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**REVIEW**

# Nanomaterial-Mediated Modulation of Plant Functional Traits and Rhizosphere Processes: Mechanistic Insights into Plant Stress Physiology

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**ABSTRACT:** Agricultural systems increasingly face interacting abiotic and biotic stresses driven by climate change and soil degradation. Plant performance under such conditions is determined by coordinated networks of functional traits governing resource acquisition, allocation, and defense. These traits also structure plant-associated microbiomes, whose activities influence nutrient cycling, stress buffering, and disease suppression. This review synthesizes current evidence that agricultural nanomaterials enhance crop stress resilience primarily by reprogramming plant functional trait networks and, through them, modulating microbiome dynamics. We analyze how nanomaterial physicochemical properties including size, surface chemistry, dissolution behavior, and redox activity determine their bioavailability and interaction with plant tissues. These interactions influence key trait categories such as root architecture, hydraulic regulation, nutrient acquisition efficiency, photosynthetic performance, and antioxidant capacity. Trait-level modulation underpins improved tolerance to drought, salinity, temperature extremes, heavy metal toxicity, and pathogen pressure. Furthermore, nanomaterial-induced shifts in plant traits reshape rhizosphere and endophytic niches, reinforcing beneficial microbial functions including nutrient mobilization, hormone regulation, pathogen suppression, and soil structural stabilization. This review proposes a trait-centric framework in which nanomaterials act as regulators of plant functional organization rather than simple growth stimulants. Future research should prioritize trait-based screening, microbiome functional monitoring, and predictive nano–ecological modeling to enable safer and more effective nanotechnology deployment for sustainable crop production.

**KEYWORDS:** Nanomaterials; plant functional traits; plant–microbiome interactions; stress resilience; rhizosphere microbiome

## 1 Introduction

There is an increasing pressure on global crop production systems by interacting pressures due to climate change, land degradation and resource scarcity [1,2]. The Food and Agriculture Organization (FAO) estimated that about 33 percent of the world soils are currently degraded with a significant part of it being contaminated by heavy metals and persistent organic pollutants [3,4], reflecting a shift from localized, single-contaminant issues toward complex, multi-stressor environments that challenge conventional remediation and management approaches [5].

At the plant level, these stresses do not act through single pathways. Instead, they disrupt coordinated physiological processes by inducing oxidative stress, osmotic imbalance, membrane destabilization, and impaired nutrient uptake. Plant response to climatic extremes is greatly stage sensitive [6,7]. For example, Matsui et al. (2021) showed that the rice is most susceptible to elevated temperatures during booting and flowering and that excessive heat causes floret sterility [8]. Similarly, Li et al. (2021) indicated vegetation dormancy in most parts of the Qinghai-Tibet Plateau is caused by pre-growing-season drought and heat stress, reducing the duration of the effective growing season [9]. Extreme rainfall events also contribute to risks including rise in soil moisture, dissolution of organic matter, mobilization of bioavailable metal fractions and reduction of Fe/Mn oxide bound heavy metals, leading to an increase in non-carcinogenic and carcinogenic risks by 10.1–188.3% [10]. Parallel shifts occur belowground, where climate extremes reorganize microbial functional gene networks involved in nutrient cycling, stress response, and pathogen dynamics. For instance, Knight et al. (2024) reported significant shifts in functional gene abundances in approximately 46% of soil microorganisms, affecting 8–61% of key functional categories related to nutrient cycling, stress response, and pathogen dynamics [11]. Such complex and interacting stresses do not therefore regulate plant responses using a single physiological mechanism but rather by a set of interacting plant functional traits the integrated morphological, physiological, and biochemical characteristics, that govern resource acquisition, allocation, and defense [12,13]. Traits such as root system architecture, hydraulic conductance, stomatal regulation, photosynthetic capacity, nutrient-use efficiency, and antioxidant potential collectively determine how plants respond to environmental stress. When trait coordination fails, plants experience carbon limitation, hydraulic dysfunction, and oxidative damage, leading to yield instability [14].

The manner by which plants react to the complex stress of their environment is a result of the coordinated changes in their functional trait sets, rather than the result of individual physiological responses [15]. Notably, the mentioned traits also control plant-related microbiomes, engineering root exudation patterns, nutrient fluid exchange rates, and immune signaling [16]. Microbiomes, in turn, affect the performance of the plant by mobilizing nutrients, buffering stress, and suppressing diseases [17]. Stress resilience thus arises as an emergent property of a coupled plant-trait-microbiome system. Fig. 1 schematically depicts these functional traits and the manner by which nanomaterials can modulate them for enhanced tolerance against drought, salinity, extreme temperatures, oxidative and heavy metals stress.

In this regard, agricultural nanotechnology is an exciting prospect yet under-theorized intervention [18]. At environmentally relevant concentrations, many nanomaterials do not behave primarily as nutrient sources or toxicants. Instead, they interact with plant membranes, organelles, and signaling networks, modulating redox balance, hormonal pathways, membrane stability, and gene expression [19–21]. Through these interactions, nanomaterials can reprogram functional trait networks that determine plant performance under abiotic and biotic stress [22]. Because functional traits also govern microbiome assembly, nanomaterials indirectly influence rhizosphere and endophytic communities [23,24], creating feedback loops that stabilize or destabilize crop resilience.

Trait-based ecological theory has long linked plant traits to ecosystem processes and microbial dynamics. Root exudation chemistry, immune signaling, and nutrient acquisition strategies define microbial niches in the rhizosphere and endosphere [25,26]. Microbiomes reciprocally reinforce plant trait expression by mobilizing nutrients, producing phytohormones, suppressing pathogens, and buffering environmental stress [27–29]. Advances in microbiome analytics now allow these interactions to be examined as an integrated system rather than as independent components [30].

In this review, we adopt a trait-centric systems framework in which nanomaterials are conceptualized as regulators of plant functional organization and microbiome assembly. We propose that plant functional traits provide a unifying axis linking molecular responses, physiological adjustments, and ecological feedbacks that underpin stress resilience. Accordingly, this review synthesizes and describes current knowledge to (i) identify nanomaterial properties that confer leverage over plant functional traits, (ii) examine trait modulation under abiotic and biotic stresses, (iii) explore trait-mediated with plant-associated microbiomes, and (iv) outline future directions for trait-informed nanotechnology in climate-smart agriculture.

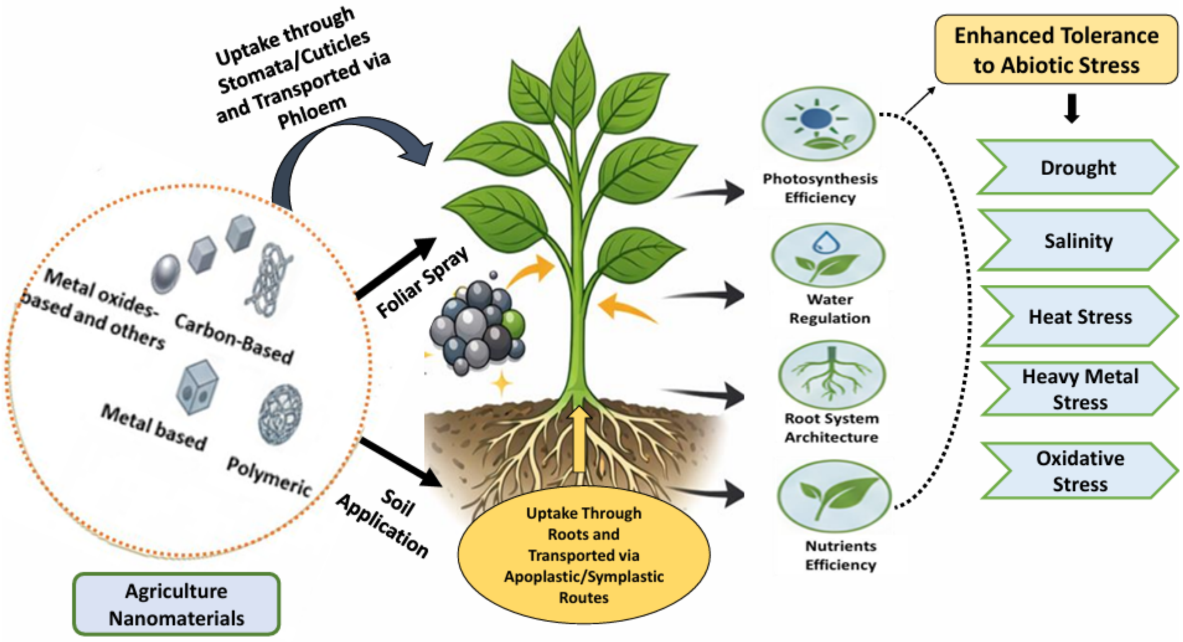

**Figure 1: Nanomaterials regulate plant functional traits that determine tolerance to abiotic stresses**. Agricultural nanomaterials (metal-, metal oxide-, carbon-based, and polymeric nanomaterials) interact with plant tissues following uptake and translocation, modulating key functional traits including root system architecture, photosynthetic efficiency, nutrient acquisition, water regulation, and antioxidant capacity. These trait-level adjustments collectively enhance plant resilience to drought, salinity, temperature extremes, heavy metal toxicity, and oxidative stress. The figure emphasizes functional traits as the primary biological leverage points through which nanomaterials influence stress tolerance.

## 2 Nanomaterials in Agroecosystems: Properties, Pathways, and Biological Leverage

Nanomaterials exposed to agricultural systems are not isolated inputs, but are rapidly assimilated into complex agroecosystems which consist of physicochemical matrices of soils, functional organization of plant structures, and heterogeneous microbial communities. Upon application, nanomaterials interact dynamically with soil minerals, organic matter, and pore water, processes that regulate their mobility, persistence, aggregation behavior, and bioavailability. Such interactions eventually command the ability of nanomaterials to either be retained in the soil matrix, interact with plant roots, translocation into plant tissues, or become available to microorganisms in the rhizosphere and endosphere [31]. Notably, these biogeochemically mediated processes characterize the main biological sites of interaction soil, rhizosphere, root surface, endosphere and phyllosphere in which nanomaterials have functional effects but not a global effect on the plant-soil continuum. Nanomaterials interact with plant roots, stems, and leaves through multiple uptake pathways (Fig. 1), ultimately influencing trait-level responses such as hydraulic conductivity, nutrient acquisition, and stress signaling [32,33]. This indicates that the effects of nanomaterials are to be understood in an ecosystem-function context, and not in the form of individual physiological reactions.

Based on this, to comprehend nanomaterials in agroecosystems it is necessary to look beyond mere chemical classification and to emphasize physicochemical characteristics that provide leverage over plant functional characteristics, instead of considering observed responses as accidental consequences.

### *2.1 Classification of Agricultural Nanomaterials*

Nanomaterials in agriculture are often categorized through their composition but from a biological perspective, their relevance lies in how distinct material classes interact with specific plant compartments and regulate functional traits. Different classes of nanomaterials with their key physicochemical properties and biological leverage points are summarized in Table 1, highlighting how surface area, redox activity, and solubility govern uptake and functional impact in plants.

