Physiology of Zinc Oxide Nanoparticles in Plants

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1 Introduction

Zinc oxide (ZnO) is a multifunctional material with unique physical and chemical properties, for example, broad range of radiation absorption, high chemical and photostability and high electrochemical coupling coefficient (Segets et al. 2009; Lou 1991). The covalence of ZnO is between ionic and covalent semiconductors and it is classified as a semiconductor in group II–VI. It has a high bond energy of 60 meV and a broad energy band of 3.37 eV. The thermal and mechanical stability makes it useful in laser technology, electronics and optoelectronics (Bacaksiz et al. 2008; Wang et al. 2005). It has multiple uses in hydrogen production, ceramic industry, biomedicine, pro-ecological systems or plant disease management (Wang 2008; Chaari and Matoussi 2012; Özgür et al. 2005; Bhattacharyya and Gedanken 2007; Ludi and Niederberger 2013; Elmer et al. 2018). ZnO has three crystal structures in nanoparticles: wurtzite, zinc-blende and rock salt (Özgür et al. 2005; Moezzi et al. 2012). Similar to other metallic engineered nanoparticles, its size range is within 1–100 nm (Marslin et al. 2017). ZnO crystals can appear as 1 D, 2 D or 3 D structures with a large variety of morphology (Kołodziejczak-Radzimska and Jesionowski 2014), which affects the toxicity and influences of the nanoparticles (Stanković et al. 2013). It was estimated that nearly 30,000 tons of ZnO NPs is used per year in various products, such as textiles, pigments, semiconductors, industrial coatings, medicines, food additives and sunscreens (Mukherjee et al. 2016; Mishra et al. 2017; The Global Market for Metal and Metal Oxide Nanoparticles 2010–2027). ZnO NPs are often used as a nanofertiliser; however, they can increase the Zn ion levels in the soil in excess of expected concentrations (Watson et al. 2015).

Many factors have an impact on the exact outcome of the ZnO NP–plant interactions, including the investigated plant species, the size of the applied particles, the

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duration or existence of pre-cultivation, the concentration and duration of ZnO exposure or the applied growth conditions, namely germination test in Petri dishes or hydroponics or pot experiment. Up to now, it has been well reviewed that how the metallic nanoparticles (including ZnO NPs) may influence the development, the photosynthetic activity or other processes there is still much lack of our knowledge (Marslin et al. 2017; Hou et al. 2018; Pullagurala et al. 2018b).

2 The Uptake and Transport of ZnO NPs in Higher Plants

The uptake and accumulation of ZnO NPs is not fully understood up to this date, but it consists of two major pathways: zinc ion release and direct nanoparticle accumulation (Poynton et al. 2011). Zinc homeostasis is regulated in plants through transporter proteins, which control the intake, mobilisation and compartmentalisation of the ion (Clemens 2001). Well-known zinc transporter protein families are as follows: ZIP (ZRT, zinc transporter proteins; IRT-like protein) are tasked with zinc uptake in the root system, root to shoot translocation is realised via HMA (heavy metal ATPases) proteins, and MTP (metal tolerance protein) is used for compartmentalisation and detoxification (Pence et al. 2000). The uptake and translocation of ZnO NPs is much less investigated. In soil, the interactions between soil grain, clay minerals and nanoparticles determine the transport, the fate and the behaviour of nanoparticles (Darlington et al. 2009). García-Gómez et al. (2018b) presented in case of several vegetables and crops that pH values or other characteristics of the soil may determine the impact of ZnO NPs on plants (Table 1c). ZnO NPs are absorbed on kaolin surfaces, followed by a dissolution (Scheckel et al. 2010). Accumulation of ZnO NPs on root surface areas is supported by multiple sources. Lin and Xing (2008) detected large amounts of nanoparticles adhered to the root epidermis in ryegrass applying scanning electron microscopy. In *Schoenoplectus tabernaemontani* ZnO NPs were observed on the root surface (Zhang et al. 2015), as well as in case of maize roots where nanoparticles were absorbed on the surface (Lv et al. 2015). The accumulation of zinc was examined in ZnO NP-treated sweet potato tubers and large amounts of Zn accumulated in the outer layers (namely the peel) of the tubers, which could have been nanoparticles (Bradfield et al. 2017; Table 1d). There are some reports of ZnO NPs invading tissues or even cells in ryegrass (Lin and Xing 2008), onion (Kumari et al. 2011), maize (Zhao et al. 2012; Lv et al. 2015), rice (Chen et al. 2018a) and *Schoenoplectus tabernaemontani* (Zhang et al. 2015). Since plants in natural conditions usually grow in the soil, the root tissues and cells are the first targets of ZnO NP "invasion", mainly at higher doses. The main symptoms of ZnO NP toxicity are reduced root length and consequently higher root diameter, sometimes fewer root hairs (Lee et al. 2013; Balážová et al. 2018; Table 1d). Some reports showed that ZnO NPs may be transported until the endodermis using both apoplastic and symplastic pathway then they can enter the vascular cylinder (Lin and Xing 2008; reviewed by Lee et al. 2013; Lv et al. 2015) but there is not much evidence of translocation to shoot as nanoparticles. Chen et al.

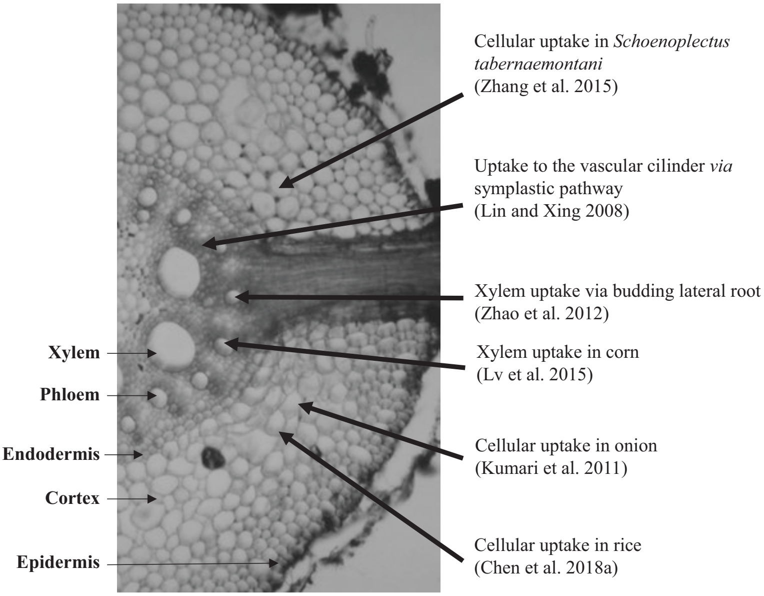

Fig. 1 Comparison of ZnO NP uptake by different plant species at the tissue level

(2018a) demonstrated the presence of ZnO NPs as dark dots both in the intercellular space and in the cytoplasm of the root cortical cells in the elongation zone which supports the dual (symplastic and apoplastic) transport theory. Besides, it was exhibited that cell organelles can be also influenced, Lin and Xing (2008) detected ZnO NPs in the nuclei and cytoplasm, as well. The root uptake and the potential transport mechanisms of ZnO NPs are depicted in Fig. 1.

