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Review

Nano-Priming against Abiotic Stress: A Way Forward towards Sustainable Agriculture

Abdul Salam [1,*], Muhammad Siddique Afridi [2], Muhammad Ammar Javed [3], Aroona Saleem [3], Aqsa Hafeez [4], Ali Raza Khan [1], Muhammad Zeeshan [5], Baber Ali [4], Wardah Azhar [1], Sumaira [6], Zaid Ulhassan [1] and Yinbo Gan [1,*]

[1] Zhejiang Key Lab of Crop Germplasm, Department of Agronomy, College of Agriculture and Biotechnology, Zhejiang University, Hangzhou 310058, China
[2] Department of Plant Pathology, Federal University of Lavras (UFLA), Lavras 37200-900, MG, Brazil
[3] Institute of Industrial Biotechnology, Government College University, Lahore 54000, Pakistan
[4] Department of Plant Sciences, Quaid-i-Azam University, Islamabad 45320, Pakistan
[5] Guangxi Key Laboratory of Agro-Environment and Agro-Products Safety, Guangxi Colleges and Universities Key Laboratory of Crop Cultivation and Tillage, Agricultural College, Guangxi University, Nanning 530004, China
[6] Department of Biotechnology, Quaid-i-Azam University, Islamabad 45320, Pakistan
* Correspondence: abdul_pk@zju.edu.cn (A.S.); ygan@zju.edu.cn (Y.G.); Tel.: +86-571-8898-2204 (Y.G.)

Abstract: Agriculture is directly linked to human life, providing food for survival and health. It is threatened by a number of challenges, such as climate change, resource depletion, and abiotic stresses, including heavy metals (HMs), salinity, drought, etc. Various strategies have been employed to palliate the phytotoxic effects of these stressors from the soil–plant system. Nanotechnological approaches have emerged as a promising tool for increasing crop productivity and promoting sustainable agriculture. Interestingly, the seed nano-priming approach has shown potential against all of the above-mentioned abiotic stress factors and has improved crop productivity. The application of nanoparticles (NPs) via seed priming is an innovative and cost-effective approach that improves seed germination and subsequent plant growth by activating plant physiological processes and providing tolerance against various stresses. The seed priming with NPs induces electron exchange and increases surface reaction capabilities related to plant cell and tissue components. This review aims to provide an overview of recent advances and research findings on seed nano-priming and the possible mechanism of plant stress-tolerance augmentation against various stresses. Furthermore, we also shed light on gaps in studies conducted in previous years, which will open new avenues for future research.

Keywords: seed priming; nanoparticles; abiotic stress; germination; plant growth; sustainability

Citation: Salam, A.; Afridi, M.S.; Javed, M.A.; Saleem, A.; Hafeez, A.; Khan, A.R.; Zeeshan, M.; Ali, B.; Azhar, W.; Sumaira; et al. Nano-Priming against Abiotic Stress: A Way Forward towards Sustainable Agriculture. *Sustainability* **2022**, *14*, 14880. https://doi.org/10.3390/su142214880

Academic Editor: Shibao Chen

Received: 23 September 2022
Accepted: 8 November 2022
Published: 10 November 2022

1. Introduction

The global population is increasing rapidly, and estimates suggest it will reach nearly 9.6 billion by 2050. Therefore, agricultural production needs to rise by 70–100% to feed the growing population [1–3]. In the present state of affairs, agriculture is facing several challenges in terms of biotic and abiotic factors that limit its productivity. Shortage of freshwater resources, climate change, and the low use-efficiency of existing agrochemicals further aggravate these stresses on crops, resulting in lower yields [4,5]. Around 70% of global water is utilized for food production, and this figure is likely to reach 83% by 2050 to meet the expanding global demand for food [6]. Salinity and drought cause billions of dollars in crop loss [7–9]. Agrochemical use is an increasingly prominent aspect of modern agriculture. A large portion of the 2.5 million tons of pesticides applied annually is either lost to the air and run-off or unable to reach the target effectively [2,10,11]. Heavy-metals contamination is another widespread and severe problem for the environment, crop productivity, and food safety [12,13]. It has been reported that around 70% of HMs and their amalgams that enter the human body come from food [14]. Moreover, the continuous release of metallic waste material in agricultural soil induces adverse effects on the soil's pH, salinity, and fertility. Global climatic conditions have further worsened the problem, imposing extra encumbrance on crop production and food security. Plants at early growth stages such as seed germination and seedling development are more prone to these environmental constraints, leading to poor growth and limited yield [15]. Innovative technologies are needed in modern agriculture to achieve crop sustainability and higher yield production. Figure 1 visualizes an overview of emerging pollutants and other abiotic stress factors inducing stress in plants and their possible counteraction with the application of different NPs.

