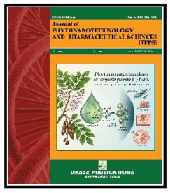
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Nanoparticle-mediated modulation of capsaicinoids and secondary metabolism in Chilli (*Capsicum annum* L.): Molecular mechanisms, phytochemical responses and future perspectives

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Abstract

Chilli is an economically important horticultural crop valued worldwide for its pungency, colour, nutritional composition and diverse health-promoting phytochemicals. Capsaicinoids, particularly capsaicin and dihydrocapsaicin, represent the characteristic secondary metabolites of chilli, while carotenoids, phenolics, flavonoids, ascorbic acid, tocopherols, glutathione and volatile compounds collectively determine its nutritional, functional and sensory quality. In this context, phytonanotechnology has emerged as a promising approach for manipulating plant physiological and metabolic processes. This review comprehensively examines the potential of nanoparticle-mediated modulation of capsaicinoids and secondary metabolism in *C. annuum*, with emphasis on nanoparticle characteristics, application routes, uptake and translocation, molecular signaling and metabolic regulation. Individual nanoparticles, including zinc oxide, selenium, iron, copper, silver, titanium dioxide and manganese nanoparticles, are discussed in relation to their potential effects on capsaicinoids and major phytochemicals. Particular attention is given to ROS-mediated signaling, antioxidant defense, calcium signaling, phytohormonal regulation, MAPK pathways and transcriptional control of phenylpropanoid and branched-chain fatty-acid pathways associated with capsaicinoid biosynthesis. The review further considers nanoparticle interactions with salinity, drought, heat, cold, heavy-metal stress and nutrient deficiency, together with their implications for fruit size, yield, colour, phytochemical composition, nutritional quality and postharvest performance.

Emerging omics technologies provide new opportunities to understand these complex interactions. Transcriptomics, proteomics, metabolomics, ionomics and epigenomics can collectively reveal how nanoparticle exposure is translated into molecular and metabolic responses. Nevertheless, direct evidence for consistent enhancement of capsaicin and dihydrocapsaicin remains comparatively limited compared with evidence for phenolics, flavonoids, antioxidant metabolism and stress tolerance. Therefore, future research should integrate nanoparticle characterization, targeted capsaicinoid profiling, molecular biology and multi-omics approaches with genotype-specific and field-scale experimentation. Particular emphasis is required on dose optimization, nanoparticle transformation, food safety, environmental fate and long-term sustainability. Overall, nanoparticle-mediated nano-elicitation represents a promising precision approach for improving phytochemical quality and stress resilience in chilli, provided that efficacy, safety and environmental sustainability are addressed simultaneously.

1. Introduction

Chilli (*Capsicum annuum* L.) is one of the most economically important vegetable and spice crops cultivated throughout tropical, subtropical and temperate regions. It belongs to the family Solanaceae and represents the most widely cultivated species of the genus *Capsicum*, comprising both pungent and non-pungent fruit types. Chilli is consumed as a fresh vegetable, dried spice, powder, oleoresin and processed food ingredient, while its bioactive constituents have attracted considerable attention in pharmaceutical, nutraceutical and food industries. The crop is particularly important because its fruits combine nutritional attributes with distinctive colour, flavour, aroma and pungency. *C. annuum* is also characterized by considerable genetic and biochemical diversity, resulting in substantial variation in fruit morphology, pungency, carotenoid accumulation and other quality attributes (Tanaka, 2025). Recent literature has emphasized the nutritional and functional importance of chilli fruits because of their abundance of capsaicinoids, carotenoids, phenolics, flavonoids, vitamins and other bioactive constituents (Ali *et al*., 2025). The increasing demand for functional foods and naturally derived bioactive compounds has consequently shifted attention from merely increasing chilli yield towards improving fruit nutritional quality