Raliya et al. (2015) detected ZnO NPs with TEM in the shoot and leaves of tomato plants but only after foliar application and not soil amendment. In Indian mustard, ZnO NPs were translocated to the leaves (Rao and Shekhawat 2014). At the same time, in soybean (López-Moreno et al. 2010) and mesquite roots (Hernandez-Viezcas et al. 2011), there were no detectable ZnO NPs, which indicates that nanoparticles entering the tissues is not a common phenomenon across all species.

It is well known that plant cell wall has pores that measure up to several nanometres (Carpita et al. 1979), which should filter out nanoparticles and prevent them from entering the cell. It has been reported that, in bacteria, ZnO NPs may increase the permeability generating “holes” in cell walls to reach the plasma membrane (Stoimenov et al. 2002; Brayner et al. 2006). Between cells, nanoparticles are most likely transported via plasmodesmata, which have a reported diameter of ~40 nm (Tilney et al. 1991). To enter the cortex, there are two possible ways: (1) entering it through the plasmodesmata as previously mentioned, or (2) potentially entering it via budding lateral roots which temporarily allow nutrients to pass the Casparian strip (Bell et al. 2003; Lv et al. 2015).

It seems that ZnO NPs may influence living cells via three distinct pathways: (1) biotransformation and release of Zn (II) ions, (2) surface interaction of nanoparticles resulting in harmful molecules such as reactive oxygen species (ROS) and (3) direct interaction of nanoparticles with cell metabolism, like photosynthesis and nutrient homeostasis (Brunner et al. 2006). ZnO NPs undergo biotransformation due to humic acid and other organic root exudates then they penetrate the root through the root pores and it is accompanied by the uptake processes, as it has been described in many studies and accumulate in tissues of plants, mainly in ionic form (Chen et al. 2018a; López-Moreno et al. 2010; Raliya et al. 2015; Balážová et al. 2018). In rice, Chen et al. (2018a) demonstrated that the plants can accelerate the degradation process of ZnO NPs, resulting in a higher Zn ion concentration. Similar results were obtained by Lv et al. (2015) in maize, proving the importance of this pathway. It is important to note that the effects of nanoparticles are more than just the release or effects of Zn ions, which has been described by numerous studies (Lin and Xing 2008; Chen et al. 2018a; Poynton et al. 2011; Zhang et al. 2015; Bradfield et al. 2017). Zn accumulation triggered by ZnO NP treatment has a lower translocation factor to shoot when compared to direct Zn ion treatment in cilantro (Pullagurala et al. 2018a, b; Table 1a), ryegrass (Lin and Xing 2008), *Schoenoplectus tabernaemontani* (Zhang et al. 2015), unlike previous examples in maize (Zhao et al. 2012) translocation factors were between 0.8 and 2.

3 ZnO NPs and Oxidative Stress

Metal oxide nanoparticles have distinct antimicrobial properties, which are well examined (Sirelkhatim et al. 2015), and one of the proposed mechanisms is the generation of ROS (Huang et al. 2008; Xia et al. 2008; Lipovsky et al. 2009). ZnO NPs will produce ROS under visible or UV light, like superoxide anion or hydrogen peroxide (Sawai et al. 1998; Padmavathy and Vijayaraghavan 2008; Zhang et al. 2008; Jalal et al. 2010) and there are even reports of ROS generation in darkness, as well (Zhou et al. 2008; Adams et al. 2015). Since the electronic band structure of ZnO immediately absorbs photons with greater energy than 3.3 eV and as a result h^+ positive holes and free electrons in conduction band are created (Seven et al. 2004). This positive hole is a strong oxidant and it will create reactive hydroxyl radicals (Zhang et al. 2012). It is also documented that nanoparticles can enhance ROS generation in plants (Wang et al. 2014; Barhoumi et al. 2015). The effect on ZnO NPs on the homeostasis of ROS seems to be dose dependent, as described by Javed et al. 2017, where lower (0.1, 1.0 and 10 mg/L) ZnO concentrations had beneficial effects in *Stevia* plants such as increased antioxidant activity, but in contrast, at higher doses ZnO had toxic effect due to oxidative burst (Table 1a).

Positively, ZnO can stimulate the enzymatic antioxidants, e.g. superoxide dismutase (SOD), catalase (CAT) or peroxidase (POX), as it has been determined by Rizwan et al. (2019) (Table 1a), wherein treated wheat SOD and POX activities increased compared to control, similarly, in cotton lipid peroxidation (LP) decreased

Table 1a Positive effects of ZnO NPs in higher plants

	Plant name	Size of ZnO NP	Duration of pre-cultivation	Concentration of the ZnO exposure	Time of exposure	Growth conditions	Plant organ investigated	Main effects (physiological/ biochemical/ morphological)[a]	Reference
Positive effect	*Allium cepa* L.	~18 nm	nd	10, 20, 30 or 40 μg/ml	Sprayed three times with 15 days interval	Six month rested bulbs planted in pots	Aboveground parts	Plant growth ↑ and earlier flowering after 20 and 30 μg/ml ZnO; seed number per umbel and 1000 seed weight ↑	Laware and Raskar (2014)
	Arachis hypogea L. var. 'K-134'	25 nm	–	100, 1000 and 2000 ppm for seed priming; 2 or 30 g/15 L for foliar spraying	3 hours seed priming; two foliar spraying	Pot and field experiment	Whole plant	Germination % ↑, seedling vigour ↑, root and shoot length ↑, plant height ↑, earlier flowering, chlorophyll content ↑, productivity ↑; foliar spraying with ZnO NPs increased pod yield	Prasad et al. (2012)
	Capsicum annuum L.	nd	14 day-long growing	0.25, 0.5 and 0.75 g	6 h	Moistened blotter paper (in Petri dishes)	Whole seedling	Concentration-dependent ↑ of seed germination, root length ↑, seedling length ↑; shoot length ↓ at the lowest concentration	Afrayeem and Chaurasia (2017)
	Caspicum annuum L. var. California	nd	29 days (?)	50 mg/L	21 days (foliar spraying once a week)	Hydroponics	Whole plant	No change in plant height, root length ↑ ns, chlorophyll content ↑ ns	Méndez-Argüello et al. (2016)
	Cicer arietinum L. var. HC-1	16–30 nm	10 days	1.5 or 10 ppm	15 days	Pot experiment (vermiculite, irrigated with nutrient solution)	Whole plant	Shoot DW ↑ at lower ZnO concentration, root growth ↓ at higher ZnO concentration, total biomass ↑; SOD and peroxidase activity↓ in shoot	Burman et al. (2013)