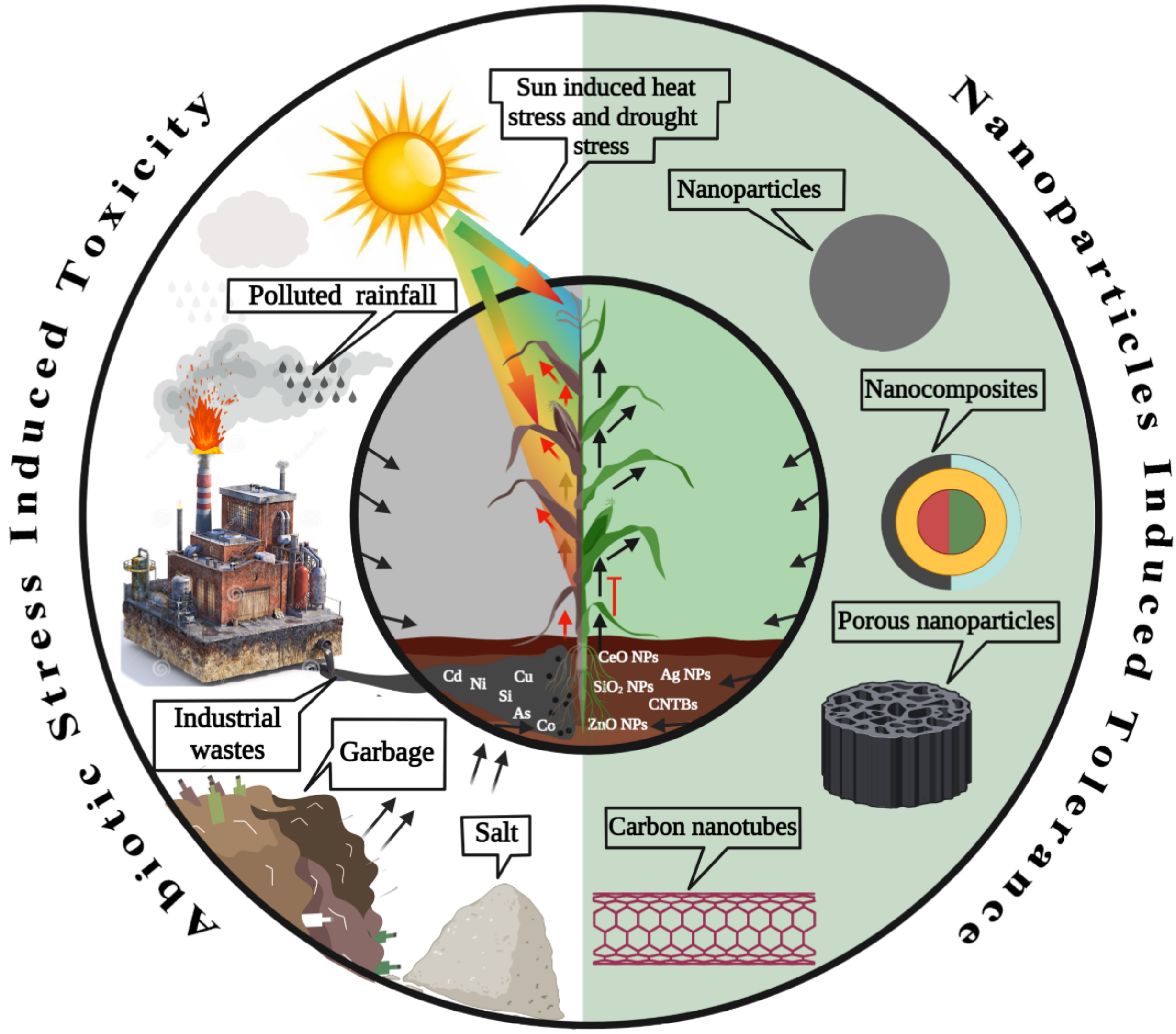

Figure 1. A schematic diagram shows different abiotic stress factors inducing stress and the potential of NPs to alleviate stress and promote plant growth.

2. Nanotechnology and Agriculture

Nanotechnology is an emerging field that has taken root in all aspects of life and has led to a new scientific revolution. Particles synthesized at the nanoscale having at least a one-dimension size of less than 100 nm form the building block of nanotechnology [16]. Nanotechnology likely provides a novel platform to achieve a dynamic balance between agricultural production and environmental sustainability. It has successfully aided the agro-technological insurgency by surveilling a critical agricultural control process in the wake of its miniature size. Furthermore, it has attracted scientists based on its many potential benefits, such as augmented stress tolerance and increased crop production, upgraded food safety and subsequent quality, absorption of enriched nutrients from the soil, depletion in agricultural inputs, and so on. The main objective of nanotechnology in agriculture is to curtail the use of chemicals, minimize the loss of nutrients during fertilization, and augment crop tolerance against biotic and abiotic stress, leading to escalated yield [17]. Nanotechnology can potentially improve the agriculture and food industries by developing innovative nanotools to improve crop stress tolerance and uplift plants' nutritional absorption [18]. These nanotools are none other than nanoparticles in the form of nanofertilizers, nanopesticides, and nanosensors to track products and nutrient levels to increase productivity as well as provide protection against biotic and abiotic stress factors [19,20]. Thus, the objective of this review lies in the domains mentioned above to aid researchers in knowing about the recent advances concerning seed nano-priming techniques and the current research progress in this field that can help shape modern-era sustainable agriculture strategies.

Nanofertilizers increase crop yield and quality by proliferating the uptake of nutrients while lowering production costs, contributing to agricultural perseverance. Many scientists are still working on nanofertilizers to know more about their underlying mechanisms. Plants absorb nanomaterials (NMs) via seed as seed priming, stomata as a foliar spray, and root as exogenously applied. Kah et al. [21] demonstrated that nanofertilizers were 18–29% more efficient than conventional fertilizers. Similarly, Liu and Lal [22] used calcium and phosphorus hydroxyapatite NPs which increased *Glycine max* productivity by 20–33% more than traditional phosphorus. Another researcher reported a 10% increase in leaf chlorophyll content by applying iron, phosphorus, and nitrogen in the southern pea plant [23]. Besides these, there are many other NPs reported, including zinc oxide (ZnO), cerium oxide (CeO_2), silicon oxide (SiO_2), CNTs (carbon nanotubes), and titanium oxide (TiO_2), which have resulted in improved plant growth and stress tolerance. SiO_2 and TiO_2 have ameliorated seed germination and nitrogen fixation and enhanced *Glycine max* growth [24,25]. Similarly, CNTs are widely used for inducing stress tolerance and improving plant growth in vegetables (i.e., cucumber, rape, tomato, etc.) as well as in crops (i.e., corn and soybean) as fertilizer [26,27]. Nanoparticles are widely used as a pesticide against biotic stress in agriculture. They are a savior of water and energy since they are utilized in lesser amounts and more infrequently than conventional pesticides [28]. Studies have suggested that silver (Ag) NPs can control *Fusarium culmorum*, *Botrytis cinerea*, *Biploaris sorokinniana*, and *Megnaporthe grisea* [29–31]. Other nanopesticides include copper (Cu) NPs, silica NMs, and Si–Ag NPs, reported to control pest diseases such as powdery mildew [32,33]. Furthermore, it is reported that gold (Au) NPs, nanodots, magnetic NPs, and carbon nanostructures are being used as nanobiosensors. Nanobiosensors are defined by their biological receptors with unique specialties towards correspondent analysts such as DNA or protein [34]. Nanobiosensors are made up of nano-sized components that act as bio-receptors on a sensor and send signals to recognition elements to recognize single or maybe multiplex solutes. The fascinating characteristics of nanobiosensors are fictionalization, miniaturization, and immobilization, which incorporate bio-components of the transduction framework into a complicated structure to enhance NM analytical performance [35].

3. Seed Nano-Priming

Seed nano-priming is one of the effective methods that alter the metabolism of seeds along with their signaling pathways, influencing germination, establishment, and plant lifecycle. Several studies have demonstrated that seed nano-priming has a variety of advantages, including enhanced plant growth and development, and higher nutritional quality. Nano-priming can regulate biochemical processes while maintaining the balance among growth hormones of plants and reactive oxygen molecules [36]. It is used to boost plant growth and metabolism, regulate physiology under abiotic stress, and improve germination synchronization. It also increases crop resistance to biotic or abiotic stress environments, which assists in minimizing the use of pesticides and fertilizers [37]. According to the latest research, seed nano-priming can stimulate various genes during germination, particularly those attributed to plant stress tolerance [38–40]. The application of nanoparticles via seed priming is an innovative area of study, and the preliminary results have been promising [41–43]. It can also be utilized for seed protection since many NPs have antimicrobial properties via antimicrobial compounds [44]. Furthermore, nano-priming can potentially target the bio-fortification of seeds to promote food production and quality [45]. After priming, nanoparticles find their way to the seed tissues and remain there. Images of confocal microscopic observation show the localization of NPs in seed tissues after 24 h priming, as shown in Figure 2 [46].

