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1 Review

2 Nanotechnology potential in seed priming for sustainable agri- 3 culture

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Abstract: Our agriculture is threatened by climate change and the depletion of resources and biodiversity. A new agriculture revolution is needed in order to increase the production of crops and ensure the quality and safety of food, in a sustainable way. Nanotechnology can contribute to the sustainability of agriculture. Seed nano-priming is an efficient process that can change seed metabolism and signaling pathways, affecting not only germination and seedling establishment but also the entire plant lifecycle. Studies have shown various benefits of using seed nano-priming, such as improved plant growth and development, increased productivity, and a better nutritional quality of food. Nano-priming modulates biochemical pathways and the balance between reactive oxygen species and plant growth hormones, resulting in the promotion of stress and diseases resistance outcoming in the reduction of pesticides and fertilizers. The present review provides an overview of advances in the field, showing the challenges and possibilities concerning the use of nanotechnology in seed nano-priming, as a contribution to sustainable agricultural practices.

Keywords: Seed nano-priming; seed coating; germination; plant resistance; nanoparticles; sustainability.

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1. Introduction

Agriculture is currently facing many challenges, including production losses due to pests, the effects of global climate change, and the depletion of natural resources (Kah et al., 2019; Lowry et al., 2019). An additional difficulty is that traditional agricultural practices have been relying on continuous application of pesticides and fertilizers, resulting in environmental contamination (Lowry et al., 2019; Zhao et al., 2020).

The world population is expected to increase to 9-10 billion by 2050, implying that food production will need to rise by 25-70% compared to current levels (Scott et al., 2018). Therefore, new technologies need to be deployed in agriculture to ensure sustainability and increase productivity (Fraceto et al., 2016; Kah et al., 2019; Lowry et al., 2019; Panpatte et al., 2016).

Nanotechnology has the potential to contribute to a new technology-based agricultural revolution (Camara et al., 2019; Lowry et al., 2019; Shakiba et al., 2020). Many nanomaterials have been developed for agricultural applications, including new solutions for soil and water remediation as well as nanofertilizers and nanopesticides, designed to reduce the applied amounts of fertilizers and pesticides, while increasing food production and quality (Camara et al., 2019; Kah et al., 2019; Zhao et al., 2020).

Nanomaterials, especially nanoparticles, have a range of applications for crop protection (Fraceto et al., 2016; Kah et al., 2019; Lowry et al., 2019). This is a major field of re-

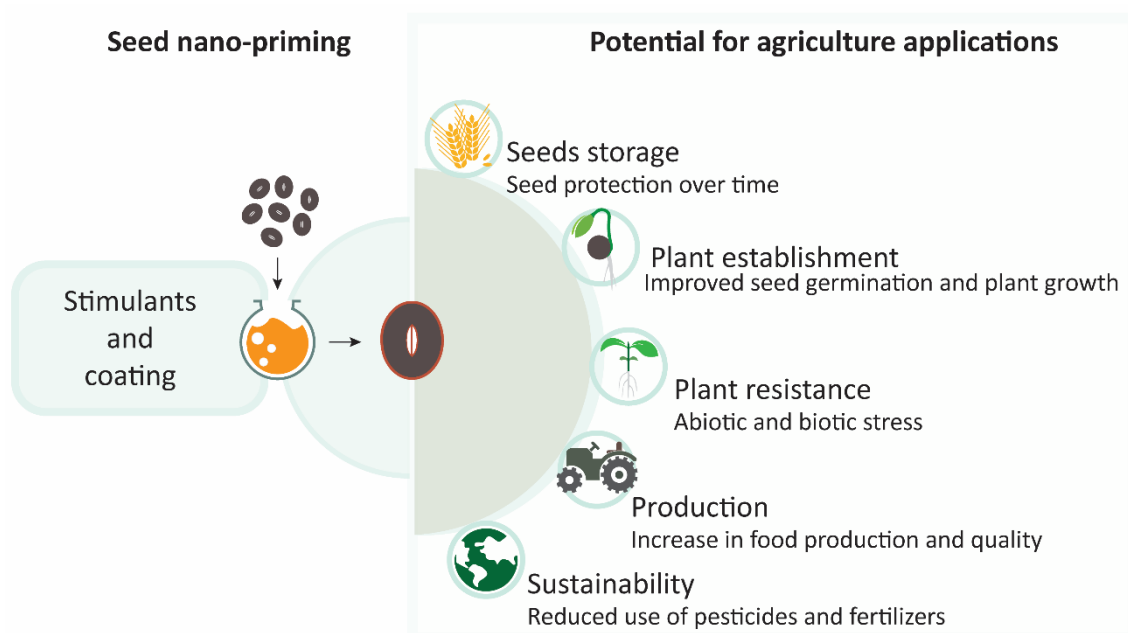
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46 search that has attracted the interest of companies in the agricultural sector, resulting in
47 the inclusion of nanoparticles in formulations (Chau et al., 2019). The use of
48 nanopesticides and nanofertilizers can contribute to pest control, plant nutrition, and
49 environmentally friendly production methods (Acharya et al., 2020; Fraceto et al., 2016;
50 Lowry et al., 2019).

51 Recent studies have shown that nanoparticles have effects on seeds and plants
52 (Acharya et al., 2020; Lowry et al., 2019; Mahakham et al., 2017; Pérez-de-Luque, 2017). Some
53 nanoparticles have side effects including the inhibition of germination or phytotoxicity
54 in seedlings (Falco et al., 2020; Hayes et al., 2020; Pelegrino et al., 2020). However, others
55 can act as stimulants, improving seed metabolism, seedling vigor, and plant growth by
56 acting in cellular signaling pathways (Acharya et al., 2020; Mahakham et al., 2017). These
57 effects depend on nanoparticle physical-chemical properties such as size, zeta potential,
58 and concentration, which are factors that determine the biological responses (Acharya et
59 al., 2019a; Pérez-de-Luque, 2017).

60 These characteristics have key roles in nanoparticle uptake and translocation in
61 plants. As example, small-sized nanoparticles cross biological barriers more efficiently
62 (Bombo et al., 2019; Hu et al., 2020; Palocci et al., 2017; Valletta et al., 2014). The surface
63 charge of the nanoparticles is also decisive. Positively or negatively charged nano-
64 particles can be taken up by the leaves and translocated to the roots. However, only neg-
65 atively charged nanos are taken up by the roots. Positive charges induce the production
66 of mucilage, which prevents their uptake by plants (Avellan et al., 2019, 2017; Spielman-
67 Sun et al., 2019).

68 Nano-priming can be applied to seeds in order to provide protection for seeds dur-
69 ing storage, improve germination, germination synchronization, and plant growth as
70 well as to increase the resistance of crops to abiotic or biotic stress conditions, which can
71 help to reduce the required quantities of pesticides and fertilizers. The use of nanotech-
72 nology for seed priming is a new area of research, although studies have already shown
73 promising results (Hussain et al., 2019; Kasote et al., 2019; Mahakham et al., 2017; Ye et al.,
74 2020). Figure 1 shows the main benefits that can result from seed nano-priming.



75
76 **Figure 1.** Seed nano-priming and its potential benefits for sustainable agriculture. In addition to provide protection for
77 seeds during storage, the use of seed nano-priming can result in improved establishment of plants in the soil with a re-
78 duced need for fertilizers. By growing faster, plants have an increased ability to compete with weeds for resources, con-
79 sequently increasing productivity and food quality. The plants may also become more resistant to abiotic and biotic
80 stresses, resulting in reduced use of pesticides.

81 The aim of this review is to provide an update concerning the potential applications
82 of seed nano-priming techniques in agriculture. Many different types of nanoparticles
83 can be used, with effects on seed metabolism and on the subsequent plant growth and
84 development.

85 **2. Seed priming and nanoparticles: Definition and potential applications**

86 *2.1. Germination and principles of seed priming*

87 Germination is one of the most important steps for the establishment of plants in
88 agriculture and is fundamental for crop quality (Acharya et al., 2020; Savassa et al., 2018).
89 The rapid development of seedlings ensures fast expansion of the leaves and elongation
90 of the roots, which favor the uptake of nutrients, their translocation through the transpi-
91 ration flow, and biomass production (Acharya et al., 2020; Chandrasekaran et al., 2020;
92 Mahakham et al., 2016). Slow germination can expose the young seedling, which is one of
93 the most vulnerable stages of plant life cycle, to many environmental stress conditions or
94 pathogens, resulting in decreases in vigor and crop productivity, leading to economic
95 losses for farmers (Acharya et al., 2019a).

96 The process of seed germination is usually divided into three phases, as summa-
97 rized in Figure 2a (Nonogaki, 2014; Nonogaki et al., 2010). It begins with imbibition (phase
98 I), when the fast water uptake triggers seed basal metabolism, as transcription, protein
99 synthesis and mitochondrial activity. In phase II (activation or lag phase), water uptake
100 is limited but the metabolism becomes hyperactive with the production of enzymes re-
101 quired for reserve mobilization and embryo development, including amylases,
102 endoxylanase, and phytase. In phase III, the seeds exhibit again fast water uptake and
103 embryo growth culminates in radicle protrusion (Ibrahim, 2016; Nonogaki et al., 2010).