**Table 1:** Physicochemical Properties of Agricultural Nanomaterials and Their Biological Leverage Points.

| Nanomaterial Class | Representative Examples | Key Physicochemical Properties | Primary Biological Interaction Zone | Functional Leverage Point | Target Plant Trait(s) | Typical Stress Context | Reference |
|---|---|---|---|---|---|---|---|
| **Primary class** | | | | | | | |
| Carbon-based NMs | Graphene oxide, carbon dots, CNTs | High surface area, electron transfer capability | Rhizosphere & cell walls | Modulation of exudation, membrane transport | Growth & allocation traits (root architecture); Hydraulic traits (osmotic adjustment) | Salinity, drought | Mukherjee et al. (2016); Pérez-de-Luque, (2017) [34,35] |
| Metal nanoparticles | Ag, Cu, Au NPs | Antimicrobial surfaces, tunable redox | Phyllosphere/root surface | Defense priming, pathogen suppression | Defense traits (immune signaling, structural defense) | Biotic stress (pathogens) | Zhao et al. (2020) [19] |
| Polymeric | Chitosan NPs, PLGA carriers, nanohydrogels | Controlled delivery, biocompatibility | Soil & rhizosphere | Targeted nutrient/hormone transport | Nutrient acquisition traits; Defense traits (stress signaling) | Combined stresses | Ioannou et al. (2020); Kaphle et al. (2018) [36,37] |
| **Others** | | | | | | | |
| Silica-based NPs | $SiO_2$ NPs | Mechanical reinforcement, low toxicity | Leaf/stomatal surfaces | Transpiration regulation | Redox traits (antioxidant activity); Nutrient acquisition traits; Hydraulic traits (root water uptake) | Drought, heat | Jalil and Ansari, (2019) [38] |
| Metal oxide NPs | ZnO, $TiO_2$, $CeO_2$, $Fe_3O_4$ NPs | High surface reactivity, redox, buffering, partial dissolution | Roots & stele | Redox regulation, micronutrient delivery | Nutrient acquisition traits (uptake and assimilation) | Drought, salinity, oxidative stress | Naseem et al. (2025; Rani et al. (2020) [39,40] |
| Nano-fertilizers | Nano-N, nano-P formulations | Slow release, high efficiency | Root−soil interface | Optimized nutrient availability | Growth & allocation traits (root proliferation, nutrient cycling) | Nutrient limitation, drought | Bhat et al. (2026; Khalifa et al. (2024) [41,42] |

**Table 1:** *Cont.*

| Nanomaterial Class | Representative Examples | Key Physicochemical Properties | Primary Biological Interaction Zone | Functional Leverage Point | Target Plant Trait(s) | Typical Stress Context | Reference |
|---|---|---|---|---|---|---|---|
| **Others** | | | | | | | |
| Plant-derived NMs | Nano-biochar, cellulose nanofibers | High porosity, organic chemistry | Bulk soil & rhizosphere | Soil structure improvement | Growth & allocation traits (photosynthetic efficiency) | Salinity, soil degradation | Kumari Sharma et al. (2024); Shahzadi et al. (2025); Singh et al. (2025) [43–45] |
| Lipid-based/foliar carriers | Liposomes, Nano emulsions | Foliar uptake, encapsulation ability | Leaf cuticle & stomata | Delivery of regulators | Photosynthetic efficiency | Heat, oxidative stress | Lu et al. (2020) [46] |

### *2.1.1 Primary Class*

#### Metallic Nanoparticles

Metallic nanoparticles such as silver (Ag), gold (Au), zinc oxide (ZnO), and iron oxide ($Fe_2O_3$) have emerged as some of the most researched agricultural nanomaterials because of their dual function of increasing micronutrient content and facilitating redox balance. In particular, ZnO and $Fe_2O_3$ nanoparticles increase micronutrient availability, which in turn helps to increase chlorophyll content, enhance photosynthesis, and improve biomass partitioning due to changes in nutrient uptake properties [47,48]. For example, Ag NPs are very useful in managing bacterial and fungal pathogens, hence improving the immunity of plants under biotic stress conditions [49]. In addition to nutrient provision, the metallic NPs have a high level of regulatory control over the redox homeostasis and antioxidant systems, which provide leverage points to adjust drought, salinity, and oxidative stress tolerance (Table 1).

#### Carbon-Based Nanomaterials

Carbon-based nanomaterials, such as carbon nanotubes (CNTs), graphene oxide, and fullerenes, have a high surface area and special electrical and mechanical properties that allow for interaction with the root-cell wall membrane interface [50]. CNTs, for example, can form nanochannels in root cell membranes, facilitating water and nutrient uptake and improving plant performance under drought and nutrient-limited conditions [51]. Graphene oxide has demonstrated the ability to modulate oxidative stress, enhance antioxidant defenses, and support the targeted delivery of agrochemicals. Instead of acting as a source of nutrients, carbon-based nanomaterials are mainly involved in membrane transport, osmotic regulation, and stress signaling, which affect plant functional responses to environmental stress [52].

#### Polymeric Nanomaterials

Polymeric nanomaterials, including chitosan NPs, PLGA carriers, and nano-hydrogels, are preferred for their biocompatibility and controlled release properties [53]. These nanomaterials allow for targeted delivery of nutrients, phytohormones, and stress-relieving compounds, which help with the coordination of growth, defense, and metabolic traits. Primarily interacting with the soil-rhizosphere interface and plant tissues, polymeric NPs help with the regulation of hormonal balance and signaling pathways, allowing for sustained trait regulation during combined abiotic and biotic stresses, where temporal coordination of growth and defense is essential [54].

### *2.1.2 Other Nanomaterials*

#### Silica-Based Nanoparticles ($SiO_2$ NPs)

Silica nanoparticles ($SiO_2$ NPs) have the ability to move through root tissues and reach aerial parts of the plant through the xylem. These NPs accumulate as phytoliths or amorphous silica. $SiO_2$ NPs promote both structural and inducible defense traits by increasing cell wall strength and triggering immune response pathways [55]. $SiO_2$ NPs also act as carriers of biomolecules and have the ability to increase soil water-holding capacity, thus playing a role in increasing resistance to pathogens and abiotic [56].

#### Nano-Fertilizers

Nano-fertilizers, such as nano-N and nano-P, enhance nutrient use efficiency by increasing nutrient retention and availability in the root-soil interface. The benefits include an increase in nutrient use efficiency and yield increase over conventional fertilizers [57]. At the trait level, nano-fertilizers enhance root development, leaf nutrient concentration, and antioxidant enzyme activity, which help in growth and abiotic stress tolerance during nutrient-deficient or water-stressed conditions [58,59].

Plant-Derived Nanomaterials

Plant nanomaterials, such as nano-biochar and cellulose nanofibers, do not have an effect on plant tissues but rather on the bulk soil and rhizosphere. Their properties increase the porosity of the soil to retain water and the availability of nutrients, contribute to root development, osmotic adjustments, and nutrient uptakes under stressed conditions such as salinity and soil degradation. These nanomaterials serve in the role of trait-level ecosystem enhancers, which assists plants and the associated microbial communities [60,61].

Lipid-Based and Foliar Nano-Carriers

The lipid-based nano-carriers include liposomes and nano-emulsions which are designed to deliver nutrients, hormones or protection factors to the foliage. They can enter into the leaf cuticles and stomata, and thus influence the photosynthetic efficiency, stomata conductance, and stress responses, particularly in the circumstances of heat and oxidative stress. Encapsulation process can also help in preserving sensitive biomolecules by avoiding degradation and can be used to release biomolecules in a controlled manner [62,63].

## *2.2 Physicochemical Properties Governing Bioavailability and Bioactivity*

### *2.2.1 Surface Area and Reactivity*

Nanomaterials have a very large surface area-volume ratio due to their nanometric size that significantly boost their reactivity and interactions with plant systems. This high surface reactivity enables them to adsorb nutrients and agrochemicals to enhance their transportation and accessibility for plants [64,65]. For example, ZnO NPs have high surface reactivity that guarantees a rapid release of $Zn^{2+}$ ions, which are significant in enzyme activation, chlorophyll formation, and alleviation of stress. Moreover, metallic NPs, including Ag and Au exhibit catalytic properties, which enable them to regulate biochemical processes in plants, thus enhancing plant biomass and stress resistance [54].

### *2.2.2 Size and Solubility*

Nanomaterials are able to enter the walls of plant cells due to their nanoscale size, increasing the ease of delivering nutrients and agrochemicals to their specific locations [66]. NPs that are 1–100 nm in length have high penetrating potential into the cuticle and root epidermis barriers. Bioavailability of NPs is affected by solubility in both water and soil [67]. It has been demonstrated that highly soluble NPs like $Fe_2O_3$ can be utilized to improve the release of bioavailable iron to plants, which is a viable solution to iron deficiencies in alkaline soils [68,69]. Conversely, engineered nanomaterials with controlled solubility can offer long-term delivery of nutrients or pesticides, which reduces the number of applications and the effects on the environment [70]. Through the utilization of their distinct categorizations and properties, nanomaterials offer efficient and accurate methods of enhancing agricultural productivity and sustainability. However, it is important to have a comprehensive understanding of the types and properties of nanomaterials in order to incorporate them into agricultural practices [71].

## 3 Modes of Nanoparticle Uptake, Translocation, and Accumulation in Plants

The interactions of nanomaterials with plants are complex, which greatly influence plant physiology, metabolism and functional performance. These interactions start at the plant interface, either root interaction or leaf interaction, and continue through internal transport and accumulation in plant tissues. Once internalized, nanomaterials can alter the properties of membranes, organelle functions, redox state, and signaling pathways, thus affect nutrient uptake, stress response, and growth regulation. In particular, these processes are not only concentration-dependent processes, but they are also greatly affected by the physicochemical properties of NPs, and all these factors contribute to the biological accessibility and intracellular fate. It is, therefore, important to understand the mechanistic aspects of nanoparticle uptake, intracellular transport, and tissue-specific accumulation to make optimal use of nanotechnology in agriculture without any unintended phytotoxicity and environmental risks [72,73].

### *3.1 Nanomaterial Uptake and Translocation*

The main entry routes for nanomaterials in plants include root uptake or foliar application, followed by transport to the target tissues. After entering the plant cells, nanomaterials are transported in the vascular tissues, mainly the xylem and phloem, depending on the application route and the physicochemical properties of the nanomaterials [74]. The uptake of nanomaterials from root tissues tends to favor upward translocation in the transpiration stream in the xylem, while foliar-applied nanomaterials have the ability to reach both xylem and phloem tissues, allowing them to be redistributed to actively metabolizing sinks like young leaves, reproductive organs, and roots.

#### *3.1.1 Root Application*

The root application method consists of the direct deposition of NPs into the soil surrounding plant roots. Initially, the root surface gets in contact with NPs and forms a negatively charged microenvironment through the root mucilage, organic acids and polysaccharides released by root hairs. This electrochemical interface is crucial in the regulation of NPs adhesion, aggregation, and mobility at the root-soil interface. This interface ensures the enhanced accumulation of positively charged NPs to the root surface [75]. However, it has also been observed that positively charged NPs do not always accumulate effectively across the root mucous layer and can accumulate selectively in the apoplast [76]. The same has been reported in metal and metal oxide NPs treated rice and wheat, which suggests that electrostatic attraction is not necessarily a guarantee of the symplastic absorption [77,78]. Following surface interaction, NPs encounter numerous anatomical and physiological barriers including root cuticle, epidermis, cortex, endodermis and the Casparian strip. Of these, the Casparian strip is a significant barrier that prevents the passive apoplastic transport of NPs into the vascular cylinder and thereby determines whether NPs stay local or are transported to distant locations. Although the root cuticle follows the same composition as the leaf cuticle, the epidermal layer in the root tip and the root hair cells are usually poorly developed, hence allowing NPs to enter the root directly through the epidermal layer.

Once the epidermal layer is crossed, NPs must cross the endodermis to reach xylem. NPs can also enter the symplastic pathway through endodermal cells into the endodermis, either bypassing the apoplastic barrier of the Casparian strip, or temporarily localizing at the Casparian strip, and then redirected. Systemic translocation of NPs is therefore impossible without symplastic entry, wherein NPs have to traverse the plasma membrane and enter the cell interior [34,79–81]. NPs have several different pathways to cross the plasma membrane, which include ion channels, endocytosis, establishment of membrane pore, and carrier protein-mediated transport. The ion channels are usually limited to passage of ultrafine NPs or ionic forms of substances that are usually less than 1 nm long. The process of endocytosis is a large and versatile pathway that enables invagination of the membrane and uptake of particles less than 1 μm in diameter into the cell interior [75,82]. In certain instances, the interaction of NPs with the plasma membrane can lead to the formation of temporary pores, allowing direct entry into the cytoplasm without the need for vesicular trafficking, as has been demonstrated for certain metal-based NPs [83]. Binding to carrier proteins associated with the plasma membrane may also provide a route for selective uptake, especially for NPs designed to resemble nutrient ions or signaling molecules [64].

### *3.1.2 Foliar Application*

One of the most common and efficient methods of nanomaterial delivery into plant systems is foliar application with a particular focus on fast and easy induction of traits and fortification of micronutrients. When nanomaterials come into contact with the leaf surface, there are two main routes of entry, which are the cuticular route and the stomatal route. The cuticle, which is a mixture of waxes, cutin, and immersed polysaccharides, is the first line of defense against external factors since it reduces water loss and the passive uptake of foreign materials [84]. Nevertheless, irrespective of its barrier property, the cuticle has been described as possessing lipophilic regions of diffusion as well as hydrophilic water-filled pore that have estimated diameter of 0.6 to 4.8 nm. Smaller-size NPs, like carbon dots, can passively diffuse through these pores and get to the underlying epidermal tissues. The diffusion of nutrients in this case relies heavily on surface chemistry, the hydrophilicity of the surface, and the modification process of the material. The ability of larger NPs to diffuse into intact cuticles is limited, and when it occurs, it is often associated with cuticle damage, pathogen emergence, aging, and environmental stress [81,85].

