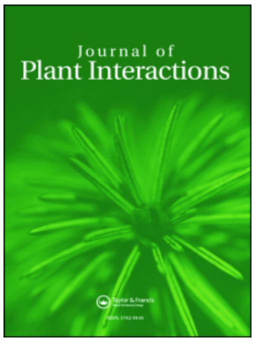

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The impact of copper oxide nanoparticles on plant growth: a comprehensive review

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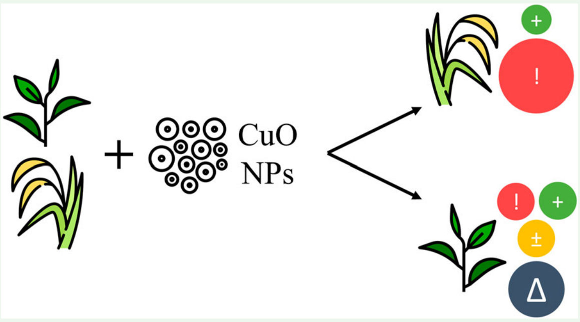
ABSTRACT
Copper oxide nanoparticles (CuO NPs) are a type of nanomaterial with unique physical and chemical properties that make them useful in various applications. CuO NPs have been studied for their potential agricultural applications, where they can have both positive and negative effects on plants, depending on factors such as concentration and duration of exposure. CuO NPs have been shown to improve plant growth and development by enhancing photosynthesis, nutrient uptake, and root growth. However, high concentrations of CuO NPs can cause oxidative stress and damage to plant cells, resulting in reduced growth and yield. Furthermore, these NPs can be taken up by plants and accumulate in various plant tissues, raising concerns about their potential impact on human health if ingested *via* the food chain. Further research is needed to determine the safe and effective application method and optimal concentration of CuO NPs in agriculture.



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Copper oxide; nanoparticles; plants

Highlights

- CuO NPs can benefit or harm plants, based on concentration and exposure time.
- Monocots are more negatively affected by CuO NPs, dicots show diverse response.
- CuO NPs impact plants based on species, concentration, and application.
- More research needed to understand CuO NPs' impact on plant growth and health.

1. Introduction

The use of nanoparticles (NPs) in agriculture can be considered a double-edged sword. While they have known positive effects as fertilizers and pesticides (Tapan et al. 2010; Madhuban et al. 2012; Tiwari et al. 2014), plants tend to uptake and translocate them, potentially disrupting their physiological processes (Li et al. 2015) and affecting their growth and development (Murali et al. 2022). The effects of NPs vary widely, primarily depending on their concentration and chemical composition (El-Moneim et al. 2021). NPs composed of essential nutrients can be used as fertilizers as they can provide nutrients to plants and are used in soil remediation projects (Du et al. 2017). In these cases, they are preferred because they release their metal content slowly, offering a longer-lasting effect compared to the immediate increase in concentration when using an ionic solution. However, NPs have been shown to inhibit plant growth at lower concentrations than their bulk forms (Song et al. 2016). Smaller NPs have demonstrated greater toxicity, penetrating the plant and even the cell wall itself (Du et al. 2011; Servin et al. 2012), although the exact mechanism of uptake remains incompletely understood (Ma and Yan 2018). Due to their variation in size and properties, including chemical composition, surface charge and surface modification, NPs can undergo different internalization processes in plants, leading to their accumulation, migration, and subsequent impact on plant growth (Karami Mehrian and De Lima 2016; Gao et al. 2023). As recently reviewed by Wang et al. (2023), plants may be able to take up nanoparticles across their entire body surface. Roots uptake nanoparticles through primary roots, pores in the root cell wall, and damaged areas, while leaves uptake nanoparticles using the pores of the periderm and stomata. Once taken up, these nanoparticles are transported within the plant *via* both the symplastic and apoplastic pathways and can move between

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different plant tissues through the xylem and phloem. Plants respond differently to NPs depending on their species due to their different physiology and also growth medium (Lin and Xing 2008; Dev et al. 2018). In general, the mechanism of the effect seems to revolve around the generation of reactive oxygen species (ROS) by the NPs, causing oxidative damage and peroxidation of plant lipids (Kamat et al. 2000; Foley et al. 2002; Reddy et al. 2016).

Copper (Cu), an abundant transition metal in the Earth's crust, is widely used and valued for its good heat and electrical conductivity. On average, the lithosphere contains 60 mg/kg of Cu, while soils typically contain 2–50 mg/kg (Oorts 2013). Cu, is an essential microelement for plants, required as a cofactor in many physiological and biochemical processes (Garcia et al. 2014). However, Cu can easily become toxic at higher-than-optimal levels. High levels of Cu are well-documented to cause oxidative stress, negative effects on the uptake of other elements, reduced photosynthetic pigment levels, and impairment of cellular components (Shabbir et al. 2020). When exposed to high Cu concentrations, plants exhibit various visible toxicity symptoms, including root and shoot growth inhibition or even plant death (Zhang et al. 2019).

Copper oxide (CuO) NPs are typically synthesized using various methods, such as chemical precipitation, thermal decomposition, and sol–gel processes (Grigore et al. 2016). In addition to these methods, the process of green synthesis has successfully produced a significant quantity of nanoparticles composed of metals or metal oxides *via* algal, fungal, plant and other biosynthesis routes (Chakraborty et al. 2022). These NPs can vary in size, shape, and surface charge depending on the synthesis method and reaction conditions (Naz et al. 2020). Furthermore, various studies have demonstrated several interesting properties, including excellent electrical conductivity, catalytic activity, and antimicrobial properties (Grigore et al. 2016; Song et al. 2019; Shehabeldine et al. 2023). These properties make them useful in a wide range of applications, including as catalysts in chemical reactions, solar cells, batteries, nanoelectronics, antibacterial agents in healthcare and environmental remediation (Boboc et al. 2017; Rafique et al. 2017). Due to their diverse uses, there are multiple pathways through which they can be released into the environment, such as through the use of raw materials, commercial synthesis, or wastewater (Brar et al. 2010; Naz et al. 2020). However, it is important to consider the potential health and environmental risks associated with the unique properties of CuO NPs. High concentrations of CuO NPs have been shown to be toxic to cells and organisms, and their small size allows them to penetrate cells and tissues, potentially having adverse effects on human health if ingested or inhaled (Hou et al. 2017). Therefore, careful assessment of the risks and benefits of CuO NPs to plants is necessary before their widespread use in various applications.

In general, CuO NPs can affect plants in two main ways. Firstly, they can release Cu, which, although an essential element, can become toxic at high doses, or they can cause particle stress by entering the plant itself (Ruttkay-Nedecky et al. 2017; Velicogna et al. 2020). The primary mechanisms of toxicity are thought to be the generation of excess ROS, leading to oxidative stress and subsequent cytotoxicity, as well as the potential for CuO NPs to cause genetic damage (Atha et al. 2012; Naz et al. 2020). If the particles release Cu ions, these ions can attach to protein thiol groups, leading to conformational changes in the proteins (Nekrasova and Maleva 2007). Another manifestation of toxicity is through the Fenton reaction, where Cu ions convert hydrogen peroxide into hydroxyl radicals, causing damage to nearby macromolecules (Chung et al. 2019).