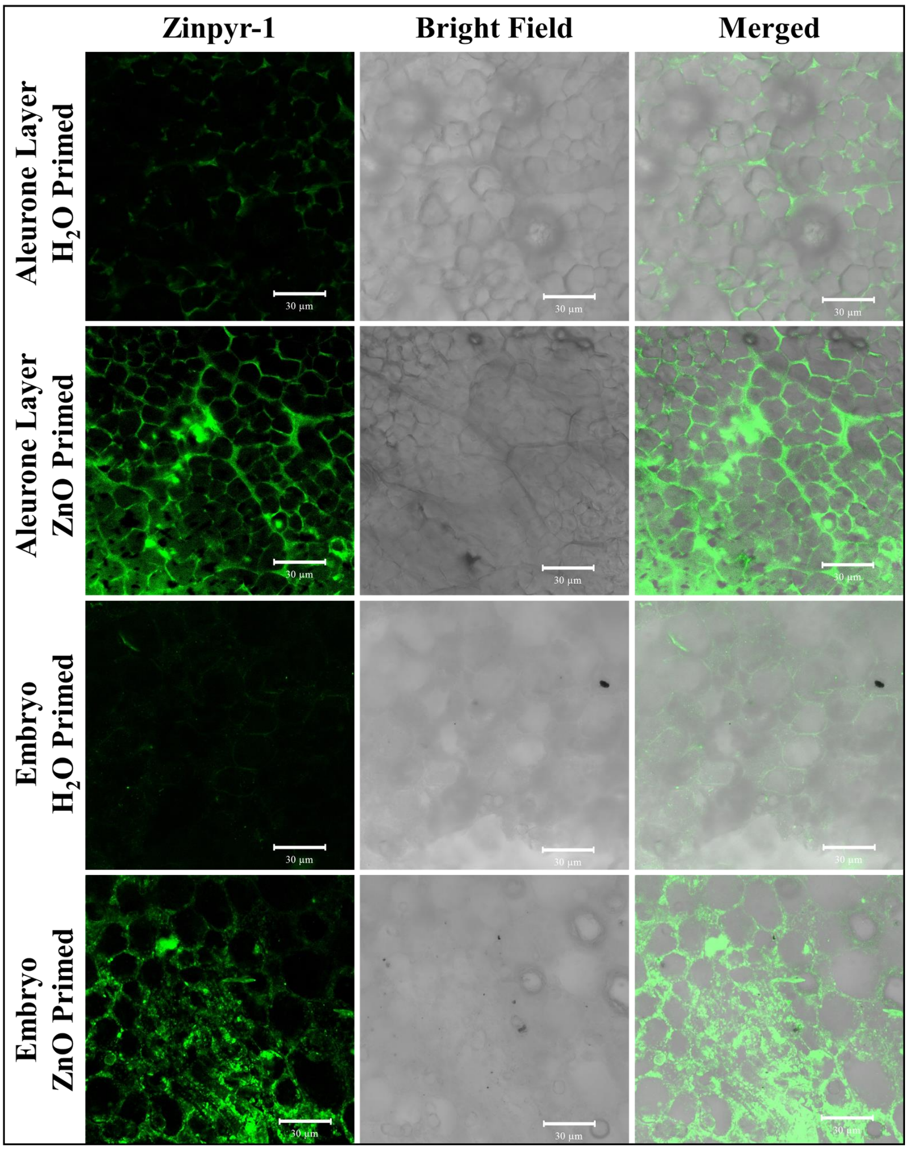

Figure 2. Nanoparticle localization in seed tissues after being primed with ZnO NPs for 24 h. ZnO NPs labeled with zinpyr-1 complex (Zinc fluorescent) localized in the seed aleurone layer and seed embryo, confirming NPs' entry to seed tissues. Reproduced with permission from Salam et al. [46], Copyright 2022, Elsevier.

4. Effect on Seed Germination

Plant life begins with the germination of seed, and productive germination is critical to the survival and conservation of plant species [47]. Plant establishment is subjected to quick and uniform seed germination, whereas poor germination makes plants vulnerable to environmental stress [48]. Consequently, knowledge about the germination and then the development of the primed seeds has great value. Seed priming is an efficient approach that leads to instant and reconcilable germination, resulting in increased plant growth [49–51]. Several studies have demonstrated that it minimizes the seedling time of emergence and produces vigorous plants that are tolerant to various abiotic and biotic stresses [52]. Current advances in seed priming, particularly the use of NPs, have been proven to be extremely promising approaches for the germination of seeds and plant development compared to traditional seed-priming methods [41,53]. Mohanlall et al. [54] reported that carbon NPs improved the growth of the root and shoot of *Vigna radiata* and *Trichilia dregeana* to a remarkable extent. In another study, rapeseed germination was up 20.2–32.5% and 91–93% during 24 and 48 h, respectively, after being primed with nanotubes, i.e., "Taunit-M," graphene, and "Taunit-MD" in comparison with non-primed seeds [55]. Similarly, some scientists found faster seed germination in cell cultures of maize, rice, tobacco, barley, switchgrass, and soybean with the application of graphene nanotubes or single-walled carbon nanohorns (SWCNHs). In 2014, Aslani et al. reported that the germination of tomato seeds was boosted by 90% using multi-walled carbon nanotubes (MWCNTs) [56].

Moreover, Das et al. [57] reported a quickened seed germination of Swiss chard by treating it with iron pyrite (FeS_2) NPs. Other researchers reported that seed priming with FeS_2 NPs enhanced seed germination and improved production of spinach, mustard, alfalfa, fenugreek, chickpea, carrot, and sesamum plants [58,59]. Some recent progress on the positive role of nano-priming as a plant growth regulator for plant growth and development is presented in Table 1. Despite all these positive outcomes of seed germination, there are also downsides to seed nano-priming, as the effect of NPs is mainly dependent on the concentration and duration of plant exposure to them. Mohanlall et al. [54] demonstrated that the application of silver and gold NPs subdued germination of orthodox seeds. Similarly, CNTs inhibited the development of the roots in *Solanum lycopersicum* L. [56]. Furthermore, seed priming with nano-CuO led to a significant reduction in seed germination of rice, and caused seed germination inhibition in soybean and chickpea [60,61]. The concentration of NPs is a key factor, and this should be carefully considered during the formulation of seed priming, as it is well known that metal-based NPs are toxic at high concentrations to all living organisms [62–64].

Table 1. Seed priming with NPs and their subsequent effect on plant growth and development.

S No.	Priming Agent	Concentration/Size	Priming Duration	Target Plant	Effect on Plant Growth and Development	Ref.
1	TiO_2 NPs, ZnO NPs, and Ag NPs	750, 1000, 1250 mg kg^{-1}/35–40 nm 750, 1000, 1250 mg kg^{-1}/100 nm 750, 1000, 1250 mg kg^{-1}/85 nm	3 min/5 times	*Capsicum annum* L.	Increased seed germination rate, seedling vigor index, root, shoot length, and CAT activity in aged chili seeds.	[65]
2	ZnO NPs	5, 10, 25, 50, 100 and 200 mg L^{-1}/15 nm	12 h	*Oryza sativa* L.	Enhanced plant Zn contents, improved seed germination, overall growth, and agronomical characteristics.	[66]
3	ZnO NPs	1, 10, 100, 1000, 5000 mg L^{-1}/20, 40, 60 nm	20 min	*Phaseolus vulgaris* L.	None of the concentrations and sizes harmed the seeds. NPs mostly detected in the seed coat, while 10 mg L^{-1} entered the inner seed and increased plant weight.	[67]
4	SiO2 NPs and MWCNTs	25, 50, 75, 100, 125 µg mL^{-1}/80.75 nm, 54.64 nm	6 h	*Brassica juncea* L.	Increased agronomic traits, silique length, and yield per silique.	[68]