On the other hand, the stomatal pathway is an incredibly effective entry pathway of larger NPs. The stomatal pores can range in size 3–10 μm × 20–25 μm length, which allows the entry of NPs during stomatal opening and active transpiration [86,87]. The accumulation of ZnO, $CeO_2$, and Ag NPs in the sub-stomatal cavities and mesophyll areas of wheat, rapeseed, and *Arabidopsis thaliana* has been reported in literature [88,89]. After entering the plant cells, nanomaterials can enter the symplast through endocytosis or apoplastically through intercellular spaces in leaf tissues. It is important to note that some NPs can actively increase their own uptake. Nano-zero-valent iron, for example, has been found to activate the plasma membrane $H^+$-ATPase, causing stomatal opening and increasing entry efficiency. Leaf morphological characteristics, such as stomatal density, abaxial and adaxial distribution, and cuticle thickness, also influence entry efficiency, although in practice, spraying the abaxial leaf surface is often not possible under field conditions [81,90]. After entering the leaves, NPs can also move around the plant. Xie et al. (2019) found that the continuous foliar application of cerium oxide NPs to common bean led to a 2.18-fold accumulation of cerium in harvested pods compared to controls [91]. Avellan et al. (2019) also found that foliar-applied gold NPs were mainly accumulated in shoots and roots, with some moving into rhizosphere soil [92]. Bueno et al. (2022) further showed that the translocation of NPs from stems to roots is easier than from leaves to leaves, indicating that the transport of NPs after foliar application is complex and organ-specific [93].

## 4 Plant Functional Traits as Primary Targets of Nanomaterials

Nanomaterials act on and selectively modulate important plant functional traits such as root development, photosynthesis, nutrient uptake, and stress metabolism. These trait-level modifications interact with rhizosphere and endophytic microbial communities to create feedback systems that maintain plant performance under stress conditions. These modifications at various levels of biological organization are translated into combined modifications of physiological performance and secondary metabolism, which together improve plant functions. These alterations represent a targeted form of reprogramming of plant functional traits such as resource acquisition, stress protection, and allocation, rather than a general promotion of growth [94,95]. Table 2 provides a review of the impacts of various nanomaterials on primary plants functional traits such as root architecture, photosynthetic activity, nutrient acquisition and stress-responsive antioxidant responses, and concludes that these materials have a regulatory role in growth rather than a promotional role.

Fig. 2 combines these results to provide a conceptualized scheme, which explains how the reprogramming of the trait by the presence of the nanomaterial is coupled with rhizosphere and endophytic microbiomes to form two-way feedback loops that have the potential to modify crop vulnerability to abiotic and biotic stresses. Collectively, both the table and figure give empirical and conceptual support to a trait-based approach to nanomaterials useful in sustainable crop stress management.

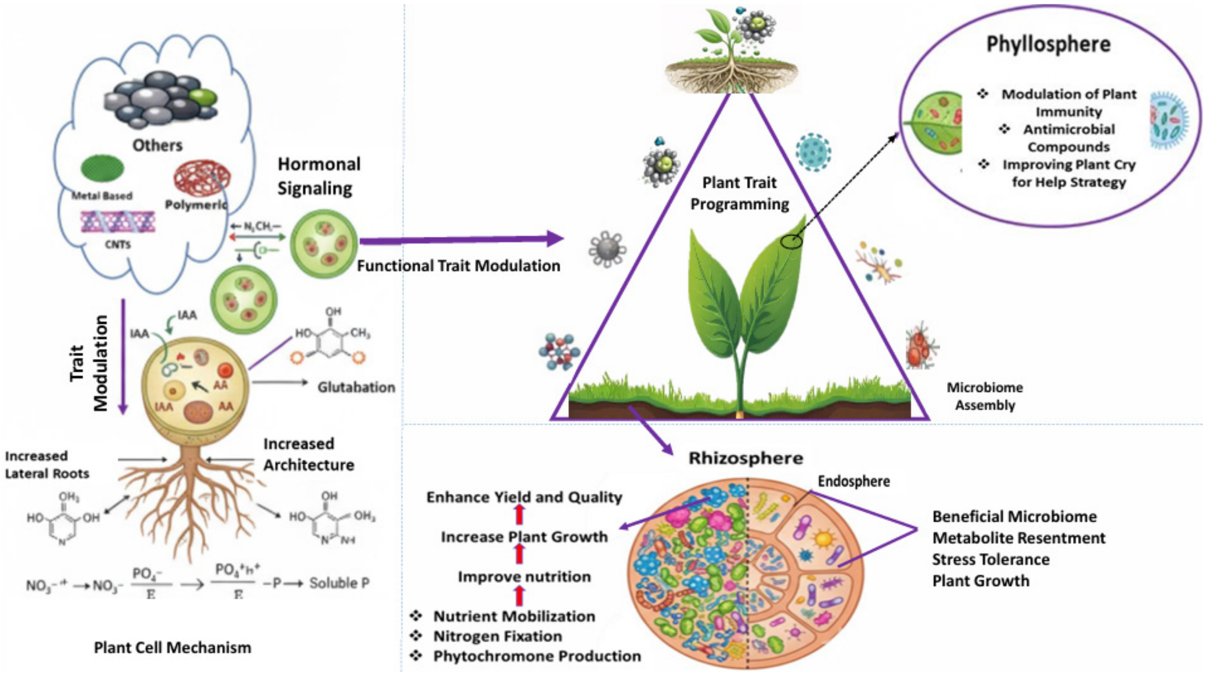

**Figure 2: Integrated nano-plant-microbiome interactions governing crop stress resilience**. Nanomaterials influence plant functional traits by altering physiological and molecular processes, including hormonal signaling and redox balance, and secondary metabolism. Trait reprogramming modifies rhizosphere and endophytic niches, reshaping microbial community composition and functional potential. In turn, beneficial microbiomes reinforce plant trait expression through nutrient mobilization, stress mitigation, and disease suppression, forming bidirectional feedback loops that stabilize crop performance under abiotic and biotic stresses.

**Table 2:** Nanomaterial-Induced Modulation of Plant Functional Traits Across Stress Contexts.

| Crop Species | Stress Type | Nanomaterial Used | Application Mode | Functional Trait Category | Specific Trait Affected | Direction of Change | Agronomic Outcome | Study Context | References |
|---|---|---|---|---|---|---|---|---|---|
| Wheat (*Triticum aestivum*) | Drought | ZnO NPs | Soil/foliar | Hydraulic traits (stomatal conductance, gas exchange) | Stomatal conductance, gas exchange | Increase | Improved water use and tolerance | Pot experiment | Raza et al. (2025) [96] |
| Tomato (*Solanum lycopersicum* L.) | Bacterial wilt (Ralstonia solanacearum) | Melatonin-decorated silica nanoparticles (MT Si NPs) | Soil | Defense traits (immune signaling); Redox traits (antioxidant enzymes); microbiome-linked | Antioxidant enzyme activity (SOD, CAT, POD, APX); SA-melatonin signaling; rhizosphere community composition | Increase antioxidant capacity and decrease disease | Suppressed bacterial wilt; improved plant growth and immunity | Pot experiment | Ijaz et al. (2024) [97] |
| Maize (*Zea mays*) | Drought | $NiFe_2O_4$ NPs | Seed priming | Growth & allocation traits (root/shoot length); Redox traits | Germination %, root/shoot length | Increase | Higher seedling vigour & biomass | Lab + growth trials | Tang et al. (2025) [98] |
| Maize (*Zea mays*) | Salinity | ZnO NPs (biosynthesized) | Soil/foliar | Hydraulic traits (RWC); Redox traits | Photosynthesis, RWC | Increase | Improved salt tolerance & growth | Controlled growth | Ashraf et al. (2025) [99] |
| Maize (*Zea mays*) | Salinity | Fe NPs (vs. Fe-EDTA, $FeSO_4$) | Pre-sowing soil treatment | Nutrient acquisition traits (Fe bioavailability); Redox traits | Fe bioavailability, chlorophyll stability, antioxidant defense | Increase | Enhanced growth and photosynthetic efficiency | Pot | Alsamadany et al. (2024) [100] |
| Sunflower (*Helianthus annuus*) | Salinity (NaCl) | NAT-BC (NTA-modified biochar) | Soil amendment | Nutrient acquisition traits (ion homeostasis); Growth & allocation traits (root architecture) | $Na^+/K^+$ homeostasis, chlorophyll content, root architecture | Increase | Reduced osmotic stress and improved biomass | Pot | Tu et al. (2025) [101] |
| Soybean (*Glycine max*) | Salt-affected soil | SiO NPs | Soil + foliar spray | Growth & allocation traits (root depth, nodulation); Redox traits | Root depth, nodulation, antioxidant capacity | Increase | Increased yield and physiological efficiency | Field | Osman et al. (2021) [102] |

**Table 2:** *Cont.*

| Crop Species | Stress Type | Nanomaterial Used | Application Mode | Functional Trait Category | Specific Trait Affected | Direction of Change | Agronomic Outcome | Study Context | References |
|---|---|---|---|---|---|---|---|---|---|
| Wheat (*Triticum aestivum* L.) | Sodic–saline soil + saline groundwater | ZnO NPs | Foliar spray | Nutrient acquisition traits; Redox traits | Antioxidant enzymes (CAT, POD, SOD), $Na^+/K^+$ balance | Increase | Improved grain nutrient content and soil enzymatic activity | Open field | Alharbi et al. (2023) [103] |
| Wheat (*Triticum aestivum* L.) | Water deficit under salt-affected soil | ZnO NPs | Foliar spray | Redox traits; Nutrient acquisition traits | SOD, GPX activity, NPK uptake | Increase | Improved biomass and membrane stability | Pot | Davoudi et al. (2024) [104] |
| Sugar beet/Cowpea | Salt stress (NaCl) | Si NPs (Au–chitosan based) | Foliar spray | Growth & allocation traits; Nutrient acquisition traits | Root colonization, IAA production, nutrient uptake | Increase | Enhanced biomass and nutrient acquisition | Pot | Francis et al. (2024; Panichikkal and Krishnankutty, (2022) [75,105] |
| Maize (*Zea mays*) | Salinity stress (NaCl) | Ag NPs | Foliar Spray/Soil Treatment | Defense traits; Redox traits (ROS scavenging) | Catalase (CAT) activity, Lipid peroxidation (MDA), Chlorophyll a | Reduction in lipid peroxidation; increase in Chl a | Full restoration of leaf dry weight; enhanced soil microbial health | Greenhouse/Pot | Martínez et al. (2026) [106] |
| Bitter gourd (*Momordica charantia* L.) | Combined metal + salinity stress | Ag NPs | Soil application with PGPR | Redox traits; Defense traits | Proline, carotenoids, antioxidant enzymes | Increase | Reduced oxidative damage and enhanced stress tolerance | Pot | Tariq and Bano, (2023) [107] |

### *4.1 Plant Growth Allocation Traits: Root and Shoot Development*

Plant growth allocation is also greatly affected by nanomaterials since they control root and shoot architecture. The NPs improve root growth and lateral root development by improving bioavailability of micronutrients, water, and uptake of nutrients. For example, ZnO NPs help to promote the growth of roots and the development of lateral roots by promoting accessibility of required nutrients [108]. On the contrary, Ag NPs improve the growth of the shoot by increasing the rate of cell division and extension of the apical meristem [109]. Carbon nanomaterials, including CNTs, provide nano-channels in the membranes of root cells, which simplifies the flow of water and nutrients through the root cell membranes, thereby supporting effective root and shoot development [110]. These modifications in growth allocation result in an improved root-to-shoot ratio, increased nutrient acquisition which provides a better platform for stress resistance and biomass accumulation. Optimizing root and shoot growth allocation allows plants to be more resilient to abiotic stresses, which guarantees survival and productivity in challenges within stressful environmental conditions [111].

### *4.2 Photosynthetic and Metabolic Traits*

Photosynthetic capacity is a functional characteristic, which connects the process of carbon fixation with growth and resistance to stress. Nanomaterials affect this property not only by increasing biomass, but also by changing the synthesis of chlorophyll, increasing light harvesting, and optimizing carbon fixation [112]. For instance, $TiO_2$ NPs boost absorbance of light and chlorophyll concentration, which optimize the efficiency of light-harvesting reactions and carbon fixation through direct contact with chloroplasts [113]. This process is further aided by carbon-based nanomaterials like graphene oxide helps in the delivery of key micronutrients such as magnesium, which is required for the production of chlorophyll [66]. Meanwhile, nanomaterials engage with metabolism to maintain productivity of photosynthesis even in the presence of stress. Metallic NPs such as $Fe_2O_3$ and ZnO are known to improve the availability of micronutrients and their functions in electron transfer, enzymatic reactions, and chlorophyll synthesis by eliminating diffusion constraints in soil-plant systems [114]. Controlled release with polymeric nanomaterials also contribute to maintaining metabolic homeostasis making sure that nutrients are available at all times with limited resources [115]. In a biochemical perspective, nanomaterials influence the major metabolic pathways that incorporate energy and stress mechanisms [116]. Stimulation of nitrogen metabolism, such as increased activity of nitrate reductase, helps in protein synthesis and meets the metabolic requirements during stress. Conversely, carbon nanomaterials maintain the redox balance by inhibiting the excess production of ROS thus maintaining the homeostasis in metabolism and preventing the oxidative inhibition of photosynthesis [117]. In sum, these interactions suggest that the efficiency of carbon assimilation is the central photosynthetic and metabolic trait that distinguishes plant performance under optimal and stress-exposed conditions, not through the induction of uncontrolled growth.