Like many cases, the key to the agricultural application of CuO NPs lies in finding the appropriate dose. Plants experience toxicity and hindered growth when exposed to high concentrations of Cu, while Cu deficiency results in various abnormal conditions, such as distortion of young leaves, necrosis, stem bending, impaired vegetative growth, and reduced grain quality in crop plants (Siddiqi and Husen 2020).

Over the last decade, an increasing number of studies have investigated the effects of CuO NPs on various plant species. These studies often employ germination indices and seedling growth parameters to assess the effects of CuO NP exposure. While it is important to study the underlying processes, these measurements provide an excellent basis for comparing CuO NP-induced responses across different plant species. Generally, these changes range from growth promotion to no effect to inhibition of seed germination and root and shoot growth, depending on both the plant species and size, as well as the experimental system employed.

The objective of this review is to collect, organize and evaluate the available studies on the relationship between plants and CuO NPs. By reviewing and organizing existing studies, this review helps consolidate the current understanding of the effects of CuO NPs on plants. It enables researchers and scientists to have a comprehensive understanding of the topic, including the range of responses observed across different plant species and experimental conditions and helps to identify gaps in the existing research, highlighting areas that require further investigation.

2. Responses of monocotyledonous plants to copper oxide nanoparticles

Studies have indicated that the responses of monocotyledonous plants to CuO NPs can vary depending on various factors, such as NP concentration, duration of exposure, and, most importantly, the specific plant species being investigated. In general, monocotyledons have shown a negative response to CuO NP treatment, with only a few exceptions.

Among the monocotyledons studied, a significant number of experiments have focused on investigating the response of rice, wheat, and maize to CuO NPs. Interestingly, the results reveal that wheat is much less sensitive to the presence of CuO NPs compared to rice or maize.

The relationship between rice (*Oryza sativa* L.) and CuO NPs has been extensively studied across various applied concentrations and experimental systems. The majority of these studies have demonstrated growth inhibition in rice when exposed to CuO NPs (Table 1). Oxidative stress induced by CuO NPs has emerged as a common factor contributing to the observed growth inhibition. In the Nipponbare cultivar of rice, the addition of CuO NPs led to increased lipid peroxidation in both root and shoot tissues, and this oxidative stress response was found to be mediated by ethylene (Azhar et al. 2023). In the Jyoti cultivar, oxidative and osmotic stress were detected after 30 days of exposure, negatively

Table 1. Studies investigating the relationship between rice (Oryza sativa L.) and CuO NPs. '-' means inhibition, while 'n.d.' marks parameters not determined.

				Effect on				
Species; cv/var, if provided	Particle size [nm]	Concentration	Medium used	Germination	Root Growth	Shoot Growth	Notes	Reference
Oryza sativa L. cv. Nipponbare	38	100, 250, 450, 600 mg/L	Petri dish, paper	n.d.	–	–	450 mg/L of CuO NPs reduced plant biomass accumulation while increased oxidative stress indicators.	Azhar et al. 2023
O. sativa var. Jyoti	<50	2.5, 10, 50, 100, 1000 mg/L	Hydroponic	–	–	–	Inhibited growth, photo-phosphorylation and carbon dioxide assimilation.	Da Costa et al. 2020
O. sativa	<50	100 µM	Hydroponic	n.d.	–	–	Inhibited growth and photosynthetic parameters.	Rai et al. 2021
O. sativa	40	0, 10, 50, 100, 500, 1000, and 2000mg/L	Petri dish, paper	–	–	–	Inhibited seed germination and early seedling growth by high concentration of CuO NPs.	Wang et al. 2020b
O. sativa	<50	62.5, 125, and 250 mg/L	Hydroponic	n.d.	–	–	Inhibited growth, oxidative stress, decreased amount of photosynthetic pigments.	Yang et al. 2020
O. sativa	43 ± 9	500, 1000 mg/kg	Soil	n.d.	–	–	Plant growth and grain fresh weight inhibition.	Peng et al. 2017
O. sativa var. Jyoti	<50	2.5, 10, 50, 100, 1000 mg/L	Petri dish, paper	–	0/–	–	Decreased germination, root and shoot length, biomass and photosynthetic parameters.	Da Costa and Sharma 2016
		100 mg/L		–	0	–		
		1000 mg/L		–	–	–		
O. sativa	<50	5 mg/L	Hydroponic	n.d.	–	n.d.	Inhibited root elongation and biomass, ROS production.	Wang et al. 2015
O. sativa Jijing No. 6	<50	25, 50, 100, 500, 1000, 2000mg/L	Petri dish, paper	0	–	0	Concentration-dependent root growth inhibition.	Yang et al. 2015
O. sativa cv. Swarna	<50	0.5, 1.0, 1.5 mM	Nano-CuO suspension saturated cotton pad	–	–	–	Growth inhibition, oxidative burst.	Shaw and Hossain 2013

Table 2. Studies investigating the relationship between wheat (*Triticum aestivum* L.) and CuO NPs. '+' indicates growth induction, '-' represents inhibition, while 'n.d.' marks parameters not determined. (RNS – reactive nitrogen species, H_2S – hydrogen sulphide).

				Effect on				
Species; cv./var., if provided	Particle size [nm]	Concentration	Medium used	Germination	Root Growth	Shoot Growth	Notes	Reference
Triticum aestivum L. cv. GK Békés	48.2 ± 6.3	150 mg/L	Petri dish, paper	n.d.	–	–	Increased ROS, RNS and H_2S content behind the growth inhibition.	Kacziba et al. 2023
T. aestivum	<30	0.1 mg/L	Petri dish, paper	+	+	+	Concentration-dependent effect, positive at lower concentrations.	Ibrahim et al. 2022
		0.2, 0.5, 1.0 mg/L		0	0	0		
		2.0, 5.0, 10 mg/L		0	–	–		
T. aestivum	14–47.4	50, 100 ppm	Foliar Spray	n.d.	+	+	Increased growth parameters. Foliar spray is more effective than soaking method.	Badawy et al. 2021
T. aestivum	14–47.4	50, 100 ppm	Grain pre-soaking	n.d.	+	+		
T. aestivum	28 ± 14	50 mg/kg	Soil	n.d.	0	0	No growth response, improved photosynthesis.	Guan et al. 2020
T. aestivum var. Pakistan-13 and NARC-11	<50	1, 5, 10 ppm	Petri dish, paper	n.d.	+	+	Positive physiological responses.	Yasmeen et al. 2018
		50 ppm		n.d.	0	+		
T. aestivum var. galaxy-13, Pakistan-13, NARC-1		25 ppm	Soil	n.d.	n.d.	+	High CuO NP concentration reduced spike length. Grain weight was increased by 25 ppm Cu NPs, while decreased by higher NPs concentrations.	Yasmeen et al. 2018
		30, 35, 40 ppm		n.d.	n.d.	–		
T. aestivum	<50	3 mg/kg	Sand	n.d.	0	0	Higher concentrations of CuO NPs inhibit root elongation.	Adams et al. 2017
		10, 30, 300 mg Cu/kg		n.d.	–	0		
T. aestivum cv. Millat-2011	12–20	0.2, 0.4, 0.6, 0.8 ppm	Petri dish, paper	0	+	+	Enhanced growth and yield.	Hafeez et al. 2015
		1 ppm		–	+	+		
		10, 20, 30, 40, 50 ppm	Hydroponic	n.d.	n.d.	+		
T. aestivum	<50	500 mg/kg	Sand	n.d.	–	–	Reduced root and shoot growth, oxidative stress.	Dimkpa et al. 2012

