more water and reduce their probability of death owing to protoplasm icing (Gao et al. 2011; Hassanein et al. 2021).

The treatment of *Dendrobium officinale* seedlings with low-concentration Na_2SeO_3 solutions significantly increases the soluble protein, free amino acid, and soluble sugar contents (Zhang et al. 2013). An analysis of rice thylakoid membrane protein components showed that the increases in the soluble protein contents at low temperatures may result from a decrease in the degradation rate or an enhancement of synthesis (He et al. 1999).

9.3 The Influence of Selenium and Nano-Selenium on Sulfur Metabolism

Although selenium is not an essential nutrient element for plants, it effectively participates in plant metabolism and has a significant alleviation effect when plants are under low-temperature stress (Feng et al. 2013; Huang et al. 2018). Nano-selenium is a nano-scale single particle that is stable and has high biological activity (Ghasemian et al. 2021). Compared with inorganic selenium, such as selenite, at the same concentration, nano-selenium is less toxic, In addition, nano-selenium can be more effectively used by organisms than inorganic or organic selenium (Hu et al. 2012).

Selenium and sulfur are elements of the same group. Sulfate and selenate have similar chemical properties. Sulfur is an important factor that affects the plant root absorption of selenium (Gupta and Gupta 2017).

At low levels, sulfur has an antagonistic effect on selenate, whereas sulfur has little effect on the absorption of selenite or selenomethionine (Djanaguiraman et al. 2010). Selenium can replace the sulfur in the sulfhydryl group of three seleno-sulfur-containing amino acids to participate in protein synthesis, thereby affecting the nitrogen, sulfur, and amino acid metabolism of plants (Feng et al. 2013; Huang et al. 2018).

The effects of exogenous sulfur on the absorption and accumulation of selenium in tobacco are dependent on the growth stage when applied, the organs exposed and the selenium and sulfur concentrations in the plants. In the early stages of tobacco growth, selenium accumulation in the whole plant and above-ground part occurs under low sulfur (75 $\mu g \cdot g^{-1}$) conditions. The accumulation of exogenous selenium in tobacco decreases as the sulfur application increases, and it has an antagonistic effect. When no exogenous selenium is applied, sulfur applications reduce the selenium content of mature tobacco leaves, revealing a selenium–sulfur antagonistic effect. When selenium is applied, the selenium content of mature tobacco leaves increases along with the sulfur application, revealing a selenium–sulfur synergistic effect (Ma et al. 2001).

When using a low-sulfur nutrient solution, selenium applications promote the absorption of sulfate ions by barley and rice seedlings, whereas sulfur starvation promotes the absorption and transportation of selenium by tomato roots. Thus, there is a relationship between selenium and sulfur that is both synergistic and mutually antagonistic (Ellis et al. 2003).

Compared with inorganic selenium, nano-selenium is more easily absorbed and used in plant metabolism, and it plays an important role in alleviating abiotic stress (Ghasemian et al. 2021).

9.4 The Mitigation Effects of Selenium and Nano-Selenium on Low-Temperature Stress

9.4.1 Regulating the Proline and MDA Contents

Under short-term low-temperature stress conditions, selenium applications can significantly increase the proline content and reduce the MDA content, thereby alleviating low-temperature stress-related damage. Proline metabolism is a typical biochemical adaptive mechanism of plants under stress conditions. Proline may function to improve plant tolerance by protecting the mitochondrial electron transport chilling chains in plants, as well as inducing the production of protective proteins and antioxidant enzymes. It aids in increasing the contents of protective substances, such as ubiquitin and dehydrin, and the activation of the corresponding anti-stress metabolic pathways (Zhang et al. 2013). Selenium applications increase the proline content and reduce the MDA content in plants, because the appropriate amount of selenium enhances glutathione peroxidase system (GSH-Px) activity and effectively reduces lipid peroxidation (Huang et al. 2018).

Appropriate selenium applications on sweet potato significantly increase the biomass, peroxidase activity, and net photosynthetic rates of the plants when under drought stress, whereas they significantly decrease the MDA level (Huang et al. 2020).

9.4.2 Promoting Protein Metabolism

It is generally believed that selenium promotes protein synthesis and metabolism in two ways. One is that inorganic selenium partially replaces the sulfur in the sulfhydryl (-SH) groups, resulting in three seleno-sulfur-containing amino acids (selenomethionine after entering the plant body, selenocysteine, and selenocysteine) that are involved in protein synthesis, thereby reducing the cysteine and methionine contents in the free amino acids. Second, selenium may be a necessary component of a tRNA ribonucleic acid chain in plants. tRNA containing selenocysteine residues exists in plants, and its main physiological function is to transport amino acids for use in proteins synthesis.

After a 10-day $^{75}Se^{4+}$ solution treatment on wheat and three kinds of pastures, 60–80% of selenium was involved in protein functions, whereas 20–30% was contained in various selenium-containing amino acids (Shang et al. 1998). In soybeans exposed to different selenium levels, 42.6–62.6% of the selenium is bound to water-soluble proteins, and protein is the main selenium-enriched component (Xie et al. 1995). Thus, selenium participates in protein synthesis and metabolism in plants.

9.4.3 Regulating Photosynthesis

Many studies show that the application of appropriate concentration selenium or nano-selenium solution can alleviate the adverse impacts when plants are exposed to low-temperature environments (Feng et al. 2013; Zhang et al. 2013). It was reported that exposure of strawberry plants to chilling stress decreased the net photosynthetic rate (Pn) (Huang et al. 2018). However, this effect could be removed by applying exogenous Se. Seedling leaves receiving different concentrations 2.5, 5, and 10 $mg{\cdot}L^{-1}$ of exogenous Se demonstrated significant increases in the Pn of 66.07%, 102.60%, and 96.18%, respectively, for Akihime, and 13.90%, 52.70%, and 6.42%, respectively, for Benihoppe, at the beginning of chilling stress (0 h) when compared with CK. With extended low-temperature exposure, the Pn decreased gradually and the application of Se retarded this decline. After 6 h of chilling stress, the Pn values of Akihime leaves in treatments of 2.5 and 5 $mg{\cdot}L^{-1}$ were significantly greater than that of the control group, increasing by 32.93% and 30.87%, respectively. After the 12-h treatment, 2.5 and 5 $mg{\cdot}L^{-1}$ increased by 28.32% and 35.27%, respectively, compared with CK. The detailed information is shown in Fig. 9.1.

The stomatal conductance (Gs) and intercellular CO_2 concentration (Ci) are closely related Pn. The Gs of strawberry leaves decreased as the exposure time to low temperature increased from 0 to 12 h. Foliar sprays containing different Se concentrations could alleviate the decline of Gs in strawberry seedlings' leaves under chilling stress. The Ci increased as the exposure time to low temperature increased from 0 to 12 h. Exposure to exogenous Se resulted in a significant decrease

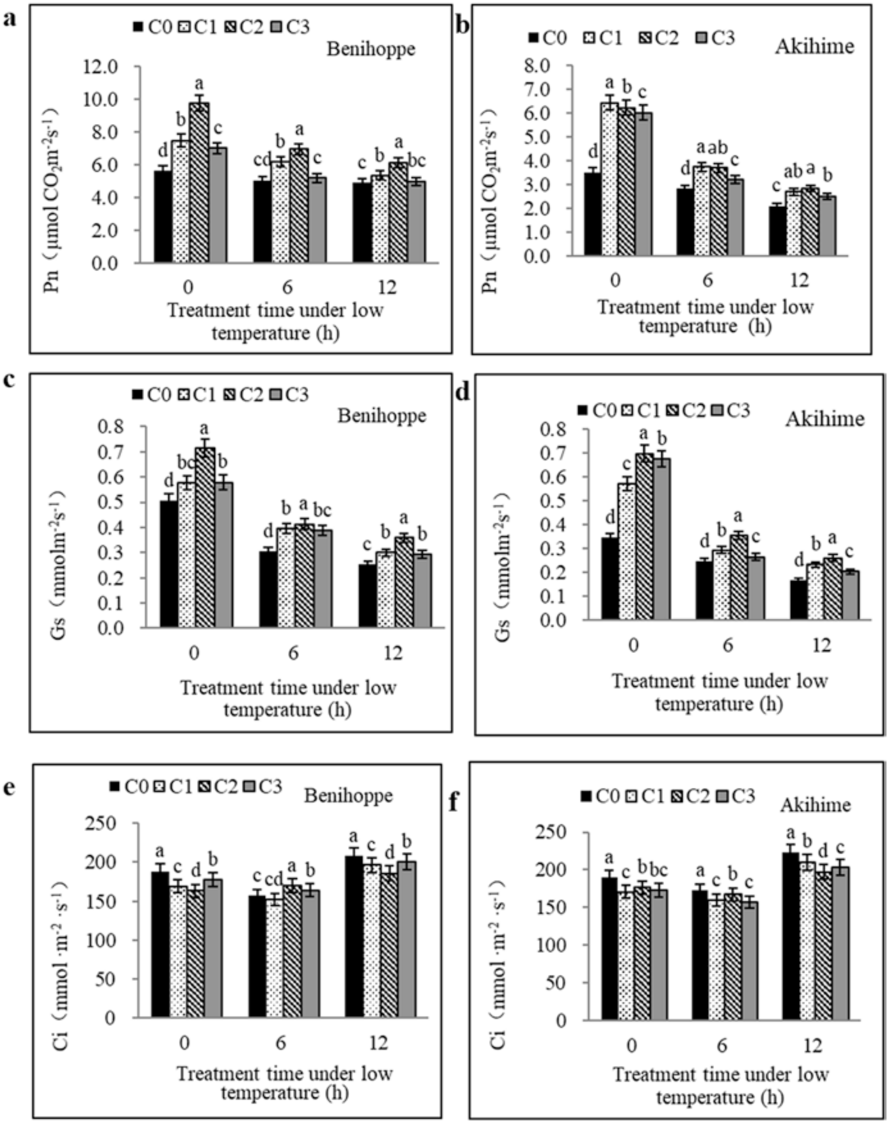

Fig. 9.1 Effects of different exogenous Se treatments (C0, 0 mg·L^{-1}; C1, 2.5 mg·L^{-1}; C2, 5 mg·L^{-1}; C3, 10 mg·L^{-1}) on net photosynthetic rate (Pn) (**a**, **b**), stomatal conductance (Gs) (**c**, **d**) and intercellular CO_2 concentration (Ci) (**e**, **f**) in leaves of two strawberry varieties under chilling stress. Bars with different letters are significantly different at the 0.05 level (LSD test). (Huang et al. 2018)

in Ci values compared with the control. For Akihime treated at 0 °C for 6 h, the Ci values of exogenous Se-treated (2.5, 5, and 10 mg·L^{-1}) strawberry leaves decreased by 8.40%, 13.77%, and 8.03%, respectively, when compared with CK. As the treatment time extended to 12 h, the leaf Ci values increased further. Applications of exogenous Se had significant stimulatory effects on Ci values. The 2.5 and 5 $\text{mg}\cdot\text{L}^{-1}$ concentrations had greater effects on both strawberry varieties than the 10 $\text{mg}\cdot\text{L}^{-1}$ concentration.

9.4.4 Regulating Respiratory Metabolism

Both the mitochondrial respiration rate and the chloroplast electron transfer rate are significantly related to the presence or absence of selenium and its level. Within a certain range (below 0.10 $\text{mg}\cdot\text{L}^{-1}$), selenium enhances the mitochondrial respiration rate and the chloroplast electron transfer rate. However, at a higher concentration ($\geq$ 1 $\text{mg}\cdot\text{L}^{-1}$), these rates decrease, indicating that selenium may be involved in energy metabolic processes in plants (Wu et al. 2000).

A low concentration of sodium selenite has a certain stimulatory effect on the respiratory rate of barley, whereas a high concentration inhibits respiration. As the sodium selenite concentration increases, the inhibitory effect becomes more obvious. When the sodium selenite concentration reaches an upper limit, the structures of the cell membrane and mitochondria are destroyed, inhibiting enzyme activity and hindering the transmission of electrons in the respiration process. Thus, the cells are basically in a dead state, and the respiratory rate is reduced (Wang et al. 2002).

9.4.5 Promoting Chlorophyll Synthesis and Metabolism

Appropriate selenium concentrations effectively enhance plant photosynthesis and increase the chlorophyll content. This may be achieved by promoting the absorption of mineral elements (e.g., P, K, Ca, Mg) related to chlorophyll synthesis by plants. Additionally, selenium stimulates the respiratory rate and the electron flow of the respiratory chain, and it can protect chloroplast enzymes. Furthermore, selenium affects the interaction of 5-aminolevulinic acid dehydratase with -SH and porphobilinogen deaminase, which regulate chlorophyll synthesis (Gupta and Gupta 2017).

Selenium may be involved in energy metabolic processes in plants. Selenium and sulfur have similar chemical properties, and there may be selenoproteins, like thioredoxin and iron-sulfur protein, in plants that can be used in photosynthesis and respiration. Additionally, it may play a similar role in transmission (Zhang et al. 2013).

Low temperatures and weak light significantly reduce strawberry seedling growth and related parameters, such as leaf chlorophyll content and photosynthetic rate, and an appropriate amount of selenium enhances strawberry chlorophyll synthesis. Foliar applications of selenium also increase the chlorophyll contents in plants. For example, when the concentration of selenium sprayed on carrot leaves is lower than 10 mg·L^{-1}, the chlorophyll content of the carrots is significantly higher than that of the control (Huang et al. 2018).

The chlorophyll content in leaves of *Nicotiana tabacum* seedlings was significantly positively correlated with the applied selenium concentration. In wheat, sodium selenite treatments revealed that selenium contributes to the accumulation of chlorophyll in the leaves and the formation of its precursor 5-aminolevulinic acid (Han et al. 2013). In soybean treated with relatively high selenium concentrations, selenium regulates the chlorophyll level through the interaction of 5-aminolevulinic acid dehydratase with -SH and porphobilinogen deaminase synthesis (Feng et al. 2013). Thus, selenium promotes and regulates the synthesis and metabolism of chlorophyll.

9.4.6 Promoting Plant Antioxidant Systems

The main biological function of selenium in animals and humans is as a component of the glutathione peroxidase system, which participates in redox reactions in the body, removes free radicals, such as lipid peroxides, and reduces peroxidative damage to the body caused by biofilms. A large number of free radicals are also produced during higher plant metabolic processes and in response to environmental stresses. These free radicals can be eliminated by corresponding enzyme systems, such as superoxide dismutase and catalase (CAT), and they can also be cleared by GSH-Px. GSH-Px has been detected in different tissues of different types of plants, and selenium applications enhance the GSH-Px activity levels in plant tissues, thereby confirming that selenium has antioxidant effects in plants (Huang et al. 2018).

In rice, sorghum, and wheat crops, selenium can increase the antioxidant capacity, improve resistance and anti-senescence abilities, and ensure normal plant growth (Peng et al. 1997; Djanaguiraman et al. 2010; Chu et al. 2010). In tomatoes grown under salt stress conditions, the application of selenium significantly increases the GSH-Px activity in plant leaves and significantly reduces the MDA content in tomato leaves (Diao et al. 2014). In sunflower seedlings, the content of the membrane peroxidation product MDA, the production rate of O^{2-}, and the generation of ROS all decrease as the selenium concentration increases, within an appropriate range, indicating that selenium eliminates excessive free radicals in plants (Habibi 2017).

9.4.7 Mode of Action

9.4.7.1 Antioxidant Mechanisms

Selenium mainly regulates the antioxidant system through three modes. First, it promotes the spontaneous disproportionation of O^{2-} into H_2O_2 without the catalysis of the superoxide dismutase enzyme. Second, it directly quenches O^{2-} and OH^{-1}

with selenium compounds, and third, it regulates the activities of antioxidant enzymes (Djanaguiraman et al. 2010).

Selenium is an essential component of the plant protective enzyme GSH-Px. The change in the GSH-Px activity caused by an exogenous selenium treatment affects the entire protective enzyme system in the plant. GSH-Px catalyzes the conversion of GSH into GSSH, thereby reducing toxic peroxides into non-toxic hydroxyl compounds. Additionally, it promotes the decomposition of H_2O_2 and the scavenging of lipid peroxides and other free radicals, thereby reducing the impact of ROS-associated superoxidation damage on biological membranes (Mroczek-Zdyrska et al. 2017).

Ascorbate peroxidase (APX) is a signal substance that regulates ROS, whereas CAT (mainly located in peroxisomes) may be responsible for removing excess ROS. Under stress conditions, selenium greatly increases the activity levels of APX and CAT enzymes (Habibi 2017).

9.4.7.2 The Ascorbic Acid–Glutathione (ASA–GSH) Cycle

The ASA–GSH cycle, which mainly exists in the cytoplasm and chloroplasts, is an important mechanism for removing H_2O_2 in plants, and it plays important roles in the defense of plants against abiotic stresses, such as low temperature, that cause oxidative damage (Huang et al. 2018).

Under low-temperature stress conditions, the increase in the ROS contents of plants stimulates increases in the activity levels of the corresponding enzymes in the ASA defense system, which enhances the defensive abilities of the plants. The components of the ASA–GSH cycle include ASA, GSH, APX, and monodehydroascorbate reductase. Both ASA and GSH are key non-metabolic antioxidants in plants that protect cell components from oxidative damage and are directly involved in the elimination of $O_2\cdot$- and $OH\cdot$. APX plays a key role in eliminating plant H_2O_2, and both ASA and APX jointly participate in the disproportionation of H_2O_2. H_2O_2 is reduced to H_2O and O_2 by the electrons of NADPH. GSH plays an intermediary role and is oxidized to GSSG, and ASA is oxidized to monodehydroascorbic acid, which can re-form ASA through monodehydroascorbate reductase action or non-enzymatic dismutation. Additionally, GSH-Px is reused in the ASA–GSH cycle. Selenium may partially replace the sulfur in GSH-Px, thereby promoting the ASA–GSH cycle, which then enhances the cold tolerance of plants (Gupta and Gupta 2017; Huang et al. 2018).

9.5 Selenium Regulates Chilling Injury, Low Temperature, and Gene Expression

GSH-Px is also known as selenium glutathione peroxidase because selenium is a component. Selenium regulates the stability of GSH-Px mRNA, and GSH-Px is involved in redox reactions in animals and plants. GSH-Px catalyzes GSH into

GSSH, reduces toxic peroxides to non-toxic hydroxyl compounds, promotes the decomposition of H_2O_2, removes free radicals, such as lipid peroxides, and reduces the effects of peroxidation on biofilms. Its activity level indirectly reflects the plant's ability to scavenge oxygen free radicals, and it plays an important plant protective role under low-temperature stress conditions (Qi et al. 2021).

GSH-Px has been detected in different types of plant tissues, and selenium increases the GSH-Px activity in plant tissues, thereby confirming the antioxidant effect of selenium in plants.

The antioxidant effect of selenium is closely related to GSH-Px activity and lipid peroxidation. A fluorescence quantitative PCR analysis of *GSH-Px* gene expression in potato leaves under different low-temperature stress conditions revealed that the expression level in the leaves of the selenium-sprayed plants was highest after a 3-h low-temperature stress, and as the low-temperature stress time, the expression level first increased and then decreased, while the control did not change significantly. It indicates that selenium may play a crucial role in the expression of *GSH-Px* genes (Kaur et al. 2016).

9.6 Progress in the Study of Selenium-Regulating Chilling Injury

9.6.1 Effects on Genomic Characteristics

Selenium applications significantly change the characteristics of genomics and proteomics. For tea roots treated with exogenous selenium and sulfur, 7877 differentially expressed unigenes have been screened, of which 4845 were upregulated and 3032 were downregulated. After a sulfur treatment, 2313 unigenes were differentially expressed, of which 1028 were upregulated and 1285 were downregulated. By comparing the transcriptomes after different treatments, a large number of selenium response-related genes, as well as metabolic pathway information, have been obtained. The metabolic pathways, such as cysteine and methionine metabolism, glutathione metabolism, and thiometabolism, are closely related to the selenium-based responses of tea plants. Some key genes of metabolic pathways, such as *ATPS1/3*, *APR*, *SAT*, *GS*, and *CS*, are upregulated (Hu 2016).

9.6.2 Effects on Proteomics Characteristics

Sodium selenite has physiological effects on peach and grape, with the soluble sugar, soluble protein, and chlorophyll contents in peach leaves increasing at the appropriate selenium concentration (20 $mg{\cdot}L^{-1}$). Proteomics analyses of peach leaves before and after selenium applications have been explored using sample phenol preparations, two-dimensional electrophoresis and mass spectrometry. A bioinformatics study on the differential proteins produced by selenium treatment has been performed. The results were as follows: (1) 1391 protein spots were detected in the two-dimensional electrophoresis results from normal peach leaves. A total of 1204 protein spots were detected in selenium-enriched leaves. After a selenium treatment, the strengths of 187 protein spots were reduced, and 33 protein spots showed significant qualitative and quantitative changes. Among them, 11 protein spots were upregulated, and 18 protein spots were downregulated. After a selenium treatment, 4 specific protein spots were missing from the leaves, and 23 proteins showing large expression differences and good dot types were selected for a mass spectrometry analysis. Complete peptide fingerprints were obtained. The peptide data were imported into the NCBI nr protein database, and 12 protein spots were identified. A bioinformatics analysis of the identified proteins revealed that most of their functional sites were in chloroplasts, with three protein spots belonging to the RuBisCO long-chain family. Protein spot 343 belongs to the oxygen-releasing complex of PSII, which could maintain its stability; protein spot 410 is lactyl glutathione lyase, and protein spot 853 is a dehydrated protein. The selenium treatment increased the expression levels of these proteins and promoted plant photosynthesis and stress resistance.

Haematococcus pluvialis has the ability to convert inorganic selenium into organic selenium, but its transformation mechanism and regulatory principles are not clear. To determine the physiological and biochemical effects of sodium selenite on *H. pluvialis* and the intracellular mechanism of selenium enrichment in *H. pluvialis*, protein expression mechanisms under sodium-selenite stress were analyzed using proteomics. *H. pluvialis* 192.80 was cultured for 10 d at different sodium-selenite concentrations. The growth of the algae was analyzed and the appropriate selenium-concentration gradient was determined.

The differences in protein expression in *H. pluvialis* after an exogenous selenium treatment were investigated. The main results were as follows: in the selenium and control groups, proteins were extracted using the TCA/acetone method for two-dimensional electrophoresis. A total of 40 significantly changed protein spots were obtained, of which 25 were upregulated and 15 were downregulated. The mass spectrometry revealed that 31 proteins were comparable with known proteins in the NCBI nr database, and 27 proteins were annotated to the database. The identified differential proteins are mainly involved in a series of cellular and molecular level regulatory processes that are involved in photosynthesis, antioxidation, amino acid metabolism, energy metabolism, ion transport, signal transmission, cell division, and cell repair.

In summary, selenium and nano-selenium play important roles in mediating cold-stress tolerance in crop plants. With the development of plant genomics, a deeper understanding of the mechanisms can be achieved, which will allow for better agricultural production practices.

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Chapter 10
Selenium and Nano-Selenium-Mediated Arsenic Stress Tolerance in Plants

Reshu Chauhan, Surabhi Awasthi, Pradyumna Kumar Singh, Sanjay Dwivedi, Sudhakar Srivastava, and Rudra Deo Tripathi

10.1 Introduction

Selenium (Se) is a trace element with antioxidant properties, protects cells from oxidative damage, boosts the immune system, and also reduces the risk of virus infections. Selenium is an essential nutrient element for humans and other animals and is also considered beneficial for plants (Garousi 2017). Selenium promotes plant growth by increasing the accumulation of nutrient elements, carbohydrates, enzymatic and non-enzymatic antioxidants, and phytohormones, which have attracted extensive research on the protection of plants from biotic and abiotic stresses (El-Ramady et al. 2020). The interest in the biological impact of Se on human health and the environment is increasing day by day due to the vital role of Se in various important pathways. In the human body, excessive Se changes to organic forms of Se like selenocysteine (SeCys), which is known as the 21st amino

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M. A. Hossain et al. (eds.), *Selenium and Nano-Selenium in Environmental Stress Management and Crop Quality Improvement*, Sustainable Plant Nutrition in a Changing World, https://doi.org/10.1007/978-3-031-07063-1_10

acid. Selenium is also an essential component of 25 various selenoproteins known to be present in the human body (Chauhan et al. 2019). The essentiality of Se for human health has been confirmed by various earlier studies (Ullah et al. 2019; Shahid et al. 2018; Ibrahim et al. 2019; El-Ramady et al. 2020). Selenium deficiency affects globally a billion people where the level of Se in the soil is naturally low including areas in China, Europe, New Zealand, Africa, Australia, and India (Lyons et al. 2003). Plants are the ultimate source of dietary Se intake for humans and other animals. A narrow window (as little as one order of magnitude) between essentiality and toxicity of Se is reported for most species (Reilly 2006). As a consequence, Se deficiency ($<40\ \mu g\ day^{-1}$) as well as toxicity ($>400\ \mu g\ day^{-1}$) is a common problem worldwide (Gupta and Gupta 2017). To avoid Se deficiency in humans and other animals, biofortification of crops with Se can be a promising strategy. In addition to this, for humans, Se can be added to many food supplements available in the market. Further to reduce environmental metalloid toxicity, plants may be used for phytoremediation of Se from soil and water.

Nanotechnology and its application have become widespread in different industries as well as in the field of agriculture. The use of nanoparticles to improve the quality of seeds, crop productivity, and yield is a promising area (Abdelhameed et al. 2019; Cheboi et al. 2021). Nanoparticles are also known to be involved in the synthesis of vitamins, proteins, fats, and carbohydrates and have also increased the photosynthetic rate. Metal nanoparticles can also neutralize different toxic substances present in the soil (Jiang et al. 2017; Siddiqui et al. 2021).

Selenium and nano-Se share some common and general characteristics but differ in their chemical and biological properties. The biological properties of Se and nano-Se for their use in human nutrition may also differ. The role of Se in human nutrition has been confirmed, whereas the recommended dose for daily intake, deficiency/toxicity levels of nano-Se, and the biological effects still need more investigation. Biofortification of edible foods with Se and nano-Se is a promising approach to support human health (El-Ramady et al. 2020). Leafy vegetables like spinach and lettuce, cereals, and fruits such as strawberry and pomegranate are commonly biofortified food (Golubkina et al. 2017; Mimmo et al. 2017; Leija-Martínez et al. 2018). Selenium nanoparticles exhibit lower toxicity, strong tendency to bind with reactive oxygen species, and higher bioavailability (El-Ramady et al. 2020).

Arsenic (As) is a class I human carcinogen and is highly toxic to all life forms. Arsenic accumulation in crop plants and subsequent contamination of the food chain threaten human health (Lindsay and Maathuis 2017). Exposure to As damages the human cardiovascular, neurological, hepatic, respiratory, and reproductive systems and also causes different types of cancer and skin diseases (Ali et al. 2019). Arsenic is present in both inorganic and organic forms in the environment, whereas the trivalent and pentavalent forms of As predominantly exist. Several studies showed that As exposure negatively affects plant growth through destruction in the chloroplast, deformations in root and shoot anatomy, and inhibition of photosynthesis and also affects the accumulation of essential nutrients (Chauhan et al. 2017; Awasthi et al. 2018). Contamination of As hampers physiochemical properties of soils and leads to loss of crop productivity and yield. Selenium acts as a protectant against various abiotic stresses in plants. Selenium is involved in the detoxification of heavy metals by alleviating the oxidative stress and antagonizing the uptake of heavy metals (Zhu et al. 2009). Selenium is a potent antagonist of As toxicity (Feng et al. 2013).

Therefore, the current chapter explores available information on the use of Se and nano-Se in the tolerance of As stress in different plants. The use of Se and nano-Se to promote plant growth is discussed. The current study also presents the role of Se and nano-Se to ameliorate As stress in plants and also the detailed understanding of Se-mediated amelioration of As toxicity by using omics approaches.

10.2 General Properties of Selenium and Nano-Selenium

Selenium is an essential trace element and the 67th most abundant element in Earth's crust. Selenium is involved in the metabolism of algae, prokaryotes, animals, and humans (Pilon-Smits 2019). Selenium is a metalloid that lies between As and bromine (Br) in the fourth period and VIA group [between sulfur (S) and tellurium (Te)] in the periodic table. It is chemically similar to S in respect to ionization potentials, bond energies, atomic size, electron affinities, and electronegativities. However, the main difference between Se and S is, S exists as oxidized quadrivalent form while Se as a reduced quadrivalent (Tinggi 2003). Selenium can exist in various oxidation states among which −2, 0, +2, +4, and +6 are most common valence states. The predominant available forms of Se to plants are inorganic, i.e., selenite (Se IV) and selenate (SeVI) (Schiavon and Pilon-Smits 2017; Chauhan et al. 2019). Selenium is a highly useful element and is globally used in various sectors such as electronics, pharmaceuticals, glass industry, paints and enamels, rubbers, plastics, and inks (Fig. 10.1). Main source of Se deposition in soil is erosion of rocks (Shahid et al. 2018). The level of Se in soil ranges from 0.01 to 2 mg/kg with a mean concentration of 0.4 mg/kg Se in soil (Fordyce 2013). Mobility and bioavailability of Se depends on the species of Se as well as the total amount of Se present in soil (Peng et al. 2017). Selenium is more mobile under oxidizing saline conditions in comparison to reducing acidic soil conditions (Antoniadis et al. 2017). Plants have the ability to accumulate Se in different plant tissues, but the amount of accumulation depends on the type of plant or plant species (Terry et al. 2000; White 2016). Nano-Se is of bright red in color and can be defined as nano-scale Se synthesized for the use in food supplements, as Se fertilizer, and for the applications in medical therapy (Gao et al. 2002). Nano-Se, i.e., nanoform of Se, also attracts more attention due to the lower toxicity and higher bioavailability (Shi et al. 2011). The advantage of nano-Se is the possibility of using Se as elemental Se, i.e., 0 oxidation state (Se^0), that shows lowest toxicity and greater bioavailability in comparison to other oxidation states (Se^4 and Se^6). Although it is very unstable and can be transformed into an inactive form, stabilization can be achieved through encapsulation with the help of suitable nano-vehicles like chitosan (Hosnedlova et al. 2018). The biological properties of nano-Se highly depend on their size, smaller particles show higher activity.

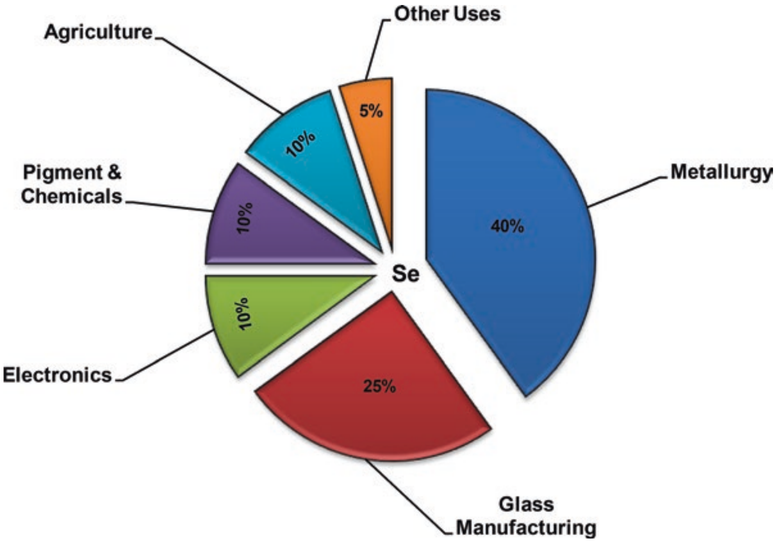

Fig. 10.1 Commercial use of Se: This figure represents the world consumption of Se in different fields. (According to United States Geological Survey; USGS 2017)

The size of nanoparticles also affects the cellular intake of nano-Se. Nano-Se has a wide range of biomedical applications. The role of nano-Se in the reduction of oxidative stress is also well reported. Nano-Se acts as a potential chemopreventive agent. Additionally, antimicrobial and antifungal activities of nano-Se as well as its protective role in metal detoxification are also reported (Yazdi et al. 2013; Hosnedlova et al. 2018; Tan et al. 2019). Selenium and nano-Se both have the potential to provide protection against oxidative stress, amelioration of environmental stress including heat stress, salinity stress, and heavy metal stress (As, Cd, and Cu), as well as also effective against cancer therapy (Djanaguiraman et al. 2018; Safari et al. 2018; Zhang et al. 2020). Prasad and Selvaraj (2014) reported that nano-Se has a potential role in protection against As-induced DNA impairment. Biosynthesized Se nanoparticle showed adsorption of Cu, Cd, and Zn. Biosynthesis of nanomaterials using plant extracts has more advantages than other biological methods because it is inexpensive and does not require any special conditions (Ramamurthy et al. 2013). The application of nano-Se for bio-fortification of crops is an effective and eco-friendly approach to minimize the Se deficiency in humans and other animals. Along with Se, the beneficial role of nano-Se is notable by fertilization of crops (Vahidi et al. 2020). Nano-Se plays an important role to regulate several physiological and biochemical processes in plants as well as in humans (Hosnedlova et al. 2018). Nano-Se has a wide application in delivery of drugs and disease diagnosis. Nano-Se is more effective than Se, thus it is preferred over other forms of Se for the treatment of various diseases like diabetes, cancer, liver fibrosis, and muscular dystrophy (Khurana et al. 2019).

10.3 Interaction of As and Se Species in Plants

Arsenic is a most toxic and carcinogenic metalloid derived from natural as well as anthropogenic sources (Awasthi et al. 2017). The pH and redox potential are primary factors that significantly control solubility as well as speciation of As in groundwater and soil (Abbas et al. 2018). In the environment, As exits in its two prevalent forms, i.e., arsenate (AsV) and arsenite (AsIII) among which AsIII is more toxic than AsV (Ahmed et al. 2022). Arsenate may replace phosphorus in DNA that disturbs phosphorylation reactions and interferes with phosphate and energy metabolism, while AsIII binds to the sulfhydryl groups of peptides and proteins and hamper their activity (Chandrakar et al. 2018). Selenium is a well-documented antagonist of As and can reduce the toxic impacts of As by scavenging and by regulation of free radicals (Chauhan et al. 2019). As discussed above, Se also exists in its different forms among which selenate (SeVI) and selenite (SeIV) are more commonly present in soil and available to plants. The interaction between As and Se is a critical factor for a detailed systematic understanding of the transportation, environmental fate, and associated toxicological effects of these metalloids in plants. The biological interactions between As and Se depend on specific biochemical forms because As and Se are metalloids with similar chemical properties that are intensely alike with different biological effects (Leybourne et al. 2022). However, the antagonistic effects or natural detoxification between As and Se have been confirmed in different plants, animals, as well as humans (Gupta and Gupta 2017; Shahid et al. 2018). Selenium-mediated amelioration of As toxicity in plants has also been confirmed by reduced As accumulation in plants and by retrieving of As-induced deficiency of nutrient elements. A marked increase in phenolic compounds, activity of enzymes of thiol metabolism, and other antioxidant enzymes like ascorbate peroxidase, catalase, guaiacol peroxidase, glutathione peroxidase on Se supplementation in rice plant inferred the role of Se as an ROS quencher, minimization of lipid peroxidation as well as in As tolerance (Chauhan et al. 2017).

The close positioning of As and Se in the periodic table shows similar electronic configuration and also the chemical characteristics. These two metalloids share the same transporter for the uptake and transportation in/within plants. Arsenite and Se (IV) both enter in plants with the help of aquaporin (Lsi1) (Ma et al. 2008; Zhang et al. 2014). Selenite also uses the transporter of As(V), i.e., phosphate transporters, for their uptake in plants (Hartley-Whitaker et al. 2002; Zhang et al. 2014). Thus, the antagonism exists between inorganic species of As and Se for the uptake and transportation in plants. Several reports inferred the role of Se in reduction of As burden in plants because of the Se as a preferable substrate for As transporters to take entry in plants (Chauhan et al. 2020; Pokhrel et al. 2020). The exposure of As damages chloroplast membrane and disturbed the photosynthetic processes as well as functionality of PS-II (Patel and Parida 2022). However, Se application during As stress is reported to repair cell integrity, recover photosynthetic efficiency, and regulate As toxicity by strengthening antioxidant potential in different plants (Table 10.1). The supplementation of Se alleviates the toxicity of As by minimizing oxidative

Table 10.1 Role of selenium and nano-selenium as a beneficial element in different plants

Plants	Findings on selenium supplementation	References
Groundnut (*Arachis hypogaea*)	Nano-Se supplementation enhanced the defense systems by activating the antioxidants under sandy soil	Hussein et al. (2019)
Wheat (*Triticum aestivum*)	Application of Se improved vegetative growth, grain yield as well as nutrient quality and nitrogen and sulfur accumulation	Lara et al. (2019), López-Bellido et al. (2019), and Boldrin et al. (2018)
Sorghum (*Sorghum bicolor*)	Application of Se and nano-Se stimulated antioxidant defense system via enhancing the activity of antioxidant enzymes	Djanaguiraman et al. (2018)
Pomegranate (*Punica granatum*)	Application of Se and nano-Se promoted maturity index and quality of fruits	Zahedi et al. (2019)
Rice (*Oryza sativa*)	Seed priming with Se improved the growth during salt stress	Subramanyam et al. (2019)
Strawberry (*Fragaria ananassa*)	Supplementation of Se in rice during different growth stages viz., seedling, tillering, booting, and mature stage, improved the accumulation of Se in the form of selenomethionine	Huang et al. (2018)
Maize (*Zea mays*)	Selenium-fortified maize improved the antioxidant content and nutraceutical value of grains and also provided salt tolerance at vegetative and reproductive stages.	Yasin et al. (2015) and Ashraf et al. (2018)
Tomato (*Solanum lycopersicum*)	Selenium reduced the cadmium uptake and also improved fruit quality and shelf life as well as storage of fruits	Lima et al. (2019) and Puccinelli et al. (2019)
Tobacco (*Nicotinia tabacum*)	Supplementation of Se and nano-Se stimulated the plant growth and root architecture	Domokos-Szabolcsy et al. (2012)

stress through the activation of genes and their respective proteins involved in the defense mechanism (Chauhan et al. 2020).

10.4 Role of Se and Nano-Se in the Defense Mechanism

Antioxidants compounds have the potential of scavenging the free radicals as well as inhibit free radicals during biochemical reactions in plants. Superoxide and hydrogen peroxide are the reaction intermediates of biochemical reactions which cause cellular damages (Devasagayam et al. 2004). Selenium acts as an antioxidant. Selenium at lower concentration is reported to act as a priming agent to enhance tolerance in plants against different abiotic stresses (Pilon-Smits et al. 2009). Selenium inhibits the accumulation of ROS like superoxide, hydrogen peroxide, singlet oxygen, hydroxyl radical, and lipid peroxide radicals during stress by acting

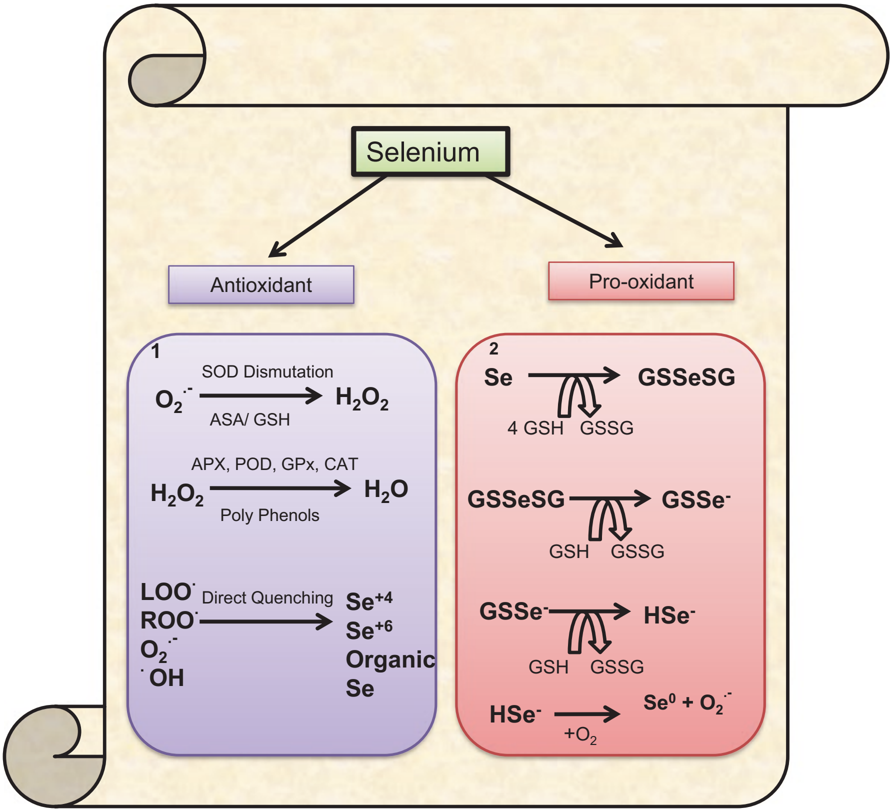

Fig. 10.2 Dose dependent behaviour of selenium: an antioxidant & pro-oxidant. 1. Selenium activates the enzymatic antioxidants [Ascorbate peroxidase (APX), Guaiacol peroxidase (POD), Glutathione peroxidase (GPx,) Catalase (CAT), Superoxide dismutase (SOD)] and non-enzymatic antioxidants [ascorbate (ASA), glutathione (GSH) and Polyphenols) to regulatereactive oxygen species (ROS) in plant cell at low dosage. Selenium also acts as a direct quencher of free radicals (LOO., ROO., O2.-, .OH). 2. Selenium also induces production of free radicals when supplies at higher concentration to plants

as a direct ROS quencher, stimulation of spontaneous dismutation of superoxide radical into hydrogen peroxide as well as by regulating non-enzymatic and enzymatic antioxidants (Feng et al. 2013). However, Se at higher concentrations also acts as a pro-oxidant, inducing an increase in ROS and lipid peroxidation (Terry et al. 2000) [Fig. 10.2]. Selenium has the potential to decrease oxidative stress by increasing the activities of antioxidant enzymes such as superoxide dismutase, peroxidase, catalase, glutathione peroxidase, etc., which leads to a decrease in reduction in lipid peroxidation (Liu et al. 2015). Zhang et al. (2019) reported that the application of selenium enhanced the biosynthesis and secretion of glutathione in

Candida utilis. The application of Se decreases the toxicity of metals such as As, Pb, Cr, and Hg in the roots of *Salvia miltiorrhiza* (Hu et al. 2015). Selenium nanoparticles in conjugation with *Cordyceps sinensis* exopolysaccharide showed enhancement of scavenging capability and superoxide anion radical (Xiao et al. 2017). Nano-selenium has a vital role in the reduction of free radicals to protect cells from damage by regulating reactive oxygen species (ROS) and glutathione peroxidases (GPx). Along with antioxidant properties, anticancer drugs, nano-selenium also increases the efficacy of these drugs. Plants mainly take up Se from soil solution in the form of selenate (SeO_4^{2-}), which is taken up inadvertently via sulfate transporters, and metabolized via the S assimilation pathway. The trace amount of selenium is important for the healthy aquatic and terrestrial environment. Nano-selenium is an effective selenium fertilizer that improves the productivity of the crop as well as effective in other fields of agriculture without compromising food security. Application of the selenium and nano-selenium not only increases the selenium content in the fruit but also induces the yield of the fruit (Yu 2005; Gao et al. 2002). Hu et al. (2008) reported an increased accumulation of Se in tea. A study by Bi et al. (2010) reported the biofortification of Se in cabbage Cao et al. (2018).

10.5 Selenium Reduces As Toxicity: Transcriptomic and Proteomic Aspect

Selenium, being an essential nutrient element and antioxidant, plays a vital role in the alleviation of As toxicity in plants (Joy et al. 2015). Pollution of As contaminates the food chain that leads to yield loss and poses health risks to humans. Integrated omics approaches and interpretation of changes in transcript and protein abundance provide a complete inventory of the genes and proteins for a detailed understanding of Se-mediated amelioration of As toxicity in plants. Selenium-mediated regulation of differential expression of As transporters confirms the Se-mediated reduction of As uptake and accumulation in rice. A study by Chauhan et al. (2020) showed higher expression of NIP1;1 in rice plants on Se supplementation during As stress which inferred the Se-mediated inhibition of upward movement of As in rice plants. Up-regulation of NIP2;1 (Lsi1), which is the main transporter for Se and As(III) transport (Zhao et al. 2010a, b), showed enhanced uptake of Se and reduced the root-to-shoot translocation of As as well as accumulation in the plant on Se supplementation during As stress. Differential expression of sulfate transporters viz., *Os03g0196000* (SULTR1;2), *Os08g0406400* (SULTR1;3), *Os01g0719300* (SULTR3;6), *Os09g0240500* (SULTR4;1), *Os10g0420400* (SULTR3;1), and *Os04g0652400* (SULTR3;3), during Se supplementation modulates uptake and transportation of As and also provides As tolerance in plants (Sengupta et al. 2011). Application of Se during As stress also showed increased abundance of the small subunit of Rubisco and chlorophyll a-b binding protein and higher expression of genes encoding these proteins which are involved in photosynthesis helped plants to gain biomass (Malik et al. 2012), thus providing tolerance

Table 10.2 Selenium-mediated modulation of gene expression involved in As detoxification

Gene name	Findings on selenium supplementation	References
OsABCG35	ABC transporters G family provides heavy metal tolerance in rice	Arenhart et al. (2014)
TIP1;2, TIP2;1; TIP2;2	Up-regulation of transporters regulates the uptake of As in the presence of selenium in rice	Chauhan et al. (2020)
SULTR1;2; SULTR1;3; SULTR3;6; SULTR4;1	Selenate and sulfate share the same transporters and regulate their uptake in *Brassica*	El-Mehdawi et al. (2018)
Os01g0702700 (OsMYB14) Os07g0634900 (OsMYB86)	MYB improved antioxidant potential through the generation of secondary metabolites in *Arabidopsis*	Roy (2016)
Os01g0586800 (OsWRKY27) Os05g0528500 (OsWRKY58) Os01g0972800 (OsWRKY17)	Repress the expression of phosphate transporters thereby reducing As uptake in *Arabidopsis*	Castrillo et al. (2013) and Awasthi et al. (2021)
Os05g0569300 (OsbZIP45) Os03g0336200 (OsbZIP30)	Modulate ABA signaling, amino acid and carbohydrate catabolism	Wang et al. (2018) and Chauhan et al. (2020)
Os08g0550700 (OsSAUR36) Os09g0437400 (OsSAUR38)	Auxin-responsive SAUR genes, involved in the growth and development of rice plant	Chauhan et al. (2020)
Os01g0868000 (OsERF99) Os05g0420300 (OsERF131)	Play a vital role in As tolerance in the presence of selenium in rice	Chauhan et al. (2020)
Os10g0529300 (OsGSTU18), Os10g0528900 (OsGSTU14	Reduce oxidative stress by increasing antioxidant potential of rice plant and an important enzyme of glutathione metabolism; help in sequestration of several heavy metals	Verma et al. (2016)
Os04g0223300 (OsAPX3)	Ascorbate peroxidase is an efficient enzyme of antioxidant system	Kumar et al. (2013)

against As toxicity (Table 10.2). Expression of the *CRTISO* gene increases fruit quality through a transcriptional up-regulation in *CRTISO*. Up-regulation of *CRTISO* gene on Se supplementation improves the carotenoid concentration as well as provides stress tolerance (Wisutiamonkul et al. 2017; Li et al. 2020). Up-regulation of genes of defense mechanism viz., glutaredoxin [*Os01g0368900* (OsGrx_C7)], glutathione-S-transferase [*Os10g0528900* (GSTU 14), *Os01g0950000* (GSTU 41)], and peroxidases [Os01g0294700 (OsPRX11), Os02g0236600 (OsPRX27), Os02g0236800 (OsPRX26)], in the presence of Se during As stress inferred As tolerance (Table 10.2). Application of Se increases the abundance of actin and tubulin protein during As stress. MYB and WRKY are the transcription factors which provide tolerance against heavy metal as MYB generates secondary metabolites that play a vital role in As tolerance (Castrillo et al. 2013). MYB transcription factors along with IAA including IAA31 and IAA14 exhibit an important role in secondary cell wall formation in rice by increasing lignin synthesis in the presence of Se during As stress (Hirano et al. 2013). WRKY is also reported to inhibit the expression of phosphate transporter that results in decreased uptake of As (Roy 2016). AP2/EREBP transcription factor is involved in the transportation of auxin that helps to reduce As-induced toxicity (Thapa et al. 2012). AUX/IAA mediates the signaling of ethylene and thus imparts tolerance against As stress (Krishnamurthy and Rathinasabapathi 2013). Pandey and Gupta (2015) reported that the supplementation of Se regulated the expression of AP2/EREBP and AUX/IAA and thus imparts tolerance against As-induced toxicity and improves plant growth. Abscisic acid is a stress hormone, and the genes involved in the expression of ABA were found significantly down-regulated by the application of Se during As stress (Yu et al. 2012; Chauhan et al. 2020).

10.6 The Proteomic Aspect of Se-Mediated Mitigation of As Toxicity

Plant proteomics is a multifaceted discipline for a detailed understanding of plant proteins' biological functions on exposure to different abiotic and biotic stresses. In plants, proteins are the key players to maintain cellular homeostasis because they act as vital executors of cellular mechanisms (Liu et al. 2019). Additionally, proteins are also very important to plants as they directly regulate the physiological characteristics of plants and are responsible for the formation of a new plant phenotype in response to adapt environmental changes. A range of proteins was found differentially expressed on Se supplementation in plants (Feng and Ma 2021; Chauhan et al. 2020). These studies reported that several defense-responsive proteins (2-Cys peroxiredoxin BAS1, chloroplastic L-ascorbate peroxidase 8, L-ascorbate peroxidase 1, Cytosolic L-ascorbate peroxidase 2, Peroxiredoxin-2E, Heat shock 70 & 90 kDa, Lactoylglutathione lyase, Glutathione S-transferase, Phenylalanine ammonia-lyase) showed higher abundance on Se supplementation during As stress in rice plant which confirms the role of Se in mitigation of As-induced toxicity. Higher abundance of different proteins such as ribulose bisphosphate carboxylase, chlorophyll a/b binding protein, glyceraldehyde-3-phosphate dehydrogenase, fructose-bisphosphate aldolase, and chloroplast 23 kDa polypeptide of photosystem II inferred improved photosynthesis in rice plant on Se supplementation during As stress. RuBisCo is the key player involved in water use efficiency, CO_2 assimilation, and photosynthesis (Dixit et al. 2015). It is reported that the up-regulation of RuBisCo during Se supplementation improves the rate of photosynthesis in the presence of As. Fructose-bisphosphate aldolase is also reported to be involved in the photosynthesis (Sun et al. 2016). Up-regulation of fructose-bisphosphate aldolase helps in the production of more reducing equivalents, i.e., NADPH, and fastens the light reaction of photosynthesis. Up-regulation of these proteins improves the photosynthetic pigments that lead to improved biomass and plant growth (Malik et al. 2012). Transporters are the main player to regulate the uptake, transport as well as accumulation of As in plants. Selenium-mediated modulation of expression of transporters responsive genes is shown to be involved in the reduction of As uptake and accumulation in plants. Supplementation of Se during As stress reduced the As-induced toxicity as As and Se compete for the same transporters for their uptake and Se is preferred over As (Kumar et al. 2014; Chauhan et al. 2020). On supplementation of Se, overexpression of OsNIP1;1 decreased the root-to-shoot translocation of As in plants. RA recent study by our group (Chauhan et al. 2020) also showed the up-regulated expression of Lsi1 (NIP2;1) transporter in the presence of Se during As stress, which not only inferred the reduced uptake of As but also the reduction of As-induced toxicity in rice plant. Selenium-mediated reduction of As accumulation is also confirmed by increased abundance of ABC transporter proteins (OsABCG5), STAR1 protein, and V type proton ATPases. ABC transporters are involved in the sequestration of As (III)–PC complexes into vacuoles in rice (Song et al. 2014) and thus lead to reduced As accumulation. Arenhart et al. (2014) reported the role of STAR1, which is an ABC transporter, in heavy metal tolerance in rice.

Exposure to As induces the production of reactive oxygen species in plants that causes oxidative stress, and to cope up with this, As-induced stress plant activates its antioxidant machinery. The proteins such as ascorbate peroxidase, glutathione S-transferase, cysteine peroxiredoxin BAS1, peroxiredoxin-2E-2, heat shock protein 70, and lactoylglutathione lyase are involved in the defense system to tolerate As-induced oxidative stress. These proteins were found in more abundance on supplementation of Se during As stress. Ascorbate peroxidase is the key player in antioxidant system. Glutathione-S transferase, an important enzyme of glutathione metabolism, helps in the sequestration of several heavy metals (Kumar et al. 2013). Cysteine peroxiredoxin BAS1 is reported as a ROS scavenger protein in plant cell (Lee et al. 2000). Peroxiredoxin is involved in the detoxification of heavy metals and also acts as a molecular chaperone similar to HSPs (Barranco-Medina et al. 2009). Thus, it can be concluded well that Se plays a very important role in the amelioration of As-induced toxicity in plants.

10.7 Conclusion and Future Prospective

The current chapter demonstrated the role of Se in reducing As burden and detoxification of As-induced toxicity in plants. Use of Se as a fertilizer not only reduces As accumulation in plants but also improved plant growth by maintaining nutrient homeostasis during As stress in plants. The regulation of ROS levels by Se can be a key mechanism for counteracting As and other environmental stresses in plants. Supply of Se fertilizer as nano-Se might prove a more promising strategy for the amelioration of As-induced toxicity because of its high bioavailability, affordability, and low toxicity. Studies are required to develop a detailed understanding about transporters for nano-Se uptake and translocation by/within plants as well as the transformation of Se species inside the plants and the volatilization from aerials plant parts. This basic knowledge would also be helpful in the utilization of Se as a priming biostimulant to complement crop growth and yield amidst As stress and other abiotic stresses.

Acknowledgment RC and SA are thankful to the Indian Council of Medical Research (ICMR) New Delhi, India for the award of ICMR-RA Fellowship [(No. 3/1/2(7)/Env./2020-NCDII & No. 3/1/2(5)/Env./2020-NCD-II respectively]. RDT is grateful to NASI, Prayagraj for the award of NASI-Senior Scientist Platinum Jubilee Fellowship.

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Chapter 11
Selenium and Nano-Selenium-Mediated Biotic Stress Tolerance in Plants

Amr H. Hashem, Amer M. Abdelaziz, Mohamed S. Attia, and Salem S. Salem

11.1 Introduction

Plants are exposed to biotic stresses such as bacteria, fungi, nematodes, insects, phytoplasma, parasitic plants, viroids, and viruses. Biotic stress agents directly deprive their host of uptake nutrients leading to reduce plant vigor continuously, and extreme cases resulted in the death of the host plant (Eid et al. 2019; Abd alhakim et al. 2022; Attia et al. 2022). Specific conditions must be present for biotic disease to develop as the following; there must be a susceptible host plant, the pathogen (fungi, bacteria, viruses, etc.), and environmental conditions conducive to disease development; these must come together in a given point in time. These conditions make up what is called the plant disease triangle. Biotic disease cannot occur if one of these pieces is missing. In every infectious disease, a series of more or less distinct events occur in succession and lead to the development and perpetuation of the disease and the pathogen. This chain of events is called a disease cycle (De Wolf and Isard 2007). Plant infection development depends on the pathogen and the host plant organ and tissue they infect (Abdelaziz et al. 2021; Abdelaziz et al. 2022). Pathogens interfere with the different physiological function(s) of the plant and lead to the development of different symptoms by different mechanisms; reduce photosynthesis, because the toxins, such as tentoxin and tabtoxin, produced by these pathogens inhibit some of the enzymes that are involved directly or indirectly in photosynthesis or by affecting the chloroplasts and causing their degeneration. In plant diseases where the pathogen infects the leaves, transpiration is usually increased due to the destruction of at least part of the protection afforded the leaf by the cuticle, an increase in the permeability of leaf cells, and the dysfunction of

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M. A. Hossain et al. (eds.), *Selenium and Nano-Selenium in Environmental Stress Management and Crop Quality Improvement*, Sustainable Plant Nutrition in a Changing World, https://doi.org/10.1007/978-3-031-07063-1_11

stomata (Doehlemann et al. 2017). Biotic plant disease is best managed through an integrated approach, which includes a combination of cultural, mechanical, biological, and chemical practices (Eid et al. 2021; Tafesse et al. 2018). Selenium (Se) has vital benefits for plant growth and stress resistance at low concentrations. However, information about the antimicrobial effect of Se of economic importance is still limited. The behavior and biological features of Se and Se nanoparticles (Se-NPs) in the nutrition of higher plants and humans may differ as to the following: 1- Bulk elemental Se is not water soluble, but Se-NPs are partially water soluble, 2- Main functions of Se plant is to increase plant growth and biomass; protect plants from abiotic/biotic stresses; deter herbivores via volatile Se But Se-NPs, increase activities of some enzymes like GSH-Px, TrxR, and GST could scavenge free radicals, have excellent bio-availability, low toxicity, and high biological activity in plants (El-Ramady et al. 2020), 3- Se-NPs were evidenced to possess extra bioactivities and functionalities as potent antioxidant, antibacterial, antifungal, and anticancer agents (Hashem and Salem 2022; Salem 2022; Menon et al. 2019). 4- Nano Se (265–530 lM concentration range) stimulated the organogenesis and the growth of root system significantly (40%) while selenate did not show these effects at any concentration moreover inhibited both callus growth and root regeneration totally in 265–530 lM concentrations (Domokos-Szabolcsy et al. 2012). 5- Bulk Se is toxic and harmful at high doses; however, Se-NPs are safe (El-Saadony et al. 2021). However, Khan et al. (2019) reported that the nanomaterials can be effective agents as carrier of active ingredients of plant defense substances, hormones, pheromones, pesticides, suppressive to fungal, bacterial plant pathogens and nematodes, and nanoparticles (NPs), by being ultra-small, may directly target virus particles thus may open a new vital field in the control of plant viruses as well as disease diagnosis (pathogen detection) may become much more quick and accurate with the use of nano-sensors. Se-NPs have effective antifungal activity in vitro against *Pyricularia grisea*, *Colletotrichum capsici,* and *Alternaria solani* on chili and tomato at concentrations of 50 and 100 ppm, respectively (Joshi et al. 2019). Moreover, Se-NPs stabilized with different coating agents on many plant pathogens, and antifungal activity of Se-NPs was not dependent on the coating agent (Vrandečić et al. 2020). This chapter reviews and discusses knowledge on Se and Se-NPs-mediated biotic stress tolerance in plants.

11.2 Selenium as Eco-Friendly Inducer

Plants possess diverse defense systems against pathogen attack. These mechanisms fail when the plant is infected by a virulent pathogen because the pathogen avoids triggering or suppresses resistance reactions, or evades the effects of activated defenses. If defense mechanisms are triggered by a stimulus prior to infection by a plant pathogen, disease can be reduced. Induced resistance is a state of enhanced defensive capacity developed by a plant when appropriately stimulated. Plants have developed a wide range of physical and chemical defense mechanisms to protect themselves against biotic stresses through metabolic, biochemical, and molecular defenses, as well as physical/structural barriers such as thorns or waxy leaves (Aldinary et al. 2021; Farrag et al. 2017). The content of Se in plants can be increased in different ways; by addition of Se to soil, soaking seeds in Se solution before sowing, hydroponic and aeroponic cultivation in a nutrient solution containing Se, and foliar application of plants with Se solution (Shanker 2006). Recent studies proved that Se has an important and effective role in protecting plants from pathogens and increasing the efficiency of physiological immunity in plants. Several reports show that when Se is added at low concentrations, it exerts beneficial effects on plant growth. Se may act as quasi-essential micronutrient by altering different physiological and biochemical traits; thus, plants vary considerably in their physiological and biochemical response to Se (El-Ramady et al. 2016). Ragavan et al. (2017) concluded that 400 mg of Se-NPs highly increased the vegetative growth such as root length, fresh and dry weight and leaf width, metabolic characteristics such as chlorophyll a, chlorophyll b, total chlorophyll, carotenoids, protein, anthocyanin, free amino acids L-proline, and leaf nitrate and yield production of Cluster bean. Also, El-Batal et al. (2016) recorded that foliar application of Se-NPs at the rate of 0.5 μg/ml is preferred for inhibiting pathogens as well as improving morphology (shoot height, number of leaves per plant, fresh, dry weight, leaf width, number of main stems), physiology (chlorophyll content, reducing sugars content, catalase (CAT), polyphenol oxidase (PPO), antioxidant activity and protein content) and yield of potato tubers. Moreover, Zahedi et al. (2019) reported that Se-NPs (especially 5–200 nm) have high biological activity in plants due to low toxicity, excellent bioavailability, and enhancement of the activities of some enzymes like GSH-Px, TrxR, and GST, which are the scavenger of free radicals.

11.3 Metabolism of Selenium in Plants

Generally, Se is absorbed by plants in several inorganic formulas such as Se, selenide, selenate, and selenite. These forms are converted to organic ones by metabolism and mostly depend on the two selenoamino acids including selenocysteine (SeCys) and selenomethionine (Hossain et al. 2021). Se may increase plant vegetative growth and biomass, protects plants from abiotic as well as biotic stresses, and supports plants against herbivores through dimethyl selenide volatile Se (Wang et al. 2020). Aphid-infected pea leaves when treated by Se recorded changes in the levels of reactive oxygen species, the activity of antioxidant enzymes, and the total antioxidant capacity (Łukaszewicz et al. 2021; Shaheen et al. 2021). During the last decade, studies related to strategies for Se biofortification in food plants for human nutrition have increased significantly because this metalloid is incorporated into human metabolism mainly as a constituent of food plants (Mora et al. 2015). Se is absorbed from soil by passive diffusion but the highest absorption rate and rapid translocation to the shoots among the inorganic and organic forms of Se, selenomethionine in wheat and canola plants is the form that present, for more Se uptake are dependent on energy expenditures, selenate is absorbed by the sulfur (S) carrier, while selenite is absorbed by the phosphate carrier (de Mello Prado et al. 2017; Kikkert and Berkelaar 2013; Li et al. 2008).

11.4 Application of Se-NPs against Mycotoxins Production

Se-NPs have great antifungal activity against production of ochratoxin A, aflatoxins, and sterigmatocystin by some biological responses like the activation of alternative pathways which result after exceeding a defined physiological beginning value. Thus, different concentrations of Se-NPs may result in the activation of diverse stress-compensation pathways. Also, the interaction between the surface of the respective Se-NPs and the cell wall facilitated the diffusion of nutrients, and therefore also affects the growth rate and mycotoxin production (Meena et al. 2021) .