### *4.3 Nutrient Acquisition Traits: Root Architecture and Transporter Activity*

The combination of structural properties of roots and nutrient uptake transporters is known as nutrient acquisition traits. These traits are enhanced by nanomaterials, depending on their capability to modify rhizosphere chemistry, root surface characteristics and nutrient transporters. Nano-assisted micronutrient uptake helps overcome physical barriers to diffusion, thereby increasing the availability of nutrients at the root surface and enhancing the expression and activity of nutrient transporters [29]. For example, ZnO and Fe NPs raising the uptake efficacy of zinc and iron, which is needed in enzyme activity and metabolic needs during stressed conditions. At the same time, the nanomaterials also impact the architecture of roots, including root length density and formation of fine roots, enhancing the capacity of plants to explore the soil [118].

### *4.4 Hydraulic and Stomatal Traits: Water-Use Efficiency and Drought Avoidance*

Hydraulic conductance and stomatal control are important plant traits that determine water balance. Nanomaterials affect these traits by modulating root water uptake, membrane water transport, and stomatal responses. Carbon nanomaterials can enhance water transport mediated by aquaporins, improving root hydraulic conductance and sustaining transpiration under moderate drought stress [14,119] At the leaf surface, nanomaterial-dependent stomatal regulation helps improve water use efficiency by optimizing carbon gain and water loss. Metallic and polymeric nanomaterials facilitate osmotic adjustment by promoting nutrient and ion regulation, thus sustaining turgor pressure under drought stress [120]. By these actions, nanomaterials improve drought avoidance and tolerance strategies by securing plant hydraulic function rather than just augmenting water supply.

### *4.5 Defense and Stress Response Traits: ROS Buffering and Signaling Plasticity*

Defense and stress response traits are the plant's ability to sense, buffer, and recover from environmental disturbances. Nanomaterials affect defense and stress response traits mainly by affecting redox homeostasis and signaling plasticity. Most NPs affect ROS metabolism by increasing the activities of antioxidant enzymes such as superoxide dismutase, catalase, and peroxidases, thus protecting the plant from oxidative stress caused by abiotic and biotic factors [94]. Moreover, nanomaterials affect hormonal and secondary metabolite signaling pathways, which prime the plant for defense without permanently activating it. This primes the plant to be more responsive to stress while reducing growth-defense trade-offs. This allows the plant to adjust defense levels depending on the stress intensity and duration [121].

These evidences indicate that nanomaterials enhance plant performance by reprogramming the complex set of plant functional traits, rather than through isolated reactions. These functional traits include how plants grow, fix carbon, absorb nutrients, transport water, and respond to defense. By reprogramming these interrelated traits, plants become more flexible and perform better as the environment changes. Based on this understanding, the following section explores how functional trait modifications induced by nanomaterials improve plant tolerance to individual abiotic stresses such as drought, salt, temperature, oxidative, and metal stresses.

## 5 Trait-Mediated Enhancement of Abiotic Stress Tolerance under Nanomaterial Application

Abiotic factors like drought, salt, high/low temperatures, and heavy metals are known to greatly restrict agricultural productivity globally by affecting water relations, nutrient uptake, photosynthesis, redox processes, and plant growth and development. Agricultural nanomaterials have been designed as multi-functional regulators that address these shortcomings at the cellular, physiological, and molecular levels. By interacting with cell walls, plasma membranes, and organelles, nanomaterials induce collective biochemical, metabolic, and transcriptional responses that enhance plant growth and stress resistance [122,123]. As conceptually illustrated in Fig. 3, nanomaterial-based reprogramming of hydraulic, osmotic, metabolic, and antioxidant functional traits defines an integrated adaptive network that enables crops to sustain growth and productivity under diverse abiotic stress conditions.

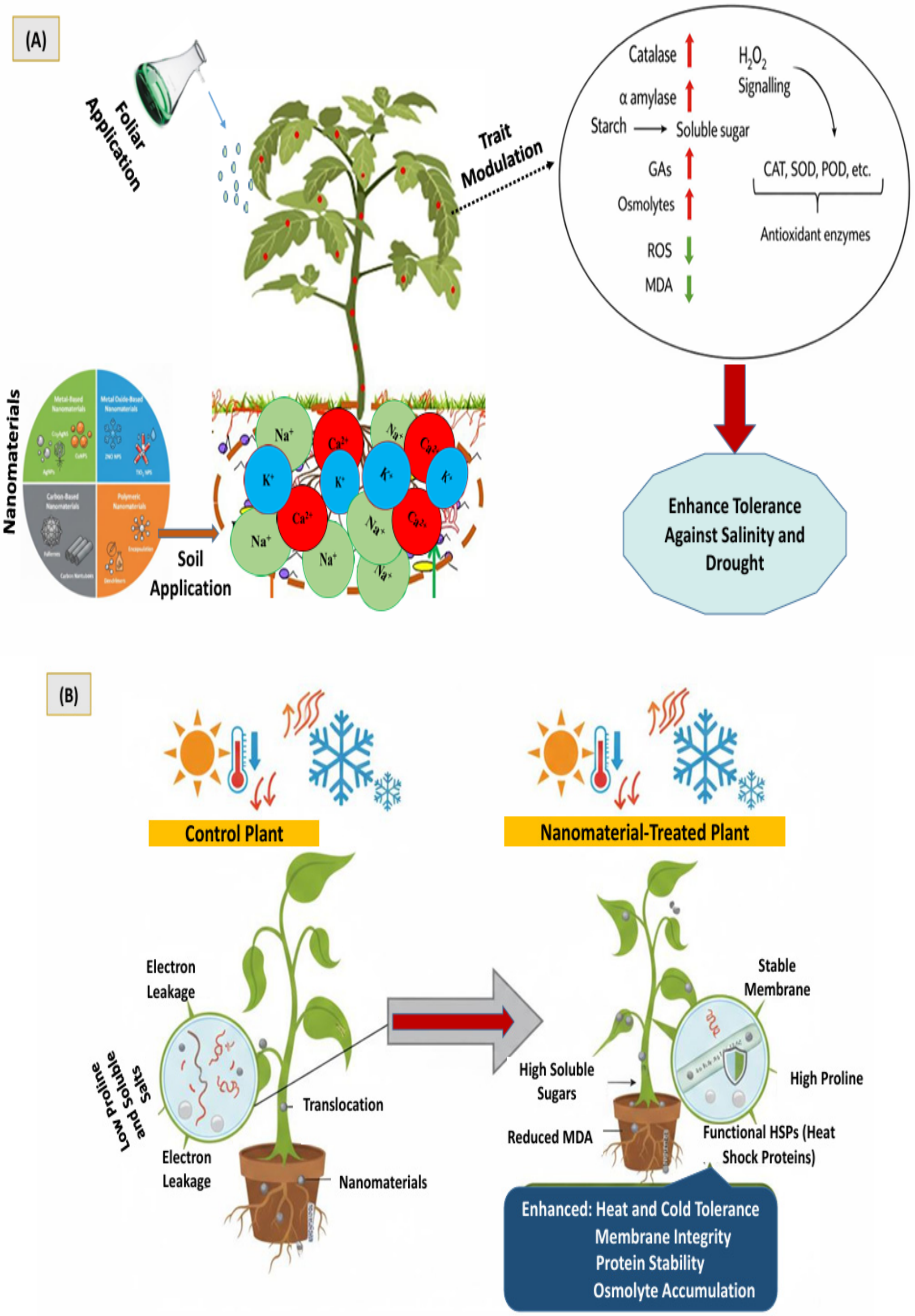

**Figure 3:** *Cont.*

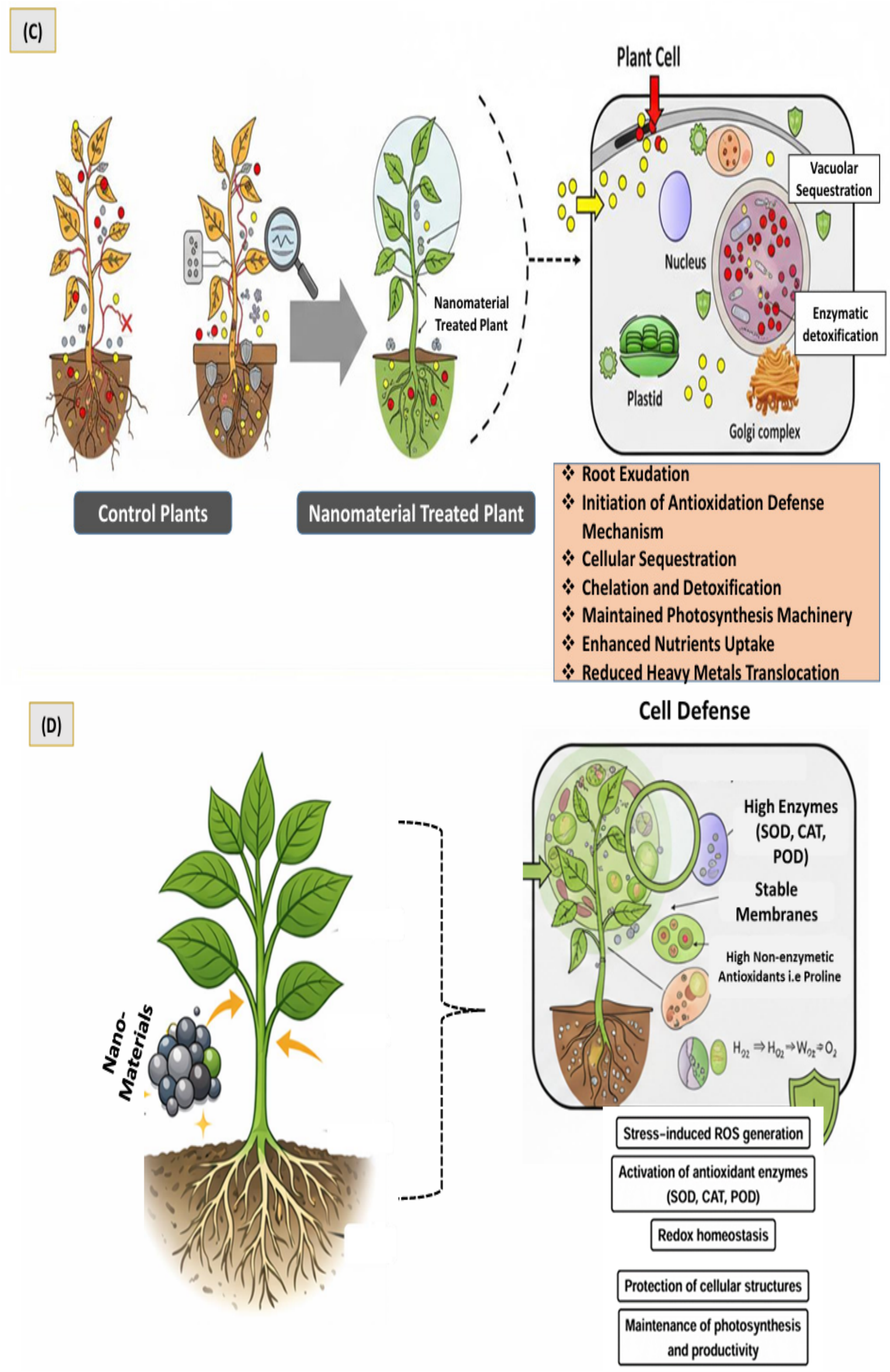

**Figure 3: Trait-specific mechanisms through which nanomaterials enhance abiotic stress tolerance**. (**A**) Hydraulic and stomatal trait regulation under drought and salinity. (**B**) Metabolic and membrane stability traits under temperature extremes. (**C**) Exclusion, sequestration, and detoxification traits under heavy metal stress. (**D**) Antioxidant and redox-regulating traits mitigating oxidative stress. Nanomaterials modulate these trait pathways to reduce physiological stress and maintain plant productivity.

### *5.1 Hydraulic and Osmotic Traits Modulation under Drought and Salinity Stress*

Drought and salinity impose severe osmotic and ionic stresses on plants, which restrict water entry, reduce turgor pressure, and impair photosynthesis, metabolism, and redox processes. Along with high/low temperatures and metal toxicity, these conditions are major global constraints on plant productivity due to their influence on hydraulic transport, nutrient uptake, and growth-related functional traits [117]. Drought and salinity tolerance in plants, therefore, demands a holistic regulation of growth-related functional traits such as root system architecture, osmotic regulation, stomatal regulation, and redox regulation [124].

Metal and metal oxide NPs (ZnO, $TiO_2$, $Fe_2O_3$, $CeO_2$), carbon-based nanomaterials (carbon nanotubes, graphene oxide), and polymeric nanocarriers have been found to possess high potential as modulators of these traits. Rather than acting as simple growth promoters, nanomaterials have been found to interact with plant tissues at the structural, physiological, and molecular levels, triggering signaling cascades that reprogram hydraulic, osmotic, photosynthetic, and antioxidant properties [62,90]. For example, Se NPs have been found to enhance drought tolerance by increasing relative water content, photosynthetic parameters, defense parameters, and biomass accumulation, with clear dose-dependent distinctions between beneficial and toxic responses [125].