impacting productivity primarily due to structural damage to the thylakoid membrane (Da Costa et al. 2020). Other studies have also suggested that damage to photosynthetic efficiency and apparatus could be a potential cause of growth inhibition (Da Costa and Sharma 2016; Yang et al. 2020; Rai et al. 2021). The outcome of CuO NP stress on rice did not appear to be influenced by the experimental system used, as inhibition of seed germination and growth of the main organs was observed in various setups, including NP suspension on filter paper (Wang et al. 2020a), soil (Peng et al. 2017), hydroponics (Wang et al. 2015), and cotton pads soaked in nano-CuO suspension (Shaw and Hossain 2013). In a rare case, while germination and shoot growth of rice seedlings were not inhibited, root length was still significantly reduced in the presence of CuO NPs (Yang et al. 2015). In conclusion, extensive studies have shown that the exposure of rice to CuO NPs leads to growth inhibition. Oxidative stress induced by CuO NPs has been identified as a common factor contributing to the growth inhibition. The inhibitory effects of CuO NPs on rice have been observed in different experimental setups, suggesting that the outcome is not significantly influenced by the specific system used.

In contrast, the results of experiments with wheat (*Triticum aestivum* L.) as the experimental subject are more complex and less consistent (Table 2). In some cases, the application of CuO NPs had a positive effect on wheat growth. For instance, when applied as foliar spray or grain pre-treatment, CuO NPs were found to increase the growth parameters of wheat plants compared to the control group (Badawy et al. 2021). Low concentrations of CuO NP suspension also showed enhancement of growth and yield of wheat in hydroponic and *in vitro* systems (Hafeez et al. 2015; Yasmeen et al. 2018) as well as in soil (Yasmeen et al. 2018). Ibrahim et al. (2022) demonstrated concentration-dependent growth responses in wheat *in vitro*, where low concentration of CuO NPs enhanced plant growth, while higher concentrations resulted in a decrease in plant growth. Conversely, other studies have shown that higher amounts of CuO can inhibit wheat growth (Dimkpa et al. 2012; Kacziba et al. 2023). When cultivated in soil, wheat growth parameters were not affected by the presence of CuO NPs at a concentration of 50 mg/kg (Guan et al. 2020). However, when grown in sand, only a concentration of 3 mg/kg of CuO NPs did not have an inhibitory effect on root growth, while higher concentrations (10, 30, and 300 mg/kg) did have an inhibitory effect (Adams et al. 2017). In summary, the response of wheat to CuO NPs is more complex and less consistent compared to rice. The effects of CuO NPs on wheat growth vary depending on various factors such as concentration and experimental conditions. In some cases, the application of CuO NPs has shown a positive impact on wheat growth, leading to enhanced growth parameters and increased yield. This positive effect has been observed when CuO NPs were applied as a foliar spray,

Table 3. Studies investigating CuO NP-induced changes in maize (*Zea mays* L.), barley (*Hordeum vulgare* L. and *Hordeum sativum* L.), green onion (*Allium fistulosum* L.), rye (*Secale cereale* L.), sorghum (*Sorghum bicolor* L.), triticale (*x Triticosecale*), perennial ryegrass (*Lolium perenne* L.) and annual ryegrass (*Lolium rigidum* L.). '+' indicates growth induction, '-' means inhibition, while 'n.d.' marks parameters not determined. (ROS - reactive oxygen species, RNS – reactive nitrogen species, H_2S – hydrogen sulphide).

				Effect on				
Species; cv./var., if provided	Particle size [nm]	Concentration	Medium used	Germination	Root Growth	Shoot Growth	Notes	Reference
Zea mays L.	<50	8 mM	Hydroponic	n.d.	–	–	Growth inhibition. Toxicity of CuO bulk particles was higher than CuO NPs.	Roy et al. 2022
Z. mays	50	500 mg/kg	Soil	n.d.	–	–	Growth inhibition, at least partly due to oxidative stress.	Pu et al. 2019
Z. mays	<50	25, 50, 100, 500, 1000, 2000mg/L	Petri dish, paper	0	–	–	Concentration-dependent phytotoxic effect.	Yang et al. 2015
Z. mays	20–40	2, 5, 10, 20, 30, 40, 50, 100 mg/L	Hydroponic	0	–	–	No effect on germination, but growth inhibition.	Wang et al. 2012
Hordeum vulgare L.	60–80	10, 25, 50, 100, 250 mg/L	Petri dish	+	+	+	Enhancement seed germination and seedling growth.	Kadri et al. 2022
H. sativum L.	30–50	300/2000/ 10000 mg/kg	Soil	n.d.	–	–	Concentration-dependent growth inhibition.	Burachevskaya et al. 2021
H. sativum spp. Distichum	30–50	300/2000mg/kg	Soil	n.d.	n.d.	–	Plant height significantly decreased by 2000mg kg−1 CuO NPs.	Fedorenko et al. 2021
H. vulgare	50 ± 10	300 mg/kg	Soil	n.d.	n.d.	n.d.	Reduced biomass after 7 days, no effect after 30 days.	Jośko et al. 2021
Allium fistulosum L.	20–100	75, 150, 300, and 600 mg/kg	Soil	0	0	0	No visible toxicity. Enhanced nutrient and allicin contents.	Wang et al. 2020a
Secale cereale L. cv. Wibro	48.2 ± 6.3	150 mg/L	Petri dish, paper	n.d.	–	–	Increased ROS, RNS and H_2S content behind the growth inhibition.	Kacziba et al. 2023
Sorghum bicolor L. cv. GK Emese	48.2 ± 6.3	50 mg/L	Petri dish, paper	n.d.	–	–	Growth inhibition, significant increase in protein tyrosine nitration, lignification.	Kacziba et al. 2023
x Triticosecale cv. GK Maros	48.2 ± 6.3	150 mg/L	Petri dish, paper	n.d.	–	–	Increased ROS, RNS and H_2S content behind the growth inhibition.	Kacziba et al. 2023
Lolium perenne L.	58 ± 45	10, 100, 500, 1000 mg/L	Hydroponic	n.d.	–	–	CuO NP-induced DNA damage. Concentration-dependent growth inhibition.	Atha et al. 2012
L. rigidum L.	58 ± 45	10, 100, 500, 1000 mg/L	Hydroponic	n.d.	–	–	CuO NP-induced DNA damage. Concentration-dependent growth inhibition.	Atha et al. 2012

grain pre-treatment, or at low concentrations in hydroponic, *in vitro*, and soil systems. However, it should be noted that the growth response of wheat to CuO NPs is concentration-dependent, with higher concentrations often resulting in inhibitory effects on plant growth. The specific effect of CuO NPs on wheat growth also appears to be influenced by the growth medium, as the inhibitory effect was more pronounced in sand compared to soil. Overall, the response of wheat to CuO NPs is characterized by a complex interplay between concentration, application method, and growth conditions, highlighting the need for further research to better understand the underlying mechanisms and optimize nanoparticle applications in wheat cultivation.