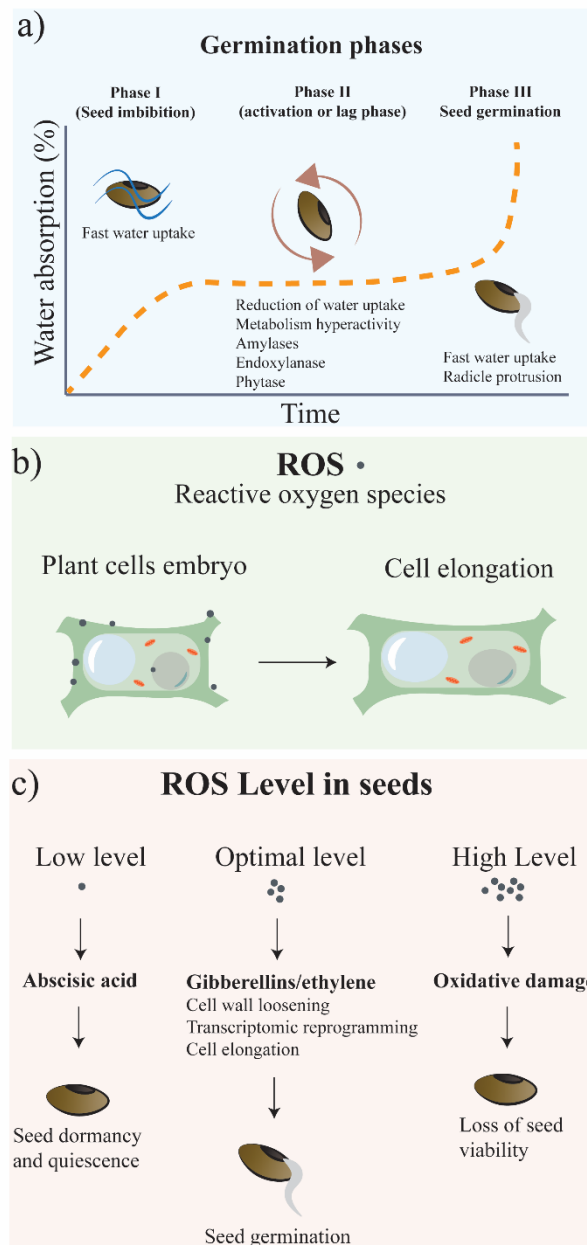


Figure 2. Germination phases and reactive oxygen species (ROS) effects. a) The germination process is subdivided into three phases: phase I (water uptake), phase II (metabolic activity, with initiation of degradation of starch reserves and preparation for embryo development), and phase III (embryo development and emergence of the radicle), b) The ROS act by destabilizing cell wall, allowing water uptake and cell elongation, c) ROS level in seeds and hormones production.

The seed germination process is finely regulated by signaling molecules that include reactive oxygen species (ROS) and phytohormones (Bailly, 2019; Choudhary et al., 2020; Oracz and Karpiński, 2016) (Figure 2b and c). Apoplastic ROS generation is directly related to cell wall loosening, which allows water uptake and cell extension (Bailly, 2019; Oracz and Karpiński, 2016). The abscisic acid and gibberellins work antagonistically to determinate seed germination or dormancy, and auxins could also act in the maintenance of seed dormancy (Wu et al., 2020). The ROS produced regulate gene expression and phytohormone signaling and the homeostasis of abscisic acid, gibberellins, auxins and ethylene, to control cellular events related to seed germination (Bailly, 2019; Choudhary et al., 2020; Shuai et al., 2016). However, when ROS levels are too high, extensive oxidative damages occur, hampering seed germination (Bailly, 2019). ROS content must be therefore spatio-temporally controlled to be enclosed in the so-called oxidative window, that ensures proper germination completion (Bailly, 2019).

123 Seed priming is a traditional technique used in agriculture to promote seed germi-
124 nation and plant establishment, based on a preliminary preparation of seeds prior to
125 sowing (Acharya et al., 2019b; Bouriouq et al., 2020; Ibrahim, 2016; Jisha et al., 2013) It is usu-
126 ally a water-based methodology whereby seeds are hydrated followed by drying, or
127 some physical methods are applied as ultraviolet light (UV) priming (Thomas T.T. and
128 Puthur, 2017). The absorption of water must be adequate to trigger the metabolic path-
129 ways for pre-germination (phases I and II), without resulting in radicle emergence (Fig-
130 ure 2).

131 This process affects the seed metabolism at molecular and cellular levels (e.g.,
132 transcriptomic reprogramming, enhanced capacity for reserve mobilization, cell wall
133 loosening, increased potential for protein synthesis and post-translational modifica-
134 tions), inducing a particular physiological state, which speeds up or even improves the
135 germination and vigor of the primed seeds on a novel imbibition (Acharya et al., 2019b;
136 Bouriouq et al., 2020; Ibrahim, 2016; Jisha et al., 2013). The moderate stress imposed by both
137 soaking and subsequent drying may also induce stress-related responses (e.g., antioxi-
138 dant mechanisms, heat-shock proteins), resulting in cross-resistance to other stress fac-
139 tors. Moreover, a faster germination shortens *per se* the exposition of the germinating
140 seeds to adverse soil conditions. Thus, seed priming has been successfully used to accel-
141 erate and synchronize germination, improve seedling vigor, and make the plants more
142 resistant to abiotic and biotic stresses, resulting in improvements of productivity and
143 food quality (Acharya et al., 2019a; Carrillo-Reche et al., 2018; Mahakham et al., 2016).

144 Different types of seed priming can be used, such as hydro-priming or hydro-
145 thermo-priming, where the seeds are hydrated using water treatment (usually limited to
146 period of 7-14 hours), which allows the occurrence of germination phase II (Lemmens et
147 al., 2019). The technique may be applied with temperature alternation (cold and hot)
148 (Noorhosseini et al., 2018). In the case of osmo-priming, solutions of low water potential
149 are used to control hydration (around 10-20%), altering seed metabolism through an ad-
150 ditional abiotic stress factor (Lemmens et al., 2019). Other methodologies such as
151 halopriming, hormo-priming, and bio-priming can be used as pre-sowing treatments,
152 using solutions containing salts (Saddiq et al., 2019), plant growth regulators (Syta et al.,
153 2019), and microorganisms (Lemmens et al., 2019), respectively.

154 2.2. Nanoparticles for seed priming

155 Seed nano-priming is a new technology that uses nanomaterials, mainly nanoparti-
156 cles, for seed priming (Kasote et al., 2019; Mahakham et al., 2017; Shukla et al., 2019). There
157 is an important difference between seed priming and seed nano-priming, since conven-
158 tional seed priming mainly employs water (hydropriming) or solutions containing sub-
159 stances (nutrients, hormones, or biopolymers) that adsorb on the seed and can result in
160 seed coating (or dressing). In seed nano-priming, the media used are suspensions or
161 nanoformulations, where the nanoparticles may or may not be taken up by the seeds
162 (Acharya et al., 2019c). Even when nanoparticle uptake occurs, the greatest fraction is re-
163 tained on the seed surface as coating (Duran et al., 2017; Falsini et al., 2019; Montanha et al.,
164 2020; Savassa et al., 2018). Such seed coating can be used with fungicides or bactericides
165 in order to protect against pathogens in the field or during storage (Gross et al., 2020).

166 One of the first studies showing the potential of nanomaterials to affect seed germi-
167 nation was reported by Khodakovskaya et al. (2009). Although seed priming was not used,
168 these authors demonstrated that carbon nanotubes could be taken up by tomato seeds.
169 The carbon nanotubes increased water uptake, resulting in tomato plants with a 2-fold
170 higher number of flowers (Khodakovskaya et al., 2013). Other studies have similarly
171 demonstrated that carbon nanotubes can modulate seed metabolism in plants such as
172 tomato, barley, soybean, and maize, increasing the gene expression of several types of
173 water channel proteins (Lahiani et al., 2013; Villagarca et al., 2012).

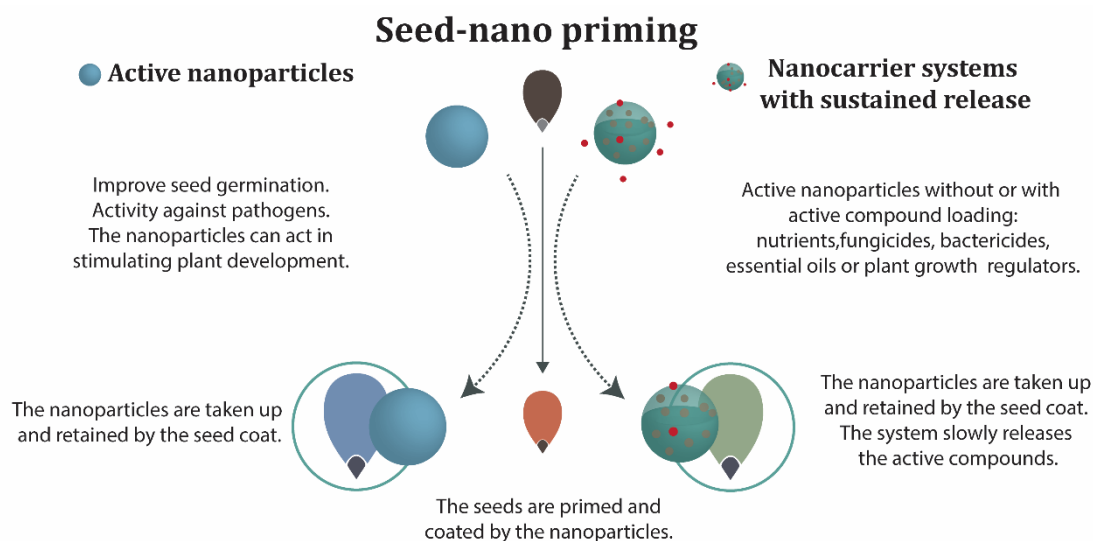
174 Different nanomaterials, including metallic, biogenic metallic, and polymeric nano-
175 particles, have also shown potential for seed nano-priming (Acharya et al., 2019c; Falsini et
176 al., 2019; Mahakham et al., 2017; Siddaiah et al., 2018), resulting in the stimulation of plant

177 growth and improvement in morphological and metabolic traits. This process can pro-
 178 mote fast root and shoot development, with changes in the expression of genes that
 179 modulate metabolic processes such as phytohormone production. Seed nano-priming
 180 changes the activity of the defense system, increasing the antioxidant levels and enzyme
 181 activities, so that the plants become more resistant to pests and other biotic and abiotic
 182 stresses under field conditions (Abdel Latef et al., 2017; Acharya et al., 2020; Duran et al.,
 183 2017; Itroutwar et al., 2019; Kasote et al., 2019; Li et al., 2019).

184 2.3. Active nanoparticles and nanocarriers systems

185 The potential applications of nanoparticles will be considered in two groups: (i) ac-
 186 tive nanoparticles and (ii) sustained release nanocarrier systems (Figure 3). Table 1
 187 shows systems that have been employed for seed priming/coating, together with their
 188 potential effects as stimulants or against biotic and abiotic stress.