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and specialized metabolite composition. In this context, strategies capable of manipulating plant metabolism while maintaining productivity are becoming increasingly important. Recent advances in *Capsicum* genomics have also provided new insights into the genetic basis of fruit quality and capsaicinoid accumulation, creating opportunities to integrate conventional crop improvement with molecular and nanotechnological approaches (Qin *et al*., 2024). The importance of chilli as a functional crop is largely associated with its rich and diverse phytochemical composition. Chilli fruits contain several classes of biologically active compounds, including capsaicinoids, carotenoids, phenolic acids, flavonoids, ascorbic acid, tocopherols and volatile constituents. These metabolites contribute to fruit colour, pungency, flavour, antioxidant capacity, nutritional quality and potential health-promoting properties. Capsaicinoids are primarily responsible for pungency, whereas carotenoids such as capsanthin, capsorubin, β-carotene and related pigments contribute to the characteristic colour of mature fruits. Phenolic compounds and flavonoids participate in antioxidant and defense responses, while ascorbic acid and tocopherols contribute to the overall antioxidant potential of the fruit. Recent comprehensive evaluation of chilli has highlighted its diverse nutritional and phytochemical profile and its potential for development into value-added functional foods (Ali *et al*., 2025). In addition, capsaicin and structurally related compounds have received increasing attention because of their potential antioxidant, anti-inflammatory, metabolic and pharmacological applications (Maharjan *et al*., 2024; Jayan *et al*., 2025). The accumulation of these compounds is not static but is influenced by genotype, developmental stage, environmental conditions, cultivation practices and stress exposure. Therefore, phytochemical composition represents the integrated outcome of genetic regulation and environmental interaction. Understanding the mechanisms controlling this metabolic plasticity is essential for developing approaches that can enhance desirable phytochemicals without adversely affecting plant growth and productivity.

Capsaicinoids are among the most characteristic specialized metabolites of chilli and are responsible for the pungency of hot *Capsicum* fruits. The major capsaicinoids are capsaicin and dihydrocapsaicin, which together account for the majority of the total capsaicinoid content, while nordihydrocapsaicin, homocapsaicin and homodihydrocapsaicin occur in smaller quantities. Capsaicinoid biosynthesis is highly specialized and occurs predominantly in the placental septum of developing fruits. Recent understanding indicates that capsaicinoid formation involves the convergence of two major metabolic routes: the phenylpropanoid pathway, which generates vanillylamine, and the branched-chain fatty-acid pathway, which supplies the acyl moiety. These two components are subsequently condensed to form capsaicinoids (Tanaka, 2025). The pathway is temporally and spatially regulated and is influenced by developmental stage and genotype. Genetic and biochemical investigations have identified several important enzymes and genes involved in capsaicinoid formation, providing opportunities for targeted metabolic manipulation (Tanaka, 2025; Wen *et al*., 2025). Capsaicin is also of considerable biological importance because it interacts with the transient receptor potential vanilloid 1 (TRPV1) receptor and has been associated with antioxidant, anti-inflammatory, analgesic, metabolic and other biological activities (Maharjan *et al*., 2024). Recent reviews have further highlighted the expanding food, pharmaceutical and industrial applications of capsaicin and related compounds (Wang *et al*., 2025; Jayan *et al*., 2025). Consequently, improving or precisely regulating capsaicinoid accumulation has significance not only for pungency but also for the nutritional, functional and economic value of chilli fruits.