Although fewer experiments have been conducted using maize (*Zea mays* L.) as an experimental subject, the results consistently show that both root and shoot growth of maize are inhibited by CuO NPs both in soil, hydroponic culture, and *in vitro* experiments (Table 3). In soil experiments, Pu et al. (2019) found that reducible Cu was the predominant form, suggesting that oxidative stress is at least partially responsible for the observed growth inhibition. In hydroponic systems, CuO NPs were observed to be transported between the root and shoot *via* the xylem and phloem (Wang et al. 2012). It has also been demonstrated that bulk CuO particles are more toxic to maize seedlings compared to nano CuO, primarily due to the higher dissolution of Cu ions in hydroponic environments (Roy et al. 2022). Additionally, increasing concentrations of applied CuO NPs significantly and concentration-dependently inhibited maize root elongation when grown of filter paper, unlike ions added in similar quantities. (Yang et al. 2015). These findings highlight the consistent negative impact of CuO NPs on maize growth and suggest that oxidative stress and copper ion dissolution are key factors contributing to the observed inhibition.

Barley (*Hordeum vulgare* or *Hordeum sativum* L.) displayed varied responses to CuO NPs depending on the experimental system, applied concentration, and exposure duration (Table 3). *In vitro* growth experiments showed that the presence of CuO NPs enhanced seed germination and seedling growth parameters (Kadri et al. 2022). However, in soil experiments, higher concentrations of slightly smaller CuO NPs significantly decreased plant growth (Burachevskaya et al. 2021; Fedorenko et al. 2021). Interestingly, in a soil study, CuO NPs at a concentration of 300 mg/kg initially reduced barley biomass over a one-week period, but after a month, the inhibitory effect disappeared completely (Jośko et al. 2021). These findings highlight that various factors such as the experimental system, applied concentration, and exposure duration can influence the response of barley to CuO NPs.

For several monocotyledonous plant species, there is limited research available on their response to CuO NPs, making it challenging to draw comprehensive conclusions (Table 3). In the case of green onions (*Allium fistulosum* L.) grown in soil treated with a wide range of CuO NP concentrations, one study found no significant changes in growth parameters (Wang et al. 2020c). A recent study investigated the effect of CuO NP treatment on sorghum (*Sorghum bicolor* L.), rye (*Secale cereale* L.), and triticale (*x Triticosecale*), and revealed that sorghum exhibited higher sensitivity compared to the other studied species. The study also identified variations in the homeostasis of reactive molecules as underlying factors related to sensitivity (Kacziba et al. 2023). Moreover, in ryegrass species (*Lolium perenne* and *L. rigidum* L.) the exposure to CuO NPs resulted in concentration-dependent growth reduction accompanied by DNA damage (Atha et al. 2012). These limited studies highlight the need for further research to better understand the response of these monocotyledonous plant species to CuO NPs and the underlying mechanisms involved.

Studies on the response of aquatic monocotyledonous plants to CuO NPs have been conducted, as shown in Table 4. In these studies, regardless of the size and concentration of CuO NP applied, the growth of both *Landoltia punctata* (G. Mey.) (Shi et al. 2011) and *Lemna minor* (L.) (Song et al. 2016; Koce 2017; Yue et al. 2018) was significantly decreased. These studies have also reported the presence of oxidative stress as an underlying symptom of the observed growth inhibition. These findings suggest that CuO NPs can negatively impact the growth and physiology of aquatic monocotyledonous plants and highlight the importance of understanding the potential ecological implications of nanoparticle pollution in aquatic ecosystems.

3. Responses of dicotyledonous plants to copper oxide nanoparticles

Studies have revealed that dicotyledonous plants can manifest varied responses to CuO NPs, which are contingent upon factors such as nanoparticle concentration, exposure duration, and the specific plant species under investigation. In comparison to monocotyledonous species, a greater number of studies have explored the interaction between dicotyledons and CuO NPs, although there are fewer concurrent and complementary investigations focused on individual species.

Table 4. Studies investigating the responses of aquatic monocot common duckweed (*Lemna minor* L.) and dotted duckmeat (*Landoltia punctata* G. Mey.) to CuO NPs. '-' represents inhibition, while 'n.d.' marks parameters not determined.

Species	Particle size [nm]	Concentration	Medium used	Effect on			Notes	Reference
				Germination	Root Growth	Shoot Growth		
Lemna minor L.	<50	150 µg/L	Hydroponic	n.d.	–	–	Dose-dependent growth inhibition. Accumulation of ROS.	Yue et al. 2018
L. minor	<50	0.1, 1, 10, 100, 1000 µM	Hydroponic	n.d.	–	–	Concentration-dependent growth inhibition.	Koce 2017
L. minor	40	10, 50, 100, 150, 200 mg/L	hydroponic	n.d.	–	–	Inhibited the plant growth, increased antioxidant enzyme activities and lipid peroxidation.	Song et al. 2016
Landoltia punctata G. Mey.	10–15	0.2, 0.6, 1 mg/L	Hydroponic	n.d.	n.d.	–	Growth inhibition and decreased chlorophyll content.	Shi et al. 2011

Table 5. Studies investigating the relationship between thale cress (*Arabidopsis thaliana* L.) and CuO NPs. '-' means inhibition, while 'n.d.' marks parameters not determined.

Species	Particle size [nm]	Concentration	Medium used	Effect on			Notes	Reference
				Germination	Root Growth	Shoot Growth		
Arabidopsis thaliana L.	30–50	10 mg/L	Hydroponic	n.d.	–	n.d.	Root cell wall damage.	Nie et al. 2020
A. thaliana (Ethylene-insensitive mutants (ein2-1, ein4 and etr1-3) and WT)	38	50, 100, 200, 300, 400 mg/L	Agar	n.d.	n.d.	–	Negative effect on shoot biomass and chlorophyll contents. ROS accumulation. Mutant plants are less sensitive.	Azhar et al. 2020
A. thaliana	<50	10 mg/L	Hydroponic	n.d.	n.d.	n.d.	Altered jasmonic acid and glucosinolates metabolism.	Soria et al. 2019
A. thaliana	60–75	0.4. mg/L	Hydroponic	n.d.	n.d.	0	Higher amount of CuO NPs suppressed rosette growth. Altered expression of 922 genes.	Landa et al. 2017
		2, 10 mg/L		n.d.	n.d.	–		
A. thaliana	30–50	10, 20 mg/L	Hydroponic	n.d.	–	–	Growth inhibition, oxidative stress and cell damage.	Tang et al. 2016
A. thaliana	30	0.5, 1 mg/L	Agar	n.d.	–	0	Growth inhibition, oxidative stress, changed pigment balance, lignin deposition.	Nair and Chung 2014
		2, 5, 10, 20, 50, 100 mg/L		n.d.	–	–		

Arabidopsis thaliana (L.), being one of the most extensively studied model organisms in plant biology, has been the subject of numerous investigations exploring its interaction with CuO NPs. The majority of these studies indicate a detrimental impact of CuO NPs on Arabidopsis growth (Table 5). Several publications highlight the ability CuO NPs to influence the expression of a wide range of genes in *A. thaliana*. For instance, a recent study demonstrated that CuO NPs caused damage to the root cell walls and downregulated genes associated in cell wall organization, leading to inhibition of root growth (Nie et al. 2020). Similarly, Landa et al. (2017) observed decreased rosette growth in *A. thaliana* exposed to CuO NPs, accompanied by alterations in the expression of various genes, including the downregulation of metal transporter and aquaporin genes and the upregulation of metallochaperone-like genes. Another study detected cell damage and oxidative stress as underlying factors contributing CuO NPs-induced growth inhibition, which were further manifested through changes in gene expression levels related to oxidative stress (Tang et al. 2016). When grown in agar media, *A. thaliana* treated with CuO NPs exhibited reduced chlorophyll content and increased anthocyanin content in its leaves This study also revealed lignin deposition and oxidative stress as consequences of altered root growth, as supported by changes in the expression levels of related genes (Nair and Chung

Table 6. Studies investigating the relationship between the members of Brassicaceae family and CuO NPs. '+' indicates growth induction, '-' represents inhibition, while 'n.d.' marks parameters not determined (ROS - reactive oxygen species).