11.5 Management of Biotic Stress in Plants by Selenium and Se-NPs

11.5.1 Antimicrobial Activity

Inorganic Se forms, such as sodium selenite (Na_2SeO_3) or sodium selenate (Na_2SeO_4), have inhibitory effects on fungi or synergistic effects with fungicides (Xu et al. 2020). Both inorganic and organic Se forms were recently reported to inhibit *Fusarium graminearum* growth in vitro (Mao et al. 2019). Mao et al. (2020), recorded the effect of four Se compounds, i.e., Na_2SeO_3, Na_2SeO_4, selenomethionine, and selenocysteine, at different concentrations. The four Se compounds at the amount of 20 mg were applied onto wheat spikes directly after inoculation at flowering. All four of the Se compounds significantly reduced the mycelial growth and deoxynivalenol toxin production. In the study by Hashem et al. (2021a), biogenic Se-NPs may be effective and economical alternatives for treating fungal plant pathogens. Bio-synthesized Se-NPs by *Bacillus megaterium* ATCC 55000, which was characterized by mono-dispersed spheres with 41.2 nm, have promising antifungal activity against *Rhizoctonia solani* in vitro and in vivo. Soaking and foliar spraying of Se-NPs 1 mM caused a significant enhancement of morphological and metabolic indicators as total chlorophyll-content carotenoids. Moreover, the application of Se-NPs induced responses regarding the total contents of phenols and total soluble protein. In contrast, total phenol contents in shoots and roots-infected plants were significantly decreased in response to the treatments with Se-NPs. Se-NPs act as a promoter and/or stressor, enhancing the antioxidant defense systems of plants, which leads to the improvement of plant tolerance. Thus, biosynthesized Se-NPs by *B. megaterium* ATCC 55000 are a promising and effective agent against *R. solani* damping-off and root rot diseases in *Vicia faba*. Bio-Se-NPs spherical with a size of

46 nm by *Lactobacillus acidophilus* ML14 can use an efficient agent against plant pathogenic fungi *Fusarium* species that caused wheat crown and root rot diseases to protect wheat crop losing, instead of using chemical pesticides with more advantages, Se-NPs have no harmful effects on seed germination, plant growth, and soil microflora, while some are beneficial to the plants. The bio Se-NPs significantly inhibited the *Fusarium* growth in the range of 20–40 μg/mL in vitro. For more, under greenhouse conditions, the wheat treated with bio Se-NPs (100 μg/mL) significantly reduced the incidence of crown and root rot diseases by 75% by significantly scavenging 88 and 92% of DPPH and ABTS radicals, respectively, and resulted in destroying fungal mycelium as well as considerably enhanced plant morphology as root and shoot length and weight, metabolic characters, higher content of pigments (chlorophyll, carotenoids, gas exchange parameters, transpiration, conductance stomata, and net photosynthesis), and yield as grain quantity and quality by 5–40% (El-Saadony et al. 2021). Se-NPs were prepared by reducing agents, and glutathione can be used as antioxidant for enhancing plant immunity and as a moderate inhibitor of the *A. solani*, a pathogenic fungus of early blight of potato. At lowest concentration (50 ppm), Se-NPs showed 8.33% inhibition, but at high concentration (800 ppm), it showed complete inhibition of the fungal growth. This antifungal effect may be linked with the fact that Se may trigger the generation of ROS, capable of reacting with intracellular thiols and forming intermediates that cause oxidative stress as a consequence of the formation of superoxide radicals (Ismail et al. 2016). Se is a micronutrient metalloid incorporated (in the form of selenomethionine or selenocysteine) in the structure of enzymes such as glutathione peroxidases, iodothyronine deiodinases, and thioredoxin reductase, which are involved in antioxidant defense, detoxification, and metabolism, respectively (Forootanfar et al. 2014). The low toxicity of Se-NPs has attracted research attention against plant diseases (Hashem et al. 2021a). Also Wu et al. (2015) reported that sodium selenite has important physiological functions for plant vegetative growth and improvement of plant fruit at low concentrations, and has been shown to have a positive effect on biotic and abiotic stress tolerance and protect plants against invertebrate herbivore destruction as well as fungal pathogens. Furthermore, containing substances in leaves and stems of cruciferous and alfalfa crops act as repellents, so that aphids, caterpillars, and spider mites not affected these plants. Wu et al. (2016) studied the effect of Se salts on spore germination and mycelial growth of the *Botrytis cinerea* in vitro and gray mold restraint in tomato, application of Se at 24 mg/L reduced spore growth of the pathogen and successfully restricted disease in collected tomato fruit. Se treatment at 24 mg/L appears to stimulate the production of intracellular reactive oxygen species in the fungal spores. These results indicate that Se has the promise for limiting gray mold rot of plant and might be positive in integrated resistance against fungal disease of postharvest fruits and vegetables caused by *B. cinerea*. Biosynthesized Se-NPs by *Trichoderma* have great potency to suppress the growth, sporulation, and zoospore viability of *Sclerospora graminicola,* and these biological activities were inversely proportional to the size of Se-NPs. Under greenhouse conditions, application of Se-NPs and *Trichoderma asperellum* together enhanced the early plant growth and suppressed downy mildew incidence as

compared to their individual application. Thus *Trichoderma* formulations along with Se-NPs can be successfully employed for controlling plant disease.(Nandini et al. 2017). Se-NPs have great advantage as less toxic to humans and animals than synthetic fungicides. They also have great potential to inhibit the growth of *Aspergillus nidulans*, *Aspergillus ochraceus,* and *Aspergillus parasiticus*, in vitro; therefore, Se-NPs could be used as a fungicide against these phytopathogens (Abdel-kareem and Ahmed Zohri 2017; Quiterio-Gutiérrez et al. 2019). Nandini et al. (2017) reported that, when applying 100 ppm of Se-NPs, the growth of the plant was not affected and it did not show any phytotoxic effect, and resulted in the decrease of the disease severity up to 6%. The application of Se-NPs increased the content of pigments in the leaves, and likewise increased the activity of the antioxidant enzymes activity and the antioxidant potency, which helped in the control of *A. solani*. Additionally, the content of non-enzymatic antioxidant compounds in fruits, such as flavonoid, glutathione, vitamin C, and phenols, was significantly increased with the application of Se-NPs (Quiterio-Gutiérrez et al. 2019). Antimicrobial effect against phytopathogens was explained by different four mechanisms such as: disruption of bacterial cell membrane; depolarization; modification of the intracellular levels of ROS and scavenging the excess of ROS; and metabolic interference by disrupting the intracellular levels of (ATP) (Huang et al. 2020). Se accumulation in plant cells and Se volatilization may affect the interactions between plants and disease causative, herbivores, and the pollinating insects (El Mehdawi and Pilon-Smits 2012); thus, Se can protect plants against a wide range of vertebrate and invertebrate fungal plant pathogens and may also have allopathic advantages (El Mehdawi and Pilon-Smits 2012). Se levels can reach up to 0.6% of *Brassica juncea* plant dry weight without any signs of toxicity and are commonly in the 0.1% range. This accumulation gives great protection to plants from caterpillar herbivory as well as fungal infection. Function of Se hyper-accumulation by plants protect *B. juncea* from caterpillar herbivory and fungal infection as *Fusarium* and *Alternaria brassicicola* in the field. Accumulation of toxic elements as Se by plants is an effective mechanism to deter insect herbivory and to confer insect toxicity (Boyd 2012; Hanson et al. 2003). Application of selenite (at a concentration of 24 mg Se/L for 3 hours) is a promising agent as an alternative to synthetic fungicides against *B. cinerea* that caused postharvest gray mold disease of fruits and vegetables by damaging the pathogen conidial plasma membrane and loss of cytoplasmic materials from the hyphae. Moreover, selenite can stimulate ROS accumulation in fungal spores that result in oxidative damage of fungal hyphae (Wu et al. 2016). Sodium selenite could control postharvest disease of fruits and vegetables caused by *Penicillium expansum* through inhibited spore germination, germ tube elongation, and mycelial spread. The inhibitory effect was positively related to the concentration of Se used (Wu et al. 2014). Se-NPs have great potency to control a broad spectrum against fungal phytopathogens and diseases at a wide spectrum of plant host especially tomatoes (Joshi et al. 2019). Also Hernández-Díaz et al. (2021) reported that biogenic reduction of elements such as Se with plant extracts has become one of the most accepted methods for NPs and Se-NPs production, as it is considered an ecological and cost-effective process without the use of chemical contaminants. These biogenic Se-NPs have great potency as a phytopathogens growth inhibition, such as *Aspergillus niger*. Finally, Se has antifungal activity against *A. fumigatus* and *C. albicans* (Shakibaie et al. 2015). Se as a bioactive micronutrient could be built up by transforming into NPs for usage as an antimicrobial element, especially for inhibition of bacterial pathogens via attached to bacterial cells and led to their complete explosion through exposure prolongation (Al-Saggaf et al. 2020). Potency of nano Se in the stabilization of the immune system and activation of the defense response give Se-NPs priority over other nanomaterials (Ikram et al. 2021). A previous study confirmed that, Se-NPs have antimicrobial activity against phytopathogens including bacteria and fungi; therefore, the application of Se-NPs in agriculture filed represents a great advantage than chemical synthetic fungicides because they are less toxic to both humans, animals, and environment than synthetic fungicides (Alagesan and Venugopal 2019). Also their application might also benefit the human diet due to the essential nature of Se in mammals (Joshi et al. 2019). Se-NPs have different possible mechanisms against bacterial and fungal plant pathogens as the following; intracellular ATP depletion, Induction of oxidative stress through ROS production, Alteration of bacterial membrane potential, disruption of bacterial membrane Inhibition of fungal spore germination (Hernández-Díaz et al. 2021).

11.5.2 Antiviral Activity

Viruses are responsible for approximately 50% of the emerging plant diseases; thus, the development of antiviral agents is a great goal, and the use of metal NPs can be a new vital opportunity for novel antiviral agents for crop protection against viral plant pathogens (Vargas-Hernandez et al. 2020). The use of NPs has great potency to minimize the problem of virus-caused diseases in agriculture. The antiviral activity of Metal NPs has been reported by many researchers in vitro and in vivo with several plants and is effective against positive- and negative-sense single-stranded RNA viruses(Vargas-Hernandez et al. 2020). Also it can enhance the physiological processes of plants in a way that provides potential benefits to growth, development, and courage defense responses (Du Jardin 2015).

11.5.3 Nematicidal Activity

Se-NPs induced systemic resistance of tomatoes to the root-knot nematode, stimulated plant growth and development through the PR-6 gene expression in the roots and leaves of plants subjected to nematode invasion, and increased the activity of proteinase inhibitors. Treatment of plants with Se-NPs reduced the invasion of plants by affecting the physiological and morphological properties of the parasites in the roots (Tables 11.1 and 11.2) (Udalova et al. 2018).

Table 11.1 Plant disease controlled by Selenium

Disease	Causative pathogen	Host	Selenium application	Mechanism of action	References
Green mold	*Penicillium digitatum*	Orange fruit	At 100 ppm se inhibit 5.56% but at 500 ppm, selenium gave 85.22% fungal growth inhibition.	Make the fungal membrane more leaky and increasing cell permeability.	(Khalifa and Sameer 2014)
Early blight	*Alternaria solani*	Tomato		Synergistic action of selenium to some fungicides	(Ismail et al. 2016)
Gray mold decay	*Botrytis cinerea*	Tomato	Se treatment at 24 mg/L	Significantly inhibited spore germination, induce the generation of intracellular reactive oxygen species in the fungal spores and damage to the conidia plasma membrane and loss cytoplasmic materials from the hyphae.	(Wu et al. 2016)
Stem rot	*Sclerotinia sclerotiorum*	Oilseed rape	(0.1 and 0.5 mg/kg of soil)	Enhanced and regulates microbial communities in soil and caused increasing nitrogen , carbohydrate metabolism. Also, se promoted the energy metabolism and amino acids of infected leaves.	(Liu et al. 2019; Xu et al. 2020)

Table 11.2 Plant diseases controlled by Se-NPs

Disease	Causative pathogen	Host	Selenium application	Mechanism of action	References
Damping-off and root rot	*Rhizoctonia Solani*	Faba bean	Synthesized biologically by *bacillus megaterium* (soaking and spraying)	Se-NPs act as a promoter and/or stressor, enhancing the antioxidant defense systems of plants	(Hashem et al. 2021a)
Crown and root rot	*Fusarium species*	*Triticum aestivum* L	Synthesized by *lactobacillus acidophilus* (100 μg/mL)	Enhancement plant growth and yield	(El-Saadony et al. 2021)

(continued)

Table 11.2 (continued)

Disease	Causative pathogen	Host	Selenium application	Mechanism of action	References
Early blight	*Alternaria solani*	Potato and tomato	By glutathione (GSH) as Product from *Saccharomyces cerevisiae*	Antioxidant activity for enhancing plant immunity and completely inhibited the fungal growth at 800 μg/ml. Induction of the enzyme activity ascorbate, glutathione peroxidase superoxide dismutase, peroxidase, and phenylalanine ammonia lyase in the leaves, and the enzyme GPX in the fruit. Regarding non-enzymatic compounds in the leaves, also increasing chlorophyll a, b, and totals whereas phenols, vitamin C, glutathione, and flavonoids were increased in fruits	(Ismail et al. 2016; Quiterio-Gutiérrez et al. 2019)
Downy mildew	*Sclerospora graminicola*	Pearl Millet	Biosynthesized by *Trichoderma* sp.	Suppressed the growth and sporulation	(Nandini et al. 2017)
Root-knot nematode	*Meloidogyne incognita*	Tomato	0.34 and 0.68 μg/mL	Induce systemic resistance, promoted plant vegetative growth and development, was involved in the *PR-6* gene expression in the roots and leaves of plants and increased the Proteinase activity of inhibitors	(Udalova et al. 2018)

11.6 Mechanisms of Selenium and Se-NPs-Mediated Biotic Stress Tolerance

11.6.1 Mechanisms for Antimicrobial Activity

In this context, nanobiotechnology might be used to boost plant yield, development, and productivity in the face of biotic stressors (Hashem et al. 2021a). Biogenic Se-NPs have also demonstrated exceptional antimicrobial activity against a variety of pathogenic microbes, including fungi and bacteria (Salem et al. 2022; Abu-Elghait et al. 2021; Korde et al. 2020; Srivastava and Mukhopadhyay 2015). Furthermore, biogenic Se-NPs serve as promoters and strengthen plants' antioxidant defense mechanism, resulting in increased plant tolerance to environmental stresses (Bai et al. 2020; Ismail et al. 2016; Zahedi et al. 2021). Plant-mediated Se-NPs have emerged as powerful antibacterial and bio-fortifying agents to minimize the devastating impacts of plant pathogenic strains among different NPs. Se-NPs derived from biogenic processes have also been demonstrated to exhibit good biocompatibility, low toxicity, renewability, and bioavailability, as well as being environmentally benign (Khiralla and El-Deeb 2015; Korde et al. 2020). *S. graminicola* growth, sporulation, spore viability, and proliferation are all suppressed by biosynthesized Se-NPs, according to another study. Plant pathogen *S. graminicola* infects maize and pearl millet crops (Nandini et al. 2017). Another study found that biogenic Se-NPs have exceptional antifungal activity against *A. solani*, which causes early blight in potatoes. They discovered that biogenic Se-NPs had a progressive inhibitory impact on the development of the pathogenic fungus in investigation (Ismail et al. 2016). They found that biogenic Se-NPs had good antifungal ability against the fungus *R. solani* (Hashem et al. 2021a). Surprisingly, they discovered that sick plants with biosynthesized Se-NPs had much higher chlorophyll and carotenoid content than control plants. Furthermore, as compared to healthy plants, foliar treatments of Se-NPs cause reactions in terms of total phenolic content and total protein content. *Pelargonium zonale* leaf-extract-mediated Se-NPs also showed great promise against *Penicillium digitatum*. According to another study. *P. digitatum* is also a plant pathogen that often causes the postharvest fungal infection known as green mold in citrus (Korde et al. 2020). In addition, plant-derived Se-NPs suppress the development of this fungus species substantially in vitro. Green-mediated Se-NPs may be an efficient and cost-effective way to treat fungal plant diseases due to their high biocompatibility. The antifungal potency of biogenic Se-NPs might be due to a variety of factors, including the generation of ROS or the disruption of inner cellular functions and structure.

Furthermore, biomolecule-assisted Se-NPs were shown to suppress the development of *Aspergillus flavus*, a harmful and saprotrophic fungus with a worldwide distribution. It's notorious for wreaking havoc on cereal grains, tree nuts, and legumes. Se-NPs' precise method of action is currently unknown. However, it has been observed that Se-NPs produce ROS that destroy the pathogens cell structure, cellular membranes integrity, and limit ATP synthetase function (Hu et al. 2019; Mosallam et al. 2018). Another mechanism for biogenic Se-NPs is to suppress growth of microorganisms by destroying the cellular structure, then attaching to the cellular membranes and modifying the DNA molecules replication, synthesis of proteins process, and nutrition various metabolic cycle; finally, it binds to the thiol groups current in protein molecules and causes cell death (El-Gazzar and Ismail 2020; Mosallam et al. 2018; Zonaro et al. 2015). In another investigation, Se-NPs have pesticidal activity against a variety of insects. The interaction of NPs with phosphorus-containing substances like DNA and RNA, which damaged these vesicles, may explain Se-NPs insecticidal potency. Se-NPs, on the other hand, have been linked to the deactivation of key enzymes as well as cell death (Hashem et al. 2021b; Salem and Fouda 2021; Salem et al. 2021). Gunti et al. (2019) produced Se-NPs using aqueous extracts from *Emblica officinalis* fruits, resulting in amorphous particles with a size of 15–40 nm.

Rhizopus stolonifer, *Fusarium anthophilum*, *A. flavus*, *A. ochraceus*, *Aspergillus brasiliensis*, and *Aspergillus oryzae* have all been shown to have antimicrobial action. Green chemistry-derived Se-NPs have been shown to exhibit antimicrobial action against plant pathogens such fungi and bacteria (Alagesan and Venugopal 2019; Joshi et al. 2019). Se-NPs produced using propolis aqueous extract have been shown to exhibit antioxidant and antibacterial effects against fungal pathogens along with Gram-positive and Gram-negative bacteria (Shubharani et al. 2019). Shoeibi et al. (2017) reported on the production of Se-NPs using green technique, and they found that it inhibited the development of phytopathogens such *A niger*. As a result, using Se-NPs in agriculture is advantageous since they are less harmful to humans and animals than chemical fungicides. Due to the necessary role of Se in mammals, their use may also improve the human diet (Joshi et al. 2019; Sengupta et al. 2014; Shirsat et al. 2015). Huang et al. (2019) suggested four mechanisms for Se-NPs mediated antimicrobial properties Fig. 11.1: 1 metabolic invasion via interruption of intracellular adenosine triphosphate (ATP) levels; (2) variation of intracellular values of ROS, (3) depolarization, and (4) biological membranes disturbances. Se-NPs have been demonstrated to suppress Gram-positive and Gram-negative bacteria cells with a level of efficacy comparable to that of Se salts. The lipo-saccharides of Gram-negative surfaces resist Se-NPs electrostatic repulsion (Tran et al. 2015). Given biosynthesized Se-NPs' strong antimicrobial activity in vitro and in vivo, it's not hard to think that green-mediated Se-NPs may be an ideal nanoproduct for killing these destructive plant diseases. Consequently, there has been little study into plant-based Se-NPs in the agricultural industries. To safeguard plants, it is critical to investigate the applicability performance of green produced Se-NPs against damaging plant diseases.

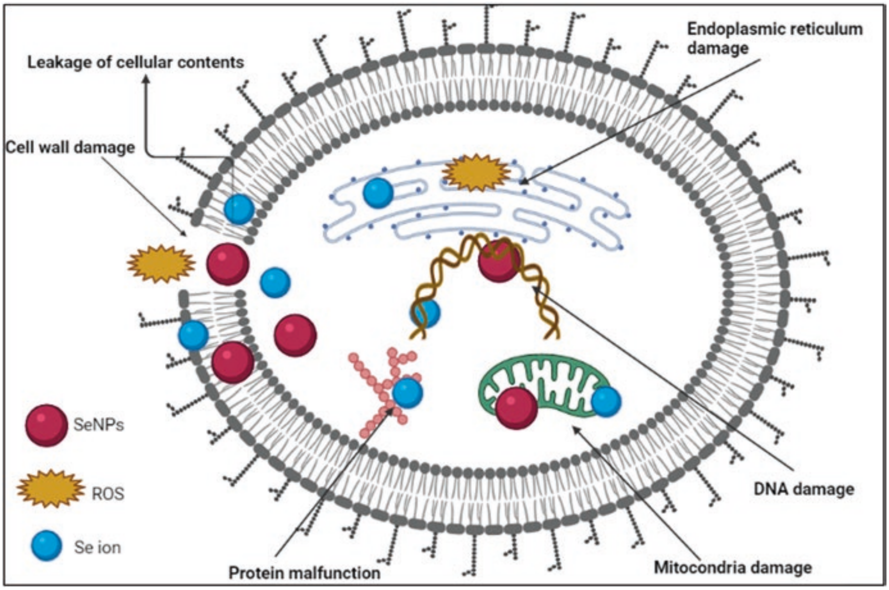

Fig. 11.1 Mechanisms for antimicrobial activity

11.6.2 Mechanism for Antiviral Activity

Virus infection is one of the most challenging issues in agricultural production, and it poses a significant danger to human food security due to the absence of an efficient management strategy. Interactions between NPs, phytopathogens of plants, and plant cell responses have gotten a lot of interest because of their antiviral potential; moreover, the impact of NPs on plants supports the concept that NPs may be used as a novel antiviral technique in agriculture (Vargas-Hernandez et al. 2020). In most cases, the viral infection cycle begins with the virus entering the host plant's cell and going through uncoating, transcription, and propagation, followed by encapsidation and amplification before invading and dispersing (Zhao et al. 2019). The antiviral activity of the NPs was demonstrated in both foliar and soil supplementation applications. Nanomaterials have been shown to have antiviral action in vitro and in vivo with various plants, and are effective against both beneficial and harmful sense single-stranded RNA viruses(Vargas-Hernandez et al. 2020). The interaction of nanomaterials with the outside of the viral infection has been described by several authors as one stage in the antiviral process. In vitro antiviral efficacy of NPs against tobacco mosaic virus (TMV) and dengue virus (type-1) was reported by Cai et al. (2019) and Ramya et al. (2015), respectively. The findings show that NPs directly inactivate virus via interactions with envelope proteins, resulting in direct damage to virus shell proteins, aggregating, and even breakage. Potato virus Y and tomato mosaic virus protein particles may similarly attach to NPs (Noha et al. 2018). Because the NPs were attached to the virus and hindered virus replication, NPs sprayed on diseased tomatoes for seven days before treatment with potato virus Y and tomato mosaic virus decreased pathogenicity and virus percentage(Noha et al. 2018). When compared to a single NP and salicylic acid (SA) administration, a combination of NPs and SA given before 3 and 7 days of infectious agent had a synergistically antiviral effect against tomato bushy-stunt virus (El-Shazly et al. 2017). These findings back up Vargas-Hernandez et al. (2020), who claim that the usage of NPs as antivirals in plants is due to the enhancement of plant defense systems that lead to plant immune and development response, in which the stress response, virulence genes, and phytohormones all play a role. Although the antiviral mechanisms of Se-NPs are unknown, recent research may give evidence of the processes involved (Lin et al. 2021; Vargas-Hernandez et al. 2020) Fig. 11.2.

11.6.3 Mechanism for Nematicidal Activity

Nematodes diseases are one of the most abundant diseases for plants. Root-knot nematodes (*Meloidogyne* spp.) cause at least 90% of all the damage caused by nematodes to crops (Castagnone-Sereno 2002; Attia et al. 2021). Chemicals are widely used for management of nematode diseases where chemicals used as soil fumigants (Kalaiselvi et al. 2017), but some of these chemicals are toxic to plants. Moreover, most of mechanisms of other metal NPs may resemble Se-NPs; therefore, these mechanisms are mentioned in Fig. 11.3. Mechanisms include 1- The physical

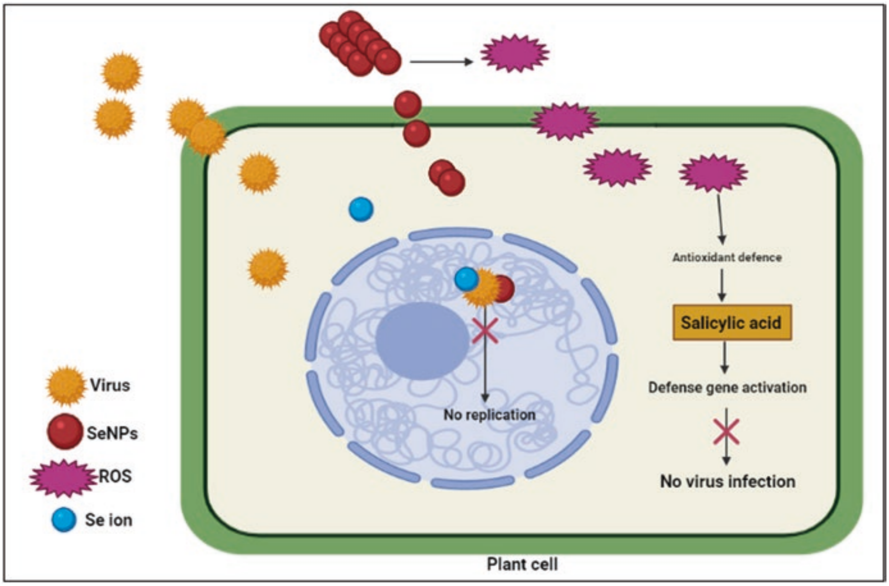

Fig. 11.2 Mechanism for antiviral activity

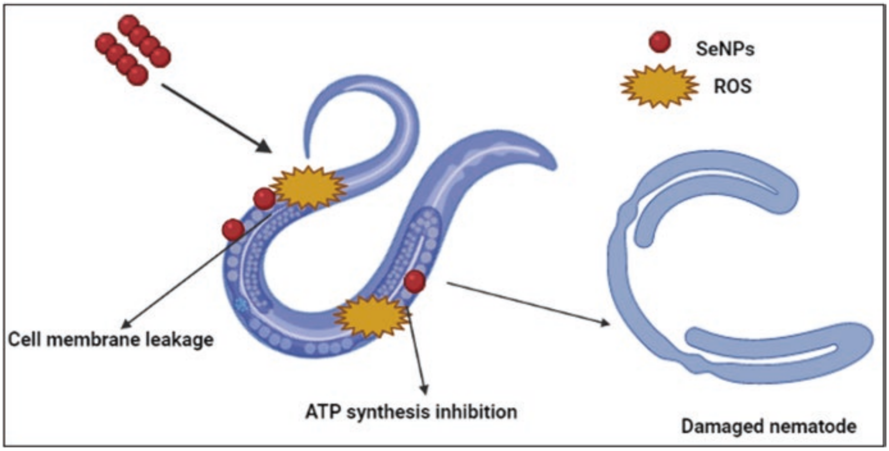

Fig. 11.3 Mechanism for nematicidal activity

structure (size, shape, and homogeneity) plays important role in the cell wall penetration of the nematode eggs which is followed by cell dysfunction (Sharon et al. 2010). 2- NPs induced oxidative stress and upregulation of sod-3 and daf-12 genes which caused the failure of reproduction in Caenorhabditis elegans worms (Roh et al. 2009). 3- Disrupting and malfunctioning of several cellular mechanisms, such as membrane permeability, ATP synthesis, and physiological response to oxidative stress in both eukaryotic and prokaryotic cells (Lim et al. 2012).

11.7 Conclusion

Biotic stress occurred by living pathogens including viruses, bacteria, fungi, and plant parasitic nematodes that inhibit the growth and yield of plant either completely or partially. Pesticides are synthetic chemicals used for management of plant diseases. Application of pesticides are efficient for controlling of plant diseases but may led to harmful effect on both environment and human. Therefore, metal nanoparticles are used for controlling plant diseases at low concentrations without any toxicity on healthy plant cells. The tolerance of biotic stress in plants is enhanced by Se and Se-NPs. The antimicrobial, antiviral and antinematode activities of Se and Se-NPs are reported. This chapter illustrates the mechanisms of plant's tolerance to pathogenic bacteria, fungi, viruses, and nematode using Se and Se-NPs.

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Chapter 12
Selenium Bioavailability and Nutritional Improvement in Crop Plants

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12.1 Introduction

The metalloid selenium (Se) is ubiquitous within the environment and its concentration in soil changes from 0.01 to 2.0 mg kg^{-1}, bringing about a normal of 0.4 mg kg^{-1}. However, Se is an indispensable micronutrient even at little concentrations, and its role in environment and food chain needs to be deeply studied. It can have harmful impacts when taken in high concentration (Terry et al. 2000). Plants are the essential store of dietary Se for creatures including humans, and its investigation needs to be significantly studied (Dumont et al. 2006). Many plant species belonging to the families Asteraceae, Brassicaceae, and Fabaceae accumulate adequate measures of Se in the leaf trichomes and epidermal cells (El Mehdawi and Pilon-Smits 2012; Pilon-Smits and Quinn 2010; Freeman et al. 2006, 2007). It is realized that the

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M. A. Hossain et al. (eds.), *Selenium and Nano-Selenium in Environmental Stress Management and Crop Quality Improvement*, Sustainable Plant Nutrition in a Changing World, https://doi.org/10.1007/978-3-031-07063-1_12

Fabaceae family includes huge number of species known to be hyper-accumulators of Se. Likely the transformation could be because of suitable Se transporters and biochemical pathways in various angiospermic clades. This development is thought to have happened throughout geological periods when seleniferous soils were more abundant than present times (Brown and Shrift 1982; Cappa et al. 2014; White et al. 2007). Metabolism of Se in higher plants is firmly related to that of sulfur because of their chemical analog similarity in having indistinguishable tetrahedral structures and pKa values (pKa2 sulfate = 1.9 versus pKa2 selenate = 1.74) against this background. Se is taken inside the plants through sulfate carriers and absorbed by sulfur acclimatizing pathways (Dumont et al. 2006; Sors et al. 2005a, b). However, low Se concentration can expand protection from stress; for example, Se at low concentrations increases the biomass of wheat seedlings under dry spell (Yao et al. 2009) and detoxifies hefty metals like arsenic (As), cadmium (Cd), mercury (Hg), and lead (Pb) in plants (Feng and Wei 2012; Lin et al. 2012; Malik et al. 2012; Mroczek-Zdyrska and Wójcik 2012; Saidi et al. 2014; Han et al. 2015). Moreover, tobacco is a monetarily significant crop around the world, and tobacco leaves are viewed as amazing to deliver Se-rich proteins, as they contain plentiful and excellent dissolvable proteins (Teng and Wang 2012). The preceding sections of the chapter are dedicated to unravel the importance of Se in enhancing the growth and yield of crop plants. In addition, a concise account on transport of Se, its bioavailability, and interaction with critical elements and heavy metals is also conversed to highlight its importance in crop improvement and food security.

12.2 Se as an Emerging Micronutrient of Immense Importance

Se helps plants to withstand various biotic (pathogens and herbivory) and abiotic stresses such as oxidative stress (El Mehdawi and Pilon-Smits 2012; Pilon-Smits and Quinn 2010; Feng et al. 2013; Quinn et al. 2011; White and Brown 2010). The last decade witnessed large interest from plant biologists to explore the importance of micronutrients in enhancing the plant metabolism through resilience and direct effect on plant metabolism and growth (Mir et al. 2020). Se is critical to upregulate the resilience against biotic as well as abiotic stressors, apart from its role in adapting various physiological and metabolic processes important for plants (Fig. 12.1). Se is known as an efficient potent mineral nutrient in many plants including several higher plants (Lyons et al. 2009; Pilon-Smits and Quinn 2010). It is an integral part of approximately 30 selenoenzymes such as formate dehydrogenases, methionine-R-sulfoxide reductase B1 (SEPX1), glycine reductases, glutathione peroxidases, tetraiodothyronine, 50-deiodinases, thioredoxin reductases, selenophosphate synthetase 2, and some hydrogenases that help cells to withstand various free radicals by controlling the oxidative metabolism in plants (Mangiapane et al. 2014). It also aids in maintaining sufficient water levels in the cells, protects cellular membranes

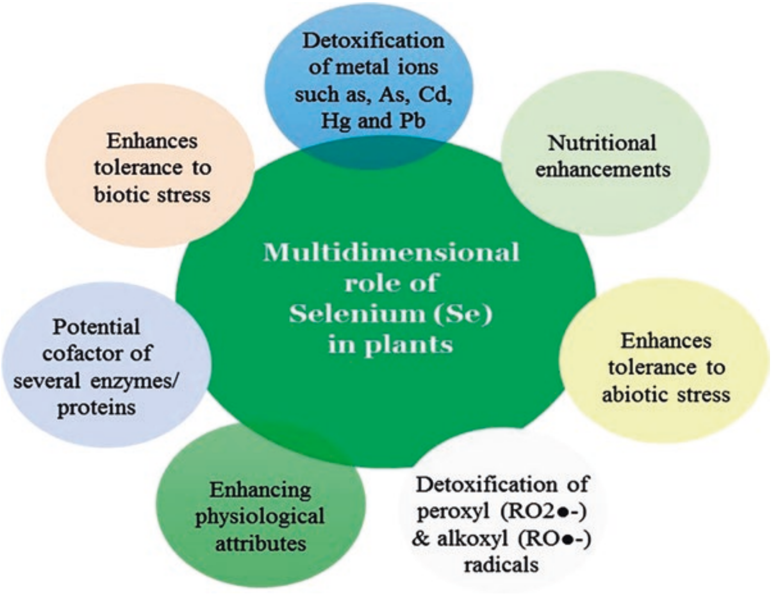

Fig. 12.1 Multidimensional role of selenium in improvement of crop plants

from the harmful effects of reactive oxygen species (ROS) by helping in detoxification of peroxyl ($RO_2^{\bullet -}$) and alkoxyl ($RO^{\bullet -}$) radicals anddirecting various antioxidant defense mechanism, etc. In addition, some hydrogenases play a significant role in avoiding cell damage because of free radicals by dealing with the oxidative metabolism in plants (Mangiapane et al. 2014). It likewise fills in as a stress buster for plants by keeping up with adequate water levels inside the cells, thereby shielding cellular membranes from adverse impacts of ROS by aiding in detoxification of peroxyl ($RO_2^{\bullet -}$) and alkoxyl ($RO^{\bullet -}$) radicals, managing antioxidant defense mechanism and so on. It also aids in releasing more light energy under conditions of heat stress, therefore maintaining the stability of photosystem (Huang et al. 2017). Moreover, enough amount of Se can aid in minimizing the disintegration of the chlorophyll. However, upon foliar, it was shown that there was a significant decline in net photosynthetic rate, and it also aids in the production of chlorophyll that improves plant–water relations and increases the effect of antioxidants (Ding et al. 2017). Moreover, Se can also enhance synthesis of higher pigment content and antioxidants in tomato fruits (Zhu et al. 2017). The accumulated heavy metals such as Pb, Cr, Cd, As, and Ni resulted in significant decrease after foliar spraying with Se fertilizers in grapes (Zhu et al. 2017). It is also reported that Se content in fruits even enhances the fruit flavor and quality after using the Se-rich fertilizers (Ryant et al. 2020).

Se is also known to decrease the biosynthesis of ethylene, the hormone that is responsible for plant senescence and fruit ripening. This confirms its possible positive impact in improving shelf life of various fruit and vegetables (Luksic and Germ

2017; Puccinelli et al. 2017). Further, it is reported that Se triggers partial stomatal closure, as revealed by the values of stomatal conductance that results in decrease in the net assimilation, hence, decreasing dry-matter production (Ryant et al. 2020). Amino acid–chelated Se is famous for its impact on pear, grape, and peach for improving net photosynthetic rate and reduced stomatal conductance and transpiration rate (D'Amato et al. 2014). It also aids in restoring the formation of ascorbic acid and polyphenolics in fruits (D'Amato et al. 2014) and hence validates its role as multitalented micronutrient. Furthermore, inorganic forms of water-soluble Se are selenite and selenate and are the foremost bioavailable forms of the element for plants (Dungan and Frankenberger 1999). However, various studies indicate that selenate accumulates more in plant tissues than selenite (Poblaciones et al. 2014), due to the upper transportation rate of selenate through the xylem (Gupta and Gupta 2017). Moreover, Se at low concentration is considered as a key element as it acts as an antioxidant, protecting against ultraviolet and pathogens. In contrast, at high concentrations, Se acts as a toxin, reducing plant growth, inducing chlorosis, inhibiting protein synthesis, and causing early death of the plant (Kaur et al. 2014). Generally, when Se concentration in plants is >1 mg kg^{-1}, it is often toxic; below this value, it is beneficial to plants (Xue et al. 2001; Malik et al. 2011) (Table 12.1).

12.3 Se Bioavailability

Se bioavailability plays a significant role in Se-enriched agricultural products and the risk assessment of Se-contaminated soils. Data on Se bioavailability is needed to survey the nutritional content of Se in plants, to frame a decision to direct biofortification and phytoremediation methodologies, likewise as dietary recommendations (Fairweather et al. 2010). The requirement for measurement of Se bioavailability is especially significant as recent suggestions of potential health benefits related to various levels of Se consumption. However, the trouble isn't clear, as these are enormous variations within the Se content within the soil-plant system. Past investigations have shown that the total Se in the soil cannot address all Se bioavailability (Zhang et al. 2014; Dinh et al. 2018), while bioavailable Se is a key parameter that decides the versatility and toxicity of Se in the soil (Li et al. 2010; Thiry et al. 2012). Whenever Se is applied to the soil, a spread of physicochemical responses happens, similar to adsorption-desorption, precipitation-disintegration, oxidation-decrease, and methylation-demethylation. In the end, Se exists in a few chemical structures and displays different migration mobility and bioavailability inside the soil. Subsequently, during a complex soil-plant system, an exact evaluation of the bioavailability of Se and consequently the factors that influence it are essential for the safe execution of biofortification and phytoremediation systems in Se-deficient and Se-contaminated regions, respectively. The bioavailability of Se is not only hooked into the whole Se content but also more significantly on the Se fraction and speciation in soils (Tolu et al. 2014; Wang et al. 2018a, b). Subsequently, Se take-up and accumulation by plants are constrained by various Se fractions and its speciation in

Table 12.1 Comprehensive review of selenium application and purpose of study on different plant species and the metabolite profiling through different techniques

Plant species	Selenium application	Metabolite/s	Profiling technique	Principle analysis	References
Lepidium sativum (Garden Cress)	0–5 mg/L in hydroponic media for 14 days exposure along with 0–2 mg/L Cd exposure	Selenium, Cadmium, phenolics	ICP-MS, GC-DAD/ HPLC-diode array detector	Plant defense mechanism; Interaction of selenium with cadmium	Elguera et al. (2013)
Lepidium sativum (Garden Cress)	0–5 mg/L in hydroponic media for 12 days exposure along with 0–2 mg/L Cd exposure.	Glyoxal, methylglyoxyal	HPLC-diode array detector	Selenium toxicity; Plant defense mechanism	Gomez Ojeda et al. (2013)
Brassica napus (Rapeseed)	50 μM Se in hydroponics media for 3 & 7 days.	Selenium, sulfur estimation	ICP-MS; GC-MS (primary metabolites); ROS analysis (Fluorescence visualization)	Selenium toxicity; Plant defense	Dimkovikj and Van Hoewyk (2014) and Ahmad et al. (2020)
Brassica rapa (Rapeseed)	Seven days exposure with 25 μM Selenium under pot experiment in greenhouse	Total phenolics, anthocyanins, chlorophyll estimation, flavonoids, Glucosinolates	Spectrophotometric analysis using UPLC-ESI	Plant defense; Health remuneration	Thiruvengadam et al. (2015)
Brassica oleracea (Cabbage)	0–0.5 mM foliar spray for 4 weeks under pot experiment.	Glucosinolates, methylselenocysteine, selenium, and sulfur	HPLC-DAD, LC-MS, ICP-MS	Health remuneration; Functions of food	Tian et al. (2016)
Brassica oleracea (Cabbage)	10, 50, 100 μM different Selenium under pot experiment in greenhouse for 4 weeks	Total polyphenolics	HPLC-FLD	Functions of food	Mahn (2017)

(continued)

Table 12.1 (continued)

Plant species	Selenium application	Metabolite/s	Profiling technique	Principle analysis	References
Brassica oleracea (Cabbage)	Exposure of 25 μM selenium for about 7 days	Glucosinolates, methylselenocysteine, selenium and sulfur, amino acid profiling	HPLC-DAD, LC-MS, ICP-MS, UPLC-DAD	For Plant defense mechanism studies; for toxicity of selenium element	Tian et al. (2018)
Arabidopsis thaliana (Thale cress)	Application of about 30 μM selenium to germinated seeds	Selenium, ROS, and reduced glutathione	ICP, Florescence microscopy, and spectroscopy	Defense mechanism; function of food	Jiang et al. (2019)
Triticum aesativum (Wheat)	0, 12, 21, 38, 68, and 120 g ha^{-1} concentrations of Selenium through foliar spray	Selenium and sulfur	Atomic absorbance spectrophotometer, GC-MS	Antioxidant defense mechanism	Lara et al. (2019)
Oryza sativa (Rice)	Soil application of 47 and 36 g ha^{-1} of Se (as sodium selenate)	Chlorophyll estimation Antioxidant enzyme; spatial distribution of selenium and micronutrients in the biofortified rice	SPAD; X-ray fluorescence microscopy	Health remuneration	De Lima Lessa et al. (2019), Huang et al. (2018), Cui et al. (2010) and Chang et al. (2020)
Zea mays (Maize)	20 g/ha selenium foliar spray under field experiment, 1 μM applied under salinity stress	Rate of photosynthesis and chloroplast structure	Atomic absorbance spectrophotometer, GC-MS	Plant defense mechanism; regulation of selenium toxicity in plant cells	Ngigi et al. (2019), Jiang et al. (2017) and Fairweather-Tait et al. (2010)

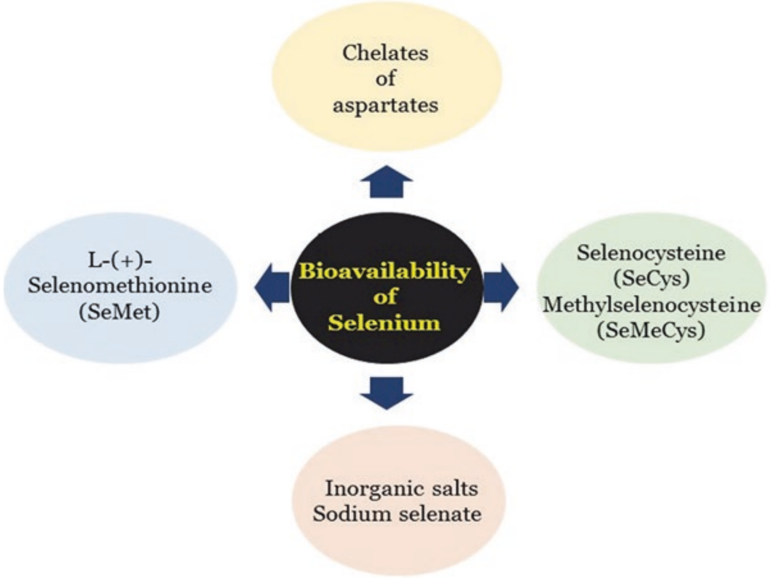

Fig. 12.2 The existing bioavailable forms of Se to crop plants

the soil (Salhani et al. 2003; Harada and Takahashi 2008). Se in soil fundamentally exists in four diverse oxidation states, specifically: Se(-II), Se(0), Se(IV), and Se(VI) (Stasinakis and Thomaidis 2010; Fordyce 2013).

Inorganic Se is the dominating form inside the soil but organic forms like selenomethionine (SeMet), selenocysteine (SeCys) and methylselenocysteine (SeMeCys) additionally are available [63] (Fig. 12.2). Among various types of Se, Se (IV) is a smaller amount soluble and available contrasted with Se(VI) (Peng et al. 2017). In addition, Se (IV) is a predominant species under reducing conditions, whereas Se(VI) is a prevalent species under oxidizing conditions. In this way (Seby et al. 1998), Se is less bioavailable under reducing acid conditions and more mobile and accessible under oxidizing conditions. In addition to different chemical structures in the soil, Se likewise exists in various geochemical fractions (Shaheen et al. 2017). The distribution of Se fraction inside the soil is organized according to its pronounced differences in solubility and bioavailability of different Se species.

Past investigations have proposed different consecutive extraction strategies to clarify the dissemination of Se fractions inside the soil (Chao and Sanzolone 1989; Qin et al. 2017). Generally, Se fractions in soil are often characterized as soluble Se (SOL-Se), exchangeable Se, and carbonate-bound Se (EXC-Se), iron (Fe)/manganese (Mn) oxide-bound Se (FMO-Se), OM-bound Se and elemental Se (OM-Se), and residual Se (RES-Se) fractions. The SOL-Se fraction is the most mobile and most effectively consumed by plants (Kamei-Ishikawa et al. 2007; Schiavon et al. 2013); it is considered as bioavailable Se (Ajwa et al. 1998; Dhillon et al. 2007). Consequently, SOL-Se portions are frequently used to assess Se bioavailability in soil and vital role in deciding Se fixations in plants (Wang et al. 2013; Dinh et al. 2017). EXC-Se fraction mainly refers to the Se(IV) bound with hydrous oxides (Ryden et al. 1987) and surface adsorbed by clay minerals (Bar-Yosef and Meek 1987; Chao and Sanzolone 1989) and humus (Zhang and Frankenberger 2003). EXC-Se fraction is definitely less bioavailable than SOL-Se but could open up for plant take-up (Kulp and Pratt 2004). Thus, both SO-Se and EXC are frequently characterized as bioavailable Se in the soil. OM-Se incorporates FA-and HA-bound Se, and records for over half of complete Se in Se-rich soils (Wang et al. 2018a, b). In the soil, the HA-bound Se is steady and hard to break down, though the majority of the FA-bound Se exists in low-molecular-weight forms and might be easily mineralized into inorganic Se and seleno-amino acids (Dinh et al. 2017; Supriatin et al. 2015). Thus, plants experience issues retaining HA-bound Se however effectively assimilate FA-bound Se. In this manner, the role of OM-Se in bioavailable Se inside the soil relies upon the extent of FA/HA-Se. FMO-Se basically refers to Se related with Fe/Mn, which is hard for plants to take-up (Ge et al. 2000). Besides, elemental Se is exceptionally insoluble and stable for plant take-up, and just a small level of nanoscale essential Se are frequently haunted by plant (Parfitt 1979). RES-Se primarily occurs in sulfide-bound Se and silicate minerals (e.g., feldspar, quartz, mica, and so forth) (Chao and Sanzolone 1989), which are inaccessible to plants (Zhang et al. 2014).

12.4 Factors Affecting the Bioavailability of Selenium

The bioavailability of Se plays a critical decisive role in agricultural products based on Se enrichment and to assess the risk associated with Se contamination. The nutritional content of Se in plants is also accomplished by assessment of its bioavailability for deciding the phytoremediation and biofortification strategies (Fairweather et al. 2010). The most common forms of silicon available in soil includes Se salts, such as elemental Se, selenate, selenide, and selenite. Among these forms, selenate is the more readily transported in plants and is poorly absorbed by the minerals in the soil. The elemental form of selenite is formed by biological or chemical reduction of selenite, a less soluble form of Se as compared to selenate. Several factors are responsible for the availability of Se in the soil; that is poor organic matter in soil, dry climatic conditions, high pH, high temperatures, and less waterlogging favor the higher ratios between selenites and selenates in soil. The following sections further elaborate the major factors responsible for the bioavailability of Se.

12.4.1 The Selenium in Soil: Chemical Complexities

The retaining of Se from soil mainly occur through precipitation which gets removed from soil through desorption, volatilization, dissolution, and leaching. All these processes are dependable on factors such as climatic conditions, physiochemical properties of soil, the type of plant, and agnomical attributes. The concentration of Se in soils is largely dependent on the absorption of Se on soil surfaces as reported by Goldberg (2011). We can conclude poor absorption of Se by soils enhances the rate of Se availability. Under reducing condition the Se(IV) is most stable and predominant form of Se in soil solution and in oxidizing conditions Se(VI) is most predominant form (Séby et al. 1998). For example, it is reported that absorption of Se in Se(IV) form is largely effected by physicochemical properties of soil such as pH, organic matter, presence of competitive anions, clays, and metal oxides (Lee et al. 2011; Violante 2013; Li et al. 2015). On the other hand, desorption also plays a critical role in the availability of Se, and low desorption rate is ultimately a detrimental factor for the uptake of Se by plants. The rate of Se desorption is found to be positively correlated with pH of soil and negatively with metal hydroxides (Li et al. 2015). For example, a pH range of 5.6 to 8.7 enhanced the Se concentration in solution phase, even though by dropping the pH from 5.6 to 3.6 results in reverse effects.

The immobilization of Se in the soils is largely influenced by complexation reactions. Earlier studies revealed that Se is involved in the complexation reactions with organic matter in soils were minerals such as aluminum and ion are richly found (Gustafsson and Johnsson 1994; Bruggeman et al. 2007; Fernandez et al. 2009; Dinh et al. 2019). Few studies also hypothesizes that Se leads complexation directly with the functional groups of organic matter (Dhillon and Dhillon 1999; Winkel et al. 2015; Dinh et al. 2019; Wang et al. 2018a, b).

The availability of Se in soil solutions is also directly influenced by dissolution and precipitation reactions (Adriano 2001). Moreover, immobilization through precipitation of Se also plays important role in Se availability. The Se-S precipitates were found to be stable at pH 7 indicating the critical role of pH in precipitation of Se (Geoffroy and Demopoulos 2011). The mobility and availability of Se are greatly influenced by its microbial transformation. In the environment, the Se is less oxidised mainly in reduced form. The reduced states of Se are grossly induced by various transformation, such as competitive electron acceptors, microbial activities, and environmental conditions (Eswayah et al. 2016). As far as environmental conditions are concerned, the Se reduction through microbes occurs through aerobic as well as anaerobic reactions (Bolan et al. 2014). The anaerobic reduction of Se is accomplished by microbes such as *Thauera selenatis*, *Sulfurospirillum barnesii,* and *Arseniciselenatis* (Stolz et al. 1999; Park et al. 2011). Microbes mostly under abiotic environmental factors also mediate the oxidation of Se (Bassil et al. 2018). For example, Liu et al. (2015) reported that once aeration in sol is improved, the microbial activities were enhanced resulting in the oxidation of Se(IV) to Se(VI). The aerobic oxidation of Se(IV) and Se(0) is also mediated by microorganisms in the diverse soils (Sarathchandra and Watkinson 1981). The biological process of Se methylation is another potential mechanism for bioavailability of Se in soils. The volatile and methylated Se is less toxic to plants (Bolan et al. 2014; Winkel et al. 2015; Vriens et al. 2016). The methylated Se is reported in soils with moderately oxidized or reduced conditions and the methylated form is usually found in reservoirs sediments (Masscheleyn et al. 1991). The biomethylation of Se is accomplished by organisms such as bacteria, fungi, and microalgae, and some plants have also been reported (Neumann et al. 2003)

12.4.2 Physio-Chemical Properties of Soil

Several factors such as organic matter, clay, pH, Eh, and presence of Fe/Al/Mn oxides greatly influence the bioavailability of Se in soils. The pH and Eh of soil play pivotal role in Se speciation and its bioavailability (Antoniadis et al. 2017; Shaheen et al. 2018). Lee et al. (2011), reported that Se is more available in alkaline soils rather than acidic soils. Due to variable charges, the soils usually tend to be negatively charged and it is reported that electrostatic repulsion occurs between the negatively charged Se(IV) and Se(VI) forms of Se (Lewis-Russ 1991). The later reaction results in release of Se from the soils thus enhancing its availability for plants.

The existence of Fe/Al/Mn oxides is another major factor for bioavailability of Se, due to their widespread ability of chelation (Muller et al. 2012). The Se (VI) is found to mediate electrostatic interaction with Fe/Al oxides (Fernandez et al. 2009). In this way, the capacity of Fe/Al oxides helps in contributing to Se availability. The soil organic matter has string cheating ability and large surface area and has been attributed to play a critical role in bioavailability of Se (Fakour et al. 2016; Ahmad et al. 2017). It is reported that low-molecular-weight organic acids augment release of Se usually found on the surface of the soil solid phase (Sharma et al. 2015; Dinh et al. 2019). In addition, it must be noted that soil organic matter generates negative surface charge leading to repulsion of Se oxyanions, thus improving the availability of Se (Dousova et al. 2015). Moreover, the higher clay content the bioavailability of Se is low (Yang et al. 2003). Due to the positive charge of clay, it has the ability to adsorb the Se oxyanions (Loganathan et al. 2014). Thus, there is a negative correlation between clay and Se availability (Feng et al. 2016).

Finally, a greater factor for accumulation of Se depends on the plant species. The plant Se accumulation capacity is related to the species, genotype, and growth stages. To some extent, this capacity determines how much Se in the soil can enter the food chain. The ability of absorbing Se from soil varies from one plant species to other (Terry et al. 2000). On the basis of accumulation of Se, plants are broadly categorized into the following three types (Schiavon and Pilon-Smits 2017):

- Se non-accumulators – these plants accumulate <100 mg Se kg^{-1} DW from soil.
- Secondary Se accumulators – these plant species accumulate 100–1000 mg Se kg^{-1} DW from soil.
- Se hyper-accumulators – plant species are the largest accumulators of Se with >1000 mg Se kg^{-1} DW.

Hartikainen (2005) reported that Se protects and promotes the growth of Se hyper-accumulators against severe conditions through the enhancement of antioxidant activity.

12.4.3 The Effects of Climatic Conditions

The climatic conditions directly influence the availability and absorption of Se in soil. Phenomenon such as deposition or soil retention of Se or sorption is driven by climatic change has largely influenced the Se availability and absorption (Jones et al. 2017). Other critical climatic factors such as evapotranspiration, temperature, aridity index, and precipitation greatly influence the Se concentration in diverse soil types (Jones et al. 2017; El-Ramady et al. 2015b). High precipitation and low temperatures are reported to decrease the accumulation of Se plants (El-Ramady et al. 2015a) Higher precipitation also results in higher leaching of Se resulting in excessive loss of Se and unavailability of Se. Agricultural management practices such as intercropping, rotation, irrigation, tillage pattern, and fertilization are critical for bioavailability of Se (Longchamp et al. 2013). The ploughing of soil helps in releasing the Se from deeper layers of soil and their by enhancing the absorption and utilization of Se by crop. The variability of Se is also dependent of plant species, supplementation of fertilizer and the climatic factor. The intercropping systems also influence the bioavailability of Se. Moreover, it is observed that supplementation of inorganic and organic fertilizers affects the availability of Se. In addition, mode of supplementation, type, and dosage of fertilizer are critical for bioavailability of Se.

12.5 Transport of Selenium in Plants

Transport of Se is a complex process demanding the uptake, translocation, and distribution of Se in plants. It is further dependent on different factors like plant species, development phase, type and amount of Se, physiological conditions, i.e., salinity and soil pH, role of membrane transporters, and mechanism used by the plants (Renkema et al. 2012; Zhao et al. 2005), and also depends on the type of soil. Alkaline soil approves selenate while acidic soil approves selenite, a diprotic weak acid with pKa1 and pKa2 of 2.46 and 7.31, respectively (Hopper and Parker 1999). These two types of Se differ mainly in their rate of absorption and mobility inside the plant (Zhao et al. 2005).

Plant roots can take up Se as selenate (SeO_2–), selenite (SeO_2–; HSeO; $HSeO^-$), or organo-Se compounds such as selenomethionine (SeMet) and selenocysteine (SeCys); however, colloidal elements of Se or metal selenides are ineffectual in absorption by plant roots (White and Broadley 2009). Among the various forms of Se, selenate (SeO_2^{4-}) is the most widespread type of bio available Se found in agricultural soils and is additionally more water soluble than selenite (Missana et al. 2009; Sors et al. 2005a, b). Mobility of selenate is higher in soil solution yet selenite has a stronger affinity to get absorbed by iron and aluminum oxides/hydroxides and to some extent to clays and organic matter (Fordyce 2013). Various experiments have been conducted on plants like Astralagus, *Beta vulgaris*, *Oryza sativa*, *Brassica oleracea*, *B. juncea,* etc. to demonstrate the relatively low rate of selenite uptake than that of selenate (Shrift and Ulrich 1969; Zayed et al. 1998). On the contrary, experiments conducted by Broyer et al. (1972) and Zhang et al. (2004) respectively showed higher rates of selenite transportation than that of selenate in *Astragalus crotolariae* and *Glycine max* (Zhang et al. 2004). Surprisingly, equal transportation rates of both selenite and selenate were observed in *Phaseolus vulgaris* in a 3-h experiment (Arvy 1993). The differences in the phosphate and sulfate concentrations in both the environment and the plant itself constitute the main reason behind these disparities.

Transporters of Se found in the root cell membrane help in the movement of Se from the soil to the plant itself. Specifically, phosphate transporter mechanism regulates the movement of selenite (Li et al. 2019), while movement of selenate occurs with the help of sulfate transporters and channels (Zhang et al. 2004; Feist and Parker 2001). The decision for the selection between these two transporters mainly depends on the nutritional status of the plant (White et al. 2004). When sulfate concentrations on the outside is higher as compared to the plant, Se preference for the transporters decreases and inducible sulfate transporters exhibit greater selectivity for sulfate over selenate than constitutive active sulfate transporters (White et al. 2004). However, in case of *Oryza sativa* and *Lycopersicon esculentum*, the presence of sulfur had almost no effect on the uptake of selenite (Zhang et al. 2006; Asher et al. 1977). Similar results were obtained in an experiment performed on Triticum spp. (Jiang et al. 2018). Also, presence of phosphorus (P) in the environment is reported to affect the uptake of Se. *Astragalus canadensis*, *Astragalus bisulcatus* (Se hyper-accumulator species), *Trifolium fragiferrum*, and *Lolium perenne* displayed a 20–70% decline in the rates of Se uptake due to ten times increase in the concentration of P (Hopper and Parker 1999; Broyer et al. 1972). Similarly, reduced P concentration within the environment leads to an increased activity of phosphate transporter genes, causing a big increase within the uptake of selenite. Wheat showed 60% rise in the uptake of selenite when grown in P deficit environment (Muchhal et al. 1996; Muchhal and Raghothama 1999). Additionally, Li et al. (2008) have also reinforced the earlier experiments highlighting the negative impact of increasing phosphorus concentration on selenite uptake, thereby elucidating selenite uptake by phosphorus transporters. However, reduction within the rates of selenate under S deficit conditions was more profound than that of selenite under P starved conditions. The possible reasons for this observation are: (i) strong effect of phosphate on the Km of selenite influx, (ii) higher affinity of phosphate transporters for selenite as compared to sulfate transporters for selenate, and (iii) varied degrees of up-regulation of genes under S or P deficit conditions (Barrow and Whelan 1989).

SeCys and SeMet are also known to be transported by the transporters that increase the uptake and signaling of cysteine and methionine within the plant. Three genes viz., SHST1, SHST2, and SHST3 encode the sulfate transporters have been isolated from an equatorial legume *Stylosanthes hamata* (Smith et al. 1997) and one gene (HVST1) was isolated from barley (*Hordeum vulgare*) (Smith et al. 1997). The uptake of selenite is not at all affected by the membrane transporters. The uptake of H_2SeO_3 is catalyzed by homologs of the rice aquaporin channel OsNIP2;1

(Pommerrenig et al. 2015) while phosphate transporters, such as rice OsPT2 are known to enhance $HSeO^{-}$ uptake (Zhang et al. 2014).

12.6 Accumulation of Selenium in Plants

Plant species change a few significant degrees in their ability to accumulate and endure Se (White et al. 2007). Based on maximum Se levels in shoot tissues inside the field, species could likewise be named Se hyper-accumulator (>1000 mg Se.kg^{1} DW), Se accumulator (100–1000 mg Sekg^{1} DW), or non-Se accumulators (Brown and Shrift 1982; White et al. 2007). Se hyper-accumulation is found in 4–5 genera from three unique families, and likely advanced autonomously in every ancestry. Indeed, even within the genus *Astragalus*, Se hyper-accumulation might have evolved multiple times, decided from its occurrence in more derived taxa that don't form a natural group with a common ancestor. The polyphyletic beginning of Se hyper-accumulation recommends that this attribute can evolve relatively easily and might be controlled by generally couple of genes. It is conceivable that there is a key gene like a transcription factor that controls a bunch of genes that together cause the disorder of hyper-accumulation and hyper-tolerance. A few studies have been carried out to have better understanding of molecular mechanism involved in Se tolerance and accumulation, both in non-hyperaccumulators and non Se accumulators (Van der Ent et al. 2013). A few quantitative trait loci (QTL) were identified that co-segregated with the upper selenate resilience in accession Columbia contrasted with *Landsber gerecta* (Zhang et al. 2006). A few Se-related genes are available within the identified QTL regions, including a selenocysteine methyl transferase (SMT) homologue, an ATP sulfurylase, and a serine acetyl transferase (SAT). In another report by Zhang et al. (2006) comparing nineteen diverse ecotypes of Arabidopsis with variable tolerance and accumulation of Se, the trait tolerance and accumulation were observed to be not associated (Zhang et al. 2006). Additionally, tolerance to selenate and selenite appeared to be controlled by different loci.

In *A. thaliana*, a transcriptome analysis was performed on plants developed with or without selenate (Van Hoewyk et al. 2008). It was discovered that genes involved in ethylene and jasmonic acid pathways were upregulated by Se. In concurrence with a role for these hormones, Arabidopsis mutants with an imperfection in genes associated with ethylene synthesis, ethylene signaling, and jasmonic acid signaling were shown to have reduced tolerance to selenate, and overexpression of a protein involved in ethylene signaling resulted in increased selenate resistance (Van Hoewyk et al. 2008).

12.7 Interaction of Selenium with Macronutrients and Heavy Metals

The Se availability and its interaction with macronutrients are being studied for long to trace their role in plant metabolism and growth. For instance, it is reported that nitrogen-based fertilizers play a pivotal role in accumulation and bioavailability of Se, hence enhancing the crop production (Cui et al. 2010). Se concentration in rice grains was found increased upon supplementation of nitrogen-based fertilizers as reported by Reis and coworkers (2018). In low Se soils, it was found that nitrogen fertilizers enhanced translocation and uptake of Se from soil (Chen et al. 2016). Following key reports further highlight the positive role played by nitrogen in Se accumulation, transport, and metabolism:

- Enhances the Se metabolism and assimilation (Kim et al. 1999)
- Promotes Se absorption in addition to P, K, S (Chen et al. 2012)
- Nitrogen fertilizers promote uptake of Se (Dinh et al. 2019)

Further, it is reported that Se uptake was influenced by phosphorus supplementation and depends on Se speciation. The bioavailability and concentration of Sein wheat are found to be enhanced by supplementation of P fertilizers. Moreover, later attribute is grossly dependent on rate of Se supplementation (Li et al. 2015). The aforementioned reports suggest that in agricultural practices for higher production, it is critical to apply P fertilizers for higher yield and Se concentration in grains.

Due to chemical similarities between sulfur and Se, it is found that both elements follow identical pathways of metabolism. Duncan et al. (2017) reported that application of S-fertilizers has significant potential on bioavailability of Se in several plant species (Duncan et al. 2017). The chemical and physical behavior of Se(IV) was found to be largely influenced by supplementation of S. the enhancement of soil organic matter, reduction in soil pH, increase in microbial activities by supplementation of S fertilizer have a net positive effect on accumulation and transport of Se(IV) (Liu et al. 2015). It must be noted even if the Se content of soil is less, the uptake and concentration of Se in plants can be enhanced by supplementation of S-fertilizers.

Due to its ubiquitous existence and high toxicity, As has been considered as the most widespread toxic heavy metal in several countries, such as Southeast Asia, China, Europe, and United States (Rahman et al. 2014). Due to the chemical similarity of Arsenic (As) and Se, it must be assumed that both may cotransport from soil to aerial parts of plants. The accumulation of Se and As is also dependent on the plant species. Furthermore, it is reported that both As and Se share similar transporters, establishing a competitive interaction (Li et al. 2016). It is observed that Se retards the transport of As to the aerial parts of plants (Camara et al. 2018). Hu et al. (2013) reported similar effects of As transport upon supplementation of Se in rice (Hu et al. 2013). Further, Se causes hindrance in transport of As from soil to root and then root to shoot in rice plants (Zhou et al. 2017).

Mercury (Hg) is another toxic element and is highly toxic to humans even in low concentrations (Wang et al. 2016). The Hg is found to be controlled by antagonistic behavior of Se in rice plants. The elemental Hg was found to be directly took up by rice leaves and then resulting in formation of Hg-Se complex in rice leaves (Chang et al. 2020). In most plant species the Hg-Se complexes is insoluble due to precipitation and hence reducing the bioavailability of Hg. Meng et al. (2014) observed drastic reduction in distribution of Hg in endosperm and embryos upon administration of Se (Meng et al. 2014).

Cadmium (Cd) is also toxic to humans and is considerably accumulated by crop plants (Hamid et al. 2019). The potential solution to Cd toxicity is accomplished by administration of Se (Affholder et al. 2019). The antagonistic approach between Cd and Se depends on factors such as dosage, Se species, and plant species. It is reported that the Cd-Se complexes formed in soil is not used or transported by the plant roots (Shanker et al. 1995). The uptake of Cd from the soil is also affected by the supplementation of Se (Huang et al. 2018). In particular, Se(IV) was found to decrease the accumulation of Cd in rice grains (Liao et al. 2016). In addition, the accumulation and transport of Cd concentration in plant tissue are also decreased by the supplementation of Se in rice crops (Huang et al. 2018). It must be kept in mind that Se and Cd employ different transporters, so negating the competitive effect for translocation from roots to aerial parts of plants. Khan et al. (2015) found that Se played a critical role in reducing the ethylene content, increasing the accumulation of proline, and enhancing the activities of enzymes such as glutathione reductase (GR) and glutathione peroxidase (GPX) under Cd stress in wheat plants (Khan et al. 2015). In summary, we can conclude that Se plays a critical role in controlling the toxicity of metal ions such as As, Cd, Hg, etc.

12.8 Conclusion and Future Perspectives

Food security is ultimately attained by improvement of crop plants through diverse range of technical inputs and use of fertilizers providing adequate supply of nutrients (Naik et al. 2021). Keeping in view the importance of nutrients most especially inorganic nutrients such as Si, P, N, Se, etc., we aimed to discuss the critical importance of Se in playing pivotal role for enhancing crop production. The important aspects such as its critical role as important micronutrient, bioavailability in soil, factors affecting its bioavailability, and then transport mechanism are discussed in detail to have great insights into the existence and role played in plant growth and metabolism. In this context, an exhaustive account of Se biofortification and its positive role in upregulating the accumulation of elements is of prime importance (Hou et al. 2020). Besides, we disused the role of Se interaction with N, P, and S and its critical role in circumventing the toxic effects of heavy metals such as As, Hg, and Cd. We believe it is pivotal to have an in-depth know-how regarding nutritional importance of Se, its existence in soil, and interactions with components of rhizosphere and root system. Moreover, transport of Se from the roots to aerial parts, its positive role in transporting or assisting the transport of other micronutrients needs to be explored at large. As briefly discussed in the last few sections of this chapter, it is the need of the hour to have a detailed understanding of role played by Se to decline the toxic effects of heavy metals on plant growth and metabolism. Moreover, understanding the role of omics techniques to unravel the molecular mechanism governing the sustainable production of crops through supplementation of micronutrients such as Se must be further unearthed (Zargar et al. 2015, 2016). To further clarify the role of Se in crop improvement scientists need to authenticate its role through field trails and trace the actual standard conditions of supplementations through precise agricultural practices.

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Chapter 13
Effect of Selenium Application on Quality Improvements of Seeds and Fruits

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13.1 Introduction

Low selenium doses have resulted in many problems for global public human health. Selenium (Se) is an essential trace element for many organisms, and it has a potential effect on humans, plants, and animals. The plant product enriched with Se is the principal source of human and animal Se intake (Puccinelli et al. 2017). However, its shortage in the soil worldwide directly affects its content in plants and can cause many diseases in humans and animals (Chu et al. 2013). Insufficient Se intake can induce epilepsy, increase fertility, and cause immunodeficiency. Se has anti-aging, anticancer, and immunity-boosting activities (Zeng and Combs 2008).

Exogenous Se supplementation is a bio-fortification strategy, which improves crop yield and quality (Du et al. 2019). Researchers have identified that appropriate Se supply could not only increase Se content in plants, but also stimulate growth and development of plants and increase the resistance and antioxidant ability of plants subjected to a stressful environment, like drought and salt stress (Zhou et al. 2020; Rady et al. 2020; Karimi et al. 2020). The primary purpose for that Se is a

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M. A. Hossain et al. (eds.), *Selenium and Nano-Selenium in Environmental Stress Management and Crop Quality Improvement*, Sustainable Plant Nutrition in a Changing World, https://doi.org/10.1007/978-3-031-07063-1_13

vital component of several proteins like the antioxidant enzyme, which can effectively remove oxygen-free radicals (Chu et al. 2013). Se assimilated within the plant in the same pathway as sulfur (S). S is reacted with the amino acids to create the organic forms; selenomethionine and selenocysteine (Sors et al. 2005). However, low amounts of Se act as an antioxidant, while high doses stand as a prooxidant in plants (Hartikainen et al. 2000). Se toxicity depends on the chemical formula and concentration of Se in environmental and biological systems (Li et al. 2010). The inorganic types of Se are selenate (Se VI) and selenite (Se IV). These forms are toxic at higher doses. Meanwhile, selenomethionine (SeMet), selenocysteine (SeCys), and Se-methyl selenocysteine (SeMeCys) represent organic forms in plants. These forms are amino acids that have abundant benefits for health (Hartikainen 2005; Arulselvi 2014).