Table 1. *Cont.*

S No.	Priming Agent	Concentration/Size	Priming Duration	Target Plant	Effect on Plant Growth and Development	Ref.
5	Ag NPs and TiO2 NPs	25, 50, 100, 200, 400 µg mL^{-1}/50–100 nm	24 h	*Solanum lycopersicum* L.	Ag NPs at 25 and 50 µg mL^{-1} increased seed germination and seedling vigor index, whereas TiO_2 NPs reduced seed germination and seedling vigor and increased antioxidant activity.	[69]
6	MnO NPs	10, 20, 40, 80 mg L^{-1}/22–39 nm	14 h	*Citrullus lanatus* L.	Improved chlorophyll contents, phenolic acids, and phytohormones.	[70]
7	Lignin NPs	80, 312, 1250, 5000, 20,000 mg L^{-1}/50 nm	8 h	*Zea mays* L.	Induced beneficial effects on root and shoot growth, increased chlorophyll, carotenoids, and anthocyanin contents.	[71]
8	Cu-chitosan NPs	0.01, 0.04, 0.08, 0.012, and 0.16% (*w*/*v*)/150 ± 12.4 nm	4 h	*Zea mays* L.	Increased α-amylase and protease enzymes also increased the total protein content in germinating seeds.	[72]
9	Cu-chitosan NPs	0.0625 mmol L^{-1}/174.2 ± 1.5 nm	N/A	*Zea mays* L.	Increased root shoot length, dry mass, leaf area, and gas exchange attributes.	[73]
10	Fe_3O_4 NPs	0, 20, 40, 80, 160 mg L^{-1}/30 nm	8 h	*Zea mays* L.	Increased seed germination and vigor, plant length, and biomass.	[74]
11	Fe_2O_3 NPs	50, 100, 150 mg L^{-1}/23 nm	14 h	*Citrullus lanatus* T.	Increased root and shoot length as well as non-enzymatic antioxidants.	[43]
12	nanoCS/TPP-GA3, nanoALG/CS-GA3	0.005 mg mL^{-1} and 0.0005 mg mL^{-1}/195, 450 nm	12 h	*Solanum lycopersicum* L.	Increased fruit production and overall productivity up to 4 fold.	[75]
13	Lignin NCs with GA3	0.5, 1, and 1.5 mg mL^{-1}/200–250 nm	30 Min	*Eruca vesicaria* and *Solanum lycopersicum* L.	Improved germination percentage, increased stem and root length as well as their fresh and dry weight both under in-vitro and in-vivo conditions.	[76]
14	Fe_2O_3 NPs	0 ppm to 600 ppm/80 nm	12 h	*Triticum aestivum* L.	Increased grain iron content, germination percentage, seed vigor index I, II and shoot length.	[77]
15	Co and MoO_3 NPs	1 L for 40 kg seeds, 0.5 mL/20 g seed/60–80 nm	2 h	*Glycin max* L.	Improved seed vigor indices and plant growth as well as biomass	[78]

N/A: data not available.

5. Effects on Plant Growth and Physiology under Abiotic Stress

Besides modulating seed germination, nano-priming has also been proven to impact other characteristics of plants, such as stability, growth, and physiology, by protecting them from abiotic stress [79–81]. This is achieved by escalating plant tolerance against abiotic stress and altering nutrient uptakes, biochemical mechanisms, cellular antioxidants, photosynthetic efficacy, and molecular mechanism [82]. Many scientists intend to learn about nano-priming effects on plant growth and physiology under abiotic stress. In 2021, Rai-Kalal et al. [83] demonstrated that, in contrast to non-primed seeds, there was more proline and catalase in SiO_2-treated Purna HI 1544 (wheat cultivar), resulting in increased tolerance against drought stress by better maintenance of biochemical balance and photosynthetic parameters. A study highlighted improved root and shoot length by applying MWCNTs on *Dodonaea viscosa* L. and *Alnus subcordata* under drought stress by increasing nutrient uptake and photosynthetic efficiency [84,85]. Another study reported that wheat nano-priming with ZnO NPs increased shoot height and improved overall plant physiology, including growth under salinity stress [86]. Similarly, nano-priming of *Brassica napus* with ZnO NPs increased shoot and root length by 25.63% and 48.17%, respectively, resulting in a significant increase in seedling growth [87]. Moreover, some researchers reported augmentation in plant growth of maize and tomatoes owing to increased chlorophyll content and anti-oxidative enzymes by priming with TiO_2 NPs, inducing resistance against salt stress [88,89]. There was also an interpretation of enhanced plant growth against temperature stress when maize seeds were nano-primed with NO NPs, as it is efficient in boosting CAT (catalase) and SOD (superoxide dismutase) activities in the plant [90]. Furthermore, Ivani et al. [91] and Hojjat and Kamyab [92] examined the nano-priming effects of SiO_2 NPs and Ag NPs on fenugreek plants under salt stress. They concluded that these NPs had increased various plant defense mechanisms (i.e., alteration in turgor pressure, opening or closing of stomata, etc.), resulting in enhanced growth characteristics. Konate et al. [93] studied the effect of magnetic NPs, particularly Fe_3O_4, on wheat seedlings and reported a positive influence on plant growth as it inhibits the uptake of HMs (Cu, Cd, and Zn), subsequently reducing toxicity in the wheat plant.

6. Effects on Plant Metabolism under Abiotic Stress

Nanoparticles can directly alter plant and seed metabolism and interrupt hormonal production, thus making plants more resistant to environmental stresses. The production of reactive oxygen species (ROS), which is involved in various metabolic pathways, is enhanced along with an increase in the mobilization of storage proteins and the level of phytohormones [94]. Moreover, NPs can increase the seed's water uptake potential, resulting in increased activity of enzymes [95,96]. Furthermore, NPs reduce the level of over-produced ROS under stress in the seed under abiotic stress conditions because of the increased activity of enzymes such as guaiacol-peroxidase, CAT, and SOD to minimize seed cell damage [97]. When seeds are stored at low temperatures for extended periods, they tend to be aged, decreasing their germination rate, producing ROS and decreasing their antioxidant level, and negatively impacting the seeds' metabolic potential [98]. The application of NPs can optimize the ROS level in seeds and enhance their germination even at late ages. Several compounds can be used to coat the biogenic NPs to reduce the level of ROS in seeds [39]. Table 2 summarizes different nanoparticles used for abiotic stress mitigation.

Table 2. Application of NPs via seed priming for mitigation of abiotic stresses and their mechanism of action.

S No.	Stress Factor	Priming Agent	Concentration/Size	Priming Duration	Target Plant	Stress Mitigation Mechanism	Ref.
1	Cobalt	ZnO NPs	500 mg L^{-1}/20 nm	24 h	*Zea mays* L.	Increased seed zinc content, decreased oxidative damage, improved antioxidant activity, photosynthetic apparatus, and ultrastructure.	[46]
2	Cadmium	ZnO NPs and Fe NPs	25, 50, 75, 100 mg L^{-1}/20–30 nm, 5, 10, 15, 20 mg L^{-1}/50–100 nm	20 h	*Triticum aestivum* L.	Increased Zn and Fe content, respectively. The NPs increased plant growth and nutrient contents while decreasing Cd uptake and, consequently, Cd toxicity.	[99]
3	Lead	ZnO and Fe_3O_4 NPs	0, 50, 100, 200, 300 and 500 mg L^{-1}/70 nm, 55 nm	16 h	*Basella alba* L.	At 200 mg L^{-1}, both NPs decreased lead uptake and reduced toxicity by reducing H_2O_2 and MDA content and increasing SOD, POD, CAT, and proline activity.	[100]
4	Manganese	SNPs	12.5, 25, 50, 100, 200 µM/23 nm	18 h	*Helianthus annuus* L.	Improved antioxidants and phenolic compounds while reducing oxidative damage and lipid peroxidation.	[101]
5	Chromium	Nitric oxide NPs	100 µM/N/A	24 h	*Oryza sativa* L.	Together with spermidine, nitric oxide reduced chromium accumulation in plants leading to reduce oxidative stress and increased carbon assimilation	[102]
6	Salt	CeO_2 NPs	500 mg L^{-1}/1.8 nm	24 h	*Gossypium hirsutum* L.	NPs localized in cotyledon and root apical meristem. Enhanced nutrient uptake, reduced ROS accumulation, and up-regulated terpene synthase genes.	[38]
7	Salt	TiO_2 NPs	40, 60, 80 ppm/25 nm	24 h	*Zea mays* L.	Enhanced phenylalanine ammonia lyase, potassium ions, and antioxidants while reducing sodium ions, MDA, and electrolyte leakage.	[89]