Species; cv./var., if provided	Particle size [nm]	Concentration	Medium used	Effect on			Notes	Reference
				Germination	Root Growth	Shoot Growth		
Brassica juncea L.	<50	4, 8 mg/L	Foliar spray	n.d.	+	+	Increased growth, biomass, chlorophyll content, net photosynthetic rate.	Faraz et al. 2022
		2, 16 mg/L		n.d.	0	0		
B. juncea	<50	20, 50, 100, 200, 400 and 500 mg/L	Semi-solid medium	n.d.	–	–	Reduced shoot and root growth. ROS generation and lipid peroxidation.	Nair and Chung 2015
B. nigra L.	53	500, 1000 mg/L	Agar	0	–	–	Decreased root length, shoot length and leaf area. ROS generation.	Zafar et al. 2017
		1500 mg/L		–	–	–		
B. oleracea L.	<50	30 ppm	Seed pre-treatment	n.d.	0	0	70 ppm CuO NP seed pre-treatment increased root length.	Vassell et al. 2019
		70 ppm		n.d.	+	+		
B. oleracea var. capitata		10 mg/plant	Foliar spray	n.d.	n.d.	–	Decreased plant weight, water content and photosynthesis.	Xiong et al. 2017
		250 mg/plant		n.d.	n.d.	–		
B. pekinensis L.	<40	10 mg/L	Hydroponic	0	+	+	Concentration-dependent response. In high amount CuO NPs induced oxidative stress.	Wang et al. 2020c
		1000 mg/L		0	–	–		
B. rapa L. var. Green and Rosie	10–100	75, 150, 300, and 600 mg/kg	Soil	n.d.	n.d.	–	Rosie variety was more sensitive to CuO NPs.	Deng et al. 2020
B. rapa ssp. rapa	25–55	50, 250, 500 mg/L	Petri dish, paper	n.d.	–	–	Growth inhibition, oxidative stress.	Chung et al. 2019

2014). In a metabolomics study, it was found that CuO NP stress disrupted the homeostasis of several metabolites involved in the jasmonic acid and glucosinolate pathways, potentially contributing to the stress responses of *A. thaliana* to CuO NPs (Soria et al. 2019). Additionally, the comparison of wild-type and ethylene-insensitive mutant *A. thaliana* plants suggested the significant role of ethylene in CuO NP-induced oxidative damage in leaves, as the mutant plants exhibited reduced sensitivity to oxidative stress caused by CuO NPs compared to the wild type (Azhar et al. 2020). In conclusion, numerous studies have investigated the interaction between *A. thaliana* and CuO NPs, revealing a detrimental impact on plant growth. Overall, these findings highlight the complex effects of CuO NPs on *A. thaliana* and provide insights into the molecular mechanisms involved in the plant's response to nanoparticle stress.

In addition to *A. thaliana*, several economically important plant species from the Brassicaceae family have been studied in relation to CuO NPs (Table 6). The response of Indian mustard (*Brassica juncea* L.) to CuO NPs varied depending on the mode of application CuO NP treatment as a foliar spray resulted in increased growth, higher photosynthetic rate, and enhanced antioxidant capacity in *B. juncea* plants, while higher concentrations had a neutral effect on growth (Faraz et al. 2022). However, when grown in a semi-solid medium, the addition of CuO NPs significantly inhibited root and shoot growth *in B. juncea*, accompanied by oxidative burst, lipid peroxidation, lignification, and downregulation of catalase and ascorbate peroxidase expression in the roots (Nair and Chung 2015). The growth of black mustard (*Brassica nigra* L.) was also inhibited in the presence of CuO NPs, along with the generation of ROS (Zafar et al. 2017). Pre-treating kale (*Brassica oleracea* L.) seeds with 70 ppm of CuO NPs had a positive effect on the subsequent growth of roots and shoots in the developed plants (Vassell et al. 2019). While foliar application of CuO NPs was beneficial in some another cases, it had detrimental effects on cabbage (*Brassica oleracea* L. var. capitata), leading to reduced biomass, chlorosis, and necrosis on the leaves (Xiong et al. 2017). Chinese cabbage (*Brassica perkiensis* L.) displayed a concentration-dependent response to CuO NPs in hydroponic system, stimulating root and shoot growth at low concentrations but causing growth inhibition at high concentrations, primarily due to oxidative stress (Wang et al. 2020b). On the other hand, bok choy (*Brassica rapa* L.) exhibited clear sensitivity to CuO NPs both in soil and *in vitro*. Comparing soil-grown Green and Rosie varieties, Rosie was found more susceptible to CuO NP-induced stress, with the nanoform of Cu was more damaging compared to bulk or ionic alternatives (Deng et al. 2020). Additionally, an *in vitro* study on turnip (*Brassica rapa* L. ssp. rapa), revealed severe changes in the oxidative homeostasis associated with CuO NP-induced growth inhibition of (Chung et al. 2019). In summary, the response of Brassicaceae plant species to CuO NPs varies depending on the mode of application and concentration, the studies highlighting the diverse and species-specific responses of Brassicaceae plants to CuO NPs.

Lettuce (*Lactuca sativa* L.) is another plant species commonly studied in in the context of the relationship between CuO NPs and plants (Table 7). Among the reports available, low concentration of CuO NP (10 mg/plant) applied as foliar spray had a positive effect on lettuce, while a higher quantity

Table 7. Studies investigating the relationship between lettuce (*Lactuca sativa* L.) and CuO NPs. '+' indicates growth induction, '-' means inhibition, while 'n.d.' marks parameters not determined.