Elevating Se content in food plants can effectively prevent Se deficiency in human food. Thus, increasing Se concentration in crops stimulates widespread concern for researchers and farmers (Song et al. 2018; Marques et al. 2020; Yan et al. 2021). Low dietary intake of Se by a human is due to obtaining foods with low Se concentration (Arulselvi 2014; Ullah et al. 2019). In this situation, there is an urgent need to apply effective strategies for increasing the organic Se concentration in edible plant products to avoid and prevent Se deficiency. Exogenous treatment of Se could mainly increment Se levels in seeds and fruits (Puccinelli et al. 2017; Babalar et al. 2019; D'Amato et al. 2020). Considerable studies have demonstrated that exogenous Se application increased Se content in the seed and fruit crops, such as wheat (Ali et al. 2017), rice (Marques et al. 2020), and tomato (Arulselvi 2014). Our objective in this chapter is to highlight the efficiency of the different strategies of Se application in improving the quality of edible portions (seeds and fruits) of plants.

13.2 Selenium (Se) in Soil

The Se concentration in soil ranges between 0.1 and 2.0 mg kg^{-1} depending on the geographical area (White 2018). Moreover, the Se level in the soil depends on the bedrock from which the soil segment originates and the geochemical mechanisms that produce the soil components. In clay soils, Se content was higher than in coarse mineral soils. The mean Se content in clay soils was 0.29 mg kg^{-1} and in coarse soils is 0.17 mg kg^{-1}. The organic soil contains the highest Se concentration (0.46 mg kg^{-1}) (Natasha et al. 2018). Se could be present in four distinct oxidation forms: selenate, selenite, elemental Se, and organic selenide. Se bioavailability in the soil varies with different soil properties and compositions. In other words, the pH, the soil redox capacity, organic matter, clay amount, and chemical form determine the bioavailability of Se in the soil (Galić et al. 2021a). Mainly, Se oxyanions (SeO_4^{2-} and SeO_3^{2-}) are highly water soluble, stable, and possibly mobile in oxic natural ecosystems.

Se speciation in the soil is controlled by three main mechanisms: oxidation vs. reduction, mineralization vs. immobilization, and volatilization. Se is more immobilized in acid and reduced soils (Li et al. 2017). In acidic soils, iron in a colloidal state and Se-squioxides produce the unavailable ferric selenite (Galić et al. 2021b). Se gently oxidizes to selenite or selenite depending on the pH of the soil. Under reductive soil conditions, pH < 4, selenite or selenate is reduced to selenide or Se metal. These forms have low mobility (Wang et al. 2017). Moreover, organic matter interacts with Se in different ways to immobilize or release Se in the soil (Dinh et al. 2017). The dominant inorganic Se forms in cultivated soils are selenite and selenate. Selenate is more water-soluble and available to take by plants under alkaline and oxidizing soil conditions (Hall 2018).

13.3 Se Uptake and Assimilation in Plants

Many factors influence the absorption of Se by plants and its accumulation in plant parts. These factors include the Se concentration in the soil, the chemical form of Se, soil pH, the redox potential of the structure of soil components, mineral contents, and rain and atmospheric precipitation. However, Se seems to be an essential micronutrient in 33 microalgae species. It is not for the higher plants. In addition, the Se form is the main factor that determines the entire amount of Se in the soil (Surai 2007). Se can be available for plants in inorganic chemical forms such as selenite (SeO_3^{2-}) or selenate (SeO_4^{2-}) or the form of seleno-amino acids like SeMet as an organic form (Jezek et al. 2012). Meanwhile, selenite represents a water-soluble and commonly available Se pool for plants. The elementary Se (Se^0) and selenides are not available for plants because they exist in reductive soil conditions (Zayed et al. 1998). In a soil environment, the ions are passively transported to the root through diffusion or mass flow mechanisms, with water uptake and pull strength resulting from the vital transpiration process. However, selenate ions and organic Se can enter the roots actively against electrochemical gradient (Terry et al. 2000).

The absorption of SeO_4^{2-} is mediated by a sulfate transporter into the plant root via the plasma membrane and is then converted into Se amino acids (Schiavon and Pilon-Smits 2017). In the Se assimilation, selenite is reduced to selenide, and then incorporated into SeCys. The synthesis of SeCys probably occurs in mitochondria, chloroplasts, and the cytosol of plant leaves, and SeCys acts as a precursor of SeMet, which can be converted to other organic Se forms via metabolic processes (Jezek et al. 2012). The uptake of SeCys and SeMet by wheat and canola is 20-fold higher than that of selenate or selenite. The reason may be due to the absorption of organic forms of Se via amino acid permease (Schiavon and Pilon-Smits 2017). Similarly, SeO_3^{2-} likely enters via a PO_4^{3-} transport pathway into the root cells (considered an active process). Selenite is reduced to other Se compounds in the root cells. Reduction of SeO_3^{2-} in enzymatic or non-enzymatic ways produces Se^{2-} which reacts with O-acethylserine, to synthesis Se-Cys. However, the accumulation of Se-Cys inhibits Se metabolism in an enzymatic way. The high content of Se-Cys in root cells, does not block Se metabolism in a nonenzymatic way (Jezek et al. 2012).

The competitive interaction of Se is related to the absorption and transition of S. Moreover, the force of competition between Se and S depends on the forms of each ion. There are similar mechanisms of their absorption, transport, and assimilation because of the chemical similarity of Se and S. Based on the competitive interactions in the availability of ions and uptake, increment of Se level in plant organs can not only limit the levels of N, P, and S but also inhibit the absorption of other heavy metals such as Zn, Mn, Fe, Cu, and Cd. In contrast, the supply with N, P, and S can minimize the absorption of Se by roots. This process maintains the available Se in the soil at a safe threshold (Kabata-Pendias 2000).

Based on the ability of plants to uptake and accumulate the Se forms, plants have been divided into three groups:

- *Se non-accumulators*: This group includes most of the plants: cereals, vegetables, fruits, and many weed species growing on common soils which can absorb up to 25 mg Se/kg of dry matter (Jezek et al. 2012). There are differences among plant species growing on an equivalent region concerning the quantity of absorbed Se. The typical extent of Se content in these plants is 0.01–1.0 mg/kg of dry matter (Zayed et al. 1998).
- *Secondary Se accumulators:* These plants growing on soils with low and medium reserve Se can absorb 25–100 mg Se/kg of dry matter. Concentrations of Se in their tissues generally exceed 1 mg/kg. Plants of this group are tolerant to soil salinization (Terry et al. 2000). This group includes many different species, like *Atriplex*, *Aster*, *Astragalus*, *Castilleja*, *Brassica*, *Comandra*, *Machaeranthera*, *Grindelija* (Zayed et al. 1998; Jezek et al. 2012).
- *Se (hyper)accumulators:* These species grow on soils rich in Se higher than 5 mg/kg of soil (Gupta and Gupta 2000). Plants can contain 100–10,000 mg Se/kg dry matter. This group includes *Machaeranthera, Astragalus, Stanleya, Cardamine, and Haplopappus*. Se accumulators can contain a hundred times more Se than Se non-accumulators growing on an equivalent soil (Jezek et al. 2012).

13.4 Strategies of Se Enrichment in Plants

13.4.1 Selenium as a Seed Priming Agent

Plant seeds can uptake Se from the external medium and assimilate it during germination. Seeds soaking with Se represents a simple, low risk, low cost, and effective method to increase plant tolerance under abiotic stress (Nawaz et al. 2013; Ibrahim 2016). The seed priming strategy increases seed vigor and synchronization of germination in many crops (Du et al. 2019). Soaking time depends on crop species in which seed hydration reaches a point where germination-related metabolic processes activate before the emergence of the radicle (Lutts et al. 2016). Many of the recent studies emphasize the standardization of seed soaking techniques to induce

Table 13.1 Effect of selenium as a priming agent on quality of germination in *Brassicaceae* plants

Plant species	Se dose	Nutritional value	References
Brassica vegetables (broccoli, cauliflower, green cabbage, Chinese cabbage, kale, and Brussels sprouts)	50 µM Sodium selenate	↑SeM, SeCys, SeMetCys without negative effects on glucosinolates	Ávila et al. (2014)
Brassica oleracea (var. italica) (broccoli) 5 days	100 µM Sodium selenate sodium selenite	Se 85 µg g^{-1} DM ↓≈polyphenols, ↑anthocyanins, ≈GLS (sulphoraphane variable among cultivars)	Tian et al. (2016)
B. oleracea (var. italica) (broccoli) *Sinapis alba* (mustard) *B. oleracea* (var. *capitata* f. *alba*) (white cabbage)	10 mg of Se L^{-1} Se oxide	↓antioxidant activity, ≈GLS content 400 µg g^{-1} DM 138 µg g^{-1} DM 382 µg g^{-1} DM	Piekarska et al. (2014)
B. oleracea (var. italica) (broccoli) *B. chinensis* (var. pekinensis) (packchoi) *B. albogabra* (kale)	30, 60, 90, 120, and 150 mg of Se L^{-1} sodium selenate	SeMet, SeMeCys 467 mg kg^{-1} 312 mg kg^{-1} 156 mg kg^{-1}	Piekarska et al. (2014)
B. oleracea (var. italica) (broccoli)	50 µM Sodium selenate	↑antioxidant activity and phenolics 132 µg g^{-1} DM	Bachiega et al. (2016)

biosynthesis of promoting hormones, early DNA replication, higher ATP biosynthesis, osmotic adjustments, and membrane reorganization through restoring their original structures and reducing leakage of metabolites (Johnson and Puthur 2021). Tables 13.1 and 13.2 report the studies of Se as a priming agent on *Brassicaceae* and *Graminaceae* plants.

Se as a seed priming agent increases seed activity and vitality (Jezek et al. 2012). Se is absorbed during the germination of seeds and improves germination quality (Chomchan et al. 2017) and growth of seedling and vitality (D'Amato et al. 2020). This element also ensures the high quality of seed germination for the establishment of healthy seedlings. Se also enhances the antioxidant and defensive substance contents and activities in plants (Frias et al. 2009). Se priming in rice seed decreased the electric conductivity (EC) of seed leachates, lipid peroxidation, higher α-amylase activity, and higher free sugars levels while inducing antioxidant systems (Khaliq et al. 2015). Furthermore, Se priming was a beneficial method in promoting the emergence and growth of rice seedlings. The improved emergence of rice seedlings after seed soaking was parallel to the enhancement of α-amylase activity, greater soluble sugars contents, and higher respiration rate (Wang et al. 2016). Priming of seed with 0.8 Se L^{-1} was more beneficial in increasing the quality of seed germination and growth of seedling than 1.0 mg Se L^{-1} (Moulick et al. 2016).

Besides its influence on quantitative parameters, Se priming may increase the quality of the edible plant parts, as recently published by Guardado-Félix et al. (2017) and Serrano-Sandoval et al. (2019) in the case of isoflavonoid contents and

Table 13.2 Effect of selenium as a priming agent on quality of germination in *Graminaceae* plants

Plant species	Se dose	Nutritional value	References
Oryza sativa (rice)	5, 10, 15, 20, mg of Se L^{-1} Sodium selenate Sodium selenite	SeMet, $SeCys_2$, 300–500 mg kg^{-1} DM ↑PAs (free and conjugated), ↓carotenoids	D'Amato et al. (2018a)
	10, 20, 30, and 40 mg of Se L^{-1} Sodium selenite	10–25 mg kg^{-1} DM ≈polyphenols	Chomchan et al. (2017)
Rice cultivars (Super and Shaheen Basmati)	15, 30, 45, 60, 75, 90, and 105 μmol L^{-1} selenium	↓electrical conductivity ↓lipid peroxidation, ↑ α-amylase activity, ↑soluble sugars, ↑enzymatic antioxidants ↑chlorophyll contents, ↓total phenolics	Khaliq et al. (2015)
Rice	50 μM sodium selenite	↑α-amylase activity, ↑soluble sugars ↑respiration rate	Wang et al. (2016)
Spring Wheat (*Triticum aestivum* L.)	0.75 μM priming application	↑the yield attributes Maintain plant water status	Nawaz et al. (2017)
Secale cereale (rye)	10 mg of Se L^{-1} Se oxide	53 μg g^{-1} DM ↓antioxidant activity, ≈GLS	Piekarska et al. (2014)

antioxidant capacity of chickpea (*Cicer arietinum* L.). In mung bean sprouts, inorganic Se can transform into organic Se compound (SeMe-SeCys) through germinant bioconversion (Tie et al. 2016). In addition, exogenous application of Se, as priming agents, increased the content of phenolic acids, especially in their soluble conjugated forms in *Oryza sativa* (D'Amato et al. 2018a). In the case of sprouted amaranth seeds, Se in the form of sodium selenite enhanced polyphenols by increasing the activity of GPX (Pasko et al. 2015).

Moreover, the supplementation of selenate or selenite increments the quality of seeds via significantly decreased content of erucic acid and increased the oleic acid fraction in rapeseed seeds (Liu et al. 2017). Furthermore, the supply of selenite (priming) increased essential fatty acids, linoleic and alpha-linolenic acids, which are precursors of polyunsaturated fatty acids of amaranth plants (Pasko et al. 2015).

13.4.2 Selenium Application in Hydroponic Nutrient Solution

Se enhances crop development and delays aging. Besides the action on the physiological mechanisms of various plants, regulated increments in Se content at safe and benefit levels of the green products. The Se application in the nutrient solution increases Se levels in seeds and fruits. Se enrichment can not only raise Se content

Table 13.3 Effect of sodium selenate applied in the nutrient solution on improving the quality of tomato (*Solanum lycopersicum* L.) fruits

Sod. Selenate dose	The results	References
0.5, 1 mg Se L^{-1}	11 mg kg^{-1} DW Decrease ethylene	Pezzarossa et al. (2013)
1.0 mg of Se L^{-1} (in the nutrient solution 2 weeks after transplanting)	In fruits (µg of Se g^{-1} DW): 10.28–11.46 ↑Se content, ↓β-carotene content, ↓ethylene, ↑delay in the onset of fruit ripening	Pezzarossa et al. (2014)
1–1.5 mg of Se L^{-1}	In fruits (mg kg^{-1} DW): 0.94–2.76 (1 mg L^{-1} treatment), 2.08–3.54 (1.5 mg L^{-1} treatment) ↑delayed fruit ripening, ↑shelf life, ↑delayed lycopene and *β*-carotene synthesis, ↑chlorophyll degradation	Puccinelli et al. (2019)

in plants but also control the plant development and improve antioxidant capability in grains. Se levels of 0.0 (as control), 0.5, 1.0, and 2.0 ppm were added to the nutrient solution to increase the growth and fruit quality of tomatoes grown under hydroponic conditions. Fruit number and fruit weight were the highest after 0.5 mg/L Se application. Fruit dry matter was the highest in the control ones. The fruit firmness showed a progressive increase with raising Se levels. The soluble solid levels were not changed by adding Se. The soluble sugar concentration was reduced with incrementing Se levels. The contents of lycopene and Se in tomato fruit positively changed with raising Se doses (Lee et al. 2007). The effect of Se application in nutrient solution on tomato fruits is shown in Table 13.3.

Selenate at 5 µM and 10 µM was added through the roots of *Solanumlycopersicon*. Se induced the phenolic substances and decreased Mo, Cu, Fe, and Mn % in roots. Application of selenate per plant with low level (2.0 mg), or high level (20.0 mg) led to Se-enrichment of fruits at a safe level. The Se-enriched fruits exhibited increased flavonoids; chalcone, kaempferol, and naringenin contents and decreased cinnamic acid content. Hence, tomato fruits could be safely improved with Se. Se enrichment might enhance the level of different nutraceutical substances (Schiavon et al. 2013). In tomatoes, the application of selenate to the hydroponic system or soil, delayed senescence, extended the vegetative period, and improved the development of fruits (Pezzarossa et al. 2013, 2014; Puccinelli et al. 2019).

Se bio-fortified fruits showed a delay in the fruit ripening. The Se application had a positive role in affirming the sensory and the post-harvest quality by decreasing ethylene formation in tomato fruits. Se at 0.5 or 1.0 mg/L increased lycopene in association with a pronounced increase in quercetin (Pezzarossa et al. 2013). Se at 1.0 mg/L significantly reduced lutein and β-carotene level in fruit. The lower β-carotene content might delay fruit ripening. Thus, Se biofortification of tomatoes might be economically beneficial for farmers. Supplementation of Se (1 mg L^{-1}) in hydroponics-enriched tomato fruits could provide a rational supplement of Se. That means that the Se in a nutrient solution is essential for producing fruits with beneficial health properties for humans (Pezzarossa et al. 2014). The Se application improved the nutritional values of tomato fruits, the forms of organic Se, MetSeCys, and SeMet in the fruits (Arulselvi 2014), and the antioxidant capacity (Castillo-Godina et al. 2016).

Interestingly, Se application has been found to delay senescence and fruit ripening in many plant species, which led to a decline in postharvest losses (Businelli et al. 2015). The delay in fruit ripening might depend on lower ethylene generation. This Se-induced decrease in ethylene synthesis might be related to the increase in the level of organic Se; SeMet compared to methionine (Met), which acts as a precursor in the biosynthesis of the ethylene (D’Amato et al. 2020).

13.4.3 Soil Application of Selenium

Because of the reduction and sorption reactions, Se must be applied in the fertilizers every year and to crops, to maintain a sufficient Se concentration in agricultural products. Utilization of the fertilizer Se by plants is usually 5–20%. The residual Se remains in an insoluble form is unavailable to the plants (Jezek et al. 2012). For this reason, to make sure long-term sustainability, Se in soils and within the organic form must be known before any biofortification strategy is widely implemented. The residual Se may be leached, volatilized, retained in the soil environment, strongly absorbed by iron or aluminum oxides, or retained in non-soluble elemental forms (Broadley et al. 2010).

Treatment of soil with selenate and selenite (0–10 mg kg^{-1}) increased the Se content in ryegrass seedlings. There is a strong correlation between shoot Se content and GSH-POX activity (Cartes et al. 2005). The higher shoot Se concentration in selenate-treated plants suggested that the activity of this enzyme was related to the chemical form of applied Se rather than with the concentration of Se in plant tissues. The soil application of selenate fertilizers proved to be more effective to increase plant Se concentrations than selenite fertilization and hence selenate is the predominant form of Se in Se fertilization of plants (Wang et al. 2013). Soil application of the trace element Se can increase organic Se forms (SeCys and SeMet) in lentil seeds (Ekanayake et al. 2015).

Se application in the soil significantly increased the Se content in dry matter of roots, straw, and wheat grains. The application of 0.2 mg Se kg^{-1} in soil created the greatest Se concentration in grain (0.732 mg/kg), straw (0.227 mg/kg), and roots (1.375 mg/kg) dry matter, whereas rock bottom dose of Se (0.05 mg Se kg^{-1} of soil) gave 0.155 mg Se kg^{-1} in grain. The results cleared that Se content was highest in wheat grain and lowest within the straw dry matter (Ducsay et al. 2009). Similarly, the soil application increased shoot dry weight and grain yield of the purple-grained wheat cultivar (202 w17) and common wheat cultivar (Shannong 129) (Xia et al. 2020). The effect of Se application in the soils to improve the nutritional values of crops is shown in Table 13.4.

The treatment of wheat plants in Australia with organic Se form may be a cost-effective strategy for increasing the organic Se content in wheat grains and high uptake of Se in animal and human foods. As stated above, the problem connected

Table 13.4 Effect of the soil application of selenium on the nutritional values of plant seeds

Plant species	Se source	Se dose	Nutritional value	References
Zea mays L. (Dekalb DKC4316, FAO 300)	Sodium selenite	200 g Ha^{-1}	↑SeMet, ↑SeCys ↑inorganic and organic Se forms, ↑xanthophyll, ↑salicylic acid, ↓hydroxycinnamic acid content, ↑antioxidant activities	D'Amato et al. (2019)
Zea mays L.	Sodium selenate	5.0–20.0 g Ha^{-1}	In grain (mg of Se kg^{-1} DW): 0.042–0.068, ↑Se concentration	Ngigi et al. (2019)
Triticum aestivum L. (cv. Jordão, bread wheat, TA)	Sodium selenate Sodium selenite	4, 20, and 100 g Ha^{-1}	In grain (mg of Se/kg DW): from 0.76 (selenate soil treatment) to 2.98 (selenate foliar spray) ↑SeMet	Galinha et al. (2014)
Glycine max L.	Sodium selenite	0.9 mg kg^{-1} of soil	In bean (mg of Se/kg DW): 75, ↑SeMet, ↑SeCys	Chan et al. (2010)
Raphanus sativus L. (cv. Saxa)	Sodium selenate	5–20 mg/pot	↑SeMet, SeCys Se in roots, 0.75–1.51 ↑phenolic, ↑cysteine, ↑glutathione, ↑glucoraphanin, ↑total N, ↓polyphenols in hydroponics, ↑cysteine, ↓glutathione, ≈polyphenols	Nothstein et al. (2016)

with the management of Se enrichment is the control of the concentration of Se applied to avoid toxicity. The researchers added Se in the form of selenate at fertilizing rates of up to 120 g ha^{-1} in field trials and 500 g ha^{-1} in pilot trials in soil and added 330 g ha^{-1} of foliar Se applied with low S concentrations (2–5 mg S kg^{-1} soil). These authors didn't observe any symptoms of toxicity in the plant with the applied treatment concentrations are 20 times higher than the doses of safe application. A soil application of 10 g Se ha^{-1} could be raising the Se content of crops (Lyons et al. 2005). However, the principal factor analysis exhibited that a higher Se concentration (20 mg/kg) was more dangerous for the physiological processes of maize plants than a low Se concentration (Naseem et al. 2021). The activity of antioxidants such as catalase, ascorbate peroxidase, glutathione reductase, and glutathione peroxidase was significantly improved with 1 ppm Se application to salt-stressed mung bean plants. Se treatment at low concentration increased Se uptake but reduced the Na^+ uptake, consequently improving the plant function in mung bean plants grown under salt stress (Kaur and Nayyar 2015).

13.4.4 Foliar Application of Selenium

Foliar applications of Se aimed to improve the Se content of seeds or fruits. Moreover, the foliar application is a powerful option for Se enrichment of agricultural outcomes. Foliar spraying enhances the effectiveness of plant protection

Table 13.5 Effect of the foliar application of selenium on the nutritional values of different crops

Plant species	Se source	Se dose	Nutritional value	References
Hordeum vulgare L. (spp. distichum)	Sodium selenite Sodium selenate	10–40 g Ha^{-1}	↑Se content	Rodrigo et al. (2013)
Oryza sativa L.	Sodium selenite	100 µM	↑Se Amino acid, ↑Non-amino acid, Se inorganic > Se organic, ↑antioxidant capacity; ↑Ca, Mg, Zn, Mn	Yin et al. (2019)
Triticum aestivum L.	Sodium selenite	37.50–112.50 g Ha^{-1}	↑Se content ↑gliadin, ↑glutenin, ↓albumin, ↓globulin, ↑iron, zinc↓ copper, ↓manganese ↑amino acids, ↑anthocyanins	Xia et al. (2019)
Triticum aestivum L.	Sodium selenite	12–120 g Ha^{-1}	↑Se content, ↑starch content, ↑total soluble sugars, ↑reducing sugars, ↑sucrose, ↑N, and antioxidant metabolism	Lara et al. (2019)
Lens culinaris Medikus (subs. Culinaris)	Potassium selenite	40.0 g Ha^{-1}	↑Se content	Rahman et al. (2013)
Cicer arietinum L.	Sodium selenite Sodium selenate	10.0–40.0 g Ha^{-1}	↑Se content ↑SeMet	Poblaciones et al. (2014)

technologies related to the priming of seed or soil application (Hong et al. 2021). Applied Se primarily enters the leaf via stomata and is moved to different plant parts *through* symplastic and apoplastic pathways. Foliar application of Se could improve the Se concentration in many plants (Andrejiová et al. 2019; Yin et al. 2019). The utilization of selenate could be more efficient for enhancing plant Se concentrations than selenite. Therefore selenate is the predominant Se form used in Se enrichment plants (Hawrylak 2013). The chemical form of Se, time of treatment, and method of application affect the relative effectiveness of the applied Se donor (Ros et al. 2016). The effect of foliar Se application on improving the nutritional values of crops is shown in Tables 13.5, 13.6, and 13.7.

13.4.4.1 Arable Crops

Different methods of Se supply were found to be effective in improving yield and quality in arable crops (Nawaz et al. 2017). Se treatment at different growth stages enhanced the antioxidant capability of wheat, overcame oxidative stress, and the effects of Se applications were the best if Se levels ranged between 20.0 and 30.0 mg Se L^{-1}. Furthermore, the Se application increased Se content in grains at the heading–blooming stage (Chu et al. 2013). The authors focused on assaying the nutritional values of seed plants after Se foliar application, as shown in Table 13.5.

Table 13.6 Effect of the foliar application of selenium on the nutritional values of tomato fruits

Plant species	Se source	Se dose	Nutritional value	References
Solanum lycopersicon Mill. (var. Durpeel and var. Uno Rosso F1)	Sodium selenate	150 g Se Ha^{-1} (at the flowering stage)	Se in fruits (mg kg^{1} DW): 0.378 (Durpeel) – 0.990 (Uno Rosso F1) ↑Se content in fruits, ≈total carotenoids, ≈vitamin C, ↑total polyphenols	Andrejiová et al. (2019)
Solanum lycopersicon L. (cv. Provence)	Sodium selenate	1 mg Se L^{-1} (at the onset of flowering)	Se in fruits (μg g^{-1} DW): 24.0–33.0 ↑delayed fruit ripening	Zhu et al. (2017c)
Solanum lycopersicum L. (cv. PKM. 1)	Sodium selenate	2.0–10.0 mg Se L^{-1} solution.	Se in fruits (μg of Se g^{-1} DW): 26.52–52.24 Se in fruits: ↑SeMet, ↑MeSeCys ↑total phenolic, ↑total protein, ↑nitrate, ↑total antioxidant activity, ↓chlorophyll, ↑Se concentrations	Arulselvi (2014)

The foliar application of Se at the tillering stage is an efficient technique for improving the yield in drought-prone regions of the world (Nawaz et al. 2017). Moreover, foliar application of Se regulates nutrient uptake, wheat yield through maintenance of turgor, and increases gas exchange attributes and antioxidant systems. A marked decline in osmotic pressure resulted from the foliar supply of Se significantly increased transpiration rate, turgor and accumulation of free amino acids, total soluble sugars, and activity of antioxidant enzymes, which increased the wheat yield by 24%. Moreover, it also increased Se contents and improved iron (Fe) and sodium (Na) uptake, and maintained calcium (Ca) contents in the straw of wheat. The Se supplement at the grain-filling stage improved the grain yield by increasing the performance of physiological metabolism (Shahzadi et al. 2017). Foliar application of a single dose of Se donor raised the Se content of lentil seed from 201 up to 2772 μg kg^{-1}. However, the application of Se did not influence grain yield. It increased SeCys and SeMet in lentil yield (Rahman et al. 2015). Nano-Se with 30 ppm as a foliar treatment at two intervals every season could increase the yield of pea plants grown in sandy soil (El-Sawy et al. 2019). Se has appositive effects on nutritional values through increasing phenolic contents in seeds of corn (Gul et al. 2017) and rice (Emam et al. 2014).

Se nanoparticles (SeNPs) at 0, 20, and 40 ppm as an environment-friendly factor were used at the vegetative stage to induce improvement in the growth of three different groundnuts (*Arachis hypogaea* L.) varieties (NC, Gregory and Giza 6). Application of SeNPs improved growth, yield, and quality of groundnuts crop. The SeNPs improved photosynthetic pigments, total sugars, antioxidants enzymes, total flavonoids, total phenols, lipid peroxidation, seed oil, and fatty acid composition (Hussein et al. 2019a, b).

Table 13.7 Effect of the foliar application of selenium on the nutritional values of tree fruits

Plant species	Se source	Se dose	Nutritional value	References
Olea europaea (Leccino cv.)	Sodium selenate	100 mg/L	Increase Se in fruits B, Mg, K, Cr, Mn, Fe, and Cu in edible parts, increase total phenols	D'Amato et al. (2017, 2018b)
Vitis vinifera L. (hutia no. 80)	Amino acid chelated	Se ≥ 0.12 g/L	Increase Se in fruits Acid invertase activity, total soluble sugar, and Se content in berries	Zhu et al. (2017a)
Vitis vinifera L. (CVs. Crimson Seedless, Red Barbara, Summer Black, and Hutai no. 8)	Amino acid-chelated Se	Organic Se content ≥60 g/L	Increase Se in fruits ↑soluble sugar; ↑soluble protein; ↑soluble solid; ≈polyphenol; ↑K and Ca; ↓Pb, Cr, Cd, As, Ni	Zhu et al. (2017b)
Prunus Persica L. Batsch (cv. Flavorcrest and cv. Suncrest) and *Pyrus communis* L. (cv. Conference)	Sodium selenate	0.1 and 1.0 mg of Se/L	Increase Se in fruits ↑fruits flesh firmness, ↑soluble solid content	Pezzarossa et al. (2012)
Pyrus communis L. (cv. Liuyuexueli)	Sodium selenite Sodium selenate	20, 40, 50, 100, 200 mg of Se/L	<40 mg L^{-1} optimal Se concentration and Se (IV) more suitable (food safety)	Deng et al. (2019)
Pyrus granatum L. (c.v. Malase Saveh)	Sodium selenate Nano-selenium	1–2 μM	↑Phenolic compounds, ↑antioxidants, ↑Anthocyanins	Zahedi et al. (2019)

13.4.4.2 Fruit Crops

Due to the antioxidant role of Se and its impact on ethylene synthesis, several studies have been conducted to examine the effects of Se enrichment on fruit quality and post-harvest life (D'Amato et al. 2020). Application of Se seemed to cause a delay in fruit ripening (Pezzarossa et al. 2014; Zhu et al. 2017c; Puccinelli et al. 2019). The retardation of ethylene biosynthesis may be beneficial because it could influence the post-harvest shelf life of tomato fruits. It also stated that this could be due to the scavenging of reactive oxygen species (ROS) production by inducing antioxidant systems, parallel with a down-regulation of ethylene biosynthesis genes (Zhu et al. 2017c).

The nutritional benefits that tomato fruits acquired with Se biofortification were the presence of SeMet and MetSeCys as the forms of Se compounds in the fruits (Arulselvi 2014), an increase in the antioxidant activity, a slightly higher level of vitamin A, and an increase in fruit firmness and total solids (Cartes et al. 2005). Tomato plants are the most commonly used crops in Se enrichment studies; the data are reported in Table 13.6.

Fortification techniques are suitable for getting a Se-enriched tomato without extreme Se absorptions (Andrejiová et al. 2019). The Se fortification of tomatoes proved to be effective in producing fruits with a longer shelf life and higher levels of Se-organic forms and antioxidant compounds.

Only a few recent studies are focused on the Se-enrichment of fruit trees (Table 13.7). The content of Se in tree fruits can be enriched by different techniques, like soil or foliar application. From the literature evaluated, the foremost used mode for Se biofortification in trees is the foliar spray. The supply of Se enhanced the Se content in the fruits of the Se-treated trees: peaches and pears (Pezzarossa et al. 2012), and table grapes (Zhu et al. 2017c), without influencing the yield. Se also confidently changes the soluble-solid content in peach and pear (Pezzarossa et al. 2012), glucose, fructose, organic acid, and protein contents in grape (Zhu et al. 2017c).

The foliar method of Se was better than the application in the soil. Since it involves a more uptake of Se, lack of residual impacts, and less consumption of Se sources, resulting in the most environmentally safe and economically acceptable method (D’Amato et al. 2014; Tedeschini et al. 2015). The foliar and fruit spraying of Na selenate influenced Se accumulation, fruit growth, and senescence in peach and pear fruit crops. Foliar Se application incremented the Se content, but the sprayed Se fruit has higher Se content than the leaf. The daily intake of pears and peach treated with 1 mg of Se L^{-1} does not induce toxicity but can even provide a rational Se supplementation for human nutrition. Inorganic Se increased in the pear juice, so the application of selenite is more proper than selenate for food safety (Deng et al. 2019). In apples and pomegranates, Se application via foliar spray improved the nutritional values of the fruit (Zahedi et al. 2019).

In apples, in addition to the increase of Se content, foliar Se application increases the flesh firmness, the soluble solids, titrable acidity, and antioxidant enzyme activities (Babalar et al. 2019). Also, in pomegranates, Se application led to an effective increase in phenolic substances, anthocyanins, and total antioxidants (Zahedi et al. 2019). Moreover, in a recent study, foliar Se application induced total phenols and flavonoids and improved salt tolerance in the grapevine (Karimi et al. 2020).

Overall, foliar application with Se resulted in the enrichment of Se content in fruits (grapes, peaches, pears, olives, apples, and pomegranates) and their derivates (oil, wine, and juice), and their nutritional quality. However, the perfect plan of Se application like dose, time, Se source, and method of application is required to prevent damage to photosynthetic molecules. The damaged chlorophyll inhibits photosynthesis and metabolism and maximizes the protection from environmental stresses and the quality of the products (Karimi et al. 2020).

Concerning the effects of foliar applications of Se (100 mg L^{-1}) on table olives (D’Amato et al. 2014), at the harvesting stage, the Se content in the edible portion of the drupes reached 6.1 µg g^{-1} and 29 µg of Se/five olives. Se biofortification also improved the quality of nutritional values of the drupes, with markedly higher increments in the levels of Mg, K, Mn, B, Fe, Cr Cu, and Na than those of the control plants. Furthermore, the five Se-enriched olives at a day would implement a quantity of K, Mg, Cu, Fe, Zn, and Mn needed by humans. Se enrichment at 50, 100, and

150 mg L^{-1} concentrations through the foliage is also sufficient for the improvement of the Se content (up to 120 μg kg^{-1}) in extra virgin olive oil (EVOO) (D'Amato et al. 2020).

Moreover, Se enrichment increased organic Se, phenol, photosynthetic pigments content in EVOO (D'Amato et al. 2014). In particular, the phenolic profiles showed that oleacein, ligustrosideaglycone, and oleocanthal were the most affected compounds and were increased by 57%, 50%, and 32%, respectively. In *Vitis* grapes supplemented with Se-amino-acid-chelated fertilizer, the Se concentration, free sugar, and invertase activity were more than in the untreated ones. Moreover, Se-fertilizer promoted the nutritional values; free sugar, water-soluble protein, soluble solids, and decreased organic acid, while it maintained the polyphenol act as antioxidants in Eurasian species. In addition, applied Se increased the Se content, nutrition values, and subsequent quality of grapes and reduced the uptake of heavy metals Cr, Ni, Pb, As, and Cd (Zhu et al. 2017a, b).

The wine originated from grape berries enriched by foliar Se application (100 mg L^{-1} selenate) contained 0.620 mg Se/L. Interestingly, the inorganic Se was up 26% of the total Se in the control wine, while in Se-enriched grape, the percentage developed to 47.5% of the Se content. The foliar application of selenate increased selenite content in enriched wine (Fontanella et al. 2017).

13.5 Conclusion

The application of Se in plant production and improvement of the quality of seeds and fruits has shown remarkable promising potential. Se application increased the antioxidant compounds and the nutritional values of crop and fruit yield. It also had economic and commercial importance due to its role in delaying fruit ripening and senescence. Indeed, Se-enriched plants provide many nutritional benefits. It is necessary to determine the applied Se-biofortification techniques and costs. The fortification strategies depend on the Se donor, dose, the period and method of application, growth stage, plant species, and agricultural conditions. Also, Se metabolism determines the Se content in the plant tissues. So, it is necessary to assess the risk resulting from the intake of the Se hyperaccumulator plants or plants treated with very high Se doses. To avoid the exceeding accumulation of Se in edible portions of the plant, it should apply organic selenium donors in the biofortification or treat the plants with low Se doses, thus restricting the risk of surpassing the recommended dietary consumption in humans.

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Chapter 14
Application of Selenium and Nano-selenium in Abiotic Stress Management, Crop Improvement, and Agro-biotechnology

Most. Waheda Rahman Ansary, Md. Hashmi Sakib, and Tofazzal Islam

14.1 Introduction

Plants are often subjected to a variety of external stresses, which cause a number of physiological, morphological, molecular, and biochemical changes in their cells. These stresses can be biotic and abiotic in nature that pose threats to the growth, development, and productivity of the plants. The most common abiotic stresses include high salinity, drought, waterlogging, radiation, extreme temperature (cold, frost, or heat), UV radiation, higher emergence of disease and pests, and heavy metal contamination, which are a major hurdle in attaining potential yield of cultivated crops worldwide (Islam et al. 2016; Ahmad et al. 2021; Aryal et al. 2020; Hossain and Islam 2021; Hossain et al. 2021a, b, 2022; Oo et al. 2020; Raza et al. 2020; Zaid et al. 2020). Drought is the main abiotic stress which occupies 45% of the arable lands and is expected to increase in the future due to global warming (Bot et al. 2000; Burke et al. 2006). On the other hand, most of the crop species are sensitive to salt stress which covers 33% of the irrigated and 20% of total cultivated agricultural land globally (Srivastava and Kumar 2015). It can reduce crop yield from 10% to 50% depending on its severity in the soils (Panta et al. 2014). Besides, heavy metal contamination, such as hexachromium (Cr), arsenic (As), cadmium (Cd), lead (Pb), mercury (Hg), and copper (Cu), due to the anthropogenic activities

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M. A. Hossain et al. (eds.), *Selenium and Nano-Selenium in Environmental Stress Management and Crop Quality Improvement*, Sustainable Plant Nutrition in a Changing World, https://doi.org/10.1007/978-3-031-07063-1_14

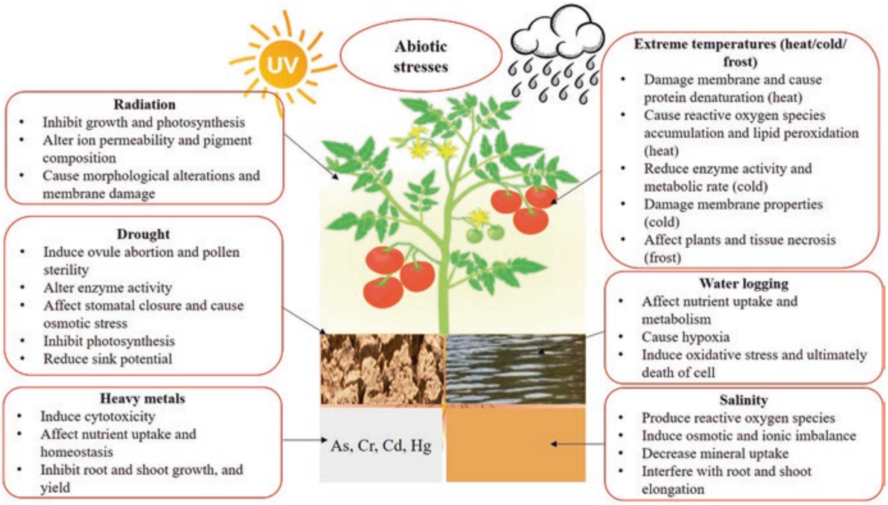

Fig. 14.1 Major abiotic stressors and their effect on crop growth and development

including excessive use of synthetic chemicals and mineral extraction, also negatively affect developmental processes, quality, growth, and yield of crop plants (FAO 2015; Manzoor et al. 2018). It is also predicted that the intensity of abiotic stresses will increase due to the limitation of freshwater associated with global climate change in the coming years (Aryal et al. 2020; Godoy et al. 2021; Hossain et al. 2022; Oo et al. 2020; Sarker et al. 2021). Therefore, eco-friendly approaches are needed to mitigate the problems associated with crop production in the stressful environment for ensuring the food and nutritional security of the ever-increasing global population. Various kinds of abiotic stressors and their detrimental effects on crop plants are shown in Fig. 14.1.

Intense research efforts are focusing on mitigation of or adaptation to biotic and abiotic stresses for sustainable crop production worldwide. The primary tools used in agricultural biotechnologies are tissue culture, genetic engineering, embryo rescue, somatic hybridization, marker aided selection and genetic analysis, and recent advancement of genome editing through CRISPR-Cas9 technology. Although all these technologies have generated a considerable number of abiotic stress-tolerant varieties (Haque et al. 2018; Islam 2019a, b; Chennakesavulu et al. 2021; Farooq et al. 2021; Hossain et al. 2022), their practical use and acceptability largely depend on politics, public perception, environmental factors, and biosafety regulations. Besides, the regulatory process to releasing a new GMO crop prior to cultivation and commercialization is lengthy and highly expensive (Godoy et al. 2021; Kumar et al. 2020). Due to the high complexity of the modified traits, only 12 among 500 transgenic crops have been approved for cultivation (Kumar et al. 2020). Therefore, a nongenetic approach such as use of selenium (Se) and nano-Se could be a safer alternative tool to fight against the environmental stressors and improvement of crop yield.

Selinium is considered as one of the most important trace elements in human and animal nutrition (Hossain et al. 2021a; 2021b; Hossain and Islam 2021). It is also a beneficial micronutrient involved in several morphological, physiological, and biochemical processes in plants. Surprisingly, both an excessive and insufficient intake of Se might have major health implications. For these dual characteristics, Se is considered as a "double-edged sword" (Hawrylak-Nowak et al. 2015). Se has different forms such as nano-Se, selenite, selenate, and selenoproteins (Chauhan et al. 2019). It is required for the activation of sulfur assimilation genes (Djanaguiraman et al. 2010). It can enhance the activity of glutathione peroxidase (GPX) enzyme and other Se-based proteins (Ardebili et al. 2015; Peng et al. 2007). At lower concentrations, Se can improve the rate of photosynthesis (Jiang et al. 2017; Zsiros et al. 2019) and stimulate the growth and quality of crop plants (Hussein et al. 2019; Zahedi et al. 2019a). In addition, several studies reported that Se strengthens the plant defense under stressful conditions, such as modifying physiological, biochemical, and epigenetic responses to water stress in corn (*Zea mays*) (Bocchini et al. 2018), reducing chilling stress in sugarcane (*Saccharum officinarum* L.) (Elsheery et al. 2020), alleviating salt stress-mitigating As toxicity in rice (*Oryza sativa*) (Hussain et al. 2020; Singh et al. 2018), mitigating salinity stress in strawberry plants (*Fragaria* × *ananassa* Duch) (Soleymanzadeh et al. 2020), managing drought stress in camelina (*Camelina sativa*) and canola (*Canola napus*) (Ahmad et al. 2021), and altering the physiological response of lamb's lettuce (*Valerianella locusta*) grown under high-temperature stress (Hawrylak-Nowak et al. 2018). The bioactivity of Se is categorized into three concentrations: (i) lower concentration is required for appropriate growth and development; (ii) moderate concentration can be stored in order to maintain homeostatic functions; and (iii) higher concentration is poisonous to all living organisms including plants (Hamilton 2004).

The nanoparticles (1–100 nm) are molecular or atomic aggregates and possess some unique chemical and physical properties. They are able to cross the cellular barrier to act on living organisms including plants (Pérez-de-Luque 2017; Singh et al. 2021). Some nanoparticles show promising activities on growth, development, and abiotic stress tolerance in plants (Islam 2019a, b; Hussain et al. 2020; Rana et al. 2021). Except for some exclusive chemical, physical, and biological properties, both Se and its nanoparticles share some common features. Nano-Se is a form of Se, which is water soluble, bright red in color, and nano-defined size in the redox state of zero (Se0). Nano-Se is widely used for nutritional supplements and treating human diseases, producing nano-medicine and other therapeutic applications (Chaudhary et al. 2016; Hosnedlova et al. 2018; Khurana et al. 2019; Song et al. 2020; Zhao et al. 2017). Furthermore, nano-Se has achieved worldwide attention due to its low toxicity, high stability, biological activity, and excellent bioavailability in plants (Abdulsalam et al. 2018; Sharma et al. 2014; Zhang et al. 2001). Similar to Se, nano-Se or Se-nanoparticles play an important role to mitigate stress and regulate the growth of plants. The toxicity of nano-Se is lower compared to other forms of Se including selenite, selenate, and selenomethionine (SeMet) (Djanaguiraman et al. 2018). Nano-Se improves the growth of cucumber under combined salinity and heat stresses (Shalaby et al. 2021). It is also used to manage the adverse effect on cut chrysanthemum (*Chrysanthemum morifolium*) flowers caused by high-temperature effect (Seliem et al. 2020). Nano-Se also alleviates NaCl stress in tomato (*Solanum lycopersicum*) (Morales-Espinoza et al. 2019), Cd and Pb toxicity in rice (Hussain et al. 2020), salinity stress in strawberry (Zahedi et al. 2019a), high-temperature stress in sorghum grains (*Sorghum bicolor*) (Djanaguiraman et al. 2018), and drought stress in strawberry (Zahedi et al. 2020), wheat (*Triticum aestivum*) (Ikram et al. 2020), and pomegranate (*Punica granatum*) (Zahedi et al. 2021). In contrast, the toxic effect of Se and nano-Se at higher doses on plants have also been reported (Awual et al. 2014, 2015a, b; Hawrylak-Nowak 2013; Neysanian et al. 2020).

Considering the recent advances in the beneficial effects of Se and nano-Se on growth promotion, biotechnological applications, and stress tolerance in crop plants (Hossain et al. 2021a, b), this chapter summarizes the effects of Se and nano-Se in alleviating environmental stressors to crop plants with particular attention to their molecular mechanisms. It also elaborates the use of Se and nano-Se in agro-biotechnologies. In addition, this chapter highlights the roles of Se and nano-Se on the growth, development, and yield of crop plants.

14.2 Uptake, Accumulation, and Transportation of Selenium in Plants

Selinium content in soil mainly depends on the inherited parent material and soil-forming processes. Organic and calcareous soils have the highest amounts of Se, but sandy soil developed under humid climate have the lowest amount of Se (Kabata-Pendias 2000). The concentration of Se in soils varies from 0.01 to 2.0 mg/kg. In clayey soils, the concentration ranges from 0.8 to 2 mg/kg; in tropical soils, it is between 2 and 4.5 mg/kg, while in seleniferous soils, the concentration can be >10 mg/kg (Adebayo et al. 2020; Fordyce 2013). Both the organic and inorganic forms of Se are available in nature. The available organic forms are selenocysteine (SeCys), selenocystathionine (SeCysth), and SeMet, and the inorganic forms are mainly elemental Se, selenide (Se^{2-}), selenite (Se^{4+}; SeO_3^{2-}), and selenate (Se^{6+}; SeO_4^{2-}) (Bodnar et al. 2012). Se uptake is vital for their effective functioning in plants; however, the uptake, accumulation, and translocation largely depend on the membrane transporters, presence of other substances, forms and concentrations of Se, soil type and conditions, plant phase, and species (Renkema et al. 2012). For example, a comparatively low rate of selenite was taken up by *O. sativa*, *Beta vulgaris*, *Brassica oleracea*, *Astragalus,* and *B. juncea* than that of selenate (de Souza et al. 1998; Shrift and Ulrich 1969; Zayed et al. 1998). In contrast, higher rate of selenite was taken up by *Glycine max* and *A. crotolariae* (Broyer et al. 1972; Zhang et al. 2003), while the transportation rate was equal in *Phaseolus vulgaris* (Arvy 1993).

Selenate is the most common type of Se found in agricultural and oxygenated soil, while selenite is dominant in anaerobic soil. Generally, selenite is tightly

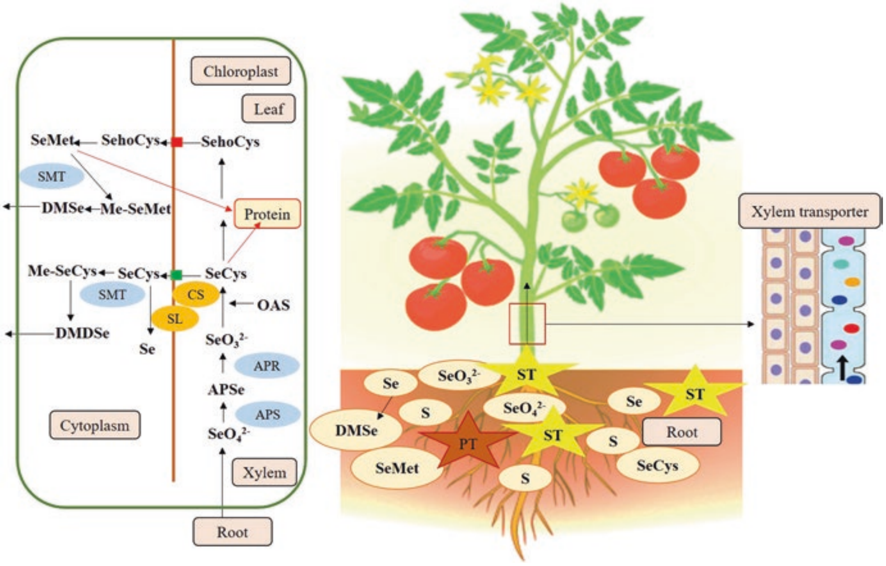

Fig. 14.2 Selenium uptake, and metabolism in plants for improving stress resistance (*S* Sulfur, *Se* Selenium, *ST* Sulfur transporter, *APS* ATP sulfurylase, *APR* APS reductase, *OAS* O-acetyl serine, *SMT* Selenocysteine methyltransferase, *CS* Cysteine synthase, *SL* SeCys lyase)

absorbed by aluminum (Al) and iron oxides/hydroxides and also by organic matters and clays. Plants mainly uptake selenate involuntarily via sulfate transporter (ST), which is more mobile and water soluble compared to selenite. Upon completion of uptake, selenate is then metabolized, reduced to selenite via the action of ATP sulfurylase (APS) and APS reductase (APR), followed by selenide through the sulfur assimilation pathway (Sors et al. 2005; Wallenberg et al. 2010; White 2016). After that, selenide couples with O-acetyl serine (OAS) to form SeCys by the action of cysteine synthase (CS), which is further converted to either methyl-SeCys (Me-SeCys) by selenocysteine methyltransferase (SMT) or Se or SeMet by SeCys lyase (SL) or other enzymes, respectively. The sulfur analog of Se can then be methylated and undergoes vaporization to a nontoxic form in the atmosphere (Fig. 14.2) (Pilon-Smits and Quinn 2010).

It is known that phosphate transporter helps to uptake selenite from soil (De Temmerman et al. 2014; Li et al. 2008). The availability of phosphate and sulfate in the plant and environment also determined the form in which Se would be taken up by the plant. Both passive diffusion (Ellis and Salt 2003) and active transport mechanisms (Li et al. 2008) are used to uptake selenite. It is well known that organic forms of Se including SeCys and SeMet can also be taken up by the plant root, but plants are unable to absorb elemental Se or metal selenides (White and Broadley 2009). Some plant growth-promoting bacteria including *Bacillus subtilis*, *B. licheniformis*, *Exiguobacterium* sp., and *Pseudomonas pseudoalcaligenes* help in the biotic transformation of highly soluble but toxic selenite to less toxic elemental Se (Javed et al. 2015). However, inhibitors of major intrinsic proteins (MIPs), $AgNO_3$, and $HgCl_2$ have a negative effect on the uptake of Se in rice root (Zhang et al. 2010, 2012).

Once Se are taken up by the plants, their effect can be noticed if accumulation and transportation can be ensured within the plant tissues. Vacuoles of the plant cells are the storehouse of Se accumulation (Mazej et al. 2008; Ximénez-Embún et al. 2004); it can be effluxed through ST (Gigolashvili and Kopriva 2014). Se concentration is relatively higher in young leaves during seedling growth (Cappa et al. 2014). Accumulation of Se ranges from 100 mg Se/kg soil to 10,000 mg/kg soil, determined by the capacity of plant tissues. Hyperaccumulators including *Neptunia*, *Astragalus*, *Xylorhiza,* and *Stanleya* species accumulate more than 1000 mg Se/kg soil, while secondary accumulators including Camelina, Aster, *Medicago sativa*, *Helianthus*, *B. napus*, *B. juncea,* and broccoli accumulate Se between 100 and 1000 mg Se/kg soil. Non-accumulators accumulate <100 mg Se/kg soil and would not survive in Se-rich soils, rather they volatilize Se as dimethyl selenide (DMSe) and their growth is hampered (Galeas et al. 2007).

Selenite uptake by root is transformed into SeMet and selenomethionine Se oxide hydrate (SeOMet), but mostly into unidentified and water-insoluble forms. Thus, Se translocation from root to shoot is lower in plants taken up by selenite than those taken up by selenate (Zhu et al. 2009). The chemical reduction of selenate to selenite and subsequent SeCys takes place at leaf chloroplast, whereas the synthesis and methylation of SeMet occur in the cytosol (Lin 2011). Transportation of Se is a complex process and is determined by the type and nature of membrane transporters, nutritional status of soil and plant, and also the transportation mechanisms (Li et al. 2008; White et al. 2004; Zhao et al. 2005). The affinity for Se decreases in the presence of a higher external surface. Again, constitutively active STs showed less affinity for sulfate over selenate compared to inducible STs (White et al. 2004). Transportation of Se is also affected by the transpiration rate, xylem loading, and the mobility nature of Se (Renkema et al. 2012). Kikkert and Berkelaar (2013) conducted an experiment in wheat and canola and observed that selenite is more mobile than SeMet, while SeMet is more mobile than either SeCys or selenate. Transportation of selenate takes place inside *Arabidopsis thaliana* via STs *SULTR1;1* and *SULTR1;2* (El Kassis et al. 2007). But in another study, fortified selenate is not transported by *SULTR1*, which indicated that *SULTR1;2* is the preferred transporter for the uptake of selenate in plant roots (El Kassis et al. 2007; Shibagaki et al. 2002).

Metabolism and gene expression in higher plants is closely associated with sulfur. Selenate and sulfur have identical tetrahedral structures and pKa values of 1.74 and 1.9, respectively (Dumont et al. 2006; Sors et al. 2005). The increased expression of genes encoding *HASTs*, primarily *SULTR1;1*, results in an increased sulfate and selenate absorption ability, and thereby improving Se concentrations in sulfur-deficient plants (Hsu et al. 2011; Terry et al. 2000; White et al. 2004, 2007). Moreover, when the development of non-accumulator and Se indicator species hindered by a lack of sulfur supply, gene expression for the genes encoding *SULTR1* and *SULTR1;2* increased in the root (El Kassis et al. 2007; Rouached et al. 2008; Schiavon et al. 2015; Shinmachi et al. 2010). Gene expression of the same genes also increased during the augmentation of Se in tissues (Hsu et al. 2011;

Inostroza-Blancheteau et al. 2013; Rouached et al. 2008; Takahashi et al. 2000; van Hoewyk et al. 2005; Zhang et al. 2006). Se hyperaccumulator constitutively expresses these genes indicating higher selenate uptake capacity (Cabannes et al. 2011; Freeman et al. 2010; Schiavon et al. 2015).

14.3 Selenium and Nano-selenium Improve Abiotic Stress Tolerance in Plants

Se and nano-Se are very important components having the physiological and antioxidant properties which attract many biologists in recent years. It does not take part in major metabolic processes in plant; however, it plays a vital role in reducing physiological stresses. The fight against tremendous abiotic stressors is mostly linked with the improvement of photosynthesis rate, strengthening immune systems, maintaining ion homeostasis, and regulating the uptake of water and nutrients (Fig. 14.3). Selenate, taken up by plant increase the hydrogen peroxide (H_2O_2) detoxifying enzymes specially ascorbate peroxidase (APX) and GPX under stressful conditions which in turn improve stress resistance capacity in plants. They are available in nature, eco-friendly, and have no toxic effect in low concentration. Thus, the interest for Se and nano-Se has sharply increased worldwide for attaining

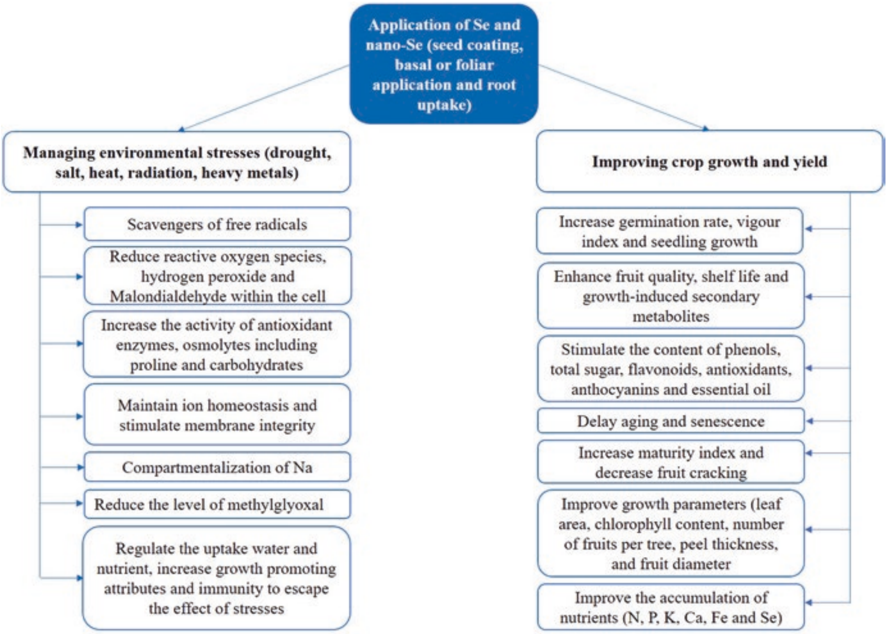

Fig. 14.3 Underlying mechanisms of selenium- and nano-selenium-induced mitigation of environmental stresses and crop yield improvement

sustainable agriculture (Hossain et al. 2021a, b; Ahmad et al. 2021; Bocchini et al. 2018; Djanaguiraman et al. 2018; Elsheery et al. 2020; Ghazi 2018; Hasanuzzaman et al. 2011, 2014; Hawrylak-Nowak et al. 2018; Hossain et al. 2022; Hussain et al. 2020; Morales-Espinoza et al. 2019; Seliem et al. 2020; Shalaby et al. 2021; Singh et al. 2018; Soleymanzadeh et al. 2020; Zahedi et al. 2019a, b; Zhang et al. 2001, 2008).

14.3.1 Tolerance to Drought Stress

Water scarcity or drought is one of the most critical environmental stresses globally that negatively affects the germination, photosynthetic rate, osmotic potential, growth, and development of plants (Fig. 14.1). In addition, it affects the production of proteins, lipids, nucleic acids, and carbohydrates. Recently, drought along with the climate change scenario has posed a severe challenge to sustainable crop production (Ahmad et al. 2020; Miao et al. 2015; Rana et al. 2013). It is very difficult to explain the length and severity of drought since it is determined by the evaporation rate, distribution of total rainfall, soil type, and its water storage capacity (Farooq et al. 2009; Trenberth et al. 2014). Depending on the intensity, wilting, dropping of leaves, yellowing, etiolation, and finally, death are the most common symptoms of drought stress in plants (Akhtar and Nazir 2013, Sapeta et al. 2013). In order to maximize agricultural production and to mitigate the impact of drought stress on crops, numerous techniques have been developed. Among them, application of Se and nano-Se is the most modern technology used to protect crop plants from the dangerous drought stress. Both Se and nano-Se play an important role by reducing oxidative damage, regulating senesce to produce antioxidants, and improving water status to increase plant tolerance to drought stress (Fig. 14.3, Table 14.1) (Ahmad et al. 2016; Nawaz et al. 2013, 2015, 2016; Zahedi et al. 2020, 2021).

Yao et al. (2009) reported that seed treatment of wheat (*T. asetivum* L. cv Shijiazhuang No. 8) with Se at the rate of 1.0, 2.0, and 3.0 mg/kg Se significantly promoted root activity; increased proline content, catalase (CAT), and peroxidase (POD) activities, as well as chlorophyll and carotenoids content; and reduced malondiadehyde (MDA) content of seedlings grown under drought stress. Production of MDA is a signaling molecule responsible for the production of reactive oxygen species (ROS) which cause oxidative damage in plants. Therefore, reduction of MDA in the cell of plant breaks down the adaptive mechanisms of oxidative stress under drought condition (Chakraborty and Pradhan 2012; Moller et al. 2007). Nawaz et al. (2013) showed that seed priming of wheat cultivars (Pashban 90 and Kohistan 97) with Se did not affect seedling biomass at normal condition; however, under drought stress, seed treating with 75 μM Se significantly increased seedling biomass, total sugar content, and free amino acids and reduced soluble protein in both cultivars. It is reported that either foliar application or seed priming with Se or combination of both potentially mitigate the adverse effect of drought stress by eliciting various physio-biochemicals attributes. Combined foliar application and

Table 14.1 Mechanisms of selenium and nano-selenium in mitigating drought stress of various crop plants

Crop plants	Mode and dose of application	Underlying mechanisms to mitigate drought stress	References
Spring wheat (*Triticum aestivum*)	Basal application of 0.1 and 0.25 mM Se	(i) Improve water status (ii) Decrease peroxidase activity (iii) Inhibit the stress-induced accumulation of proline	Kuznetsov et al. (2003)
Soybean (*Glycine max*)	Foliar application of 21g/ha Se	Increase the activity of antioxidant and glutathione peroxidase	Habibi et al. (2006)
Wheat (*T. aestivum*)	Seed priming with 1.0, 2.0, and 3.0 mg Se/kg	(i) Increase the content of proline, chlorophyll and carotenoids (ii) Increase the activity of catalase and peroxidase (iii) Reduce malondiadehyde	Yao et al. (2009)
Rapeseed (*Brassica napus*)	Seed treatment with 25 μM Se	Enhance antioxidant defense and methylglyoxal detoxification systems	Hasanuzzaman and Fujita (2011)
Wheat (*T. aestivum*)	Irrigation plus application of 1.0 mg Se/kg	Increase antioxidant activities and membrane integrity	Yao et al. (2012)
Olive (*Olea europaea*)	Foliar application of 50 and 150 mg Se /L	(i) Regulate water status and photosynthesis rate (ii) Increase the activity of some antioxidants (iii) Reduce Malondialdehyde content	Proietti et al. (2013)
Rice (*Oryza sativa*)	Foliar application of 0.03 mM Se	(i) Increase the levels of amylose and phenolic compounds (ii) increases lignin, cellulose and pectin contents in rice straw	Emam et al. (2014)
Wheat (*T. aestivum*)	Foliar application of 40 mg Se /L	(i) Maintenance turgor pressure and gas exchange characteristics (ii) Enhance antioxidant system	Nawaz et al. (2015)
Maize (*Zea mays*)	Foliar application of 40 mg Se/L	(i) Increase the activity of antioxidant enzymes (ii) Enhance water potential at leaves	Nawaz et al. (2016)
Wheat (*T. aestivum*)	(i) Seed priming with 75 μM Se (ii) Foliar application and fertigation with 7.06 and 7.35 μM Se, respectively	Maintenance plant water status	Nawaz et al. (2017)

(continued)

Table 14.1 (continued)

Crop plants	Mode and dose of application	Underlying mechanisms to mitigate drought stress	References
Maize (*Z. mays*)	Basal application of 150 mg Se	(i) Increase proline, K concentrations and nitrogen metabolism in aerial parts of plants (ii) Activate stress tolerance gene such as phytoene synthase which is required for maintaining leaf carotenoid contents, sorbitol dehydrogenase, regulate the level of osmolytes and alcohol dehydrogenase	Bocchini et al. (2018)
Cauliflower (*B. oleracea*)	Foliar application of 100 ppm sodium selenite solution at 10 ML/ application	Increase antioxidant activity and phenolic compound	Hachmann et al. (2019)
Wheat (*T. aestivum*)	Foliar application of 25 and 50 mM Se	(i) Improve chlorophyll contents and photosynthetic efficiency (ii) Increase antioxidant defense system components and osmoprotectants	Rady et al. (2020)
Wheat (*T. aestivum*)	Exogenous application of 30 mg nano-Se /L	Improved plant growth parameters (plant height, shoot and root length, fresh weight and dry weight, leaf length, area and number)	Ikram et al. 2020
Strawberry (*Fragaria* × *ananassa* Duch)	Foliar application of 50 and 100 mg nano-Se/SiO_2/L	(i) Improve the activity of antioxidant enzymes such as catalase, ascorbate peroxidase, guaiacol peroxidase and superoxide dismutase (ii) Reduce lipid peroxidation and hydrogen peroxide (H_2O_2) content (iii) Increase membrane stability, relative water content and water use efficiencies	Zahedi et al. (2020)
Pomegranate (*Punica granatum*)	Foliar application of 20 mg nano-Se /L (10 and 50 nm size)	(i) Increase the phenolic content, osmolytes concentration, and abscisic acids (ii) Reduce stress-induced lipid peroxidation and H_2O_2 content (iii) Enhance the activity of antioxidant enzymes.	Zahedi et al. (2021)

seed priming with Se at the rate of 7.06 and 75 μM significantly improved antioxidant properties [APX, superoxide dismutase (SOD), POD, and CAT], osmoprotectant (glycine betanin, total phenolic content, anthocyanin, and flavonoids), water potential, osmotic potential, turgor pressure, proline, total soluble sugar, total free amino acids, total chlorophyll contents and yield component in Canadian and Australian camelina, and UAF and AARI canola (Ahmad et al. 2021). Moreover, Ghouri et al. (2021) stated that the foliar application of 10 mL of combined Se and silicon (Si) was more effective to control drought stress and improve the growth performance of rice rather than any of the single one by reducing water loss and increasing chlorophyll content.