(continued)

Table 1a (continued)

	Plant name	Size of ZnO NP	Duration of pre-cultivation	Concentration of the ZnO exposure	Time of exposure	Growth conditions	Plant organ investigated	Main effects (physiological/ biochemical/ morphological)[a]	Reference
	Cucumis sativus L. 'Poinsett 76'	8 nm	–	50, 100, 200, 400, 800 and 1600 mg/L	Until 65% of the seeds were germinated	Petri dishes (germination test)	Whole plant	Germination % ↑ at 400–1600 mg/L concentration, root length ↑ at 200–800 mg/L ZnO NP	de la Rosa et al. (2013)
	Coriandrum sativum L.	24 ± 3 nm	–	100, 200 and 400 mg/kg (soil)	35 days	Pot experiment (soil)	Leaves	Photosynthetic pigment content ↑; lipid peroxidation ↓ at 400 mg/kg ZnO NP	Pullagurala et al. (2018a)
	Daucus carota L. cv. Pusa Rudhira	nd	nd	50, 100 and 150 ppm	nd	Field experiment with foliar ZnO NP spraying	Whole plant	Number of leaves ↑, root length and root diameter ↑ at 100 ppm ZnO combined with 50 ppm FeO NP	Elizabath et al. (2017)
	Fagopyrum esculentum Moench	<50 nm	–	50, 500, 2000 and 4000 ml/L	1 week or 3 days (?)	Petri dishes with wet filter paper (germination test)	Whole plant	Biomass ↑at low Zn NP but ↓ ns at higher conc., root growth and the number of root hairs ↓ at high ZnO NP; MDA content ↓, SOD and peroxidase activity ↓	Lee et al. (2013)
	Fragaria x ananassa Duch. cv. Chandler	nd	–	50, 100 or 150 ppm	135 days	Field experiment	Shoot	Plant height ↑; 150 ppm ZnO + 150 ppm FeO had a positive effect on the growth parameters and fruit yield	Kumar et al. (2017)
	Gossypium hirsutum L.	2–54 nm	7 days	0, 25, 50, 75, 100 and 200 mg/L	21 days	Hydroponics	Whole plants	Root length and shoot length ↑; photosynthetic pigment level and total soluble protein content ↑, SOD and POX activity ↑; MDA level and CAT activity ↓	Venkatachalam et al. (2017b)

	Hordeum vulgare L.	30 nm	–	0, 5, 10, 20, 40 and 80 mg/kg	7 days germination then 21 days cultivation	Petri dishes (germination) then pot experiment	Whole plant	No effect on seed germination and root elongation; SOD activity ↓, CAT activity ↑	Doğaroğlu and Köleli (2017)
	Lactuca sativa L.	90 ± 10 nm	–	0, 1, 10 and 100 mg/kg (soil)	7 weeks	Pot experiment (soil)	Whole plants	Biomass and photosynthetic rate ↑ at 10 mg/kg ZnO NP	Xu et al. (2018)
	Phaseolus vulgaris L. var. red hawk kidney	93.8 or 84.1 nm	–	62.5, 125, 250 and 500 mg/kg (soil)	45 days	Soil (pot experiment)	Whole plant	No effect on germination, pod production and chlorophyll content. Coated ZnO NPs increased root and leaf length	Medina-Velo et al. (2017)
	Phaseolus vulgaris L. var. Valentino	nd	33 or 44 days	25, 50, 100 and 200 ppm	nd	Field experiment with foliar ZnO NP spraying at 33 and/or 44 days after sowing	Whole plant	Shoot length and root length ↑; chlorophyll a + b content ↑ and ↑ ns at higher ZnO concentration	Ewais et al. (2017)
	Sesamum indicum L.	12 ± 3 nm and 18 ± 2 nm	–	0.1, 0.25, 0.5, 1 and 2 g/L	nd	Soil (pot experiment)	Whole plant	Root length and shoot length ↑, photosynthetic pigment content ↑ mainly at lower concentration	Narendhran et al. (2016)
	Solanum lycopersicum L. cv. PKM-1	35 nm	20 days	2, 4, 8 or 16 mg/L	15, 30 or 45 minutes	Sand then sandy loam	Whole plant	Shoot length and root length ↑ and ↑ ns; photosynthetic activity, carbonic anhydrase activity and antioxidant enzyme activities ↑ in a dose- and duration-dependent way	Faizan et al. (2018)

(continued)

Table 1a (continued)

	Plant name	Size of ZnO NP	Duration of pre-cultivation	Concentration of the ZnO exposure	Time of exposure	Growth conditions	Plant organ investigated	Main effects (physiological/ biochemical/ morphological)[a]	Reference
	Solanum lycopersicum L. hybr. ‘tomato cherry super sweet 100’	25 ± 3.5 nm	Seed priming for 1 h	0, 10, 100, 250, 500, 750 and 1000 mg/L	5 days	Petri dishes (germination test)	Whole plant	Germination % ↓ at 1000 mg/kg concentration	Raliya et al. (2015)
			14 days before foliar or soil application of ZnO NP	0, 10, 100, 250, 500, 750 and 1000 mg/L or /kg (soil)	Foliar spraying or soil exposure on 14-day-old plants, then analysis on the 28th, 40th and 66th day	Pot experiment (soil)	Whole plant	Foliar application: plant height ↑ ns and ↓ ns, root length ↑ at 100–250 mg/kg but ↓ ns at higher concentration, chlorophyll content ↑ at 1000 mg/kg; soil exposure: plant height ↑ at 250–500 mg/kg, root length ↓ at higher concentration, chlorophyll content ↑ and ↑ ns	
	Stevia rebaudiana Bertoni	34 nm	–	0, 0.1, 1.0, 10, 100 or 1000 mg/L	4 weeks	Culture medium	Shoots formed from nodal regions	Highest percentage of shoot formation at 1 mg/L ZnO; steviol glycoside content ↑ and oxidative stress ↑; concentration-dependent phytotoxic effects at higher ZnO concentration	Javed et al. (2017)