Species; cv./var., if provided	Particle size [nm]	Concentration	Medium used	Effect on Germination	Effect on Root Growth	Effect on Shoot Growth	Notes	Reference
Lactuca sativa L.	<50	100, 1000 mg/L	Hydroponic	n.d.	–	–	Inhibited growth, photosynthesis. Oxidative stress.	Xiong et al. 2021b
L. sativa var. ramosa Hort.	40–200	100, and 1000 mg/L	Foliar application	n.d.	–	–	Changed nutrient status, oxidative stress.	Xiong et al. 2021a
L. sativa cv. Vanda	13.0 ± 0.1	20 mg of CuO/plant	Soil/Foliar	n.d.	0/+	0/+	Enhanced root Ca, Mg, S, Ag, Cu, Mo V and Zn content upon irrigation with CuO NPs. Foliar application increased leaf number.	Kohatsu et al. 2021
L. sativa	6.6 ± 0.2	0.2, 2, 20, 40 µg/mL	Petri dish, paper	0/+	0/+	n.d.	Low concentrations (≤ 20 µg/mL) are beneficial.	Pelegrino et al. 2020
		80, 150, 300 µg/mL		–	–	n.d.	High amount of CuO NPs decreased root growth and antioxidant capacity, moreover disturbed nitric oxide homeostasis.	
L. sativa cv. batavia blonde dorée	40–60	10 mg/plant	Foliar spray	n.d.	n.d.	+	Increased plant dry weight.	Xiong et al. 2017
		250 mg/plant		n.d.	n.d.	–	High foliar dose decreased plant weight, photosynthetic activity and water content.	
L. sativa	10 ± 8	0.02, 0.04, 0.4, 4, 8 mg/L	Petri dish	0	–	n.d.	CuO NPs were more toxic than ionic form.	Liu et al. 2016
L. sativa	10–100	5, 10, and 20 mg/L	Hydroponic	n.d.	–	0	Reduced root length and increased ascorbate peroxidase activity.	Hong et al. 2015

Table 8. Studies investigating CuO NP-induced changes in soybean (*Glycine max* L.), spinach (*Spinacia oleracea* L.), and mung bean (*Vigna radiata* L.). '+' indicates growth induction, '-' represents inhibition, while 'n.d.' marks parameters not determined.

				Effect on				
Species; cv./var., if provided	Particle size [nm]	Concentration	Medium used	Germination	Root Growth	Shoot Growth	Notes	Reference
Glycine max L.	40	2, 5, 10 mg/L	Hydroponic	n.d.	–	n.d.	Root growth inhibition, oxidative stress.	Liu et al. 2021
G. max	<50	5, 15, 30, 45, 60, 100 mg/L	Petri dish, paper	0	+	0	Concentration-dependent effect on root and shoot growth.	Adhikari et al. 2012
		200, 400, 600 mg/L		0	–	–		
Spinacia oleracea L.	20–100	400 mg/kg	Soil	n.d.	n.d.	0	No visible toxicity.	Rawat et al. 2021
S. oleracea L. var. Pusa Bharti	<50	1.2×10^{-4}, 1.2×10^{-3} mol/Kg of soil	Soil	n.d.	0	n.d.		Singh and Kumar 2020
		1.2×10^{-2} mol/Kg of soil	Soil	n.d.	0	–	High applied dose decreased plant biomass (probably shoot growth was inhibited).	
S. oleracea	<50	10, 100 mg/L	Soil	n.d.	0	0	No significant toxic effect.	Singh and Kumar 2016
		1000 mg/L		n.d.	–	–		
Vigna radiata L.	1–30	1, 10 mg/kg	Soil	0	0	0	Concentration-dependent effect on seed germination and shoot growth.	Subpiramaniyam et al. 2021
		100 mg/kg		–	0	-		
V. radiata	10–50	20, 50, 100 mg/L	Agar	n.d.	–	0	Negative effect on root growth, concentration-dependent effect on shoot growth. Oxidative stress.	Gopalakrishnan Nair et al. 2014
		200, 500 mg/L		n.d.	–	–		

in the same form became harmful (Xiong et al. 2017). In another study, supplementing *L. sativa* plants with 20 mg of CuO NPs through foliar spray increased leaf number and dry weight, while irrigation with CuO NPs enhanced macro- and microelement content in the roots (Kohatsu et al. 2021). Conversely, higher concentrations of CuO NPs applied as foliar spray significantly inhibited lettuce growth and induced changes in oxidative status (Xiong et al. 2021b). In a different study, lower amounts of CuO NPs slightly improved germination and root growth of lettuce seedlings *in vitro*, but higher concentrations disrupted nitric oxide signaling, resulting in reduced antioxidant capacity, germination, and root elongation (Pelegrino et al. 2020). Previous *in vitro* research demonstrated that CuO NPs were more toxic than Cu ions and inhibited the root growth in lettuce seedlings (Liu et al. 2016). Using a hydroponic growth system, both low (Hong et al. 2015) and high (Xiong et al. 2021a) concentrations of CuO NPs decreased root growth in lettuce, attributed to changes in oxidative homeostasis and an increased antioxidant response. In summary, the effect of CuO NPs on lettuce growth is influenced by the concentration and method of application, highlighting the concentration-dependent and method-specific effects of CuO NPs on lettuce growth and oxidative status.

The response of soybean (*Glycine max* L.) to CuO NPs has been relatively understudied, and the available results show mixed outcomes (Table 8). In hydroponic conditions, CuO NP inhibited soybean root growth in a concentration- and exposure time-dependent manner, accompanied by increased Cu levels and oxidative stress (Liu et al. 2021). Conversely, in an *in vitro* study conducted on filter paper, low levels of CuO exposure had a positive impact on soybean root elongation. However, as the concentration increased, both root and shoot growth were significantly inhibited (Adhikari et al. 2012).

To date, only a limited number of studies have examined the interaction between spinach (*Spinacia oleracea* L.) and CuO NPs, and notably, all of these studies focused on soil-grown plants. (Table 8). The findings of these studies suggest that, except at high concentrations (1000 mg/L) where CuO NPs inhibited plant growth (Singh and Kumar 2016), spinach plants generally exhibited no or moderate growth responses to CuO NPs (Singh and Kumar 2016, 2020; Rawat et al. 2021).

Based on the very limited available information, it appears that mung bean (*Vigna radiata* L.) is relatively sensitive to exposure to CuO NP (Table 8). In a recent study, when grown in soil supplemented with low amounts of CuO NPs, seed germination, root growth, and shoot growth were not affected, but at a higher concentration (100 mg/kg), it significantly inhibited germination and shoot development while not impacting root elongation (Subpiramaniyam et al. 2021). In a previous study, CuO NP were found to inhibit root growth across a wide range of concentrations *in vitro*, accompanied by increased lipid peroxidation and lignification, while shoot biomass was only reduced at high concentrations of CuO NPs (Gopalakrishnan Nair et al. 2014).

Among several dicotyledonous plant species, only isolated studies are available thus far, which will be discussed below, grouped according to the effects of CuO NPs.

Some dicotyledonous plant species have shown a clear concentration-dependent response to the presence of CuO NPs, with low amounts of CuO NPs having a positive effect but higher concentrations inhibiting plant growth in the same experiment (Table 9). For example, *in vitro* treatment of chickpea (*Cicer arietinum* L.) with CuO NPs at concentrations of 1–60 mg/L improved root and shoot growth, while higher concentrations in the range of 100–600 mg/L severely inhibited growth parameters (Adhikari et al. 2012). Similarly, in an another *in vitro* study, high concentrations of CuO NPs significantly decreased buckwheat (*Fagopyrum esculentum* Moench.) root elongation, while lower amounts had no effect on this organ (Lee et al. 2013). In the case of tomatoes (*Solanum lycopersicon* L.) grown in various media,

Table 9. Concentration-dependent effect of CuO NPs. Studies investigating CuO NP-induced changes in chickpea (*Cicer arietinum* L.), buckwheat (*Fagopyrum esculentum* Moench.), tomato (*Solanum lycopersicon* L.) and candyleaf (*Stevia rebaudiana* Bertoni.). '+' indicates growth induction, '-' means inhibition, while 'n.d.' marks parameters not determined.