Table 2. *Cont.*

S No.	Stress Factor	Priming Agent	Concentration/Size	Priming Duration	Target Plant	Stress Mitigation Mechanism	Ref.
8	Salt	ZnO NPs	50, 100 and 500 mg L^{-1}/12–21.0 nm	24 h	*Triticum aestivum* L.	Changed polypeptide patterns which resulted in improved plant growth, photosynthetic pigments, overall photosynthetic efficacy, and leaf ultrastructure.	[86]
9	Salt	ZnO NPs	0.1%, 0.2%, 0.3%/N/A	12 h	*Spinacia oleracea* L.	Reversed salt stress-induced reduction in biochemical and growth attributes, improved antioxidant defense system.	[103]
10	Salt	CeO_2 NPs	100 µMol/4.1 nm	8 h	*Brassica napus* L.	Improved ROS scavenging ability and up-regulated salicylic acid-related genes.	[104]
11	Salt	CeO_2 NPs	100 µMol/8.5 nm	1, 3, 8 h	*Brassica napus* L.	Increased seed waster and NPs uptake capacity, increased α-amylase activity of seed, and consequently improved plant nutrient content.	[105]
12	Drought	zero-valent Cu NPs	5.556 mg L^{-1}/30–40 nm	8 h	*Zea mays* L.	It decreased drought-induced damage by enhancing ROS-scavenging enzymatic activity, and light-harvesting pigments.	[106]
13	Drought	ZnO NPs	5, 10, 15, 25, 50 ppm/20–30 nm	24 h	*Oryza sativa* L.	Increased plant growth attributes, biomass, proline, SOD, POD, and CAT levels while reducing MDA content.	[107]
14	Drought	Fe_2O_3 NPs	0, 25, 50, 75, and 100 ppm/N/A	24 h	*Linum usitatissimum* L.	Increased plant growth, biomass, and yield attributes improved antioxidant enzymatic activity while decreasing oxidative damage.	[108]
15	Drought	Si NPs	0, 100, 200, 500 mg L^{-1}/25 nm	N/A	*Calendula Officinalis* L.	Si NPs at higher levels deposited in root cell walls after priming which resulted in enhanced germination indices and subsequent growth attributes under drought stress.	[109]

N/A: data not available.

As seed nano-priming is a water-based technique, where seeds are first hydrated properly and later dried, or some physical method can be used such as ultraviolet light (UV) [110], it follows that adequate water must be provided to induce the metabolic pathways for pre-germination without fear of radicle emergence. This process affects seed metabolism at the cellular and molecular levels (e.g., enhanced capability for protein synthesis, post-translational modifications, cell wall loosening, reserve mobilization, and reprogramming of transcriptome). The seed's germination and vigor are speeded up by nano-priming [111,112]. Stress-related responses such as heat-shock proteins and antioxidant mechanisms are activated in response to the hydration and drying process, improving cross-resistance against other abiotic stresses. In addition, the period of exposure of germinating seeds under unfavorable soil conditions is shortened by aggravated germination.

The primary metabolites synthesized in primary metabolic pathways are directly involved in plant metabolism and growth. ROS-induced signaling events primarily regulate the activation of secondary metabolism. In addition, ROS serves as a signal for other messengers such as brassinosteroids (BRs), nitric oxide (NO), ethylene (ET), salicylic acid (SA), and jasmonic acid (JA). These messengers can directly or indirectly regulate secondary metabolism [113]. Nanoparticles can induce mitogen-activated protein kinase (MAPK) cascades, enhanced cytoplasmic Ca^{2+}, and ROS as signaling transduction cascades. For instance, in CeO_2-primed cotton seeds, the ROS induction genes and conserved Ca^{2+} transduction cascade genes were expressed in root transcripts [38]. In *Arabidopsis*, Ag NPs stimulate ROS induction and Ca^{2+} bursts by modifying the physiology of the plant [114]. Calcium levels and signaling pathway proteins have been shown to boost rice growth primed with Ag NPs [115]. These studies also concluded that Ag NPs or free ions resemble Ca^{2+} or signaling molecules. They may bind with the Ca^{2+}/Na^{+} ATPases, Ca^{2+} channels, and Ca^{2+} receptors [116].

Different NPs perform diverse roles in plant metabolism when seeds are primed with them. Khodakovskaya et al. [117] reported the uptake of CNTs by tomato seeds, which increased their water uptake capacity and doubled the number of flowers in tomato plants. Several studies have supported the positive effects of CNTs on the metabolism of plant seeds such as maize, soybean, barley, and tomatoes, by enhancing the gene expression of different water channel proteins [118,119]. Seeds of *Vigna radiate* L. primed with a low concentration of Cu NPs improved seed germination and metabolism [120]. The metabolic activity of plants is also reported to be positively affected by Si NPs [121]. ZnO NPs also play a key role in plant metabolism as they are necessary for various enzyme activities such as SOD and dehydrogenases [122]. The nitrogen metabolism enzymes (glutamate dehydrogenase, nitrate reductase, and glutamine synthase) help absorb nitrates and can transform the inorganic nitrogen into organic nitrogen. The activities of these enzymes were enhanced with Ti NPs, resulting in the plants' improved fresh and dry weight [123]. Nanoparticles also affect the synthesis of secondary metabolites in medicinal plants. For instance, the essential oils of *Thymus vulgaris* were affected adversely by water stress, while the application of TiO_2 NPs reversed drought- stress-induced changes and improved essential-oil content. This could be attributed to the unique chemical and physical properties of NPs in favor of plant metabolism [124].

7. Priming-Induced Molecular Responses against Abiotic Stresses

Nanoparticles can interact with plant cells and settle in different cell compartments. The seed nano-priming alters biochemical pathways and gene expression profiles during or after seed germination [125]. The first stage of seed germination is the imbibition phase, in which the seed takes up water. Seed priming with NPs at this stage can cause the activation of seed-located water channel genes, i.e., aquaporin (AQP) genes that enhance the water uptake capacity of the seeds [39,126]. When seeds of different crops such as soybean, corn, and barley are sprayed with MWCNTs, the expression of AQP genes is induced [126]. When rice seeds (*Oryza sativa* L. cv. KDML 105) were primed with Ag NPs, overexpression of AQP genes was observed [39]. AQP genes enable water transport across biological membranes and aid in transferring ROS (such as H_2O_2), nutrients, and gases (NH_3 and CO_2), eventually resulting in enhanced germination rates and subsequent growth. An et al. [38] analyzed the transcriptome profile of CeO_2 NPs-primed cotton seeds coated with polyacrylic acid under saline and non-saline conditions. Under no salinity stress, 7799 variable genes were expressed in the seeds primed with NPs compared to the control. While under salt stress, ten ion homeostasis regulating genes and 13 ROS pathway genes were expressed in seeds, resulting in salt stress tolerance and improved growth. Ye et al. [40] observed that MnSOD (Mn superoxide dismutase) was upregulated in primed seeds which enhanced the SOD enzyme levels to avoid the phytotoxic effects caused by the ROS. Primed seeds were also better resistant to biotic stresses compared to controlled seeds. The expression of genes for polyphenol oxidase, peroxidase, and phenylalanine ammonia-lyase was upregulated in seed primed with chitosan NPs which impart them resistance against oomycete *Schlerospora graminicola* i.e., cause of downy mildew disease [127]. Plaksenkova et al. [128] demonstrated the over-expression of miRNA-156 and miRNA-159 in the barley seeds primed with ZnO NPs. These microRNAs impart resistance to plants against abiotic stress factors.