189 Active nanoparticles are nanoparticles that themselves can cause a biological effect,
 190 acting as a stimulant, an anti-pathogen, or both (Mahakham et al., 2017; Rizwan et al., 2019;
 191 Siddaiah et al., 2018). Nanocarriers with sustained release features are systems where the
 192 nanoparticle (being itself active or not) is loaded with an active ingredient (biological or
 193 synthetic) and provides extended release of this compound over time (Camara et al., 2019;
 194 Falsini et al., 2019; Kumar et al., 2020; Shakiba et al., 2020).



195 **Figure 3.** Seed nano-priming. The nanoparticles can be defined as (i) active nanoparticles, which are systems that can
 196 have a stimulatory effect on plant growth and development, or (ii) nanocarrier systems providing sustained release,
 197 where the nanoparticles can be active or inactive, and are loaded with an active ingredient.
 198

199 Metallic nanoparticles are an example of active nanoparticles that can be prepared
 200 employing either chemical or biological synthesis (Kasote et al., 2019; Mahakham et al.,
 201 2017; Maswada et al., 2018). Polymeric nanoparticles are other potentially active systems,
 202 since many of the polymers used for their preparation present biological activity (Divya
 203 et al., 2019; Li et al., 2019; Sathiyabama and Muthukumar, 2020). These systems can be used
 204 for sustained release after being loaded with substances including pesticides, fertilizers,
 205 biological compounds, or even other nanoparticles. The sustained release of these sub-
 206 stances can result in higher biological activity and reduced toxic effects (Bravo Cadena et
 207 al., 2018; de Oliveira et al., 2019; Falsini et al., 2019). Many products that are used for seed
 208 priming can be loaded into nanocarrier systems, consequently improving their biological
 209 activities (Bravo Cadena et al., 2018; Falsini et al., 2019; Pereira et al., 2019).

2.3.1. Active nanoparticles

Metallic nanoparticles, including those produced using biogenic processes, are systems that are normally smaller than 100 nm. These systems have received special attention for seed nano-priming, since many of them are prepared with metals that play important roles in plant metabolism (Das et al., 2018a).

Some examples of these metals are iron, zinc, and manganese. Iron is a co-factor for enzymes such as cytochrome P450s and Fe(II)/2-oxoglutarate-dependent oxygenase, which makes it an essential nutrient in various metabolic pathways, including respiration and photosynthesis (Guha et al., 2018; Kasote et al., 2019). Zinc is another metal essential for plant metabolism. Around 30% of the global lands is deficient in this micronutrient, leading to problems in sugar production and the synthesis of cell membranes, hormones, and proteins, affecting seedling vigor, photosynthesis, and plant defense systems (Itrotwar et al., 2019; Savassa et al., 2018). Manganese acts as a co-factor for enzymes as superoxide dismutase (involved in antioxidant response) and the oxygen-evolving complex of photosystem II (Ye et al., 2020).

Seed nano-priming using nanoparticles based on these metals has shown considerable potential for agricultural applications. For example, Dileep Kumar et al. (2020) primed chilli seeds with metal oxide nanoparticles (zinc, titanium, and silver) and found that zinc oxide nanoparticles improve germination and seedling development (shoot and root length), while these effects are not observed for the other tested metal based nanoparticles (titanium and silver). According to Rizwan et al.⁵³, priming sorghum seeds with iron oxide nanoparticles improves the seed germination, water content, and photosynthesis (Rizwan et al., 2019).

Biogenic nanoparticles prepared using biological extracts from plants, fungi, or bacteria can have high contents of phytochemicals compounds, including phytochemicals rich in hydroxyl and carbonyl functional groups, such as phenolics, flavonoids, terpenoids, sugars, and proteins. These compounds are natural reducing agents for metals and can act as capping that stabilizes the nanoparticles in colloidal solutions (Acharya et al., 2019c; Mahakham et al., 2016).

As an alternative methodology for the synthesis of metallic nanoparticles, green synthesis is more economical compared to chemical methods, and has the advantages of increasing biocompatibility and avoiding the use of toxic chemicals (Acharya et al., 2019c). Many biogenic metallic nanoparticles have been shown to present improved biological effects as well as lower (or no) phytotoxicity compared to metallic nanoparticles synthesized using chemical methods (Itrotwar et al., 2019; Kannaujia et al., 2019).

Some metallic nanoparticles can become toxic to seeds or plants due to the re-oxidation process. For example, silver nanoparticles can be re-oxidized (from Ag^0 to Ag^+ ions) within seeds and plants, and the ionic form can inactivate proteins and enzymes, resulting in toxic effects (Kannaujia et al., 2019). However, bioactive compounds present as coatings on biogenic nanoparticles can act as stabilization agents, avoiding the re-oxidation reaction and consequently increasing the biocompatibility of metallic nanoparticles (Kannaujia et al., 2019; Spagnoletti et al., 2019). Different biogenic metallic nanoparticles have been shown to be able to enhance seed germination, improve plant growth and development, and increase the levels of chlorophyll and antioxidants (Acharya et al., 2020; Das et al., 2018b; Kasote et al., 2019; Mahakham et al., 2016).

Itrotwar et al., (2019) found that biogenic zinc nanoparticles produced using brown seaweed (*Turbinaria ornata*) extracts were able to increase the plant development and the level of antioxidant compounds. Mahakham et al., (2016) showed that aged maize seeds, primed with biogenic gold nanoparticles synthesized using galangal rhizome extracts, showed improved germination with a 3-fold increase in the seed emergence vigor index compared to the control, in addition to increased chlorophyll content. Mahakham et al., (2016) found that priming rice seeds with biogenic silver nanoparticles produced using kaffir lime leaf extract increased the α -amylase activity and water uptake of the seeds, improving both germination and plant biomass. Kasote et al., (2019) primed watermelon

264 seeds with biogenic iron nanoparticles produced using onion extracts, which resulted in
265 metabolic improvements in the plants and enhancement of the innate immune system.

266 Biogenic metallic nanoparticles can act as delivery systems, since many secondary
267 metabolites may adhere on the nanoparticle surface. These metabolites can have differ-
268 ent biological actions that improve plant metabolism and growth (Ittroutwar et al., 2019;
269 Raja et al., 2019). Also, many biological extracts have fungicidal or bactericidal proper-
270 ties and can be used in the protection against pathogens (Fraceto et al., 2018; Maroufpour
271 et al., 2020). Furthermore, metallic or biogenic metallic nanoparticles can be taken up by
272 seeds more easily due their small sizes, and trigger secondary metabolites more effi-
273 ciently, providing stronger action in development of the embryo (Kasote et al., 2019;
274 Mahakham et al., 2017, 2016).

275 2.3.2. Sustained release nanocarrier systems

276 Biopolymeric nanoparticles are systems that can be made from polysaccharides, li-
277 pids, and proteins, resulting in nanoparticles that are biodegradable and biocompatible,
278 besides being able to be designed to respond to different environmental stimuli (Camara
279 et al., 2019; Fraceto et al., 2016; Shakiba et al., 2020). These systems can be loaded with var-
280 ious substances including fungicides (Gao et al., 2020; Maluin et al., 2020), essential oils
281 (Campos et al., 2019; de Oliveira et al., 2019; Kavetsou et al., 2019), plant growth regula-
282 tors (Falsini et al., 2019; Pereira et al., 2017; Yi et al., 2015) and fertilizers (Guo et al., 2018)

283 Polymeric nanoparticles used for seed coatings are normally larger than 100 nm
284 (Falsini et al., 2019), providing slow release of active compounds used to modify plant
285 metabolism or to combat pathogens (Falsini et al., 2019; Kumar et al., 2020; Muthukrishnan
286 et al., 2019; Shakiba et al., 2020). Numerous nanocarrier systems based on biopolymers
287 have the potential to be used for seed treatment, including alginate (Du et al., 2019; Ji et
288 al., 2019), zein (Oliveira et al., 2019; Qi et al., 2020), cellulose (Coelho et al., 2018; Zhang et
289 al., 2017), synthetic biopolymers (poly-epsilon-caprolactone, poly(lactic-co-glycolic acid),
290 and poly(lactic acid)) (Shakiba et al., 2020), and lipid nanoparticles (Campos et al., 2015; da
291 Silva Santos et al., 2019).

292 Chitosan is another biopolymer that has been used to prepare nanocarrier systems
293 for agricultural applications. This polymer has fungicidal properties and also acts in
294 plant metabolism, activating defense mechanisms (Chandra et al., 2015; Kashyap et al.,
295 2015; Maluin et al., 2020). The concentration of this biopolymer is a key consideration,
296 since high concentrations block seed germination (Sathiyabama and Muthukumar, 2020).
297 This effect is because oligosaccharides and polysaccharides can elicit physiological re-
298 sponses in plants, high concentrations causing cell apoptosis, while low concentrations
299 have stimulant effects (Li et al., 2019).

300 Biopolymeric nanoparticles can be used as carrier systems for metal micronutrients,
301 allowing a slow release of these compounds. Saharan et al., (2016) showed that the prim-
302 ing of maize seeds with chitosan nanoparticles containing copper induced α -amylase
303 and protease activities and promoted reserve mobilization, thus favoring seedling
304 growth. In contrast, the treatment with bulk copper led to inhibitory effects. Similarly,
305 the priming with zinc-loaded chitosan nanoparticles induced the activity of hydrolytic
306 enzymes in maize seeds, favoring germination.

307 Nanocarrier systems for plant growth regulators have shown potential for seed
308 priming, providing improvements from seed germination up to production (Falsini et al.,
309 2019; Pereira et al., 2019). Falsini et al., (2019) used lignin nanoparticles containing
310 gibberellic acid to coat arugula and tomato seeds. They observed an improved biological
311 activity of the gibberellic acid in inducing seed germination and plant growth when the
312 phytohormone was nanoencapsulated. The ability of active nanoparticles or nanocarrier
313 systems to increase seed germination can be explained by the fact that at optimal con-
314 centrations, nanoparticles are able to penetrate the seed coat, increasing the number of
315 holes in the coat and consequently increasing water uptake and oxygen transfer (Guha et
316 al., 2018; Joshi et al., 2018; Khodakovskaya et al., 2013).