	Triticum aestivum L.	34.4 nm	–	25, 50, 75 and 100 ppm	24 h seed priming	Soil (pot experiment)	Whole plant	Plant height ↑, biomass ↑, photosynthetic pigment content and activity ↑, Zn content ↑ concentration-dependently	Munir et al. (2018)
	Vigna radiata L.	~18 nm	–	0, 20, 40, 60, 80 and 100 mg/L	3 h then germinating for 7 days	Germination test	Whole plant	Germination % ↑; root and shoot length ↑ and ↑ ns	Jayarambabu et al. (2014)
	Vigna unguiculata L.	30 nm	–	250, 500 and 750 ppm	6 hours seed treatment	Soil (pot experiment)	Whole plant	Seedling length ↑, germination % ↑, seedling fresh weight ↑ and vigour index↑, shoot and root length ↑, productivity ↑	Srinivasan et al. (2017)
	Vigna unguiculata L.	75 nm	–	0, 100, 500, 1000 and 2000 ppm	Overnight seed soaking	Wet filter paper (Petri dishes) and pot experiment	Whole seedling	High ZnO NP uptake, positive effects on plant growth	Suriyaprabha et al. (2018)

[a] ↑ indicates significant and ↑ ns indicates non-significant increase, while ↓ refers to significant decrease and ↓ ns to non-significant reduction

Table 1b Stress alleviating effects of ZnO NPs in higher plants

	Plant name	Size of ZnO NP	Duration of pre-cultivation	Concentration of the ZnO exposure	Time of exposure	Growth conditions	Plant organ investigated	Main effects (physiological/ biochemical/morphological)[a]	Reference
Stress alleviation	*Triticum aestivum* L. ecotype 'Stolichna' and 'Acveduc'	nd	–	1:100	Seed pretreatment for 4 hours	Sand culture	Leaves	Negative effects of drought ↓; antioxidant enzyme activity and water content of the leaves ↑, stabilised photosynthetic pigments	Taran et al. (2017)
	Leucaena leucocephala (Lam.) de Wit	2–64 nm	5 days	25 mg/L	15 days	Hydroponics	Whole plants	Alleviation of Cd- and Pb-induced stress: total soluble protein and photosynthetic pigment content ↑, lipid peroxidation ↓ in leaves; antioxidant enzyme (SOD, CAT, POX) activities ↑	Venkatachalam et al. (2017a)
	Oryza sativa L.	15–137 nm (68.1 avg)	50 days	100 mg/L	6 days	Hydroponics	Whole plants	As(III) and As(V) accumulation of the roots ↓ after ZnO NP treatment, but had no effect on As(V) content in the shoots	Wang et al. (2018b)
	Triticum aestivum L.	20–30 nm	15 days	0, 25, 50, 75 and 100 mg/kg	Four foliar spraying: 2, 4, 6 and 8 weeks after sowing	Soil from a polluted field (pot experiment)	Whole plant	Plant growth ↑, photosynthesis ↑ and grain yield ↑; Cd content ↓; electrolyte leakage ↓; SOD and POD activity ↑ in leaves; generally Cd toxicity ↓	Hussain et al. (2018)
	Triticum asestivum L. var. Lassani-2008	20–30 nm	Seed priming for 1 h	0, 25, 50, 75 and 100 mg/L	124 days	Pot experiment (soil contaminated with Cd)	Whole plant	Plant height ↑, spike length ↑, photosynthetic pigment content ↑, Cd content of root and shoot↓; POD and SOD activity ↑ in leaves	Rizwan et al. (2019)

[a] ↑ indicates significant and ↑ ns indicates non-significant increase, while ↓ refers to significant decrease and ↓ ns to non-significant reduction

Table 1c Mixed or concentration-dependent effects of ZnO NPs in higher plants

	Plant name	Size of ZnO NP	Duration of pre-cultivation	Concentration of the ZnO exposure	Time of exposure	Growth conditions	Plant organ investigated	Main effects (physiological/ biochemical/ morphological)[a]	Reference
Mixed or concentration-dependent effect	*Allium cepa* L.	<35 and 50 nm	Until the roots reached 2–3 cm in length	10, 100 and 1000 μg/ml	18 h	Glass beaker, darkness, watered	Root	Dose-dependent genotoxicity of meristematic cells	Demir et al. (2014)
	Allium cepa L.	~50 nm	3 days	5, 10 and 20 μg/ml	3 days	Hydroponics	Root	Root growth ↓ concentration-dependently	Ghodake et al. (2011)
	Allium cepa L.	20 nm	–	10, 20, 30 and 40 mg/L	10 days	Wet filter paper (germination test)	Whole seedling	Mitotic index ↓ and number of chromosomal abnormalities ↑ at 30–40 mg/L ZnO NP, germination % and seedling growth ↑ns at lower concentration	Raskar and Laware (2014)
	Allium sativum L.	4 nm	Until roots of the bulbs reached 2 cm length	0, 10, 20, 30, 40 and 50 mg/L	24 h	Beakers with water	Roots	Concentration-dependent root growth and mitosis inhibition. Mitotic aberrations	Shaymurat et al. (2012)
	Arabidopsis thaliana	20–45 nm	–	20, 50, 100 and 200 mg/L	14 days	1/2 MS media	Whole plant	Lateral root number ↑, imbalance in nutrient homeostasis	Nair and Chung (2017)
	Avena sativa L.	nd	–	750, 1000 and 1250 mg/kg seed	10 min priming	Wet paper and field experiment	Whole plant	Germination %, seedling vigour and yield ↑ at low concentration, root and shoot length ↓ at higher doses; however, no toxicity was observed	Maity et al. (2018)

(continued)

Table 1c (continued)