Several studies have been performed, but still, extensive research is required to better understand the molecular mechanisms taking place after seed priming with NPs and the expression of resistance genes. Variable NPs with variable coatings are used for priming purposes, and each produces a different response at the molecular level. Moreover, NPs can serve as co-factors or signals that can improve the regulation of gene transcription related to abiotic stress responses [94].

8. Effects on Photosynthesis under Abiotic Stress

Photosynthesis is the process of conversion of sunlight energy into organic compounds taking place in higher plants, some microorganisms, and algae [129]. Nano-priming of the seeds has found its way into the plant's photosynthesis mechanisms. Seed priming with ZnO NPs has improved photosystem and gas-exchange attributes resulting in increased photosynthetic activity [46]. The improved photosynthetic efficiency is attributed to the protective role of ZnO NPs against oxidative damage induced by abiotic stress. Lower concentrations (0.01%) of aluminum oxide (Al_2O_3) NPs on *Hibiscus sabdarifa* L. cultivars significantly enhanced the biochemical functions (proline, proteins, soluble sugars, chlorophyll a and b, and carotenoid levels), physiological properties, growth characteristics (fresh and dry mass, root and shoot length, and dry mass), and the activity of various antioxidant enzymes (ascorbate peroxidase (APX), CAT, peroxidase (POD), and SOD) [130]. The increase in photosynthetic rate could be attributed to the stimulation of water splitting in the electron transport system, as Pradhan et al. [131] observed in the case of Mn NPs. Rubisco (Ribulose-1, 5-bisphosphate carboxylase/oxygenase) is the key enzyme in photosynthesis that integrates CO_2 into biological compounds. Rubisco activity is induced by TiO_2-primed chickpeas [132]. In *Mentha piperita*, TiO_2 (200 mg L^{-1}) enhanced the carotenoid and chlorophyll a and b content [133]. Similarly, Yang et al. [134] observed that TiO_2 priming raised Rubisco activity and enhanced photosynthesis by water splitting and oxygen evolution, normalizing the provision of light energy from photosystems (PS II and PS I) and light absorption in the chloroplast.

Iron plays its part in the electron transport system of photosynthesis and respiration, helping photosynthesis, reproduction, and initial seed germination [135]. Rui et al. [136] reported that the need for natural sources of iron in *Arachis hypogaea* could be replaced by iron oxide (Fe_3O_4) priming. This enhanced the Fe level, chlorophyll content, root and shoot length, and activity of phytohormones (abscisic acid and gibberellic acid) and antioxidant enzymes. The growth and photosynthetic rate of rice seedlings could be enhanced by priming with low zero-valent iron NPs (nZVI). When physiological and biochemical changes in nZVI-primed *Oryza sativa* were observed, there was a significant increase in expression of *OsGAMYB* and *OsGA3Ox2* (to mediate mobilization of seed storage food reserves efficiently and control the activity of hydrolases) [137]. The photosynthetic pigments content was enhanced by applying Al_2O_3 and TiO_2 NPs in wheat leaves [138]. Moreover, in soybean, Rubisco activity [139], stomatal conductance, and transpiration rate were promoted by CeO_2 NPs [140]. Gold NPs stimulated oxygen evolution and the electron transport chain in mung bean leaves [141].

It was reported by Abdel-Latef et al. [142] that when ZnO NPs were used as a priming agent for lupin seeds, they elevated photosynthetic pigments and growth parameters (fresh and dry weight, root and shoot length) by alleviating salt-stress-induced changes. Hussain et al. [42] reported that under cadmium (Cd) stress, SiO_2 NPs–primed seeds increased the chlorophyll a and b content, carotenoid content, photosynthetic rate, plant biomass, and reduced Cd uptake, antioxidant enzyme activity, and ROS production. Seed germination and plant growth were reported to be elevated when sorghum seeds were primed with Fe_3O_2 NPs [143]. Biomass and photosynthetic pigments were increased when treated with 500 mg L^{-1} concentration of Fe_3O_2 NPs, while leaf water content was enhanced by 100 and 500 mg L^{-1} concentrations. The enhanced photosynthetic parameters improved biomass production and maintained biochemical balance, alleviating the drought stress from the wheat seedlings (cultivar HI 1544) when they were primed with 15 mg L^{-1} of SiO_2 NPs [83]. Similarly, Abou-Zeid et al. [86] observed an increase in root and shoot growth and improved photosynthesis and ultra-structure of leaves when wheat cultivars were primed with ZnO NPs. Silicon dioxide NPs have also been reported to enhance the photosynthetic rate of plants by inducing the synthesis of photosynthetic pigments [144]. However, further investigation is needed to explore the molecular mechanisms underlying NPs' improved photosynthesis and related attributes.

9. Effects on Nutrient Uptake and Regulation

Nanotechnology has become a promising candidate for boosting the food and agricultural industries. Nanofertilizers can be used to replace conventional chemical fertilizers, which will reduce environmental pollution [145]. The application of NPs has increased since the discovery of their benefits with regard to nutrition and stress tolerance. Such nano-formulations are developed which can attach, absorb, encapsulate, and entrap the active molecules. Nanofertilizers are available in various modes such as aerosol dusting, fertigation drip tape, seedling root drip, seed priming, and foliar sprays [146]. Nanoparticles affect plant physiology, growth, and morphology [86]. Physiological features may be affected by changing the SOD, CAT activity, total phenolic content (TPC), chlorophyll content, and ROS formation [113]. Morphological changes may depend on physiological attributes such as phosphorus and nitrogen metabolism, enhanced photosynthesis, and increased enzyme activity [147]. Plant growth includes parameters such as biomass, root and shoot length, and leaf area. MWCNTs are used as nanofertilizers that induce development and growth, and enhance supplement nutrition, antioxidant defense, aquaporin expression, and photosynthesis [148]. The increase in leaf growth, plant height, and chlorophyll content was observed when MgO, MgH, ZnO, and CuO NPs were used as fertilizers and foliar sprayed on crops [149]. However, over-concentration of these NP-derived fertilizers could induce toxicity in plants [150].

Priming seeds with NPs benefits the germination process, which may be attributed to the grain's efficient nutrient and water uptake. Priming *Citrullus lanatus* with Ag NPs improved their germination, growth, quality, and yield even when stored for long periods [151]. Laware and Rasker [152] observed that TiO_2 elevates seedling growth and germination rate along with the increase in the activity of protease and amylase. Silver NPs reduced sulfur, phosphorus, and magnesium concentration and enhanced potassium content in oriental lilies [153].