317 In another work with tomato seed priming, Pereira et al., (2019) reported that chi-
318 tosan-based nanocarrier systems of gibberellic acid were able to improve not only initial
319 seedling growth but also fruit production under field conditions. In this study, the seed
320 nano-priming were able to increase the production in 225.5 % and 178,8% for chi-
321 tosan/tripolyphosphate and alginate/chitosan nanoparticles containing gibberellic acid,
322 respectively. The method used to prepare this nanoparticles do not involve organic sol-
323 vents, being interesting method aiming a sustainable agriculture. (Jiménez-Arias et al.,
324 2020; Pereira et al., 2017)

325 The improvement of the biological efficacy of active compounds by nanocarrier sys-
326 tems is associated to the enhancement of physical-chemical proprieties. Effects such as
327 increased solubility, protection against degradation, and greater bioavailability can re-
328 duce the required concentration of the active compound and minimize toxic effects
329 (Fraceto et al., 2016; Lombardo et al., 2019). Several studies have shown that seed-nano
330 priming can be more efficient than conventional methods and can contribute to im-
331 proved agricultural practices (Acharya et al., 2019a; Bravo Cadena et al., 2018; Mahakham et
332 al., 2017). Many systems defined as nanopesticides or nanofertilizers, used in the control
333 of pests or for plant development, have the potential for use in seed nano-priming
334 (Camara et al., 2019; Fischer et al., 2019; Lowry et al., 2019).

335 2.4. Seed nano-priming and effects on plant metabolism under abiotic and biotic stresses

336 Abiotic and biotic stresses lead to reduced production and economic losses. Abiotic
337 stresses are environmental factors such as drought, flood, heat or cold, salinity, or nutri-
338 ent-deficient soils. Biotic stresses are caused by microbial pathogens (bacteria or fungi),
339 insects, or weeds that compete for nutrients (Camara et al., 2019; Zhao et al., 2020).

340 The use of seed nano-priming in agriculture can improve the quality of seeds and
341 increase resistance against stress conditions. Nanoparticles can act directly against path-
342 ogens, as well as alter the metabolism of seeds and plants, consequently enhancing the
343 innate immune system, altering hormone production, and making the plants more re-
344 sistant to diseases or abiotic stress (Panyuta et al., 2016).

345 The nanoparticles uptake under seed coating can promote the ROS production, act-
346 ing in different metabolic pathways, increase the level of active gibberellins, and the
347 mobilization of storage proteins (Chandrasekaran et al., 2020). Also, the effect of nanopar-
348 ticles in increasing water uptake by the seeds can cause sufficient stress to activate ger-
349 mination, increasing the activities of enzymes in phases I and II of the process (Acharya et
350 al., 2019c; Joshi et al., 2018) (Figure 4a). Seed nano-priming has been shown to increase
351 germination, since these systems are able to keep ROS levels in the optimum range com-
352 prised by the oxidative window that promotes seed germination (Figure 4b). (Kasote et
353 al., 2019; Guha et al., 2018)

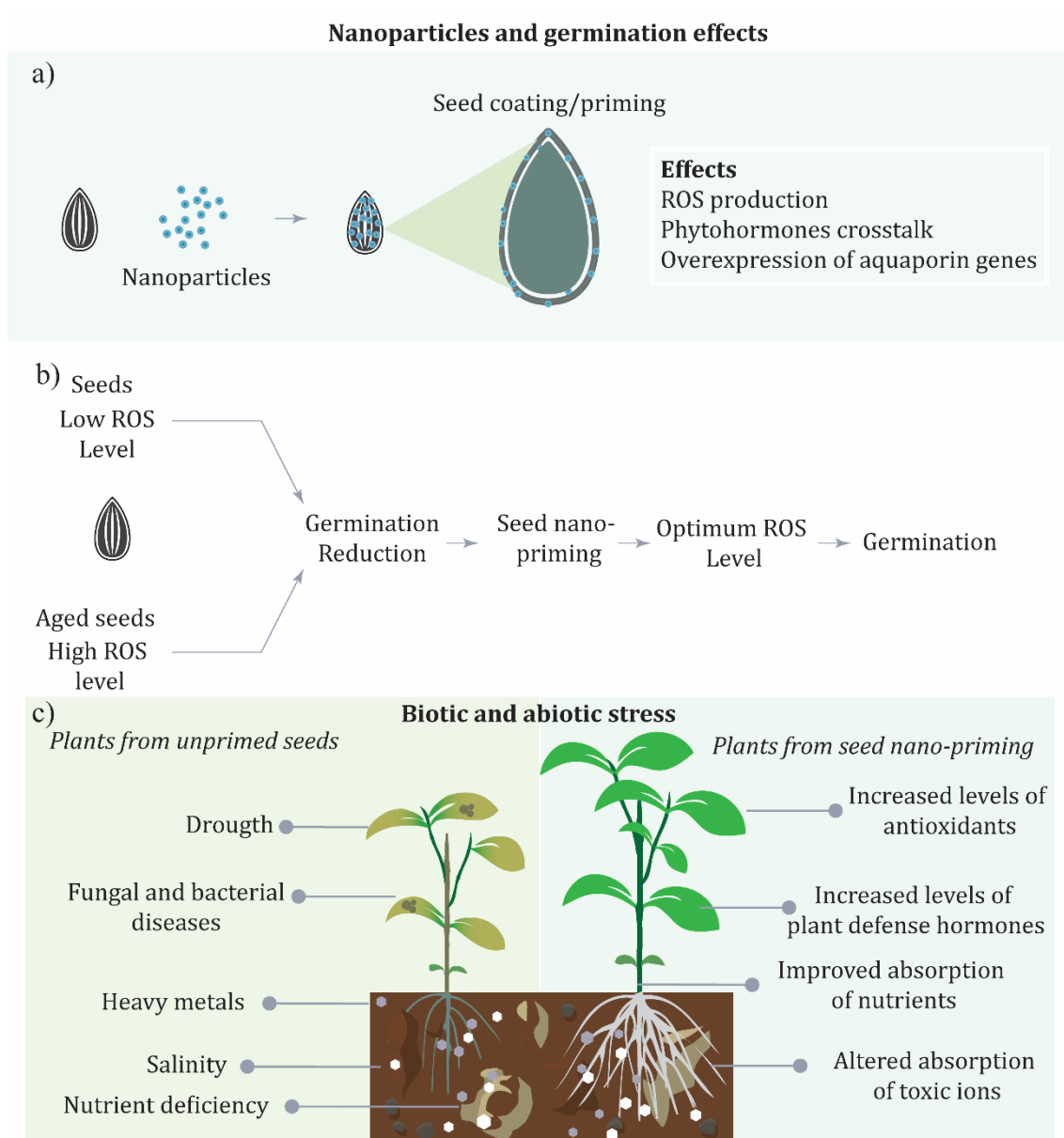


Figure 4. Effects of seed nano-priming on seeds and plants under abiotic and biotic stresses. a) Effects of seed nano-priming during the germination, b) effects of seed nano-priming on ROS levels, and c) potential effects under biotic and abiotic stress.

Under stress conditions, nanoparticles can act to reduce seed ROS levels, due to increased activity of enzymes such as superoxidase dismutase, catalases, and guaiacol-peroxidase, hence reducing seed cell damage (Guha et al., 2018).

The storage of seeds for long periods at low temperatures results in aging, which can heavily decrease the germination rate (Mahakham et al., 2016). After long periods, the seed cells initiate processes that increase ROS generation and reduce antioxidant levels, causing metabolic side effects that result in a reduction of the germination index (Guha et al., 2018).

The use of biogenic metallic nanoparticles has been shown to be able to control reactive oxygen species at optimum levels, resulting in improved germination of aged seeds. The biogenic nanoparticles can be coated with many compounds that are natural reducing agents and act to decrease ROS levels in seeds (Acharya et al., 2019c; Guha et al., 2018; Mahakham et al., 2017).

2.4.1. Biotic stress

Seed protection is required at different times during agricultural practices. In the field, the seeds and seedlings need to be protected against insects, fungi, and bacteria that can damage the seed and reduce germination or seedling growth. During harvesting and storage, seeds carry microorganisms from the field. These may shorten the shelf-life of the product or lead to the accumulation of microbial metabolites that make the products dangerous for consumption (Schmitt et al., 2020).

In the field, the use of fungicides and neonicotinoids for seed coating can reduce the damage caused by these organisms during plant establishment (Gross et al., 2020). This method has shown excellent potential compared to foliar applications (Farias et al., 2019; Matyjaszczyk, 2017). Relative to foliar treatment, the use of pesticides for seed treatment can reduce the amounts of the chemicals applied in the field as well as decrease the number of runs of agricultural machines on the land (avoiding soil compaction); so, the technique can be considered economically and environmentally advantageous (Matyjaszczyk, 2017).

Seed coating techniques employ fungicides that may be released in the field during the sowing process, resulting in environmental contamination. For example, pesticides such as carbofuran and thiran are highly toxic and persistent in the environment (Chau et al., 2019), so the consumption of treated seeds by animals such as granivorous birds can lead to poisoning or death (Gross et al., 2020).

Because nanoparticles are reactive and physiochemically dynamic materials, they tend to heteroaggregate in environmental media (Lowry et al., 2012). This can result in an effective seed coating, limiting the release of these compounds in the environment (Lowry et al., 2012).

Nonetheless, the use of nanoparticles for seed priming and coating can provide eco-friendly solutions. Many of these systems are nontoxic, biodegradable, and can increase the bioefficacy of active ingredients used at low concentrations (Bravo Cadena et al., 2018; Mahakham et al., 2017; Sathiyabama and Muthukumar, 2020).

Several systems have been shown to be effective against pathogens. Ahuja et al., (2019) demonstrated that iron(II) sulfide nanoparticles were more effective than the fungicide carbendazim to control the fungus *Fusarium verticillioides* in rice seeds. Silver nanoparticles are active against plant pathogens, including *Aspergillus flavus*, *Aspergillus niger*, *Aspergillus fumigatus*, and *Colletotrichum capsica*, showing great potential for seed protection. Metallic nanoparticle systems can be used for both seed priming and seed protection, as demonstrated for nanoparticles composed of iron (Ahuja et al., 2019), copper (Abdel Latef et al., 2017), silver (Mahakham et al., 2017), and silica (Bravo Cadena et al., 2018). Sathiyabama and Muthukumar, (2020) primed rice seeds with chitosan/guar nanoparticles, which resulted in increased plant development and higher levels of chlorophyll and carotenoids, the nanoparticles showing anti-fungal activity (71%) against the rice pathogen *Pyricularia grisea*. For pearl millet, Nandhini et al., (2019) showed that seed nano-priming and foliar application of zinc nanoparticles reduced downy mildew caused by *Sclerospora graminicola*.