				Effect on				
Species	Particle size [nm]	Concentration	Medium used	Germination	Root Growth	Shoot Growth	Notes	Reference
Cicer arietinum L.	<50	5, 15, 30, 45, 60 mg/L	Petri dish, paper	0	+	+	Low concentrations of CuO NPs increased growth parameters, while higher amounts inhibited plant growth.	Adhikari et al. 2012
		100, 200, 400, 600 mg/L		0	–	–		
Fagopyrum esculentum Moench	<50	50, 500 mg/L	Petri dish	n.d.	0	n.d.	High amount of CuO NPs inhibited root growth.	Lee et al. 2013
		2000, 4000 mg/l		n.d.	–	n.d.		
Solanum lycopersicon L.	18.4 ± 5.5	20 µg/ml	Agar	0	+	+	Concentration-dependent effect of CuO NPs on plant growth. High CuO NP concentration limited plant growth in agar medium, with underlying oxidative stress.	Ahmed et al. 2018
		200 µg/ml		0	0	+		
		2000 µg/ml		0	–	–		
		20 µg/ml	Hydroponic	n.d.	+	+		
		200, 2000 µg/ml		n.d.	0	0		
		20 µg/ml	Soil	n.d.	+	+		
		200, 2000 µg/ml		n.d.	0	0		
Stevia rebaudiana Bertoni regenerants	25–30	2 mg/L	Agar	n.d.	+	+	Low concentrations of CuO NPs increased growth parameters, while higher amounts inhibited plant growth.	Ahmad et al. 2020
		20 mg/L		n.d.	+	+		
		200 mg/L		n.d.	–	–		
		2000mg/L		n.d.	–	–		

CuO NPs exerted a concentration-dependent effect on plant growth, promoting growth at low concentrations, but either have no effect or a negative effect on plant biomass at higher concentrations, regardless of the growing conditions (soil, agar, or hydroponics), (Ahmed et al. 2018). The observed growth inhibition was associated with oxidative stress and changes in photosynthetic properties. Furthermore, in a recent study, a similar concentration-dependent effect was observed in candyleaf (*Stevia rebaudiana* Bertoni) regenerant plants, where supplementation of agar medium with 2–20 mg/L CuO NPs increased root formation, plant length, and steviol glycoside content, while higher concentrations between 200 and 2000mg/L significantly decreased these parameters (Ahmad et al. 2020).

In some cases, research has shown that CuO NPs have had a positive effect on plant growth, as summarized in Table 10. For instance, when pigeon pea (*Cajanus cajan* L.) seedlings were cultivated in soil containing a relatively low concentration of CuO NPs (20 ppm), their growth performance showed a significant increase (Shende et al. 2017). In the case of sweet potato (*Ipomoea batatas* L.), two varieties treated with CuO exhibited longer roots in response to low concentrations of nanoparticles, particularly in the Covington variety, which also showed higher lignin content (Bonilla-Bird et al. 2020). Similarly, in a previous study conducted by Ochoa et al. (2017), it was found that supplementing the soil of green pea (*Pisum sativum* L.) plants with CuO NPs positively influenced their root elongation.

In contrast to other studies, the application of CuO (NPs) on bell pepper (*Capsicum annuum* L.) did not have any significant effect on plant growth or productivity (Table 10) (Rawat et al. 2018).

For certain plant species, only negative effects were observed in response to CuO NPs exposure, as mentioned

Table 10. CuO NPs with positive/no/negative effect. Studies investigating CuO NP-induced changes in pigeon pea (*Cajanus cajan* L.), sweet potato (*Ipomoea batatas* L.), green pea (*Pisum sativum* L.), bell pepper (*Capsicum annum* L.), cucumber (*Cucumis sativus* L.), alfalfa (*Medicago sativa* L.) and white mustard (*Sinapis alba* L.). '+' indicates growth induction, '-' represents inhibition, while 'n.d.' marks parameters not determined.

				Effect on				
Species	Particle size [nm]	Concentration	Medium used	Germination	Root Growth	Shoot Growth	Notes	Reference
Cajanus cajan L.	33	20 ppm	Soil	n.d.	+	+	Increased height, root length, fresh and dry weights.	Shende et al. 2017
Ipomoea batatas L.	10–100	25/75/125 mg/kg	Soil	n.d.	+	n.d.	Exposed to 25 mg CuO NP/kg, var. Covington plants had longer roots and higher macroelement content.	Bonilla-Bird et al. 2020
Pisum sativum L.	10–100	50 mg/kg	Soil	0	+	+	Positive effect on root elongation.	Ochoa et al. 2017
		100 mg/kg		0	+	0		
Capsicum annum L.	20–100	125, 250, 500 mg/kg	Soil	n.d.	0	0	No significantly effect on plant growth or development.	Rawat et al. 2018
Cucumis sativus L.	n.d.	100, 200, 400, 600 ppm	Petri dish, paper	–	–	n.d.	Severely inhibited germination and root growth.	Moon et al. 2014
Medicago sativa L.	10–100	5, 10, and 20 mg/L	Hydroponic	n.d.	–	n.d.	Reduced root growth and catalase activity, increased ascorbate peroxidase activity.	Hong et al. 2015
Sinapis alba L.	<50	10, 100, 1000 mg/L	Petri dish, paper	–	–	n.d.	Concentration-dependent inhibition of germination and root growth.	Landa et al. 2016

Table 11. Mixed effect of CuO NPs. Studies investigating CuO NP-induced changes in cilantro (*Coriandrum sativum* L.), shiny elsholtzia (*Elsholtzia splendens* willd.), willow (*Salix integra* Thunb.) and eggplant (*Solanum melonegra* L.). '+' indicates growth induction, '-' means inhibition, while 'n.d.' marks parameters not determined.

				Effect on				
Species; cv./var., if provided	Particle size [nm]	Concentration	Medium used	Germination	Root Growth	Shoot Growth	Notes	Reference
Coriandrum sativum L.	10–100	20 mg/kg	Artificial soil	–	0	–	Reduced germination, shoot growth and element content.	Zuverza-Mena et al. 2015
		80 mg/kg		–	0	0		
Elsholtzia splendens Willd.	43 ± 9	100, 200, 500, 1000 mg/L	Hydroponic	0	–	n.d.	No effect on germination, inhibited root growth.	Shi et al. 2014
Salix integra Thunb. 'Yizhibi'	40	100 mg/kg	Soil	n.d.	+	–	100 mg/kg CuO NPs increased root growth and decreased shoot elongation, while 500 mg/kg NPs inhibited plant growth.	Qu et al. 2022
		500 mg/kg		n.d.	–	–		
Solanum melongena L.	25–55	100 mg/L	Petri dish, paper	0	+	–	Concentration-dependent effect on germination and root growth. General inhibition of shoot growth.	Baskar et al. 2018
		250 mg/L		–	0	–		
		500, 1000 mg/L		–	–	–		