Nutrient priming is another technique in which seeds are saturated in a particular concentration of nutrients before sowing [154]. Water uptake efficiency, nutrient availability, and germination are boosted when seeds are primed with either micro- or macronutrients. During germination, osmosis for water regulation is elevated by micronutrient seed priming [154]. For example, the yield of mung beans was enhanced when primed with sodium molybdate dihydrate for 5 h [155]. Similarly, when macronutrients such as potassium are used, they increase stress tolerance against environmental conditions in plants [156]. Priming with Zn solutions was reported to increase the grain yield of chickpeas and wheat [157]. Zinc priming may mimic the zinc in zinc-deficient soils and enhance the crop's nutrient absorption and growth. Zinc sulfate heptahydrate ($ZnSO_4.7H_2O$) priming increased seed production by up to 9% in chickpeas compared to non-primed seeds [158]. Nutrient priming not only increases nutrient availability but also improves plant stress tolerance. Ascorbic acid (antioxidant and essential nutrient) and plant extracts induce the antioxidant potential of plants and protect them from oxidative stress damage [159,160]. Under salinity stress, it also improves the germination rate of *Agropyron elongatum* [161].

Nano-priming can be combined with nutrient priming to enhance its effects. Several studies have come up with positive results. The photosynthetic rate, growth, and seed germination could improve *Zea mays* seedlings when primed with macronutrient NPs such as $Mg(OH)_2$ [162]. Similarly, it is reported that priming with MgO NPs has improved seed vigor and germination in *Vigna radiata* [163]. In rice and wheat field trials, Zn nutrition has been reported to enhance productivity as well as grain nutrient quality [66,164]. In black-eyed pea plants, Fe content and seedling vigor can be alleviated using foliar sprays of Fe-NPs (500 mg L^{-1}) [23]. Das et al. [165] found that nano-pyrite could efficiently replace NPK (nitrogen, phosphorus, potassium) fertilizers for rice cultivation. Seed germination and growth could be raised using low concentrations of nZVI (40–80 µmol L^{-1}) in peanuts [166]. Yoon et al. [167] demonstrated that in *Arabidopsis thaliana*, photosynthesis and biomass could be boosted by using nZVI (500 mg kg^{-1} soil). It increased the plant Fe content and promoted the levels of micro and macro-nutrients such as Zn, Mg, Mn, and P. However, to date, no study has reported the potential of nZVI in fields. Therefore, further research is required to investigate the role of nano-priming in aggravating plant nutrition under abiotic stresses in field trials.

10. Effects on Plant Antioxidant Defense Systems

Antioxidant enzymes play a crucial role in plant defense systems against biotic and abiotic stress [46,168]. The stress factor triggers the overproduction of ROS (H_2O_2, O_2, and O^-) that cause oxidative stress, including lipid peroxidation and cellular damage, which disturb cell functionality. ROS generation and their scavenging should be balanced for plant survival and better functioning, and this state of homeostasis is achieved by the plant's antioxidant defense system [169–171], which generally increases as it encounters stress-induced overproduction of ROS. Scavenging over-produced ROS by various antioxidant enzymes has a crucial role in developing tolerance in plants against abiotic stress and maintaining the balance of biochemical state of the cell [172]. Several studies have reported that seed priming with NPs is shown to positively regulate the plant's antioxidant defense system [46,89,107,108]. Mazhar et al. [107] have reported that ZnO NP priming has increased SOD, POD, and CAT activity in rice under drought stress. SOD is the first line of defense against ROS-induced oxidative and cellular damage [173]. Seed priming with Ag NPs and TiO_2 NPs improved SOD, POD, CAT, and carotenoid contents in *Solanum Lycopersicum* [69,89]. Previously, it has been stated that seed priming with TiO_2 NPs increased phenylalanine ammonia-lyase (PAL) activity along with other antioxidants in maize under salt stress. Phenylalanine ammonia-lyase has great importance in the phenylpropanoid pathways of plants [174]. Phenylpropanoid compounds are the precursors of various phenolic compounds that have a wide range of functions in plants and play essential roles in various pathways such as plant defense against biotic and abiotic stress, signal transduction, and interaction with other organisms [175,176]. Regab et al. [101] reported that the application of sulfur (SNPs) as priming agents has improved the antioxidant compounds (ascorbic acid, total flavonoid, total phenolic contents) in sunflower seedlings under manganese stress, and the increase in the production of antioxidants due to SNPs stimulates the detoxification machinery of plants, resulting in dismutation of ROS. Flavonoid and phenolic compounds serve as free radical scavengers because of their hydroxyl groups and their roles as hydrogen/electron-donating agents, singlet oxygen quenchers, and metal chelators, protecting the plant against oxidative stress caused by elicitors [177,178]. Similarly, Si nano-priming together with Pseudomonas inoculation increased antioxidant activity (based on DPPH radical scavenging and ß-carotene/linoleic acid (BCB) bleaching tests) by 85.3% and 86.3% in *Melissa officinalis* L. [172]. Kumar et al. [179] reported that Ag NP priming enhanced antioxidant enzymes such as SOD, POD, CAT, and APX and higher soluble sugar concentrations in *Psophocarpus tetragonolobus* L. CAT and APX are considered crucial regarding ROS detoxification, which protects plant cells from oxidative damage [46]. Nano-ceria seed priming has been reported to alleviate ROS-induced damage in cotton seedlings under salinity stress [38].

11. Crosstalk with Plant Growth-Promoting Microbiota

Plants nurture an array of phyto-microbiota, particularly rhizobacteria in the below-ground ecosystem, which mutually establish a relationship to underpin each other's ecological and physiological functions through various communication sources [176,180,181]. Plant growth-promoting microbiota positively influences plant health and fitness by employing direct and indirect mechanisms [182,183]. They are a group of microbes inhabiting the plant rhizosphere zone that synthesize plant growth regulators at low concentrations and regulate plant biochemical processes that lead to improved plant growth and development [175,176,184]. These microbial communities perform substantial biological roles, including nutrient cycling, plant protection, and abiotic stress alleviation [3,185]. Yasmin et al. [186] applied ZnO NPs alone and with "Phytoguard", a PGPR consortium, and reported higher growth attributes in combined treatment than individually, under salt stress. They determined that the increase in growth under combined treatment was a result of reducing MDA content and improving photosynthesis and antioxidant activity, which led to reduced salt toxicity. Recently, Akhtar et al. [187] reported that SiO_2 NPs and PGPR strains modulate wheat plants' physiological and metabolic reactions and induce tolerance under drought stress environments. This evidence was strengthened by Galal's study [188], which demonstrated that ZnO NPs significantly modulate the defense system and enhance plant growth and tolerance against abiotic stresses. Interestingly, nano-silica did not show any hazardous effect on soil bacteria. Nonetheless, it stimulated PGPR growth and multiplied the bacterial population in soil that might serve as biofertilizers for plant growth and productivity [187]. Raliya et al. [189] stated that foliar spray of ZnO NPs enhanced the rhizosphere zone, increasing rhizosphere enzymes (acid phosphatase, alkaline phosphatase, phytase) and plant root growth. Dai et al. [190] reported that exogenously applied CeO_2 NPs decreased the general rhizosphere zone but increased the PGPR zone. The concentration level of NPs plays a crucial role and should be carefully considered before being applied to secure optimum benefits [62–64]. The exploitation of beneficial microbes and NPs is an emerging and valuable approach in the present era, as the application of NPs at optimum concentration and plant growth-promoting rhizobacteria (PGPR) both induce stress tolerance and promote plant growth [191–195]. However, the synergistic effect and the chemistry of plant-associated microbes with NPs need to be explored further, in depth, on a molecular basis to fully understand the mechanism. The schematic diagram in Figure 3 illustrates the proposed pathways of priming induced tolerance against abiotic stress.