Siddaiah et al., (2018) showed that the treatment of millet seeds with chitosan nanoparticles resulted in alteration of the innate immune system of the plants and increased resistance against pathogens. The treatment improved the levels of antioxidant enzymes and increased expression of proteins involved in the salicylic acid pathway, which is related to plant resistance responses against biotrophic pathogens. The field studies of Choudhary et al., (2019) showed that the treatment of maize seeds with zinc-containing chitosan nanoparticles resulted in plants with higher activity of antioxidant enzymes and lignin concentrations, making the plants more resistant to pathogens. Bravo Cadena et al., (2018) showed that silica nanoparticles loaded with cinnamon essential oil and applied to pea seeds acted as seed primers and provided bactericidal activity against *Pseudomonas syringae* pv. *psii*, even at low concentrations. The use of essential oils with fungicidal or bactericidal properties for seed priming is a promising eco-friendly alternative

425 to chemical fungicides or bactericides (Bravo Cadena et al., 2018; Campos et al., 2019; de
426 Oliveira et al., 2019).

427 Techniques employed during the storage of cereals include the control of humidity
428 and temperature to minimize the growth of microorganisms, as well as the use of chemi-
429 cal products, although the latter may be viewed negatively by consumers, who prefer
430 natural products (Schmitt et al., 2020). For this purpose, the use of biopolymers or essen-
431 tial oils with activities against pests can provide a greener alternative to agrochemicals,
432 avoiding problems associated with residual contamination.

433 2.4.2. Abiotic stress

434 Harvest yields can be drastically decreased by soil salinity and contamina-
435 tion(Maswada et al., 2018). Salinity represses plant growth due to water and nutritional
436 deficits and direct ionic effects on plant metabolism (Abdel Latef et al., 2017). Contamina-
437 tion with heavy metals may be both anthropogenic (due to fertilizer applications, indus-
438 trial processes, atmospheric deposition following waste incineration, and discharges of
439 sewage and sludge) and geogenic (due to natural atmospheric deposition or regional
440 geological processes) (Barbieri et al., 2018; Hussain et al., 2019; Qayyum et al., 2017).

441 Ye et al., (2020) showed that jalapeño seeds primed with manganese nanoparticles
442 presented improved root growth under saline conditions, modulating the distribution of
443 sodium between roots and shoots. The highest concentration was found in the shoots,
444 which the authors attributed to a higher plants response mechanism to avoid root dam-
445 age caused by high concentrations of salts changing the osmotic process and hormone
446 regulation.

447 Maswada et al., (2018) reported that sorghum seeds treated with nano-iron(III)
448 showed improved germination, with the plants showing increased chlorophyll contents
449 and improved growth under saline conditions. These results indicate that this system
450 could be used not only to improve seed germination, but also to avoid stress conditions.
451 In another study, priming lupin seeds with zinc nanoparticles improved plant develop-
452 ment under saline conditions, due to increased levels of photosynthetic pigments, phe-
453 nols, organic molecules, and antioxidant enzymes (Abdel Latef et al., 2017).

454 In a case of heavy metal contamination, Rizwan et al., (2019) showed that priming of
455 wheat seeds with iron and zinc nanoparticles reduced the absorption of cadmium, re-
456 sulting in low cadmium concentrations in the grains. Hussain et al., (2019) also demon-
457 strated that seed priming with silicon nanoparticles were able to reduce the cadmium
458 concentration in wheat roots, shoots and grain.

459 Soil deficiency of nutrients such as iron and zinc can affect the production of
460 phytohormones involved in plant defense responses, including jasmonic acid and sali-
461 cylic acid (Choudhary et al., 2019; Kasote et al., 2019). Kasote et al., (2019) primed watermel-
462 on seeds with biogenic iron nanoparticles prepared using onion extract. The plants
463 showed increased levels of jasmonic acid and of its precursor cis-(+)-12-oxo-
464 phytodienoic acid during the early seedling stage, which could increase the resistance to
465 stress.

466 Nguyen et al., (2020) showed that maize seed priming with cooper nanoparticles can
467 enhance drought resistance in plants. The leaves kept high water content, increased the
468 levels of anthocyanin, chlorophyll and carotenoids and reduced the oxidative stress.

469 These results showed the potential of seed-nano priming to relieve plant stress
470 caused by saline conditions, drought, the presence of heavy metals, or nutrient deficien-
471 cy, with the modulation of metabolism to resist stress conditions and improve plant
472 growth (Figure 4 c). The use of seed nano-priming to trigger plant resistance to abiotic
473 stress is a strong alternative to avoid side effects of global climatic crisis or anthropogen-
474 ic and geogenic effects, in order to reduce losses in the field production.

475 2.5. Effects on microbiota

476 The effect of seed nano-priming on plant microbiota is a fairly new area requiring
477 further studies. The interaction between plants and microorganisms is essential for agri-

478 culture, since these symbiotic relations are important for the absorption of nutrients, de-
479 fense against pathogens, plant quality, and productivity (Shcherbakova et al., 2017).

480 The foliar application of nanoparticles can modulate the root microbial community.
481 Raliya et al., (2016) showed that foliar application of zinc nanoparticles to mung beans led
482 to an extension of the rhizosphere zone, with root volume increasing by 58.9%. They also
483 reported increases in the activity of rhizosphere enzymes such as acid phosphatase
484 (98.07%), alkaline phosphatase (93.02%), and phytase (108%). These factors are extreme-
485 ly important for the uptake of nitrogen and phosphorus by plants.

486 Dai et al., (2020) found that roots exposed to cerium oxide nanoparticles decreased
487 the rhizosphere bacterial community, but enhanced the growth of microorganisms that
488 promote plant growth.

489 Others studies have reported side effects in the soil microbiota following amend-
490 ments with nanoparticles. Zhang et al., (2020) found that silver nanoparticles (at 100
491 mg/kg) altered the soil pH and negatively affected microorganisms involved in nitrogen,
492 carbon, and phosphorus cycles. In another study, Li et al., (2020) showed that the
493 amendment of soils with silver nanoparticles (10.4 mg kg⁻¹) reduced plant development
494 and resulted in silver bioaccumulation.

495 Other metallic nanoparticles, such as titanium and zinc nanoparticles, have been
496 found to affect the soil microbiota, depending on the concentration and the duration of
497 exposure (Chavan and Nadanathangam, 2020; Zhai et al., 2019). Apart from the intrinsic
498 properties (chemical nature, size, coating) and concentration, the impact of nanoparticles
499 on plant root and rhizosphere microbiota are largely dependent on soil texture, pH, or-
500 ganic matter content, and fertilization (Hamidat et al., 2016; Santaella and Plancot, 2020;
501 Simonin et al., 2018).

502 Few studies have investigated how seed nano-priming might affect the interactions
503 of microorganisms with roots. Rahman et al., (2020) showed that seed priming using plat-
504 inum nanoparticles stabilized with poly(vinylpyrrolidone), resulted in side effects on the
505 root microbiota of pea plants, with a decrease in mycorrhizal fungi and rhizobial coloni-
506 zation, while these effects were not observed for the same system with gold or silver na-
507 noparticles.

508 More studies in this field must be encouraged in order to elucidate the mechanisms
509 by which seed-nano priming can affect seed metabolism and alter the microbiome se-
510 lected by the roots during development of the plant. Many nanoparticle systems have
511 shown great potential for use in agriculture, but could be toxic towards soil microbiota.
512 The treatment of seeds may offer a safer way to improve the establishment of plants and
513 avoid side effects in the soil, since the treatment is performed on the seeds, avoiding ap-
514 plications in soils.

515 2.6. Improving crop quality and production

516 Seed nano-priming can increase the productivity of different crop species, due to
517 the positive effects on plant metabolism and development. Fast root development in-
518 creases the potential of the plant to access nutrients and water, accompanied by faster
519 expansion of the leaf area, consequently increasing the use of light energy for plant
520 growth.

521 The effects on the innate immune system can improve the resistance against patho-
522 gens, so that smaller quantities of pesticides need to be applied. Consequently, the con-
523 centrations of residual agrochemicals in food are lower, making the products safer for
524 consumption. These effects have been demonstrated in studies evaluating the effects of
525 seed priming, up to harvest, in species with agronomical value.

526 Yasmeen et al., (2017) showed that in wheat plants, seed priming with iron and
527 copper nanoparticles led to improvements of spike length, number of grains per spike,
528 and grain weight. Rahman et al., (2020) reported that priming of pea seeds with platinum
529 nanoparticles stabilized with poly(vinylpyrrolidone) increased production by 163.5%,
530 although the seed weight was reduced by 66.7%.

531 Acharya et al., (2020) demonstrated the potential benefits of priming watermelon
532 seeds with biogenic silver nanoparticles produced using onion extracts. The results re-
533 vealed a burst in plant development and increased metabolic activity throughout the life
534 of the plant, resulting in production increases between 31.6% and 35.6%.

535 Pereira et al., (2019) reported that the priming of tomato seeds with algi-
536 nate/chitosan nanoparticles containing gibberellic acid greatly improved fruit produc-
537 tion, increasing productivity by almost 4-fold.

538 Another issue concerns biofortification. For example, the treatment of seeds with
539 iron, zinc, and manganese nanoparticles resulted in plants and grains with higher con-
540 tents of these minerals (Sundaria et al., 2019). Other studies have also reported that in-
541 creased concentrations of these elements in roots, shoots, leaves, or grains can result in
542 vegetables richer in essential minerals (Rizwan et al., 2019; Sundaria et al., 2019).

543 Seed nano-priming can be an effective way to reduce the amounts of fertilizers ap-
544 plied to crops. A major problem in agriculture is that only 30-50% of the nitrogen and
545 45% of the phosphorus applied in the field are absorbed by the crops (Das et al., 2018b).
546 These losses can be harmful to the environment, since they can lead to the eutrophica-
547 tion of aquatic systems and contamination of native terrestrial ecosystems. The use of
548 seed nano-priming has been shown to improve root development and increase the pro-
549 duction of enzymes required for nutrient uptake, which would enable reductions of the
550 amounts of fertilizer used in the field (Guha et al., 2018).