	Plant name	Size of ZnO NP	Duration of pre-cultivation	Concentration of the ZnO exposure	Time of exposure	Growth conditions	Plant organ investigated	Main effects (physiological/ biochemical/ morphological)[a]	Reference
	Beta vulgaris L.	<100 nm	–	0.075, 0.84, 1.68 or 3.36 g ZnO NP/ kg (soil) which was equivalent to 20, 225, 450 and 900 mg Zn/kg (soil)	7–10 + 35 days	Calcareous or acidic soil (pot experiment)	Whole plant	Biomass ↓ ns at 900 mg/kg Zn (calcareous soil); oxidative enzyme activities ↓ (calcareous soil)	García-Gómez et al. (2018b)
	Brassica oleracea var. capitata L. cv. Golden Acre	17.4 ± 4.9 nm	–	0.001, 0.1, 1, 10, 100, 500 and 1000 μg/ml	6 days	Wet filter paper (germination test)	Root	Germination and root elongation is less sensitive to NPs than to free ions	Pokhrel and Dubey (2013)
	Cucumis sativus L.	<100 nm	–	0.075, 0.84, 1.68 or 3.36 g ZnO NP/ kg (soil) which was equivalent to 20, 225, 450 and 900 mg Zn/kg (soil)	7–10 + 35 days	Calcareous or acidic soil (pot experiment)	Whole plant	Biomass ↓ ns at 900 mg/kg Zn (calcareous soil); oxidative enzyme activities ↓ (calcareous soil)	García-Gómez et al. (2018b)
	Daucus carota L. cv. Danvers Half Long	30–40 nm	16 weeks	0.5, 5, 50 and 500 mg/kg DW (soil)	13 weeks	Pot experiment (sand)	Whole plant	Root and total biomass ↓ dose-dependently; Zn accumulation in the taproot periderm	Ebbs et al. (2016)
	Glycine max L.	8 nm	–	500, 1000, 2000 and 4000 mg/L	Until 65% of control roots were 5 mm long	Petri dishes with wet filter paper (germination test)	Whole plant	Germination was not affected; root elongation ↑at 500 mg/L but ↓ at 2000 mg/L ZnO NP	López-Moreno et al. (2010)

	Glycine max L.	10 nm	18 days	50, 100 and 500 mg/kg (soil)	48 days	Soil (pot experiment)	Whole plant	Altered nutritional values of soybean	Peralta-Videa et al. (2014)
	Lactuca sativa L.	<100 nm	–	0.075, 0.84, 1.68 or 3.36 g ZnO NP/kg (soil) which was equivalent to 20, 225, 450 and 900 mg Zn/kg (soil)	7–10 + 35 days	Calcareous or acidic soil (pot experiment)	Whole plant	Germination % (acidic soil); oxidative enzyme activities ↓ (calcareous soil)	García-Gómez et al. (2018b)
	Pennisetum glaucum L.	<50 nm	–	0, 100, 250, 500, 750 and 1000 mg/L	7 days	Petri dishes (germination test)	Whole plant	Germination % ↓; root length ↑ but ↓ at 500–1000 mg/L. concentration; shoot length ↑ ns and ↓ ns	Jain et al. (2017)
	Phaseolus vulgaris L. cv. Contender	<100 nm	–	0.075, 0.84, 1.68 or 3.36 g ZnO NP/kg (soil) which was equivalent to 20, 225, 450 and 900 mg Zn/kg (soil)	7–10 + 35 days	Calcareous or acidic soil (pot experiment)	Whole plant	Germination % ↓ (acidic soil); photosynthetic pigments ↓ (acidic soil); oxidative enzyme activities ↓ (calcareous soil)	García-Gómez et al. (2018b)
	Phaseolus vulgaris L. var. Pinto Saltillo	<50 nm	–	1, 3 and 6 mg/L	120 days	Pot experiment with irrigation of ZnO NP	Whole plant	No change in root length; shoot length ↓ ns; no change in chlorophyll content	Medina-Péréz et al. (2018)
	Phaseolus vulgaris L. var. red hawk	93.8 or 84.1 nm	–	125, 250 and 500 mg/kg (soil)	87 ± 11 days (until maturity)	Soil (pot experiment)	Produced seeds	ZnO NPs have low residual transgenerational effects on the properties of produced seeds	Medina-Velo et al. (2018)

(continued)

Table 1c (continued)

	Plant name	Size of ZnO NP	Duration of pre-cultivation	Concentration of the ZnO exposure	Time of exposure	Growth conditions	Plant organ investigated	Main effects (physiological/biochemical/morphological)[a]	Reference
	Pisum sativum L.	<100 nm	–	0.075, 0.84, 1.68 or 3.36 g ZnO NP/kg (soil) which was equivalent to 20, 225, 450 and 900 mg Zn/kg (soil)	7–10 + 35 days	Calcareous or acidic soil (pot experiment)	Whole plant	Photosynthetic pigments ↓ (acidic soil); oxidative enzyme activities ↓ (calcareous soil) but ROS ↑ (acidic soil)	García-Gómez et al. (2018b)
	Raphanus sativus L.	<100 nm	–	0.075, 0.84, 1.68 or 3.36 g ZnO NP/kg (soil) which was equivalent to 20, 225, 450 and 900 mg Zn/kg (soil)	7–10 + 35 days	Calcareous or acidic soil (pot experiment)	Whole plant	Germination % ↑ (acidic soil); oxidative enzyme activities ↓(calcareous soil)	García-Gómez et al. (2018b)
	Salicornia persica 'Akhani' ecotype	50 nm particle size, 677,450, Sigma–Aldrich	10 days	100 and 1000 mg/L	14 days	1/2 MS medium	Whole plant	Concentration-dependent inhibition of plant growth: shoot length ↓, root length ↓ and root diameter ↑ at 1000 mg/L concentration. Loss of root tip viability, RNS and ROS ↑, oxidative stress	Balážová et al. (2018)
	Solanum lycopersicum L. cv. cerasiforme	<100 nm	–	0.075, 0.84, 1.68 or 3.36 g ZnO NP/kg (soil) which was equivalent to 20, 225, 450 and 900 mg Zn/kg (soil)	7–10 + 35 days	Calcareous or acidic soil (pot experiment)	Whole plant	Germination % ↓ (acidic soil); oxidative enzyme activities ↓ (calcareous soil)	García-Gómez et al. (2018b)

	Solanum lycopersicum L. cv. Moneymaker	nd	3 weeks	0, 200, 400 and 800 mg/L	2 weeks	Pot experiment (soil)	Whole plant	Plant growth ↓ at 400–800 mg/L concentration, and photosynthetic rate ↓, chlorophyll content ↓ but carotenoid content ↑ at 400–800 mg/L concentration, SOD, CAT and APX activity ↑ concentration-dependently	Wang et al. (2018a)
	Trifolium alexandrium L.	nd	–	750, 1000 and 1250 mg/kg seed	10 min priming	Wet paper and field experiment	Whole plant	Germination %, seedling vigour and yield ↑ at low conc., root and shoot length ↓ at higher doses; however no toxicity was observed	Maity et al. (2018)
	Triticum aestivum L.	<100 nm	–	0.075, 0.84, 1.68 or 3.36 g ZnO NP/kg (soil) which was equivalent to 20, 225, 450 and 900 mg Zn/kg (soil)	7–10 + 35 days	Calcareous or acidic soil (pot experiment)	Whole plant	Biomass ↓ ns at 900 mg/kg Zn (calcareous soil); oxidative enzyme activities ↓ (calcareous soil)	García-Gómez et al. (2018b)
	Zea mays L.	<100 nm	–	0.075, 0.84, 1.68 or 3.36 g ZnO NP/kg (soil) which was equivalent to 20, 225, 450 and 900 mg Zn/kg (soil)	7–10 + 35 days	Calcareous or acidic soil (pot experiment)	Whole plant	Photosynthetic pigments ↑ ns (acidic soil); oxidative enzyme activities ↓ (calcareous soil)	García-Gómez et al. (2018b)