Zahedi et al. (2020) demonstrated that foliar application of nano-Se (25 mg/L) or nano-Si (125 mg/L) or their combination Se/SiO_2 (50 and 100 mg/L) promoted growth and yield parameters of strawberry plants under both normal and drought conditions (30, 60, and 100% FC). Interestingly, plants treated with 100 mg/L nano-Se/SiO_2 showed higher levels of key osmolytes including proline and carbohydrate and stored more photosynthetic pigments compared to other treatments. The increased drought tolerance ability in strawberry plants in the said study was linked with the increasing activity of CAT, APX, guaiacol peroxidase (GPOX), and SOD and reduced lipid peroxidation (LPO) and H_2O_2 content. Another study reported that 30 mg/L nano-Se significantly increased plant growth parameters (plant height, shoot and root length, fresh weight and dry weight, leaf length, area, and number) under drought stress when two wheat varieties (drought-tolerant and drought-susceptible) were treated exogenously with 10, 20, 30, and 40 mg/L nano-Se at trifoliate stage, while 40 mg/L gradually decreased morphological parameters in both varieties (Ikram et al. 2020). Furthermore, Zahedi et al. (2021) stated that foliar application of 10 and 50 nm nano-Se at the rate of 20 mg/L increases the phenolic content, osmolytes concentration, antioxidant enzymes, and abscisic acids in pomegranate plant (12 years old) compared to the control treatment under drought stress. However, treatment with 10 nm nano-Se was more effective compared to the 50 nm nano-Se.

Due to the lack of available water during the drought stress, photosynthetic rate decrease. Se and nano-Se help to improve photosynthetic rate by maintaining water status determined by the plant species, growth stages, stress duration, and intensity. At the same time, increasing proline means improving the nutrient status of the plant since proline acts as a source of nitrogen and carbon. Moreover, proline plays a vital role in the protection of the biomolecules against denaturation, osmotic potential, adjusting cell pH, and scavenging the hazardous free radical and ROS (Farooq et al. 2009). The capability of the plant to use water efficiently and protect membrane integrity determines the drought tolerance ability of the plant. In general, during drought stress, plants protect transpiration by closing their stomata. However, Se does not reduce the water use or transpiration, rather they regulate water uptake capacity and slightly increase transpiration rate (Kuznetsov et al. 2003; Proietti et al. 2013). Similarly, nano-Se also increases membrane integrity and relative water content during drought stress (Zahedi et al. 2020).

Several other studies also reported the application of Se to alleviate drought stress in different crop plants (Table 14.1) (Emam et al. 2014; Germ 2008; Habibi 2013; Ibrahim 2014; Kostopoulou et al. 2015; Nawaz et al. 2015, 2016; Sajedi et al. 2011; Tadina et al. 2007; Wang 2011). However, still there is very limited reports on the use of nano-Se (Ikram et al. 2020; Zahedi et al. 2020, 2021). Since nano-Se is effective against other abiotic stresses like salinity (Badawy et al. 2021; Ghazi 2018), and heat (Seliem et al. 2020; Shalaby et al. 2021), further research is necessary to evaluate the effect of nano-Se in mitigating drought stress in various crop plants.

14.3.2 Tolerance to Salinity Stress

Salinity is a severe problem that affects plant growth, development, and metabolism. It reduces the uptake of water and nutrients even in the presence of water due to a high level of osmotic pressure, and subsequently, it alters plant physiology, cell division, elongation, pigmentation, ion concentrations, gaseous exchange, and photosynthesis. In addition, it increases respiration rate and oxidative stress markers, such as hydroxyl anion (OH^-), H_2O_2, and superoxide (O_2^-) radical. Ultimately, plants die due to severe oxidative damage under high salinity stress (Abdul Qados 2015; Babitha et al. 2015; Desoky et al. 2019; Kong et al. 2005; Rady et al. 2019; Tsai et al. 2004; Zaki and Rady 2015; Zhu 2003). To combat the harmful effects of ROS, plants have their own defensive system. However, the enzymatic and nonenzymatic antioxidants of plants are not sufficient to defend under severe stress conditions and need to boost up antioxidant defense efficacy by adding additional adjuvants under a variety of stresses, including salt stress (Alharby et al. 2021; Azzam et al. 2021; Mekdad et al. 2021a, b; Rady et al. 2021; Seleiman et al. 2021). Although high dose of Se can cause a variety of problems in plants including inadequate photosynthesis, excessive generation of ROS, trouble in opening and closing of stomata, oxidative damage, and selenosis (Saffaryazdi et al. 2012), Se and nano-Se increase the tolerance ability against salt stress by reducing Na^+ accumulation, maintaining ion homeostasis, increasing photosynthesis, and enhancing antioxidant activities (Mozafariyan et al. 2016; Rahman et al. 2021; Regni et al. 2021; Sheikhalipour et al. 2021).

The level of Na^+ increased with the increment of salinity level and reduced K^+. Foliar application of 50 ppm nano-Se improved N^+ and K^+ contents in coriander leaves compared to the control (0 ppm nano-Se) plant and also decreased the ratio of Na^+/K^+, while this ratio increased as the salinity level increased (Ghazi 2018). Similarly, Ashraf et al. (2018) noticed that foliar application of 20 and 40 mg Se/L decreases the accumulation of toxic Na^+ in different parts of maize plant under salinity and improved growth. Se reduced Na^+ by compartmentalization in vacuoles and increased bond with the cell wall. Other stress tolerance attributes such as the increased activity of antioxidant enzymes and reduction of H_2O_2 and MDA were also observed. There is an antagonistic relationship between Na^+ and K^+ during salinity stress causing an imbalance in the cell homeostasis, nutrient deficiency, delayed growth, and finally, plant death (Yu and Assmann 2016). However, Se and nano-Se exhibit a meaningful influence on cell homeostasis by maintaining the ratio of K^+/Na^+. It is also suggested that Se upregulates *ZmNHX1* gene expression in root cells which may be responsible for the compartmentalization of Na under extreme salinity (Jiang et al. 2017).

Notably, the photosynthesis rate reduces during the salinity stress which has a detrimental effect on overall growth and development. Se improves stomatal conductance, transpiration, pigmentation, and photosynthesis in maize plant treated with 1 μM Se and increases salt tolerance capacity when exposed to 100 mM NaCl (Jiang et al. 2017). Similarly, Habibi (2017) found that sunflower (*Helianthus* *annuus*) seeds priming with 5 mg/kg Se increased photosynthetic pigment such as anthocyanins and carotenoids when subjected to salinity stress (15 ds/m NaCl). These photosynthetic pigments also help to increase the efficiency of photosystem II, the content of chlorophyll a and b, the rate of photosynthesis, and remarkably reduced H_2O_2 and MDA. Hence, Se and nano-Se avoid the severe damage caused by salinity stress by restoring pigmentation, chloroplast membrane integrity, and photosynthetic capacity.

Activation of enzymatic and nonenzymatic antioxidants and reduction of ROS are very common mechanisms to reduce the oxidative stress in plants caused by different abiotic stress including salinity stress. Ascorbate-glutathione cycle, thioredoxin (Trx), and glutaredoxin (Grx) systems were the most efficient in scavenging ROS in chloroplasts, suggesting that these systems play an important role in Se-mediated scavenging of H_2O_2 and reducing oxidative damage under salt stress. Rady et al. (2021) showed that leafy nourishment of common bean (*P. vulgaris*) with nano-Se at the rate of 0.5, 1.0, and 1.5 mM significantly improved relative water content, cell membrane integrity, free proline, and soluble sugar and minimized oxidative stress markers such as hydrogen peroxide, leakage of electrolytes, and peroxidation of membrane lipid (MDA) compared to the non-treated plants grown in saline soils with EC up to 57.55–7.61 dS/m. The activity of antioxidant properties including CAT, SOD, POX, APX, and glutathione reductase (GR) also increased. Considerable reduction of Na^+ content was observed where the ratio of K^+/Na^+ increased, and the best result was obtained in the plant treated with 1 mM nano-Se. Similar to this study, Elkelish et al. (2019) reported that foliar application of 5 and 10 μM Se increased the levels of nonenzymatic antioxidants [ascorbate (AsA), glutathione (GSH), phenolic compounds] and the accumulation of osmolytes (proline, sugars, and K^+) in wheat seedlings. In addition, fighting against ROS and LPO, upregulation of gene expression, and higher transportation of Na^+ to vacuoles are observed during salinity stress.

The involvement of methylglyoxal (MG) detoxification system may be another mechanism of Se to increase salt tolerance capacity. MG is a highly reactive cytotoxic component produced intracellularly by several enzymatic and nonenzymatic processes and detected in plant under optimal growth condition. However, the accumulation of MG increases when plants are exposed to environmental stresses. Overexpression of glyoxalase (Gly) enzymes decrease MG accumulation and oxidative stress as well as optimizing GSH equilibrium and antioxidant enzyme activity under stress circumstances (Yadav et al. 2008). This finding is also supported by Hasanuzzaman et al. (2011) that the exogenous application of Se in rape seed exposed to salinity stress increased L-ascorbate and GSH contents, elevated the GSH/GSSG (glutathione disulfide) ratio, and upregulated the activity of antioxidant enzymes and Gly system, which control the level of MG and ROS and efficiently maintain cell homeostasis.

Several other studies also reported the application of Se and nano-Se in managing salinity stress in different crop plants (Table 14.2) (Diao et al. 2014; Habibi and Aleyasin 2020; Hasanuzzaman et al. 2011; Hashem et al. 2013; Hawrylak-Nowak 2009; Hu et al. 2013; Kong et al. 2005; Mozafariyan et al. 2016; Morales-Espinoza et al. 2019; Regni et al. 2021; Shalaby et al. 2021; Sheikhalipour et al. 2021; Soleymanzadeh et al. 2020).

Table 14.2 Mechanisms of selenium and nano-selenium in alleviating salinity stress of various crop plants

Crop plants	Mode and dose of application	Underlying mechanisms to mitigate salinity stress	References
Sorrel (*Rumex acetosa*)	Exogenous supply of 1–5 µM Se	(i) Promote antioxidative and osmoregulatory activity (ii) Enhanced the accumulation of water-soluble sugars, and modified cellular ultrastructure	Kong et al. (2005)
Cucumber (*Cucumis sativus*)	Exogenous application of 5 and 10 µM Se	(i) Reduce the content of chloride ion (ii) Increase antioxidant activity and proline accumulation	Hawrylak-Nowak (2009)
Rapeseed (*B. napus*)	Seedling treated with 25 µM Se	Enhance antioxidant defense and MG detoxification systems	Hasanuzzaman et al. (2011)
Melon (*C. melo*)	Exogenous application of 2, 4, and 8 µM Se	(i) Inhibit lipid peroxidation (ii) Increase SOD and POD enzymes activity	Hu et al. (2013)
Canola (*Canola napus*)	Foliar spraying of 5 mg/L Se	(i) Increase the content of endogenous proline, magnesium and phosphorus ion (ii) Enhance catalase activity	Hashem et al. (2013)
Tomato (*Solanum lycopersicum*)	Exogenous application of 0.05 mM Se	(i) Increase the activity of SOD, GR, glutathione peroxidase, thioredoxin reductase, ascorbate, GSH and NADPH contents (ii) Enhance ROS scavenging activity	Diao et al. (2014)
Tomato (*S. lycopersicum*)	Exogenous application of 5 and 10 µM Se	(i) Increase photosynthetic pigments (ii) Improve the integrity of cell membranes by increasing leaf relative water content	Mozafariyan et al. (2016)
Sunflower (*Helianthus annuus*)	Exogenous application of 5 mg/kg Se	(i) Improve carotenoids and anthocyanin (ii) Increase antioxidant defense system components GPx (iii) Reduce MDA and H_2O_2 content	Habibi (2017)
Maize (*Z. mays*)	Exogenous supply of 1 µM Se	(i) Increase SOD and APX (ii) Upregulate *ZmMPK5, ZmMPK7,* and *ZmCPK11* genes in the roots (iii) Regulate Na^+ homeostasis	Jiang et al. 2017
Coriander (*Coriandrum sativum*)	Foliar application of 50 ppm nano-Se	(i) Improve N^+ and K^+ contents in leaves (ii) Reduce Na^+ content (iii) Maintain K^+/Na^+ ratio	Ghazi (2018)

(continued)

Table 14.2 (continued)

Crop plants	Mode and dose of application	Underlying mechanisms to mitigate salinity stress	References
Maize (*Z. mays*)	Foliar application of 20 and 40 mg Se/L	(i) Reduce Na^+ by compartmentalization in vacuoles (ii) Increase bond with the cell wall (iii) Reduce H_2O_2 and MDA	Ashraf et al. (2018)
Tomato (*S. lycopersicum*)	1, 5, 10, and 20 mg/L nano-Se	(i) Increase Flavonoids, Phenols, Lycopene, and β-carotene, titratable acidity, soluble solids (ii) Increase APX, GPx, CAT, SOD (iii) Reduce pH	Morales-Espinoza et al. (2019)
Wheat (*T. aestivum*)	Foliar application of 5 and 10 μM Se	(i) Increase Carotenoids, proline, soluble sugar and water content (ii) Reduce stress-induced Proline oxidase, MDA and H_2O_2 content (iii) Enhance the activity of γ-glutamyl kinase, SOD, CAT, GST, APX, GR	Elkelish et al. (2019)
Strawberry (*Fragaria* × *ananassa* Duch)	Exogenous application of 10 μM nano-Se	(i) Alleviate NaCl-induced lesion to PSII functioning (ii) Increase the activity of CAT and phenylpropanoid derivatives contents (salicylic acid, catechin, and caffeic acid) (iii) Decrease the content of oxidants	Soleymanzadeh et al. (2020)
Soybean (*G. max*)	Foliar application of 50 μM Se and 50 μM Se + 1 mM boron	(i) Enhance antioxidant defense system (ii) Increase the activity of glyoxalase systems	Rahman et al. 2021
Olive (*O. europaea*)	Exogenous supply of 10 and 30 mg/L Se	(i) Restore ion homeostasis by increasing the release of Ca^{2+} (ii) Reduce toxic effects of gaseous exchange on leaf (iii) Improve photosynthesis Mitigate the reduction of relative water content in leaves	Regni et al. (2021)
Bitter melon (*Momordica charantia*)	Foliar spray of 10 and 20 mg/L chitosan-Se nanoparticles	(i) Increase antioxidant enzyme activity, proline concentration, relative water content, and K^+, (ii) Decrease MDA and H_2O_2 oxidants and Na aggregation in plant tissues	Sheikhalipour et al. (2021)

14.3.3 Tolerance to High- and Low-Temperature Stresses

In the recent climate change scenario, temperature stress (heat/cold) has received the greatest attention due to its significant effect on cell division, plant growth, yield, and plant distribution. High temperature affects enzymatic activities and its metabolism. Photosynthesis is a critical component of plant cellular function that is heavily influenced by heat stress. Photosystem II, Rubisco, cytochrome b559, and plastoquinone are negatively influenced by high temperatures (Carmo-Silva et al. 2012). If the surrounding temperature rises (>10–15 °C), immediately the shock response generates to avoid heat stress (Du et al. 2018; Haghighi et al. 2014).

Vegetative plants are more sensitive to temperature stress. Hawrylak-Nowak et al. (2018) reported that foliar or soil application of Se enhanced the thermotolerance of lamb's lettuce through the action of antioxidant enzymes including CAT and GPOX and decreased GSH among low-molecular-weight nonenzymatic antioxidants to remove excess H_2O_2, when lettuce plant was exposed to heat stress (35 °C). The content of phenolic compounds was not affected by Se under heat stress; however, at normal temperature, Se-biofortified plants accumulate significantly more phenolic compounds than the non-treated plants. Heat stress (day/night, 40/30 °C) remarkably reduced growth traits (total chlorophyll contents, photosynthesis, stomatal conductance, transpiration rate), antioxidant enzyme activities, membrane stability index, and increased intercellular CO_2, LPO, non-photochemical quenching (NPQ). Foliar application of Se at the rate of 8 μM improved all the growth parameters, level of osmolytes, and antioxidant activity. Improvement of antioxidant mechanisms drastically reduced ROS, thereby minimizing LPO in cucumber plants grown under heat stress (Balal et al. 2016).

Similar to Se, nano-Se is also effective to control thermal stress by different processes including LPO. Seliem et al. (2020) used *Lactobacillus casei* to fabricate nano-Se having the dimension between 50 and 100 nm and reported that green synthesized nano-Se accelerated physiological and biological profiling of two sensitive cultivars of chrysanthemum (Sensual and Francofone) under heat stress (up to 41.6 °C). Besides, biogenic nano-Se improved the activity of CAT and POD (up to 150 mg/L nano-Se), and reduced electrolyte leakage and polyphenol oxidate (up to 200 mg/L nano-Se. Furthermore, nano-Se improved percent pollen germination, photosynthetic rate, facilitated a higher level of unsaturated phospholipids, increased antioxidant enzyme activities, and reduced the concentration of oxidants when 10 mg/L nano-Se was foliar sprayed during the booting stage of grain sorghum grown under heat stress (day/night, 38/28 °C) (Djanaguiraman et al. 2018). In addition, nano-Se at the rate of 5 and 10 mg/L significantly modified the expression of heat stress transcription factor *HSFA4A*, thereby activating specific signaling pathways and altering metabolism (Safari et al. 2018). *HSF* subfamily alters the expression of genes responsible for plant adaptations to the different stress conditions (Guo et al. 2016).

A high amount of ROS is produced during low-temperature or chilling stress. Antioxidant enzymes (CAT, SOD, APX), particularly those involved in the AsA-GSH cycle, play an important role against stress-induced oxidative damage. Foliar application of 5 mg/L Se significantly reduced the effect of oxidative damage caused by chilling stress after 6 h at 0 °C through improving gas exchange capacity and producing AsA-GSH cycle-related enzymes including APX, GR, dehydroascorbate reductase (DHAR), and monodehydroascorbate reductase (MDHAR) in strawberry seedlings (Huang et al. 2018). Similarly, Chu et al. (2010) demonstrated that wheat seedling treated with 0.5 and 1.0 mg/kg Se significantly increased chlorophyll content and seedlings biomass where 2.0 and 3.0 mg/kg Se only increased chlorophyll content rather biomass under cold stress. In addition, the activity of antioxidant enzymes, such as CAT and POD, and antioxidant compounds (anthocyanins, flavonoids, and phenolic compounds) was improved by different Se concentrations (0.5, 1.0, 2.0, and 3.0 mg/kg), while none but 1.0 mg/kg Se reduced MDA and superoxide radical production in wheat seedlings under cold stress, suggesting that production of antioxidant enzymes or compounds and reduction of free radicals and membrane LPO are determined by the dose of Se. Therefore, at appropriate concentration, both Se and nano-Se reduce the damage caused by high- and low-temperature effects on different crop plants by increasing the photosynthetic rate, antioxidant enzyme activity levels, reducing ROS, and promoting the AsA-GSH cycle (Table 14.3).

14.3.4 Responses to Heavy Metal Toxicity

Plants are sessile in nature and face a wide variety of environmental stresses including heavy metals, having a specific gravity >5 and an atomic mass >20 (excluding alkali metals), and are potentially harmful even at low concentrations (Bhat et al. 2020; Rascio and Navari-Izzo 2011). As, Cd, Pb, and Hg are the most frequently occurring toxic nonessential heavy metals for plant metabolism among the 53, and can significantly lower agricultural production once their concentration exceed the recommended levels (Edelstein and Ben-Hur 2018; Gupta et al. 2010; Kavamura and Esposito 2010). Population growth, urbanization, industrial activities, fertilization, treated wastewaters, sewage sludge, and the weathering of the minerals in soil accumulate vast amounts of heavy metals, which were easily absorbed into the food chain via soil buildup and plant uptake (Di et al. 2017; Gupta et al. 2010; Nagajyoti et al. 2010; Sharma 2012; Singh et al. 2010). Heavy metals have been linked to the inhibition of essential physiological processes in plants, such as photosynthesis, gaseous exchange, respiration, mineral feeding, and nutrient absorption (Ali et al. 2013; Li et al. 2013; Sardar et al. 2022); Yadav et al. 2014) as well as the overproduction of various ROS (Li et al. 2013; Singh and Prasad 2014; Singh et al. 2010).

Recently, a lot of researches have been carried out on minimizing heavy metal contaminations in various crops through Se and nano-Se (Table 14.4). Low Se

Table 14.3 Mechanisms of selenium and nano-selenium in reducing temperature stress in various crop plants

Crop plants	Mode and dose of application	Underlying mechanisms to mitigate heat/cold stresses	References
Wheat (*T. aestivum*) (cold stress)	Exogenous application of 0.5, 1.0, 2.0, and 3.0 mg/kg Se	(i) Increase antioxidant compounds (anthocyanins, flavonoids, and phenolic compounds) and enzymes (CAT and POD) (ii) Reduce MDA and superoxide radical	Chu et al. (2010)
Rapeseed (*B. napus*) (heat stress)	Foliar application of 25 µM Se	(i) Upregulate antioxidant defense (ii) Decrease LPO, MG and H_2O_2 (iii) Enhance the activity of MDHAR, DHAR, GR, GPX, CAT, Gly I, and Gly II	Hasanuzzaman et al. (2014)
Wheat (*T. aestivum*) (heat stress)	Exogenous application of 2 and 4 mg/L Se	(i) Elevate the activity of both enzymatic (CAT and APX activities) and nonenzymatic (anthocyanins, carotenoids, and L-AA contents) antioxidants (ii) Decrease H_2O_2 and MDA	Iqbal et al. (2015)
Cucumber (*C. sativus*)	Foliar application of 8 µM Se	(i) Improve the level of osmolytes, antioxidants activity (ii) Reduce ROS	Balal et al. (2016)
Maize (*Z. mays*) (heat stress)	Exogenous application of 5–15 µM Se	(i) Increase SOD, APX, GR, MDHAR, GPX (ii) Reduce POX and H_2O_2	Yildiztugay et al. (2017)
Lamb's lettuce (*Valerianella locusta*) (heat stress)	Exogenous supply of 50 mg d/m^3 Se	(i) Decrease Proline, APX and H_2O_2 (ii) Increase GPx, CAT, GSH,	Hawrylak-Nowak et al. (2018)
Strawberry (*Fragaria* × *ananassa* Duch) (cold stress)	Exogenous application of 5 mg/L Se	(i) Increase ascorbic acid, SOD, CAT, POD, DHAR (ii) Decrease GR, APX, MDHAR, MDA and H_2O_2	Huang et al. (2018)
Wheat (*T. aestivum*) (heat stress)	Exogenous supply of 5 and 10 mg/L nano-Se	Modify the expression of heat stress transcription factor HSFA4A	Safari et al. (2018)
Chrysanthemum (*Chrysanthemum morifolium*) (heat stress)	Exogenous supply of 50–200 mg/L nano-Se	(i) Improve the activity of CAT and POD (ii) Reduce electrolyte leakage and polyphenol oxidate	Seliem et al. (2020)
Tea (*Camellia sinensis*) (cold stress)	Foliar application of 2 mg/L Se	(i) Increase SOD, POD, CAT and APX to cope up with oxidative damage (ii) Reduce MDA and H_2O_2 (iii) Regulate changes in secondary metabolites	Liu et al. (2021)

(continued)

Table 14.3 (continued)

Crop plants	Mode and dose of application	Underlying mechanisms to mitigate heat/cold stresses	References
Cotton (*Gossypium hirsutum*) (heat stress)	Foliar application of 150 g/L Se	(i) Slow down the production of ROS (ii) Keep the plant green to improve photosynthesis and supply carbohydrate for longer time	Saleem et al. (2021)

levels minimize heavy metal toxicity by preventing oxidative stress in oilseed rape caused by Cd and Pb (Wu et al. 2016); regulating photosynthesis, transpiration rate, and substomatal CO_2 in grape, peach, and pear (Feng et al. 2015); detoxifying Cd toxicity through vacuolar sequestration; forming phytochelatins and cell wall absorption (Riaz et al. 2021); reducing Cd uptake, ROS accumulation, balancing nutrients and increasing H^+- and Ca^{2+}-ATPase activities in rice (Lin et al. 2012); and limiting accessibility, absorption, and translocation of Hg (IHg and MeHg) in rice (Zhang et al. 2012).

The movement of heavy metals from ground to aerial parts of the plant significantly inhibited by the foliar application of Se resulted in reduced heavy metal concentration in xylem sap (Gao et al. 2018; Wan et al. 2019). Earlier, Wang et al. (2014) reported that Se might facilitate the increase of apoplastic obstacles in root endoderm and is therefore restricting apoplastic movement of heavy metals including Hg and MeHg when 5 μg/g Se was foliar applied to rice plant. In addition, Shahid et al. (2019) described the application of 9 μM Se in potato plant grown for 48 days under As (40 μM) and/or Cd (40 μM) stress impeding As and Cd accumulation in plant tissue and Cd- and As-induced alteration in the nitrogen metabolism (14.5).

Moreover, Azimi et al. (2021) demonstrated that exogenous application of Se (10 mg/L) and CS-Se nanoparticles (5 and 10 mg/L) in Moldavian balm plant was effective to lessen the negative effect of Cd stress (2.5 and 5 mg/kg) through enhancing the content of proline, phenols, antioxidant enzymes activities, and some essential oils and reducing the level of MDA and H_2O_2. This study also suggested that lower dose of CS-Se nanoparticles (5 mg/L) was more effective than the higher dose of CS-Se nanoparticles (10 mg/L). Proline is a multifunctional amino acid that functions as a signaling molecule. Based on prior research, it can be stated that proline plays an essential role in the reduction of plant stress through maintaining cellular osmotic pressure and membrane integrity, preventing protein denaturation, and neutralizing harmful ROS (Ahmad et al. 2021; Elkelish et al. 2019; Farooq et al. 2009; Rady et al. 2021; Yao et al. 2009; Zahedi et al. 2020). Se also mitigated Al-induced toxicity in the root of ryegrass by activation of the POD enzyme and spontaneous increasing dismutation of O_2 to H_2O_2 (Cartes et al. 2010). Phyto-availability of Pd occurs when phosphate was added to a Pb-containing growth medium. Again, under phosphorous-deficient situation, Se reduced the toxicity of Pb at low concentration

Table 14.4 Mechanisms of selenium and nano-selenium in managing heavy metal stress in various crop plants

Crop plants	Mode and dose of application	Underlying mechanisms to mitigate heavy metal stress	References
Perennial ryegrass (*Lolium perenne*) (Al stress)	Exogenous application of 0–10 μM Se	(i) Activate POD enzyme (ii) Increase dismutation of O_2 to H_2O_2 spontaneously	Cartes et al. (2010)
Rice (*Oryza sativa*) (Cd stress)	Exogenous application of 3 μM Se	(i) Reduce Cd uptake and ROS accumulation (ii) Balance nutrients (iii) Increase H^+- and Ca^{2+}-ATPase activities	Lin et al. (2012)
Rice (*O. sativa*) (Hg and MeHg stress)	Foliar application of 5 μg/g Se	Restrict apoplastic movement	Wang et al. (2014)
Oilseed rape (*B. napus*) (Pb and Cd stress)	Exogenous application of 5, 10, 15 mg/kg Se	(i) Decrease oxidative damages, SOD and POD (ii) Increased MDA accumulation	Wu et al. (2016)
Faba bean (*Vicia faba*) (Pb stress)	Exogenous application of 1.5 and 6 μM Se	(i) Modification of the activity of GPX, POD and CAT (ii) Reduce LPO and H_2O_2 accumulation	Mroczek-Zdyrska et al. (2017)
Pak Choi (*B. rapa* subsp. *chinensis*) (Hg stress)	Exogenous application of 2.5 mg/kg Se (iv)	Reduced Hg bioaccumulation	Tran et al. (2018)
Tomato (*S. lycopersicum*) (Cd stress)	Exogenous application of 10 μM Se	(i) Enhance the activity of antioxidant enzymes that protect cellular structures by neutralizing reactive free radicals (ii) Increase the activity of SOD, CAT, APX, GR and osmolytes (proline and glycine betaine)	Alyemeni et al. (2018)
Potato (*S. tuberosum*) (As and Cd)	Exogenous application of 9 μM Se	(i) Hinder Cd accumulation in plant tissue (ii) Reduce Cd- and As-induced alteration in the nitrogen metabolism	Shahid et al. (2019)
Radish (*Raphanus sativus*) (Cd stress)	Exogenous application of 2, 4, and 8 mg/L Se	(i) Decline the Cd uptake, transport and distribution in roots and in leaves (ii) Enhance biomass acquisition, chlorophyll biosynthesis and fluorescence (iii) Increase the activity of enzymatic antioxidative protection system	Amirabad et al. (2020)

(continued)

Table 14.4 (continued)

Crop plants	Mode and dose of application	Underlying mechanisms to mitigate heavy metal stress	References
Moldavian balm (*Dracocephalum moldavica*) (Cd stress)	Exogenous application of 5 mg/L CS-Se nanoparticles	(i) Enhance the content of proline, phenols, antioxidant enzymes activities, and some essential oils (ii) Reduce the level of MDA and H_2O_2	Azimi et al. (2021)
Rice (*O. sativa*) (Cd stress)	Exogenous application of 3 mM Se + Si	(i) Regulate gene expression (ii) Sequester Cd in the root cell walls and organelles (iii) Reduce Cd transfer to the aerial parts	Huang et al. (2021)
Coriander (*C. sativum*) (Cd stress)	Seed priming with 5, 10, and 15 mg/L nano-Se	(i) Increase growth attributes, chlorophyll content, total soluble sugars, leaf relative water content, and gas exchange parameters (ii) Improve antioxidant response through increasing CAT, APX and POD activity (iii) Protect cellular structures through scavenging free radicals and ROS (iv) Detoxify H_2O_2	Sardar et al. (2022)

through modification of the activity of GPX, POD, and CAT and reducing H_2O_2 accumulation (1.5 or 6 μM) in faba bean (Mroczek-Zdyrska et al. 2017).

Seed priming with nano-Se at the rate of 0, 5, 10, and 15 mg/L improved growth parameters, total soluble sugar, chlorophyll content, and gas exchange parameters in coriander crop which were conversely reduced by Cd toxicity. In addition, nano-Se improved antioxidant responses by increasing CAT, APX, and POD activity, strengthening cells through detoxifying H_2O_2, and scavenging free radicals and ROS (Sardar et al. 2022). It is worth mentioning that different biotic and abiotic factors including soil pH, temperature, plant type, size and root systems, water conditions, and microbes affect the ability of Se and nano-Se to reduce heavy metal uptake in plants (Feng et al. 2021). Sometimes Se supply may enhance the phytoaccumulation of heavy metals including As in *Thunbergia alata* (Bluemlein et al. 2009) and Cu and Cd in mustard (Fargašová et al. 2006), wheat, and pea (Landberg and Greger 1994). In addition, a higher concentration of Se may act as toxic and reduce plant growth probably linked with the disturbance of the mineral balance of plants, such as accumulation of large amounts of calcium and phosphorus in shoot tissues (Hawrylak-Nowak 2008). Therefore, proper understanding of the activity and concentration of Se is required before application of Se to alleviate different abiotic stresses.

14.3.5 Responses to Elevated UV Radiation

Enhanced UV radiation has a significant effect on agricultural production. Several studies showed that elevated UV radiation affects morphological, biochemical, and anatomical properties of plants, determined by the intensity, plant species, and growth stages (Gaberščik et al. 2001; Yao et al. 2014). Most of the time, it is regarded as stress to plants, triggering the activity of phenyl-propanoid cycle, reducing leaf area and total biomass, causing alterations in various plant organs, affecting the photosynthesis and content of mineral elements in plants, and retarding growth (Jin et al. 2017; Kataria et al. 2014; Rozema et al. 2002), although the ambient UV radiation can also regulate the growth and development of plant (Björn 2015; Golob et al. 2017; Jansen et al. 2012; Peng and Zhou 2010; Shen et al. 2014). It is worth mentioning that both heat and drought stresses are related to high radiation including UV radiation (Golob et al. 2019).

In this scenario, Se plays an important role by stimulating plant growth when exposed to UV-B radiation through the alleviating oxidative stress and ROS content (Ekelund and Danilov 2001; Germ et al. 2005; Golob et al. 2019; Hartikainen et al. 2000; Nawaz et al. 2015; Seppänen et al. 2003; Xue et al. 2001). Elevated UV-B is one of the most studied radiation stresses having negative effect on plant growth parameters, chlorophyll content, protein content, nutrient content including N and Fe, and yield. In contrast, it increased MDA, H_2O_2, proline content, and Zn and Mn concentration in the grain of winter wheat. However, foliar application of Se (30 mg/kg) increased chlorophyll content, plant growth parameters, grain protein content, grain N, Fe, Cu, and Se concentration under UV-B and suggested that, to some extent, Se can improve the yield and quality of winter wheat exposed to enhanced UV-B (Yao et al. 2013). The impact of UV radiation can be different in different growth stages of the plant. Enhanced UV-B affects the quality and yield of wheat in heading and flowering stages than the whole growth stage. Therefore, protective measures (Se application) should be taken during flowering and heading stages (Yao et al. 2014).

Similarly, Breznik et al. (2005) evaluated the effect of Se on two buckwheat species, common (*Fagopyrum esculentum* Moench) and tartary [*F. tataricum* (L.) Gaertn.] exposed to UV-B radiation. Foliar spray of Se at the rate of 1 g/m^3 mitigated the negative effect of UV-B stress. UV-B reduced the effective quantum yield of photosystem II in both buckwheat species which was alleviated by the addition of Se. Se treatment also increased biomass in common buckwheat. However, in contrast, Se-treated hybrid buckwheat showed inferior yields under elevated UV radiation although the level of UV-protective substances, such as UV-absorbing compounds and anthocyanins, were improved (Golob et al. 2018).

Although several studies are available regarding the application of Se in reducing the adverse effect of UV stress from different crop plants, still there is no report on the use of nano-Se to mitigate elevated UV radiation stress in crop plants. Since nano-Se is gaining importance to reduce the negative effect of various abiotic stresses through improving the activity of antioxidant enzymes, photosynthetic pigments, and the content of proline and some essential oils, as well as reducing oxidative damage, and the level of MDA and H_2O_2 (Badawy et al. 2021; Ghazi 2018; Shalaby et al. 2021; Seliem et al. 2020; Seleiman et al. 2021), further research is necessary to evaluate their effect in mitigating enhanced UV radiation stress in various crop plants.

14.4 Impacts of Selenium and Nano-selenium on Crop Improvement and Agro-biotechnologies

Selinium is an essential micronutrient for humans and animals, and at low concentration, it has been used not only to improve the biotic and abiotic stress tolerance ability in crop plants, but also to increase crop growth, development, and yield (Hossain et al. 2021a, b; Ahmad et al. 2021; Bocchini et al. 2018; Elsheery et al. 2020; Hawrylak-Nowak et al. 2018; Hussein et al., 2019, 2020; Singh et al. 2018; Zahedi et al. 2019a). Therefore, they are now widely used as phytofortifier and growth regulator to improve the quality of food crops and feed supplementation (El-Kinany et al. 2019; Reis et al. 2020; Szarka et al. 2020) (Table 14.5). However, the physiological reactions of plants differ significantly to the administration of Se fertilizers (El-Ramady et al. 2015).

Table 14.5 Impact of selenium and nano-selenium on the growth performance in crop plants

Crop plants	Mode and dose of application	Effects on crop growth and yield	References
Lettuce (*V. locusta*)	Fertilization with 0.1 mg kg−1 Se	(i) Stimulate the growth of seedlings (ii) Diminish lipid peroxidation	Xue et al. (2001)
Bitter gourd (*M. charantia*)	Seed priming with 2 mg/L Se	Improve germination, seed performance and antioxidant activities	Chen and Sung (2001)
Green tea (*C. sinensis*)	Foliar application of 50 g/L Se	(i) Increase numbers of sprouts and the yield (ii) Improve sweetness and aroma of green tea leaves (iii) Reduce bitterness from leaves (iv) Enhance total amino acid and vitamin C contents	Hu et al. (2003)
Soybean (*G. max*)	Foliar application of 50 ppm Se as sodium selenate	Protect antioxidative parameters during senescence	Djanaguiraman et al. (2005)
Tomato (*S. lycopersicum*)	2.5 µM Se and 1 µM nano-Se	(i) Increase shoot and root dry weight, fresh weight and biomass (ii) Improve chlorophyll content (iii) Increase relative water content	Haghighi et al. (2014)

(continued)

Table 14.5 (continued)

Crop plants	Mode and dose of application	Effects on crop growth and yield	References
Valencia orange	Spraying of 50 ppm sodium selenite (Se source) + 0.1 % potassium silicate + 0.5 % potassium sulphate + 0.5 % boric acid	Enhance growth factors, nutritional status, fruit quality and yield	Ibrahim and Al-Wasfy (2014)
Pear (*Pyrus bretschneideri*), grape (*Vitis vinifera*), and Peach (*Prunus persica*)	Foliar spray of amino acid-chelated 0.017 g/L Se	(i) Protect photosystem II (ii) Improves photosynthesis, maximum and effective quantum yield of PSII, and the photochemical quenching	Feng et al. (2015)
Cucumber (*C. sativus*)	6 μM selenite 6–20 μM selenate	Upregulate mitochondrial dehydrogenases activity by selenite-impaired photosynthetic pigments accumulation and chlorophyll fluorescence parameters	Hawrylak-Nowak et al. (2015)
Coriander (*C. sativum*)	Exogenous application of Se (25 and 50 ppm), nano-Se (25 and 50 ppm), and glycine betaine (5 and 10 mM)	(i) Increase the contents of proline, ascorbic acid, photosynthesis rate, and the major constituents of coriander essential oil including linalool, geranyl acetate, camphor, δ-terpinene, and α-pinene (ii) Improve growth parameters	El-Kinany et al. (2019)
Pomegranate (*P. granatum*)	Foliar application of 1 and 2 μM Se and nano-Se	(i) Increase maturity index and decreased fruit cracking (ii) Improve growth parameters (leaf area, chlorophyll content, number of fruits per tree, peel thickness, and fruit diameter), nutrient content (N, P, K, Ca, Fe and Se) in leaves, and yield (iii) Increase total sugar, phenolic compounds, antioxidants and anthocyanins contents	Zahedi et al. (2019b)
Tomato (*S. lycopersicum*)	Foliar application of 3 mg/L sodium selenate or nano-Se	Increase shoot and root biomass fruit production, and postharvest longevity	Neysanian et al. (2020)
Wheat (*T. aestivum*)	Foliar application of 30 mg/L	Increase plant height, shoot length, shoot fresh weight, shoot dry weight, root length, root fresh weight, root dry weight, leaf area, leaf number, and leaf length	Ikram et al. (2020)
Barley (*Hordeum vulgare*)	Nano-Se stabilized by PVP C15 (8 ± 2 kDa) and ascorbic acid	Improve number of seed germination	Siddiqui et al. (2021)
Rice (*O. sativa*)	Seed priming and foliar application of 6.25 mg/L nano-Se	Increase grain yield	Badawy et al. (2021)

Generally, the growth-promoting effects of Se and nano-Se vary greatly due to the variation in plant species, growth stage, duration and concentration of exposure, size, shape, and solubility of the nano-Se (Nagdalian et al. 2021; Romero et al. 2019). In the sector of agronomy and agriculture, both Se and nano-Se are successfully utilized to supply different macro- and micronutrients including Se, which is required for appropriate crop growth and development. Due to the influence of Se and nano-Se, plant growth improves even under adverse conditions. They improve germination rate, vigor index, and seedling growth in the early stage of ontogenesis (Lyons et al. 2009; Siddiqui et al. 2021). Moreover, they can delay aging and senescence in crop plants (Chen and Sung 2001), increase shelf-life of fruit (Pezzarossa et al. 2012), improve aroma and sweetness, and reduce bitterness in tea leaves (Hu et al. 2003). In a study, Hussein et al. (2019) observed the effect of nano-Se on the growth of three different groundnut cultivars (NC, Gregory, and Giza 6) which are mostly affected by the concentration of nano-Se and type of groundnut cultivars. Foliar application of 20 and 40 ppm nano-Se at vegetative stage increased the growth of two cultivars of groundnut, including Gregory and Giza 6 linked with the alteration in photosynthetic pigments, and improved antioxidant enzymes (CAT, POD, APX), LPO, and the content of phenols, total sugar, and flavonoids, while the growth parameters were negatively affected in cultivar NC. In another study, Siddiqui et al. (2021) showed that the highest number of seed germination was achieved in barley by the Se-nanoparticles stabilized by Polyvinylpirrolidone (PVP) C15 (8 ± 2 kDa) and ascorbic acid at a concentration of 4.65 μg/mL.

Zahedi et al. (2019b) reported that foliar applications of both Se (1 and 2 μM) and nano-Se (1 and 2 μM) have beneficial effects on morphological, vegetative, and organoleptic properties and yield in pomegranate. Both Se and nano-Se significantly increased maturity index and decreased fruit cracking. In addition, Nano-Se at the rate of 2 μM significantly improved growth parameters (leaf area, chlorophyll content, number of fruits per tree, peel thickness, and fruit diameter), nutrient content (N, P, K, Ca, Fe, and Se) in leaves, and yield. Moreover, total sugar, phenolic compounds, antioxidants, and anthocyanins contents were also improved by the application of 2 μM nano-Se in pomegranate. Along with improving growth parameters and nutrient status, Se and nano-Se also increase crop yield by producing various growth-induced secondary metabolites. El-Kinany et al. (2019) described the effect of Se (25 and 50 ppm), nano-Se (25 and 50 ppm), and glycine betaine (5 and 10 mM) on coriander plants grown under salt stress. Exogenous application of Se and glycine betaine improved the contents of proline, ascorbic acid, photosynthesis rate, and the major constituents of coriander essential oil including linalool, geranyl acetate, camphor, δ-terpinene, and α-pinene. In addition, all the growth parameters tested were significantly improved by the application of Se and glycine betaine compared to nano-Se and control treatment.

Besides, the effect of foliar application of Se was reported on stimulating growth, fruit quality, and yield of other crop species including potato (Turakainen 2007), tomato (Haghighi et al. 2014; Neysanian et al. 2020), soybean (Djanaguiraman et al. 2005), lettuce (Xue et al. 2001), green tea leaves (Hu et al. 2003), pear, grape, and peach (Feng et al. 2015), cucumber (Hawrylak-Nowak et al. 2015), bitter gourd

(Chen and Sung 2001), orange tree (Ibrahim and Al-Wasfy 2014), sorghum (Djanaguiraman et al. 2010), and pepo plants (Germ et al. 2005). In contrast, an excess Se may act as toxic to non-tolerant plant species, and subsequently decrease germination and growth rates, as well as cause leaf chlorosis and black spots (Awual et al. 2014, 2015a, b; Hawrylak-Nowak 2008, 2013; Neysanian et al. 2020; Pezzarossa et al. 2012), where some plants remain unaffected (Hsu et al. 2011).

Biofortification of plants with nutrients such as Se is one of the main targets of plant biotechnology (Khan and Hell 2008). Se biofortification involves the uptake and accumulation of Se in agricultural food products through different biotechnological and agronomical approaches such as genetic engineering, modifying nutrient uptake channels, plant breeding, and manipulation of agricultural practices. It is a promising strategy to increase the nutritional status of food crops and improve the dietary intake of nutrients in the human body (Zhu et al. 2009; Borrill et al. 2014). Se accumulation, tolerance, and volatilization by plants can be improved by genetic engineering through sulfur-related enzymes. For example, Pilon-Smits et al. (1999) reported the overexpression of APS (a key enzyme for selenate to selenite transition) in *B. juncea*, resulting in selenate reduction; however, plants with APS transgenics accumulated and tolerated more Se. The overexpression of SMT was also observed in *B. juncea* which enhanced Se accumulation (LeDuc et al. 2004). Moreover, the overexpression of SMT and γ-glutamyl-Me-SeCys in shoots were found by introducing SMT gene of *Astragalus bisulcatus* (two-grooved poison vetch) in *A. thaliana* (Ellis et al. 2004; Pilon-Smits and LeDuc 2009; Sors et al. 2005). Interestingly, double transgenic crop (crossed of APS and SMT *B. juncea*) accumulated higher Se (up to 9 times) than wild type (LeDuc et al. 2004), and most of the Se in the double transgenics was Me-SeCys form. ST is also a potential target to improve the efficiency of genetically engineered Se-enriched crops at the molecular level. Furthermore, plant-microbe interaction is an important area to improve Se biofortification.

Plant secondary metabolites that play an important role in sustainable agriculture are influenced by Se accumulation in plants. Se changes the synthesis of sulfur-containing secondary (S-secondary) compounds with nutritional value such as glucosinolates (GLS) which take part in the plant defense system against insects and herbivores. In mammals, isothiocyanates produced through the hydrolysis of GLS act as cancer-preventing agents (Dinkova-Kostova 2013). Se affects the production of protein and amino acids and also exerts an additional effect on N-secondary compounds that act as a scavenger of free radicals like phenolics. Phenylalanine (Phe) is the substrate for phenolic biosynthesis. Moreover, Met (methionine), Phe, Tyr (tyrosine), and Trp (tryptophan) are the precursor of GLS. Therefore, Se accumulation is very crucial in plants having the significant effect on the biosynthesis of both types of secondary products that are beneficial for plants as well as animals (Barickman et al. 2013; Robbins et al. 2005; Schiavon et al. 2013). Fertilization of tomato with 5 and 10 μM Se increases the phenolic compound in leaf. Moreover, foliar spray of 2 and 20 mg selenate in Se-biofortified tomato fruits improved the level of flavonoids naringenin, chalcone, and kaempferol having antioxidant properties (Schiavon et al. 2013). It is worth stating that multiple bioactive components can be maximized in a single plant but need to consider the interactions between Se and the main metabolic pathways of the plant to avoid potential interference with the production of other phytochemicals.

14.5 Conclusion and Future Perspectives

To feed the ever-increasing population in the world, intense research efforts are needed to be carried out worldwide. However, increasing environmental stresses and emergence of diseases and pests due to global climate change are considered major limiting factors for crop production for ensuring food security. Se and nano-Se show promise to improve environmental stress tolerance in plants, increase crop yield, and modify plant features such as higher nutrient content and long storage life, and improve the production of essential oil. Their uses in agro-biotechnologies have also been increased. Nano-Se is one of the most potentially used forms of Se. Nano-Se's fascinating properties lead to its use not only in the modern clinical sectors, but also to achieve sustainable agriculture by improving crop growth and reducing environmental stresses. Beneficial effects of the application of Se and nano-Se to alleviate environmental stresses and improve crop yield are documented in many reports. Although molecular mechanisms of the effect of Se on plants and other living cells are largely known, the precise roles of nano-Se in plants are poorly understood. It is necessary to know the accurate form, dose, and timing of application of Se and nano-Se on plants to get the highest benefit from this micro-element. Further studies are needed to elucidate the precise roles of Se and nano-Se in alleviation of environmental stresses for ensuring future food and nutritional security of the increasing population of the world under the changing climate.

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Chapter 15
Selenium Toxicity and Tolerance in Plants: Recent Progress and Future Perspectives

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15.1 Introduction

Selenium (Se) was discovered by Jons Jakob Berzelius, who named it after the Greek goddess of the moon 'selene'. Nowadays, Se is one of the most actively examined metalloids due to its beneficial effects on plants, animals, and humans. Although Se is not utilized as an essential nutrient, it is taken up by higher plants primarily from the soil. Globally, total soil Se concentration is typically within the range 0.01–2.0 mg kg^{-1} with an overall mean of 0.4 mg kg^{-1} (Johnson et al. 2010). Selenate being present in soil solution enters the plant in conjunction with the sulphate uptake machinery, while selenite is absorbed in association with phosphate uptake and aquaporins (Schiavon and Pilon-Smits 2017). Organic Se forms (e.g. selenomethionine, selenocysteine) found in relatively small amounts in the soil may enter the root cells via amino acid transporters with affinity to transport cysteine and methionine (Trippe and Pilon-Smits 2021). Selenite as the more toxic Se form is partly converted to organic forms like selenomethionine (SeMet) in the root cells, while most of the absorbed selenate is translocated into the shoot via xylem (Shrift and Ulrich 1976; Zayed et al. 1998). The sites of the assimilation are mainly leaf chloroplasts. In the first step, selenate is activated by ATP sulphurylase (APS) yielding adenosine 5′-phosphoselenate (APSe) which is then reduced by APS reductase resulting in selenite formation. Selenite is further reduced to selenide (Se^{2-}) either by the activity of sulphite reductase or by a non-enzymatic reduction with glutathione. The latter mechanism seems to be more energetically favourable (Hsieh and Ganther 1975; Trippe and Pilon-Smits 2021). In the following step, cysteine synthase complex catalyses the incorporation of selenide into selenocysteine (SeCys).

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M. A. Hossain et al. (eds.), *Selenium and Nano-Selenium in Environmental Stress Management and Crop Quality Improvement*, Sustainable Plant Nutrition in a Changing World, https://doi.org/10.1007/978-3-031-07063-1_15

The detoxification of SeCys occurs via various alternative ways. SeCys can be converted to the less toxic selenomethionine (SeMet) and volatile dimethyl-selenide (DMSe), or it can be converted to elemental Se (Se^0) and alanine. The formations of methyl-selenocysteine (MeSeCys) and the volatile dimethyl-diselenide (DMDSe) are further possible SeCys detoxification mechanisms and are characteristic of hyperaccumulator plant species (Pilon-Smits and Quinn 2010; Trippe and Pilon-Smits 2021). Selenium in low quantities has a beneficial effect on plants' physiological processes, as it promotes organ growth and vegetative-reproductive development in healthy plants and enhances tolerance in plants exposed to abiotic or biotic stresses (Kolbert et al. 2019a; Hasanuzzaman et al. 2020). However, at elevated dosages, Se causes toxicity in the susceptible plant species. Se phytotoxicity is associated with multiple underlying mechanisms as indicated by recent experimental results.

In the following sections, we discuss these phytotoxicity mechanisms of elevated Se doses as well as the tolerance mechanisms against Se toxicity developed by plants.

15.2 Selenium Toxicity and Toxicity Mechanisms

15.2.1 Se Toxicity and Proteins

Selenium is a non-essential microelement for higher plants; however, its uptake and metabolism have an effect on plant metabolism. Like other micronutrients, the effect of Se is dose-dependent: In small concentration, it has proven to be beneficial for plants, while excess Se content can lead to toxic processes (Molnár et al. 2018a, b). The dose of Se to exert its toxic symptoms is generally above 5 mg kg^{-1} DW (Reilly 1996); however, it's dependent on plant species, for example, in rice, 2 mg kg^{-1} DW has been proven to be toxic (Tripathi and Misra 1974), while Dutch clover can accumulate 330 mg kg^{-1} (Mikkelsen et al. 1989). The toxic symptoms of high Se content are usually chlorosis, withering and decreased biomass production (Hawrylak-Nowak et al. 2015; Lehotai et al. 2016a, b; Molnár et al. 2018a, b). Behind these symptoms are various molecular background processes: disturbances in hormonal balance, nutritional state and primary carbon metabolism, protein toxicity and changes in ROS and RNS levels resulting in nitro-oxidative stress (Kolbert et al. 2016; Kolbert et al. 2019b). We must note that in case of exogenous Se addition, Se-induced phytotoxicity seems to be connected with the method of Se application. Yin et al. (2019) have found that different Se forms and application methods have distinct effects on Se accumulation, photosynthetic efficiency or antioxidant parameters of rice, either at vegetative or reproductive stage. Namely, root application of Se, mainly in the form of methyl-selenocysteine (MeSeCys) or selenite, had more significant influence on biomass production and Se accumulation than foliar dressing. At the same time, foliar spraying of Se as selenate was shown to be more harmful at higher concentrations for field-grown cowpea (*Vigna unguiculata*) plants (Lanza et al. 2021). The visual symptoms of Se toxicity occurred as necrotic spots on the leaves (at 50–100 g^{-1} Se per ha), while total chlorosis, the formation of brown necrotic lesions and senescence were detected at higher Se dosage.

To evaluate the threat of selenium to the proteome, the uptake and metabolism of this element have to be reviewed briefly. Se could be uptaken as inorganic selenate or selenite, or as organic selenoamino acids, like SeCys and SeMet (White and Broadley 2009). The metabolism of selenium is via the sulphur assimilation pathway, which will reduce selenate to selenite and incorporate it into SeCys. SeCys can be converted to various organic forms, and among them is SeMet (Kolbert et al. 2019a).

In organisms, in which Se is essential, there encoded a specific tRNA that can integrate selenocysteine to various selenoproteins (Carlson et al. 2018; Tobe and Mihara 2018). For higher plants, Se is not essential; however, the incorporation of selenoamino acids is still present (White 2016). The similarity of cysteine and SeCys will result in a competition for plant cysteine tRNA, resulting in a selenoamino acid integration into plant protein synthesis (Stadtman 1990). The non-specific selenoprotein formation is one of the main toxic processes of Se in higher plants, resulting in harmful changes in the active protein pool. SeMet is considered to be more stable compared to SeCys, and its incorporation in proteins is generally harmless (Stadlober et al. 2001). It is important to note that trans-sulfuration process, which has been detected in yeast (Lazard et al. 2015; Plateau et al. 2017), can revert SeMet to SeCys, resulting in higher flawed selenoprotein levels.

The toxic effect of selenoamino acid assimilation is associated with structural differences, resulting in an altered non-functional protein with altered redox potential (Hondal et al. 2013). Cysteine is often found in the active sites of proteins, and changes in this amino acid will affect enzyme kinetics (Kim and Gladyshev 2005; Hazebrouck et al. 2000). SeCys can also affect cofactor or ion binding (Aldag et al. 2009). There has been evidence that Se can replace sulphur in protein Fe-S clusters, which are essential to chloroplastic and mitochondrial electron transport (Hallenbeck et al. 2009). In summary, SeCys incorporation during proteins synthesis is usually toxic to the plant. Selenoproteins are predominantly degraded via the ubiquitin proteosome pathway (Smalle and Vierstra 2004), preventing cytotoxic effects.

15.2.2 Se Toxicity and Reactive Species

The signaling of different reactive species is important in all physiological and developmental processes in plants. Almost all abiotic stress factors can induce changes in ROS (reactive oxygen species), RNS (reactive nitrogen species) or RSS (reactive sulphur species) metabolism as a response, which can increase the plant tolerance or contribute to the toxicity. Se is not an exception to this rule: Nitro-oxidative stress is considered to be one of the main toxic mechanisms.

The connection between ROS and Se stress is evident as early as the Se metabolism: glutathione reduces selenite to selenide, which results in superoxide anion (Chen et al. 2007). This can enhance the transcription of antioxidant response genes (Van Hoewyk et al. 2008) and the metabolism of antioxidants (Dimkovikj and Van Hoewyk 2014). Se can also generate superoxide anion in mitochondria (Vallentine et al. 2014). This oxidative response has been associated with decreased activity of tricarboxylic acid cycle in roots (Dimkovikj and Van Hoewyk 2014). Selenite also decreased the aconitase activity, which contains an Fe-S cluster as a possible target for Se toxicity (Verniquet et al. 1991). In in vitro experiments, iron-sulphur containing ferredoxin from chloroplasts has been treated with selenite. This resulted in a rapid decrease in enzyme activity and destabilization of Fe-S cluster, proposing another impact of Se on electron transport chains (Fisher et al. 2016). The inactivation of antioxidant metabolism and depletion of glutathione will evoke an altered cellular redox state and oxidative stress (Hugouvieux et al. 2009; Grant et al. 2011). ROS accumulation can damage macromolecules, e.g. lipid peroxidation which has been documented in response to excess Se (Mostofa et al. 2017; Gouveia et al. 2020). Protein oxidation can also occur, which will change the active protein pool eventually resulting in protein degradation (Berlett and Stadtman 1997; Dunlop et al. 2002). Oxidized proteins have been reported in response to Se (Sabbagh and Van Hoewyk 2012; Vallentine et al. 2014), further emphasizing the significance of ROS metabolism in Se toxicity.

Compared to ROS, the role of RNS in abiotic stress is a newer, active field of study. The connection between RNS and Se has been examined; however, the results are still unclear. It has been reported that Se can alter endogenous NO levels (Lehotai et al. 2012; Chen et al. 2014a), and NO metabolism mutants *nia1nia2* and *gsnor1–3* had altered response compared to the control. *nia1nia2 Arabidopsis* plants showed to be sensitive to Se in contrast to wild type or *gsnor 1–3*. Both *Arabidopsis* mutants had lower NO levels than wild type, suggesting the role of NO/GSNO in Se tolerance (Lehotai et al. 2016a). Peroxynitrite is another major RNS, formed from the reaction of superoxide and NO. In RNS signaling, peroxynitrite can induce protein tyrosine nitration, one of the main RNS signaling processes. Se treatment can alter peroxynitrite levels and protein tyrosine nitration in plants (Lehotai et al. 2016b; Molnár et al. 2018a, b; Kolbert et al. 2018). The connection between tyrosine nitration and Se tolerance is still diverse; however, it's suggested that changes in protein tyrosine nitration pattern contribute to Se toxicity by changing the active protein pool. Data on other RNS-mediated macromolecule modifications: S-nitrosation, lipid and nucleic acid nitration, are scarce. The importance of these macromolecule modifications in RNS signaling has been shown, suggesting their possible role in Se toxicity.

In the case of RSS, connections between Se stress and RSS metabolism have been insufficiently documented. Chen et al. (2014b) have reported that in selenite-treated rapeseed, increasing concentration of Se reduced root growth, and it was closely correlated with the inhibition of endogenous H_2S generation in root tips. It can be hypothesized that due to the similarity between sulphur and selenium, and the connection between RSS and other reactive molecules, RSS could be involved in Se stress. This connection is needed to be visualized in further studies.

15.2.3 Se Toxicity and Hormonal Status

Plants have different strategies to respond to metalloid toxicity, one is the regulation of hormone levels. Many studies showed that auxin, ethylene, jasmonic acid, and cytokinin play a crucial role to protect the plants against selenium (Se). Among the phytohormones, auxin signaling is essential for the normal plant growth and development, and auxin can interact with other hormones (Casanova-Sáez and Voß 2019). Ethylene is a gaseous molecule which regulates many fundamental aspects of plant life cycle such as leaf and flower senescence, fruit ripening, germination (Corbineau et al. 2014; Miransari and Smith 2014; Wilson et al. 2014) and root development (Ivanchenko et al. 2008; Lima et al. 2009; Huang et al. 2013). Malheiros et al. (2019) observed that 10 μM Se down-regulated ethylene biosynthesis genes (ACS2, ACS6, ACO1, ACO7) and also down-regulated the expression of auxin biosynthesis genes (YUCCA1, YUCCA3) in rice (*Oryza sativa* L.) roots under Se toxicity. Selenite treatment inhibited auxin accumulation but increased cytokinin level in *Arabidopsis thaliana* primary root (Lehotai et al. 2012). As known, cytokinin controls cell division, organ and growth development. Jiang et al. (2018) demostrated that selenium-tolerant *Arabidopsis* mutant with a loss-of-function mutation in a terpenoid synthase gene (TPS22) contain less cytokinin level and reduced gene expression of cytokinin receptors (AHK3, AHK4).

Jasmonic acid (JA) belongs to the jasmonate compounds, and it has a role in the response to biotic and abiotic stress. *Arapidopsis* ethylene or jasmonate biosynthesis or signaling (*acs6*, *ein2* and *jar1*) mutants plants showed less resistance to selenite and selenate the two major forms of Se compared to control (Tamaoki et al. 2008; Van Hoewyk et al. 2008). The Se-sensitive *Arabidopsis* 'Wasilewskaya' ecotype showed enhanced selenite resistance when it was treated with methyl jasmonate (MeJA) as a jasmonate acid derivate or 1-aminocyclopropane-1-carboxylic acid (ACC) precursor of ethylene (Tamaoki et al. 2008). About the toxicity, these results suggested that plant hormones are essential to protect the plants from Se stress.

15.2.4 Se Toxicity and Nutritional Homeostasis

Selenium (Se) excess interrupts mineral balance in plants, causing adverse changes in the quantitative composition of essential nutrients, as has been confirmed by the recent study of Ulhassan et al. (2019). They found a decline in the transportation of micronutrients (Fe, Zn, Mn) and macronutrients (Ca, Mg, P, K) both in the leaves and roots in selenite-treated *Brassica napus* plants.

Se ions interact with nutrients in plant tissues, thus disrupting the physiological processes they regulate. The interaction between Se and essential elements depends on the quantitative proportions, causing antagonistic and synergistic effects (Hawrylak-Nowak and Matraszek-Gawron 2020).

Kabata-Pendias (2011) observed that increased Se levels in plants suppress the concentrations of nitrogen (N), phosphorus (P) and sulphur (S), as well as several amino acids; thus, high Se concentrations inhibit the absorption of metals, mainly manganese (Mn), zinc (Zn), copper (Cu) and cadmium (Cd). Maize plants treated with selenite (5–100 μM) showed high phosphorus and calcium (Ca) content in shoots, but reduced potassium (K) content (Hawrylak-Nowak 2008). In addition, Feng et al. (2009) found that selenite (10–100 mg kg^{-1} of soil) suppressed the uptake of P, calcium (K), magnesium (Mg), Cu, Zn and arsenic (As) in the Se accumulator Chinese brake fern (*Pteris vittata* L.). In the case of cucumber, the toxicity threshold for selenate and selenite was between 20 and 80 μM. Hawrylak-Nowak et al. (2015) measured the macronutrients concentrations in the aboveground cucumber organs. Their experiment showed that 60 μM of selenite significant decrease in N amounts in plants. Also the Mg concentrations decreased only under a highly phytotoxic selenite concentrations (40 and 60 μM). The effects of Se on Ca concentration depended on the chemical form of Se added to the growth media. Whereas selenite treatments between 30 and 60 μM significantly decreased the Ca concentration in the dose-dependent manner, the exposition of plants to selenate resulted in a slightly higher concentration of Ca, but a significant increase was noted only in the presence of 40 and 80 μM Se applied as selenate. About nutritional homeostasis and the toxicity, these researches suggested that plant nutritional homeostasis is necessary for normal growth and development in case of excess selenium.

15.3 Se Tolerance and Its Background

15.3.1 Se Tolerance Mechanisms

It has been proved that high Se concentration, mainly in Se-rich areas (e.g. USA, Canada, South America) (Gupta and Gupta 2017), does not always seem to be disadvantageous for plants. Numerous researchers have established that plant species having the ability to tolerate and to (hyper)accumulate Se in their younger leaves and reproductive organs are more resistant against herbivores and pathogens (Freeman et al. 2006; Statwick et al. 2016; Mechora 2019; Pilon-Smits 2019).

The ability of plants to tolerate and (hyper)accumulate Se depends on external and internal factors. External factors can be the Se concentration in the soil or water, the chemical form (selenate, selenite or organic) of Se, pH, etc. which affect Se availability for plants (detailed in White 2017). Since the uptake and metabolism of Se are executed via S assimilation pathway, the abundance or the absence of S and Se is also determinative (White 2018).

One of the intrinsic agents is the presence of different sulphate transporters (SULTRs) localized in the membrane of root cells which are responsible for the uptake of Se dominantly in the form of selenate (SeO_4^{2-}). Non-accumulators (e.g. *Arabidopsis thaliana*), Se-accumulators (e.g. *Brassica juncea*) and Se-hyperaccumulators (e.g. *Astragalus bisulcatus*, *Stanleya pinnata*) all have SULTR1,1;2 homologs, but the expression level of their encoding genes is different; in the hyperaccumulators, these genes show high constitutive expression (White 2018). The transport of Se from root to shoot can be regarded as another intrinsic factor. In both non-accumulators and (hyper)accumulators, Se is translocated predominantly as selenate. The primary Se assimilation through which selenate is converted to selenoamino acids, selenocysteine (SeCys) and selenomethionine (SeMet) in a multistep procedure takes place in the chloroplasts of mesophyll cells (details in Guignardi and Schiavon 2017; White 2017). Besides, selenate can be sequestered in the vacuole in both non-accumulators and (hyper)accumulators (Freeman et al. 2006; Guignardi and Schiavon 2017; White 2017). The third internal factor might be the way of secondary metabolism, namely, fate of SeCys and SeMet. Similar to Cys and Met, Se-amino acids may incorporate into peptides and proteins using the metabolic pathways of S analogues (summary by Zhang et al. 2020). At 'optimal' Se concentration, this replacement can be beneficial in human aspect, because of producing Se-enriched (selenized) crops (broccoli, potato tubers, onion bulbs, edible seeds and grains), containing Se predominantly as selenomethyl selenocysteine (SeMSeCys) or selenocysteine ($SeCys_2$) and possessing higher antioxidant capacity (Gupta and Gupta 2017; Chauhan et al. 2019; Zhang et al. 2020). But at 'supraoptimal' Se concentration, when excess amount of selenate gets taken up by plants, selenate may be sequestered in the vacuoles of the mesophyll cells, or selenate can be converted to SeCys in the plastids. Either in non-accumulators like *Arabidopsis* or (hyper)accumulators such as *Brassica juncea* or *Astragalus biculcatus*, if the extra SeCys replaces Cys in key enzymes, it may cause dysfunctionality and toxicity. Therefore, the fourth point of view is the way of detoxification. In order to avoid Se toxicity, SeCys is transformed to less harmful SeMet which gets through methylation by cytosolic S-adenosyl-methionine: methionine methyl transferase (MMT) producing Se-methylselenomethionine (SeMSeMet) (White 2018). We must note that SeCys also can be methylated to selenomethyl selenocysteine (SeMSeCys) by selenocysteine methyltransferase (SMT) enzyme, but SMT is missing in non-accumulators, while both enzymes can be found in Se-hyperaccumulators (Gupta and Gupta 2017). In non-accumulators, SeMSeMet can be metabolized to dimethylselenide (DMSe) which is later volatilized (Pilon-Smits and Quinn 2010), or to γ-glutamyl-SeMSeMet (γ-Glu-SeMSeMet) (White 2017). Though Se-(hyper)accumulators have both MMT and SMT enzymes, the production and accumulation of SeMSeCys and its derivative, γ-glutamyl-SeMSeCys (γ-Glu-SeMSeCys), occur to be dominant in the shoot and reproductive tissues (Freeman et al. 2006; White 2016). Later, SeMSeCys is converted to volatile dimethyl diselenide (DMDSe) (Valdez Barillas et al. 2012; Kolbert et al. 2019a).