551 3. Concerns

552 Although nanoparticles have potential for use in seed priming or seed coating, cau-
553 tion must be exercised in the application of nanomaterials. The safe use of these systems
554 demands the development of appropriate regulations based on sound research, not only
555 in agriculture, but also in many other industrial sectors (Kah et al., 2018; Scott et al., 2018).
556 Legal frameworks are required for industrial production of nanomaterials, treatment of
557 industrial waste, and agricultural applications, together with evaluation of the fates of
558 these nanoparticles in the environment, considering their possible ecotoxicity.

559 Agricultural activities are connected with many ecosystems that may be directly
560 impacted by nanomaterials (Lowry et al., 2019). Therefore, it is crucial to understand the
561 mechanisms of action of these materials and to develop nanoparticles that are safe in
562 both the field and the wider environment.

563 Before seed treatment, it is necessary to evaluate the conditions employed for prim-
564 ing, considering the nanoparticle size and concentration, and the duration of exposure,
565 since these factors can cause side effects such as germination inhibition, reduced plant
566 development, detrimental alterations of metabolism and cell structure, and modification
567 of root-microbiota interactions (Duran et al., 2017; Rahman et al., 2020; Rizwan et al., 2019).

568 It is essential to understand how the physical-chemical properties of nanoparticles
569 affect seeds and other associated organisms, in order to be able to design nanoparticles
570 that are both effective and present minimal toxic effects (Camara et al., 2019).

571 The different kinds of nanoparticles cited in this article (metallic, biogenic metallic
572 and polymeric nanoparticles) not only differ in their physical chemical characteristics,
573 but also in their biological activity. The design of these nanoparticles for seed priming
574 can be used for different strategies, as example seed protection, biofortification, plant re-
575 sistance against pests and abiotic stresses or even the mix of this effects.

576 However, the use of nanoparticles for seed priming can provide great advantages.
577 The treatments in seeds reduce the exposition of nanomaterials compared with foliar
578 and soil applications. Another positive point is the low concentrations of nanoparticles
579 used for seed priming, that can be a through a controlled form by factories, avoiding
580 high release of this materials in the environment. Probably, the residual of nanoparticles
581 in plants will be very small or even none, but studies are necessary to elucidate how dif-
582 ferent nanoparticles as metallics, metallics biogenic and polymeric interact with the
583 plant development.

584 **4. Conclusions**

585 Nanotechnology is a promising area for exploitation in agriculture, and seed-nano
586 priming is one of the tools that can be employed to promote sustainability. These sys-
587 tems can promote the establishment of plants, as well as provide protection against bio-
588 tic and abiotic stresses, resulting in improvements of productivity and food quality.



589 There are many issues that need to be addressed concerning the industrial produc-
590 tion of these technological systems and their application in the field, including scale-up,
591 seed priming conditions, and toxic effects in plants and other organisms. However, it is
592 clear that the adoption of nanoparticle systems can alter crop management, with reduc-
593 tion of the applied quantities of pesticides and contamination risks, resulting in agricul-
594 tural practices that are safer for farmers, consumers, and the environment.




595 **Declaration:** The authors declare that they have no competing interests.




596 **Author's contribution:** Anderson do Espirito Santo Pereira: Conceptualization, Writing -
597 original draft - review & editing, Halley Caixeta Oliveira: Conceptualization, Writing -
598 original draft - review & editing, Leonardo Fernandes Fraceto: Conceptualization, Writ-
599 ing - original draft - review & editing and Catherine Santaella: Conceptualization, Writ-
600 ing - original draft - review & editing




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Table 1. Nanoparticles employed for seed priming and coating, showing the nanoparticle systems, their characteristics, and the main effects on the species evaluated. Each article is classified according its application: A1 (seed priming), A2 (effects in the field), A3 (effects against pathogens), and A4 (relieving abiotic stresses).



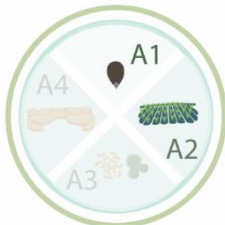
Nanoparticle system	Characteristics	Main effects	Applications	Reference
<i>Biogenic silver nanoparticles produced using kaffir lime leaf extracts</i>	Spherical nanoparticles with particle size of 6-26 nm.	Concentrations: 10 and 20 mg mL ⁻¹ . Species: Rice seeds (<i>Oriza sativa</i> L. cv. KDML 105). Effects: Increases of water uptake and aquaporin gene expression, enhanced α -amylase activity (1.2-1.3-fold higher than control group), faster germination, high vigor index of seedlings, and increases of root, shoot, and seedling biomass. The seeds showed greater uptake of silver ions compared to the silver nanoparticles.		Mahakham et al., 2017
<i>Iron oxide nanoparticles</i>	Particle size <50 nm, with surface area of 180 m/g ² .	Concentrations: 10, 50, 100, and 500 mg L ⁻¹ . Species: Sorghum (<i>Sorghum bicolor</i> (L.) Moench) KDML 105. Effects: The treatments increased seed germination and plant growth. Treatment at 500 mg mL ⁻¹ increased photosynthetic pigments and, biomass. Treatments at 100 and 500 mg mL ⁻¹ increased the relative water content in leaves.		Maswada et al., 2018




Biogenic iron nanoparticles produced using onion extracts	Particle size of 19-30 nm, with low-crystalline or amorphous Fe ₂ O ₃ .	<p>Concentrations: 20, 40, 80, and 160 mg L⁻¹ Species: Watermelon (<i>Citrullus lanatus</i> (Thunb.) Matsum and Nakay varieties). Effects: Treatment with the nanoparticles increased germination and growth of shoots and roots. The nanoparticles did not cause adverse antioxidant and chlorophyll effects, compared to the effects of the bulk counterparts (FeCl₃ and Fe₂O₃). The nanoparticles were taken up and translocated into the seed endosperm. Increased non-enzymatic antioxidant levels and induction of jasmonates-linked defense responses in the seeds.</p>		Kasote et al., 2019
Zinc oxide and iron oxide nanoparticles	Zinc oxide nanoparticles with sizes of 20-30 nm; iron oxide nanoparticles (Fe ₃ O ₄) with sizes of 50-100 nm.	<p>Concentrations: Zinc nanoparticles at 25, 50, 75, and 100 mg L⁻¹; iron nanoparticles at 5, 10, 15, and 20 mg L⁻¹. Species: Wheat (<i>Triticum aestivum</i> L.). Effects: The seed priming (high concentrations) improved plant development, increasing the spike length, plant biomass, and photosynthetic pigments, while reducing cadmium uptake. The zinc nanoparticles reduced cadmium levels in shoots, roots, and grains by 38%, 55%, and 83%, respectively. The iron nanoparticles reduced cadmium levels in the shoots, roots, and grains by 54%, 56%, and 84%, respectively. The plants presented high concentrations of Zn and Fe after seed priming.</p>		Rizwan et al., 2019
Silicon nanoparticles	Spherical nanoparticles with size around 90 nm.	<p>Concentrations: The nanoparticles were evaluated at concentrations of 300, 600, 900, and 1200 mg L⁻¹. Species: Wheat (<i>Triticum aestivum</i> L.). Effects: The seeds treated with nanoparticles and germinated in soil contaminated with cadmium showed increases of plant biomass, photosynthetic rate, and levels of carotenoids and chlorophylls <i>a</i> and <i>b</i>, while there was decreased formation of reactive oxygen species and antioxidant enzymes</p>		Hussain et al., 2019




Biogenic zinc nanoparticles produced using brown seaweed (<i>Turbinaria ornata</i>) extracts	Spherical and hexagonal nanoparticles with average size of 15-52 nm.	<p>activity. Cadmium uptake by the plants was reduced, with the greatest effect for the concentration of 1200 mg L⁻¹.</p> <p>Concentrations: Nanoparticles at concentrations of 5, 10, 25, 50, 100, and 200 mg L⁻¹. Species: Rice (<i>Oryza sativa</i> L.). Effects: The treatment at 10 mg L⁻¹ had the greatest effect, increasing seed germination, vigor index, and seedling development. The plants showed high contents of antioxidant enzymes. There was a dose-response accumulation of zinc in the seedlings, according to the concentration used for seed priming.</p>		Itroutwar et al., 2019
Nanoparticles of zinc, titanium, and silver	Zinc oxide nanoparticles (35-40 nm), titanium oxide nanoparticles (100 nm), and silver nanoparticles (85 nm), with spherical, cylindrical, and needle-like morphologies, respectively.	<p>Concentrations: Nanoparticles at concentrations of 750, 1000, and 1250 mg kg⁻¹. Species: Chilli (<i>Capsicum annuum</i> L.). Effects: The zinc nanoparticles increased germination, as well as shoot and root growth. These effects were not observed for the titanium and silver nanoparticles. Evaluation against the pathogens <i>Aspergillus flavus</i>, <i>Aspergillus niger</i>, <i>Aspergillus fumigatus</i>, and <i>Colletrotrichum capsica</i> showed that silver nanoparticles at 1000 and 1250 mg kg⁻¹ could reduce pathogen infection.</p>		Dileep Kumar et al., 2020
Chitosan/tripolyphosphate nanoparticles	Nanoparticles with size of 259.4 ± 4.7 nm, PDI (polydispersity index) of 0.28 ± 0.0016, and zeta potential of 40.0 ± 2.9 mV.	<p>Concentrations: Nanoparticles at concentrations of 1-100 µg mL⁻¹. Species: Wheat (<i>Triticum aestivum</i> L.). Effects: The nanoparticles promoted plant development, increasing the chlorophyll content at low concentration (5 µg mL⁻¹), and showed metabolic effects, with enhancement of auxin content in roots and shoots.</p>		Li et al., 2019