Nanomaterials ameliorate osmotic stress and ionic toxicity in salinity stress conditions through the regulation of $Na^+/K^+$ homeostasis and decrease oxidative damage. $Fe_2O_3$ and ZnO NPs have shown the ability to enhance chlorophyll content, antioxidant properties, and growth indices by inhibiting sodium uptake in plants like wheat [126,127]. These findings indicate an enhancement in the regulation of ions and the stability of metabolism rather than the mere effect of a nutritional enhancement. Mechanistically, NPs interact with cell walls, membranes, and organelles to trigger biochemical and genetic reactions that enhance stress protection in cells [128,129]. The carbon-based nanomaterials, including multi-walled carbon nanotubes, enhance drought tolerance by raising the water uptake capacity, hydraulic permeability, and physiological attributes. The use of $SiO_2$ NPs also enhances structural aspects of roots, including the density of roots in their lateral direction, root-shoot ratio, which increases the capacity of soil exploration and absorb water during drought and salinity stress environments [130,131]. Besides inorganic NPs, polymeric nanomaterials such as hydrogel aid in overcoming drought challenges by assisting the soil to retain water and release it to the roots at the same speed, thus ensuring the plant is in a steady water state regardless of changes in water availability [132]. At the cellular level, nanomaterials also help in osmotic adjustment by accumulating compatible solutes (such as proline and soluble sugars) and by regulating ion transporters via ABA signaling, which helps in maintaining turgor pressure [133,134].

Taken together, these results suggest that NPs-induced drought and salt tolerance is a complex phenomenon that arises from the integrated regulation of hydraulic, osmotic, root, and redox traits, rather than from the action of individual biochemical properties. At the trait level, improvements are NPs type and dose-dependent, with metal oxide NPs (ZnO, $Fe_2O_3$, $TiO_2$) promoting ionic and antioxidant properties, carbon nanomaterials enhancing water uptake efficiency, and polymeric hydrogels maintaining soil water content (Table 2).

### *5.2 Membrane Stability and Metabolic Plasticity under Extreme Temperatures*

Among the dynamic environmental elements, one of the most harmful stresses is thought to be the constant rise in temperature. Elevated temperature increases the generation of ROS and triggers oxidative stress in crop plants [135]. This leads to the degradation of membrane lipids, disruption of cellular balance, and impairment of various metabolic functions. Ultimately, these effects result in cell death within the plant. Furthermore, heat stress inhibits carbon fixation, increases the breakdown of chlorophyll, and inhibits photosystem II and electron flow. These results interfere with the photosynthesis process, resulting in diminished plant growth. On the contrary, these plants' defense mechanisms, secondary metabolism, respiration, and the synthesis of proteins and nucleic acids are all impacted by low temperatures [136]. During times of heat stress, plants produce a number of molecular chaperones and heat shock proteins [137]. Heat shock proteins help other proteins maintain their fidelity in stressful situations and are involved in the resistance to heat stress [138]. Multiwall carbon nanotubes have been shown to increase the gene expression of heat shock proteins, such as HSP90 [139]. Additionally, the use of $TiO_2$ NPs via stomata opening regulation lessened the impact of heat stress [140]. Also, $TiO_2$ NPs activate the antioxidant defense system to reduce the oxidative stress and cellular damage, and regulate phytohormone levels and defense-related genes to enhance plant stress adaptation [141]. Polymeric NPs with reflective coatings reduce leaf temperature, further mitigating heat-induced oxidative stress. Under cold stress, graphene oxide and $SiO_2$ NPs enhance membrane fluidity and stimulate osmolyte accumulation, preventing ice crystal formation and preserving enzymatic function [67,142]. These nanomaterials also stabilize chloroplast membranes and maintain electron transport, preserving carbon assimilation and energy production. In addition, NPs modulate metabolic pathways related to nitrogen and carbohydrate metabolism, allowing plants to maintain biomass accumulation under temperature extremes [143]. In general, temperature tolerance mediated by nanomaterials is an integrated phenomenon that arises from the maintenance of membrane integrity, photosynthetic efficiency, and metabolic homeostasis. $TiO_2$, carbon-based, and polymeric NPs protect chloroplasts, regulate ROS, and maintain energy and nitrogen metabolism, with comparative analyses showing differences in efficacy for heat and cold stress (Table 2).

### *5.3 Exclusion, Sequestration, and Detoxification under Heavy Metals Stress*

Nanomaterials may alleviate heavy metal stress via various pathways such as chelation, sequestration as well as adjusting antioxidant defense characteristics. NPs can decrease the amount of metal uptake or compartmentalize metals in vacuoles, reduce oxidative damage to plant tissues by increasing root exudation and regulation of metal transporters. A number of studies show that metal oxide and carbon-based nanomaterials enhance tolerance of plants to cadmium, lead, and arsenic stress, stabilizing photosynthetic and nutrient acquisition characteristics [40,144,145]. The presence of heavy metal, such as cadmium, lead, and arsenic, disturbs the uptake of nutrients, forms ROS, and interferes with the metabolic processes. Nanomaterials reduce stress caused by heavy metals by enhancing mechanism of exclusion and detoxification. Iron oxide and magnesium oxide NPs fix metals in the soil making them less bioavailable and preventing the uptake by roots [146]. Silicon-based NPs reinforce the cell walls and minimize the infiltration of metals into the root tissues and internalized NPs subsidize phytochelatin formation and vacuolar metals sequestration while reducing cytosolic toxicity. ZnO NPs act as ROS-scavenging NP that helps membranes and proteins to avoid oxidative damages under the influence of metal stress [147]. For instance, ZnO NPs application prompted the development of effective heavy metal tolerance mechanisms by infiltrating a series of biochemical pathways in a cascade pattern to prevent heavy metal oxidative stress-induced cell injury in *Leucaena leucocephala* [148]. Moreover, Samani et al. (2024) found out that Nano-silica is a useful soil amendment, enhancing the nutrient availability and suppressing the adverse effects of heavy metals on *Calendula officinalis* [149]. The pretreatment of wheat with FeO and Se NPs had lowered oxidative stress and Cd uptake and enhanced ($p < 0.05$) synthetic and non-synthetic gas exchange, gene expression, and *Triticum aestivum* biomass [150]. These protective functions enhance the efficiency of photosynthesis, optimize root to shoot biomass ratios, and strengthen the activity of antioxidant enzymes, all of which work in combination to enhance plant performance in metal-polluted environments. There is evidence in the literature that metal oxide NPs in comparison to carbon-based NPs can be exceptionally beneficial in lowering metal levels. Taken together, these results highlight that the tolerance of the heavy metals by nanomaterials is founded on two metal exclusion/sequestration and metabolic/antioxidant reinforcement mechanisms. Metal oxide NPs do not only reduce metal uptake, but carbon and Si NPs result in ROS buffering effects, root-to-shoot transfer, and stability of photosynthesis (Table 2).

### *5.4 Oxidative Stress Modulation and Antioxidant Defense Systems under Abiotic Stress Conditions*

Overproduction of reactive oxygen species is a frequent effect of drought, salinity, extreme temperatures and heavy metal stress. Nanomaterials affect ROS and improve antioxidant capabilities at various levels. $CeO_2$ nanoparticles can directly eliminate reactive oxygen species through the redox cycling between $Ce^{3+}$ and $Ce^{4+}$ ions, which can neutralize superoxide radicals and hydrogen peroxide, while $TiO_2$ nanoparticles can help stabilize electron transport in chloroplasts and mitochondria to decrease ROS production [151,152]. ZnO and Ag NPs stimulate enzymatic antioxidants, including superoxide dismutase, catalase, and ascorbate peroxidase to stabilize cellular redox homeostasis. The non-enzymatic antioxidants, including glutathione and ascorbate, are stimulated by carbon-based NPs (graphene oxide), which guarantees a long-lasting detoxification performance in the presence of the stressor [135,153]. This type of ROS control maintains photosynthetic activity, membrane integrity, enzymatic activity and metabolic stability that enables plants to survive in stressed condions. Finally, ROS regulation by NPs is predetermined by the combined action of enzymatic and non-enzymatic processes in any type of stress. Comparative evidence shows that $CeO_2$ and $TiO_2$ have direct influence on ROS, ZnO and Ag enhance enzymatic antioxidants, while carbon-based nanomaterials preserve the detoxification capacity thereby collectively safeguarding photosynthesis, membrane, and metabolism (Table 2).

### *5.5 Hormonal Signaling and Gene Regulation under Abiotic Stress Conditions*

Nanomaterials also regulate the plant hormonal signaling and mitigating stress response pathways. They regulate the endogenous concentrations of abscisic acid, auxins, cytokinins, gibberellins, jasmonic acid and salicylic acid, thus combining the notion of stress with growth and development. For example, $TiO_2$ NPs can improve jasmonic acid and salicylic acid and reduce ethylene levels and can enhance salt tolerance in cucumber, whereas CaO and CuO NPs can stimulate the movement of auxins and increase cytokinins and gibberellins balance to optimize plant development under salinity stress [154–156]. The plant transcriptome reveals the presence of signals from NPs that enhance stress-responsive transcription factors, including AP2C1, and induce genes that participate in antioxidant pathways, water transport, and osmolyte biosynthesis. It is also noted that epigenetics, such as histone acetylation, take place during ZnO nanoparticle treatment [55,157]. Signaling molecules like nitric oxide and ROS are secondary messengers, which trigger downstream pathways that organize integrated responses to stress [158]. In conclusion, the results indicate that nanomaterials contribute to stress resilience by integrating hormonal responses with transcriptional mechanisms. (Table 2).

### *5.6 Targeted Delivery and Controlled Release under Abiotic Stress Conditions*

The stress tolerance is improved spatiotemporally through the delivery systems through nano-carriers that facilitate targeted and sustained release of nutrients, growth regulators, and antioxidants. For instance, chitosan polymeric carriers can deliver nitrogen to rice seedlings with maximum efficiency during drought conditions, whereas lignin-based biodegradable carriers improve the retention and bioavailability of zinc and iron in wheat when applied to the roots or leaves [159]. By employing such delivery system, nanomaterials can embrace their maximum functional effects on the plant traits with minimised environmental loss and off-target effects. These outcomes these studies demonstrate that precise nanocarrier-mediated delivery, at the level of space and time is crucial in terms of achieving trait-level results. Chitosan-derived and lignin-based nanocarriers enhance local nutrient and stress-relieving compounds delivery to enhance persistent modulation with a reduced off-target activity of functional traits (Table 2).

## 6 Trait-Mediated Enhancement of Biotic Stress Tolerance under Nanomaterial Application

Biotic stress is one of the biggest causes of crop failure around the world and is always a challenge for efficient farming. Biotic stress is caused by living organisms that attack plants, such as fungi, bacteria, viruses, insects, nematodes, and other herbivores. Unlike abiotic stress, biotic stress often causes extreme nutrient depletion, infection and even it has the potential to drive a crop to its death if the plant's defense mechanisms are not strong enough [160,161]. At the functional level, biotic stress disrupts plant defense traits, growth allocation traits, and metabolic stability traits, thereby impairing yield formation and quality. In this context, nanotechnology is a promising, eco-friendly, and efficient method for addressing biotic stress in plants. It acts by enhancing the plants' defense traits, improving resistance signaling, and directly reducing the populations of pathogens and pests [162]. Although nanomaterials mainly exhibit trait-mediated effects, its use can also cause unexpected effects on a microbial community. NPs synthesized chemically can cause changes in rhizosphere and endophytic microbial community by influencing root exudation, nutrient conditions, or microbial signals, but green-synthesized NPs are typically more environmentally friendly [163]. The recognition of these effects is essential in exploiting the nano-trait-microbiome nexus in a sustainable manner. It is worth noting that the enhancement of plant defenses when exposed to nanomaterials also alters microbial recruitment and microbial communication in the rhizosphere and phyllosphere. The trait-mediated effects of nanomaterials on plant-associated microbiomes under biotic stress are presented in Table 3, which describes how various nanomaterials affect microbial communities in the rhizosphere, phyllosphere, and endosphere to improve disease resistance and plant growth.