Plant secondary metabolism, increasingly referred to as specialized metabolism, comprises interconnected biochemical pathways that produce compounds involved in plant defense, environmental adaptation, signalling, pigmentation, reproduction and interactions with other organisms. In chilli, important specialized metabolic pathways include phenylpropanoid, flavonoid, carotenoid, terpenoid and capsaicinoid biosynthesis. These pathways are closely connected with primary metabolism because their precursors originate from amino acids, carbohydrates, fatty acids and other primary metabolites. The phenylpropanoid pathway, for example, provides the aromatic precursor required for capsaicinoid biosynthesis, whereas branched-chain amino-acid metabolism contributes to the formation of the fatty-acid moiety. Recent advances in capsaicinoid research have demonstrated that the pathway is regulated by multiple structural genes, transcriptional regulators and developmental signals rather than by a single metabolic reaction (Tanaka, 2025; Wen *et al*., 2025). Similarly, recent multi-omics research has increased understanding of the complex regulatory networks governing capsaicinoid accumulation and identified potential targets for metabolic engineering (Krishna *et al*., 2026). Secondary metabolites therefore represent dynamic biochemical traits that can respond to developmental and environmental signals. Their manipulation through controlled agricultural interventions offers an opportunity to improve fruit quality, antioxidant capacity and stress resilience simultaneously. However, metabolic enhancement needs to be balanced against possible trade-offs between secondary-metabolite accumulation, growth and yield.

Phytonanotechnology represents an emerging interdisciplinary field that integrates nanoscience with plant biology, crop production and sustainable agriculture. Nanoparticles possess distinctive physicochemical characteristics, including small particle size, high surface-area-to-volume ratio, tunable surface chemistry and enhanced reactivity, which provide opportunities for their application in agriculture. Nanomaterials have been investigated as nanofertilizers, nanopesticides, nanocarriers, nanostimulants and nanoelicitors. Their potential applications include improving nutrient-use efficiency, facilitating controlled delivery of agrochemicals, enhancing plant growth and increasing tolerance to environmental stresses. Recent research has demonstrated that nanoparticle responses in *Capsicum* are highly dependent on particle composition, size, morphology, concentration, application route and plant developmental stage (Díaz-Parra *et al*., 2025). Similarly, broader reviews have emphasized the potential of phytonanotechnology for sustainable agriculture while identifying challenges related to nanoparticle behavior, plant uptake, environmental fate and toxicity (Peng and Qin, 2024). In chilli, metal and metal oxide nanoparticles have been investigated for their effects on growth, nutrient acquisition, antioxidant defense, stress tolerance and fruit quality. However, the application of nanotechnology should not be viewed simply as a method for supplying nutrients. Instead, nanoparticles may act as biologically active stimuli capable of modifying signaling networks and metabolic pathways. This perspective provides the foundation for exploring nanoparticles as potential regulators of specialized metabolism in *C. annuum*.

Despite rapid progress in agricultural nanotechnology, the specific relationship between nanoparticle exposure and capsaicinoid-centered secondary metabolism in chilli remains insufficiently explored and integrated. Recent research has substantially expanded knowledge of the effects of nanoparticles on *Capsicum* growth, development, nutrient responses and stress tolerance (Díaz-Parra *et al*., 2025), while independent advances in capsaicinoid biology have clarified the biochemical and genetic basis of pungency (Tanaka, 2025; Wen *et al*., 2025). At the same time, nanoparticle-assisted elicitation has emerged as a promising approach for manipulating plant specialized metabolism (Vyavahare *et al*., 2025). These developments provide a strong rationale for examining the interface between phytonanotechnology and chilli phytochemistry. Accordingly, this review focuses on nanoparticle-mediated modulation of capsaicinoids and other secondary metabolites in *C. annuum*, with particular emphasis on nanoparticle uptake, transport and bioaccumulation; ROS, calcium and phytohormone signaling; phenylpropanoid and branched-chain fatty-acid pathways; capsaicinoid biosynthetic genes and enzymes; and changes in phenolics, flavonoids, carotenoids and antioxidant compounds. The review further examines nano-elicitation, nanoparticle-mediated stress adaptation, omics approaches, nano–plant–microbiome interactions, phytotoxicity and food-safety considerations. Particular attention is given to the factors responsible for variation in plant responses, including nanoparticle type, size, concentration, surface properties, application route, genotype and developmental stage. Such an integrated perspective may facilitate the development of precision phytonanotechnology approaches for producing chilli fruits with enhanced functional quality while maintaining crop productivity and ensuring environmental and consumer safety.