<p><i>Biogenic gold nanoparticles synthesized using galangal rhizome extracts</i></p>	<p>Spherical nanoparticles with size of 10-30 nm.</p>	<p>Concentrations: Nanoparticles at concentrations of 5, 10, and 15 ppm. Species: Maize (<i>Zea mays</i> L.). Effects: The treatment at 10 ppm improved the emergence from aged seeds by 83% and seed vigor index by 3-fold, compared to the control. The plants showed increased chlorophyll content. The nanoparticles were detected in the seeds, roots, and shoots.</p>		<p>Mahakham et al., 2016</p>
<p><i>Manganese(III) oxide nanoparticles</i></p>	<p>Spherical nanoparticles with size of 50 nm and zeta potential of 29.2 ± 1.8 mV.</p>	<p>Concentrations: 0.1, 0.5, and 1 mg mL⁻¹. Species: Jalapeño (<i>Capsicum annuum</i> L.). Effects: Under salt stress conditions, the seedlings showed greater root length (around 55% greater than for the control). Molecular evaluation (expression of manganese superoxide dismutase) showed that the seed priming could control oxidative stress. Seed priming avoided changes of proteins, lignin, or distribution of nutrients, which are effects caused by salt stress in plants. The nanoparticles were taken up by the seeds and formed nanoparticle-corona complexes.</p>		<p>Ye et al., 2020</p>
<p><i>Iron(II) sulfide aqua nanoparticles</i></p>	<p>Spherical nanoparticles with size around 6-20 nm</p>	<p>Concentration: 30 µg mL⁻¹. Species: Rice (<i>Oryza sativa</i> L.). Effects: The treatment of seeds with nanoparticles resulted in increased germination, vigor index, and root length. Evaluation against the fungus <i>Fusarium verticillioides</i> showed that the nanoparticles presented anti-fungal activity, with 10-fold greater efficiency than the fungicide carbendazim for control of the fungus and reduction of rice rot.</p>		<p>Ahuja et al., 2019</p>




<i>Copper nanoparticles</i>	Nanoparticles with sizes of 25, 40, and 80 nm, and zeta potentials of 15-25 mV.	<p>Concentrations: 1, 10, 100, and 1000 mg Cu L⁻¹. Species: Common bean (<i>Phaseolus vulgaris</i> L.). Effects: The effects depended on nanoparticle size and concentration, with low concentrations and larger nanoparticles increasing plant weight. High concentrations inhibited seed germination, independent of nanoparticle size.</p>		Duran et al., 2017
<i>Chitosan nanoparticles of and carbon nanotubes</i>	Chitosan nanoparticles with size of 95 ± 2 nm and zeta potential of +123.5 mV; carbon nanotubes with size of 40 ± 0.4 nm and zeta potential of -8.5 mV	<p>Concentrations: 10% of both nanomaterials were used, with a concentration of 20 µg L⁻¹. Species: Common bean (<i>Phaseolus vulgaris</i> L.). Effects: Seed priming with the nanomaterials led to side effects. The plants presented reduced growth parameters, stress effects (increases of electrolyte leakage and hydrogen peroxide), and reduced concentrations of carbohydrates, proteins, and vitamin C. The authors evaluated the same systems for foliar treatment, with the results showing improvement of plant quality. The carbon nanomaterial led to a reduction of 30 days for harvesting the crop.</p>		Abdel-Aziz et al., 2019
<i>Zinc nanoparticles</i>	Zinc nanoparticles with size of 20 nm and spherical shape, and sizes of 40 and 60 nm with elongated shapes.	<p>Concentrations: 1, 10, 100, 1000, and 5000 mg L⁻¹. Species: Common bean (<i>Phaseolus vulgaris</i> L.). Effects: None of the treatments affected germination. After 5 days, higher fresh weight was obtained for the treatment with 40 nm nanoparticles. Few nanoparticles were detected in the cotyledons, with the greatest part being retained in the seed coat.</p>		Savassa et al., 2018


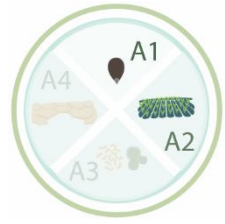

<i>Chitosan nanoparticles</i>	Chitosan nanoparticles with sizes of 20-170 nm.	<p>Concentrations: 0.5, 1, 1.5, 10, 15, and 20 mg mL⁻¹. Species: Rice (<i>Oryza sativa</i> L.). Effects: The nanoparticles increased seed germination, seedling growth, and plant weight.</p>		Divya et al., 2019
<i>Zinc nanoparticles</i>	Mean size of 21.3 nm	<p>Concentrations: 20, 40, and 60 mg L⁻¹. Species: Lupin (<i>Lupinus termis</i> L.). Effects: A saline condition was imposed by the use of 150 mM NaCl. The treatment at 60 mg L⁻¹ mitigated the stress condition, avoiding reductions of growth parameters (root and shoot lengths; fresh and dry weights) and photosynthetic pigments. Soluble sugar and protein contents were increased, lipid peroxidation was reduced.</p>		Abdel Latef et al., 2017
<i>Biogenic silver and gold nanoparticles produced using onion extract</i>	<p>Silver nanoparticles with size of 11.6 ± 2.40 nm and zeta potential of -2.20 ± 0.29 mV, with spherical and ellipsoidal morphology; gold nanoparticles with size of 93.68 ± 2.06 nm and zeta potential of -8.51 ± 1.26 mV, with anisotropic morphology.</p>	<p>Concentrations: Silver nanoparticles at 31.3 µg mL⁻¹ and gold nanoparticles at 31.3 µg mL⁻¹. Species: Onion (<i>Allium cepa</i> L.) Effects: The studies were performed for 2 years; the treatments resulted in increases of seedling emergence, number of leaves, plant weight, and productivity, compared to unprimed and hydro-primed seeds. The results also showed metabolic effects, with increases of chlorophylls <i>a</i> and <i>b</i>. The gold nanoparticles provided better results than the silver nanoparticles. The uptakes of nanoparticles by the onion seeds were 29.75% for silver nanoparticles and 4.86% for gold nanoparticles.</p>		Acharya et al., 2019a



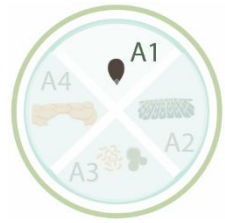
<p><i>Platinum nanoparticles stabilized with poly(vinylpyrrolidone)</i></p>	<p>Nanoparticles with size of 3.2 ± 0.8 nm and spherical morphology.</p>	<p>Concentrations: Concentrated solution at 1.0 mM. Species: Pea (<i>Pisum sativum</i> L.). Effects: Seed priming for 3 hours resulted in side effects, with decreases of germination and root length. The treatment reduced colonization by microorganisms (arbuscular mycorrhizal fungi and rhizobia).</p>		<p>Rahman et al., 2020</p>
<p><i>Biogenic silver nanoparticles produced using Phyllanthus emblica</i></p>	<p>Nanoparticles with size of 10-35 nm, irregular shape, and zeta potential of -23.8 mV.</p>	<p>Concentrations: 0, 5, 10, 25, and 50 mg L⁻¹. Species: Wheat seeds (<i>Triticum aestivum</i> L.). Effects: The biogenic silver nanoparticles reduced ROS production by root systems compared to non-biogenic silver nanoparticles, although the effects differed according to the wheat variety. The non-biogenic silver nanoparticles reduced the germination index, while the biogenic nanoparticles at a concentration of 10 mg L⁻¹ increased root growth. Coating with plant extract reduced nanoparticle uptake by wheat seeds.</p>		<p>Kannaujia et al., 2019</p>
<p><i>Chitosan guar nanoparticles</i></p>	<p>Nanoparticles with size of 122 nm, PDI of 0.358, and zeta potential of -30 mV.</p>	<p>Concentrations: 0.05, 0.1, and 0.2%. Species: Rice (<i>Oryza sativa</i> L.). Effects: At concentrations of 0.05% and 0.1%, the nanoparticles promoted seed germination, while the use of 0.2% reduced seed germination. The plants showed increases of root and shoot lengths as well as of fresh and dry weights. The levels of chlorophyll and carotenoids were increased. The formulation showed anti-fungal activity (71%) against the rice blast pathogen <i>Pyricularia grisea</i>.</p>		<p>Sathiyabama and Muthukumar, 2020</p>

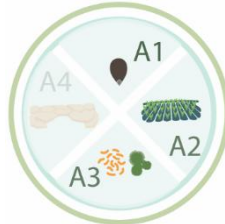
Iron nanoparticles	Nanoparticles with size of ~80 nm and zeta potential of -44 mV.	<p>Concentrations: 25, 50, 100, 200, 300, 400, 500, and 1000 $\mu\text{g mL}^{-1}$. Species: Wheat (<i>Triticum aestivum</i> L.), types WL711 (low-iron genotype) and IITR26 (high-iron genotype). Effects: Increased germination index at 300 and 400 $\mu\text{g mL}^{-1}$. The best treatment for WL711 was 200 $\mu\text{g mL}^{-1}$, which increased shoot and root lengths by 64% and 46%, respectively. High concentrations caused inhibition of plant growth. At 25 $\mu\text{g mL}^{-1}$, the concentrations of iron at harvest were 45.7% (IITR26) and 26.8% (WL711).</p>		Sundaria et al., 2019
Zero-valent iron nanoparticles (priming of aged seeds)	Nanoparticles with size of 33.8 ± 3.59 nm and zeta potential of -39 mV.	<p>Concentrations: 10, 20, 40, 80, and 160 mg L^{-1}. Species: Rice (<i>Oryza sativa</i> L.). Effects: At 20 mg L^{-1}, there was increased water uptake, while above this concentration, the water uptake decreased by 25-50%. Increases were observed for root and shoot lengths, chlorophyll and carotenoid levels, and amylase and protease activities. Control of ROS levels and membrane integrity was the greatest at 20 mg L^{-1}. The highest concentration (160 mg L^{-1}) had negative effects on seedling growth. Iron content in roots and shoots increased in line with the nanoparticle concentration.</p>		Guha et al., 2018
Biogenic silver nanoparticles and turmeric nanoemulsions	Turmeric nanoemulsion with particle size of 171.3 \pm 0.52 nm, PDI of 0.25, and zeta potential of -1.23 ± 0.16 mV; biogenic silver nanoparticles with size of 141.3 \pm 0.78 nm, PDI of 0.18 \pm 0.03, and zeta poten-	<p>Concentrations: 10-fold diluted turmeric nanoemulsion and biogenic silver nanoparticles at 31.3 $\mu\text{g mL}^{-1}$. Species: Watermelon (<i>Citrullus lanatus</i> (Thunb.) Matsum. & Nakai). Effects: The biogenic nanoparticles reduced the germination time. There were increases of the catabolism of disaccharides (sucrose) to monosaccharides (fructose and glucose), shoot length, stem diameter, and chlorophyll content. There was no difference in the concentration of phenolic compounds, compared to the control. Productivity increased by between 31.6% and 35.6%. The formulations were taken</p>		Acharya et al., 2020