(continued)

Table 1c (continued)

	Plant name	Size of ZnO NP	Duration of pre-cultivation	Concentration of the ZnO exposure	Time of exposure	Growth conditions	Plant organ investigated	Main effects (physiological/ biochemical/ morphological)[a]	Reference
	Zea mays L. Golden variety	24 ± 3 nm	–	0, 50, 100, 200, 400, 800 and 1600 mg/L	15 days	Petri dishes with wet filter paper (germination test)	Whole plant	Temperature may alter the plant-ZnO NP interaction, e.g. at 20 °C germination ↓ at 400 and 1600 mg/L, while at 25 °C germination ↓ only at 400 mg/L	López-Moreno et al. (2017)
	Zea mays L. cv. Zhengdan 958	30 ± 5 nm	1 week	2, 5, 10, 15, 20, 40, 60, 80 and 100 mg/L	7 days	Hydroponics	Whole plant	Zn accumulation; ZnO NPS mainly occurred in the rhizodermis	Lv et al. (2015)
	Zea mays L. cv. NK-199	17.4 ± 4.9 nm	–	0.001, 0.1, 1, 10, 100, 500 and 1000 µg/ml	7 days	Wet filter paper (germination test)	Root	Germination and root elongation is less sensitive to NPs than to free ions; ZnO caused tunnelling-like effect in the root tips	Pokhrel and Dubey (2013)
	Zea mays L.	386–1116 nm	30 days	100, 200, 400, and 800 mg/kg (soil)	30 days	Pot experiment	Whole plant	High Zn accumulation and translocation to shoot	Zhao et al. (2012)

[a] ↑ indicates significant and ↑ ns indicates non-significant increase, while ↓ refers to significant decrease and ↓ ns to non-significant reduction

Table 1d Negative effects of ZnO NPs in higher plants

	Plant name	Size of ZnO NP	Duration of pre-cultivation	Concentration of the ZnO exposure	Time of exposure	Growth conditions	Plant organ investigated	Main effects (physiological/ biochemical/ morphological)[a]	Reference
Negative effect	*Allium cepa* L.	~50 nm	3 days	5, 10 and 20 μg/ml	3 days	Hydroponics	Root	Concentration-dependent root growth inhibition	Ghodake et al. (2011)
	Allium cepa L.	<100 nm	Grown until 2–3 cm root lenght	25, 50, 75 and 100 mg/L	4 h	Hydroponics	Root	Lipid peroxidation ↑, chromosomal aberrations ↑ and mitotic index ↓	Kumari et al. (2011)
	Allium sativum L.	4 nm	Until radicals reached 2 cm length	10, 20, 30, 40, 50 mg/L	24 hours	Beakers with water	Root	Concentration-dependent root growth and mitosis inhibition, mitotic aberrations	Shaymurat et al. (2012)
	Arabidopsis thaliana ‘Col-0’	~44 nm	5 days at 4 °C (in dark)	400, 2000 and 4000 mg/L	18 days	1/2 MS medium	Whole plant	Seed germination % ↓, number of leaves ↓, root elongation ↓	Lee et al. (2010)
	Beta vulgaris L. cv. Detroit	<100 nm	–	3, 20 and 225 mg Zn/kg (soil)	60 and 90 days	Calcareous or acidic soil (pot experiment)	Leaves	6–12-fold higher Zn content and ROS ↑ in leaves (acidic soil), MDA content ↑, altered photosynthetic pigment ratios	García-Gómez et al. (2018a)
	Brassica juncea L.	<100 nm	Germination	0, 200, 500, 1000 and 1500 mg/L	96 h	Hydroponics	Whole plant	Plant biomass and chlorophyll ↓, lipid peroxidation and proline content ↑	Rao and Shekhawat (2014)

(continued)

Table 1d (continued)

	Plant name	Size of ZnO NP	Duration of pre-cultivation	Concentration of the ZnO exposure	Time of exposure	Growth conditions	Plant organ investigated	Main effects (physiological/ biochemical/ morphological)[a]	Reference
	Brassica napus L. cv. Hayola 401	<50 nm	–	5, 10, 25, 50, 75, 100, 125, 250 and 500 mg/L	6 days	Petri dishes (germination test)	Whole plant	Germination % ↓ns, root length ↓, shoot length ↓ ns and ↓	Kouhi et al. (2014)
	Carthamus tinctorius L. cv. Isfahan	nd	Until the two leaf stage	0, 10, 100, 500 and 1000 mg/L	Three spraying with 14 day intervals	Soil (pot experiment)	Leaves (?)	Malondialdehyde (MDA) content ↑	Hafizi and Nasr (2018)
	Cucumis sativus L.	50 nm	–	2000 mg/kg (soil)	8 weeks	Soil (pot experiment)	Whole plant	Soil dehydrogenase activity ↓; no change in biomass and shoot length; root length ↓ ns	Kim et al. (2011)
	Cucumis sativus L.	≤50 nm	2 h	10, 20, 50, 100, 200 and 500 mg/L	5–12 days	Petri dishes (filter paper or soil)	Whole plant	Germination % ↓ns, root length and shoot length ↓	Kumar et al. (2015)
	Glycine max L.	<50 nm	7 days	500 ppm	3 days	Hydroponics	Whole plant	Severe oxidative burst, changes in protein expression	Hossain et al. (2016)
	Helianthus annuus L. hybr. Kongo	nd	2 weeks	0.6 and 6 mg/l	1, 2 and 3 weeks	Hydroponics	Whole plant	Plant growth and protein production ↓	Sturikova et al. (2018)