Last but not least, it must be noted that Se-hyperaccumulator species such as *Stanleya pinnata* has evolved the process of degradation of malfunctioning Se-containing proteins via the ubiquitin-26S proteasome pathway (Sabbagh and Van Hoewyk 2012).

At tissue level, in non-accumulators and indicators, Se accumulation was found in the mesophyll and vascular tissue of the leaves, while in hyperaccumulators that was dominant in younger leaves (mainly in trichomes and leaf edges) and reproductive tissues supporting the hypothesis that Se accumulation in these plant parts may protect the embryo and the sensitive younger leaves from herbivores and pathogens (Freeman et al. 2006; Pilon-Smits 2019).

15.3.2 Se Tolerance and Reactive Species

Several reports have established that Se toxicity due to the pro-oxidant ability of excess Se is accompanied by nitro-oxidative stress (Van Hoewyk 2013; Chen et al. 2014a; Kolbert et al. 2016), but relatively a few studies deal with the relationship between Se tolerance and reactive species. In Se-hyperaccumulator *Stanleya pinnata*, Freeman et al. (2010) found higher levels of ascorbic acid, glutathione and nonprotein thiols in comparison to secondary Se accumulator *Stanleya albescens*. Moreover, after the treatment with 20 µM selenate for 10 weeks, the superoxide accumulation detected in *S. pinnata* leaves was lower compared with *S. albescens*. Similarly, hydrogen peroxide content occurred to be lower, too. All these findings suggested that Se tolerance may be in connection with the increased antioxidant content, decreased ROS level and up-regulated sulphur assimilation. Not surprisingly, in the leaves of control *S. pinnata*, the genes encoding glutathione S-transferase (GST), two glutaredoxins, catalase (CAT) and dehydroascorbate reductase (DHAR) were more highly expressed, and in the roots, the genes encoding ferredoxin, two glutaredoxins and a glutathione peroxidase (GPX) were up-regulated resulting in a higher antioxidant capacity of the Se-hyperaccumulator species.

A few years ago, Kolbert et al. (2018) observed that in case of two *Astragalus* species (Se-hyperaccumulator *A. bisulcatus* and Se-sensitive *A. membranaceus*), the meristem cells of root tips of *A. membranaceus* showed 50% or 85% viability loss after the treatment with 50 or 100 µM selenate. This was in part due to increased superoxide levels, while in the root tips of tolerant *A. bisulcatus*, selenate had no effect on superoxide levels. Furthermore, enhanced NO and peroxynitrite formation was detected as an effect of 50 µM Se in the root of sensitive *A. membranaceus*, but in *A. bisulcatus* root tips, Se treatments had no effect on the examined reactive nitrogen species (RNS) levels which can be due to its Se-hypertolerance.

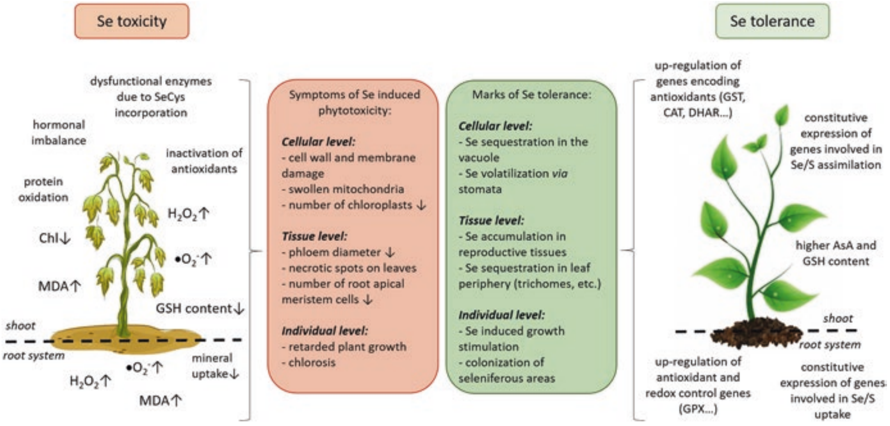

Fig. 15.1 Schematic model of the symptoms of Se toxicity and the marks of Se tolerance in higher plants. *Chl* chlorophyll, *MDA* malondialdehyde, $\bullet O_2^-$ superoxide anion, H_2O_2 hydrogen peroxide, *GSH* glutathione (reduced), *AsA* ascorbic acid, *GST* glutathione S-transferase, *CAT* catalase, *DHAR* dehydroascorbate reductase, *GPX* glutathione peroxidase. (Based on Freeman et al. 2006; White 2017; Both et al. 2020; Gouveia et al. 2020; Lanza et al. 2021)

15.4 Conclusions and Future Perspectives

Based on the results of the reports, Se acts as a double-faced element for plants. Small amount of Se can an antioxidant, while at higher concentrations, Se occurs to function as a pro-oxidant resulting in not only the overproduction of reactive oxygen species (ROS) and lipid peroxidation but nitrosative stress, hormonal and nutritional imbalance or synthesis of malfunctional selenoproteins, and consequently chlorotic plants with inhibited growth, as well. These findings are summarized in Fig. 15.1. It seems that Se tolerance and capability of Se accumulation depend on many external factors (e.g. concentration and availability of Se) and their interplay with various internal agents, such as the presence of sulphate transporters and basically high expression levels of genes encoding antioxidants or involved in S assimilation.

Though many studies have dealt with Se toxicity, there are still many questions about the relationship of Se toxicity and phytohormones or RNS/RSS. Furthermore, the nitro-oxidative background of Se tolerance also needs deeper insights.

Acknowledgements This work was supported by The National Research, Development and Innovation Office (Grant no. K135303).

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Chapter 16
Manipulation of Selenium Metabolism in Plants for Tolerance and Accumulation

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16.1 Introduction

Selenium (Se) is an essential element for many life forms. Humans, in particular, require trace Se as a key component of selenocysteine (SeCys), which is recognized as the 21st protein amino acid and is typically embedded at the catalytic site of 25 known selenoproteins (Labunsky et al. 2014; Carlson et al. 2018). Human selenoproteins exhibit a wide range of functions in cellular metabolism, resulting in critical health effects. In particular, they favor the immune system and defense mechanisms against free radicals and oxidative stress and regulate thyroid metabolism and spermatogenesis (Rayman 2020; Lima et al. 2021).

The United States Recommended Dietary Allowance for Se in adults is 55–75 μg/day (National Academy of Sciences 2000), while the threshold of chronic Se intake that might cause toxicity is 400 μg/day (Institute of medicine 2000; Vinceti et al. 2018). Although cases of chronic selenosis, i.e., the condition caused by excessive Se, were documented in Enshi, (China) (Huang et al. 2013) and in Punjab (India) (Hira et al. 2004; Chawla et al. 2020), Se deficiency is a more frequent condition, and the number of people who are suffering from it is increasingly growing on a global scale (Jones et al. 2017). Se deficiency manifests subtly as augmented susceptibility to viral infections, cancers, and other diseases (Lima et al. 2021; Schiavon et al. 2020). Acute selenosis can also occur in humans and is generally caused by the ingestion of Se-rich chemical products and excessive amounts of dietary Se supplements (MacFarquhar et al. 2010).

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M. A. Hossain et al. (eds.), *Selenium and Nano-Selenium in Environmental Stress Management and Crop Quality Improvement*, Sustainable Plant Nutrition in a Changing World, https://doi.org/10.1007/978-3-031-07063-1_16

Plants represent a major source of Se to humans, and therefore Se consumption ultimately depends on the concentration of available Se in soil, as well as on the plant capacity to take up and convey Se to the aboveground produce (Yang et al. 2021). Globally, Se concentration in soils is generally very low, but a few soils termed "seleniferous" naturally contain elevate amounts of Se (more than 100 mg Se/kg). Other soils are high in Se due to anthropogenic Se contamination and need reclamation (Khamkhash et al. 2017).

Intriguingly, plant do not require Se for their growth and metabolism, but this element at low concentration can induce several beneficial effects in them, such as a greater growth and resistance against abiotic and biotic stress (Chauhan et al. 2019). At high concentration, however, Se generates toxicity in plants causing protein misfolding or acting as a prooxidant agent through the redox cycling with thiols and by producing reactive oxygen species (Van Hoewyk 2013; Kolbert et al. 2019).

Plants do not appear to possess specific mechanisms for Se uptake; thus, Se is likely transported across cell membranes nonspecifically through the action of transport proteins for other nutrients (Trippe and Pilon-Smits 2021). Though, certain plants, termed Se hyperaccumulators, are believed to own specific transporters that assist Se uptake and are hypothesized to be responsible for their extraordinary ability to accumulate Se in their shoot (>1000 mg Se/kg) when growing in seleniferous soils (White et al. 2016, 2018). Also, Se hyperaccumulators have evolved specific biochemical pathways that allow them to avert Se toxicity and whose metabolites serve ecological functions (Pilon-Smits 2019). On this account, Se-hyperaccumulators offer a fascinating genetic pool for the selection of candidate genes to transfer to non-hyperaccumulators through genetic engineering. So far, sulfur-related proteins that mediate Se transport or are involved in Se assimilation or detoxification (including volatilization) have been overexpressed in non-hyperaccumulators using different manipulation strategies, resulting in enhanced capacity of plants to accumulate and tolerate Se (Pilon-Smits and LeDuc 2009). However, as the development of Se-enriched plants has become particularly attractive for both phytoremediation and biofortification scopes, this requirement has prompted research to identify novel molecular targets unrelated to S transport and metabolism.

16.2 Genetic Engineering of Se Accumulation and Tolerance

16.2.1 Manipulation of Selenium Transport

Among Se species present in terrestrial ecosystems, selenate is the most available in oxic soils, while selenite dominates under anoxic conditions, as those in flooded soils (Winkel et al. 2015; Shahid et al. 2018). Organic selenocompounds can be appreciably present in seleniferous soils and derive mainly from the decomposition of Se-hyperaccumulator litter (Pilon-Smits 2019). Once in the soil, these compounds, especially the Se-amino acids, can be readily taken up by plants thus contributing to Se cycling (Winkel et al. 2015).

Plants take up both selenate and selenite ions, but neither ion can cross the root cell membranes through Se-specific transporters. Selenate, in particular, makes use of sulfate transporters (SULTRs) for the entry into cells owing to its chemical similarity to sulfate (Schiavon and Pilon-Smits 2017a; Trippe and Pilon-Smits 2021). However, the hypothesis that other transporters beside SULTRs may be responsible for selenate movement within the plant cannot be excluded.

SULTR1;2 is the major root high-affinity transporter involved in the primary sulfate uptake. The mutation of SULTR1;2 in *Arabidopsis* resulted in enhanced Se tolerance through restriction of selenate uptake and accumulation in the plant, but mutations in other sulfate transporters did not appear to modulate Se tolerance (El Kassis et al. 2007). The Se-hyperaccumulator *Stanleya pinnata* has a very high expression of the gene encoding SpSULTR1;2 (Wang et al. 2018), which, contrary to non-hyperaccumulators, is not subjected to the canonical feedback regulation operated either by the availability of sulfate or the S state of the plant (El Mehdawi et al. 2018). Therefore, SpSULTR1;2 could have higher specificity for Se over S, which would explain the high Se/S ratios observed in *Stanleya pinnata* and, perhaps, the S-independent seasonal variation in Se concentration in different plant organs of different Se-hyperaccumulators. If this will be corroborated, the transfer of *SpSultr1;2* into crops or high biomass plants would have the potential to increase their Se storage capacity, thus greatly improving the effectiveness of biofortification and phytoremediation programs, respectively. Overexpression of *Sultr1;2* transporter from non-hyperaccumulators could also result in higher rates of Se uptake in transgenic plants, even though competition with sulfate will be more significant at the root surface.

Selenite entry into the plants is also assisted by nonspecific mechanisms including aquaporins (e.g., NIP2.1, Lsi1) and phosphate transporters (Zhao et al. 2010a, b; Zhang et al. 2014; Schiavon and Pilon-Smits 2017a). The overexpression of the phosphate transporter OsPT2 in rice conferred a greater uptake capacity of selenite with a consequent increase in the accumulation of Se in the rice grains (Zhang et al. 2014). Furthermore, glutathione (GSH) applied to rice plants was effective in promoting the selenite transport (Zhang et al. 2015). This observation makes it plausible that genetic engineering of GSH content in the roots can be applied to control the absorption of selenite, but the hypothesis remains to be ascertained. Since selenite is the prevalent form of Se available in paddy fields where rice plants are commonly grown, understanding how plants take up selenite from anoxic soils will be useful for rice engineering in regions where dietary Se is low and mainly relies on this crop as the main food source.

I should be noted that increasing the accumulation of Se in plants by enhancing their capacity to absorb Se, both in the case of selenate and selenite, carries the risk that plants may not tolerate a high Se concentration in their cells. Reduced selenium tolerance often results in a drop in plant biomass and a reduction in productivity, which is not an intended event.

Once absorbed, selenite is readily assimilated within cells, whereas selenate can move in the plant likely through the assistance of sulfate transporters (El-Mehdawi et al. 2018; White et al. 2004, 2016). The gene encoding the low-affinity sulfate transporter *Sultr2;1* that is responsible for sulfate loading into the xylem was found to be largely more expressed in *S. pinnata* than in non-hyperaccumulators, thus leading to the hypothesis that perhaps it explains the exceptional accumulation of Se in the hyperaccumulator shoot (El Mehdawi et al. 2018).

In addition to *Sultr 1;2* and *Sultr2;1*, other *Sultr* genes could be considered potential targets of genetic engineering, such as those involved in sulfate/selenate entry into plastids (SULTR3 group), or in sulfate/selenate translocation into sink organs, like *Sultr1;3*. In this regard, the study by Wang et al. (2018) offers a nice overview of different sulfate transporters upregulated in the leaves and roots of *S. pinnata* compared to the related non-hyperaccumulator *S. elata* that could be investigated.

The same study revealed the extraordinary expression of a gene encoding the amino acid transporter LYSINE HISTIDINE TRANSPORTER1 (LHT1), a homolog of amino acid permease (AAP), in roots of *S. pinnata*. It is reasonable that Se-amino acids, either methylated or not, can enter the root cells by engaging amino acid permeases with broad substrate specificity (Schiavon et al. 2020). This hypothesis arises from the evidence that proline competes with cysteine (Cys) and methionine (Met) for the uptake by the plant (Frommer et al. 1993), and some plants like durum wheat (*Triticum turgidum*) and spring canola (*Brassica napus*) show a preference for Se-amino acids over inorganic Se (Zayed et al. 1998; Kikkert and Berkelaar 2013). At present, LHT1 is under investigation to confirm its function in the transport of Se-amino acids.

Very recently, it has been reported that the transporter NRT1.1B belonging to the family of peptide transporters (PTRs) that assists nitrate transport also manifests the transport capacity of SeMet (Zhang et al. 2019). Consistently, NRT1.1B overexpression in rice plants was associated with higher SeMet loading into the grains. This gene could therefore be a particularly interesting target for biofortification.

A summary of the main studies on Se transport is reported in Table 16.1.

16.2.2 Manipulation of Genes Implied in Selenate Reduction

Being similar to sulfate, selenate is assimilated along the S pathway in plastids to be converted into Se-amino acids. Therefore, the first attempts to manipulate Se metabolism targeted enzymes that function in sulfate assimilation. The first reaction of the process involves the activation of sulfate/selenate to adenosine 5′-phosphosulfate/selenate (APS/APSe) by the enzyme adenosine triphosphate sulfurylase (APS) (Bohrer et al. 2015). This step is considered to be limiting for selenate assimilation (White et al. 2016, 2018; Lima et al. 2018), and the overexpression of adenosine triphosphate sulfurylase isoform 1 (APS1) in *Brassica juncea* and *A. thaliana* has successfully overcome this limitation by promoting the reduction of selenate to

Table 16.1 List of transporters in involved Se uptake for different plant species

Plant species	Transporters	Se species	Reference(s)
Arabidopsis thaliana L.	SULTR1;2,	Selenate	El Kassis et al. (2007)
Astragalus racemosus (HA), *Astragalus bisulcatus* (HA), *Astragalus glycyphyllos* (n-HA), *Astragalus drummondii* (n-HA)	SULTR group 1, 2 and 4	Selenate	Cabannes et al. (2011)
Brassica juncea L. Czern. (n-HA), *Stanleya elata* L. (n-HA), *Stanleya Pinnata* L. (HA)	SULTR1;1, SULTR1;2, SULTR 2;1	Selenate	Schiavon et al. (2015), Wang et al. (2018) and El Mehdawi et al. (2018)
Oryza sativa L. (n-HA)	NIP2;1	Selenite	Zhao et al. (2010a, b)
Oryza sativa L. (n-HA)	(OsPT2)	Selenite	Zhang et al. (2014)
Triticum aestivum L. (n-HA)	SULTR1;1, SULTR4;1	Selenate	Shinmachi et al. (2010)
Oryza sativa L. (n-HA)	NRT1.1B	SeMet	Zhang et al. (2019)
Eruca sativa mill. (n-HA), *Diplotaxis tenuifolia* (n-HA)	SULTR1;1, SULTR1;2, SULTR 2;1	Selenate	Dall'Acqua et al. (2019)

n-HA non-hyperaccumulators, *HA* hyperaccumulators

APSe (Pilon-Smits et al. 1999). Transgenic *Brassica juncea* plants, in particular, when treated with selenate contained more organic Se than wild-type plants, which conversely accumulated more selenate (Pilon-Smits et al. 1999). Interestingly, these transgenics showed superior Se tolerance than wild type, although accumulated two- to three-fold more Se, possibly because they assimilated Se more easily. In *A. thaliana*, the overexpression of APS1 led to increased amounts GSH and its precursor cysteine (Sors et al. 2005). High levels of GSH are critical in antioxidative processes (Noctor et al. 2018; Hasanuzzaman et al. 2019) and may also explain greater tolerance of transgenics to Se (Grant et al. 2011).

More recently, the adenosine triphosphate sulfurylase isoform 2 (APS2) of *S. pinnata* has been identified as a new potential target of genetic engineering (Jiang et al. 2018). APS2 has both plastidial and cytosolic localization in non-Se hyperaccumulators *A. thaliana* and *Stanleya elata*, while only cytosolic in *S. pinnata* (Bohrer et al. 2015; Jiang et al. 2018). A transcriptomic study revealed amazing levels of Aps2 gene transcripts in *S. pinnata* compared to *S. elata* and predicts the hypothesis that high APS2 expression may be responsible for the Se hypertolerance trait typical of the hyperaccumulator.

In the later stages of S/Se assimilation, reactions are driven by the action of adenosine 5-phosphoreductase (APR) and sulfite reductase (SiR). APR converts APS/APSe to sulfite/selenide (White et al. 2018). Similar to APS, APR is supposed to be critical in controlling the assimilatory flow of selenate into Se-amino acids. The overexpression of APR from *Pseudomonas aeruginosa* in *A. thaliana* resulted in an increase in tolerance to Se and accumulation of organic Se (Sors et al. 2005). Also, APR knockout mutants of *A. thaliana* showed a decrease of their ability to accumulate and tolerate Se, likely because of the concurrent reduction of GSH levels and increase of reactive oxygen species (ROS) generation (Grant et al. 2011).

Regarding SiR, preliminary studies have not highlighted a key role for this enzyme in the tolerance and accumulation of Se, as neither overexpression nor knockdown of SiR did not produce any specific phenotype in *A. thaliana*. Therefore, SiR does not appear to be a potential candidate for the genetic engineering of plants to be enriched in Se.

16.2.3 Manipulation S-Related Genes for Averting Se-Amino Acid Incorporation into Proteins

As previously mentioned, Se-hyperaccumulating plants have evolved specific biochemical pathways to thrive in seleniferous soils and become hypertolerant to high Se concentrations accumulated in their tissues. In one of these pathways, the enzyme selenocysteine methyltransferase (SMT) plays a noteworthy role (Schiavon et al. 2017a; Chen et al. 2019). SMT prevents SeCys misincorporation into proteins via its methylation into methyl-selenocysteine (MetSeCys), therefore significantly reducing toxicity stemming from the generation of malformed proteins. MetSeCys is the dominant Se form in Se-hyperaccumulators, while non-hyperaccumulators mainly contain selenate or selenomethionine (SeMet) (Schiavon et al. 2017a; White et al. 2016, 2018). However, SMT activity was also determined in some Se-accumulators, such as broccoli (Lyi et al. 2005), and MetSeCys was quantified in broccoli, radish, rice, potato, and carrot (Amato et al. 2020). In Se non-hyperaccumulator *Astragalus drummondii*, although the SMT gene was identified, SeCys methylation activity was though absent (Sors et al. 2009). Induced mutation of the SMT gene in *A. drummondii* provided some SMT activity, but the mutated enzyme was not yet as active as its counterpart in the hyperaccumulator *A. bisulcatus* (Sors et al. 2009). Recently, a novel SMT has been identified in *B. juncea*, which can methylate both homocysteine and SeCys substrates (Chen et al. 2019). Overexpression of this enzyme in tobacco plants increased the accumulation of total Se and MeSeCys (Chen et al. 2019). Thus, the gene encoding SMT attains great attention as an appealing candidate for the genetic engineering of staple crops with fortified levels of Se. In fact, an increase in the synthesis of MetSeCys in the edible produce is a desirable trait because this metabolite is a reservoir of methylselenic acid which in humans determines greater resistance to certain types of cancer (Lima et al. 2021). The formation of MetSeCys can be a relevant metabolic step to be transferred also to the plants employed for Se phytoremediation, because MetSeCys can be further metabolized to volatile nontoxic dimethyldiselenide (DMDSe) dispersed in the air (White et al. 2018; Chauhan et al. 2019). On this account, the SMT gene has been cloned and characterized from different plant species (Çakir and Ari 2013; Lyi et al. 2005; Zhu et al. 2009; Neuhierl and Bock 1996; Sors et al. 2009). For example, SMT from the Se hyperaccumulator *Astragalus bisulcatus* was cloned and overexpressed in *A. thaliana* and *B. juncea* plants, which produced MetSeCys after being fed with selenite (Ellis et al. 2004; LeDuc et al. 2004). In addition, both transgenics contained more total Se but were more tolerant to Se than the wild-type plants due to increased volatilization rates of Se in the form of DMDSe.

Another gene belonging to the S/Se metabolism that has been tested for its potential in improving the tolerance to Se while decreasing the accumulation of Se amino acids responsible for proteins misfolding is the one that codes for the enzyme cystathionine-β-synthase (CβS). This enzyme converts SeCys to seleno-cystathione, which is the substrate for the synthesis of SeMet. When CβS from *A. thaliana* was overexpressed in *B. juncea*, plants exhibited higher Se volatilization rates (at least two- to threefold than the wild type) and greater tolerance to Se (van Huysen et al. 2003), therefore confirming that SeCys conversion to seleno-cystathione is rate-limiting, for the formation of volatile Se. In this case, plants produced volatile dimethylselenide (DMeSe) from methionine (Met). The specific route involves methionine being initially methylated by S-adenosyl-L-Met:L-Met S-methyltransferase (MMT) to form Se-methyl Se-methionine (SeMeMet), which is the precursor of the volatile DMeSe typically produced by Se non-hyperaccumulator plant species (Chauhan et al. 2019; Schiavon and Pilon-Smits 2017a). Whether overexpressing SeMeMet can cause an actual increase of Se volatilization has not been verified yet.

In addition to improving the flow of SeCys toward the formation of volatile compounds for averting nonspecific incorporation of Se-amino acids into proteins, plants can break down SeCys into alanine and elemental Se through the activity of selenocysteine lyase (Sec-lyase) (SL) (White et al. 2016). Garifullina et al. (2003) overexpressed a mouse SL in *A. thaliana*, which resulted in the reduced content of Se in proteins and concomitant greater Se accumulation. Interestingly, when the overexpression of SL was targeted to the cytosol, the plants were more tolerant to Se, but when it was targeted to the chloroplast, plants behaved in the opposite way, being quite sensitive to Se. One possible hypothesis is that elemental Se released from SeCys breakdown replaced Fe in Fe-S clusters of electron-transfer proteins functioning in photosynthesis, making them less stable and active (Hallenbeck et al. 2009).

A chloroplastic SL homolog of the mouse SL was identified in *A. thaliana* and named CpNifS. Its overexpression in *A. thaliana* allowed plants to accumulate more Se in their tissues and be more tolerant to it than the wild type. In addition, plants contained less S in proteins, which means a lower rate of Se-amino acid embedding in proteins and a concomitant increase in S concentration (Van Hoewyk et al. 2005). Therefore, the flow of Se was probably diverted to pathways that produce less toxic forms of Se.

The main differences between Se-hyperaccumulators and non-hyperaccumulators in Se and S metabolism are reported in Table 16.2.

Table 16.2 Differences between Se hyperaccumulator and non-hyperaccumulator plant species with respect to Se/S metabolism and main Se forms accumulated

Se hyperaccumulators	Se non-hyperaccumulators
High specificity for Se over S resulting in high Se/S ratio	Low specificity for Se over S resulting in low Se/S ratio
High Se metabolic flow. Unique APS2	Low Se metabolic flow
Additional pathways for Se detoxification	No specific pathways for Se detoxification
Se volatilization as dimethyldiselenide (DMDSe)	Se volatilization as dimethylselenide (DMSe)
High Se-amino acid uptake	Low Se-amino acid uptake
Se mainly accumulated in organic forms. Major organic form of se stored: SeMeCys	Se mainly accumulated in inorganic forms. Major organic form of Se stored: SeMet

16.2.4 Manipulation S-Unrelated Genes for Increasing se Tolerance

In recent years, genetic engineering has targeted other genes, not related to S/Se metabolism but rather to antioxidant defense, for modulating plant Se tolerance and accumulation. For example, overexpression of the selenium-binding protein gene *SBP1* in *A. thaliana* enhanced the resistance of plants to selenite (Agalou et al. 2005) and cadmium (Hugouvieux et al. 2009). SBP1 has many potential metal-binding sites and can chelate selenite, but not selenate, with a ligand to protein molar ratio of 1:1 (Schild et al. 2014). In this Se-SBP1 assemblage, selenite is reduced to form an R-S-Se(II)-S-R-type complex. SBP1 in *A. thaliana* is reported to be associated with cellular S demand as it is upregulated by S starvation and reduces plant sensitivity to multiple stresses through a GSH-dependent mechanism (Zechmann 2020). Furthermore, overexpression of SBP1 can prevent the oxidative stress generated by selenite that may be responsible for mitochondrial damages and dysfunction (Dimkovikj and Van Hoewyk 2014).

Similar to SBP1, the overexpression of the ethylene response factor ERF96 in *A. thaliana* resulted in enhanced tolerance to selenite due to low Se accumulation and increased antioxidant activity (Jiang et al. 2020). In contrast, ERF96-silenced plants were more sensitive to selenite than the wild type. In *A. thaliana*, the ERF96 gene is typically upregulated by selenite, and the mechanism by which it confers greater tolerance to Se is that it reduces the expression of selenite/phosphate transporters PHT1;1 and PHT2;1, thus restricting selenite uptake and allocation in the plant. Furthermore, transgenics overexpressing ERF96 exhibited superior activity of antioxidant enzymes (e.g., catalase, CAT, and glutathione peroxidase, GPX), contained more GSH and decreased ROS accumulation when compared to the wild-type plants. Interestingly, two allelic lines defective in the expression of the gene encoding the cytosolic ascorbate peroxidase (APX1) were Se resistant and accumulated more Se than the wild type (Jiang et al. 2016). Also in this case, Se tolerance was attributed to greater activity of antioxidant enzymes CAT, GPX, and glutathione reductase (GR), and increased synthesis and accumulation of GSH.

The role of GSH in improving Se tolerance by acting as powerful antioxidant was also proved by Bañuelos et al. (2005), who overexpressed GSH synthase in *B. juncea* thus increasing its capacity to tolerate and accumulate Se (Bañuelos et al. 2005), and by Zhou et al. (2018), who reported increased expression of the glutathione S-transferase family gene GST-u4 in leaves of the Se-hyperaccumulator *Cardamine hupingshanensis*, supporting the formation of glutathione-chelated selenate to form Se-binding phytochelatins (PCs) to be transferred into the vacuoles for Se sequestration via ATP-binding cassette transporters (ABCC).

Another fascinating gene unrelated to S/Se metabolism that may be of interest for genetic engineering is the one encoding a broccoli methyltransferase (*BoCOQ5–2*) involved in the ubiquinone biosynthetic pathway and reported to stimulate selenium volatilization in both bacteria and transgenic *A. thaliana* plants (Zhou et al. 2009, 2010). Ubiquinone has antioxidant functions, and thus it would act in cells by protecting them and more specifically mitochondria from oxidative stress generated by excess Se (Bentinger et al. 2007). When BoCOQ5–2 was expressed in *A. thaliana*, plants volatilized three times more Se in the form of DMDSe than the wild type and became more tolerant to Se (Zhou et al. 2009). The increase in tolerance was primarily attributed to the restriction of ROS generation rather than to a direct effect of manipulation of the ubiquinone pathway.

Additional genes of interest have been discovered in *A. thaliana* (Van Hoewyk et al. 2008), *S. pinnata* (Wang et al. 2018), and *C. hupingshanensis* (Zhou et al. 2018) with key roles in Se detoxification pathways and that may alter Se metabolism. More specifically, the genes of interest are those involved in the transamination of SeCys or its oxides (e.g., L-cysteate and L-cysteine-sulfinate), selenoprotein degradation, synthesis and signaling of ethylene and abscisic acid, glutamyl cycle by recycling glutamate from GSH-conjugates (e.g., glutamyl cyclotransferase (GGCT2;1), and selenation reactions (e.g., genes coding for aryl sulfotransferases). In the last case, the flow of selenate in the S pathway was found to be diverted to form phosphoadenosine 5′-phosphoselenate (PAPSe) and used for selenation in the root of the Se hyperaccumulator *C. hupingshanensis*; thus, selenide, SeCys, and selenoprotein formation was prevented when plants were subjected to high Se doses (Zhou et al. 2018).

With respect to genes that control Se-protein degradation, in the study by Zhou et al. (2018), the genes coding for E3 ubiquitin-protein ligase MUL1, RNF13, and the ubiquitin- conjugating enzyme E2 7 were upregulated by Se in the roots, with gene expression levels similar to those reported for *Stanleya pinnata* (Sabbagh and Van Hoewyk 2012). Therefore, expressing these genes in Se non-hyperaccumulators might be relevant for reducing the toxicity stemmed from the generation of malformed proteins under Se stress.

16.3 Potential of Genetic Engineering for Se Biofortification and Phytoremediation

Studies conducted so far indicate that several S-related and unrelated genes could be valid candidates for manipulating plant tolerance and accumulation of Se in crops to be fortified or in high biomass plants for use in phytoremediation of Se-polluted soils (Fig. 16.1) (Zhu et al. 2009; Pilon-Smits and LeDuc 2009; Schiavon and Pilon-Smits 2017b).

Even though high Se levels in harvestable plant parts are desirable for both biofortification and phytoremediation, some specific traits appear to be more suitable than others depending on the phytotechnology applied. For example, in the case of biofortification, we aim at increasing the accumulation of Se in edible plant organs mainly in the forms most available to humans and most beneficial to health. Therefore, genes whose overexpression might favor the entry of Se into the plants and its flow along the S assimilation pathway to produce elevated amounts of SeMet and MetSeCys are the main targets to be addressed by genetic engineering. As for phytoremediation, genes promoting Se accumulation, root-to-shoot translocation, and further volatilization into the atmosphere are the most attractive to be overexpressed. In both phytotechnologies, however, increasing the plant tolerance to Se is mandatory to avoid an unintended reduction of plant growth and yields, which could otherwise hinder the final outcome of plant enrichment with Se.

It should be noted that, despite the promising results obtained in laboratory and greenhouse tests, only a few field testing have been performed to assay the capacity

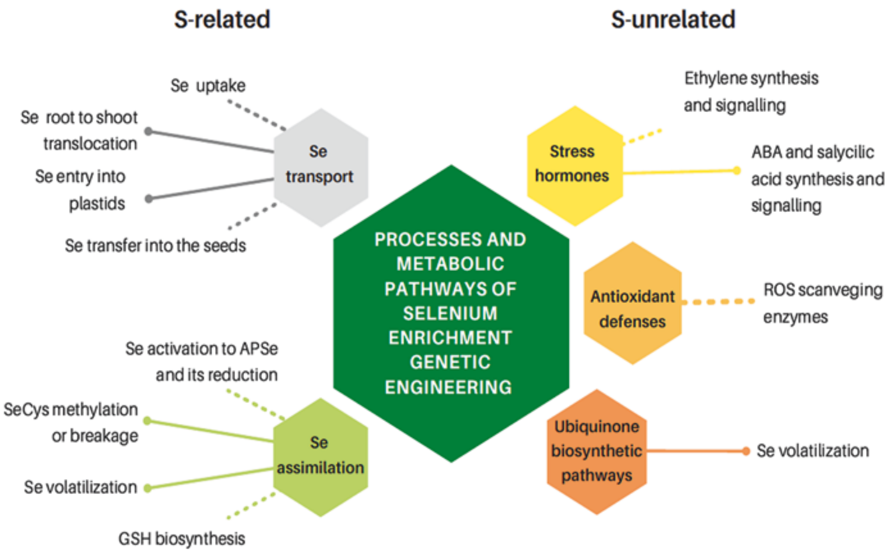

Fig. 16.1 Survey of principal S-related and unrelated processes/pathways targeted by genetic engineering for plant Se enrichment

of transgenics to accumulate and tolerate Se or remediate Se-contaminated sites by increasing Se volatilization rates. This is mainly to the fact that in many countries, the cultivation of transgenics is not allowed, and their use in biofortification and phytoremediation technologies poses some concerns and is less accepted by the populations than agronomic biofortification and conventional breeding (Zhu et al. 2009).

Transgenic lines of *B. juncea* overexpressing either chloroplastic SL or SMT manifested increased capacity for Se phytoremediation when grown under field conditions (Bañuelos et al. 2007). They could indeed accumulate up twofold more Se in their shoot from Se-contaminated saline sediments and produced more biomass than wild-type plants.

Further small-scale experiments testing transgenics used *B. juncea* lines overexpressing genes encoding the enzymes APS, γ-glutamyl-cysteine synthetase (ECS), and glutathione synthetase (GS) (Bañuelos et al., 2005). The transgenic plants showed greater biomass yield and, in the case of APS transgenics, up to 4.5-fold more Se accumulation than wild-type plants.

These studies on the whole support the evidence that genetic engineering can feasibly generate plants that are really effective for Se phytoremediation purposes, as well as crops fortified with Se. In particular, wide transcriptomic studies conducted so far in Se-hyperaccumulators and accumulators have provided a pool of genes from which to draw to create transgenics with altered Se accumulation or metabolism (e.g., Çakir et al. 2015; Van Hoewyk et al. 2008; Wang et al. 2018; Zhou et al. 2018). Studies from Çakir et al. (2016) and Huang et al. (2010) additionally suggest a potential role of several miRNAs (i.e., small RNA molecules controlling targeted gene translation) in the modulation of Se metabolism which deserve a deeper investigation (Fig. 16.2).

With respect to Se biofortification, a feasible avenue for improving enrichment of plants with Se could include attempts to overexpress targeted gene(s) in specific plant tissues and organs and produce anticarcinogenic compounds (e.g., MetSeCys) that can be extracted in appreciable quantities. In the case of phytoremediation, genes whose overexpression could increase Se tolerance and accumulation and especially promote Se volatilization into nontoxic forms appear the best candidate for the genetic engineering of plants ideally suited for the cleanup of Se-contaminated soils.

16.4 Considerations and Future Directions

A number of genes and metabolic pathways have been identified as potential targets of Se genetic engineering for the generation of transgenics with superior capacity of Se enrichment. However, although a promising tool, the use of transgenics in phytoremediation and biofortification is still largely limited and far from being accepted by local populations in several countries. To overcome this limitation, new molecular tools like CRISPR/Cas9 could be used to modify the genetic code of the plants

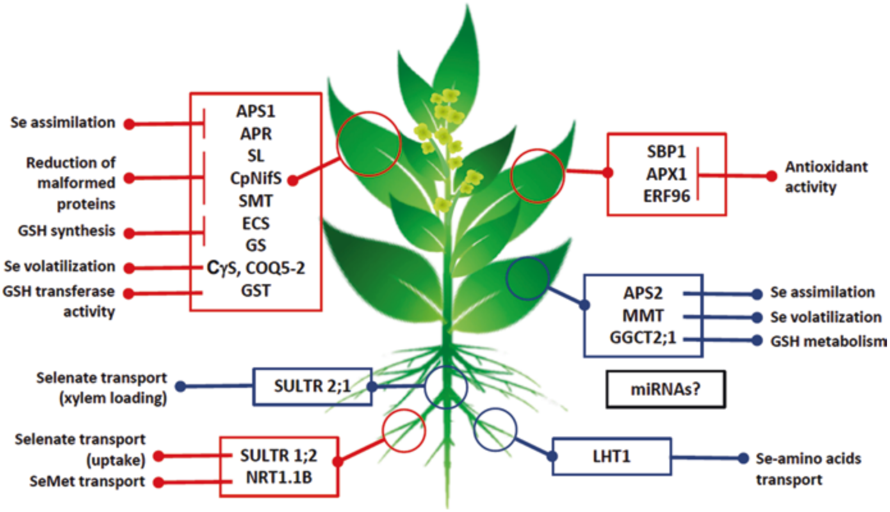

Fig. 16.2 Survey of genes overexpressed in plants and conferring increased Se tolerance and accumulation (reported inside red squares) and promising genes yet to be tested (reported inside blue squares). APX1 is the only among these genes whose loss of function was found to be associated with enhanced Se tolerance and accumulation. For all genes, the metabolic target or the process in which they are implied is indicated on the side. The role of miRNAs in the control of Se metabolism is unknown and might deserve investigation

without introducing foreign DNA, with the aim of generating plants that possess transporters (e.g., SULTR) or enzymes (e.g., APS, APR, etc.) with constitutive expression or high specificity for Se. In this case, the technology would benefit from the high-throughput sequencing of hyperaccumulator genomes to generate plants with greater Se storage capacity and tolerance that may gain better public acceptance.

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Chapter 17
Biological Activity of Selenium in Plants: Physiological and Biochemical Mechanisms of Phytotoxicity and Tolerance

Barbara Hawrylak-Nowak

17.1 The Physicochemical Similarity of Selenium to Sulphur Determines the Biological Activity of Selenium in Plants

Selenium (Se) is an essential trace element for most organisms, including humans. However, it is toxic at concentrations exceeding the physiological tolerance threshold of a given organism. The chemical form of this element is also of great importance for its toxicity. Organisms for which Se is essential need this element for the biosynthesis of the 21st protein amino acid, i.e. selenocysteine (SeCys), which is a component of approximately 25 specific selenoproteins in the human organism (Van Hoewyk 2013). However, the essential Se metabolism in vascular plants is believed to have been lost during evolution, as deduced based on plant genome analysis demonstrating no evidence of a SECIS element in the coding regions of selenoprotein transcripts (Zhang and Gladyshev 2009). Selenium can be incorporated readily and non-specifically into various functional plant metabolites, some of which may be advantageous to plants (Schiavon and Pilon-Smits 2017). Therefore, in recent years, researchers have shown a growing interest in plant Se metabolism. The importance of this element for plants and the mechanisms of its phytotoxicity are still the object of genetic, molecular, physiological, and ecological studies.

The chemical properties of Se highly resemble those of sulphur (S). However, the radius of the Se atom is larger than that of S: the radii of Se^{2-} and S^{2-} are 0.191 nm and 0.174, respectively (White et al. 2004). These slight differences in the size and ionic properties of S and Se atoms may cause irreversible changes in the protein structure and disturb the catalytic functions of enzymes in Se-sensitive

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M. A. Hossain et al. (eds.), *Selenium and Nano-Selenium in Environmental Stress Management and Crop Quality Improvement*, Sustainable Plant Nutrition in a Changing World, https://doi.org/10.1007/978-3-031-07063-1_17

plants (Terry et al. 2000; Hasanuzzaman et al. 2020). The chemical and physical properties of Se are very similar to those of S, which is an essential macronutrient to all organisms. It is crucial for the uptake, translocation, and biological activity of Se. Like S, Se can exist in four main oxidation states: −2, +2, +4, and + 6. It commonly occurs as selenide (−2), elemental Se (0), selenite (+4), and selenate (+6). Each of these oxidation states exhibits different chemical properties. In nature, Se occurs in inorganic and organic forms, forming compounds with approximately 16 other elements (Kabata-Pendias 2010).

Due to the similarity to S, all plants can take up and metabolize Se relatively easily and fast via the S metabolic pathway. For example, in *Arabidopsis*, two high-affinity sulphate transporters (SULTR1;1 and SULTR1;2) are involved in the uptake and transport of selenate within plants. In Se hyperaccumulators, the constitutive expression of genes encoding SULTR1 and SULTR1;2 in roots results in high selenate absorption ability (Raina et al. 2021). Moreover, SeO_3^{2-} and SeO_4^{2-} ions, i.e. the chemical analogues of SO_3^{2-} and SO_4^{2-} ions, respectively, can be assimilated to organic Se forms, such as SeCys and selenomethionine (SeMet). The assimilation of Se is thought to compete with S assimilation. Selenium compounds also undergo biological methylation, and the volatile products of this reaction contribute to the geochemical cycle of the element in nature (Terry et al. 2000; White et al. 2004; Kabata-Pendias 2010; Schiavon and Pilon-Smits 2017).

Selenium in plants can be incorporated into other S compounds, e.g. glucosinolates and their associated aglycons or (seleno)glutathione (Schiavon and Pilon-Smits 2017). It can also be part of Fe-Se clusters, since the chloroplastic NifS-like enzyme releasing elemental S from cysteine (Cys) for the synthesis of Fe-S clusters may also use SeCys as a substrate (Van Hoewyk et al. 2005). Another Se-containing metabolite is Se-allyl-L-cysteine sulfoxide synthesized in *Allium* species from selenoglutathione or SeCys substrates (González-Morales et al. 2017). Moreover, different plant species can also produce other organic Se metabolites, e.g. selenoecholine, selenobetaine, and selenotaurine or volatile dimethylselenide (DMSe) and dimethyldiselenide (DMDSe) (Chauhan et al. 2019).

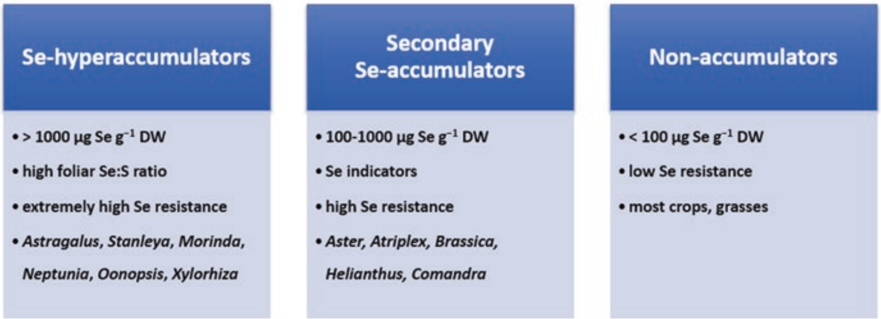
As emphasized above, Se and S metabolism in plants is closely interrelated both at the stage of ion uptake, transport, subsequent compartmentalization, assimilation, and/or volatilization. This phenomenon critically determines the biological activity of Se in plant organisms.

17.2 Plants Vary in the Resistance and Ability to Accumulate Selenium

The current stage of knowledge does not classify Se as an element necessary for plants. However, recent experiments show that a low concentration (most often a few micromoles) Se exerts a positive influence on plant growth and resistance to some biotic and abiotic stress factors. It may therefore act as a beneficial element for plants altering several biochemical and physiological processes (Hawrylak-Nowak et al. 2018b; Hasanuzzaman et al. 2020). Selenium is very unevenly distributed in the Earth's crust, and its phytoavailability in soils is often low. In many areas of the world, the level of this element in soils is low/deficient in terms of dietary requirements. On the other hand, there are regions where the level of Se in soils is very high and its intake is higher than a certain threshold; then the element may be harmful to all living organisms (Oldfield 2002). While the Se concentrations in most natural soils are between 0.01 and 2.0 mg Se kg^{-1}, seleniferous soils are characterized by substantially higher levels of the element, i.e. from 2 to 1200 mg kg^{-1} (White 2018).

Although all plants have the ability to uptake and metabolize Se, they differ in their Se tolerance and capability to accumulate this element in aboveground organs. Therefore, three types of plants have been distinguished: Se hyperaccumulators, secondary Se accumulators, and non-accumulators (Fig. 17.1; Terry et al. 2000). The first group consists of a few species that are capable of active and specific accumulation of Se during their growth in soils with high Se levels. They are resistant to high Se concentrations. During growth on seleniferous soils, these species are capable of accumulation of over 1000 µg Se g^{-1} DW (0.1–1.5%) showing no symptoms of Se toxicity (White et al. 2007; Galeas et al. 2007; Lima et al. 2018).

The occurrence of Se hyperaccumulators in nature has been reported for at least 90 years. However, there has been increasing interest recently in using these amazing organisms in studies of Se metabolism in plants (Lima et al. 2018). No Se hyperaccumulators have been found in regions with low Se levels in the soil. Several *Stanleya*, *Astragalus*, *Neptunia*, *Morinda*, *Xylorhiza*, and *Oonopsis* species represent this group of plants. The greatest number of Se hyperaccumulator species represents the Fabaceae family (Terry et al. 2000; Gupta and Gupta 2017). Nevertheless, there is no close relationship between the Se accumulation ability and the plant family (Wrobel et al. 2020). The best-characterized Se hyperaccumulator is *Astragalus bisulcatus* (Fabaceae), which can accumulate up to 15,000 µg Se g^{-1} DW. This species grows in the south-western regions of the USA characterized by a naturally high concentration of Se in the soils (Galeas et al. 2007). It is assumed that



Se-hyperaccumulators	Secondary Se-accumulators	Non-accumulators
• > 1000 µg Se g^{-1} DW	• 100-1000 µg Se g^{-1} DW	• < 100 µg Se g^{-1} DW
• high foliar Se:S ratio	• Se indicators	• low Se resistance
• extremely high Se resistance	• high Se resistance	• most crops, grasses
• *Astragalus, Stanleya, Morinda, Neptunia, Oonopsis, Xylorhiza*	• *Aster, Atriplex, Brassica, Helianthus, Comandra*	

Fig. 17.1 Classification of plants in terms of their capability of selenium accumulation and tolerance

these species require Se for proper growth. Due to the high content of Se in their tissues, these species are highly toxic to humans and animals (Terry et al. 2000).

Not all species growing in seleniferous soils are able to accumulate Se. Even within one genus, there are large species differences, e.g. the genus *Astragalus* includes both Se-accumulators and species that do not accumulate this element. Some species can grow in the same habitat and yet accumulate very different amounts of Se (Terry et al. 2000; Lima et al. 2018). An extraordinarily high foliar Se:S ratio is believed to be one of the characteristic features of Se hyperaccumulators (White et al. 2007). However, Se is not disposed evenly in their tissues, and its levels may vary over the vegetative season. Generally, the highest foliar concentrations of Se are recorded in early spring. They are higher in younger leaves and reproductive tissues than in older leaves (Pilon-Smits and Quinn 2010). A study conducted by Galeas et al. (2007) suggests a specific flow of Se in hyperaccumulators during their vegetative season: from root to young leaves in spring, then Se remobilization from older leaves to generative parts in summer and retranslocation to roots in autumn. An ecological advantage of the capability of accumulation of abnormally high concentrations of Se in tissues is the protection of such plants against herbivore and pathogen attacks (Schiavon and Pilon-Smits 2017). Therefore, the ability to repel harmful organisms might have contributed to the evolution of Se hyperaccumulators (White 2018).

The second group of plants, known as secondary Se accumulators or Se indicators, is species that grow on soils with a low/medium level of this element and accumulate from several hundreds to 1000 μg Se g^{-1} DW. They do not require this element for proper growth. Secondary Se accumulators take up this element in direct proportion to the amount available in the soil. Some species of the genera *Atriplex*, *Comandra*, *Aster*, and *Brassica* are examples of this type of plants (Terry et al. 2000; Ellis and Salt 2003). Some researchers suggest that secondary Se accumulator species probably do not have any Se-specific metabolic pathways; they take up and metabolize Se and S ions indiscriminately, merely at increased rates in comparison to non-accumulator species (Pilon-Smits and Quinn 2010). A recent study carried out by Ogra et al. (2017) on two Se accumulator species, Indian mustard and garlic, have shown that both species supplemented with selenate and SeMet accumulate organic Se mainly as methylselenocysteine (MeSeCys) and γ-glutamyl-Se-methylselenocysteine (γ-GluMeSeCys). They suggest that Indian mustard may have a specific metabolic pathway for selenohomolanthionine (SeHLan) biosynthesis.

Most crops and grasses generally contain below 20 μg Se g^{-1} DW and are unable to accumulate Se in an amount exceeding 100 μg Se g^{-1} DW, even if they grow in Se-rich soils. They are Se-sensitive and cannot survive under excessive amounts of Se in the soil, showing stunted growth, chlorosis, and metabolism disorders. Such plants are regarded as non-accumulators (Terry et al. 2000; Gupta and Gupta 2017). They can tolerate low concentrations of Se in the rhizosphere through limitation of Se uptake and translocation to their aboveground organs (White et al. 2004) and rapid Se sequestration inside the vacuoles of mesophyll cells (Raina et al. 2021). However, S-rich plant species, like *Brassicaceae*, are characterized by two- to fivefold higher Se content than cereals grown in the same area (Terry et al. 2000; Gupta and Gupta 2017). Research conducted by Eurola et al. (1989) showed that, among non-hyperaccumulator species, onion and Brassicaceae vegetables had a higher Se level than other vegetables growing in soils supplemented with selenate in Finland.

17.3 Main Causes of Selenium Phytotoxicity: Malformed Selenoproteins and Oxidative/Nitro-Oxidative Stress

In higher plants, Se is toxic at concentrations exceeding the tolerance threshold, which is different for Se accumulators and for non-accumulators. Significant inhibition of root and shoot growth is a more characteristic consequence of excessive exposure to Se. In some cases, enhanced bioaccumulation of Se, especially in non-accumulators, can cause toxicity symptoms, e.g. leaf curl, reduction of the leaf blade surface, chlorosis, and necrosis (Fig. 17.2; Terry et al. 2000; Hawrylak-Nowak et al. 2015). In maize, the toxic effect of Se, mainly when it was supplied as organic SeMet, was manifested by a large increase in the concentration of anthocyanins in leaves (Hawrylak-Nowak 2008a, b, c). In turn, in cowpea grown in field conditions,

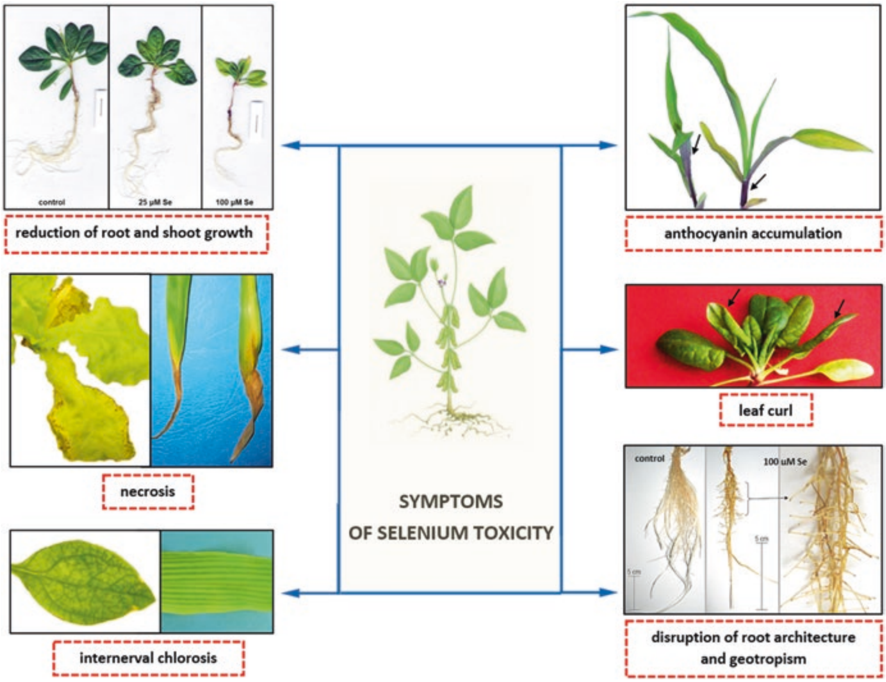


Fig. 17.2 Common visible symptoms of selenium toxicity in plants

foliar application of selenite exceeding 50 g ha^{-1} caused necrotic brown spots on leaves and deposition of pink salt in the interior. The leaf lesions were located mainly close to the trichomes (Silva et al. 2018). Microprobe X-ray fluorescence (μ-XRF) spectroscopy revealed a simultaneously elevated accumulation of Se and calcium (Ca) within necrotic lesions on the leaves of cowpea treated with foliar application of high selenate levels. Disarrangement of the upper epidermis was observed as well (Lanza et al. 2021).

The accumulation of huge quantities of Se in the root system of selenite-treated plants may induce significant alterations in the root architecture (Lehotai et al. 2012) and disturbances in the geotropic reaction of these organs (unpublished data; Fig. 17.2). This phenomenon may be influenced by damaged root ultrastructure (Ulhassan et al. 2019), highly disturbed metabolism of the root cells (Hawrylak-Nowak et al. 2015), loss of cell viability in the root apex, and/or hormonal imbalance (Lehotai et al. 2012).

The bioavailable chemical form of Se has considerable importance not only for its uptake and translocation but also for phytotoxicity. Selenite exhibits higher toxicity to most species than selenate (Hawrylak-Nowak 2013; Hawrylak-Nowak et al. 2015; Łukaszewicz et al. 2019). The translocation of selenate from the root system to shoots is easier and faster than that of either organic Se or selenite, since selenite is largely retained in root cells where it is quickly transformed into organic phytotoxic Se forms (Zayed et al. 1998). When both selenite and selenate are available in the growth media, the prevalent pattern is that of selenite. Selenite can probably inhibit the translocation of selenate to aboveground organs and is more hazardous at high concentrations than selenate (Guerrero et al. 2014). Organic Se forms, e.g. SeCys and SeMet, can be taken up by plants as well (Terry et al. 2000). Their toxicity is higher than that of the inorganic forms of this element, especially selenate. SeCys and SeMet can be directly misincorporated into proteins, and SeCys can additionally induce protein-thiol oxidation, which leads to disturbances in many physiological and molecular processes (Lazard et al. 2017). Moreover, it has recently been found that SeMet contributes to oxidative stress through an effect on hormone homeostasis (enhanced ethylene biosynthesis and reduced auxin production) and on plant primary metabolism (Malheiros et al. 2020).

In contrast to Se accumulators, non-Se-accumulating plant species (e.g. crops) are unable to discriminate efficiently the absorption of Se as selenate and S as sulphate during transport and assimilation of these elements (Bañuelos et al. 2017). Therefore, non-specific incorporation of Se-amino acids, i.e. SeCys and SeMet, into proteins is regarded as the major cause of Se phytotoxicity (Brown and Shrift 1981). The malformed selenoprotein hypothesis emphasizes that Se toxicity appears when $tRNA^{cys}$ accidentally binds to SeCys instead of Cys during the translation process, thereby producing malformed and thus toxic selenoproteins. This hypothesis is supported by studies on transgenic plants, which suggest that diversion of SeCys away from non-specific protein misincorporation is related to enhanced Se resistance (Van Hoewyk 2013). In comparison to Cys, SeCys is larger, more easily deprotonated, and has greater nucleophilicity; thus, it is more reactive in redox reactions

(Hondal et al. 2012; Lazard et al. 2017). SeMet can be generated from SeCys during a three-step enzymatic process (Schiavon and Pilon-Smits 2017). It has been found that SeMet is the principal Se-amino acid in non-accumulator species (Brown and Shrift 1982).

The replacement of Cys with SeCys may interfere with the formation of disulphide bridges in proteins, which may weaken their stability, possibly leading to their inactivation or aggregation (White et al. 2004; Lazard et al. 2017). It has been reported that the bond between the Se atoms of SeCys is longer, weaker, and thus more labile than the disulphide bond, which may cause slight fluctuations in the protein tertiary structure (Terry et al. 2000). Proteins having selenosulphide or diselenide bonds are expected to have lower redox potentials than proteins with disulphide bridges, which can disturb the catalytic activity of enzymes (Hondal et al. 2012). Moreover, Se reduces the rate of protein synthesis, since SeMet substituted for Met probably interferes with the formation of the peptide bond (Terry et al. 2000).

Through their pro-oxidative action, toxic concentrations of Se induce oxidative stress in plants (Hartikainen et al. 2000). Reduced concentrations of non-enzymatic antioxidants, e.g. reduced glutathione (GSH) and L-ascorbic acid (L-AsA), found in Se-exposed plants are believed to be involved in an increase in the accumulation of reactive oxygen species (ROS) (Freeman et al. 2010; Ulhassan et al. 2019). GSH biosynthesis can probably be reduced due to the Se/S competition for uptake and assimilation (Schiavon et al. 2020). Also, decreased activities and levels of the expression of antioxidant enzymes, such as catalase (CAT), glutathione reductase (GSH-Px), and dehydro-ascorbate reductase (DHAR), may be responsible for a reduced level of cell protection against ROS (Ulhassan et al. 2019). The presence of selenoproteins in mitochondria and chloroplasts may weaken electron transport, thereby increasing the accumulation of superoxide (Van Hoewyk 2013). Furthermore, the transformation of selenocompounds into H_2Se or selenols (SeCys, MeSe, RSeH: GSeH, etc.), which are easily oxidized with simultaneous production of ROS, contributes to induction of oxidative stress (Lazard et al. 2017). Consequently, plants treated with toxic Se concentrations exhibit increased accumulation of harmful lipid peroxidation products (Hartikainen et al. 2000; Łabanowska et al. 2012; Hawrylak-Nowak et al. 2015). Oxidative stress induced by Se can be linked not only to ROS overproduction but also to an impaired methylglyoxal (MG) detoxification system. MG is a very reactive cytotoxic compound formed in cells both through non-enzymatic and enzymatic reactions. Se triggers MG toxicity by decreasing the activities of glyoxalases I and II, by which MG is largely neutralized (Mostofa et al. 2017). The pro-oxidative activity of Se seems to explain its toxicity when the intracellular concentration of this element exceeds the antioxidant defences and methylation capacity; it may also be responsible for programmed cell death (Spallholz 1997).

Besides ROS, Se phytotoxicity induces changes in the concentrations of reactive nitrogen species (RNS), i.e. peroxynitrite and nitric oxide (NO). Thus, researchers suggest consideration of nitro-oxidative stress, in addition to oxidative stress, as an underlying cause of Se toxicity (Kolbert et al. 2016). As shown by Chen et al. (2014), the selenite-induced oxidative injury is a consequence of generation of

NADPH oxidase-dependent ROS in the roots of wild-type field mustard. The authors assumed that NO increased the production of ROS through enhancement of the expression of several *Br_Rbohs* genes encoding NADPH oxidase. They claimed that endogenous NO performed a toxic function in mustard under selenite-induced stress by initiating ROS burst. Furthermore, the reduction of selenite to SeCys may generate additional inorganic Se intermediate metabolites that can also provoke oxidative stress (Van Hoewyk 2013. Accordingly, an augmented level of H_2O_2 in *Arabidopsis* primary roots was found. It exhibited a positive correlation with both cell mortality and bioaccumulation of Se applied as selenite (Lehotai et al. 2012). Furthermore, glutathione-mediated non-enzymatic reduction of selenite can produce selenodiglutathione (GS-Se-SG), which has higher toxicity than selenite and can induce mitochondrial superoxide over-accumulation and cytotoxicity (Wallenberg et al. 2010). As suggested by Łabanowska et al. (2012), under Se exposure, carbohydrate molecules serving as electron traps can participate in the production of long-lived radicals.

Recent results reported by Kolbert et al. (2019) demonstrate that Se phytotoxicity targets the plant proteome, i.e. the whole set of proteins expressed by the genome, cell tissue, or organism at a certain time and in specified conditions. It has been demonstrated that not only seleno- and oxy-proteins but also nitro-proteins are produced as a result of Se stress. Certain plants are able to limit Se-induced proteomic damage via redirection of SeCys away from protein synthesis, thus preventing the formation of Se proteins. Furthermore, proteasomes, i.e. protein complexes that degrade unneeded or damaged proteins by proteolysis, can eliminate malformed selenoproteins, oxyproteins, and nitroproteins.

One of the factors by which trace elements influence the metabolic and physiological processes of plants is their interaction with essential nutrients. Many research reports have shown that Se ions can disturb the mineral balance in plants (Hawrylak-Nowak 2008a, b, c; Ríos et al. 2008a, b; Łukaszewicz et al. 2019; Ríos et al. 2013). Due to the SeO_4^{2-} and SO_4^{2-} antagonism, the ratio between these ions in the medium influences their uptake and accumulation. However, synergism can also occur between them when the concentrations of S and Se in the growth medium are relatively low, causing increased accumulation of S and Se and the end products of assimilation of these elements in plants (Lyons et al. 2005; Ríos et al. 2008a, b). In field conditions, the interactions between S and Se are very complicated, as S fertilization can improve the availability of Se in soil but inhibit selenate uptake by plants (Stroud et al. 2010).

It has been found that selenite rather than selenate exerts a stronger impact on the nutritional mineral status in plants, especially in the case of N, P, Mg, S, and Zn (Ríos et al. 2008a, b). In a study conducted by Hawrylak-Nowak (2008a, b, c), selenite treatment increased maize shoot P and Ca contents, while K declined with an increasing Se concentration. Since phosphate transporters are involved in selenite transport (Gupta and Gupta 2017), the plant P level can be particularly affected by selenite treatments. In cucumber treated with selenite or selenate, the shoot K, P, and S bioconcentrations were especially highly disturbed by toxic concentrations of Se. In turn, the N level was generally maintained unchanged (Hawrylak-Nowak et al. 2015). Feng et al. (2009) suggest antagonistic and synergic effects of Se on the uptake of Ca, Mg, and K at low and high Se concentrations, respectively, in Chinese brake fern, which is a Se accumulator. It has also been suggested that damage and changes in the permeability of root cell membranes induced by increased lipid peroxidation may contribute to mineral homeostasis disorders (Hawrylak-Nowak et al. 2015).

17.4 Mechanisms of Selenium Resistance and Tolerance

As mentioned above, the non-specific incorporation of SeCys and SeMet into proteins causes disturbances in their structure and functions. However, Se-hyperaccumulating species can tolerate high Se levels in their tissues and colonize seleniferous soils due to the effective metabolic detoxification of Se by sequestration of the element in vacuoles, production of non-toxic Se metabolites, e.g. non-protein amino acids, and/or efficient volatilization of Se compounds (White 2018).

In Se hyperaccumulators, the enzyme SeCys methyltransferase (SMT) found in plastids transforms SeCys to non-protein amino acid methyl-SeCys, thereby preventing its misincorporation into proteins and toxic action (Schiavon and Pilon-Smits 2017). The additional possible Se tolerance mechanisms in Se-hyperaccumulating species are based on sequestration of methyl-SeCys in epidermis cells (Freeman et al. 2010) and transformations of organic Se to alkylated volatile Se species, e.g. dimethyldiselenide (DMDSe) (Ellis and Salt 2003; Wrobel et al. 2020). It has been found that Se hyperaccumulators treated with SeO_4^{2-} store Se predominantly as methyl-SeCys, while non-accumulators such as *Arabidopsis* and secondary accumulators such as *Brassica juncea* accumulate primarily SeO_4^{2-}, indicating differences in Se metabolism. Moreover, interesting Se sequestration patterns, which are not observed in non-hyperaccumulating taxa, have been detected in Se hyperaccumulators: approximately 90% of Se was accumulated as methyl-SeCys in leaf epidermis or leaf hairs (Freeman et al. 2006). In turn, oilseed rape metabolized SO_3^{2-}/SO_4^{2-} into various organic Se forms, mainly SeMet, whereas SeCys, i.e. a precursor of non-protein Se-amino acid, was not detected in the seeds and leaves of this species (Seppänen et al. 2018). Furthermore, hyperaccumulator species translocate Se more effectively in the xylem (from root to shoot) and phloem (from leaves to generative organs) than non-accumulators and differ in their tissue Se accumulation patterns (Pilon-Smits 2019).

The levels of L-ascorbic acid, GSH, non-protein thiols, and total S were higher in the Se-hyperaccumulator *Stanleya pinnata* than in the secondary Se-accumulator *Stanleya albescens*. This suggests that the tolerance to Se may be related to improved antioxidant capacity and increased S accumulation (Freeman et al. 2010). The multiomics research on Se tolerance in the Se-hyperaccumulating species *Cardamine enshiensis* revealed that GSH, flavonoid, and lignin biosynthetic pathways can be of great importance in protecting plants from Se-induced stress (Huang et al. 2021).

Although the Se tolerance mechanisms have similar features, there is genetic variation between populations of individual species with regards to the degree of Se accumulation, as demonstrated in the case of *Stanleya pinnata* (Parker et al. 2003). Tamaoki et al. (2008) reported that both ethylene and jasmonic acid (JA) are important compounds for enhancement of Se resistance in Arabidopsis. It was found that augmented accumulation of ROS was connected with increased ethylene and JA biosynthesis in a Se-tolerant *Arabidopsis* ecotype. Similarly, auxin and ethylene may increase Se tolerance, since their reduced levels caused greater sensitivity to Se in *Arabidopsis*; simultaneously, high concentrations of cytokinin contributed to considerable enhancement of plant resistance to selenite (Lehotai et al. 2012). Recently, a novel Se tolerance mechanism has been proposed, in which endoplasmic reticulum-assisted degradation (ERAD) is involved in the elimination of misfolded selenoproteins (Van Hoewyk 2018).