**Table 3:** Trait-Mediated Effects of Nanomaterials on Plant-Associated Microbiomes.

| Nanomaterial Type | Plant Host | Microbiome Compartment | Trait Driver | Microbial Community Shift | Functional Microbial Response | Stress Context | Evidence Level | Reference |
|---|---|---|---|---|---|---|---|---|
| Melatonin-decorated $SiO_2$ NPs | Tomato (*Solanum lycopersicum* L.) | Rhizosphere | Redox traits and (melatonin–SA pathway) | Decrease *Ralstonia solanacearum*; increase beneficial taxa (*Gemmatimonadaceae*, *Anaerolineaceae*) | Disease suppression; enhanced microbiome stability | Bacterial wilt | 16S rRNA amplicon sequencing + metabolomics | Ijaz et al. (2024) [97] |
| Silica nanoparticles ($SiO_2$ NPs) | *Astragalus* spp. | Rhizosphere | Redox traits (Root exudation & systemic acquired resistance (SAR)) | Decease Pathogen-helper bacteria (*Pseudomonas*, *Microbacterium*); increased microbial diversity and network complexity | Alleviated Fusarium root rot; enhanced antioxidant enzyme activity (APX, CAT, POD) | Fusarium root rot | 16S rRNA sequencing + metabolomics + co-inoculation bioassays | Ai et al. (2025) [164] |
| Silica nanoparticles ($SiO_2$ NPs) | Tomato (*Solanum lycopersicum* L.) | Root endosphere | Nutrient acquisition traits; defense traits (priming) | Increased endophytic diversity (Rhizobium, *Sphingobium*, *Mitsuaria*) | Enhanced resistance to bacterial wilt | Bacterial wilt | High-throughput sequencing | Wang et al. (2025) [165] |
| Silica nanoparticles | Arabidopsis (*Arabidopsis thaliana*) | Phyllosphere & rhizosphere | Defense trait (SAR induction) | Enrichment of beneficial microbial taxa | Immune priming against pathogens | Biotic stress | Transcriptomics + microbiome profiling | El-Shetehy et al. (2021) [166] |
| Metal oxide nanoparticles (CuO, ZnO, $Fe_2O_3$) | Tomato (*Solanum lycopersicum*) | Rhizosphere | Defense trait: redox trait | Shift in community composition; decreased pathogen abundance | Suppression of soil-borne disease | Bacterial wilt | 16S rRNA sequencing | Jiang et al. (2022) [167] |
| Copper–Silver (Cu–Ag) nanoparticles | Rice (*Oryza sativa*) | Endosphere (leaf) | Defense trait: redox trait (PAL activity, ROS) | Increased Beneficial endophytes (*Burkholderiales*, *Micrococcales*, *Rhizobiales*) | Suppression of *Xanthomonas oryzae* pv. *oryzae*; enhanced stress resistance and growth-promoting functions | Bacterial leaf blight (BLB) | 16S rRNA sequencing + enzymatic activity assays | Ning et al. (2025) [15] |
| Silica nanoparticles ($SiO_2$ NPs) | Pakchoi (*Brassica chinensis* L.) | Rhizosphere | Growth & allocation traits (exudation/ metabolites) | Increased *Rhodobacteraceae*, *Paenibacillus*, *Chaetomium* | Enhanced carbon and nitrogen cycling | Contaminated mine soil | 16S rRNA + ITS sequencing + GC-MS metabolomics | Tian et al. (2020) [168] |

**Table 3:** *Cont.*

| Nanomaterial Type | Plant Host | Microbiome Compartment | Trait Driver | Microbial Community Shift | Functional Microbial Response | Stress Context | Evidence Level | Reference |
|---|---|---|---|---|---|---|---|---|
| ZnO nanoparticles (ZnO NPs) | Tea (*Camellia sinensis* L.) | Phyllosphere (epiphytic and endophytic) | Growth & allocation traits (photosynthesis/shoot) | Altered phyllosphere microbial community composition | Potential enhancement of plant health and productivity | General growth improvement | 16S rRNA sequencing + metabolomics | Chen et al. (2024) [169] |
| Silver (Ag) and Copper (Cu) nanoparticles | Wheat (Triticum aestivum L.) | Endosphere/rhizosphere interface | Defense traits; redox traits (PR genes, ROS) | Decreased *Tilletia indica* pathogen abundance | Suppression of fungal growth; enhanced plant resistance | Karnal bunt | *In vitro* + gene expression + pot assays | Jabran et al. (2025) [170] |
| $Fe_3O_4$ engineered nanomaterials (ENMs) | Maize (*Zea mays* L.) | Rhizosphere | Nutrient acquisition traits; growth & allocation traits (exudation) | Increased Nitrogen-fixing bacteria, decreased iron-redox bacteria; increased PGPR-related taxa | Altered carbon cycling; plant growth promotion | Nutrient stress | 16S rRNA sequencing + GC-MS metabolomics | Zhang et al. (2020) [171] |
| Graphene oxide (GO) | Soybean (*Glycine max* L.) | Rhizosphere | Growth & allocation traits; nutrient acquisition traits | Enrichment of beneficial bacterial genera (*Sinorhizobium*, *Sphingomonas*) | Enhanced nutrient cycling, PGPR support | Nutrient stress | 16S rRNA sequencing | Qiao et al. (2025) [172] |

### *6.1 Disease Stress and Defense-Related Trait Modulation*

Nanomaterials regulate plant defense traits against pathogenic fungi, bacteria, and viruses by integrating direct antimicrobial activity and host-mediated resistance traits. Ag-NPs showed a 46% increase in antifungal activity and suppressed *Fusarium* wilt in chickpea by 73.3% without influencing seed germination and soil microbes [173]. Similarly, ZnO NPs suppressed *Ralstonia solanacearum* in tomato and improved growth traits by increasing barrier and antimicrobial defense traits [174]. $CeO_2$ NPs showed broad-spectrum antifungal activity in wheat, which supports pathogen exclusion and cellular defense trait stability [175], while $TiO_2$ NPs at 40 mg $L^{-1}$ suppressed disease severity in wheat by regulating ROS-mediated signaling traits [176]. Biopolymer-derived NPs, chitosan NPs, also play a role in developing pathogen resistance by priming systemic acquired resistance (SAR) and regulating traits of plant defense. Nanoparticles can enhance structural and chemical defense properties through ROS signaling, hormone regulation, and the induction of antimicrobial metabolites. NPs can also indirectly influence the phyllosphere and rhizosphere microbiomes to promote antagonistic microbes that inhibit pathogens, which offers a trait-mediated microbial shield against biotic stress [177–179]. Nanomaterials also improve root defense and rhizosphere protection by inhibiting nematode attack and soil-borne pathogens, as evidenced for ZnO- and $SiO_2$ NPs in various crops [180,181]. Nanomaterials also Collectively, these studies indicate that nanomaterials integrate structural, redox, and transcriptional defense traits to improve disease resistance (Table 3).

### *6.2 Pest Stress and Resistance-Related Trait Enhancement*

Insect pests and mites impose substantial yield penalties by damaging photosynthetic tissues, depleting stored resources, and acting as vectors for plant diseases, thereby compromising both growth and defense-related traits [182]. NP-based methods have great potential in pest management by inducing plant defense traits without significantly affecting non-target species. The application of low concentrations of Ag NPs can effectively reduce the population of phytophagous mites on tomato plants without affecting beneficial mites, indicating a selective pest control mechanism [183]. Similarly, the application of Zn NPs resulted in complete mortality of *Sitophilus oryzae* and reduced *Rhyzopertha dominica*, establishing their effectiveness in postharvest protection [184]. Silicon-based NPs improved physical and biochemical resistance in tomato against *Helicoverpa armigera* and root-knot nematodes [185]. Cu NPs showed higher pest mortality with minimal effects on predators [186]. Treatment of rice or maize grains showed 97% pest mortality in 7–14 days [187]. In addition to their role in pest management, nanomaterials also improve root system architecture, redox signaling pathways, and secondary metabolite synthesis, which collectively contribute to beneficial plant-microbe interactions, thus strengthening biotic stress tolerance (Table 3).

## 7 Mechanistic Integration: The Nano-Trait-Microbiome Nexus

Plant-associated microbiomes in the rhizosphere, endosphere, and phyllosphere act as an extension of plant functional traits, which affect nutrient uptake, disease resistance, and stress tolerance [188,189]. Conventional microbiome engineering using probiotics is often unpredictable and unstable in the long term [31]. Nanomaterials bring in a mechanistic component that indirectly affects microbiome composition, diversity, and activity by plant-mediated traits. NPs are able to influence root exudation and extracellular metabolites, which influence microbial colonization under both optimal and stressful conditions [190,191]. Nano-Cu, Zn, Fe, and chitosan are examples of plant protection nanomaterials that reduce the incidence of diseases and alter rhizosphere and phyllosphere microbiomes [192,193]. However, their unregulated use, especially Ag NPs, may suppress favorable microbial plants and raise the number of pathogens [194].

These findings reiterate that the interaction between microbiomes cannot be explained based on toxicity alone but rather interpreted based on a trait-based and mechanistic approach.

On the ecosystem level, the growth of plants and their productivity are ultimately affected by the management of nutrients, control of pathogens, and resistance of stress by plant-associated microbiomes. All physicochemical properties of plants (root morphology, immune systems, hormonal regulation, exudate composition, etc.) influence the dynamics of microbiome communities, rather than simple colonization patterns [195]. Overall, nanomaterials influence the plant-microbiome interface in the primary way, by modulation of the host functional properties that define the recruitment and maintenance of the microbiome. The nano-plant-microbiome interface based on functional traits is conceptually depicted in Fig. 4, and examples of microbiome effects based on these traits under the application of nanomaterials are presented in Table 3.

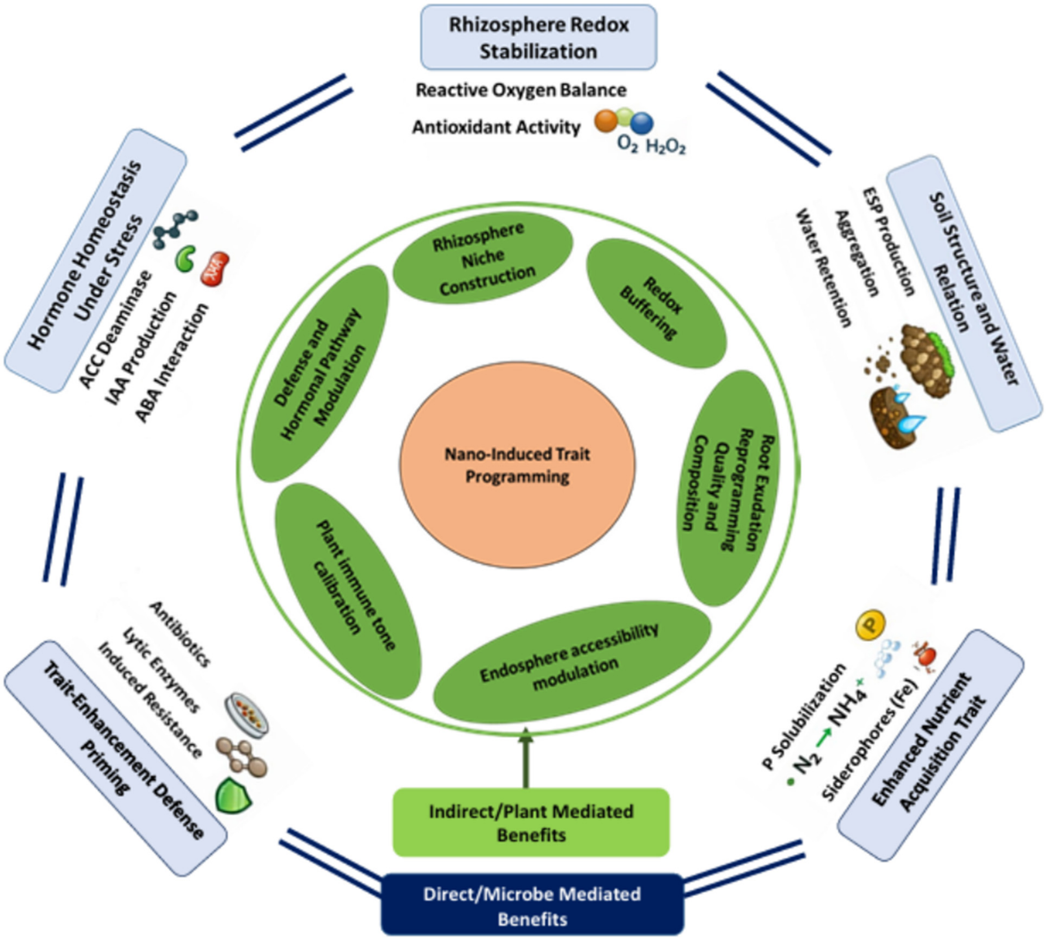

**Figure 4: Functional reprogramming of plant-associated microbiomes under nano-induced trait modulation**. Nanomaterial-driven reprogramming of plant functional traits alters root exudation patterns, redox status, and defense signaling, creating new ecological niches that shape microbial functional capacities rather than only community composition. These microbiomes provide key ecosystem services, including nutrient mobilization (e.g., phosphorus solubilization, nitrogen fixation), stress hormone regulation (e.g., ACC deaminase activity), redox buffering, pathogen suppression, and soil structural stabilization through extracellular polymeric substances. These functional services feedback to reinforce plant trait performance, forming a dynamic plant–microbiome partnership that enhances resilience under abiotic and biotic stress.