	Ipomoea batatas var. Georgia jet	30–40 nm	7 days	100, 500 and 1000 mg/kg DW (soil)	130 days	In potting mix, under natural conditions	Tubers	Biomass and number of tubers ↓ at 1000 mg/kg ZnO; >70% of the accumulated Zn was in the flesh (compared to the peel)	Bradfield et al. (2017)
	Lemna minor L.	20 nm	nd	0, 0.03, 0.3, 1, 10, 30 mg/L for 1 or 7 days; 0, 1, 10 mg/L for 6 weeks	1 day, 1 week or 6 weeks	Hydroponics, 1/2 Hutner's medium	Whole plant	Photosynthetic efficiency of PSII ↓ after 1 day; biomass and root length↓ after 1 week; Zn content ↑ and growth ↓ until 6 weeks	Chen et al. (2018b)
	Lolium perenne L.	20 ± 5 nm	2 weeks germination+1 week	10, 20, 50, 100, 200 and 1000 mg/L	12 days	Hydroponics	Root	Plant biomass ↓, root tissue degradation	Lin and Xing (2008)
	Medicago sativa L. 'WL 535'	8 nm	–	50, 100, 200, 400, 800 and 1600 mg/L	Until 65% of the seeds were germinated	Petri dishes (germination test)	Whole plant	Germination % ↓ at 800-1600 mg/L conc., root length ↓ at 400-1600 mg/L ZnO NP	de la Rosa et al. (2013)
	Oryza sativa L.	nd	1–3 days	10, 100, 500 and 1000 mg/L	7 days	Moistened filter paper	Root	No change in germination %; root length ↓ and number of roots ↓at 100–1000 mg/L	Boonyanitipong et al. (2011)

(continued)

Table 1d (continued)

	Plant name	Size of ZnO NP	Duration of pre-cultivation	Concentration of the ZnO exposure	Time of exposure	Growth conditions	Plant organ investigated	Main effects (physiological/ biochemical/ morphological)[a]	Reference
	Oryza sativa L. ssp. japonica	<50 nm	14 days	25, 50 and 100 mg/L	7 days	Hydroponics	Whole plant	Biomass ↓, photosynthetic pigment content ↓, root length ↓, shoot length ↓; oxidative damage; root-to-shoot transport of ZnO NPs	Chen et al. (2018a)
	Oryza sativa L.	≤50 nm	2 h	10, 20, 50, 100, 200 and 500 mg/L	5–12 days	Petri dishes (filter paper or soil)	Whole plant	No change of germination %, root length and shoot length	Kumar et al. (2015)
	Oryza sativa L. Jijing No.6.	<50 nm	–	0, 25, 50, 100, 500, 1000 and 2000 mg/L	2 h priming then germination for 5 days	Wet filter paper (germination test)	Whole plant	Germination % was not affected at 2000 mg/L concentration, root length ↓ at 100–2000 mg/L, shoot length was not affected	Yang et al. (2015)
	Pisum sativum L. cv. Negret	<100 nm	–	3, 20, and 225 mg Zn/kg (soil)	30 and 60 days	Calcareous or acidic soil (pot experiment)	Leaves	6–12-fold higher Zn content and ROS ↑ in leaves (acidic soil), MDA content ↑, altered photosynthetic pigment ratios	García-Gómez et al. (2018a)

	Schoenoplectus tabernaemontani	19–47 nm	4 weeks	10, 100 and 1000 mg/L	3, 7, 14 and 21 days	Hydroponics	Whole plant	Growth inhibition and zinc accumulation	Zhang et al. (2015)
	Solanum lycopersicum L. 'Bombyx'	30 nm	nd	10, 25, 50 and 75 nmol/L	48 h	Soft agar (in Petri dishes)	Whole plant	Vigour index ↓, Azotobacter-treatment ameliorated ZnO tolerance	Boddupalli et al. (2017)
	Solanum lycopersicum L. 'Roma FV'	8 nm	–	50, 100, 200, 400, 800 and 1600 mg/L	Until 65% of the seeds were germinated	Petri dishes (germination test)	Whole plant	Germination % ↓ at 800–1600 mg/L concentration, root length ↓	de la Rosa et al. (2013)
	Solanum lycopersicum L.	<50 nm	–	0, 100, 250, 500, 750 and 1000 mg/L	7 days	Petri dishes (germination test)	Whole plant	Germination % ↓ at 750–1000 mg/L; root length ↓ at 500–1000 mg/L. concentration; shoot length ↓ at 750–1000 mg/L ZnO NP	Jain et al. (2017)
	Solanum melongena L.	18 nm	nd	100, 250, 500 and 1000 mg/L	15 days	Petri dishes (germination test)	Whole plant	Shoot length ↓ and root length ↓	Baskar et al. (2018)
	Triticum aestivum 'HD 2967'	30 nm	nd	10, 25, 50 and 75 nmol/L	48 h	Soft agar (in Petri dishes)	Whole plant	Vigour index ↓, Azotobacter-treatment alleviated ZnO toxicity	Boddupalli et al. (2017)

(continued)

Table 1d (continued)

	Plant name	Size of ZnO NP	Duration of pre-cultivation	Concentration of the ZnO exposure	Time of exposure	Growth conditions	Plant organ investigated	Main effects (physiological/ biochemical/ morphological)[a]	Reference
	Triticum aestivum L.	<100 nm	–	500 mg/kg	14 days	Grown in sand	Whole plant	Root growth ↓; bioaccumulation of Zn as Zn-phosphate in shoot; lipid peroxidation ↑, GSSG ↑, peroxidase and catalase activity ↑ in root, chlorophyll content ↓ in shoot	Dimkpa et al. (2012)
	Triticum aestivum L.	<50 nm	–	0, 100, 250, 500, 750 and 1000 mg/L	7 days	Petri dishes (germination test)	Whole plant	Germination % ↓ and root length ↓ from 250 mg/L ZnO NP; no change in shoot length	Jain et al. (2017)
	Triticum aestivum L.	≤50 nm	2 h	10, 20, 50, 100, 200 and 500 mg/L	5–12 days	Petri dishes (filter paper or soil)	Whole plant	Germination % ↓ ns, root length and shoot length ↓	Kumar et al. (2015)
	Triticum aestivum L.	15.37 nm	15 days	0, 100 and 200 mM	7 days	Hydroponics	Whole plant	Seedling fresh weight ↓, chlorophyll content ↓, H_2O_2 content and lipid peroxidation ↑, antioxidant enzyme activities ↓	Tripathi et al. (2017)