Non-accumulators can avoid incorporation of SeCys into proteins either by breaking down this amino acid to alanine and elemental Se (Van Hoewyk et al. 2005) or by transforming SeCys to volatile DMSe (Schiavon and Pilon-Smits 2017). The transformation of SeMet and SeCys to volatile Se compounds is an effective strategy increasing plant tolerance to Se. Generally, Se is volatilized as DMSe in non-accumulators and as DMDSe in Se-hyperaccumulators (White 2018). The resistance to Se in Se-sensitive non-accumulator plants can be increased via genetic engineering. Overexpression of key enzymes responsible for Se detoxification in hyperaccumulators, such as SMT, may lead to increased Se tolerance in non-accumulators. Such transgenic plants may be useful in Se phytoremediation. They are also of great interest to medical practitioners and nutritionists due to the presence of organic Se forms with potentially high anticancer activity (Ellis et al. 2004). Recent comparative transcriptomics experiments reported by Zhou et al. (2018) indicated that the storage function, transamination, oxidation, and selenation play vital roles in Se tolerance in *Cardamine hupingshanensis* (Brassicaceae) – a novel species included in the group of Se hyperaccumulators. Additionally, a dissimilar degradation pathway for malformed Se proteins improved Se tolerance in this species.

17.5 Beneficial Role of Selenium in Plants: Growth-Promoting Effects and Enhanced Stress Tolerance

Recent research has demonstrated that Se can be regarded as a beneficial element to plants (Baker and Pilbeam 2015). This was mainly indicated by research proving the growth-stimulating effect of low Se concentrations and its positive influence on plant resistance to various abiotic and biotic stresses (Seppänen et al. 2003; Hawrylak-Nowak et al. 2018b). Selenium plays its beneficial role as a growth-promoting agent and stress modulator mainly by inhibition of ROS production and over-accumulation via the following pathways: (i) modulation of the levels and activity of non-enzymatic and enzymatic antioxidants, (ii) stimulation of the spontaneous dismutation of $O_2^{\bullet -}$ to H_2O_2, and (iii) direct ROS quenching (Feng et al. 2013; Chauhan et al. 2019). Other mechanisms can be associated with the influence of Se on the integrity and stability of photosystems and photosynthesis machinery, which in consequence leads to limited ROS formation (Chauhan et al. 2019). In *Brassica napus*, exogenously applied Se markedly improved plant growth by increasing the uptake of essential mineral elements, photosynthetic efficiency, and gas exchange parameters. It also elevated the concentrations of water-soluble proteins and sugars (Ulhassan et al. 2019). Selenium can also act as an anti-senescent agent and support plants in the maintenance of cellular function and structure, thereby contributing to the improvement of plant growth and development (Kaur et al. 2014).

Appropriate Se concentrations are highly effective in mitigation of cell oxidative damage induced by various environmental stressors. Selenium ions may regulate or improve the function of the injured photosynthetic machinery and/or repair the chloroplast ultrastructure to rebalance the electron transfer chain (Feng et al. 2013). Some results suggest that Se may activate protective mechanisms mitigating the effects of photooxidative stress in potato chloroplasts (Seppänen et al. 2003). In these experiments, the synergistic effect of Se on the transcription level of chloroplast antioxidant enzymes, such as Cu/Zn superoxide dismutase (Cu/ZnSOD) and GSH-Px, was demonstrated. Moreover, decreased lipoperoxidation in thylakoid membranes has been suggested to protect and stabilize enzymes involved in the biosynthesis of photosynthetic pigments (García Márquez et al. 2020).

In plants exposed to heat stress, Se fertilization may improve yields by alleviation of ROS-induced injuries through activation/modulation of the cellular antioxidant machinery (Hasanuzzaman et al. 2014; Iqbal et al. 2015; Balal et al. 2016; Hawrylak-Nowak et al. 2018a). Under heat stress, disruption of AsA-GSH cycle components resulting in overproduction of ROS was detected. Nevertheless, supplementation with Se enhanced enzyme activities and the plants accumulated higher concentrations of GSH and L-AsA (Hasanuzzaman et al. 2014). Exogenous Se was also found to modify physiological responses of cucumber exposed to short-term cold. The Se-supplemented plants showed increased foliar content of proline and reduced lipid peroxidation in root tissues both directly after chilling and after re-warming (Hawrylak-Nowak et al. 2010).

The effect of exogenous Se on plants grown under salt stress is well documented, as many salt-exposed species reacted very positively to Se supplementation (Hawrylak-Nowak 2009; Diao et al. 2014; Jiang et al. 2017; Atarodi et al. 2018). As recently shown by Elkelish et al. (2019), Se supplementation protected wheat plants against salt-induced oxidative stress and strengthened stress tolerance by up-regulating antioxidant systems, enhancing osmolyte biosynthesis, and preventing excessive bioaccumulation of Na^+. Moreover, Jiang et al. (2017) demonstrated that the shoot K^+ accumulation increased and the root Na^+ level decreased at a low Se concentration. The authors found that Se can up-regulate the *ZmNHX1* gene in root cells, which may be involved in the compartmentalization of Na^+ in conditions of excessive salinity. Similarly, in rice treated with Se prior to salinity stress, Subramanyam et al. (2019) showed increased transcript levels for OsNHX1, an important Na^+/H^+ antiporter responsible for Na^+ sequestration in the vacuole. The role of free proline in the Se-induced enhancement of plant resistance to salinity is ambiguous. Its level fluctuates in plants supplemented with Se and exposed to salt stress. In some salt-stressed species, the level of this amino acid can increase under the influence of exogenous Se, which is associated with simultaneous growth stimulation (Hawrylak-Nowak 2009). In turn, the Se growth-promoting effect on other species was not connected with a significant increase in foliar accumulation of proline (Hawrylak-Nowak 2015). Se-induced stabilization of the proline level in leaves and limited loss of this amino acid from roots were demonstrated in other plants (Regni et al. 2021).

Selenium ions can also be effective in counteracting the stress associated with toxic trace elements. Exogenous Se has been found to prevent their uptake and negative impact on plants. Under Cd- and As-induced phytotoxicity, the supplementation of potato with Se reduced the accumulation of Cd and/or As in plants and modulated the metabolism of N and carbohydrates. The enhanced C-metabolism and decreased N losses associated with the Se supplementation improved plant growth (Shahid et al. 2019). In experiments with Cd-exposed cucumber (Hawrylak-Nowak et al. 2014), the enrichment of the growth medium with Se caused decreased lipid peroxidation and reduced Cd and phytochelatin (PC) accumulation in root tissues. The leaf cell membranes exhibited improved stability, but the growth-promoting effect of Se was not pronounced. A positive impact of low Se concentrations on the maintenance of the structure and fluidity of chloroplast biomembranes was demonstrated by Filek et al. (2010) in Cd-exposed rape. The enhanced Fe uptake and bioaccumulation under Se supplementation can be regarded as one of the mechanisms of reducing both metal toxicity (Feng et al. 2009) and the negative impact of salt stress (Atarodi et al. 2018) on plants, since Fe is a key component of chloroplasts and the photosynthetic electron transport chain. In turn, in a summary of the considerations on the mechanisms underlying the Se-mediated restriction of the uptake of some toxic metals, Feng et al. (2021) pointed to the co-precipitation of Se and metals in soil as a key factor limiting the uptake of metal ions by plants. The downregulation of genes encoding proteins involved in Cd uptake may also be important (Feng et al. 2021). As in many other cases, the chemical form of Se may also play a significant role in the amelioration of some negative effects caused by toxic metals. In Ni-exposed lettuce treated with a low dose of selenate, the root growth was stimulated, while selenite in general intensified the phytotoxicity of Ni. Although a decreased concentration of this metal was detected in the roots, the Ni level in the shoot increased, regardless of the Se form (Hawrylak-Nowak and Matraszek-Gawron 2020). In turn, in Cd-exposed pak choi, both chemical forms of Se mitigated Cd-induced oxidative stress, but selenite caused a decrease in shoot Cd accumulation, whereas selenate increased it (Yu et al. 2019).

The protective effect of Se is related not only to its antioxidant activity. This element has been found to exert a multidirectional effect on various physiological processes, especially on water balance. The protective influence of exogenous Se in water-deficit conditions may result from its direct impact on more effective water uptake from the soil (through stimulation of water uptake by roots) and/or its inhibitory effect on the intensity of transpiration and thus water loss from plant tissues (Kuznetsov et al. 2003). Recently, Han et al. (2022), who compared the effectiveness of selenite and selenate in mitigation of drought stress in tobacco, demonstrated that both chemical forms were useful, but the beneficial effects of selenate exceeded those associated with the application of selenite.

The accumulation of toxic Se compounds can effectively protect plants against fungal and other pathogen and herbivore attacks. The accumulation of Se in tissues has been found to protect plants against fungal infections and invertebrate herbivores, which become poisoned after feeding on Se-rich leaves (Hanson et al. 2003). Similarly, aphids evidently distinguished and avoided Se-containing leaf tissues (Hanson et al. 2004). It was later found that differences in the Se assimilation pathway allow achievement of maximum Se bioconcentrations, which are indispensable for introduction of sufficiently high doses of toxic Se compounds into the organisms of herbivores resulting in poisoning of the pests. This led to the evolution of plant species with an ability to colonize seleniferous soils (Schiavon et al. 2017; White 2018). Selenium hyperaccumulation not only can protect plants against Se-sensitive pathogens and herbivores but can simultaneously reduce neighbouring vegetation by deposition of plant biomass with extremely high Se content (elemental allelopathy) (Pilon-Smits 2019).

17.6 Selenium Biofortification Improves the Quality of Yield

Selenium uptake and assimilation by plants affects the S and nitrogen (N) metabolic pathways; therefore, current investigations are focused on the influence of Se exposure on the biosynthesis and accumulation of S and N secondary metabolites to enhance the nutraceutical profile of food (D'Amato et al. 2020). Selenium can be incorporated into several secondary Se metabolites of SeMet and SeCys (Malagoli et al. 2015; White 2018). The effect of Se enrichment on the content of these phytochemicals has been evaluated in several studies. The impact of Se on the products of plant specialized metabolism in Se-enriched plants is presented in Table 17.1.

Phenolic compounds, i.e. N-containing secondary metabolites, are formed in the shikimate and phenylpropanoid pathways (Tohge and Fernie 2017). As shown by Hawrylak-Nowak et al. (2018a), Se biofortification of lamb's lettuce not only enhanced the thermo-tolerance of the plant but also improved its nutritional value. The foliar concentrations of total phenolics, chlorogenic acid, and flavonoids in Se-supplemented plants growing at an optimal temperature were significantly elevated, and the plant biomass was simultaneously enriched with Se. The authors suppose that low concentrations of Se are able to stimulate the phenylpropanoid pathway, but only in optimal thermal conditions. Similarly, in experiments on hydroponically grown Se-biofortified strawberry reported by Mimmo et al. (2017), enhanced accumulation of flavonoid and polyphenol compounds was found in

Table 17.1 Effects of exogenous selenium on the level of secondary metabolites in selected crop plants

Plant species	Experimental conditions	Form, dose, and method of Se application	Effects of Se on secondary metabolites	References
Basil (*Ocimum basilicum*)	Natural conditions; soil	Selenate; foliar application of 30, 60, or 120 mg Se L^{-1}	Increased the content of soluble phenols in leaves	Oraghi Ardebili et al. (2015)
Basil (*O. basilicum*)	Heated glasshouse; hydroponic cultivation	Selenate; 4, 8, or 12 mg Se L^{-1} applied to the nutrient solution	Elevated level of total phenolics and rosmarinic acid in leaves	Puccinelli et al. (2020)
Basil (*O. basilicum*)	Climate chamber; soil substrate	Selenate; foliar application of 1–50 mg Se L^{-1}	Increased the concentration of total phenolic compounds in leaves	Hawrylak-Nowak (2008a, b, c)
Broccoli (*Brassica oleracea* var. *italica*)	Greenhouse; hydroponic cultivation or soil substrate	Selenate; 25 μM Se applied to the nutrient solution or soil substrate	Reduced accumulation of total glucosinolates, mainly glucoraphanin, in leaves and florets	Tian et al. (2018)
Celery (*Apium graveolens*)	Field conditions; soil	Se nanoparticles; foliar application of 5 mg Se-NPs L^{-1}	Increased accumulation of total phenols and flavonoids (rutin, apigenin, ferulic acid, p-coumaric acid, luteolin, kaempferol) in leaves, enhanced antioxidant activity of leaves	Li et al. (2020)
Coriander (*Coriandrum sativum*)	Greenhouse; soil substrate	Se nanoparticles; foliar application of 25 or 50 Se-NPs L^{-1}	Increased essential oil yield and enhanced accumulation of essential oil constituents: Camphor, linalool, geranyl acetate, α-pinene, δ-terpinene in fruits	El-Kinany et al. (2019)
Endive (*Cichorium endivia*)	Greenhouse; open hydroponic floating system	Selenate; 1, 2, 4, or 8.0 μmol L^{-1} applied via fertigation or foliar spray	Increased the concentration of total phenolic compounds in leaves	Sabatino et al. (2019)
Lamb's lettuce (*Valerianella locusta*)	Climate chamber; soil substrate	Selenate; foliar or soil application of 50 mg Se L^{-1}	Elevated level of total phenolics, chlorogenic acid, flavonoids in leaves	Hawrylak-Nowak et al. (2018a)
Lemon balm (*Melissa officinalis*)	Greenhouse; hydroponic cultivation	Selenite; 0.2 or 5 μM applied to the nutrient solution	Elevated caryophyllene, caryophyllene oxide, z-citral, citral, and geranyl acetate contents in leaves	Tavakoli et al. (2020)

(continued)

Table 17.1 (continued)

Plant species	Experimental conditions	Form, dose, and method of Se application	Effects of Se on secondary metabolites	References
Rocket (*Eruca sativa*)	Growth chamber; hydroponic cultivation	Selenate; 5, 10, 20, or 40 μM Se applied to the nutrient solution	Reduced accumulation of total glucosinolates and individual glucosinolates, decreased concentration of some phenolic compounds in leaves	Dall'Acqua et al. (2019)
Strawberry (*Fragaria* × *ananassa*)	Climate chamber; hydroponic cultivation	Selenate; 10 μM Se or 100 μM Se applied to the nutrient solution	Increased flavonoid and phenolic compounds in fruits	Mimmo et al. (2017)
Tomato (*Solanum lycopersicon*)	Greenhouse; unknown method of cultivation	Selenate; foliar application of 1 mg Se L^{-1}	Increased concentrations of flavonoids and tocopherols in fruits	Zhu et al. (2018)
Tomato (*S. lycopersicon*)	Climate chamber; hydroponic cultivation	Selenate; 5–100 μmol L^{-1} applied to the nutrient solution or via foliar spray at 2 or 20 mg Se per plant	Increased level of quercetin, quercetin-hexose-deoxyhexose pentose, naringenin chalcone, and kaempferol, and a decrease in cinnamic acid derivatives in fruit peels; stimulated biosynthesis of phenolics in leaves	Schiavon et al. (2013)

addition to an increased fruit Se concentration. These substances were found to contribute to the organoleptic traits and antioxidant capacity of strawberry fruits. Moreover, the content of total soluble solids (TSS) and the sweetness index of the Se-biofortified strawberries were elevated, which can exert a positive effect on the fruit taste. Another example demonstrating that the quality of plant products can be favourably modified to some extent by Se supplementation is Se-biofortified sweet basil (Hawrylak-Nowak 2009). In this species, foliar spraying with a Se solution (3–20 mg L^{-1} as selenate) increased the total content of phenolic compounds (up to 44% vs. the control). A similar impact of Se on the accumulation of selected phenolics in basil was also confirmed later in natural conditions (Oraghi Ardebili et al. 2015). Biofortification with Se modifies the phenylpropanoid pathway mainly by enhancing the enzymatic activity of phenylalanine ammonia-lyase (PAL), i.e. a crucial enzyme in phenylpropanoid metabolism and biosynthesis of secondary metabolites from the group of phenolic compounds (Oraghi Ardebili et al. 2015; García Márquez et al. 2020). Proteomic analysis demonstrated that proteins involved in phenylpropanoid biosynthesis were up-regulated in Se-biofortified tomato fruit causing increased flavonoid accumulation (Zhu et al. 2018). The phenomenon of the improved accumulation of phenolics may be also attributed to the Se-affected hormonal homeostasis, especially that of salicylic acid (SA), JA, and ethylene, leading to defence-related responses (Tamaoki et al. 2008; Oraghi Ardebili et al. 2015). In turn, Dall'Acqua et al. (2019) reported reduced levels of some phenolic compounds, i.e. kaempferol-3,4′-diglucoside, kaempferol-3-glucoside, and kaempferol-3-(2-sinapoil-glucoside)-4′-glucoside in salad rocket and quercetin-3,3,4′-triglucoside, quercetin-3,4′-diglucoside, and kaempferol-3.4′-diglucoside in wild rocket under selenate exposure. The authors suggest that Se may affect the shikimate pathway, i.e. the entry to the biosynthesis of phenylpropanoids, in various ways, i.e. by redirecting one of the final products of this pathway – phenylalanine from production of phenolics to serve as a substrate for glucosinolate biosynthesis or by direct inhibition of enzymes involved in the shikimate pathway.

In comparison to control plants, Se-biofortified tomatoes had higher concentrations of some flavonoids (naringenin chalcone and quercetin) in their fruits after foliar Se application and a higher level of phenolic compounds in their leaves after administration of Se through the roots (Schiavon et al. 2013). In turn, increased accumulation of phenolic acids and anthocyanins was detected in two differently pigmented lettuce genotypes supplemented with Se (Pannico et al. 2019). Biofortification with Se also increased the rosmarinic acid content in basil (Puccinelli et al. 2020). Furthermore, the presence of selenosugars, possibly originating from the cell wall, has been described in Se-supplemented plants (Aureli et al. 2012). The results reported by Bañuelos et al. (2012) revealed the presence of non-protein methylselenocysteine (MeSeCys) in Se-enriched fruits of Opuntia cactus pear. This compound is nutraceutically very interesting, since it is one of the least toxic and thus the safest chemical forms of Se, simultaneously characterized by high anticarcinogenic activity (Yang and Jia 2012). As an element that enhances the accumulation of many compounds with strong antioxidant properties, Se was found to increase the antioxidant capacity in Se-enriched leafy vegetables (Ríos et al. 2008a, b), herbs (Oraghi Ardebili et al. 2015; Tavakoli et al. 2020), and edible sprouts (Woch and Hawrylak-Nowak 2019).

Recently, Se nanoparticles (Se-NPs), i.e. bioavailable and low-toxic Se forms with high efficiency, were used for enhancement of the yield and quality of various crops (El-Ramady et al. 2020). Li et al. (2020) revealed that foliar application of Se-NPs in celery increased the concentration of total phenols, flavonoids, L-ascorbic acid, β-carotene, arginine, and tryptophan and enhanced the antioxidant capacity of plants, probably by regulating the α-linolenic acid pathway. The foliar application of Se-NPs also increased the nutraceutical potential of fruits of coriander grown under salinity by increasing the essential oil yield and the concentration of the major constituents of essential oil (El-Kinany et al. 2019).

Selenium treatment can also exert direct or indirect positive effects on the post-harvest storage of some crops. For example, Se application can delay the decline in firmness, titratable acidity, and weight loss during the storage of tomato (Zhu et al. 2016) and guava (Choudhary and Jain 2018) fruits. The reduced production of ethylene detected in Se-treated basil stored for 5 days may indicate that Se enrichment can prolong the shelf-life of basil leaves (Puccinelli et al. 2020). In turn, foliar spraying with selenate improved the respiratory potential in young chicory, but not in plants at harvest time (Germ et al. 2007). An indirect influence was associated with the reduction of the germination rate and mycelial growth of some detrimental fungi (Puccinelli et al. 2017).

17.7 Conclusions

Selenium accumulated in plants from the soil is then ingested by animals and humans with food, and in this way, Se is easily incorporated into the food chain. Although plants do not require Se for proper growth and development, the process of phytoaccumulation and further volatilization of Se can be applied in both crop biofortification in Se-deficient regions and phytoremediation of areas contaminated with this element. The biological activity of Se and plant resistance to this element are strictly dependent on the species, age, and developmental stage of plants, the phytoavailable chemical form of Se, and environmental factors influencing its uptake and accumulation. Therefore, plants can react to the presence of Se both positively and negatively (Fig. 17.3). Despite the increasing knowledge of plant responses to the presence of Se, a number of issues regarding the specific mechanisms of its toxicity and resistance in Se accumulators and non-accumulators still need elucidation. In particular, the molecular and physiological processes determining the beneficial effects of this element in crops in the changing climate conditions may be of key importance. In this aspect, the use of low-toxic Se nanoparticles with high bioavailability and efficiency may prove very promising in the future. Moreover, the knowledge of the factors controlling the uptake, translocation, and assimilation of different chemical forms of Se will help to prevent their negative impact on the primary and secondary metabolism in Se-enriched plants.

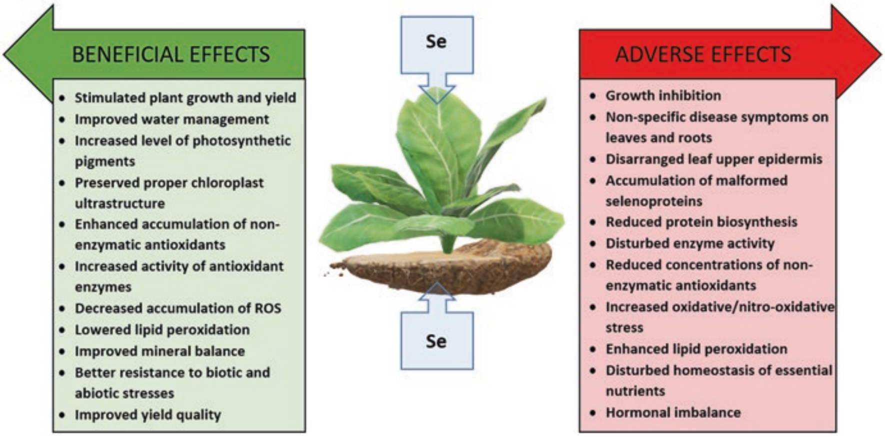


Fig. 17.3 Beneficial and adverse effects of selenium on plant growth and metabolism

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Chapter 18
Use of Selenium Accumulators and Hyperaccumulators in Se-Phytoremediation Technologies: Recent Progress and Future Perspectives

Simeng Li and Corrine Liu

18.1 Introduction

Selenium (Se) is an essential micronutrient for most organisms, including many bacteria, plants, animals, and humans (White and Broadley 2009). In nature, Se is slowly released from certain Cretaceous shale sediments (Kulp and Pratt 2004). The levels of Se in most soils are within a low range from 0.01 to 2.00 mg/kg, with an average of approximately 0.40 mg/kg (Tan et al. 2002). When Se level exceeds 10 mg/kg in soil, it may become toxic due to its nonspecific replacement of sulfur (S) in proteins and other S-containing compounds (White and Broadley 2009). In some areas, especially those with dry climate conditions and alkaline soils, as a result of soil cultivation and/or fossil fuel excavation, Se may accumulate to reach as high as 100 mg/kg in soils (Tan et al. 2002).

When the level of Se in the soil is too high to be considered as healthy for crop growth, it is necessary to remove the excess Se using remediation technologies. Among the various remediation options, phytoremediation stands out because of its minimal ecological impact and low maintenance cost (Wan et al. 2016). Phytoremediation of Se-contaminated soils relies on the use of Se accumulators and/or hyperaccumulators. Selenium accumulators are plants that grow particularly better in the presence of Se. Among Se accumulators, plants that are able to accumulate 0.1–1.5% or more (w/w) Se on a dry weight basis are categorized as hyperaccumulators. Many plants, such as silver-leafed milkvetch (*Astragalus bisulcatus*)

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M. A. Hossain et al. (eds.), *Selenium and Nano-Selenium in Environmental Stress Management and Crop Quality Improvement*, Sustainable Plant Nutrition in a Changing World, https://doi.org/10.1007/978-3-031-07063-1_18

and desert prince's plume (*Stanleya pinnata*), have demonstrated significant effectiveness in alleviating Se toxicity (Alford et al. 2012; Freeman et al. 2010; Parker et al. 2003). Because many Se accumulators and hyperaccumulators are also capable of converting the accumulated Se into volatile forms (i.e., phytovolatilization), it is possible to clean up contaminated soils by releasing those Se-containing compounds into the atmosphere.

Another issue as common as Se toxicity is Se deficiency. Large regional variations of Se concentrations in grains (e.g., rice) have been widely observed in studies (Banuelos et al. 2007; Fordyce et al. 2000; Wang et al. 2013). According to a recent global survey, low Se levels are particularly prevalent in major rice-producing and rice-consuming countries like China and Thailand, whereas Se levels are relatively higher in rice from the United States and India (Zhu et al. 2009). In areas with inadequate Se in the soil, growing proper Se-rich crops (usually Se accumulators and hyperaccumulators) is a practical solution to offset deficiency, but close monitoring throughout the plant life cycle is required to optimize Se concentrations in crops within the narrow range.

When using Se accumulators and hyperaccumulators for Se phytoremediation, understanding how plants take up and metabolize Se and identifying affecting factors are critical for better effectiveness. In this chapter, the current theory on Se uptake and metabolism is first introduced (Sect. 18.2), followed by brief discussions on Se phytoremediation technologies in both terrestrial and aquatic systems (Sect. 18.3). Factors that influence Se phytoremediation are reviewed in Sect. 18.4. Lastly, future prospects of Se phytoremediation are explored (Sect. 18.5).

18.2 Selenium Uptake, Metabolism, and Speciation

Selenium may exist in various forms in different soils, including naturally occurring organic forms such as selenide (Se^{2-}), selenate ($HSeO_4^-$), selenite (SeO_3^{2-}), elemental selenium (Se), and organic selenium (Li et al. 2017). Among the different forms, $HSeO_4^-$ is the predominant readily bioavailable species in most soils (Fordyce et al. 2000; Kotrebai et al. 1999; Tan et al. 2002). Being a chemical analog of sulfur (S) in the periodic table, Se shares many chemical similarities. For example, Se^{2-} resembles sulfide (S^{2-}) in many ways. Just like S^{2-}, Se^{2-} mostly exists in alkaline conditions; hydrogen selenate ion (HSe^-) is formed in neutral conditions; hydrogen selenide (H_2Se) occurs in acid conditions. Selenates are highly water-soluble like sulfate (SO_4^{2-}); it is a good oxidizer that can be reduced to Se^{2-} or elemental Se. Selenite is the Se analog of the sulfite ion (SO_3^{2-}) (Guo et al. 2000). In its inorganic forms, Se commonly replaces a small portion of the S in sulfide ores of many metals (Kulp and Pratt 2004). Selenite is the predominant inorganic species in most soils. To optimize the performance of Se phytoremediation using Se accumulators and/or hyperaccumulators, it is necessary to understand the molecular mechanisms of Se uptake, transformation, accumulation, tolerance, and speciation.

18.2.1 Plant Uptake of Selenium

Due to the chemical similarities between Se and S, ionic Se can be taken up by many plants via the mediation by S transporters present in the root cell membranes (Fig. 18.1). Studies on translocation factors of canola and wheat found that $HSeO_4^-$ was the most mobile Se species in these two plants (Eiche et al. 2015; Renkema et al. 2011). The uptake of $HSeO_4^-$ is mediated by transporters of SO_4^{2-} that are located in the root cell membranes (Sors et al. 2005). Depending on the plant species and nutritional status, the selectivity of these transporters varies. Translocation of Se ions is influenced by the xylem loading and transpiration rates, which differs

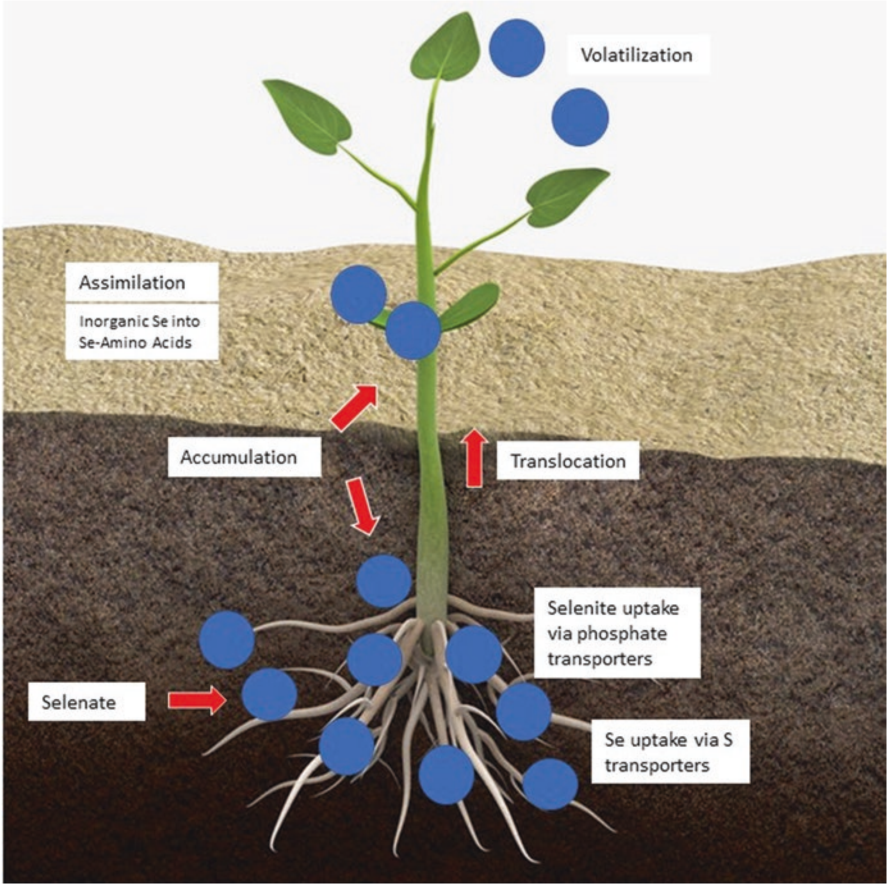

Fig. 18.1 Possible fates and transport pathways of selenium in plants. Selenate is the most bioavailable form of selenium in most soils. The uptake and accumulation of selenate begin from the plant root, followed by selenate relocation to the shoot and leaves. The plant can assimilate inorganic selenate and convert it into various organic forms including selenocysteines (SeCys). Volatile forms of organic Se can be emitted into the atmosphere

among different plants (Li et al. 2008). Meanwhile, the nutritional status inside and outside the plant also affects the preference of SO_4^{2-} transporters. Sulfate is preferred when sulfate concentrations are higher in the soil environment, vice versa. Different SO_4^{2-} transporters in the same plant may have contrasting selectivity for SO_4^{2-} and $HSeO_4^-$. In general, inducible SO_4^{2-} transporters also demonstrated preference for SO_4^{2-} when compared with constitutively active SO_4^{2-} transporters. The mechanism of $HSeO_4^-$uptake by plants has been well established, but little is known about Se^{2-} uptake. Passive diffusion was used to explain Se^{2-} uptake for decades. However, it has been found in some recent long-term hydroponic experiments that Se^{2-} uptake could be impacted by phosphate (PO_4^{3-}) in the soil. These results suggest that passive diffusion is not sufficient to explain Se^{2-} uptake by plants; it is possible that Se^{2-} uptake is actively affected by PO_4^{3-} transporters (Hopper and Parker 1999).

18.2.2 Accumulation Metabolism in Plants

The accumulation of Se mostly occurs in the vacuoles inside plant cells. In general, younger leaves accumulate more Se than older ones during seedling growth (Ramos et al. 2010; Wu et al. 1988). Hyperaccumulator plants are capable of accumulating more Se in their cells without any toxic effects. Hyperaccumulators and accumulators are able to thrive in Se-rich soils and show no toxic effects despite a large amount of accumulated Se in the biomass (e.g., 1000 mg Se/kg dry mass), while non-accumulators cannot survive when the accumulated Se is above 100 mg Se/kg dry mass (Gupta and Gupta 2017).

In the plant, inorganic Se is first converted into adenosine phosphoselenate via the hydrolysis catalyzed by ATP sulfurylase (APS) and then reduced to form selenite by APS reductase (APR). Selenite is further reduced into selenide by sulfite reductase (Saffaryazdi et al. 2012). In certain plants, selenite can also be reduced by glutathione or glutaredoxins (Gupta and Gupta 2017). Afterward, selenide forms SeCys by coupling with O-Acetyl serine (OAS) via the catalysis by cysteine synthase. Determined by plant species and environmental conditions, SeCys can either be converted into elemental Se through SeCys lyase, be methylated to methyl-SeCys by selenocysteine methyltransferase (Me-SeCys), or form selenomethionine (SeMet) by a group of different enzymes. Both SeCys and SeMet bestow Se tolerance and can be vaporized further as dimethyl diselenide (DMDSe) in hyperaccumulators or dimethyl selenide (DMSe) in other plants (Schiavon and Pilon-Smits 2017). The major metabolism steps are illustrated in Fig. 18.2.

Various species also exhibited different traits that appear to optimize their accumulation capacity. Several studies reported that the Se hyperaccumulator *Stanleya pinnata* had less competitive inhibition by S than the non-accumulating *Stanleya elata* and *Brassica juncea*. Comparing these species, it was found that *Stanleya pinnata* consistently had the highest level of expression of the S transporter genes SULTR1;2 and SULTRI2;1, indicating that the amount of the genes expressed in

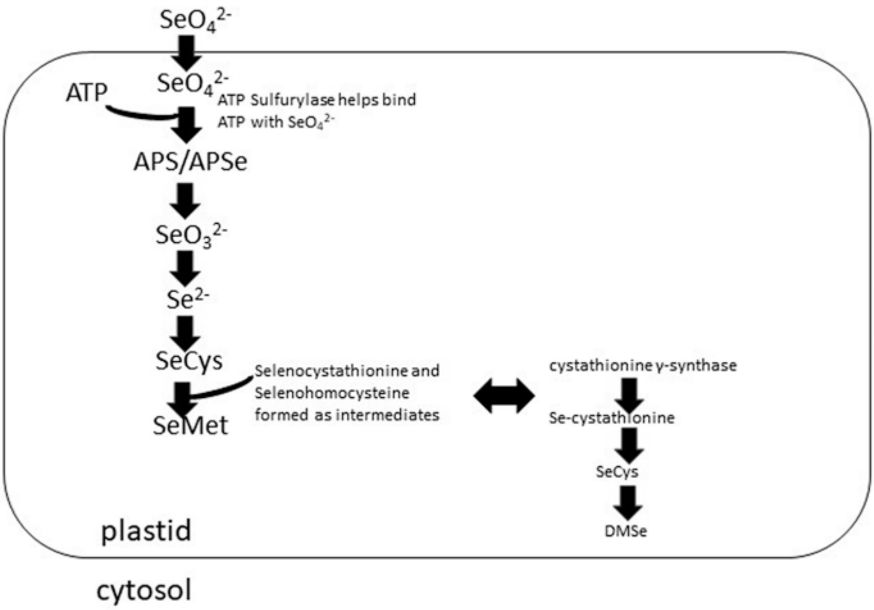

Fig. 18.2 Brief mechanism for Se metabolic activities. Selenate enters cells through its competition against sulfur via sulfur transporters in the plasma membrane of roots. Selenate is methylated into SeCys and SeMet, both of which can be safely accumulated in plants. After its transport to plant leaves through xylems, selenate is assimilated to DMSe and DMDSe via a variety of sulfur metabolism enzymes

this plant species could be a contributing factor to its accumulation capacity (Ohno et al. 2012; Schiavon et al. 2015). Another possible mechanism for Se tolerance in hyperaccumulators is the ability to store organic Se forms into specific compartments away from where key biochemical processes take place (Chan et al. 2009). Recent studies have identified that non-hyperaccumulator species mainly have Se restricted to their vascular tissues, as opposed to hyperaccumulators' ability to store Se in other areas such as in the leaves and/or vacuoles of epidermal cells (Zhu et al. 2009). Excess Se concentrations can promote the generation of reactive oxygen species (ROS), leading to oxidative stress (Battin and Brumaghim 2009). Hyperaccumulators seem to have antioxidant defense systems in place to mitigate the impacts of oxidative damages caused by the excess Se they possess. Glutathione synthetase (GHS) functions as a major defense mechanism against oxidative stress, and the genes mediating its production were expressed higher in the hyperaccumulator *Stanleya pinnata* as compared to the non-hyperaccumulator *Stanleya elata* (Lindblom et al. 2013).

Previous studies showed that high levels of Se accumulation could result in reactive oxygen species (ROS) formation and cause oxidative stress in plants (Battin and Brumaghim 2009; Ebrahimi et al. 2015; Ramos et al. 2010). Increased levels of ROS may be formed when electron flows during plant photosynthesis are impeded by increased Se-derived stress or malfunction. In a recent study, a reduced electron flux as impacted by Se accumulation was observed in *Stanleya albescens*, which led to increased ROS in the plant cells (Freeman et al. 2010). In addition, the increase of ROS may also be a result of the reactions between selenite and reduced glutathione (GSH). For example, when two *Stanleya* species were treated using superoxide and hydrogen peroxide over 10 weeks, those receiving 20 μM of selenate had higher accumulation of superoxide in leaves than those receiving 10 μM. The results shown in Fig. 18.3 also indicated that *Stanleya pinnata* demonstrated to be a Se hyperaccumulator because ROS were not significantly higher despite Se treatments and its photosynthesis was not negatively impacted, whereas *Stanleya albescens* could only be considered as an Se accumulator (Freeman et al. 2010).

When using phytoremediation for Se-contaminated soils, the accumulated Se will be vaporized as dimethyl diselenide (DMDSe) when Se hyperaccumulators are planted or dimethyl selenide (DMSe) when non-accumulators are grown. These vapor forms of Se (i.e., DMDSe and DMSe) are nearly 600 times less toxic compared with elemental Se. Particularly in hyperaccumulators, due to the catalysis by

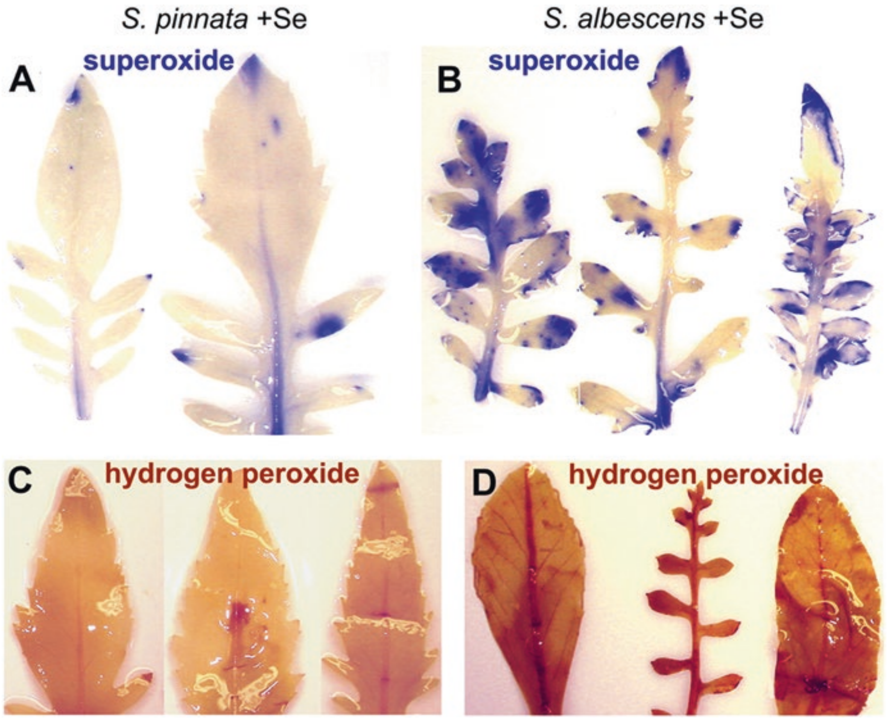

Fig. 18.3 Reactive oxygen species (ROS) staining visualization of Se-induced superoxide and hydrogen peroxide in *Stanleya pinnata* and *Stanleya albescens* leaves over 10 weeks. A and B are superoxide accumulation in leaves of "*S. pinnata* + 20 μM selenate" and "*S. albescens* + 20 μM," respectively. C and D are hydrogen peroxide accumulation in leaves of "*S. pinnata* + 20 μM selenate" and "*S. albescens* + 20 μM," respectively. (Reprinted from Freeman et al. 2010)

selenocysteine methyltransferase, SeCys and SeMet are methylated to nontoxic Me-SeCys and Me-SeMet, which can be safely accumulated till a significantly higher level in plant biomass. So far, a large variety of plants have been studied for their potential to remediate Se-contaminated soils and agricultural drainage water. Examples of such applications are given in Table 18.1.

As shown in Table 18.1, many different plant species have been studied as Se accumulators and hyperaccumulators. Due to the different molecular mechanisms responsible for Se tolerance and accumulation, the accumulation capacity on a dry mass (DM) basis of these plants may significantly vary. For example, *Astragalus racemosus* could accumulate 14,920 mg/kg DM of Se, while *Triticum aestivum* was able to accumulate 387 mg/kg DM of Se (Eiche et al. 2015; Knight and Beath 1937). Among all the plant species listed in Table 18.1, *Astragalus* species

Table 18.1 Accumulation capacities (in leaves) on a plant dry mass basis of Se accumulators and hyperaccumulators

Plant species	Common name	Accumulation capacity (mg Se/kg dry mass of plant)	Location	References
Brassica juncea	Indian mustard	931	Punjab, India	Eiche et al. (2015)
Triticum aestivum	Wheat	387	Punjab, India	Eiche et al. (2015)
Astragalus praelongus	Stinking milkvetch	2925	Fort Collins, CO, USA	Alford et al. (2012)
Astragalus bisulcatus	Two-grooved milkvetch	13,685	Fort Collins, CO, USA	Jong et al. (2015)
Stanleya pinnata	Desert princesplume	3713	Fort Collins, CO, USA	Jong et al. (2015)
Buchloedactyloides	Buffalo grass	340	Davis, CA, USA	Wu et al. (1988)
Trifolium fragiferum	Strawberry clover	900	Riverside, CA, USA	Hopper and Parker (1999)
Astragalus crotalariae	Salton milkvetch	2175	Truckhaven, CA, USA	Beath et al. (1941)
Astragalus racemosus	Creamy milkvetch	14,920	Laramie, WY, USA	Knight and Beath (1937)
C. Hupingshanensis	Wheat	1965	Enshi, China	Yang et al. (2013)
Spinacia oleracea L.	Spinach	3890	Mashhad, Iran	Saffaryazdi et al. (2012)
Allium sativum	Garlic	1355	Ithaca, NY, USA	Kotrebai et al. (1999)
Brassica oleracea	Broccoli	876	Grand Forks, ND, USA	Roberge et al. (2003)
Brassica napus L.	Oilseed rape	646	Helsinki, Finland	Ebrahimi et al. (2015)

(milkvetch) had the highest levels of Se accumulation in general, ranging from 2175 to 14,920 mg/kg DM of Se.

18.2.3 Plant Speciation in Plants

Many different Se-containing compounds (including but not limited to selenide, selenate, and selenite) exist at the same time in plants. Recently, these compounds have been identified by using a variety of characterization techniques such as high-performing liquid chromatography inductively coupled plasma mass spectrometry (HPLC-ICP-MS) and electrospray ionization mass spectrometry (ESI-MS) (Freeman et al. 2010). The rate of Se accumulation is largely dependent on the Se species being absorbed by plants. Studies on Se absorption kinetics showed that selenate could be more efficiently taken up by plants compared with any other Se species. The various Se species also exist in different parts of a plant. For example, in selenate-enriched plants, selenate, Se-MeSeCys, SeMet, and selenate are more abundant in shoot extracts, whereas SeMet, selenate, and selenite have been found in larger quantities in root extracts. In selenite-enriched plants, SeMet, selenite, and SeMetSeOxide are the predominant species in soot extracts, whereas SeMet and Se-MeSeCys are more common in root extracts (Gupta and Gupta 2017).

By the use of a μ-X ray fluorescence spectrometer for elemental analysis, researchers (Freeman et al. 2010) have localized the accumulation of Se in young leaves of *S. pinnata* in distinct globular areas, particularly near the leaf margins and tip (Fig. 18.4a); meanwhile, the distribution of Se was all over the leaf edge in *S. albescens*, not in discrete areas (Fig. 18.4b). The remarkable difference in the spatial distribution of Se in plant leaves reflected one of the reasons how Se hyperaccumulators could tolerate higher levels of Se without disrupting the major biochemical processes in plant cells. The images taken by a scanning electron microscope (SEM) coupled with energy dispersive spectroscopy (EDS) further revealed that Se was accumulated in all the tested epidermal cells in *S. pinnata* (Fig. 18.4e, e), but no detectable Se was found in the epidermal cell walls (Fig. 18.4g). There was also no detectable Se in vascular or mesophyll tissues of *S. pinnata*. The highest levels of Se in *S. pinnata* were found in an organelle which resembled a small vacuole (Fig. 18.4f). According to the line scan taken across a rupture of *S. pinnata* leaf, little Se was accumulated in the cuticular layer (Fig. 18.4h). Unlike the Se-hyperaccumulator *S. pinnata*, only slightly detectable Se was found in one enlarged peripheral epidermal cell in *S. albescens* (Fig. 18.4d).

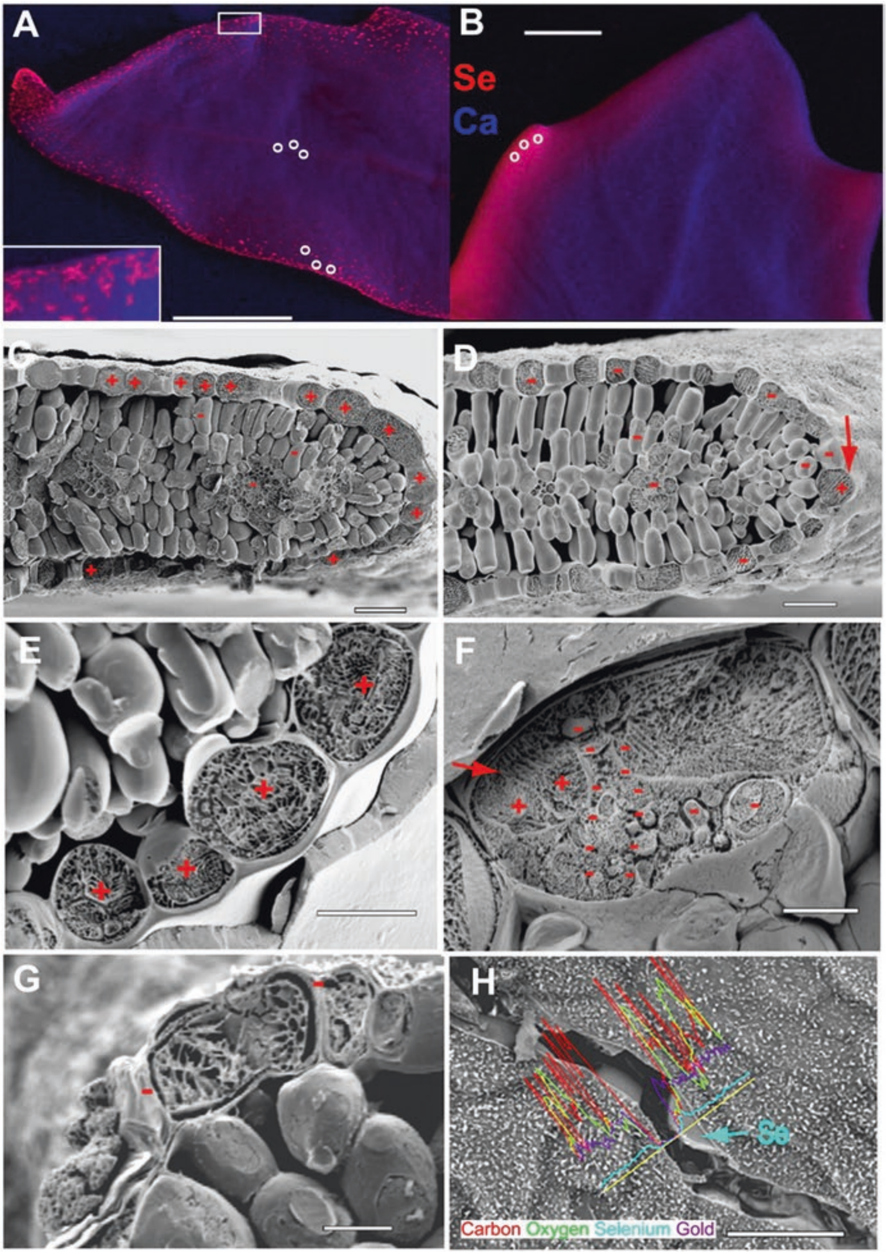

Fig. 18.4 Localization and speciation of Se in *Stanleya pinnata* and *Stanleya albescens* leaves. (Reprinted from Freeman et al. 2010)

18.3 Selenium Phytoremediation Studies

Owing to its environmental friendliness, cost-effectiveness, and various long-term benefits, phytoremediation is an increasingly popular technology based on the use of plants for site cleanup. During phytoremediation, metals (or any other contaminant(s) in concern) are first removed from the contaminated soil via plant uptake through plant roots and then translocated to the upper parts of the plant (Li et al. 2008). The contaminant can be accumulated in the plant and be metabolized into its various forms. Eventually, the contaminant can be eliminated from the contaminated site by plant harvesting or through volatilization in less toxic forms (Susarla et al. 2002). Phytoremediation technologies can be used alone to address the issue of Se toxicity due to the excess amount in soil, but they can also be used to produce green fertilizers when applied in combination with biofortification.

18.3.1 Selenium Phytoremediation in Terrestrial Systems

Concerning the environmental and health risks associated with crops growing in seleniferous soils that may contain high levels of Se up to 100 mg/kg, extensive studies have been conducted to investigate the behavior, transformation, transport, and fate of Se in terrestrial systems (Alford et al. 2012; Eiche et al. 2015; Roberge et al. 2003; Wu et al. 1988). Phytoremediation technologies have been widely used in the United States and many other countries to prevent the transport of mobile forms of Se from irrigated areas with seleniferous soils and/or to remove accumulated Se from soils using plant bioaccumulation and/or volatilization (Schiavon and Pilon-Smits 2017; Zhu et al. 2009).

The use of plants (either Se accumulators or hyperaccumulators) for the removal of Se from contaminated areas is a less invasive and less expensive alternative for conventional physical and chemical approaches. Depending on the goals of remediation, different plant processes can be optimized to achieve better performance. In phytoextraction, plants take up excess Se from seleniferous soils, translocate the absorbed Se to various parts (e.g., shoot and leaves), and accumulate Se until the plant tolerance levels are reached. Afterward, the exploited plants can be harvested for reutilization (e.g., fertilizer production). In phytovolatilization, plants may convert Se to its volatile forms (e.g., DMSe and DMDSe) which will be released into the atmosphere via transpiration.

The selection of proper plant species for Se phytoremediation is often determined through a matrix of different ecological and economic factors. In general, an ideal plant species for Se phytoremediation should (i) grow well under local climatic and weather conditions, (ii) produce a large quantity of biomass in a short time, (iii) be competitive against other non-accumulator plants, (iv) possess a high level of tolerance for Se, (v) be exceptional in accumulating or volatilizing Se, and (vi) have the possibility to generate economic values. Popular species for terrestrial applications are mostly in the *Brassica* family, such as *Brassica juncea* L. (Indian mustard) and *Brassica napus* L. (canola).

The adoption of Se hyperaccumulators for Se remediation requires the consideration of many tradeoffs and careful evaluations. Although Se hyperaccumulators such as *Astragalus racemosus* (creamy milkvetch) demonstrate many desirable features for Se phytoremediation like their remarkable ability to take up, translocate, accumulate, and volatile Se, they are usually wild species that are difficult to obtain and grow (Harris et al. 2014). These plants are also often slow-growing species and come in small sizes. Because of the very high concentrations of Se accumulated in hyperaccumulators, their large-scale applications should be carefully assessed for potential impacts on the local ecological systems. While many herbivores avoid consuming Se hyperaccumulator plants, honeybees do not. The large ingestion of Se may affect the health of honeybees and the quality of honey. Therefore, much research in recent years has been focused on identifying and manipulating new target genes that are responsible for Se hyperaccumulation and tolerance. Through gene engineering, it is possible to produce new species with improved features for Se phytoremediation. For example, the overexpression of ATPS, CGS, and SMT genes in non-accumulator *Brassica* species has demonstrated significant improvements in Se accumulation (ATPS and SMT), volatilization (CGS), and/or tolerance (ATPS, CGS, and SMT). Some recent studies conducted in California have reported successful field applications of ATPS and SMT transgenic *B. juncea* for the remediation of Se-contaminated sediments (Banuelos et al. 2005, 2007).

18.3.2 Selenium Phytoremediation in Aquatic Systems

Many aquatic plants, such as *Typha angustifolia* L. (cattail) and *Scirpus acutus* Muhl. *ex* Bigelow (bulrush), have been used in aquatic systems (e.g., constructed wetland) to remove selenate and/or selenite from agricultural or industrial wastewater. In a pilot study, the microcosms planted with cattail (*Typha angustifolia* L.) and muskgrass (*Chara* spp.) were able to remove aqueous Se by 75% and 74% with 15 days, respectively (Nattrass et al. 2019). In another study, the co-application of *Typha angustifolia* L. and bulrush (*Scirpus acutus* Muhl. *ex* Bigelow) in a 36-ha constructed wetland in California demonstrated high removal of selenite (on average 89%) from oil refinery wastewater, partly precipitated in the sediments and partly incorporated into plant tissues, with up to 30% of the Se completely removed through phytovolatilization (Hansen et al. 1998). In constructed wetlands, most of the Se in the influent would be captured via either sediment adsorption or plant uptake, while a small fraction would be volatilized through plant transpiration. Hence, periodical harvest of plant biomass and replacement of sediments are required to maintain well-functioning systems. The harvested plant biomass can be properly managed to create economic values for being applied as fertilizers or animal feeds, if no other contaminants preclude it.

18.4 Affecting Factors During Field Phytoremediation

Phytoremediation is a plant-based technology for managing Se in seleniferous soils. Although field studies are essential for the development of sustainable and resilient phytoremediation strategies for soil and water remediation, field research and field data remain limited nowadays. The implementation of phytoremediation technologies requires the integration of a broad range of knowledge, such as the fate and transport of Se, plant behaviors and responses, sustainable agronomic practices for long-term crop production, etc. Under field conditions, the major factors that may affect the performance of Se phytoremediation include (i) selected plants for phytoremediation, (ii) agronomical practices for crop production, (iii) unwanted consumption of Se-accumulating plants, (iv) water management strategies for less effluent generation, (v) the presence of competing ions against Se uptake, (vi) soil salinity, (vii) the presence of toxic compounds at high concentrations, (viii) adverse climatic and weather conditions, and (9) community acceptance of phytoremediation. The most frequently encountered factors have been discussed further in this section.

18.4.1 Plant Selection for Se Phytoremediation

The efficacy of Se phytoremediation is largely dependent on the plants selected or bred for field applications. As shown in Table 18.1, the accumulation capacity of plants may vary significantly, as well as the growth patterns of these plants. To optimize cost-effectiveness of phytoremediation technologies, crop cultivation techniques and transgenic technologies are often used. For instance, the black rice (Jinlong No.1) cultivated by Chinese researchers could accumulate up to 6.5 mg/kg DM of Se, and the black wheat cultivated by another Chinese group was able to accumulate 112.8% additional Se compared with normal species (Wang et al. 2013; Wu et al. 2015). Recent developments in gene engineering techniques have made it possible to improve the capabilities of non-accumulator plants in terms of selenium uptake and accumulation. For example, the introduction of selenocysteine methyltransferase gene of *Astragalus bisulcatus* (two-grooved poison milkvetch) into *Arabidopsis thaliana* (Thale cress) enabled the overexpression of Se-methylselenocysteine and γ-glutamyl methylselenocysteine in the shoots of the latter, thus increasing its accumulation of Se (Sors et al. 2005). In addition, Se-relevant genes in *Arabidopsis thaliana* has also been mutagenized to enhance the efficiency of the breading of Se-enriched crops, during which genetic engineering served as a supplementary technique to breeding (Pilon-Smits and LeDuc 2009).

18.4.2 Crop Rotation in the Field

In order to maintain constant biomass production, reduce plant diseases (e.g., Alternaria black spot, Rhizoctonia root rot, Fusarium, etc.) and mitigate insects and weeds, rotations among different phytoremediation crops under field conditions should be considered as part of the phytoremediation strategies. Crop rotations may also enable deeper site cleanup through Se phytoextraction from different zones of the soil profile. In Se-sensitive areas, selected crops should be tried in rotation with other agronomic crops (e.g., tomatoes, cotton, wheat, etc.) for long-term maintenance.

18.4.3 Predators Frequenting Crops and Soils

In agricultural regions, it is particularly important to identify insects frequenting crops and soils during Se phytoremediation, especially with flowering plant species such as Indian mustard and birdsfoot trefoil as they tend to attract more potential predators, which could be harmful or beneficial to other crops growing nearby. The biological cycle of Se should be monitored in long-term field phytoremediation. Bioaccumulation and biomagnification may occur in the food chain. There are several factors that may affect bioaccumulation, including the bioavailability of Se in soil, plant species, mobility of insects, and the feeding behavior of the food chain consumers. Many herbivores such as grasshoppers (*Dissosteria pictipennis* Brunner) can avoid consuming high Se plants, but predators of grasshoppers such as mantises (*Litaneutria minor* Scudder) often cannot avoid ingesting Se accumulated in their prey (Table 18.2). Therefore, high concentrations of Se in Se hyperaccumulator plants (e.g., *Brassica* plants) and the subsequent bioaccumulation by insects and animals may cause concerns considering the toxic effects of excess Se on birds and mammals that feed on insects (Banuelos 2000). In addition, plant seedlings may also be directly consumed by some animals such as ground squirrels that forage throughout the winter.

Table 18.2 Selenium concentrations detected in tissues of grasshoppers (*Dissosteria pictipennis* Brunner) and mantis (*Litaneutria minor* Scudder) from four different sites at Kesterson Reservoir

	Total Se in soil (mg/kg soil)	Extractable Se in soil (mg/L)	Se in grasshopper (mg/kg insect)	Se in mantis (mg/kg insect)
Site 1	0.60 ± 0.03	0.05 ± 0.02	1.2–9.8	9–22
Site 2	53.7 ± 17.5	0.72 ± 0.63	9.1–27.5	31–52
Site 3	0.10 ± 0.09	0.02 ± 0.01	3.7–7.0	10.2–18.0
Site 4	4.2 ± 2.3	0.16 ± 0.04	1.0–4.6	5.5–10.3

Adapted from Banuelos (2000)

18.4.4 Water Management Strategies

Water is necessary for plant growth in phytoremediation. Minimum irrigation water usage and maximum biomass production would contribute to the optimal cost-effectiveness of phytoremediation. Based on the data derived from a multiyear study, plant yields increased as more irrigation water was used up to the reference evapotranspiration (Banuelos 2000). The increased biomass production indicated that more Se could be extracted from the soil. If the same amount of biomass could be produced with less water, growers would be more likely to use phytoremediation rather than other conventional methods. In a study on the influence of field irrigation practices on biomass and Se accumulation of different plant species, it was found that irrigations increased the Se concentrations in plant tissues of *Brassica hyssopifola* Kuntze (summer weed) and *Melilotus indica* (winter weed). The growth of root systems is also known to be simulated by irrigation scheduling. Some plants are able to develop deeper roots in response to planned water deficits, thus being able to access bioavailable Se in the deeper subsoil horizons. In addition, water management in the field may also influence Se phytovolatilization and microbial activities in the soil.

18.5 Future Prospects

With a growing number of field investigations on Se phytoremediation, increasing evidence shows that many different plant species have the genetic potential to remove Se from contaminated soils. To optimize the performance of Se phytoremediation, it is critical to identify Se accumulators and hyperaccumulators in phytoremediation research. As an emerging technology, field research on Se phytoremediation, despite its importance in developing sound phytoremediation strategies, is still in the nascent stage. An integrated approach needs to be adopted for future field studies on Se phytoremediation, and such an approach shall balance factors such as crop selection, crop rotation, irrigation, water management strategies, chemical and mineralization in soils, pest control, harvest strategies, biomass usage, economic viability, and social acceptance (Banuelos 2000). Long-term field studies that are conducted to evaluate the performance of phytoremediation in removing Se from soils and reducing Se in drainage effluent should be encouraged. In addition, biomass generated could be considered for biochar production and/or hydrogel synthesis (Li and Chen 2020).

With the continuous advances in gene engineering, new genes and proteins from Se accumulators and hyperaccumulators that promote Se tolerance, accumulation, and volatilization can be discovered and introduced to high-biomass crops. However, before launching large-scale applications of transgenic plants for Se phytoremediation, their potential ecological implications (e.g., impacts on ecosystems, pollinators, herbivores, food chains, and microbial activities) should be carefully discussed and weighed against the cons and pros of other alternatives.

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Chapter 19
Selenium in Food Chain in Relation to Human and Animal Nutrition and Health

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19.1 Introduction

Selenium (Se) was discovered in 1817 by Swedish chemist J. Jacob Berzelius, who was investigating the cause of the sudden illness that occurred in the majority of sulfuric acid production factory workers. It was understood that the by-product, which was released during the production of sulfuric acid, was an element that has not yet been defined. This element was named Se, derived from the Greek word “selene,” which means goddess of the moon. Its importance was emphasized in 1957, and its role in human and animal health began to be investigated in the 1960s (Baltaci et al. 2016; Gupta and Gupta 2017). Se is found in soil, water, rock, lake, ocean, atmosphere, and biosphere in different proportions, and its distribution between countries also varies considerably (Ren and Guo 2004). Therefore, the endogenous level of Se, an essential element naturally found in the body, is affected by both geographical region differences and age group differences in the same region (Park et al. 2011; Rayman 2012). The difference of Se from other semimetals is that it is incorporated into proteins by a common translation mechanism as part of the 21st amino acid, selenocysteine (SeCys) (Kryukov et al. 2003; Papp et al. 2007). There are about 100 selenoprotein families known so far. The functional properties of only a few of the 25 selenoproteins identified so far in humans have been elucidated. The main function of many selenoproteins, such as glutathione peroxidase (GPx), thioredoxin reductase (TrxR), and iodothyronine deiodinases (DIOs), is to regulate the redox mechanism and prevent oxidative damage (Tinggi 2008). While oxidative stress may be the main factor underlying many health problems, it can also appear due to diseases. For this reason, especially in recent years, it has been emphasized how important it is to use Se supplements to strengthen antioxidative defense. Although its biochemical functions have not yet been fully elucidated, it

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M. A. Hossain et al. (eds.), *Selenium and Nano-Selenium in Environmental Stress Management and Crop Quality Improvement*, Sustainable Plant Nutrition in a Changing World, https://doi.org/10.1007/978-3-031-07063-1_19

has been revealed that Se deficiency is associated with the formation of many health problems such as neurodegenerative diseases (Aaseth et al. 2016; Varsi et al. 2017), diabetes (Solovyev et al. 2019), cardiovascular diseases (Kuria et al. 2020a), cancer (Vinceti et al. 2018; Kuria et al. 2020b), Keshan disease (Alehagen et al. 2016), immune system weakness (Huang et al. 2012). Regarding the world-threatening COVID-19 pandemic, Se has been found to be resistant to RNA viruses and chronic inflammatory conditions. For this reason, it has been suggested that adequate Se intake may effectively prevent the new coronavirus SARS-CoV-2 and may alleviate the course of the disease (Alexander et al. 2020). The levels of Se in the body, whose toxicity causes many health problems up to death, are primarily regulated by urinary excretion.

19.2 Selenium in Animal Tissue

Products such as meat, milk, and eggs of animals fed with foods high in Se contain high levels of Se; on the other hand, the element concentration of the products of animals fed with low Se content is low. Therefore, the total amount of Se in the animal reflects the Se content of the foods they consume (Combs and Combs 1986a). Less Se accumulates in the muscles than in other organs. The main chemical form of Se is selenomethionine (SeMet) in plant foods and is SeCys in animal tissues. Distribution, absorption, and excretion of Se in the body mainly depend on its total amount in the diet and its chemical form. In addition, the amount of Se taken depends on the vitamins, heavy metals, and sulfur components in the food (Underwood 1977).

19.2.1 Absorption, Metabolism, and Excretion of Selenium

All forms of Se, organic and inorganic, are readily absorbed, mainly in the lower end of the small intestine. Studies conducted in experimental animals and humans have shown that the absorption of Se is around 80%. The absorption of organic compounds is higher than inorganic compounds. The absorption of SeMet from the gastrointestinal tract is over 90%, while that of selenite is around 60% (Stewart et al. 1987). The absorption of Se varies depending on whether it is taken with food or taken alone as an organic or inorganic supplement (Sirichakwal et al. 1985). As in humans, the absorption of Se in animals depends on many factors other than its chemical form. For example, vitamins A and E and protein increase the absorption of Se; vitamin C, mercury, arsenic, and sulfur reduce the absorption (Fairweather-Tait 1997). Se taken into the body is transported from the intestine to the liver in the blood. It is reduced to selenide and binds to α- and γ-globulins in target tissues and various organs. It is then included nonspecifically as SeMet and specific selenoproteins as SeCys (Linder 1988).