	tial of -1.23 ± 0.16 mV.	up by the seeds.		
<i>Multi-walled carbon nanotubes</i>	Nanotubes with diameter of 13-14 nm.	Concentrations: 70, 80, and 90 $\mu\text{g mL}^{-1}$. Species: Wheat (<i>Triticum aestivum</i> L.). Effects: Increases of seed germination, root length, number of root hairs, shoot length, plant weight, number of stomata, and size of average length of vascular systems (xylem and phloem). At 90 $\mu\text{g mL}^{-1}$, there were increases of 21% and 27% for spike length and weight, respectively, 20% for the number of spikelets, and 32% for grain production.		Joshi et al., 2018
<i>Nano-pyrite (FeS₂)</i>	Nanoparticles with sizes in the range 25-100 nm, with spherical morphology	Concentrations: 50 $\mu\text{g mL}^{-1}$. Species: Rice (<i>Oryza sativa</i> L.). Effects: Increased α -amylase activity and improved germination. Field studies showed that seeds treated with nano-pyrite (FeS_2), with seedlings grown in the field without fertilizers, had the same productivity found for untreated seeds, with seedlings grown in the presence of fertilizers.		Das et al., 2018b
<i>Mesoporous silica nanoparticles containing cinnamon essential oil</i>	Nanoparticles with size of ~100 nm and pores of around 2-2.8 nm.	Concentration: 2 mg mL^{-1} . Species: Pea seeds (<i>Pisum sativum</i> L.). Effects: The seeds showed fast germination and in biological evaluations against <i>Pseudomonas syringae</i> pv. pisi, the cinnamon essential oil provided a 90,000-fold increase in bactericidal activity in comparison the oil non-encapsulated.		Bravo Cadena et al., 2018
<i>Copper and iron nanoparticles</i>	Copper nanoparticles with sizes of around 15-30 nm; iron nanoparticles with sizes of around 20-30 nm.	Concentrations: 20, 25, 30, 35, and 40 ppm Species: Wheat (<i>Triticum aestivum</i> L.) seeds of varieties galaxy-13, Pakistan-13, and NARC-11. Effects: Different effects were observed, depending on the wheat variety and the nanoparticle priming. The nanoparticles increased starch degradation, glycolysis, and the tricarboxylic acid cycle. Both types of nanoparticle increased the sugar content and superoxide dismutase activity, while the		Yasmeen et al., 2017

Cobalt and molybdenum oxide nanoparticles	Both types of nanoparticle had sizes of 60-80 nm and spherical morphology.	<p>copper nanoparticles had greater potential to improve stress tolerance. Treatment with the iron and copper nanoparticles at 25 $\mu\text{g mL}^{-1}$ increased the spike length, the number of grains per spike, and the grain weight. However, high concentrations decreased all these parameters, depending on the wheat variety.</p> <p>Concentrations: 1 L of stock commercial solution for 40 kg of seeds. Species: Soybean seeds (<i>Glycine max</i> (L). Merr.). Effects: The nanoparticles increased seed germination and, when associated with plant growth regulators (auxin and gibberellic acid), increased the shoot and root length and dry biomass. The molybdenum oxide nanoparticles increased the activities of amylases and lipase.</p>		Chau et al., 2019
Biochar nanoparticles produced from rice and wood sawdust	Nanoparticles with sizes of ~22-56 nm and spherical morphology.	<p>Concentrations: 0.5, 5, and 50 mg L^{-1}. Species: Rice (<i>Oryza sativa</i> L.) and tomato (<i>Lycopersicon esculentum</i> Mill.). Effects: For rice, the treatments with rice biochar nanoparticles increased seed germination, with the exception of the highest concentration (50 mg L^{-1}). The treatments increased root growth by 50%, compared to the control, and also increased the plant biomass. The biochar nanoparticles showed no stimulant effects on tomato seeds. For the other species, the nanoparticles presented side effects.</p>		K. Zhang et al., 2020
Chitosan nanoparticles loaded with thiamine	Nanoparticles with size of 560 nm, polydispersity <1, and zeta potential of 37.7 mV.	<p>Concentration: 0.1%. Species: Chickpea (<i>Cicer arietinum</i> L.) Effects: The nanoparticles increased seed germination, induced a 10-fold increase of the auxin level in seedlings, and increased the quantity of secondary roots.</p>		Muthukrishnan et al., 2019

Lignin nanoparticles loaded with gibberellic acid	Nanoparticles with sizes around 200-250 nm, polydispersity of 0.17-0.38, and spherical morphology.	<p>Concentrations: 0.5, 1, and 1.5 mg mL⁻¹. Species: Arugula (<i>Eruca visicaria</i> (L.) Cav. subsp. <i>sativa</i>), tomato (<i>Solanum lycopersicum</i> L. cv. Ciliegino), and chickpea (<i>Cicer arietinum</i> L.). Effects: The effects varied according to the time of sowing after the treatment. For the arugula seeds, the formulations improved germination and increased the stem and root lengths and the plant biomass. Similar effects were observed for tomato seeds, varying according to the parameter and the concentration used. The system could be taken up by the seeds and provided a seed coating.</p>		Falsini et al., 2019
Chitosan nanoparticles loaded with gibberellic acid	Alginate/chitosan nanoparticles with 450 ± 10 nm, PDI of 0.3 and zeta potential of -29 mV. Chitosan/tripolyphosphate nanoparticles with 195 ± 1 nm, PDI of 0.3 and zeta potential of 27 mV. Spherical morphology	<p>Concentrations: 0.05, 0,005, and 0,0005 mg mL⁻¹. Species: tomato (<i>Solanum lycopersicum</i> var. <i>cerasiforme</i>). Effects: The chitosan nanoparticles had a biological response according the concentration. The chitosan nanoparticles improve the shoot and root dry weight with 30 days. After 90 days the seeds treated with chitosan nanoparticles containing gibberellic acid, improve the shoot plant length and weight. Also improve the production of fruits in 225% for chitosan/tripolyphosphate and 178% for alginate/chitosan nanoparticles. The plants treated with alginate/chitosan nanoparticles loaded with gibberellic acid increase the fruit weight in 30%</p>		Pereira et al., 2019
Biogenic silver nanoparticles produced using the fungus <i>Macrophomina phaseolina</i>	Nanoparticles with size of 5-30 nm.	<p>Concentrations: 10, 20, and 50 µg mL⁻¹. Species: Soybean (<i>Glycine max</i> (L.) Merr.). Effects: The nanoparticles showed bactericidal effects against gram-positive and gram-negative bacteria. There were no observed effects on germination or seed development.</p>		Spagnoletti et al., 2019

Chitosan nanoparticles	Nanoparticles with size of 400 nm and spherical morphology.	<p>Concentration: 250 mg kg⁻¹. Species: Pearl millet (<i>Pennisetum glaucum</i> (L.) R.Br.). Effects: The chitosan nanoparticles increased seed germination. The treated seeds showed increased resistance against downy mildew disease caused by the biotrophic oomycete <i>Sclerospora graminicola</i>. The seed priming improved the innate immune system. The plants showed increased the expression of genes of phenylalanine ammonia lyase, peroxidase, and polyphenoloxidase. The plants overexpressed PR1 and PR5 proteins, markers of salicylic acid pathways.</p>		Siddaiah et al., 2018
Biogenic zinc oxide nanoparticles produced using <i>Eclipta alba</i> extracts	Nanoparticles with size of 32 nm.	<p>Concentrations: 50, 100, 150, 200, 250, and 500 ppm. Species: Pearl millet (<i>Pennisetum glaucum</i> (L.) R.Br.). Effects: <i>In vitro</i>, at 100-250 ppm, the nanoparticles increased seed germination and vigor. In the field, at 200 and 250 ppm, there were increases of plant growth (fresh weight and surface leaves). The combination of seed-nano priming and the foliar application of nanoparticles inhibited sporulation and growth of <i>Sclerospora graminicola</i>.</p>		Nandhini et al., 2019
Chitosan nanoparticles containing copper	Nanoparticles with size of 374.3 ± 8.2 nm and zeta potential of 22.6 mV	<p>Concentrations: 0.01, 0.04, 0.08, 0.12, and 0.16% w/v. Species: Maize seeds (<i>Zea mays</i> L.). Effects: Inhibitory effects on plant development were induced only by the highest concentration. The other concentrations improved seed germination and seedling growth by inducing α-amylase and protease activities and promoting reserve mobilization.</p>		Saharan et al., 2016

<p><i>Chitosan nanoparticles containing zinc</i></p>	<p>Nanoparticles with size of 387.7 ± 4 nm, spherical morphology, polydispersity of 0.22, and zeta potential of +34 mV.</p>	<p>Concentrations: 0.01, 0.04, 0.08, 0.12, and 0.16% w/v. Species: Maize seeds (<i>Zea mays</i> L.). Effects: The nanoparticles showed anti-fungal activity against <i>Curvularia lunata</i>. The seeds showed increased germination, due to high activity of α-amylases and protease enzymes. The combination of seed-nano priming and application of the nanoparticles to leaves increased the activities of antioxidant enzymes and of phenylalanine ammonia lyase and polyphenol oxidase. Lignin accumulation was also increased. In field experiments, the seeds/plants treated with nanoparticles were less susceptible to diseases, compared to the control. The grain yield increased by 39.8% and the seeds showed higher zinc contents.</p>		<p>Choudhary et al., 2019</p>
<p><i>Molybdenum nanoparticles combined with the bacteria Mesorhizobium ciceri ST282 and Bacillus subtilis Ch13</i></p>	<p>Nanoparticles with size of 35-50 nm.</p>	<p>Concentrations: 10 mg L⁻¹ of nanoparticles, 10⁸ CFU mL⁻¹ of <i>M. ciceri</i> ST282, and 10⁷ CFU mL⁻¹ of <i>B. subtilis</i> Ch13. Species: Chickpea (<i>Cicer arietinum</i> L.). Effects: Priming of the seeds with nanoparticles plus microorganisms resulted in increases of germination, plant growth, harvest yield, and antioxidant activity.</p>	<p>Shcherbakova et al., 2017</p>	

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