	Vigna angularis L.	Nanorods with ~64 nm length	1 week	0–200 μg/ml then 200 μg/ml	1 + 2 or 3 weeks	Hydroponics	Whole plant	Germination % ↑; root length ↓ and ↓ ns, while shoot length ↑ ns and ↑; ROS ↑, induction of oxidative stress, chlorophyll and carotenoid content ↓	Jahan et al. (2018)
	Vigna radiata L.	≤50 nm	2 h	10, 20, 50, 100, 200 and 500 mg/L	5–12 days	Petri dishes (filter paper or soil)	Whole plant	Germination % ↓ ns, root length and shoot length ↓	Kumar et al. (2015)
	Zea mays L. Zhengdan No. 958.	<50 nm	–	0, 25, 50, 100, 500, 1000 and 2000 mg/L	2 h priming then germination for 7 days	Wet filter paper (germination test)	Whole plant	Germination % was not affected at 2000 mg/L conc., root length ↓ at 500–2000 mg/L, shoot length root length ↓ at 2000 mg/L	Yang et al. (2015)
	Zea mays L. Golden variety	24 ± 3 nm	–	0, 400 and 800 mg/kg (soil)	84 days	Pot experiment (soil)	Whole plant	Stomatal conductance, photosynthesis and yield of corn plants ↓ at 800 mg/kg ZnO NP; no change in shoot length	Zhao et al. (2015)

[a] ↑ indicates significant and ↑ ns indicates non-significant increase, while ↓ refers to significant decrease and ↓ ns to non-significant reduction

along with an antioxidant enzyme (SOD and POX) activity increase (Venkatachalam et al. 2017b; Table 1a).

Nonetheless, numerous studies focused on toxic effects, like oxidative stress and malondialdehyde (MDA) formation expressing lipid peroxidation as a response to larger doses of ZnO NPs. Mukherjee et al. (2014) described oxidative stress in green peas treated with 500 mg/kg (soil) ZnO NPs. An oxidative burst was observed in soybean (Hossain et al. 2016), in beet and pea (García-Gómez et al. 2018a) and in safflower (Hafizi and Nasr 2018) (Table 1d). In onion, a concentration-dependent increase of LP was detected, followed by a decreased mitotic index and an increased number of chromosomal aberrations suggesting a genotoxic effect of ZnO NPs (Kumari et al. 2011), which was further supported by Shaymurat et al. (2012) in garlic and Ghosh et al. (2016) in onion, tobacco and broad bean. Dose-dependent activation of SOD, CAT and ascorbate peroxidase (APX) was observed in tomato, while the plants showed growth retardation at higher (400–800 mg/L) ZnO NP concentration (Wang et al. 2018a; Table 1c). In *Salicornia* a significant increase in ROS and reactive nitrogen species (RNS) levels were displayed, coupled with a significant MDA increment. Peroxidase and APX activity declined, while Mn SOD, Fe SOD and cAPX were induced in response to the treatment (Balážová et al. 2018; Table 1c). Furthermore, in rice ZnO NP treatment triggered positive response of antioxidant enzymes was examined at molecular level, where levels of CSD1, CSD2, CATa, CATb, CATc, MSD1, FSD1, APXa and APXb were measured and mostly upregulated (Chen et al. 2018a). Summarily, we can say data published up to now suggest that ZnO NPs may act controversially in respect of oxidative processes depending on several factors like concentration, duration of exposure, age of the plant, the application of priming, etc.

4 ZnO NPs Influence Nutrient Homeostasis and Photosynthetic Efficiency

The last unexplained biochemical mechanism of ZnO NP effect is the impact on nutrient homeostasis and photosynthesis. As seen previously, different concentrations of ZnO have different effects on photosynthesis ranging from beneficial to toxic effects. In cilantro (Pullagurala et al. 2018a) chlorophyll content increased in response to the treatment, the same as in case of peanut (Prasad et al. 2012), cotton (Venkatachalam et al. 2017b) or bean (Ewais et al. 2017) (Table 1a). Foliar application of 10 ppm ZnO caused an increment of phosphorus and chlorophyll content in cluster bean (Raliya and Tarafdar 2013). On the contrary, in green peas (Mukherjee et al. 2014), Indian mustard (Rao and Shekhawat 2014), corn (Zhao et al. 2015), *Arabidopsis* (Wang et al. 2015) and wheat (Tripathi et al. 2017) chlorophyll content attenuated in ZnO-treated plants (Table 1d). In rice, a significant decline of chlorophyll content was observed and upon the examination of chlorophyll synthesis genes CHLD and CHLM expression levels reduced as response to the treatment cells, followed by the increment of root diameter (Balážová et al. 2018) or lateral root number (Nair and Chung 2017), which suggests the potential reorientation of root cells like in stress-induced morphogenic responses (SIMR, Potters et al. 2007) (Table 1c and 1d).

In the background of these negative processes, probably Zn content of the different plant organs was increased, causing changes in the physiological homeostasis, like lipid peroxidation, oxidative stress, nutrient imbalance or decreased protein production, as here we previously discussed.

5.2 ZnO NP Affects Reproductive Processes

Although there are many data about the impact of ZnO NPs on vegetative growth, it is noteworthy to mention that these agents may influence the reproductive traits of the plants, as well. There are both positive and negative impacts published. Laware and Raskar (2014) discovered that foliar spraying with ZnO NP may cause earlier flowering and elevated seed production of onion. Similarly, induced productivity of cowpea (Srinivasan et al. 2017; Table 1a) and bean (Ewais et al. 2017) was recorded after ZnO NP foliar application. At the same time, in pot experiments filled with treated soil bean exhibited a decrease of fruit number and seed number per pod (Medina-Pérez et al. 2018).

6 Stress Alleviation by ZnO NPs

In some cases, stress-alleviating effect of ZnO NPs was also exhibited, for example in case of drought-stressed wheat (Taran et al. 2017), Cd- and Pb-stressed *Leucaena leucocephala* (Venkatachalam et al. 2017b) or As-treated rice (Wang et al. 2018b) (Table 1b).

7 Conclusions and Future Perspectives

Nowadays, ZnO nanoparticles (NPs) seem to be an indispensable part of our life due to the wide range of its usage (e.g. medicines with anticancer and antimicrobial activities or nanofertilisers in agriculture), therefore their emission to the environment and food chain remarkably has grown. Here, we tried to overview that plants being immovable how evolve strategies to protect themselves from these abiotic stress factors, but it was also proved that ZnO NPs may mitigate the negative effects of other toxic agents like heavy metals. Though there are an increasing number of reports dealing with the impact of ZnO NPs on plants, there is still little evidence of the potential translocation from root to shoot and there is only a few information about the anatomical changes in the root and/or shoot-like cell wall modifications triggered by ZnO NPs.

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