There is uncertainty about the transport mechanisms of dietary Se across the intestinal epithelial membrane. However, it is known that the absorption of selenate occurs via a sodium-mediated carrier transport mechanism shared with sulfur, while selenite uses passive diffusion (Fairweather-Tait 1997). Absorption of SeMet occurs by competition between methionine and its seleno analog. In contrast, inorganic forms of Se compete with inorganic sulfur compounds for absorption (McConnell and Cho 1965). Although there is evidence that the enteric absorption of seleno-amino acids other than SeMet is not active and physiologically controlled, the mechanisms are unclear. The findings indicate SeCys transport across the duodenal wall does not proceed against a concentration gradient and is not inhibited by cysteine. There is some evidence that there is no physiological or homeostatic control of the enteric absorption of inorganic or organic Se. However, there is no supporting explanation that SeCys can be actively transported in humans by the exact transport mechanism used by the sulfur analog (Barbezat et al. 1984). Of the multifunctional anion exchangers known to carry sulfur, the SLC26 gene family members also mediate the transport of inorganic Se to the intestinal brush border (Mount and Romero 2004).

Se is mainly stored in red blood cells, the heart, spleen, liver, tooth enamel, and nails. Although the most critical role in the excretion of Se is in the kidneys, the bile, pancreas, and intestine are other auxiliary organs. In addition, it is known that there is a small amount of Se excretion with sweating and hair loss (Linder 1988).

19.3 Absorption, Metabolism, Excretion, and Homeostasis of Selenium in Human

19.3.1 Absorption and Metabolism of Selenium

The absorption of dietary Se is still a research topic that has not received the attention it deserves and has not been fully elucidated. It is thought that Se absorption is not homeostatic and does not affect its bioavailability. The bioavailability of Se depends on its chemical form, which affects its intracellular distribution in the body. The intestinal absorptions of selenocompounds differ slightly from each other. This absorption rate also depends on individual parameters such as Se and health status, age, and gender (Burk and Hill 2009). The organic (SeMet and SeCys) and inorganic (selenites or selenates) selenocompounds are absorbed in the small intestine by methionine transporters and anion transporters, respectively. Studies in cell culture and living organisms have shown that almost any dietary selenocompound can be used to produce SeCys-bearing tRNA and thus for selenoprotein biosynthesis (Takahashi et al. 2017). Selenoamino acids carried by the B^0 amino acid transporter follow a transcellular pathway similar to their sulfur-containing analogs. Se is found in the diet in the forms of selenite, selenate, SeMet, and SeCys (Gammelgaard et al.

2011). Although the absorption of selenate, SeMet, and SeCys is very efficient (70–90%), the absorption of selenite is less efficient (around 60%) (Vindry et al. 2018).

SeMet is the main chemical form of Se in the human diet. It is absorbed in the same sodium transport system as methionine and is metabolized in the liver in the same way as methionine (Schrauzer 2000). The majority of SeMet-containing proteins are produced both within the cell and in the circulation. It is estimated that about 1 in 8000 methionines in a well-supplied individual is replaced by a SeMet residue (Burk et al. 2001). SeMet must be converted to SeCys before it becomes a source of selenide, but Se from exogenous SeCys is released directly as a selenide. The metabolism of inorganic and organic forms of Se in the body is different, but selenide (H_2Se) is the end product for both metabolic transformations. It is used directly as Se donors to synthesize selenoproteins and is absorbed by unmediated passive diffusion. Se is reduced to selenite via selenodiglutathione (GS–Se–GS) using glutathione reductase and nicotinamide adenine dinucleotide phosphate (Combs and Gray 1998; Pilon-Smits and Quinn 2010). In other words, selenite is stimulated by reduced glutathione in the gut to form GS-Se-GS and be further assimilated by the gastrointestinal tract. Selenate, which follows the extracellular pathway to cross the intestinal barrier, is then reduced to selenite. It is still unclear whether the transit of selenite through enterocytes is extracellular or intracellular (Vindry et al. 2018).

19.3.2 Excretion of Selenium

The biological half-life of Se in the body is estimated to be about 100 days (Griffith et al. 1976). Actual retention times depend on the state of Se present, the level of Se intake, the specific form of the element ingested, the composition of the diet, and the health status of the organism exposed to Se. Se is excreted from the body in different ways: in the urine through the kidneys, in the feces from the gastrointestinal tract, in expired air through the lungs, and through loss of hair and skin cells. The rates and amounts of each type of excretion depend on the level and form of the element in the diet (Beath et al. 1934). Several studies of Se excretion have been performed in animals with a single dose of ^{75}Se tracer. These studies demonstrated that urinary ^{75}Se excretion was directly related to Se intake, but not fecal ^{75}Se. Breath ^{75}Se excretion became important only with the intake of large amounts of Se. Thus, in light of previous studies, it has been determined that the urinary tract is the primary pathway for regulating whole-body Se under physiological conditions, and expiration is significant under potentially toxic conditions (Pedrosa et al. 2012).

19.3.2.1 Urinary Excretion of Selenium

The urinary tract is the predominant excretion route for Se in humans (Yang et al. 1989). Fifteen to twenty percent of all ingested Se is excreted by the kidneys within a few days (Pedrosa et al. 2012). The urinary excretion rate of Se depends on the level of intake in the diet. When the amount of Sein the diet increases, the level of Se excreted in the urine increases. When fed a diet low in Se, the urinary Se level is halved or less (Robinson et al. 1973; Thomson and Robinson 1986). These findings highlight the importance of the renal system in regulating intrabody Se levels. The most common Se metabolite in humans is trimethylselenonium ion (TMSe). Based on the result of improved analytical methods, it is believed that TMSe is not an important component of human urine under normal conditions. However, several studies have reported that TMSe is the main form of Se in the urine and may be a biomarker of too much Se intake (Suzuki et al. 2005). TMSe production increases with increased Se intake, and TMSe production promotes urinary excretion of Se. TMSe is responsible for up to 50% of the total Se normally present. In another study, it was reported that TMSe is not found in all urine samples, and there may be a genetic variation affecting its elimination. The main determinant of TMSe formation is the INMT gene on chromosome 7, and therefore urinary excretion of TMSe varies significantly between both individuals and populations (Kuehnelt et al. 2015). Although all these findings are still under investigation, it is thought that the previously accepted pathways regarding TMSe, the end product of excretion, may need to be reevaluated (Kuehnelt et al. 2005). Many different chemical forms of Se are determined in the urine, including SeMet, SeCys, selenite, selenate, and selenocholine (Robinson et al. 1985). Recently, selenosugars (Se-containing carbohydrates) have been found in the urine of rats fed selenite. The three selenosugars found in human urine are selenosugar 1 (methyl-2-acetamido-2-deoxy-1-seleno-β-D-galactopyranoside), its analog selenosugar 2 (methyl-2-acetamido-2-desoxy-1-seleno-β-D-glucopyranoside), and its deacylated analog selenosugar 3 (methyl- 2-amino-2-deoxy-1-seleno-pD galactopyranoside) (Kobayashi et al. 2002). The most important of these carbohydrates, which are the main elimination products of Se, is selenosugar1 (Kuehnelt et al. 2005; Gammelgaard et al. 2012). The major urinary form of Se is 1β-methylseleno-*N*-acetyl-D-galactosamine, a monosaccharide derivative and organoselenium compound (Kobayashi et al. 2002).

19.3.2.2 Fecal Excretion of Selenium

Fecal Se involves considerably unabsorbed dietary Se, along with Se found in intestinal, pancreatic, and biliary secretions (Levander and Baumann 1966). According to the research conducted with mice, the fetal excretion rate is 20% when fed with sufficient dietary Se and is 30% at moderately high Se intake. At moderately high Se intake, fecal Se excretion plateaued. Se taken in large amounts did not cause a change in the amount of stool, but it increased urinary excretion. This suggests that the fecal and urinary excretion mechanisms are different and that fecal Se excretion is negligible in excessive dietary Se intake (Pedrosa et al. 2012).

19.3.2.3 Pulmonary Excretion of Selenium

Another route of excretion is the elimination of the dimethyl selenide (DMSe) form by breathing. Pulmonary excretion of Se is mainly essential in excessive Se intake. In a study investigating the kinetics of DMSe, 300 μg of ^{77}Se as selenite was administered to a subject. It was found that 11% of the dose given in the form of DMSe was exhaled within 10 days (Kremer et al. 2005). Excess Se, which is detoxified by consecutive methylation, forms volatile DMSe and other methylated species. DMSe causes a garlic-like odor on the breath to indicate Se intoxication (McConnell and Roth 1966).

19.3.2.4 Selenium Excretion Through Hair and Nails

Although it is not very important in terms of homeostasis, excretion with hair and nails is one of the excretory pathways. Many researchers use Se levels in hair and nails to measure the body's assessment of total Se (Chen et al. 1980). This practical and noninvasive method is also suitable for evaluating chronic Se exposure (Longnecker et al. 1996).

19.3.3 Selenium Homeostasis

The rate of accumulation of Se in tissues varies as 30% in muscle, 30% in liver, 15% in kidney, 10% in plasma, and 15% in other tissues. SeMet reserves firstly maintain Se homeostasis in the liver and kidney (Mistry et al. 2012). Stored Se is used when food intake of Se is not sufficient for selenoprotein synthesis (Schrauzer 2000).

19.4 Selenoproteins

Se is a fundamental component of selenoproteins, which play an essential role in several biological functions such as thyroid hormone metabolism, immune function, reproductive health, and DNA synthesis. It also acts as an antiaging and protective against cancer by playing a role in antioxidant defense (Cabaraux et al. 2007; Suttle 2010). The human genome includes 25 genes for selenoproteins. In 25 mammalian genes, 30 selenoproteins have been defined in the last years, but the function of about 50% of them is not yet known (Mostert 2000; Kryukov et al. 2003; Lazard et al. 2017).

Selenoproteins with known enzyme function are named according to these functions, as before: GPx1–4 and GPx6 (glutathione peroxidases), SEPHS2 (selenophosphate synthetase 2), MSRB1 (methionine sulfoxide reductase B1), DIO1–3 (iodothyronine deiodinase 1–3), and TXNRD1–3 (thioredoxin reductase 1–3) (Mariotti et al. 2012). Selenoproteins with no known function were formerly named as selenoprotein followed by a letter, e.g., selenoprotein P. They are now often characterized by the root SELENO followed by the same letter, for example, SELENOP for selenoprotein P (Gladyshev et al. 2016).

19.4.1 Glutathione Peroxidase

Glutathione is one of the most abundant thiols in cells and is the primary reducing agent of glutathione peroxidase enzymes. Glutathione peroxidases (GPx) are from a family of antioxidants. They are selenoenzymes that break down lipid and hydrogen peroxides inside and outside the cell by using glutathione as a substrate. There are eight members of GPx identified in rodents and humans, which are characterized by similar properties but differ in their sites of action and chemical forms (Brigelius-Flohe and Maiorino 2013). Five of these are selenoproteins (i.e., GPx1–4, GPx6), while the remaining three (GPx5, GPx7, and GPx8) are cysteine-containing (Guillin et al. 2019). By controlling hydroperoxide levels, GPXs assist in many cellular processes such as detoxification, maintenance of the integrity of cell membranes, cell signaling, and oxidative protein folding (Brigelius-Flohe and Flohe 2017).

19.4.1.1 Glutathione Peroxidase-1

Glutathione peroxidase-1 (GPx1) was the first GPx enzyme, and the first selenoprotein identified (Mills 1957; Rotruck et al. 1973). GPx1 is a cytosolic protein highly expressed in the liver, lung, kidney, and erythrocytes and is widely found in the body. It is the enzyme whose main activity is antioxidant and first affected by Se deficiency (Flohé 1989; Fairweather-Tait et al. 2010). It plays a role in the regulation of lipid metabolism. As the only member expressed in erythrocytes, it effectively scavenges hydrogen peroxide (H_2O_2) and protects them from oxidative stress. It is responsible for the regulation of redox homeostasis in the liver (Tan et al. 1984). Mice overexpressing GPx1 have increased obesity, hyperglycemia, hyperinsulinemia, and insulin resistance (McClung et al. 2004). It has been shown that GPx1 overexpression causes chronic hyperinsulinemia by regulating pancreatic insulin production and secretion (Wang et al. 2008). GPx1 mediates many effects on glucose metabolism by acting directly on pancreatic β-cells (Huang et al. 2018).

19.4.1.2 Glutathione Peroxidase-2

Glutathione peroxidase-2 (GPx2), first described in 1993, is from the family of hydroperoxide-reducing thiol peroxidases. It has a 65% sequence homology with GPx1. Both are homotetrameric proteins with the same kinetic and substrate properties; however, GPx2 is assumed to have a stronger preference for organic hydroperoxides (Chu et al. 1993). While GPx1 levels decrease rapidly in Se deficiency, GPx2, prior and predominant among other selenoproteins, is kept relatively constant (Wingler et al. 1999; Brigelius-Flohé et al. 2001). It is predominantly expressed in the epithelium of the whole gastrointestinal tract and human liver (Chu et al. 1993). GPx2 is epithelium-specific with a dominant expression in the epithelial layer of the gastrointestinal tract additionally in the bladder, lung, and breast epithelium (Komatsu et al. 2001; Cho et al. 2002). It was suggested that GPx2 acts as a barrier against the absorption of bacteria-induced or food-borne hydroperoxides due to its specific localization in the gastrointestinal tract (Chu et al. 1993; Chu and Esworthy 1995). This allegation was also proven in the cell culture model (Wingler et al. 2000).

GPx2 expression is also subject to Wnt regulation, involved in numerous cellular processes (e.g., body axis patterning, cell fate specification, cell proliferation, and migration), especially during embryogenesis, tissue regeneration, and cell proliferation (Kipp et al. 2007, 2012). The expression of GPx2 in the intestinal epithelium varies according to localization. GPx2 decreases progressively from the ground to the lumen surface in crypts of the rectum and colon. GPx2 was distributed on an equal basis in crypt ground, whereas it was more concentrated in cells at the luminal surface and in structures capping the nuclei at the apical pole (Florian et al. 2001).

In an experimental study, low Se levels in rats promoted carcinogenesis in the early stages of tumor development. However, it has been suggested that even after Se supplementation, it does not stop the progression of the tumor (Yang et al. 2012). Therefore, there is a need to elucidate the mechanisms of selenoproteins before advocating the anticancer properties of Se. Although it has been discussed since ancient times that low Se levels may cause the development of many different types of cancer (Shamberger and Frost 1969; Medina and Shepherd 1981), there is an opinion that excessive secretion of certain selenoproteins is also effective in the growth of cancer. Minimum three selenoproteins named thioredoxin reductase 1, selenoprotein 15, and GPx2 are known to combine tumor-promoting and tumor-suppressing functions. The dual role of GPx2 during carcinogenesis has been extensively analyzed in mice and cancer cell lines (Kipp and Muller 2015).

GPx2 was found to be upregulated in various types of inflammation and some epithelium-derived tumors (Mörk et al. 2003; Chiu et al. 2005). GPx2 expression increases in many tumors of epithelial origin. Moderately differentiated colorectal tumors (Banning et al. 2008), colorectal adenocarcinomas (Murawaki et al. 2008), ductal mammary carcinomas (Naiki-Ito et al. 2007), squamous cell carcinomas (Walshe et al. 2007), and adenocarcinomas of the lung (Woenckhaus et al. 2006) are some examples for tumor kinds which lead to excess GPx2 expression. Additionally, GPx2 is highly expressed in prostate tumors (Naiki et al. 2014) and hepatocellular carcinomas (Suzuki et al. 2013).

19.4.1.3 Glutathione Peroxidase-3

Glutathione peroxidase-3 (GPx3) is an extracellular protein secreted into plasma after synthesized in renal proximal tubule cells (Whitin et al. 2002; Olson et al. 2010). It is transported through a plasma to tissues associated with the bronchi, intestinal epithelium, and membranes of type II pneumocytes (Burk et al. 2011). The kidneys act as a local pool for Se (Malinouski et al. 2012), and the pool accounts for roughly 20% of circulating Se (Burk and Hill 2005). GPx3 is expressed in the early stage of the placenta, where it is necessary to decrease H_2O_2 during the duration of decidualization (Xu et al. 2014). Besides this, the epididymis is the other tissue expressing from GPx3, which is excreted into its lumen. By catalyzing the reduction of hydrogen peroxides required for thyroid hormone synthesis, GPx3 protects the thyroid gland cells, thyrocytes against peroxidative damage (Beckett and Arthur 2005). GPx3 is one of the most highly expressed selenoproteins in the thyroid gland. Although it has been suggested that GPx3 may play a role in the polymerization of colloidal thyroglobulin, further studies are needed to elucidate the mechanism (Schmutzler et al. 2007). TXN and GRX are alternative reducing substrates of GPx3 besides glutathione (Maiorino et al. 2007). In addition, serum GPx3 levels were high in two different studies conducted in patients with metabolic syndrome without type 2 diabetes (Baez-Duarte et al. 2014) and in obese or overweight patients (Baez-Duarte et al. 2012). In studies with mice, it has been observed that loss of GPx3 increases platelet activation and delays bleeding time, thus increasing thromboembolism and causing large brain infarcts (Jin et al. 2011).

19.4.1.4 Glutathione Peroxidase-4

Glutathione peroxidase-4 (GPx4), initially called “phospholipid hydroperoxide glutathione peroxidase,” was purified from pig liver and characterized as lipid peroxidation inhibiting enzyme (Ursini et al. 1982). GPx4 leads to three different isoforms called mitochondrial, nuclear, and cytosolic GPx4 to initiate alternative transcription (Moreno et al. 2003). Cytosolic GPx4 is expressed in the liver, lung, brain, and kidney; nuclear GPx4 is expressed in testes and mitochondrial GPx4 sperm cells (Fradejas et al. 2015). The cytosolic isoform of GPx4 has been recognized as the main regulator of regulated necrotic cell death called ferroptosis (Yang et al. 2014). In contrast to cytosolic GPx4, mitochondrial and nuclear isoforms are almost entirely expressed in different spermatogenic cells, conferring specific functions there (Conrad et al. 2005; Puglisi et al. 2012). Mitochondrial GPx4 contributes to the formation of the mitochondrial capsule by oxidizing and so polymerizing mitochondrial capsular proteins. Thus, the complete rigidity and stability of the spermatozoan midpiece are ensured (Maiorino et al. 2005; Schneider et al. 2009). The nuclear isoform of GPx4 performs the same function, except that its target protein is protamine (Conrad et al. 2005).

Although GPx4 shares common features with GPx members, they are structurally, functionally, and biochemically quite different. GPx4 is monomeric, thus reducing complex peroxides in lipids, including cholesterol and phospholipid hydroperoxides, regulating the activity of cyclooxygenases and lipoxygenases (Conrad 2009; Brigelius-Flohé and Maiorino 2013). GPx4, the only enzyme that can detoxify complex hydroperoxides in membrane compartments most effectively, is required to prevent lipid peroxidation-induced cell death in vivo and in vitro (Seiler et al. 2008). GPx4 is effective in regulating the 5- and 15-lipoxygenase pathways (Fairweather-Tait et al. 2010).

The increased expression of GPx4 can protect against DNA damages by oxidation, oxidative stresses, and also carcinogenesis (Zhuo and Diamond 2009). Overexpression of GPx4 was observed to protect mice from liver damage by reducing oxidative stress and apoptosis (Ran et al. 2004). Mitochondria-specific overexpression of GPx4 protected mice from ischemia/perfusion-induced cardiac dysfunction (Dabkowski et al. 2008). This also prevents protein loss in cardiac mitochondria as associated with type 1 diabetes, allowing the heart to function properly (Baseler et al. 2013). GPx4 has a powerful cytoprotective function in neurons of different parts of the brain, such as the cerebellum, cortex, and hippocampus (Hambright et al. 2017), hepatocytes (Carlson et al. 2016), motor neurons (Chen et al. 2015), renal tubular cells (Friedmann Angeli et al. 2014), endothelium (Wortmann et al. 2013), and photoreceptor cells (Ueta et al. 2012). GPx4 is necessary for the continuation of life, and its function cannot be performed by any other protein (Ran et al. 2004).

19.4.1.5 Glutathione Peroxidase-6

Homotetrameric glutathione peroxidase 6 (GPx6) is a close homolog to GPx3. It is a selenoprotein in humans but a cysteine-containing enzyme (CysGPx) in rodents and other species (Kryukov et al. 2003). It is thought that CysGPx is the ancestral form of GPxs due to phylogenetic analysis (Toppo et al. 2008). It is expressed on the cytosol of the olfactory epithelium. The fact that GPx6 has not been purified yet and the lack of kinetic analyzes causes insufficient information about it, including the olfactory system (Dear et al. 1991; Tanaka et al. 2012). It performs the functions of detoxification of reactive oxygen species (ROS) (Fradejas et al. 2015).

In the study, which was carried out to examine the phenotype of hereditary and common neurodegenerative Huntington's disease, a synthetic lethal screening methodology called SLIC was developed for the mammalian central nervous system. By application of SLIC, the GPx6 gene was identified as a modulator of mutant Huntington toxicity. It was determined that overexpression of GPx6 can significantly attenuate both behavioral and molecular phenotypes in a mouse model of Huntington's (Shema et al. 2015).

19.4.2 Iodothyronine Deiodinases

The iodothyronines deiodinases (DIOs) with catalytic properties are divided into three different groups: type I, II, and III (DIO1, DIO2, and DIO3, respectively) (Dentice and Salvatore 2011). DIO1 is found in the plasma membrane of the thyroid, kidney, and liver; has both inner and outer ring deiodination activities; and is powerfully inhibited by propylthiouracil. DIO1 can convert T4 to T3 or rT3 and T3 to T2 and uses rT3 as a substrate (Bianco et al. 2002). DIO2 is expressed in the endoplasmic reticulum of the brain, muscle, pituitary; catalyzes only outer ring deiodination; and converts T4 to T3, activating the iodothyronines. DIO3 is found in the plasma membrane of the brain, skin, placenta; it can inactivate the iodothyronines by inner ring deiodination and catalyzes the degradation of T4 to rT3 and T3 to T2 (Fekkes et al. 1982; Bianco et al. 2002). According to the results of the studies investigating the effects of thyroid on bone metabolism and development, DIO1 was not detected in bone cells; DIO2 activity was determined in osteoblasts, and DIO3 activity was determined in osteoblasts, osteoclasts, and chondrocytes. While DIO3 is expressed during prenatal development, expression of DIO2 begins postnatally and continues throughout life to guarantee an euthyroid skeleton (Capelo et al. 2008; Williams et al. 2008).

19.4.3 Selenoprotein P

Selenoprotein P (SelP) plays a role in transporting Se to tissues (Gammelgaard et al. 2011). SelP contains about 60% of plasma Se, depending on the amount of Se in the body (Akesson et al. 1994; Burk et al. 2001; Perrone et al. 2015). It is an extracellular glycoprotein synthesized in the liver, an important organ for Se homeostasis, and highly expressed in the brain and testicles (Fairweather-Tait et al. 2010). The only selenoprotein with more than one SeCys residue in its sequence is SelP. It can contain approximately 10 SeCys residues, with the C-terminal domain a maximum of 9 and the N-terminal domain one (Saito et al. 2004). It is also an antioxidant that scavenges the peroxynitrite radicals caused by the reaction of superoxide ions with nitric oxide (Ducros and Favier 2004).

19.4.4 Thioredoxin Reductase

Thioredoxin reductase (TrxR or TXNRD), a mammalian selenoprotein, is oxidoreductase required for NADPH-dependent reduction of endogenous cofactors such as thioredoxin or glutathione (Lee et al. 2013). Isoforms of TrxR support the cellular functions of various thioredoxin (Trx) proteins by keeping active site disulfides in the reduced dithiol state using NADPH (Urig and Becker 2006; Lee et al. 2013).

These enzymes were found to evolve from glutathione reductases and are located at the penultimate C-terminal of Sec (Gladyshev et al. 1996; Tamura and Stadtman 1996). There are three different isoenzymes of TrxR: TR1, TR2, and TR3. TR1 is a cytosolic and nuclear protein whose main function is to control reduced thioredoxin status. TR1, whose main function is to control reduced thioredoxin status, is a cytosolic and nuclear protein that exhibits broad substrate specificity (Arnér and Holmgren 2000). Thioredoxin/glutathione reductase (TGR, TR2, or TrxR3) is a protein with an additional N-terminal glutaredoxin domain, unlike other animal thioredoxin reductases (Sun et al. 2001). TR2, a close homolog of TR1, can catalyze many reactions specific to the thioredoxin and glutathione systems. It is a testis-specific thiol regulator (Urig and Becker 2006) and has been associated with the formation and isomerization of disulfide bonds in the sperm maturation phase (Su et al. 2005). TR3, which is involved in the control of ROS levels, keeps thioredoxin and glutaredoxin 2 in a reduced state. It plays an active role in regulating mitochondrial redox homeostasis and cell signaling (Prasad et al. 2014). TR1 and TR3 are essential proteins required for embryonic development in mammals (Conrad et al. 2004; Jakupoglu et al. 2005). The main important cellular functions of the Trx system are the promotion of cell viability and replication, inhibition of apoptosis, cell growth factor in DNA synthesis, antioxidant defense systems, and redox modulation of signaling pathways (Nordberg and Arnér 2001; Rundlöf and Arnér 2004; Arnér and Holmgren 2006; Arnér 2009).

19.4.5 Other Selenoproteins

Table 19.1 summarizes the localization and main functions of selenoproteins.

19.5 The Role of Selenium on Animal Health

The biological importance of Se and its discovery as a nutritional factor stemmed from studies conducted in Europe on brewer's yeast during World War II. Se is a toxin blamed for poisoning farm animals, and successive discoveries regarding its biological role in living organisms have proven that it can pose a severe economic threat to agriculture. While Se compounds are thought to be carcinogenic, it has been reported that Se may protect against liver necrosis in rats (Schwarz and Foltz 1957). It was subsequently found that economically important farm animals such as turkeys, chickens, sheep, pigs, and cattle are sensitive to changes in Se content. It has been reported that Se can control exudative diathesis (ED), growth depression, and death in chickens. It has been found that some diseases in cattle and sheep can be controlled by Se. Se given to pigs has been reported to positively increase farm yield percentages (Patterson et al. 1957; Levander 1986; Oldfield 2003). Se supplementation has been shown to provide effective results in disease states that do not

Table 19.1 Human selenoproteins and their functions

Protein	Localization	Functions	References
Methionine-R-sulfoxide reductase (MsrB1)	Nucleus and cytosol	Catalyzes repair of the R-enantiomer of oxidized methionine residues with thioredoxin as reductant	Epp et al. (1983) and Ren et al. (1997)
(MsrB2 and MsrB3)	Mitochondria, cytoplasm, and endoplasmic reticulum		
Selenoprotein 15 kDa (Sep15)	Endoplasmic reticulum	A sensor and quality control of protein folding; redox functions; protects secretory cells against development of carcinoma	Behne et al. (1997), Fairweather-Tait et al. (2010) and Suttle (2010)
Selenoprotein N (SelN)	Skeletal muscles, placenta, brain, lung, endoplasmic reticulum	Muscle development; cell proliferation; calcium homeostasis; redox signaling	Arbogast and Ferreiro (2010)
Selenoprotein W (SelW)	Skeletal muscles, brain, heart, prostate, colon	Muscle development; calcium-binding; antioxidant in human lung cancer cells; protects the developing myoblast	Yao et al. (2013) and Li et al. (2018)
Selenoprotein S (SelS)	Endoplasmic reticulum, plasma membranes	Eliminates the misfolded proteins from endoplasmic reticulum; regulates the inflammation and immune response	Curran et al. (2005) and Cox et al. (2013)
Selenoprotein K (SelK)	Endoplasmic reticulum, heart, spleen, immune cells	Possible antioxidant and development activity; regulates immunity and cancer	Liu et al. (2012) and Marciel and Hoffmann (2019)
Selenoprotein V (SelV)	Testes	Protects oxidative injury and endoplasmic reticulum stress	Zhang et al. (2020)
Selenoprotein M (SelM)	Brain, lung, kidney, neuronal cells, endoplasmic reticulum, perinuclear region, Golgi	Antioxidant activity; protein folding	Papp et al. (2010), Pitts et al. (2013) and Jiang et al. (2019)
Selenoprotein H (SelH)	Brain, spleen, nucleus	Transcription factor; increases the cell viability; regulates the glutathione synthesis	Mehta et al. (2013) and Cox et al. (2016)
Selenoprotein T (SelT)	Ubiquitous	Regulator of endoplasmic reticulum homeostasis; tissue development and homeostasis; plays specific functions in endocrine cells; exerts regenerative and neuroprotective actions	Anouar et al. (2018)

(continued)

Table 19.1 (continued)

Protein	Localization	Functions	References
Selenoprotein O (SelO)	Mitochondria	Redox control	Han et al. (2014)
Selenium binding protein (SBP1)	Golgi	Protein degradation; intracellular transport; cell differentiation; cellular motility; redox modulation	Otsuka et al. (2015) and Elhodaky and Diamond (2018)
(SBP2)	Ribosomes		
Selenophosphate synthetase 2 (SPS2)	Liver, kidney, testis, cytoplasm	Selenoprotein biosynthesis	Tamura et al. (2004)
Mitochondrial capsular selenoprotein (MCSeP)	Sperm mitochondrial capsule	GPx4 storage; protects sperm cells from oxidative damage	Ursini et al. (1999) and Ingold et al. (2015)

respond to other treatments and are often of unknown etiology. In the late 1950s, it was realized that Se added to the diets of rats and chicks could replace vitamin E to prevent liver, vascular, muscle, and hepatic lesions (Schwarz and Foltz 1957). Studies have confirmed that Se is a supplement to vitamin E and an essential nutrient.

19.5.1 Functions and Evaluation of Selenium in Animals

Se, an essential element in animal nutrition, must be taken in sufficient amounts with the diet. The concept of “Se status” is used to ensure that the biological functions of Se are maintained at the most appropriate level and indicate its adequate level in the body. The Se status of an organism reflects the Se level in the environment (Ahmed et al. 1998; Rederstorff et al. 2006). The primary source of Se for animals is soil, and it is found in the soil in the form of selenide, selenium sulfide, selenium sulfate, and selenium cyanate salts (Halilova 2008; Ullah et al. 2019). Even if there is enough Se in the soil, it is not in proper form, the pH of the soil is acidic, the mineral composition of the soil, and the amount of precipitation affect the transfer of Se to the forage crops grown there (Dabak et al. 2002). Se is found in all cells and tissues in the animal body. Its concentration varies depending on the tissue, Se level in the ration, and the chemical form of the element. The ration Se form also affects the Se concentration in the tissues (Underwood and Suttle 1999). Tissue and blood Se levels of animals that consume plants grown in Se-rich or poor soils as feed are also affected in parallel (Kucuk 2014). Animals fed low Se feeds accumulate relatively low amounts of the element in their tissues, products such as eggs and milk. In contrast, animals fed high Se feeds yield products with higher concentrations (Combs and Combs 1986b).

The status of the element Se depends on many factors such as dietary intake, absorption, excretion, and bioavailability (Ermidou-Pollet et al. 2005). After dietary intake, the bioavailability and toxicity of Se in humans and animals depend on its chemical form and concentration. Organic forms are more bioavailable and less toxic than inorganic forms (Ammar and Couri 1981; Spallholz et al. 1990). Other factors such as breed, age, health, and nutritional status can also affect the body's level of uptake and distribution. Se requirement can also be affected by the presence or absence of other nutrients and elements such as vitamin E, lipids, proteins, amino acids, copper, mercury, sulfur, arsenic, and cadmium (Hassan et al. 1990; Arthur et al. 1999; Cetin et al. 2002). It is an essential trace element that has important functions in the vascular endothelium, heart and skeletal muscles, blood cells, kidneys, and cellular membranes in animals and is necessary for the normal continuation of metabolism (Humann-Ziehank 2016; Mehdi and Dufrasne 2016). The biological function of Se in animals is realized by the selenoproteins found in the tissues. Se plays a role in the defense system as a part of enzymes such as glutathione peroxidase (GSHPx), iodothyronine deiodinase, and thioredoxin reductase (Burk et al. 2003; Fairweather-Tait et al. 2010). Selenoproteins take part in the immune system, reproduction, growth, and development functions in the body (Surai 2000). The basic chemical form of Se in animal tissues forms the prosthetic group of the GPx enzyme. Inorganic Se taken with the diet is absorbed as SeMet or SeCys by entering into the structure of amino acids produced by the rumen microflora. The amount of vitamin A, vitamin E, and ascorbic acid in the ration increases the absorption of Se (Combs and Combs 1984). One of the important duties of Se and vitamin E is to show an antioxidant effect (Surai 2000; Cetin et al. 2002). Se, which protects the cell membrane against oxidation from free oxygen radicals by forming enzymatic and nonenzymatic defense mechanisms, is an essential component of the antioxidant defense system of the organism (Hostetler et al. 2003). It is known that Se added to ruminant diets at different physiological stages strengthens the immune system, increases glutathione peroxidase enzyme activity, and is therefore effective against oxidative stress (Kucuk 2014).

Se exerts a synergistic effect by helping to retain vitamin E in plasma lipoproteins (Weiss et al. 1990; Mehdi and Dufrasne 2016). In animals, 87% of *selenious* acid is absorbed from the intestines and 97% from the lungs within 4 h after ingestion. On the other hand, elemental Se is absorbed 57% from the lungs and 50% from the intestines. Most circulating Se disperses into the plasma and passes to the tissues, while a significant portion of Se in the plasma is bound to proteins. Ingested Se accumulates in the liver, spleen, and kidneys at high concentrations and brain, muscle, and erythrocytes at low concentrations. The intake time of Se accumulates in high concentrations, first in erythrocytes and then in hair and nails (Floriañczyk 1999; Atessahin 2001).

19.5.2 Deficiency Symptoms of Selenium in Animals

In order to evaluate the effects of Se in animals, it is important to know the boundary between potentially toxic Se levels and the levels of Se necessary for healthy living (Combs and Combs 1986e). Knowing the diseases that may occur in the deficiency or excess of an element is very important in animal feeding strategies and losses in the livestock economy (Ahmed et al. 1998; Cetin et al. 2002). Se deficiency in farm animals is essential because it creates pathological changes that cause substantial financial losses every year. Se activity is determined by the amount and type of Se compounds present in the soil, plant species, climatic conditions, soil pH, and the content of Se antagonists such as arsenic, sulfur, and lead.

Diseases caused by Se deficiency mainly occur in areas where soils are acidic and rare compounds such as selenium sulfide are abundant. It has been reported that disease rates are higher after cold and rainy weather and in areas heavily fertilized with superphosphate and sulfur (Bednarek and Bik 1994). Se deficiency generally causes degenerative changes in animal tissues, reproductive disorders, growth defects, immune disorders, and increased susceptibility to cardiovascular diseases. Although the deficiency affects all animal species, ruminants, mostly lambs and goats, appear more susceptible. Exudative diathesis, pancreatic fibrosis, dystrophy, decrease in hatching rate and egg production, development and feathering disorders in poultry are the conditions observed in Se deficiency (Jianhua et al. 2000; Surai 2000; Cetin et al. 2002; Rederstorff et al. 2006; Fordyce 2013; Zheng et al. 2019). Se deficiency impairs fertility in the reproductive system, leading to the formation of ovarian cysts and increased embryonic mortality in the post-insemination period (Hemingway 2003; Palmieri and Szarek 2011). Se and vitamin E deficiency include white muscle disease, infertility, abortion, weak and premature or stillbirths, ovarian cysts, metritis, mastitis, delayed conception, estrus irregularity or latent estrus, and low fertility fertilization, diarrhea, and decreased immune response in cattle. Diseases have been reported to take shape (Wuryastuti et al. 1993; Puls 1994; Dabak et al. 2002).

In chickens, Se prevents disorders due to deficiency and improves meat or egg production characteristics. In recent years, organic Se, especially in yeast enriched with Se, has become widespread. Se yeast is a mixture that contains some of the different chemical forms of Se. It contains approximately 40% SeMet, 15% SeCys, and, to a lesser extent, analogs combined with other amino acids. It has been suggested that the use of organic Se is more advantageous in increasing the Se in animal products such as meat, milk, and eggs by improving animal health and performance (Mahan 1999; Wolffram 1999). The biological usefulness of Se sources also affects the Se requirement. Se can be given to animals as inorganic forms such as selenate and selenite, and organic forms such as SeMet and SeCys (Mahan 1999; Wolffram 1999; Cetin et al. 2002).

Organic Se is obtained from *Saccharomyces cerevisiae*, a yeast that grows in a medium containing high levels of Se. In feeds, Se is found in organic form and mainly as SeMet. Therefore, animals have adapted to this form of Se (Surai 2000).

Organic Se is stored in body proteins, while inorganic Se is excreted (Canogulları et al. 2009). It has been reported that the Se-rich yeast additive to chicken feeds increases the Se and vitamin E content in eggs and the enzymatic activity of GSH-Px and improves egg quality (Swanson 1987; Sluis 2007). The problems caused by deficiency have been widespread in many countries and have caused problems in agriculture for many years. Se supplementation has been effective in treatment.

19.5.2.1 Diseases Related to Selenium Deficiency in Animals

Although the symptoms and clinical signs associated with Se deficiency in animals are well defined, it is complicated to detect subclinical deficiencies that do not cause clinical signs and take many years. These effects may include suppressed growth and reproductive problems and impaired immunity. Although the effects are temporary and do not result in definitive symptoms, they are significant for the overall consequences for livestock. Se supplementation has been shown to provide benefits, even where no apparent deficiency is observed clinically. It has been shown that when Se supplementation is given to sheep with low blood Se without clinical signs, positive changes in body weight gain, fleece weight gain, and quality are observed (Langlands et al. 1991a). White muscle disease in livestock such as cattle, sheep, pigs, and horses, exudative diathesis and pancreatic degeneration in poultry, and liver necrosis in pigs can be counted among the most common diseases with clinical findings due to Se deficiencies. Some occur widely in many countries and have caused problems in agriculture for many years. Many also respond to vitamin E, but not as effectively as Se (Oldfield 1990).

White Muscle Disease

White muscle disease (WMD) occurs in Se and vitamin E deficiency in farm animals in many parts of the world. It is more common in lambs, calves, and chickens and affects horses, goats, poultry, and nonfarm animals such as rabbits and deer (Radostits et al. 1994; Fordyce 2013). WMD is the most common and most economically important related to Se deficiency in livestock. White muscle disease, named after the characteristic lightening of muscle color accompanied by calcium deposits, is a degenerative disease of striated muscles (Arthur 1992). The disease occurs in animals fed low Se-containing foods grown on Se-poor soils. Se deficiency occurs as a result of plants not getting enough Se, especially in sulfate-rich lands. Vitamin E losses that occur during the natural and mowed drying of grasses or silage production play a role in the emergence of this disease (Dabak et al. 2002). In some regions, the increased use of corn silage with low Se and vitamin E content and low tocopherol hay silage instead of straw in cattle and sheep diets cause more Se deficiency (Moxon and Olson 1974). WMD causes hyaline degeneration of skeletal muscle cells in various body parts, including the diaphragm, heart muscle, and tongue. White muscle disease, nutritional muscular dystrophy, presents clinically as myocardial dystrophies, usually in young calves and lambs. There are acute forms of WMD affecting the heart muscle and chronic forms of delayed WMD affecting the skeletal muscles (Maas et al. 1990; Radostits et al. 1994). Acute WMD is when animals die within a few days of birth after sudden physical exertion such as breastfeeding or running. Tachycardia, arrhythmia, resting dyspnea, and cyanosis are clinical symptoms (Beytut et al. 2002). Chronic WMD is the most common form of the disease and usually develops between 3 and 6 weeks.

Affected animals have difficulty standing up and walking and have respiratory distress. Thus, the disease is termed “hard lamb disease” among sheep breeders (Oldfield 1990). Changes in tongue muscles interfere with sucking and swallowing, causing milk to flow from the nostrils. Animals affected by hypomelanosis are more susceptible to respiratory and stomach infections (Aleman 2008). An increased peroxidative mechanism in muscle tissue is believed to play a role in the pathogenesis of the disease. It has been shown that calves fed a diet deficient in vitamin E and/or Se reduce the antioxidant enzyme glucose-6-phosphate dehydrogenase activity in heart and leg muscles (Kennedy et al. 1993). When the laboratory findings of sick animals are examined, it is seen that serum creatine kinase and aspartate aminotransferase levels increase. It is observed that blood, plasma, and serum Se and serum vitamin E levels have decreased, and GSH-Px activity in erythrocytes has decreased.

In treating the disease, oral or injectable Se and vitamin E combinations should be given to lambs and kids immediately after birth (Dabak et al. 2002). Selenoprotein W deficiency, which has antioxidant properties and is found in the heart and skeletal muscles, is also seen in white muscle disease. It is stated that subcutaneous administration of Se and vitamin E in the last few months of pregnancy in regions where the disease is frequently seen will benefit protection from the disease (Levander 1991; Arthur 1992; Fairweather-Tait et al. 2010).

Exudative Diathesis

Exudative diathesis (ED) is a disease caused by Se and vitamin E deficiency that mostly affects 3–6-week-old chicks and young turkeys, ducks, and quails less frequently. The disease usually manifests itself with diffuse edema in the subcutaneous adipose tissue due to impaired permeability of capillaries in the abdomen, chest, wings, and neck region. Due to the blood in the fluid, the abdomen and other areas take on a bluish-green color. Animals with exudative diathesis are anemic and hypoproteinemic (Jenkins et al. 1993; Zheng et al. 2019). With a slow growth rate, loss of appetite and condition, weakness develops in the legs, and eventually, they die. ED in low Se cereal diets often coexists with other Se-deficient conditions, such as WMD. Vitamin E supplementation is ineffective if animals have a severe Se deficiency, but adding 0.5 mg/kg of Se to the diet has been shown to prevent ED (Patterson et al. 1957; McDowell 1992). Chicks with exudative diathesis have low Se-dependent GSH-Px activities and increased glutathione levels in their tissues.

The administration of organic and inorganic forms of Se in poultry has been reported to prevent exudative diathesis effectively. In addition, it has been reported that organic Se is more effective on feathering in developing broilers (Mahan 1999; Cao et al. 2017). It is thought that the relationship between Se and vitamin E in protecting capillary cell membranes from lipid peroxidation is effective in preventing exudative diathesis. Exudative diathesis can be wholly prevented with dietary Se. The disease is prevented by diets containing at least 100 IU of vitamin E/kg in the severe absence of Se (less than 0.02 ppm) (Noguchi et al. 1973).

Hepatosis Dietetica

Hepatosis dietetica (HD) is a disease that affects young pigs, caused by a lack of dietary Se and/or vitamin E. Young animals usually have lower serum levels of Se and Vit E than adults' risk of deficiency because they need more during growth (Fontaine et al. 1977; Fordyce 2013). Since Se forms part of glutathione peroxidase, an enzyme that acts on free radicals, it also has a protective effect on Vitamin E, related to methionine and cysteine levels, respectively (Bunk and Combs 1981). Low levels of plasma Se are also associated with low levels of plasma GSH-Px activity. Classical lesions result from oxidative damage to the endothelium. The cells most severely affected in the pig are hepatocytes (liver cells) and muscle cells in the heart and skeletal muscles. Pathological lesions associated with deficiency include serous transudate accumulation in the pericardium, chest, and abdomen, as well as gastric erosions and ulcers. Necrotic liver degeneration most commonly occurs when animals are between 3 and 15 weeks old, and affected pigs may show some signs of circulatory distress such as lethargy, cyanosis, and malaise. Affected animals experience vomiting, staggering, and muscle tremors of the shoulders, resulting in death (Mahan et al. 1999; Pallares et al. 2002; Helke et al. 2020). When tissues are evaluated histologically, considerable hepatic necrosis and bleeding areas are irregular; some lobules are swollen and red. The gallbladder is often edematous. There is myocardial necrosis and pulmonary edema. It may show cardiomyocyte degeneration, interstitial hemorrhage, focal mineral deposition, and infiltration (Van Vleet 1982; Pallares et al. 2002). Death and liver lesions can be prevented by providing Se supplements. It has been observed that organic Se yeast given to pigs in the growing stage is more effective on Se storage in muscles than inorganic Se. In contrast, inorganic Se is more effective on glutathione peroxidase (Mahan et al. 1999). HD is one of the rare Se deficiencies seen in animal feeds with appropriate regulation of legal Se supplementation levels.

The Effect of Selenium Deficiency on the Reproductive System

Reproductive performance and quality of many economically important animal species are adversely affected by Se deficiency. Prenatal nutrition and Se deficiency appear to be important factors in the etiology of placental retention, one of the most common fertility disorders (Rutigliano et al. 2008). This disorder results from the inability of the fetal placenta to separate from the maternal crypts in the caruncles, which occurs within 2 to 8 h postpartum in approximately 10% of calving dairy cows. Therefore, retentions refer to placentas that remain attached to the uterus for more than 12 h. It has been shown that placental retention decreased from 17.5% to zero in dairy cows supplemented with both Se and vitamin E (McDowell 1992). The positive effects of Se supplementation on reproductive problems are associated with GPx activity (Mehdi and Dufrasne 2016). Se-dependent GSH-Px protects the placenta, which undergoes rapid postpartum degeneration. The enzyme metabolizes peroxides into less biologically active forms to protect cell membranes against the negative consequences of oxidation (Rutigliano et al. 2008). The placental tissue pulls leukocytes toward itself immediately after birth, that is, it has a chemotactic effect. Se, with its antioxidative protection mechanism, can prevent both destruction and adhesion of membranes (Hemingway 2003; Cook and Green 2007). Se deficiency has been associated with postpartum paraplegia and uterine inflammation, as well as labor problems resulting from decreased uterine muscle tension (Moeini et al. 2009). The most common fertility problems in subclinical Se deficiency in cows are irregular estrus, weak signs of estrus, delayed ovulation, early embryonic death, ovarian cysts, increased number of inseminations per pregnancy, prolonged reconception interval, retention, secundinarum, and metritis (Goff 2005; Cook and Green 2007). Se supplementation to pregnant animals reduces the incidence of retention, cystic ovary, and metritis that may occur in the postpartum period. It has been reported that cows diagnosed with metritis also accelerate the healing process and shorten the postpartum reconception time (Hemingway 2003; Patterson et al. 2003; Overton and Yasuı 2014). Hemingway stated that prenatal Se and vitamin E administration decreased the retention rate observed after calving from 20% to 13% in animals (Hemingway 2003). It is stated that Se supplementation before and during the warmer months can improve heat stress-induced infertility by reducing oxidative stress (Megahed et al. 2008). It has been found that mastitis-metritis-galactia syndrome in pigs is closely related to Se deficiency (Hostetler and Kincaid 2004). The most effective way of supplementing Se to animals is the use of mineral-enriched salt preparations. It has been reported that high pregnancy rates can be achieved following Se supplementation (Mehdi and Dufrasne 2016). It has been determined that the oocyte follicular fluid Se values of cows with fertility problems are lower than those of normal cows (Paszkowski et al. 1995). It has been reported that 1 ppm Se added to diluted semen increases motility and oxygen consumption in 13 out of 15 ejaculates of sperm. Optimum egg fertilization is 100% in females who take Se and vitamin E supplements and continue to receive adequate nutrition, while other groups are only 40% (Surai 2000). It is stated that Se added to the diet as a supplement provides live birth weight gain and increases the chance of survival of lambs (Langlands et al. 1991b).

The Effect of Selenium Deficiency on the Immune System

The immunoprotective roles of Se in the immune system and its effect on neutrophil function are important. There is strong evidence that Se functions biochemically in bovine neutrophils (Boyne and Arthur 1979). In many animal species, Se deficiency does not directly reduce neutrophil counts but does affect some of the functions associated with cytosolic GPx1. In cases of Se deficiency, glutathione peroxidase activity is not found in neutrophils, while the activity is effective in the presence of sufficient Se. On the other hand, Se deficiency in cattle does not affect the ability of neutrophils to phagocytize bacterial cells. Deficiency causes a significant reduction in the ability of phagocytic neutrophils to kill ingested bacteria. It was observed that antimicrobial activity decreased in the neutrophils of rats with experimental Se deficiency (Serfass and Ganther 1975). It has been shown that circulating erythrocyte and neutrophil production increases after Se supplementation in cattle (Morgante et al. 1999). Se has antiproliferative and anti-inflammatory functions (Katarzyna et al. 2012). Se levels in cows are effective in defense of udder tissue against bacteria. Se and vitamin E provide neutrophil migration to the mammary gland and increase the protective effects of neutrophils against bacteria to alleviate clinical symptoms of mastitis and shorten the duration of infection. Studies have shown that after 8 weeks of Se supplementation with 0.2 mg/kg diet, the incidence of mammary gland infections in dairy cows is reduced by up to 60%. In general, Se deficiency results in immunosuppression, whereas supplementation of low doses of Se promotes enhancement and restoration of immunological functions (Wang et al. 2021). The effect of Se on the immune mechanism occurs in taking part in many Se-dependent functions and playing a role in intracellular mechanisms.

There is evidence that Se is involved in both the innate immune system, such as macrophages and the adaptive immune system, where T and B lymphocytes are present (Turner and Finch 1991). Se affects the immune function of cattle mainly through specific and nonspecific immunity. Specific immunity includes humoral immunity and cellular immunity, both of which depend on T and B lymphocytes. Se can promote the proliferation and differentiation of lymphocytes and accelerate the secretion of cytokines (Ru-Duan et al. 1992). Se has been shown to increase immune responses to both innate and experimental immunogens such as tetanus toxoid, typhoid toxin, and immunoglobulins (Ammar and Couri 1981; Spallholz et al. 1990). Among the changing immune characteristics in Se-deficient animals are decreased neutrophil counts, defective neutrophil function, increased antibody titers against bacterial and mycotic antigens, increased H_2O_2 release during neutrophil phagocytosis, decreased neutrophil fungicidal activity, decreased natural killer cell activity, and increased mortality due to candidiasis (Ammar and Couri 1981; Spallholz et al. 1990; McKenzie et al. 2002). The negative impact of the immune system in Se deficiency may increase the risk of infectious abortion against parasitic, bacterial, or viral diseases (Humann-Ziehank 2016). It is stated that species differences, supplement dose amounts, and antigen types are significant in the complexity of the immune system and the relationship between Se and immunity. Se and vitamin E have been shown to affect immune function and are often given together in practice. In weaning pigs and sheep, antibody production increases when Se or α-tocopherol is given alone, but more when given together (Peplowski et al. 1980). Many nutritional deficiencies are associated with a compromised immune system, and Se deficiency has been found to increase susceptibility to parainfluenza three virus in lambs and infectious bovine rhinotracheitis virus in cattle (Reffett et al. 1988a, b).

19.5.3 Diseases Related to Selenium Accumulation in Animals

In animals, selenosis is generally observed in two clinical forms, acute known as blind stagger, and chronic, known as alkaline disease. Feeds with a Se content higher than 20–30 ppm in feed nutrition cause acute selenosis, and doses below 3–5 ppm cause chronic and subacute Se toxicity (Raisbeck 2020; Tinggi 2003; Kim et al. 2006; Nuttal 2006). Since the poisoning symptoms are similar to the metallic poisoning symptoms, it was determined that there was a high amount of Se in the examination. However, since seleniferous plants and soils also contain elements such as Mo, Te, and Cr, the proof that Se is the main toxic factor became clear with the same toxicity observed in experiments with Se compounds.

It has been stated that the endemic distribution of some diseases in farm animals is associated with high Se concentrations in the soil and seleniferous plant species (Combs and Combs 1986c). The Se cycle in the ruminant food chain starts from the soil and includes plant resources that depend on its assimilation from the soil. The soil is the main source of Se for plants, the animals that eat these plants, and the humans who consume these foods. The Se content of most soils ranges from 0.1 to 2 mg/kg, with an average concentration of 0.2 mg/kg and significant geographical variability (Wang et al. 2016). Plants that contain Se in the soil at higher rates in alkaline environments are divided into three groups according to their Se levels. In the first group, seleniferous plants such as Astragalus, Haplopapus, and Stanleya, which contain 100 ppm and higher Se in their structure, are called indicator plants. Plants in the second group contain 25–100 ppm of Se and are called secondary Se absorbers or facultative accumulators. Aster, Atriplex, Castilleja, Gyria, Comandra, Grindelia, and Mentzelia are plants in this group. Plants such as wheat, corn, cabbage, and onions accumulate less than 25 ppm of Se (Atessahin 2001; Kucuk 2014). Se taken from plants becomes toxic by replacing the sulfur in cysteine and methionine in the body. Se toxicity is affected by the amount and frequency of doses administered, the properties of the applied compound, and the presence of combining, reducing, diluting, or synergistic substances in the medium. In addition, the type of animal affected by toxicity, its sensitivity, the efficiency of absorption, and the elimination mechanism after ingestion are also important in terms of toxicity. It is known that the elements fluorine, molybdenum, chromium, vanadium, cadmium, zinc, cobalt, nickel, and uranium increase the toxicity of Se (Muth and Binns 1964; Hassan et al. 1990; Cetin et al. 2002). Although there are differences in sensitivity to Se among animal species, the level of Se that the body can tolerate is determined as 2 ppm by National Research Council (NRC 1980). However, it has been determined that the tolerance level in sheep is higher than stated due to long-term high consumption of Se (Biswas et al. 2006; Echevarria et al. 1988). When looking at the ratio studies between "effective dose" and "toxic dose" for the possible toxicity of Se, it was stated that it could be seen as a valuable therapeutic agent when used appropriately (Muth and Binns 1964). The condition that develops due to the consumption of inappropriate Se in the diet is called Se poisoning (selenosis-selenosis). Selenosis is a condition that affects horses, cattle, pigs, and poultry, causing neurological diseases such as alkaline disease in sheep and cattle, blind staggers in cattle, and paralysis in pigs (Tinggi 2003; Kim et al. 2006; Nuttal 2006; Raisbeck 2020).

19.5.3.1 Acute Selenosis

Acute selenosis may present as sudden death with few clinical signs when toxic doses are taken. Clinical manifestations that begin between 1 h and 24 h after exposure generally belong to the gastrointestinal, cardiovascular, and respiratory systems. In acute poisoning, heart rate and respiration increase, but the pulse are weak and irregular. Dyspnea is a prominent finding, and poisoned animals may be cyanotic. Symptoms such as polyuria, severe abdominal pain, hearing impairment, teeth grinding, and runny nose are seen. Death is due to circulatory and/or respiratory failure and usually occurs within a day or two after exposure (Van Vleet 1982; Smyth et al. 1990; Ahmed et al. 1998; Tinggi 2003; Raisbeck 2020). In addition, symptoms such as decreased interest in eating, visual impairment, locomotor disorders, salivation, lacrimation, decreased hair growth, difficulty swallowing, paralysis, and collapse occur (Atessahin 2001; Kim et al. 2006; Raisbeck 2020).

Toxicity primarily affects the central nervous system. The most common symptoms after toxicity are staggered walking, teeth grinding, colic, and vision loss. Excessive sweating is common in horses. Diarrhea may occur, especially in animals that survive longer. Vomiting is a common finding in pigs and may occur in other species. It has been reported that blood pressure drops even before clinical signs appear (Casteel et al. 1985; Raisbeck 2020). In general, it is stated that the acute lethality of Se compounds taken orally is significantly less than that given parenterally. The most commonly studied form of Se, sodium selenite (Na_2SeO_3), has an average oral LD50 of about 5.9 mg Se/kg (body weight) and a parenteral LD50 of 2.0 mg Se/kg (body weight). It has been noted that oxidation state and water solubility are two important determinants of acute toxicity of Se compounds (Cummins and Kimura 1971; Combs and Combs 1986d). Se, which is taken into the body in different ways, is detoxified by methylation with the effect of many enzymes in the organism. S-adenosylmethionine is needed for the methylation of Se. As a result of the metabolism of Se, DMSe and trimethylselenium (TMSe) are formed. The most characteristic sign of acute selenosis is "garlic breath," resulting from the pulmonary excretion of volatile methylated Se metabolites such as DMSe. One of these metabolites, DMSe, has a garlic odor and is eliminated by inhalation, and the most important metabolite, TMSe, is eliminated through urine (Combs and Combs

1986d; Atessahin 2001; Raisbeck 2020). Pathological findings include liver and kidney congestion, fatty metamorphosis and focal necrosis of the liver, endocarditis and myocarditis, degeneration of smooth muscles of the gastrointestinal tract, gallbladder, and bladder, and erosion of long bones (Combs and Combs 1986d). Acute Se intoxication causes myocardial necrosis in cattle, sheep, pigs, and possibly horses. This may be evident as pale streaks and hemorrhagic areas in the myocardium and accumulation of edema in the lungs.

Acute myocardial necrosis with postnecrotic fibrosis has often been seen in intoxication with selenate. The diagnosis of Se intoxication is based on the traditional triad of clinical signs, biochemical and pathological lesions, and chemical analysis. Sudden death or sudden malaise, anorexia, pulmonary edema, cardiac arrhythmia, and shock, especially after a change in diet, should prompt an intelligent diagnostician to include acute selenosis in the list of differential diagnoses (Glenn et al. 1964; Raisbeck 2020).

19.5.3.2 Chronic Selenosis

Chronic selenosis is a condition that occurs after prolonged exposure to high Seroughages and seleniferous grains. This condition, seen in farm animals such as cattle, horses, and sheep, is expressed as alkaline disease. The disease causes weight loss, hair loss, coarse hair, nail deformities, nail necrosis, joint stiffness, lameness, myocardial atrophy, cirrhosis, and anemia (NRC 1983; O'Toole and Raisbeck 1995; Koller and Exon 1986; Atessahin 2001; Raisbeck 2020). Among the Se compounds that cause chronic toxicity, soluble inorganic salts (Na_2SeO_3 and Na_2SeO_4) are among the more toxic types. SeMet and SeCys have relatively moderate chronic toxicity, while insoluble forms of Se (elemental Se, sodium selenide, selenium disulfide, and diphenyl selenide) are among the least toxic species (Combs and Combs 1986d).

Myocardial necrosis in cattle, sheep, and pigs is seen in both chronic and acute toxicity of inorganic Se salts. Myocardial damage also occurs in calves exposed to selenate in the womb (Yaeger et al. 1998; Raisbeck 2020). Se has been shown to suppress the immune system in ruminant animals. High dietary Se from inorganic Se salts, L-SeMet, suppressed primary antibody response in fed calves and antelopes. Situations, where immunosuppression is measurable, occur at dietary concentrations less than necessary for other effects to be seen. These results indicate that animals exposed to chronically high dietary Se have an increased risk of infectious disease (Raisbeck et al. 1997; Raisbeck 2020). Characteristic transverse hoof cracks with loss of mane and tail in horses and cattle several weeks or months after exposure to Se suggest chronic selenosis. Tissue Se concentrations measured to determine toxicity damage may vary depending on the tissue sampled, the chemical form of Se taken, the type of assay used, and other Se-binding elements such as mercury (Witte et al. 1993; Nuttal 2006). Blood, serum, urine, liver, kidney, nail, and hair samples for Se analysis are used. Whole blood and liver concentrations are more affected by short-term changes and remain elevated longer after a toxic dose.

Exposure to inorganic Se, especially during feed supplements, blood, and liver Se concentrations greater than 1 ppm in pets, increases the likelihood of selenosis (Raisbeck 2020). As Se accumulates in keratinized structures such as nails and hair, it is metabolically inert and therefore more reliable than liver or blood in determining long-term Se exposure. Hair Se concentrations in cattle or horses in regular Se diets are usually less than 1 ppm. Concentrations greater than 5 ppm indicate excessive Se exposure, and the best example is the tail in cattle and the mane and tail in horses (Davidson-York et al. 1999; Davis et al. 2014). In order to prevent Se toxicity in the livestock sector, removing animals from Se soils and closing these areas for livestock production are one of the most effective ways. However, grains and grasses grown in these areas can be reused by mixing them with produce from areas with low Se soils.

19.5.3.3 The Effects of Selenium Excess on the Reproductive System

Olson argued that the effects of Se excess on reproductive performance, such as reducing pregnancy rates and the number of healthy births and weaning, have major economic consequences (Olson 1969; Raisbeck 2020). Se is easily transferred through the placenta and secreted into milk, so symptoms of selenosis can be observed in lactating animals (Guyot et al. 2007). Female rats exposed to seleniferous wheat-containing 3 ppm Se have been shown to have increased miscarriage rates (Olson 1986). Various malformations have been observed in embryos of chickens fed a diet supplemented with 8 ppm Se (Na_2SeO_3) and in chick embryos treated with Se salts while in the egg (Sukra et al. 1976). Chronic selenosis prolongs the duration of anestrus in cattle, resulting in decreased fertility and the growth of ovarian cysts (NRC 1983; Combs and Combs 1986d; Koller and Exon 1986). Se experimentally reduced pregnancy and brood size in pigs (Wahlstrom ad Olson 1959). There are reports that Se exposure reduces fertilization in cattle and sheep (Dinkel et al. 1963; Raisbeck 2000).

19.6 The Role of Selenium on Human Health

Se is known as an essential trace element that has great importance in protecting human health and especially in nutrition (Tajaddini et al. 2015). Se is an element that plays a role in many mechanisms in the body, especially in thyroid hormone metabolism, antioxidant defense, regulation of the immune system, reproductive system functions, and homeostasis of the human body, and participates in many enzymes as a cofactor (Rayman, 2000; Hoffmann and Berry 2008; Iglesias et al. 2013). Sources of Se for humans are food, water, and air, respectively. Se is found in foods mostly in organic form as SeMet, SeCys, and methyl selenocysteine, but less frequently in the inorganic form of selenate and selenite (Lu et al. 1995; Shiobara et al. 1998). The bioavailability and toxicity of Se depend on its chemical form and concentration, and organic forms are more bioavailable and less toxic than inorganic forms (Garberg et al. 1988; King 2001). Selenite and selenate are found in water, SeCys is found in foods of animal origin, and SeMet is found in foods of plant origin (Barceloux 1999; Roman et al. 2014). The most abundant type of Se in the diet is SeMet. Na_2SeO_3 and sodium selenate (Na_2SeO_4), inorganic salt forms, are generally used in food fortification and dietary supplementation (Boosalis 2008; Mueller et al. 2009; Davis et al. 2017). Se is an indispensable component of the important metabolic pathways of the human body. As an integral component of selenoproteins in mammals, Se has an impact on human health and disease (Stadtman 1996; Gladyshev et al. 2004; Rayman 2012). Proteins with Se in the form of SeCys in their active site are defined as selenoproteins, and these proteins need Se to function (Brown and Arthur 2001; Beckett and Arthur 2005). Se compounds show their effectiveness by entering into the structure of selenoproteins as SeCys and playing a role in synthesizing them. Selenoproteins are necessary antioxidant enzymes in cancer and other chemical toxicities; they regulate thyroid hormone and thyroid functions, are structural proteins in sperm for reproductive function, and reduce virulence in some viral infections (Weeks et al. 2012). These proteins are involved in redox homeostasis, redox regulation of signaling cascades, and transcription factors (Labunskyy et al. 2014; Brigelius-Flohé and Flohé 2017).

19.6.1 Deficiency Symptoms of Selenium in Human

Epidemiological studies have revealed that Se deficiency can cause significant health problems in many countries of the world. Deficiency is due to an imbalance between the nutritional requirement of the organism and the bioavailable element. Geochemical factors and eating habits can also cause Se deficiency. Parenteral or enteral nutrition, vegetarian regimens, some formula feeding, and total parenteral nutrition can cause Se deficiency (Neve et al. 1985; Mertz et al. 1989; Akkus et al. 1991). Se deficiency is frequently observed in countries whose soils are not rich in Se, such as parts of China (Fordyce 2007; Li et al. 2012). In addition, it has been reported that Se deficiency plays an essential role in the formation and progression of symptoms of heart diseases, arrhythmia, stroke, infertility, prostate cancer, nephropathy, autoimmune and other immune diseases, and thyroid diseases (Mistry et al. 2012; Hendrickx et al. 2013; Ruseva et al. 2013; Roman et al. 2014). It is stated that Se deficiency may also be associated with aging, cancer, insulin resistance, diabetes, cardiovascular, and neurodegenerative diseases (Rayman 2008; Hurst et al. 2010; Rayman 2012; Hatfield et al. 2014). Both innate and adaptive immunity are impaired in Se deficiency, and individuals with insufficient Se intake are at risk of impaired antiviral defense, immune response, and increased autoimmunity (Bellinger et al. 2009; Verma et al. 2011). As an anticancer compound, Se is involved in regulating proliferation, migration, and cancer cell apoptosis. Se deficiency can cause functional and structural disorders in many organs and systems. The diseases that often occur due to Se deficiency are dilated cardiomyopathy

(Keshan disease) and endemic osteoarthropathy (Kashin-Beck disease) (Suetens et al. 2001; Pedrero and Madrid 2009; Chen 2012).

19.6.1.1 Keshan Disease and Its Etiology

Keshan disease (KD) is defined as endemic cardiomyopathy observed in the Keshan region of China in 1935 (Yang et al. 1984; Yang et al. 1988). The disease is a common cardiomyopathy picture in women of reproductive age and children between the ages of 2 and 10 (Chen 2012). The most accepted hypothesis is Se deficiency since the soil is deficient in Se in areas where the disease occurs (Liu et al. 2002; Tan et al. 2002; Zhou and Wang 2015). A Coxsackie virus isolated from Keshan's patient caused severe cardiac pathology when administered to Se-deficient mice, concluding that Se has a protective effect against the virus that can damage the heart muscle. Based on epidemiological, laboratory, and other studies, KD is considered to be a biogeochemical condition caused by various factors, including viral infection, especially Se deficiency (Vanderpas et al. 1990; Ge and Yang 1993; Beck et al. 1994). It has also been suggested that deficiencies of molybdenum, boron, and other nutrients, as well as Se, may play a role in the pathogenicity of KD (Fang et al. 2002). It has also been suggested that deficiencies of molybdenum, boron, and other nutrients, as well as Se, may play a role in the pathogenicity of KD (Fang et al. 2002).

Features of Keshan Disease

Histopathologically, KD is characterized by multifocal necrosis and fibrous replacement of the myocardium. Multifocal myocardial necrosis (MMN) is the leading and most characteristic feature of KD (Nezelof et al. 2002). Symptoms can range from dizziness, weakness, loss of appetite, and nausea in acute cases to subacute restlessness and mild heart enlargement. Latent-type patients may not be aware that they are affected. It may occur as an incidental finding on a routine physical examination or autopsy (Ge and Yang 1993). It was determined that Se levels and GPx activities in hair, nails, and blood of people with Keshan disease were lower than control groups (Zhu et al. 1993).