### *7.1 Plant Microbiomes as Trait-Responsive Systems*

Plants are actively involved in the recruitment and optimization of beneficial microbial assemblages based on trait-mediated mechanisms. The root system architecture defines the spatial niches, while root exudates, consisting of sugars, amino acids, organic acids, flavonoids, nicotine, and other secondary compounds, act as selective chemical signals that mediate the colonization of microbes. Immune and defense signals further modulate this process, favoring the establishment of compatible microbial assemblages and suppressing the growth of opportunistic pathogens, thus supporting the idea of a tightly integrated functional unit between the plant and its microbiome [196]. The assembly of the microbiome is particularly sensitive during the developmental phase, when root signaling, exudation, and immune system activity are highly dynamic. During the early developmental phase, plant-microbe communication networks are highly responsive to external disturbances, whereas in later stages, the microbial assemblages are more stable and better protected [154]. Various plant tissues support different microbial assemblages, which are structured in non-random ways, and the functional role of microbes also differs between wild plants and domesticated crops. When the conditions are calm and non-stressful, the microbial communities are likely to display adaptive tolerance. However, when plants are exposed to pathogens, the distinction between helpful shifts and growth inhibition becomes more significant [197].

### *7.2 Nanomaterials as Indirect Engineers of the Plant Microbiome*

Plant-associated microbiomes can hardly be restructured by direct antimicrobial action of nanomaterials. They rather operate as indirect engineers by modulating plant functional traits which determine microbial recruitment, niche construction and community stability. This trait-centered mechanism can be used to explain why changes in the microbiome are more closely related to plant functions than NPs exposure.

#### *7.2.1 Trait-Driven Microbial Recruitment and Niche Construction*

The nanoparticle exposure will have the potential to remodel the root architecture, homeostasis of hormones status and synthesis of the defense metabolites leading to substantial changes in the root exudation patterns, which assemble rhizosphere community. Disturbances in the auxin and reactive oxygen species (ROS) signaling are often used to increase lateral root formation and root surface area, increasing the niche of microbial colonization. Root priming involves the enhancement of exudate release by nanoparticles with varying chemical compositions, thereby increasing the attraction of beneficial microbes [155,172]. Trait based modulation is also affected by the dynamics of time. At early growth phases, further release of sugars, amino acids, and organic acids prefer colonization by short-chain fatty acid (SCFA)-producing and pathotrophic microorganisms [198]. In this manner, nanomaterials indirectly regulate microbial succession by modulating hormonally and metabolically controlled plant traits.

#### *7.2.2 Effects on Rhizosphere Versus Endophytic Microbiomes*

The root system of plants harbors two distinct microbial communities: the rhizosphere, which refers to the soil that is in close association with the root, and the endosphere, which refers to the internal root tissues after the removal of epiphytes. Both communities are essential for plant growth and stress resistance [199]. However, they differ based on reactions to environmental disturbances. Relative to the rhizosphere, the endosphere microbiome is normally more sensitive due to the difference between filtering and functional specialization [200]. But the implication of these differences to plant growth during abiotic stress are not clearly known. Plant-root exudates are major sources of differences in microbial composition. These metabolites can mobilize nutrients and act as signals to attract, activate, or repel microbes which helps in regulating rhizosphere microbial community assembly [201–203]. The metabolite composition is different among species, leading to interspecific variation in microbiome composition and stress tolerance [204,205].

Nanomaterials are interacting more efficiently with rhizosphere microbiota through root morphological and exudative changes and immune system responses, which frequently cause community changes. Endophytic microbiota are safeguarded by barriers and immune systems, and thus, functional changes are more likely to occur than compositional changes. These interactions underscore the dominance of trait-mediated microbial filtering over nanoparticle-microbe interactions [206–208]. Experimental evidence has verified context-dependent interactions: ZnO NPs increased soybean resistance to aluminum toxicity while increasing endophytic diversity and the abundance of beneficial genera such as *Aureimonas*, *Luteimonas*, and *Sphingomonas* [209]; biosynthesized Ag NPs controlled Mucor racemosus in agricultural crops [210]; selenium NPs in rice increased endophytic community structure and the abundance of *Azospirillum* [211]. In general, nanomaterials interact with endophytic microbiota primarily through host trait and stress response modifications rather than antimicrobial activities. Representative examples of nanomaterial-induced, trait-mediated shifts in rhizosphere and endophytic microbial communities across crops and stress contexts are summarized in Table 3.

### *7.3 Direct Effects of Nanomaterials on Plant-Associated Microbiomes*

NPs can directly influence plant-associated microbial communities through physicochemical mechanisms such as disruption of cell envelopes, reactive oxygen species (ROS) generation, and release of metal ions. Metal-based, metal oxide, and carbon-based NPs have been shown to selectively suppress or enrich microbial taxa, including nitrogen fixers and biocontrol agents, depending on their composition, size, surface chemistry, and exposure dose [212,213]. For instance, exposure to $TiO_2$ and ZnO NPs drastically reduced populations of nitrogen-fixing and methane-oxidizing bacteria while increasing the abundance of bacteria capable of degrading refractory organic pollutants, particularly members of the *Sphingomonadaceae* family [214]. Ag NPs can shift microbial communities by reducing ammonia oxidizers and *Proteobacteria* while promoting *Acidobacteria* and *Bacteroidetes* [215], yet *arbuscular mycorrhizal* colonization of wheat roots often remains largely unaffected [216]. Similarly, Ag NPs significantly reduced ammonia oxidizers and *Proteobacteria*, while promoting *Acidobacteria*, and *Bacteroidetes*. Exposure to $C_{60}$ fullerenes led to a three- to four-fold decrease in fast-growing bacterial densities [217], and $TiO_2$ or amine-modified polystyrene nanospheres reduced rhizospheric bacteria in *Lactuca sativa*, inhibiting plant growth [191] Carbon-based nanomaterials altered microbial populations in *Oryza sativa* rhizosphere [218], while CNTs did not significantly affect microbial populations in *Solanum lycopersicum* [219]. Plant-associated microbial communities often display resilience, reorganizing around plant-regulated niches rather than collapsing entirely under nanoparticle exposure [163]. These observations highlight that the ultimate functional consequences of nanomaterial exposure are shaped not only by direct microbial toxicity but also by the plant's ability to modulate microbiome composition and activity, paving the way for ecosystem-level effects on nutrient cycling, disease suppression, and stress tolerance (Fig. 4).

### *7.4 Indirect Functional Consequences: Nutrient Cycling, Disease Suppression, and Stress Tolerance*

Nanomaterials have an indirect effect on plant performance by reorganizing microbial rhizosphere activity and plant-microbe interactions. Bacterial diversity in the rhizosphere stimulates the production of bioactive compounds, such as siderophores, lipopeptides, and exopolysaccharides, which regulate nutrient availability and plant health [220,221].

**Nutrient cycling:** Siderophores chelate metals such as Fe, Zn, and Cu, increasing micronutrient bioavailability and mitigating toxicity from nanomaterials [222–225]. Nanomaterials can alter soil enzyme activity and microbial nitrogen and carbon cycling, but high concentrations (e.g., $CeO_2$, Ag, Zn, Ti NPs) can impair nitrogen fixation and rhizobia symbiosis [226,227].

**Disease suppression:** Plant defense mechanisms promoted by the microbiome are enhanced as nanomaterials selectively increase the abundance of species known to produce antimicrobial and signaling compounds, thus improving resistance to soil-borne pathogens without necessarily affecting microbial diversity [228,229].

**Stress tolerance:** Exopolysaccharides produced by microbes interact with nanomaterials to reduce oxidative stress, such as in selenium NPs that form C-O-Se bonds, thereby improving antioxidant activity [230,231].

On the whole, the indirect functional effects of nanomaterials and the microbiome are contingent on microbial activation, plant-mediated filtration, and environmental factors. When coupled with beneficial microbial groups such as PGPR, mycorrhizae, and rhizobia, nanomaterials can be used to improve nutrient availability, inhibit pathogens, and make plants more resilient to environmental factors, thus providing a platform for sustainable and climate-smart agriculture (Fig. 4).

### *7.5 Feedback Loops, Signaling Pathways, and Trait Plasticity under Stress*

Plant responses to nanomaterials are mediated by feedback mechanisms involving plant properties, microbiota, and nanomaterials. Plants modulate their rhizosphere and endosphere microbial communities through root system architecture, exudation, and immune responses, and microbial metabolites. Key feedback loops, signaling pathways, and trait plasticity mechanisms underlying nano-plant-microbiome interactions are synthesized in Table 4.

**Table 4:** Mechanistic Pathways and Feedback Loops in the Nano–Trait–Microbiome Nexus.

| Nanomaterial Property | Plant Signaling Pathway | Functional Trait Reprogrammed | Microbiome Feedback | Stress Tolerance Outcome | Knowledge Gaps | Reference |
|---|---|---|---|---|---|---|
| ROS-scavenging/redox regulation | ABA signaling | Water-use efficiency | Enhanced microbial stability | Drought tolerance | Field validation | Joksimović et al. (2025) [232] |
| Slow nutrient release (nano-fertilizers) | IAA (auxin) signaling influence | Increased root proliferation & architecture | Promotion of microbial recruitment and nutrient cycling | Nutrient stress tolerance | Long-term soil/microbiome effects | El-Saadony et al. (2021) [233] |
| Nanocarrier delivery of phytohormones | Modulation of ABA, SA, JA pathways | Secondary metabolism activation | Microbiome shifts responding to hormone signaling | Abiotic & biotic combined stress tolerance | Mechanism of root-to-microbe signaling | Tripathi et al. (2025) [234] |
| Metal/oxide NP as signaling elicitors | ROS/NOS signaling and JA pathways | Secondary metabolite biosynthesis | Stimulates ROS-tolerant microbes | Oxidative stress mitigation | Dose-response & specificity across species | Liu et al. (2021) [121] |
| Si/polymeric NMs reinforcing barriers | Stress signal integration (ABA, JA, SA) | Cell wall strength, osmotic balance | Microbiome adapts to altered rhizodeposits | Salt & heavy metal tolerance | Multi-omic integration *in situ* | Zhu et al. (2019) [235] |
| Nanopriming of seeds | Early signaling adjustments (IAA, ROS) | Improved germination & root growth | Early microbiome colonization shifts | Combined environment stress | Mechanistic link seed priming in microbiome | Yu et al. (2023) [236] |
| Surface Functionalization | Secondary metabolism | Exudate profile shifts | Signal molecule modulation | Biotic stress resistance | Transgenerational effects | Lala, (2021) [237] |

These metabolites including siderophores, phytohormones, and exopolysaccharides regulate nanomaterial mobility, nutrient availability, and stress protection [234]. Stresses and nanomaterials treatment trigger plasticity responses in plant roots, which selectively favor beneficial microbes that promote nutrient acquisition, suppression of pathogens, and stress resistance. Beneficial microbes affect plant hormonal pathways (auxin, ethylene, jasmonic acid, salicylic acid), which regulate root growth, stress-responsive gene expression, and systemic resistance [33,238]. A moderate level of NM exposure enhances these feedbacks, while high exposure levels could disrupt the regulation of signaling, symbiotic functions, and resilience [239].

## 8 Environmental, Ecological, and Socio-Economic Considerations

### *8.1 Nanomaterial Fate, Persistence, and Potential Risks in Agroecosystems*

Plants being important components of the ecological system play extremely important roles in the uptake of matter into the system. When anything is introduced in the food chain, this may create imbalances in the ecosystem, which affect the different components of the ecosystem. In this aspect, the growing use of engineered nanomaterials in plant agriculture requires a more detailed knowledge of what happens to nanomaterials in the environment. Once applied, nanomaterials experience a range of physical, chemical, and biological processes, such as aggregation, dissolution, surface reactions with water systems, soil organic matter, and minerals. These mechanisms influence the mobility and reactivity of nanomaterials in soil-plant systems, which determine their effectiveness [240]. However, there have been very limited studies on the fate and toxicity of NPS with the environment.

The effects of nanomaterials on plants are obviously two-sided. On the one hand, there are nanomaterials, which were shown to induce seed germination and plant growth [241]. Alternatively, nanomaterials may also be used to prevent plant diseases from insects and pests when incorporated as nano-enhanced pesticides or insecticides [242]. The increasing application of nanomaterials in agriculture is specific to define the need to understand their phytotoxicity, their fate in the environment and their ultimate fate. Translocation of NPs into plant systems is among the most widespread issues and may become potentially hazardous to human and animal health via food chain. The accumulation of NPs in the edible parts of plants, fruits or seeds is one of the routes of exposure to herbivores and humans who consume them [54]. This is why the mechanisms of uptake, bioaccumulation, and translocation of NPs have to be known in order to establish the foundation on the basis of which environmental and health risk assessment might be developed. By doing so, the future of nanomaterials use in agriculture finally lies in creating a balance between their agricultural benefits and eco-friendliness in line with the principles of science and policy regulation [243].