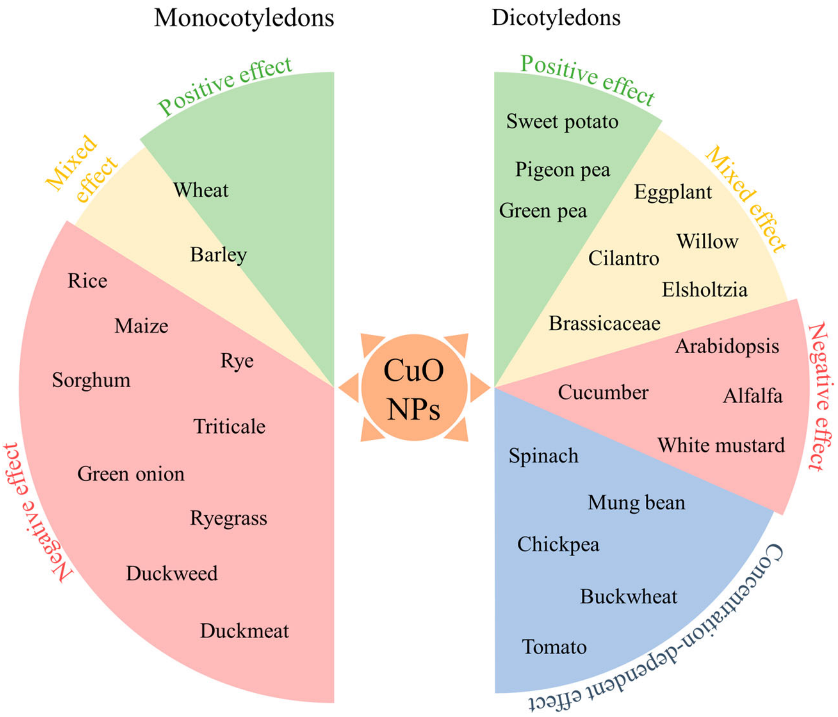

Figure 1. Influence of CuO nanoparticles on the growth responses of monocotyledonous and dicotyledonous plant species based on available literature.

in Table 10. For instance, when cucumber (*Cucumis sativus* L.) was treated with CuO NPs, both seed germination and root growth were severely inhibited This treatment also resulted in a change in protein expression pattern compared to the control group (Moon et al. 2014). Similarly, in an *in vitro* study with white mustard (*Sinapis alba* L.) seeds, their germination and subsequent root elongation were dose-dependently inhibited by CuO NPs (Landa et al. 2016). Moreover, hydroponically grown alfalfa (*Medicago sativa* L.) plants treated with CuO NPs showed a significant reduction in root elongation. This was accompanied by downregulated catalase and increased ascorbate peroxidase activity (Hong et al. 2015).

In some cases, mixed effects of CuO NPs on plants have been reported, where it is not possible to clearly determine the direction of the change caused by the treatment (Table 11). Such a mixed response was observed when CuO NPs were added to the growth media used for cilantro (*Coriandrum sativum* L.) germination. The addition of CuO nanoparticles to the artificial soil negatively influenced germination, while root elongation of the germinated seedlings remained unaffected. However, shoot growth was decreased in the presence of the 20 mg/kg CuO NP treatment (Zuverza-Mena et al. 2015). In another study, it was found that the germination of shiny elsholtzia (*Elsholtzia splendens* Willd.) was not affected by CuO NPs. However, the root growth of shiny elsholtzia was significantly inhibited by the NPs (Shi et al. 2014). In a recent study, willow (*Salix integra* Thumb., 'Yizhibi') exposed to 100 and 500 mg/kg CuO NP in soil showed contrasting effects. Lower concentrations of CuO NPs increased root growth and reduced shoot length, while high concentrations significantly inhibited the growth of willow (Qu et al. 2022). Similarly, in an *in vitro* study, root growth of eggplant (*Solanum melongena* L.) was affected by

CuO NPs in a concentration-dependent manner, ranging from promotion to inhibition. However, shoot growth of eggplant was decreased by all treatments, accompanied by oxidative stress, DNA damage, and decreased total chlorophyll content (Baskar et al. 2018).

4. Conclusions

In conclusion, the studies discussed in this review highlight the complex and varied growth responses of different plant species to CuO NP exposure. The growth response depends on several factors, including the plant species, concentration of CuO NPs, method of application (foliar spray, soil supplementation, hydroponics), and duration of exposure.

Considering higher taxonomic categories, the overall available evidence suggests that most monocotyledonous plants were negatively affected by exposure to CuO NPs, although the extent of damage depends on several factors. Among the species studied so far, only two, namely wheat and barley, have shown evidence that CuO NPs can have a positive effect on monocot growth. On the other hand, the response of dicotyledonous plant species to CuO NPs is much more diverse, with both positive and negative outcomes depending on the species, concentration, and exposure time being examined. For certain plant species such as spinach, mung bean, chickpea, buckwheat, and tomatoes, the growth response to CuO NPs exhibited a concentration-dependent pattern. Generally, lower concentrations of CuO NPs had a positive or neutral effect on root and shoot growth, while higher concentrations inhibited growth parameters (Figure 1). This concentration-dependent response suggests that there might be an optimal range of CuO NP concentration for promoting plant growth, beyond which toxicity effects become more prominent.

Different plant species within the same family, such as *A. thaliana*, *B. juncea*, *B. nigra*, and *B. oleracea*, exhibited varying growth responses to CuO NPs. *A. thaliana* generally displayed detrimental effects on growth, including root growth inhibition, altered gene expression, oxidative stress, and changes in metabolite profiles. Brassica species showed mixed responses, with some varieties showing increased growth, while others experienced growth inhibition, oxidative burst, and altered gene expression. This suggests that genetic variation and species-specific traits play a role in determining the response to CuO NPs.

According to the available data, the effect of CuO NPs on plant growth is influenced by several key factors, including:

- Concentration of CuO NPs: Different concentrations of CuO NPs have been found to have varying effects on plant growth, ranging from promotion to inhibition.
- Mode of application: The method of CuO NP application, such as foliar spray, soil amendment, hydroponics, or *in vitro* studies, can affect plant growth responses.
- Plant species and genotypes: Different plant species and even different genotypes within the same species can exhibit different sensitivities to CuO NPs. Available results suggest that wheat is relatively tolerant among the monocotyledons, whereas no specific species can be identified among the dicotyledons with a similar general higher tolerance.

Although a growing body of research on the relationship between plants and CuO NPs is becoming available each year and the existing research provides valuable insights into the effects of CuO NPs on plant growth, there are several gaps that require further research fully understand the potential impact of CuO NPs on plant growth and health.

In future studies:

- Mechanistic understanding: Further research is needed to fully understand how CuO NPs interact with plants at the cellular and molecular levels, including the specific pathways and signaling mechanisms involved in growth responses and oxidative stress induction.
- Standardized experimental protocols: Developing standardized protocols for assessing the effects of CuO NPs on plant growth will improve result reproducibility and enable better comparisons between studies, enhancing our understanding of the overall impacts of CuO NPs on plants.
- Ecological implications: Extending research to diverse plant communities and natural ecosystems is necessary to fully grasp the ecological implications of CuO NP exposure, including long-term effects on plant growth, biodiversity, and ecosystem functioning.
- Interactions with other stressors: Investigating the interactive effects of CuO NPs with other environmental stressors, such as drought, temperature extremes, and chemical pollutants, provides a more realistic assessment of the potential risks posed by CuO NPs in complex environmental scenarios.

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