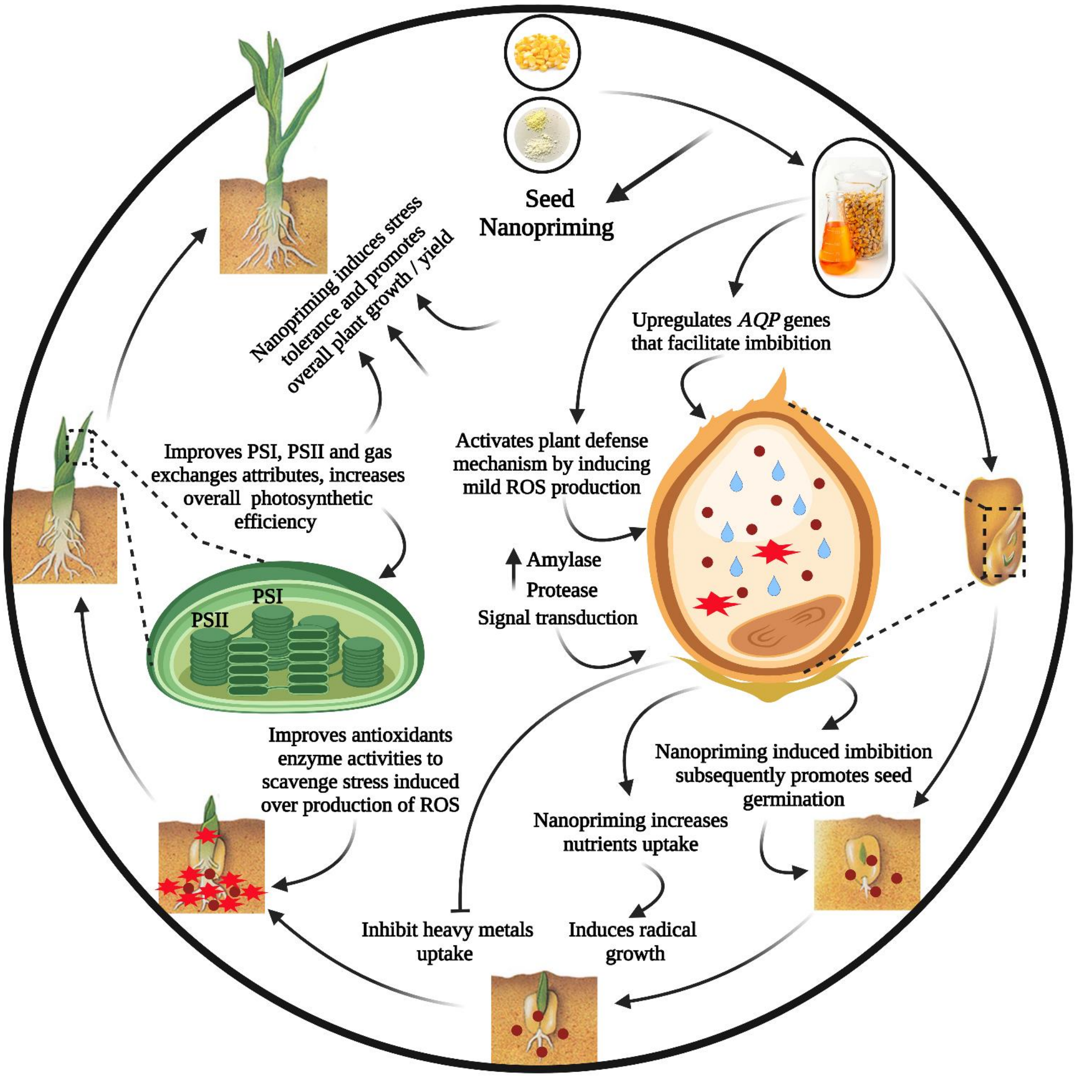

Figure 3. Seed nano-priming induced regulation of abiotic stress tolerance and growth enhancement. After entering seed tissue, NPs induce the expression of AQP genes (seed-located water channel genes), resulting in water uptake and promoting germination. NPs induce mild ROS production that serves as a signal transduction cascade leading to an activated plant defense mechanism. Abiotic stressors cause the overproduction of ROS, resulting in oxidative damage. In contrast, NPs protect the plant by enhancing antioxidant enzymes (SOD, POD, CAT, etc.) that scavenge over-produced ROS and maintain redox homeostasis. NPs increase plant nutrient uptake and improve plant photosynthetic efficiency, ultimately improving overall plant growth and development.

12. Conclusions

In the current state of the world, agriculture is facing many biotic and abiotic constraints which cause concern over food security and safety. Certain aspects of traditional agriculture, involving the extensive use of fertilizers, agrochemicals, and pesticides, pollute the environment and threaten the food chain. Thus, innovative and environmentally friendly strategies must be developed and implemented to cope with these issues in order to promote agricultural sustainability. Nanotechnology exploitation via seed priming could be a user-friendly alternative to achieve this goal. It has been tested as a simple and cost-effective approach that could potentially be the future solution for agricultural sustainability. Nano-priming promises to move the traditional farming system to sustainable agriculture, augmenting tolerance to biotic and abiotic stresses and ultimately enhancing crop productivity. Seed nano-biofortification through nano-priming aims to reduce the harm that runoff fertilizer and other agrochemicals can cause to the environment. All these factors together can guarantee the prevalence of a safer system for farmers and consumers, and can mitigate the damage to the ecosystem caused by traditional farming methods. However, the exact mechanisms behind the positive effects of NPs against abiotic stress are not yet fully explored. In the future, extensive research is needed to dissect the underlying mechanisms of nano-priming-induced changes and subsequent stress tolerance at the molecular and hormonal levels. Moreover, the concentration of NPs and exposure time should be optimized for maximum plant growth and production to produce the desired outcomes. Intensive laboratory tests based on concentration optimization are highly recommended before the large-scale use of nanoparticle-based materials in field trials. Moreover, introducing new NPs and the crosstalk of NPs with phytohormones and plant-growth-promoting bacteria is a new field that requires further study. The synergistic interaction of NPs is currently lacking in the literature regarding their role in enhancing plant growth and stress management. In this paper, we have reviewed previous research. Further studies into nano-priming should focus on the synergistic interaction of nano-materials for stress mitigation, opening new avenues for the direction of future research.

Author Contributions: Conceptualization, A.S. (Abdul Salam) and. A.R.K.; methodology, A.S. (Abdul Salam) and M.S.A.; formal analysis, A.S. (Abdul Salam) and M.A.J.; investigation, A.S. (Abdul Salam), A.S. (Aroona Saleem) and A.H.; resources, A.S. (Abdul Salam) and M.Z.; writing—original draft preparation, A.S. (Abdul Salam), M.S.A., M.A.J., A.H. and A.S. (Aroona Saleem); writing—review and editing, B.A., A.H., Z.U., S. and W.A.; visualization, A.S. (Aroona Saleem) and A.H.; supervision, Y.G.; project administration, A.S. (Abdul Salam) and Y.G.; funding acquisition, Y.G. All authors have read and agreed to the published version of the manuscript.

Funding: This work was supported by the National Key R & D Program of China (2021YFF1000400); Zhejiang Provincial Natural Science Foundation of China (Grant No. LZ22C130002); and the National Natural Science Foundation of China (Grant No. 31570183).

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: Not applicable.

Acknowledgments: The authors thank Jiaxuan Qi for reviewing and formatting the manuscript.

Conflicts of Interest: The authors declare no conflict of interest.

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