Blood and hair Se levels in people living in KD-affected areas indicate that Se deficiency is common, and there are significant differences between populations of KD and non-KD regions. The urinary excretion of Se has also differed significantly between KD and non-KD areas residents. This difference has been attributed to a greater intake of more diverse diets and animal foods in urban areas (Yin 1979; Yang et al. 1983). Se deficiency has also been implicated in Keshan disease, and supplementation with Se as Na_2SeO_3 has proven life-saving (Xia et al. 1990; Ge and Yang 1993). Among children aged 1 to 12 years afflicted and treated with Se, the incidence of KD was significantly lower, and GPx activities were increased (Yang et al. 1984).

Oral administration of Na_2SeO_3 tablets has been reported to be the most effective method to reduce KD incidence, morbidity, and disease-related deaths. In addition, for the control of KD, the use of selenized salt prepared by adding Na_2SeO_3 at the rate of 15 mg selenite/kg to the domestic salt is provided. It has been observed that the incidence of KD has decreased significantly since the introduction of such interventions. These results may be related to better-living conditions, possibly due to the availability and use of Se supplements and as a result of improved living and economic conditions, at least with the availability of a more varied and better diet. While it is clear that Se supplementation has largely eliminated endemic KD in China, there are concerns that marginal Se deficiency still causes cardiac problems (Wu et al. 1997; Lin et al. 2004).

19.6.1.2 Kashin-Beck Disease and Its Etiology

Kashin-Beck disease (KBD) is an endemic degenerative osteoarthropathy seen not only in China but also in other Se-deficient regions. The disease is observed more frequently in children up to 13 years of age compared to other age groups (Mathieu et al. 1997; Moreno-Reyes et al. 1998; Navarro-Alarcon and Cabrera-Vique 2008; Stone 2009). Although the etiology of the disease is attributed to Se deficiency as the cause is seen in soils with low Se, many possible causes such as iodine deficiency have been suggested (Zhilun et al. 1993; Suetens et al. 2001; Yao et al. 2011). Recently, etiological studies of KBD have mainly focused on low environmental Se and its interaction with mycotoxins in foods such as nivalenol (NIV), deoxynivalenol (DON), and T-2 toxin (Stone 2009). It has been hypothesized that the presence of fulvic acid (FA), a water-soluble aromatic polymer component of the soil, at high levels in drinking water in NBD regions may be a factor (Jiang and Xu 1989). It has been shown that oxy and hydroxy groups in FA can generate free radicals that can interfere with the cell membrane and cause increased lipid peroxidation when GPx activity is reduced (Peng et al. 1999). The hydroxylation of collagen molecules leads to uneven bone formation and decreased mechanical strength characteristic of KBD (Yang et al. 1992). Other factors may also play a role in the etiology of KBD, which has many possibly related causes, such as KD.

There may be nutritional imbalances and deficiencies in other inorganic nutrients such as phosphates, manganese, and Se (Levander 1987). Nutritional deficiencies, particularly Se, may contribute to the onset of the disease, associated with the stress of malnutrition, harsh living conditions, and the intense cold during the long winter of many KBD endemic areas. It is stated that general nutritional status, economic conditions, and improvements in medical services in rural areas of China reduce the incidence of KBD in the affected areas (Ge and Yang 1993). Kashin-Beck disease is characterized by shortening of the fingers and toes and changes resembling rheumatoid arthritis. Oxidative stress resulting from Se deficiency may lead to joint lesions, cartilage necrosis, and bone deformation in the future (Suetens et al. 2001; Navarro-Alarcon and Cabrera-Vique 2008; Yao et al. 2011). KBD is an osteoarthropathy characterized by chronic disabling degeneration and necrosis of the joints, epiphyseal plate cartilages of the arms and legs. It becomes evident during childhood and adolescence and leads to varying degrees of disability throughout adult life, possibly stunting. Clinically, weakness is followed by joint stiffness and pain. Advanced cases show typical signs of joint enlargement and limb deformity (Diplock 1987). The clinical symptoms of the disease are limb joint enlargement, pain, and limitation of movement. Characteristic pathological changes in KBD patients include excessive apoptosis in epiphyseal plaque chondrocyte, developmental impairment of secondary ossification endochondral, and chondrocyte necrosis in the deep layer of articular cartilage. In articular cartilage, the sulfation of extracellular matrix proteoglycan is essential in maintaining normal cartilage metabolism. Se supplementation can improve cartilage matrix metabolism (Guo et al. 1997).

19.6.1.3 Selenium and Cancer

Both clinical and epidemiological many animal studies have reported the relationship between Se level and cancer incidence and mortality (Shamberger and Frost 1969; Novotny et al. 2010). Several hypotheses have been proposed regarding the carcinostatic properties of Se compounds. We can list these as the antioxidant role of Se, its ability to strengthen immunity, its effect on the metabolism of carcinogens, its role in protein synthesis and cell division, and the formation of anticancer Se metabolites (Spallholz 2001). The most widely accepted hypothesis is that cancer develops due to damage caused by reactive oxygen radicals due to Se deficiency (Lu and Jiang 2005). It is thought that the earliest and most important protective mechanism in the preneoplastic process is the antioxidant effect of Se (Bjornstedt and Fernandes 2010). Although it is defined as an important anticarcinogen, Se is antimutagenic and anticarcinogenic at nutritional doses, while it can be mutagenic, toxic, and even carcinogenic at high doses (Rayman 2005; Letavayova et al. 2008). Antioxidant GPx, redox regulatory TrxR, and DIOs, the hormonal regulator of metabolism, eliminate DNA-damaging H_2O_2 and lipid hydroperoxides. By blocking the production of ROS and malondialdehyde, these selenoproteins regulate the redox signaling system in many cancer types and provide anticarcinogenic effects through genetic and epigenetic ways (Powis et al. 1996; Lu and Jiang 2005; Combs and Lü 2006).

Because of these effects, Se-containing GPxis thought to be an important factor in the emergence of Se anticancer properties (Lu and Jiang 2005). It is stated that Se supplementation may depend on basal Se status, amount of Se administered, chemical form and dosage, and type and stage of cancer (Brigelius-Flohé and Kipp 2016). It has been shown that when Se supplementation is applied to patients with BRCA1 gene mutations, which can be seen in familial breast cancers, chromosome breaks are reduced (Kowalska et al. 2005). It is thought that increasing p53 activity through selenoproteins may have an important role in stopping angiogenesis in early lesions of cancer (Zeng 2002). Se deficiency has been shown to reduce DNA methylation in Caco-2 cells and rat liver and colon. Thus, changes in DNA methylation may be a potential mechanism by which inadequate dietary Se increases liver and colon tumorigenesis (Davis and Uthus 2002). Certain Se metabolites (hydrogen selenide, methylselenol, selenodiglutathione) may be anticarcinogenic by inhibiting cell proliferation and neoangiogenesis and stimulating cell death through apoptosis. Substantial human epidemiology studies demonstrate the role of Se in cancer prevention and an inverse relationship between dietary Se levels and specific cancer risk. Since the anticarcinogenic roles of selenoproteins will be less in Se deficiency, correction of nutritional Se deficiency increases the anticarcinogenic effect by increasing selenoprotein expression (Combs and Lü 2006).

While some studies indicate that Se status is an independent indicator of overall cancer risk and mortality, other reports have shown that the risk of certain types of cancer is associated with lower Se (Kornitzer et al. 2004; Akbaraly et al. 2005). In both case-control studies and meta-analyses, it has been reported that Se deficiency may be a risk factor for lung cancer (Knekt et al. 1998; Hartman et al. 2002; Zhuo et al. 2004). Studies report that low Se status is associated with a four- to fivefold increase in prostate cancer risk (Brooks et al. 2001; Van den Brandt et al. 2003; Li et al. 2004; Etminan et al. 2005).

Regarding Se protection against colon cancer, studies have reported a statistically significant inverse correlation between toenail Se levels and colon cancer risk for both sexes (Ghadirian et al. 2000). A significant inverse relationship has also been reported between Se levels and the incidence of adenomatous polyps in patients under 60 years old (Fernández-Bañares et al. 2002; Jacobs et al. 2004). Se level with bladder (Hartman et al. 2002), brain (Brooks et al. 2001), esophagus (Etminan et al. 2005), head and neck (Michaud et al. 2005), ovary (Knekt et al. 1998), pancreas (Ghadirian et al. 2000), thyroid (Garland et al. 1995), stomach (Van den Brandt et al. 1994; Thompson et al. 2002), and melanoma (Clark et al. 1996; McNaughton et al. 2005) found inverse associations for risks for cancers or precancerous lesions. Selenite can oxidize cell membrane thiols and prevent the formation of the tumor layer, thereby impairing the immune activity of the tumor, making it vulnerable to destruction. For the carcinostatic properties of Se, it is an appropriate expression to strengthen the immune system by Se. Se is necessary for the maintenance of immune function, and the stimulation of the immune system can be achieved with Se supplementation. In experiments with mice, Se supplementation has been shown to increase the cellular immune response of the T-cell and nature killer cell systems.

In humans, it is stated that activation of both Se and vitamin E strengthens all aspects of the immune system through stimulation of interleukins and other associated T-cell genes (Kiremidjian-Schumacher and Roy 1998). Another hypothesis discussed is that Se interferes with the metabolism of carcinogens derived from normal metabolism (Spallholz 2001). It can react directly with carcinogens to prevent them from binding to DNA or forming reactive Se metabolites that render carcinogens noncarcinogenic (Ip and Lisk 1997).

Se can prevent cancer through its effects on the cell cycle and protein synthesis. Many Se compounds have been shown to affect cell viability and DNA integrity in cell culture (Spallholz 1994). For example, selenite stops the cell cycle of cancer cells at low concentrations by inhibiting cell division and protein synthesis (Combs and Gray 1998). Another hypothesis explains the carcinostatic activity of Se supplementation with the formation of Se metabolites that are toxic to cancer cells, such as hydrogen selenide and several methylated Se compounds. In addition, it has been shown that some selenoproteins such as methylselenol increase the synthesis of glutathione transferase enzyme, increasing the detoxification of carcinogens, which in turn reduces carcinogenesis (Ip and Lisk 1997). The methyl selenide anion is formed in the body from dietary selenite and less common naturally occurring Se compounds such as SeMet and L-Se-methyl selenocysteine as synthetic methylselenic acid (Ip et al. 2000; Whanger 2004). Cell culture studies show that Se compounds that form methyl selenides can stop the growth of cancer cells and induce apoptosis (Zou et al. 2000).

19.6.1.4 Selenium and Thyroid

The thyroid gland is the organ in which Se is found in the highest concentration relative to organ weight in the human body. The concentration of the element correlates with blood levels (Dickson and Tomlinson 1967; Aaseth et al. 1990; Kohrle 1999). For thyroid hormones to function in the organism, thyroxine (T4) must be deionized to triiodothyronine (T3). It is known that iodothyronine deiodinase-1, which produces T3 from T4 in the periphery, is enzyme-containing Se (Berry et al. 1991). The most important development in understanding the role of Se in human metabolism has been discovering type 1 iodothyronine deiodinase selenoenzyme, which is responsible for the peripheral conversion of T4 hormone T3. Type 2 deiodinase, which was discovered later and responsible for the conversion of T4 to T3 in the brain, and type 3 deiodinase, which is responsible for the deactivation of T4 and T3, are also SeCys enzymes (Hawkes and Keim 2003). DIOs are a family of enzymes containing SeCys responsible for catalyzing thyroid hormone activation and keeping thyroid hormone concentration under control in both fetal and adult tissues or cells (Kohrle et al. 2005; Negro 2008).

Se is necessary for the synthesis and storage of thyroid hormones and the proper functioning of the DIO enzyme system, which is involved in hormone synthesis (Behne et al. 1990; Croteau et al. 1995). There are three isoenzymes of iodothyronine deiodinase that catalyze the conversion of thyroxine (T4) to the biologically active hormone T3. DIO1 is mainly in the liver, kidney, thyroid, and pituitary; DIO2 is in the thyroid, central nervous system, pituitary, and skeletal muscle; and DIO3 is found in the pregnant uterus, placenta, embryonic liver, embryonic and neonatal brain, and neonatal skin (St Germain et al. 2005). Thyroid gland cells are protected by the antioxidant effect of glutathione peroxidase, an enzyme-containing selenoprotein, against the oxidative damaging effect of H_2O_2, which they need for the iodination process during hormone synthesis (Corvilain et al. 1993). H_2O_2 production is the rate-limiting step in thyroid hormone synthesis and is regulated by TSH. Therefore, serum Se levels play a decisive role in GPx activity and thyroid functions (Duntas 2010).

The increase in GPx level reduces the oxidative damage caused by H_2O_2, which is physiologically necessary for thyroid hormone synthesis and reactive oxygen radicals. However, when there is Se deficiency, there is a decrease in GPx activity and, as a result, an increase in H_2O_2 and TPO levels (Contempre et al. 1996). It is known that antioxidant enzymes such as GPx and TrxR protect thyrocytes against oxidative stress when the Se intake in the body is sufficient (Sun et al. 1999; Becker et al. 2000).

Therefore, it is stated that the efficacy of Se on the thyroid may be related to increasing antioxidant enzyme activities and may be associated with decreasing inflammatory activity (Kohrle and Gartner 2009). There are many hypotheses about the protective effect of Se on thyroid tissue. It can reduce the expression of human leukocyte antigen (HLA-DR) on the thyrocyte surface. It can lead to a decrease in the concentration of antithyroid antigens and antibodies. It can control the immune response dependent on B lymphocytes. It can inhibit proinflammatory cytokines and may decrease prostaglandin and leukotriene synthesis. It can protect thyroid tissue from oxidative stress. It can optimize thyroid hormone synthesis and transport by inducing selenoprotein synthesis (Shchedrina et al. 2010; Schomburg 2012; Dharmasena 2014). Se is needed for the enzyme iodothyronine deiodinase (ID-I), which converts T4 (thyroxine) from thyroid hormones to selenoprotein T3 (triiodothyronine). Se affects the thyroid with GPx and DIO1 enzymes. In Se deficiency, GPx decreases, and H_2O_2 increases, causing intoxication on the thyroid gland and thus cretinism. Therefore, Se deficiency also increases the diseases caused by iodine deficiency (Goyens et al. 1987; Reilly 1998; Kohrle and Gartner 2009).

Se optimizes GPx activity and simultaneously reduces TPO-antibody titers and improves hypothyroidism. Therefore, optimization of GPx activity is vital (Wu et al. 2015; Hu and Rayman 2017). Se deficiency is associated with an increased prevalence of thyroid diseases. The clinical improvements observed in thyroid diseases appear to be due to the optimization of GPxs due to their anti-inflammatory potential.

19.6.2 Selenium Toxicity in Human

It is known that insufficient intake Se causes some diseases. However, excessive amount and duration of Se intake will cause acute or chronic poisoning due to its toxic effects. As with Se deficiency, the geographic region is also important in high Se intake. Toxic effects due to excessive intake are frequently observed in countries with high Se levels in their soils. High Se-contaminated areas are located in North America, Ireland, Israel, the northern part of Australia, and South America (Tsunoda et al. 2000). The toxicity of Se is related to the chemical form of the ingested Se, its ability to enter cells, its ability to expel, detoxification activity, exposure route, frequency, and duration. Toxicity is also related to age and physical structure. Given these determinants of Se toxicity, it is challenging to establish safe levels for exposure to the element (Goehring et al. 1984; Tsunoda et al. 2000).

When Se is taken in excess, it shows prooxidant properties; it can cause DNA damage by inducing free radical production (Letavayova et al. 2008). High-dose Se administration reduces cell proliferation, resulting in DNA fragmentation and induction of cancer cell apoptosis (Wallenberg et al. 2010). Se toxicity (selenosis) symptoms of selenosis can be acute or chronic. In addition to nausea, vomiting, abdominal pain, and diarrhea, serious toxic effects such as neurological dysfunction may also be observed (Navarro-Alarcon and Cabrera-Vique 2008; Fordyce 2013). Chronic exposure to high doses of Se may cause liver damage, impaired hematopoiesis, hair loss, infertility, nail breakage, redness, garlic-like lousy breath, dental disorders, and neurological disorders (Akkus et al. 1991; Li et al. 2012; Duntas and Benvenga 2015). Although the positive effects of Se supplementation are seen in individuals with Se deficiency, it is necessary to be careful about the prooxidant effect and possibly metabolic disease risks (Drutel et al. 2013).

19.6.3 Selenium and Apoptosis

Apoptosis, called programmed cell death, is a metabolic process that plays a critical role in embryonic development, immune regulation, and tumor regression. It is a typical event that occurs at the end of the life cycle of most cells, except brain, heart, and cancer cells. The death receptor-mediated (extrinsic) and mitochondrial (intrinsic) pathways are identified as two apoptotic signaling pathways. The extrinsic apoptosis pathway is initiated by interacting a ligand with receptors such as transmembrane CD95, tumor necrosis factor receptor, and TRAIL receptor and consequent activation of membrane-proximal caspases (caspase-8 or caspase-10). The intrinsic pathway is initiated by mitochondrial outer membrane permeability (MOMP), which releases proteins into the cytosol generally localized in the space between the inner and outer mitochondrial membranes (Green 2000; Johnstone et al. 2002). In addition to its anticancer properties, Se also regulates proliferation, migration, and cancer cell apoptosis (Combs 2015). Certain drugs, proteins, and event signals that alter the integrity of cellular mitochondria induce apoptosis, and Se compounds cause mitochondrial swelling, an event that leads to apoptosis (Lemasters et al. 1998; Wakabayashi and Spodnik 2000). It is stated that it does this by creating oxidative stress in cells by reacting with glutathione by using the prooxidant property of Se. This produces free radicals, superoxide, and other ROS (Spallholz 1997). Oxidative stress-induced by Se is thought to be the primary cause of Se-induced apoptosis. The Se-induced apoptosis pathway involves inducing a shift in the intracellular redox state, shifting to a more oxidizing environment, cross-linking of thiol groups of mitochondrial proteins, mitochondrial swelling, and release (Kim et al. 2006). The inhibition of apoptosis by Se deficiency is one of the factors thought to be influential in cancer formation. In cell cultures, sufficient has been shown to inhibit the growth of cancer cells by increasing apoptosis and/or reducing cell proliferation (Lu 2001). In addition, in cell culture studies, it has been shown that Se increases cell proliferation at low levels, increases the expression of many cell cycle-related genes, and consequently reduces apoptosis (Zeng 2002). Hydrogen selenide is an important factor in Se anticarcinogenesis due to multiple metabolic pathways. Its oxidative metabolism produces superoxide anion (O_2) and H_2O_2; their formation causes DNA single-strand breaks that lead to S phase/G2 cycle arrest and cell death via apoptosis (Kaeck et al. 1997; Jiang et al. 2002). This mechanism appears to mediate selenite-induced apoptosis, as the genotoxic and proapoptotic effects of selenite on leukemia, breast, or prostate cancer cells are blocked by a superoxide dismutase or its mimetics (Zhong and Oberley 2001; Jiang et al. 2002). Even at very low concentrations, both SeMet and selenite can protect keratinocytes, melanocytes, and fibroblasts from UV-induced cell death and apoptosis. Processes behind these effects include inhibition of oxidative DNA damage, lipid peroxidation, apoptosis, suppression of inflammatory and immunosuppressive cytokine release, and modulation of p53 activity (McKenzie 2000; Rafferty et al. 2003). The biological action of Se depends on both its specific chemical form and its concentration.

High Se levels induce oxidation and cross-linking of protein thiol groups and the formation of ROS, ultimately leading to cell death. Se compounds also trigger the loss of mitochondrial function and the release of proapoptotic proteins such as cytochrome C from the mitochondria into the cytosol. Thus, the pathway in Se-induced apoptosis involves forming an intracellular oxidizing environment, followed by the induction of mitochondrial dysfunction, cytochrome C release, caspase-3 activation, and DNA fragmentation (Kim et al. 2006). Many studies have provided the basis for the conclusion that Se compounds can induce apoptosis. Inhibition of cell growth, loss of cell viability, or DNA fragmentation induced by Se compounds, leukemia HL-60 (Cho et al. 1999), liver carcinoma HepG2 (Zhu et al. 2000), colon cancer HT29 and SW480 (Stewart et al. 1997), and glioma A172 and T98G cells (Zhu et al. 1996). Se administration increases GPx1, 4, and TrxR1 activity in vascular endothelium and smooth muscle and reduces apoptosis induced by LDL and thiols. Experimental studies show that GPx1 suppresses ischemia-induced apoptosis (Maulik et al. 1999; Steinbrenner et al. 2006).

19.7 Conclusions

Although more than two centuries have passed since the discovery of Se, its role in human health is still not fully explained. Current studies show that several selenoproteins fight to inhibit tumor cell growth, while some of them support it. Similar contradictions exist for many other Se-related health issues. The mechanism of Se has not yet been fully elucidated, and there are still many question marks. For all these reasons, it is necessary to give due importance to Se and to eliminate confusion by prioritizing more molecular and epidemiological studies.

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Chapter 20
Multifaceted Role of Phyto-assisted Selenium Nanoparticles (SeNPs) in Biomedical and Human Therapeutics

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20.1 Introduction

Selenium is an important trace element necessary for human and animal immune systems to act properly and prevent some lethal or degenerative diseases (Khurana et al. 2019). Selenium is a key ingredient, which serves as coenzyme and cofactor for many enzymes and selenoproteins of the human body. It protects cells and tissues against oxidative injuries and stress (Hosnedlova et al. 2018). Selenium is also essential for regulating iodine and free radical levels in the body, as well as potentially improving disease resistance (Rayman 2000). The cellular equilibrium between oxidants and antioxidants is disrupted by selenium deficiency, which can intensify oxidation-related risks, especially when the body is under extreme oxidative stress. The use of selenium additives can attenuate certain liver-related degenerative diseases caused by the accumulation of heavy metals, toxic elements, intake of alcohol, and chemotherapy (Amin et al. 2017; Gao et al. 2014). Because of its outstanding antioxidant properties, selenium attracts the interest of researchers and clinicians. Furthermore, a selenium deficiency in the human body can lead to vascular, osseous, muscular, and immune-related problems (Agarwal and Behari 2007). Therefore, it is critical to meet the daily requirement of this essential nutrient via selenium supplementation, particularly for those who are deficient in selenium (Bai et al. 2020). In food supplements or additional products, the availability of Se content shows a challenging problem of bioavailability and adsorption. The use of supplements containing SeNPs has the potential to improve the bioavailability and efficiency in such edible food products. Due to the increasing popularity of SeNPs-based food supplements, they have been considered as food additives and medicinal products for people with selenium deficiency (Hosnedlova et al. 2018).

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M. A. Hossain et al. (eds.), *Selenium and Nano-Selenium in Environmental Stress Management and Crop Quality Improvement*, Sustainable Plant Nutrition in a Changing World, https://doi.org/10.1007/978-3-031-07063-1_20

On the other hand, high doses of selenium can lead to serious illnesses. Because of this, it is important to maintain the therapeutic dosage at the appropriate levels (Akbari et al. 2017; Alam et al. 2019). The toxicity of Se can be influenced by the amount of selenite, methyl selenium, and selenite in the food crops (Liu et al. 2018; El-Ramady et al. 2014). The above mentioned issues with high selenium doses in mind which have enabled nanotechnology have emerged as a burgeoning field of research with possible therapeutic uses in both the medical and nonmedical fields (Hosnedlova et al. 2018). Nano-sized selenium has garnered attention globally due to its use as a therapeutic agent and a major component of a dietary supplement (Vera et al. 2016; Singh et al. 2019). In addition, SeNPs possess antibacterial (Gunti et al. 2019), anti-cancer properties (Krishnan et al. 2019), an extraordinary sensing abilites (Anu et al. 2017), heavy metal detector capacities (Park et al. 2011), and as a selective agent in drug delivery (Deng et al. 2018).

20.2 Plant-Derived SeNPs: Alternative Approaches

Physical, chemical, and biological methods can be used to make SeNPs. The reduction of selenite salts, for instance, sodium selenite (Na_2SeO_3), to elemental Se (Se°) in the chemical synthesis of nanomaterials requires the use of a variety of dangerous chemical substances (Sowndarya et al. 2017; Kora and Rastogi 2016). The reduction of selenious acid (H_2SeO_3) into SeNPs of various sizes and morphologies was described in a specific study (Zhang et al. 2004) using an ascorbic acid solution in the presence of polysaccharides. In the synthesis process, the polysaccharides were used to stabilize the nano-selenium center, while ascorbic acid served as a reducing agent. Many other researchers have also published using quercetin, gallic acid, and polymer extracellular substances to synthesize SeNPs (Khurana et al. 2019; Kora and Rastogi 2016). The pH, light, ultrasonic sounds, and temperature-assisted reduction of selenite salts into SeNPs also provide the other physical and chemical methods of synthesis for SeNPs. Using a pulsed laser ablation technique and ultrasound-assisted synthesis, various experiments have reported physical methods to synthesize SeNPs (Khan et al. 2019). Unfortunately, due to the high costs and other significant environmental issues, the physical and chemical methods of nanoparticles synthesis have become ever more disadvantaged. The use of chemically made nanoparticles for medical and pharmaceutical applications has been discouraged due to their dangerous effects. Therefore, the biosynthesis of SeNPs using plants and microbes has been suggested as a feasible and traditional alternative strategy to cope with such hazards (Alagesan and Venugopal 2019).

Emerging attempts and research have also been involved in the biological synthesis of SeNPs and have resulted in an environmentally sustainable and nontoxic approach. In the biological synthesis of SeNPs, the application of various plant extracts is a less toxic, simple, and cost-effective approach compared to other biological synthesis procedures, using enzymes from microorganisms, particularly fungi and bacteria (Fig. 20.1) (Husen and Siddiqi 2014; Cui et al. 2018; Alam et al.

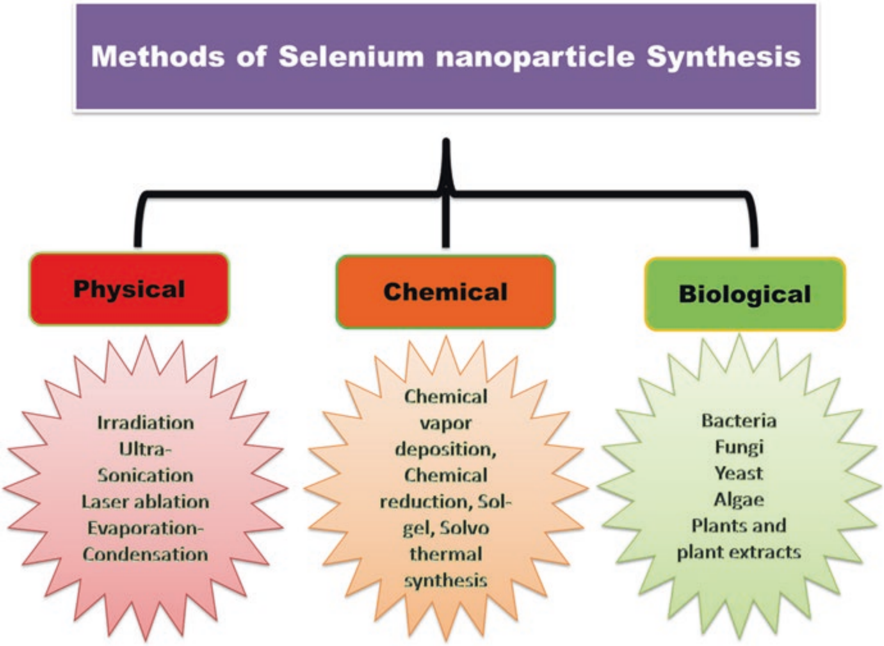

Fig. 20.1 Demonstrate the methods employed in creation of selenium nanoparticles by variety of physical, chemical, and biological agents

2019; Gunti et al. 2019). Several plant species have been successfully used to synthesize SeNPs. The phenolic acids, cinnamic acid, flavonoids, alkaloids, tannins, sesquiterpenes, monoterpenes, and other secondary metabolites in the plant extracts can serve as reducing and possible stabilizing agents in phytofabrication of SeNPs (Javed et al. 2020a, b; Javed and Nadhman 2020).

20.2.1 Phytofabrication of SeNPs

Due to their excellent biomedical properties, plants-based synthesis is more advantageous than other standard synthesis methodologies for the biosynthesis of SeNPs. The synthesis of SeNPs using natural stabilizing and reducing agents is an eco-friendly and cost-effective technique. The manufacture of nanoparticles using plant extracts began in the early twentieth century, and various plant species have been investigated for their ability to decrease and stabilize SeNPs. Using natural stabilizing and reducing substances to synthesize SeNPs is an environmentally friendly and cost-effective way of producing the nanoparticles. In the early twentieth century, plant extracts were used to synthesize nanoparticles, and many plant species have been explored for their capacity to reduce and stabilize the formation of nanoparticles. The utilization of *Aloe vera* leaf extract in the production of SeNPs has been proven (Fardsadegh and Jafarizadeh-Malmiri 2019). It has been demonstrated that *Aloe vera* leaf extract contains a wide variety of natural reductants and stabilizers, including phenolic compounds, flavonoids, sterols, vitamins, organic acids, enzymes, lignin, polysaccharides, and proteins, which are all secondary metabolites of plants and function in the reduction of Se salt. These chemical constituents are critical in the eco-friendly synthesis and stability of SeNPs (Sánchez et al. 2017). Numerous studies were carried out using plant extracts from various plant components, including the stem, flower, bark, root, and shoot to fully understand the significant nature of eco-friendly green production of stable SeNPs. Likewise, according to Sharma et al. (2014), the (raisin) extract green which uses *Vitis vinifera* for the synthesis of SeNPs acts as a reducing and stabilizing agent. A study conducted by Anu et al. (2017) revealed that the green synthesis of SeNPs with various shapes and sizes was developed in the presence of garlic clove extract (*Allium sativum*). In a similar manner, many other studies have been described to investigate the biosynthesis of SeNPs by using the leaf extracts of *Dillenia indica* (Krishnan et al. 2020), *Ocimum tenuiflorum* (Liang et al. 2020), *Prunus amygdalus* (Sadalage et al. 2020), *Spermacoce hispida* (Krishnan et al. 2019), *Zingiber officinale* fruit extract (Menon et al. 2019), *Carica papaya* latex (Rajasekar and Kuppusamy 2021), Roselle plant extract (Sawant and Sawant 2020), and bark extract of *Cinnamomum zeylanicum* (Alghuthaymi et al. 2021). There are several factors that impact SeNPs adaptability, stability, and biocompatibility. These include the type of plant extract employed, its optimum concentration, and the physicochemical reaction parameters and may reflect various surface Plasmon resonance bands (Alam et al. 2019). However, industrial-scale synthesis of plant-derived SeNPs necessitates protocol adjustment in order to synthesize nanoparticles of similar size and form. To optimize synthesis, it is also necessary to regulate the physicochemical properties of the reaction circumstances, which is a complex process. The biological applications of SeNPs are dictated by their size, structure, and biochemical characteristics, which are dependent on the experimental parameters (Table 20.1). However, the industrial production of phytofabricated nanomaterials is still in its infant stage. This is due to the fact that it requires a comprehensive understanding of the mechanism of selenium salt reduction using secondary metabolites from plants, as well as the collaborative response of reaction physicochemical parameters.

20.2.2 SeNPs Green Synthesis Protocol

The green nanoparticle synthesis protocols using plants adopt simple methodologies which can be carried out with minimum ease and instrumentation. Different plant parts such as leaves, buds, nuts, bulbs, vegetables, and seeds are washed with distilled water, diced into pieces or small fragments, and boiled in distilled water to obtain an aqueous extract. Purification of the aqueous plant extract can be accomplished by a variety of processes, including centrifugation and filtration. SeNPs can be synthesized using a combination of selenium salts, selenium oxides, selenium

Table 20.1 List of plants used for synthesis of SeNPs with size, shape, and their biopotential applications

S. No.	Entry name of plants	Size (nm)	Shape	Applications	References
1.	*Allium sativum*	40–110	Spherical	Cytotoxicity study	Anu et al. (2017)
2.	*Allium sativum*	24	Spherical	DNA targeted chemotherapy	Ezhuthupurakkal et al. (2017)
3.	*Allium sativum*	8–52	Spherical	Antimicrobial activity	Jay and Shafkat (2018)
4.	*Aloe vera*	50	Spherical	Antibacterial and antifungal activity	Fardsadegh and Jafarizadeh-Malmiri (2019)
5.	*Asteriscus graveolens*	20	Spherical	Cytotoxicity study	Zeebaree et al. (2020)
6.	*Citrus reticulata*	70	Spherical	Anti-algal activity	Alvi et al. (2021)
7.	*Clausena dentata*	46	Spherical	Larvicidal activity	Sowndarya et al. (2017)
8.	*Diospyros montana*	4–16	Spherical	Antioxidant, antimicrobial and anticancer activity	Kokila et al. (2017)
9.	*Emblica officinalis*	20–70	Spherical	Antioxidant, antimicrobial activity and biocompatibility studies	Gunti et al. (2019)
10.	Fenugreek	50–150	Oval	Cytotoxicity study	Ramamurthy et al. (2013)
11.	*Ficus benghalensis*	20–140	Spherical	Photocatalytic activity	Tripathi et al. (2020)
12.	Hawthorn	113	Spherical	Antitumor activity	Cui et al. (2018)
13.	*Leucas lavandulifolia*	56–75	Spherical	Antibacterial activity	Kirupagaran et al. (2016)
14.	*Orthosiphon stamineus*	88–141	Ball	Cytotoxicity study	Sivakumar and Jeganathan (2018)
15.	*Pelargonium zonale*	40–60	Spherical	Antibacterial and antifungal activity	Fardsadegh and Jafarizadeh-Malmiri (2019)
16.	*Psidium guajava*	8–20	Spherical	Antibacterial and cytotoxicity study	Alam et al. (2019)
17.	*Spermacoce hispida*	47	Spherical	Cytotoxicity study	Krishnan et al. (2019)
18.	*Spermacoce hispida*	120 ± 15	Rod	Antioxidant, antibacterial, anti-inflammatory, and anticancer activity	Vennila et al. (2018)
19.	Tea extract	83–160	Spherical	Antioxidant activity	Zhang et al. (2018)
20.	*Theobroma cacao*	1–3	Spherical	Antioxidant activity	Mellinas et al. (2019)
21.	*Withania somnifera*	40–90	Spherical	Antioxidant, antibacterial, antiproliferative, and photocatalytic	Alagesan and Venugopal (2019)

(continued)

Table 20.1 (continued)

S. No.	Entry name of plants	Size (nm)	Shape	Applications	References
22.	*Prunus amygdalus*	150–330	Irregular	Antibacterial activity	Sadalage et al. (2020)
23.	*Azadirachta indica*	153–278	Spherical	Antibacterial and cytotoxicity study	Mulla et al. (2020)
24.	*Zingiber officinale*	100–150	Spherical	Antimicrobial and antioxidant	Ezhuthupurakkal et al. (2017)
25.	Lemon	90–100	Rod	H_2O_2 sensing	Sawant and Sawant (2020)
26.	*Gracilaria corticata*	50–250	Spherical	Antibacterial and anticancer activity	Mirzaei et al. (2021)

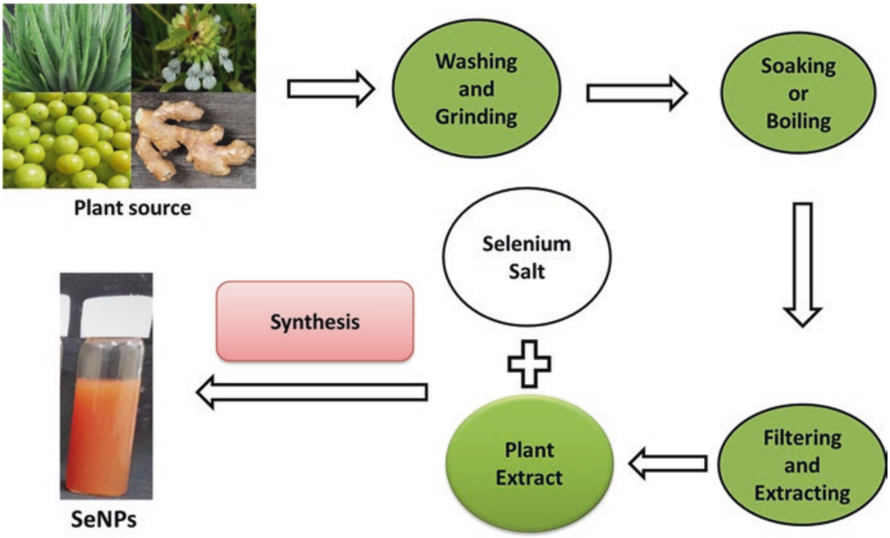

Fig. 20.2 Flowchart illustrates green synthesis of selenium nanoparticles from plant source

acids, amorphous selenium, and plant extracts at a wide range of temperatures and pH. At room temperature, the plant extract is simply mixed with various concentrations of selenium acid/oxide/salt solutions, and their conversion to SeNPs occurs within minutes in a one-pot, one-step, and environmentally friendly process. Since phytochemicals act as natural reducing and stabilizing agents, there is no need to add an external hazardous stabilizing/capping agent. The reaction mixture is then further incubated to reduce the metal salt, and the color change is used to monitor the reaction. Finally, the NPs can be collected using high-speed centrifugation, washed vigorously in solvent or water, and stored for future use. Figure 20.2 illustrates a brief green synthesis protocol of SeNPs. To determine the elemental composition, exact morphology, and other physicochemical properties of SeNPs, a variety of well-known characterization techniques may be used. While a comprehensive discussion of such characterization techniques is beyond the reach of this study, a quick summary of the most relevant and commonly used techniques is presented (Gunti et al. 2019; Alagesan and Venugopal 2019).

20.3 Methods Used for Characterization of SeNPs

The two main methods for determining the exact morphology and precise structures of SeNPs are transmission electron microscopy (TEM) and scanning electron microscopy (SEM). High-resolution transmission electron microscopy (HR-TEM), energy-dispersive X-ray spectroscopy (EDX), atomic imaging, and scanning tunneling microscopy are examples of ancillary techniques developed in accordance with breakthroughs in electron microscopy. These techniques have been used to describe SeNPs not only in terms of shape but also in terms of their elemental composition and adherence to support materials. Another invaluable tool for elucidating the size, crystallinity, and composition of SeNPs is X-ray diffraction (XRD). This approach is widely used to calculate SeNP grid parameters. The X-ray photoelectron spectroscopy (XPS) technique is used to efficiently assess the elementary composition through surface analysis of SeNPs. In addition to the characterization techniques described above, the gas adsorption and desorption technique is often used to gather information on the particular SeNP surface areas to determine their pores and volumes. This knowledge is particularly useful in characterizing porous SeNPs and in correlating their structure with their catalytic aspects (Gunti et al. 2019; Alagesan and Venugopal 2019).

20.4 Biomedical Potential of Phytofabricated SeNPs

Approximately 9.6 million people died from cancer globally in 2018, making it the world's second leading cause of death after heart disease. Mutations in proto-oncogenes and critical tumor suppressor genes are the most common causes of cancer (Javed et al. 2020a, b). Major human cancers include cervical, colorectal, stomach, thyroid, liver, lung, breast, and prostate cancer. Breast and prostate cancer are the most common cancers in women and men, respectively, worldwide (Nounou et al. 2015). Surgery to remove tumor tissues, chemotherapeutic cell killing, endocrine therapy, and radiation elimination of the most aggressive cancer cells are aspects of conventional cancer treatment. When it comes to treating cancer or tumor cells, hormone therapy and immunotherapy are two less indispensable approaches to take into account. However, these treatments frequently cause abnormalities in the patient's body, resulting in the damage of many normal cells and important organs, as well as lowering the patient's quality of life (Damyanov et al. 2018; Farokhzad and Langer 2006). Cancer cells possess intrinsic characteristics that distinguish them from normal living cells, such as angiogenesis (the creation of new blood vessels) and permeability of the capillary and lymph drainage systems. In order to develop powerful nanodrugs that may be utilized to treat cancer cells selectively and precisely, nanotechnologists are taking advantage of the diverse microenvironment in cancer cells (Farokhzad and Langer 2009).

Bioactive and biologically accessible, selenium nanoparticles play an important role in numerous oxidoreductive reactions. For plants and animals, selenium nanoparticles have a variety of regulatory effects that promote their normal functioning, as well as numerous health benefits (El-Ramady et al. 2014; Skalickova et al. 2017). Selenium nanoparticles are used as antioxidants to protect cells from free radical damage, anticancer agents to treat cancer, antimicrobial agents to inhibit the growth of a variety of pathogenic microbes, an antidiabetic substitute to control diabetes, and hepatoprotective agents to reduce metal toxicity.

20.4.1 SeNPs in Cancer Treatment

The approaches to cancer detection, diagnosis, and treatment may be influenced by cancer nano-biotechnologists. When different concentrations of plant-derived SeNPs were given to human cancer cell lines such as lung malignancies, human cervical carcinoma, and liver malignancy, they demonstrated potential anticancer properties, according to the researchers (Ramamurthy et al. 2013; Schneider et al. 2010). Current research looks into the effectiveness of plant-derived SeNPs in the treatment of cancers such as colon, prostate, skin, and ovarian as well as leukemia and major brain tumors that originate from glial cells in the brain (Schneider et al. 2010). It is probable that SeNPs derived from plants will be investigated in the future for the treatment of gliomas, particularly in cases when excision is not possible (brain stem glioma). SeNPs derived from plants can also be investigated for their potential application in targeted drug delivery to treat these deadly gliomas. Phytofabricated SeNPs with a small size and spherical form, produced at neutral pH, are powerful anticancer drugs (Cui et al. 2018). According to the findings of the study, the addition of phenols, flavonoids, flavanols, amino acids, alkaloids, cardiac glycosides, saponins, galactomannan, and polysaccharides in the plant extract helps to stabilize the biochemical corona of nanomaterials. The applicability and promise of plant-derived SeNPs as a future option to counteract the damaging impacts of various cancerous cells are further enhanced by these chemical compounds (Ramamurthy et al. 2013).

The use of laminarin polysaccharides to produce SeNPs (LP-SeNPs) was demonstrated in another study, which indicated that the SeNPs with an average diameter of 60 nm displayed a spherical structure and the propensity to persuade toxicity in human hepatocarcinoma cells. The LP-SeNPs were eventually determined to activate multiple mitochondrial pathways, causing apoptosis and blocking autophagy’s late phase. In human liver cancer cells, plant-derived SeNPs were also found to decrease and ameliorate the antiapoptotic protein Bcl-2 expression and the inhibitory effects of Bcl-2 (B-cell lymphoma 2) on Beclin-1 (Cui et al. 2019). SeNPs have the capacity to cause oxidative stress and inflammation in cells by releasing reactive oxygen species into the environment. This has the effect of decreasing cell viability. Plant-derived SeNPs influence the fate of HepG2 cells by increasing ROS levels while decreasing mitochondrial potential and glutathione levels. It has been observed that DNA damage in HepG2 cells caused by SeNPs causes cell cycle arrest, which ultimately results in cell death (Zeebaree et al. 2020). In vitro studies have shown that the phytofabrication of SeNPs using the leaf extract of *Withania somnifera* can reduce the viability of adenocarcinomic human alveolar basal epithelial cancer cells. Human alveolar basal carcinoma cells are affected by the SeNPs, which cause chromosomal instability and mitotic arrest, according to the researchers (Alagesan and Venugopal 2019). One more research team (Rajasekar and Kuppusamy 2021) reported that SeNPs mediated by *Carica papaya* latex seemed to have a significant impact on breast cancer cells, causing apoptotic alterations such as chromosomal condensation, fragmentation, and the creation of the apoptotic body in the breast cancer cells. Plant-derived SeNPs cause cytotoxicity in cancer cells by causing considerable changes in nuclear morphology and important events such as nuclear condensation.

SeNPs that have been biosynthesized show a strong antileukemia potential. Biosynthesized SeNPs effectively restrict the growth of acute myeloid leukemia cells (AML) by boosting their antioxidant capability and delimiting the expression of c-Jun activation domain-binding protein 1 and thioredoxin 1. A second mechanism by which SeNPs execute their antileukemia effects on leukemia cells is by the efficient removal of free radicals by SeNPs, which in turn prevents the lipid peroxidation caused by free radicals (Vera et al. 2016). A few studies have demonstrated the anticancer potential of SeNPs derived from plants against human AML cells. However, the scope of these studies has been limited. Because of oxidative stress generated by ROS, plant-derived SeNPs have prospective applicability in most cancers, osteoporosis, and coronary heart diseases (Rajasekar and Kuppusamy 2021). Plant-derived SeNPs can be explored for the development of effective chemotherapeutic medications by considering their antioxidant capacity as well as their cytotoxic effects on cancer cells.

Plant-derived SeNPs enter cells through endocytosis, which is mediated by receptors. With a specific acidic pH condition and a redox imbalance, malignant cells can be differentiated. SeNPs continuously generate free radicals, which disrupts the mitochondrial membrane, causing protein leakage, and increases endoplasmic reticulum stress, causing membrane breakdown. The rupture of the mitochondrial membrane allows different proteins to leak out and induces apoptosis by activating caspases. The activation of different molecular pathways, including NF-B, Wnt/β-catenin, MAPK/Erk, PI3K/Akt/mTOR, and apoptotic pathways, is managed by this cellular stress state. Through its oxidative and inflammatory stress signaling pathway, NF-B affects cellular homeostasis. The MAPK/Erk, VEGF, PI3K/Akt/mTOR, and Wnt/β-catenin pathways, on the other hand, are critical in carcinogenic signaling and must be activated (Ikram et al. 2021). The inhibition of cellular proliferation and the obstruction of growth-promoting signals in the tumor microenvironment were induced by the control of these pathways by plant-derived

SeNPs. Furthermore, the biosynthesized SeNPs cause cancer cells to alter their signaling pathways, resulting in a reduction in their proliferation. Finally, the disruptive cellular activities cause DNA fragmentation, which causes cell cycle arrest and cell death (Khurana et al. 2019).

20.4.2 Antidiabetic Properties

Diabetes is caused by a variety of causes, including poor eating habits, stress, a lack of physical activity, obesity, inflammation, heredity, and the passage of time. However, the good news is that there are several preventative strategies (such as careful monitoring of blood cholesterol, blood pressure glucose levels, physical activity as well as dietary modification) that may be utilized to control diabetes and its potentially fatal effects (Souto et al. 2011; Fan et al. 2020). Subcutaneous injections of insulin, a protein hormone, are used as a first-line treatment for the management of diabetes in people with type 2 diabetes (Twigg et al. 2019). A side effect of the repeated daily insulin injections is the formation of painful and uncomfortable sores at the injection site, as well as fat accumulation at the location of the injection, hypertrophy, and trypanophobia (Wong et al. 2017). Insulin, which is secreted by the pancreas, regulates the amount of glucose taken up from the diet. When the pancreas fails to produce enough insulin, a metabolic condition known as diabetes mellitus develops, where the glucose level in the blood rises slightly above average. Endothelial dysfunction produces an upsurge in the oxidative stress, which causes the progression and increased severity of diabetes. Diabetes is divided into two groups based on insulin secretion: type I diabetes and type II diabetes. In the first type, the body produces a lesser amount of insulin as a result of genetic defects, viral infection, autoimmunity, and acute poisoning, which results in organ failure. The second type is a more spread pathogenic condition and is exacerbated by poor diet management and lack of exercise, all of which lead to resistance against insulin. Increased blood glucose levels can also lead to various conditions such as liver, eye, kidney, and heart damage (Guan et al. 2018).

Selenium is a trace element that plays a role in a variety of activities in the human body, including immunological function and antioxidant defense mechanisms (Agarwal and Behari 2007). The recommended daily consumption of selenium for people is 55 μg and should not exceed 400 μg, according to the US National Academy of Sciences (Ungvári et al. 2014). Se is considered hazardous to adults if they receive a dosage greater than 700 μg per day (Fan et al. 2020). Researchers in the field of nanotechnology are becoming more and more interested in the study of selenium and its beneficial effects on people and animals on a regular basis. It has been demonstrated in the literature that there is a link between the selenium content in the blood and diabetes. Diabetic patients show a high concentration of selenium relative to a non-diabetes individual (Galan-Chilet et al. 2017; Cancarini et al. 2017).

To reduce the oxidative and inflammatory effects, the body of a diabetic patient needs more antioxidant species, and selenium has active antioxidant and anti-inflammatory properties. Moreover, the size of an element has a significant impact on its biomedical application. Therefore, SeNPs are becoming increasingly popular for diabetes treatment. Type I and type II diabetes can both be effectively treated with SeNPs because they can reduce oxidative damage while also sensitizing insulin, which can be used as an anti-hypoglycemic agent in the treatment of diabetes (Al-Quraishy et al. 2015). Researchers investigated the hypoglycemic effect of SeNPs in diabetic rats with type I diabetes that had been injected with streptozotocin (STZ). The findings revealed that SeNPs likely exacerbated hyperglycemia and high cholesterol in the diabetic rat models by inducing insulin-mimetic activity, which also prevented hepatic and renal histological injury (Zeng et al. 2018). On the other hand, the same models were used to develop SeNPs derived from polysaccharide of *Catathelasma ventricosum*, and the results of this study revealed that polysaccharide SeNPs had antidiabetic activity when compared to native SeNPs. In another study, dose-dependent chitosan-stabilized SeNPs (CSS-SeNPs) were synthesized to verify the effect of their anti-diabetes in a 2.0 mg^{-1} dose-dependent rat model, and the results showed antidiabetic effects (Mohamed et al. 2021).

By using plants as reactants for SeNP synthesis, nanoparticles with great biocompatibility can be generated without the need for additional stabilizing and capping chemicals (Anu et al. 2017). Plant-derived SeNPs are widely accepted as one of the possible alternatives for controlling the severe diabetes due to their non-toxigenic nature. SeNPs synthesis mediated by leaf extract of *Hibiscus sabdariffa* (roselle plant) was developed in order to investigate the antioxidative effects in diabetic rats induced by streptozotocin (STZ) (Fan et al. 2020). Streptozotocin is an antibiotic medication generated from the bacteria *Streptomyces achromogenes* that has a broad spectrum of activity. Streptozotocin is a pancreatic beta-cell-specific cytotoxin; hence, it is used to induce diabetes in mouse models. STZ reduces the antioxidant capacity of SOD, CAT, GR, and GPx in rats while inducing a rise in nitric oxide and malondialdehyde (MDA) levels (Liu et al. 2018). On the surface of cells, STZ binds to GLUT 2 (glucose transporter 2) receptors and competes with glucose molecules to induce phosphorylation of the Akt protein. Apart from that, by increasing the quantity of ROS (reactive oxygen species) and RNS (reactive nitrogen species) production, STZ causes apoptosis and cytotoxicity in the cells. Finally, STZ causes oxidative stress, which results in a mitochondrial cleavage, DNA fragmentation, decrease in testosterone levels, and lowering the antioxidant potential of antioxidant enzymes such as SOD and CAT, which ultimately lead to cell death. In STZ-induced rats, phytofabricated SeNPs were internalized through receptor-mediated endocytosis and inhibited the generation of ROS and RNS by boosting the antioxidant capability of SOD and CAT, as well as increasing serum testosterone and lipid levels (Al Nahdi et al. 2017).

Unfortunately, there is only a limited data available on the antidiabetic effects of SeNPs derived from plants. One of the study found that SeNPs synthesized from polysaccharides of *C. ventricosum* may considerably lower blood sugar level, improve body weight, and elevate antioxidant enzyme capacity and lipid levels in streptozotocin-induced rats (Liu et al. 2018). It has also been demonstrated that the green synthesized SeNPs increase insulin release as well as the proliferation of cells. The ROS scavenging capability of SeNPs, as well as modulations of HSP70 and SIRT1, is thought to be part of the SeNPs anti-diabetes mechanism.

The exact antidiabetic mechanism of plant-assisted SeNPs is unknown, and it requires further pharmacological testing and chemical research. While the strong antidiabetic potential of the plant-derived SeNPs is being taken into consideration in rats and mice, we can clearly assume that plant-derived SeNPs may prove to be a helpful and effective tool for the design of nanomedicines in the near future for the treatment of human diabetes (Khurana et al. 2019; Krishnan et al. 2020).

20.4.3 Antioxidant Application Potential

An important role in the body is played by antioxidants, which interact with free radicals and stabilize them. They also help to prevent harmful chain reactions from occurring and convert free radicals into harmless by-products of the manufacturing process. Antioxidants help to control oxidative stress and are important in the treatment of degenerative disorders caused by free radicals. Naturally occurring and synthesized antioxidants, however, are only moderately efficient due to low bioavailability because of poor absorption, difficulty crossing over the plasma cell membranes, and later breakdown during delivery. The plant-derived nanoparticles, on the other hand, contain potential antioxidant functional groups that are more stable, have a more regulated release, are more biocompatible, and possess superior antioxidant profiles (Khalil et al. 2020). Plant-derived SeNPs are well-known for their strong antioxidant properties, which have been demonstrated in earlier studies (Qiu et al. 2018; Gunti et al. 2019; Menon et al. 2019). This is because SeNPs derived from plants contain a high concentration of nano-selenium, which plays an important role in the production of selenoenzymes, such as glutathione peroxidase, which aids to safeguard tissues and cells from free radicals when applied in vivo (Vera et al. 2016; Du et al. 2017). Furthermore, another study found that SeNPs derived from *Mucuna pruriens* and *Aloe vera* have remarkable antioxidant capacity (Fardsadegh and Jafarizadeh-Malmiri 2019; Menon et al. 2019) which protect cells from oxidative damage (Kalishwaralal et al. 2018).

A recent publication suggests a possible explanation for the antioxidant activity of plant-derived SeNPs, i.e., the presence of surface functional groups that stabilize and cap the nanoparticles which are derived from secondary plant metabolites (Vennila et al. 2018). Nutritionists and physicians commonly recommend that people consume selenium-fortified foods (such as nuts, mushrooms, and cereals) to maintain good health (El-Ramady et al. 2014). Because they are derived from plants and may be utilized as natural antioxidant anchoring agents in food packaging material, the plant-based SeNPs are considered to be highly biocompatible when used to replace synthetic antioxidants in the packaging material (Wadhwani et al. 2016; Vera et al. 2016). Due to their significance, phytofabricated SeNPs may be potential future alternatives for the cosmetics industry. They can be used in the formulation of antiaging creams and sunscreens.

20.4.4 Antimicrobial Applications

Traditionally, when it comes to treat microbial diseases, the use of medicinal plants and their derivatives has been recognized to be a conventional method (Abalaka et al. 2010). The antibiotics designed in the early twentieth century were effectively used to control several Gram-positive and Gram-negative bacterial infections (Singh et al. 2014). By interfering with the translation process, most antibiotics target bacterial ribosomes and inhibit their growth or dismantle ribosomal subunits (Dimauro and Davidzon 2005). Many antibiotics have been found to cause a range of negative side effects in both humans and animals. According to endosymbiotic hypothesis, the mitochondrion is derived from bacteria, and the structural and molecular components of the protein expression system in bacteria and humans are fundamentally identical in structure and function. Therefore, similarities between mitochondrial and bacterial ribosomes indicate that many antibiotics may induce side effects that, in certain circumstances, and could be misinterpreted as mitochondrial myopathy (Xing et al. 2006). Researchers have discovered that excessive dosages of bactericidal antibiotics can result in mutations and metabolic alterations in the host cell, which can then determine the development of extremely harmful oxidative radical species (Kim et al. 2011).

With the advent of antibiotic resistance in most of the harmful bacterial strains, infectious bacterial illnesses are becoming increasingly concerning. In order to combat microbial illnesses more effectively while also causing the least amount of damage to host cells, it is unavoidable to search for effective antimicrobial compounds. A potent antibacterial agent selenium (Se) and its derivatives such as selenium sulfide are widely used in medicine to treat illnesses caused by microbes. Although selenium (Se) is an element that occurs naturally (Khiralla and El-Deeb 2015; Sadalage et al. 2020), an excess of Se creates harmful consequences and leads to selenosis (Gunti et al. 2019; Menon and Shanmugam 2020). Therefore, recent research has concentrated on reducing the harmful effects of selenium while simultaneously increasing its bio-functional properties. As a result of their outstanding antibacterial potential and biocompatibility, plant-derived SeNPs are considered superior to elemental selenium in several applications (Gunti et al. 2019; Fardsadegh and Jafarizadeh-Malmiri 2019).

To successfully produce plant-derived SeNPs with nontoxic properties, excellent antibacterial action at low doses, and bioactivity, additional research must be conducted. Antimicrobial potential of plant-derived SeNPs has been investigated extensively. The antibacterial function of plant-mediated SeNPs may be due to their smaller size when compared to microbes, which allows them to penetrate microorganism cell membranes and induce cell death (Menon and Shanmugam 2020). Plant-mediated SeNPs with small dimensions and more rounded shapes can have greater accessibility into the bacterial cell (Zonaro et al. 2015). As a result, it is widely accepted that the antimicrobial potential of plant-mediated SeNPs is inversely proportional to their size and that the antimicrobial potential increases as the size of plant-mediated SeNPs decreases (Zonaro et al. 2015). Plant-derived SeNPs have long been known for their antibacterial action against bacterial strains of both Gram-positive (*Staphylococcus aureus*) and Gram-negative (*Escherichia coli*, *Klebsiella pneumoniae*, and *Proteus* sp.). Due to the weak peptidoglycan cell wall of Gram-negative bacteria, SeNPs are apparently more efficient against them. Moreover, the antibacterial ability of SeNPs produced with *Psidium guajava* leaf extract was found to display high antibacterial activity against *Staphylococcus aureus* and *Escherichia coli* (Alam et al. 2019).

Plant-derived SeNPs are also effective against fungi that cause diseases in humans. SeNPs biosynthesized with fruit extract of *Phyllanthus emblica* exhibit antifungal activity against food-borne pathogens like *Aspergillus flavus*, *Aspergillus brasiliensis*, *Aspergillus oryzae*, *Fusarium anthophilum*, and *Rhizopus stolonifer* (Gunti et al. 2019; Fardsadegh and Jafarizadeh-Malmiri 2019). Antimicrobial activity of plant-derived SeNPs may be mediated by either the formation of ROS or the breakdown of the integrity of the cell membrane, depending on the source. Plant-mediated SeNPs also defeat microbial activity by a mechanism known as cell wall disruption, followed by binding to the cell membrane, causing changes in DNA replication, protein synthesis, and other processes associated with normal cell functions. Finally, the SeNPs bind to the thiol or sulfhydryl groups present in membrane proteins, causing denaturation and cell death. However, the precise antimicrobial action of plant-derived SeNPs remains unknown (Agarwal and Behari 2007; Yan et al. 2018).

20.4.5 Antiviral Properties of SeNPs

There has been a major threat to human health posed by viral infectious diseases. For example, enterovirus-71 (EV71) is a virus that causes mouth, hand, and foot disease and has emerged as a severe public well-being threat throughout the world (Zhang et al. 2015). Similarly, the influenza virus continues to be an extremely infectious pathogen that affects thousands of individuals each year during several seasonal outbreaks (Tao et al. 2017). In order to prevent the surfacing of new viral particles from cell membranes, various types of antiviral medications have been developed as a primary source of protection. The use of synthetic medications, on the other hand, has led to emergence of drug-resistant virus strains, which are extremely dangerous to human health and can be fatal (Nguyen et al. 2012). In addition, drug tolerance reduces the antiviral efficacy of synthetic antivirals by a factor of two (Antipov and Pokryshevskaya 2019). Rapid assay designs and innovative technology are required to successfully combat this alarming situation which is spreading fast. Due to recent advancements in the synthesis of different nanomaterials, they are now considered a premier choice for the treatment of infectious viral diseases. The antiviral effects of the biosynthesized SeNPs have been demonstrated to be extremely effective. Selenium is a trace element that regulates several critical biological processes, as well as specific enzyme modulations, and which potentially eliminate reactive oxygen species from the environment (Li et al. 2017). Because of the important function that selenium plays in the immune system and defense processes, a selenium shortage could result in a high risk for getting a viral infection. The antiviral potential of plant-derived SeNPs has, unfortunately, only been reported in a few research papers. The biogenic SeNPs, on the other hand, have gotten a lot of interest lately because of their unique antibacterial potential as an integral element of selenoproteins (Khurana et al. 2019). SeNPs were found to have antiviral activity against the influenza virus, according to a recently published study. In the laboratory, it was demonstrated that the oseltamivir-coated SeNPs have the ability to stimulate the production of ROS, which in turn triggers the activation of caspase-3 death. Additionally, ROS were controlled in order to activate the Akt and P53 signaling pathways, which prevented malignant cells from proliferating further (Li et al. 2017).

20.4.6 Hepatoprotective Applications

Animal liver is the most vital organ because it carries out a wide range of metabolic functions and is therefore susceptible to serious injury (Bai et al. 2020). Hepatocyte injuries are not only a major health concern for people, but they are also a significant ailment in aquaculture species such as fish, which exhibit liver color changes and enlargements as a result of these injuries (Kunjiappan et al. 2015). It has been proven that several analgesics and pyretics, such as acetaminophen (APAP), can be utilized to treat hepatic damage in people. It is quite safe and beneficial to take APAP medication. Acute nephrotoxicity and hepatotoxicity are caused by an overdose of the APAP (Kon et al. 2004; Amin et al. 2017; Yan et al. 2018). The production of severe kidney and liver damage by APAP is thought to be the result of two molecular pathways. In the first molecular mechanism, the N-acetyl-p-benzoquinone imine (NAPQI) accumulates, as a result of enhanced P450 3A4 (CYP3A4) and CYP2E1 (P450 2E1) activity, resulting in increased P450 3A4 (CYP3A4) and CYP2E1 (P450 2E1) expression (Dahlin et al. 1984). An increase in reactive nitrogen species (RNS) such as peroxynitrites and nitric oxide, which is considered independent of NAPQI production, is another molecular cause of APAP toxicity (NO) (Al Nahdi et al. 2017). It is believed that an increased level of RNS is responsible for increased protein nitration and subsequently enhanced proteolysis (Hinson et al. 2002; Abdelmegeed et al. 2013). These stresses result in mitochondrial malfunction, which includes a decrease in the membrane potential of the mitochondria, inhibition of respiration, and an increase in mitochondrial oxidative stress (Kon et al. 2004; Abdelmegeed et al. 2013; Al Nahdi et al. 2017). Due to APAP overdose, the endpoint of such mitochondrial dysfunction is the commencement of necrosis and apoptosis in the kidney and liver (Amin et al. 2017; Yan et al. 2018).

Plant-derived SeNPs, which have emerged because of recent nanotechnological breakthroughs in nano-medicine, have drawn the attention of scientists and clinicians who are striving develop potentially viable treatment for severe liver diseases. Because of their antioxidant capacity, *Spermacoce hispida* aqueous extract mediated SeNPs (Sh-SeNPs) were examined for their hepatoprotective activities against APAP toxicity (Amin et al. 2017; Ikram et al. 2021). It was discovered that plant-derived SeNPs could be conjugated with S-allyl-glutathione (SAG), a physiologically active ligand, to form (SAG-Sh-SeNPs), which increased the biological activity of the SeNPs significantly. It has been proven that SAG-Sh-SeNPs protect mitochondrial activity, which results in the protection of the kidneys and liver against APAP toxicity in mice (Krishnan et al. 2020). Additional studies have been conducted on the chitosan-stabilized (CS) SeNPs to determine their hepatoprotective properties. Diseased mice were treated with CS-SeNPs, which reduced their hepatocyte necrosis and their serum alanine transaminase, lactate dehydrogenase, and aspartate transaminase levels. SeNPs were found to protect hepatocyte necrosis by slowing lipid oxidation and increasing glutathione peroxidase, catalase, and superoxide dismutase activity (Bai et al. 2020). Because of the function of CS-SeNPs in the management of hepatoprotective damage in mice, there has been widespread agreement that plant-derived SeNPs can be a useful and efficient prospective hepatoprotective therapy in the future for the treatment of human hepatocyte injuries. There have only been a few research studies conducted to report the effects of plant-derived SeNPs on human hepatocyte injuries and other liver disorders; therefore, it is important to investigate the potential of plant-derived SeNPs to protect the liver from a variety of hepatic injuries in the near future.

20.5 Conclusions

In the twenty-first century, the biogenesis of nanomaterials to develop formulations has significant potential to control illnesses by creating smart drug delivery models to distribute medicines to the targeted locations. According to reports, a large number of nanobiotechnology-based products are available on the market. Considering the significance of plant-based SeNPs and the green synthesis routes for biocompatibility and safety, it is expected that plant-based SeNPs will emerge as a major therapeutic tool with the potential to treat deadly cancers and a wide range of other devastating disorders such as neurological disorders, diabetes, viral diseases, antimicrobial drug resistance, antifungal drug resistance, and many other devastating disorders. Owing to their high efficacy, biocompatibility, and antimicrobial capability, it is not hard to think that plant-based SeNPs might be useful in the production of commercial substances. Plant-based SeNPs function as a cofactor for a variety of antioxidant enzymes, and these nanoparticles are predicted to change the cosmetics industry by allowing for the nano-formulations of antiaging and skin-clearing treatments. Taking into account the importance of selenium in immune system enhancement, plant-based SeNPs are likely to be employed in the commercial production of antiviral vaccines. Many studies have cited SeNPs derived from plants as a key reason. However, further research is needed to understand the link between nano-selenium and selenium, as well as the molecular alterations that are responsible for therapeutic variations. Furthermore, knowing the kinetics or variety of selenoproteins in the presence of plant-based SeNPs is critical for improving our knowledge of the pharmacological effects of plant-based SeNPs. To understand the in vivo mechanism of action of SeNPs, biologists, chemists, pharmacists, doctors, and physicists will need to work collaboratively. Such initiatives are likely to increase the use of SeNPs in the pharmaceutical sector for the development of personalized therapeutic medicines.

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