### *8.2 Risks to Soil Microbial Networks and Ecosystem Functions*

The basic functions of the ecosystems, including the nutrient recycling, soil aggregation, carbon fixation, and control of the soil-borne pathogens depend on soil microbial communities. Their exposure to nanomaterials can specifically disrupt the high interconnections of these communities and, hence, have an impact on the plant-associated microbiomes, including the phyllosphere. In this respect, chemically synthesized nanoparticles which are more active and persistent have a higher probability of interfering with the microbial diversity and ecosystem processes, whereas green-synthesized nanoparticles seem to be relatively harmless [244]. It is also important to note that while the overall microbial diversity may be only mildly affected, a slight shift in the composition of keystone populations, functional groups, or microbial interaction networks may cause disproportionate in ecosystem [245]. Issues of interest especially are the non-target effects on beneficial soil microorganisms including nitrogen fixing microbes, mycorrhizal fungi, decomposers and soil invertebrates that collectively make soils functionally stable. NPs which are capable of generating reactive oxygen species or leaching metal ions will impose great selective pressure on vulnerable microbial populations, and may result in less functional redundancy and ecosystem resilience. One consequence of this process of selective filtering is its effect on the stress-tolerant phenotype of microbial networks, which in turn can impact nutrient cycling rate and feedbacks between microbes and plants [246]. On the contrary, nanomaterial induced plant functional properties such as stabilization of root exudation patterns, optimization of root system architecture, and improvement of immune signaling, could reduce the detrimental influence to some extent by providing a good root environment for beneficial microorganisms.

In this context, ecological impacts of nanomaterial exposure tend to be dose-dependent. Nanomaterials can be used to increase microbial activity, metabolism efficiency, and plant diversity at low doses but can lead to plant damage at high doses [247,248]. For example, 5 mg $kg^{-1}$ and 50 mg $kg^{-1}$ of Ag and Zn NPs induced microbial abundance and diversity in the rhizosphere of *Medicago truncatula* [249], but 10–100 mg $kg^{-1}$ of ZnO did not impact much on Cyanobacteria growth on *Lactuca sativa* [250]. These results underscore the reality that the impact of nanomaterials is not bad but it depends on the concentration level, exposure duration and the ecology. To this end, Fig. 5 provides a conceptual map of the potential environmental and health hazards associated with the utilization of nanomaterials, focusing on routes of exposure, susceptible ecological units, and the necessity to perform risk assessment at the system level, which is no longer predictable using acute toxicity indicators. This will involve an evaluation of the stability of microbial network, plasticity of plant traits as well as functional redundancy, all of which are likely to contribute significantly to predicting the future results of the ecosystem and the safe usage of nanomaterials in sustainable agriculture.

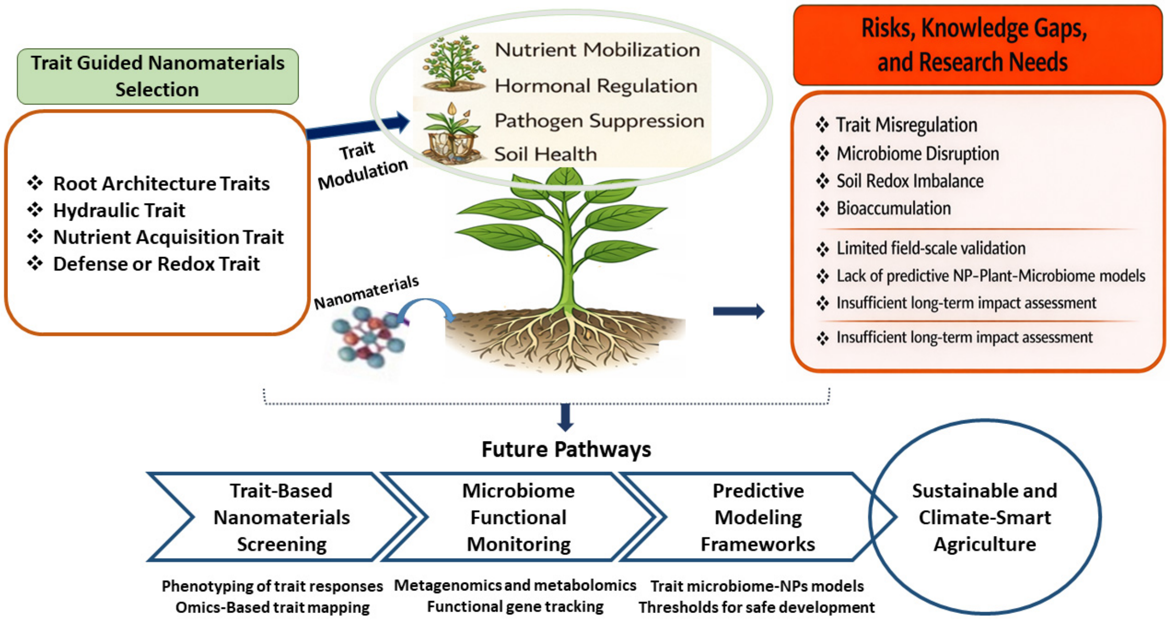

**Figure 5:** Conceptual framework of future research directions and knowledge gaps in trait-guided nanotechnology for sustainable agriculture. The figure highlights the balance between nanomaterial-enabled trait regulation and potential ecological risks, while identifying key research needs such as limited field validation, lack of predictive nanoparticle-plant-microbiome models, and insufficient understanding of long-term impacts. It outlines trait-based design, microbiome-informed strategies, and predictive frameworks as pathways toward climate-smart agriculture.

### *8.3 Sustainability, Regulatory, and Scalability Challenges*

Sustainable use of nanomaterials in agriculture requires the use of strategies to reduce environmental impact. To enhance the effectiveness of polymeric or lipid vesicles, NPs can be encapsulated to increase their stability and reduce environmental leakage [251]. The controlled-release formulations can deliver nutrients or pesticides precisely hence causing no environmental contamination. Furthermore, a mixture of nanomaterials and tools of precision agriculture, including nanosensors, will enable the accurate application of nanomaterials based on the immediate status of soil and plant health according to real-time monitoring. These methods, combined with adequate waste disposal mechanisms significantly lower the environmental risks associated with nanomaterials [252].

#### *8.3.1 Current Regulations on Nanomaterial Use*

Although the advances in the sphere of nanotechnology are tremendous, the regulatory frameworks surrounding the use of nanomaterials in agricultural practices remain underdeveloped in most regions of the world [37]. The existing policies are primarily focused on overall security of the chemicals and do not consider any special features of NPs. As an example, the European Union has policy on nanomaterials replacement, registration, evaluation, and restriction of chemicals, but these rules remain in progress [253]. The regulatory bodies in other nations like United States like Environmental Protection Agency (EPA) and Food and Drug Administration (FDA) are only starting to analyze the environmental and health impact of nanomaterials. Nevertheless, the absence of standard testing tests and decades-long safety data are now significant barriers to nanomaterial regulation [254].

#### *8.3.2 Recommendations for Safe Application*

There should be safety protocols and evaluations to utilize the nanomaterials in agriculture safely. The most important practices are running ecotoxicological experiments to determine the long run effect of nanomaterials on soil, water, and non-target species [190]. Introduction of an acceptable limit of concentration and labeling standard of nanomaterial-based agricultural products are imperative steps towards overcoming the risks involved. Cooperation between researchers, industry and governmental agencies is one of the key aspects of creating the best practices of production, use and disposal of nanomaterials [255]. Additionally, education campaigns can be a decisive element in the responsible nanotechnology use in the field of agriculture to make sure that the benefits of nanotechnology are derived without harming the natural environment and human life [256]. The transformational power of nanomaterials technology in agriculture can be positively exercised to ensure responsible use of the technology in agriculture in which the ethical issues of environment and health are considered through the process of creating sustainable practices and good regulations. These practices are necessary to achieve larger results at a high degree of ecological sustainability.

## 9 Future Perspectives and Research Gaps

### *9.1 Trait-Guided Nanomaterial Selection and Screening*

Since nanomaterials possess greater potential to influence plant functions by affecting functional traits other than being direct plant growth regulators, the next advancements in the use of nanotechnology in agriculture should not be limited to an outcome-based metric of improvement, like better yield or biomass. It should concentrate on the selection of nanomaterials on the basis of characteristics. High-throughput phenotyping could be an effective fast way of screening nanomaterials that promote root architectural plasticity, hydraulic regulation, nutrient acquisition efficiency, immune priming, and redox homeostasis [22]. Despite the observed promising results in laboratory and greenhouse conditions, there is still a large gap in extrapolating trait-level responses to a variety of field conditions. The characteristics of nanomaterials and plants can be influenced by soil type, variation in climate conditions, type of crops, and practices used in their management. In this manner, trait-based field-level screening methods are imperative to allow reproducibility and applicability to agriculture [257].

### *9.2 Microbiome Functional Monitoring and Trait-Mediated Engineering*

Microbiome engineering using nanomaterials is a promising approach for sustainable agriculture. Instead of directly modifying microbial populations, nanomaterials function mainly as plant-mediated filters by modulating root exudation patterns, immune responses, and nutrient uptake. This indirect mechanism can selectively promote beneficial microbial groups such as nitrogen-fixing bacteria, phosphate-solubilizing microbes, biocontrol agents, and short-chain fatty acid-producing bacteria, thus improving nutrient turnover, disease control, and stress resilience [258]. Nevertheless, microbiome interactions are extremely dependent on context. Inconsistencies between nanomaterial characteristics, plant species, and native microbial assemblages can lead to non-responsive or harmful effects [259]. Future studies should thus progress from diversity metrics to functional microbiome analysis, such as metagenomics, metabolomics, and functional gene analysis, to more accurately forecast macroscopic effects.

### *9.3 Predictive Modeling, Dose Thresholds, and Risk Pathways*

One of the most important research gaps is the lack of accessible predictive models that connect nanomaterial properties with the regulation of plant traits, microbiome, and environmental risk. This is because nanomaterial interactions are usually dose-dependent and nonlinear. Long-term research on nanomaterial persistence, cumulative effects, interactions with agrochemicals, and multi-cropping cycle effects is still limited [260,261]. Future research should target trait-based micro homeostasis models and microbiome risk assessments to establish safe operational ranges. This is crucial for preventing unintended consequences, such as trait dysregulation, microbiome disruption, soil redox, and bioaccumulation.

### *9.4 Toward Sustainable and Climate-Smart Nanotechnology Applications*

The combination of nanomaterials and real-time phenomic observation has a synergistic potential for agricultural applications. By acting on the indirect pathways, this combination can selectively increase beneficial microbial populations, such as nitrogen-fixing bacteria, phosphate-solubilizing bacteria, biocontrol agents, and short-chain fatty acid producers [257]. Future directions are oriented to the interplay between nexus of nanomaterial-driven trait management and environmental risk as presented in Fig. 5. It illustrates the balance between potential uses of nanomaterial-enabled trait regulation and possible environmental and ecological hazards, with clearly defined research imperatives and knowledge gaps. The intersection of trait screening, microbiome functional observation, model development frameworks, and enabling regulatory frameworks offers a model of safe, scalable, and climate-resilient agricultural nanotechnology. These approaches must be coordinated in order to promote food security without compromising the ecosystems and soil health.

## 10 Conclusions

This review synthesizes emerging evidence that agricultural nanomaterials enhance crop stress resilience primarily by reprogramming coordinated networks of plant functional traits and, through them, reshaping plant-associated microbiomes. Rather than acting solely as nutrient sources or antimicrobial agents, nanomaterials influence hydraulic regulation, nutrient acquisition, photosynthetic capacity, redox balance, and defense signaling traits that collectively determine plant performance under environmental stress. Because these traits govern the ecological niches that structure rhizosphere and endophytic communities, nanomaterial-induced trait shifts propagate to microbiome assembly and function, generating feedback loops that can stabilize nutrient cycling, stress buffering, and disease suppression. This trait-centric perspective reframes nanotechnology in agriculture from an input-driven approach to a systems-regulatory strategy. It emphasizes that the success of nanomaterials depends not only on their composition but on how their physicochemical properties align with plant functional organization and ecological context. While promising laboratory and greenhouse findings demonstrate the potential of nanomaterials to improve stress tolerance, significant knowledge gaps remain regarding long-term soil persistence, non-target microbiome effects, trophic transfer, and field-scale performance under variable environments. Future research should prioritize trait-based screening platforms, functional microbiome monitoring, and predictive modeling of nano–plant–microbiome interactions across environmental gradients. Integrating nanotechnology with plant breeding, phenomics, and soil ecological management will be essential for translating laboratory insights into climate-resilient cropping systems. By adopting a trait-guided and ecologically informed framework, agricultural nanotechnology can move toward safer, more efficient, and more sustainable contributions to global food security.

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