2. Nanoparticles used in chilli production

Nanoparticles (NPs) represent an increasingly important component of modern agricultural nanotechnology because their nanoscale dimensions, high surface-area-to-volume ratio, surface reactivity and tunable physicochemical properties allow them to interact with plants in ways that differ from conventional bulk materials. Agricultural nanoparticles have been investigated as nanofertilizers, nanoelicitors, nanopesticides, nanocarriers and biostimulants, with applications ranging from seed treatment and nutrient delivery to stress mitigation and crop protection. Nanoparticles can enter plants through seeds, roots and leaves and subsequently move through apoplastic and symplastic pathways; however, their uptake and translocation depend strongly on nanoparticle type, size, surface charge and concentration (Zhang and Su, 2024). In chilli, these characteristics are particularly relevant because nanoparticle exposure may influence not only growth and nutrient acquisition but also antioxidant metabolism, stress responses and the accumulation of specialized metabolites such as capsaicinoids, phenolics and carotenoids.

2.1 Metal nanoparticles

Metal nanoparticles include elemental forms of silver (Ag), gold (Au), copper (Cu), iron (Fe), zinc (Zn) and selenium (Se), among others. Their agricultural significance arises from their distinctive electronic, catalytic and redox properties, as well as their ability to release metal ions under particular environmental conditions. Essential micronutrient-based nanoparticles such as Zn, Fe, Cu and Se may simultaneously function as nutrient sources and physiological stimulants when applied at appropriate concentrations. Their nanoscale structure can alter nutrient availability and interaction with plant tissues compared with conventional salts. Zinc is particularly important in plant metabolism because it participates in numerous enzymatic reactions, protein synthesis, membrane stabilization and regulation of gene expression. Similarly, iron is essential for electron transport, chlorophyll formation and numerous redox reactions, while copper participates in photosynthetic and antioxidant enzymes. Selenium, although, not considered an essential nutrient for higher plants, can at appropriate concentrations stimulate antioxidant defenses and improve tolerance to environmental stresses. Nanoparticle-based delivery may therefore provide opportunities for improving nutrient-use efficiency and plant resilience. Recent reviews of nanofertilizers emphasize their potential to improve nutrient availability and delivery efficiency while reducing losses associated with conventional fertilizer systems (Ayenew *et al*., 2025).

2.2 Metal oxide nanoparticles

Metal oxide nanoparticles include zinc oxide (ZnO), titanium dioxide (TiO_2), iron oxides (Fe_3O_3 and Fe_3O_4), copper oxide (CuO), magnesium oxide (MgO) and manganese oxide nanoparticles. These materials have received considerable attention because of their chemical stability, surface reactivity, catalytic properties and, in several cases, their ability to provide essential mineral elements. ZnO nanoparticles are particularly relevant to chilli production because Zn is involved in several physiological and biochemical processes associated with growth and stress tolerance. Iron oxide nanoparticles may influence Fe availability, chlorophyll formation and electron transport, while TiO_2 nanoparticles have been investigated for their potential effects on photosynthetic performance and antioxidant metabolism. CuO nanoparticles may provide both micronutrient and antimicrobial functions, although, excessive Cu exposure can induce oxidative stress.

The biological performance of metal oxide nanoparticles is strongly dependent on particle size, morphology, surface properties, dissolution behavior and application concentration. Consequently, identical nominal concentrations of two different metal oxide nanoparticles may produce substantially different physiological outcomes. Recent nanofertilizer research emphasizes that the nano-formulation, rather than merely the elemental nutrient concentration, must be considered when interpreting plant responses (Ayenew *et al*., 2025). The same principle is particularly important for chilli, where changes in nutrient and redox status could subsequently influence phenylpropanoid metabolism, antioxidant capacity and capsaicinoid biosynthesis.

2.3 Carbon-based nanomaterials

Carbon-based nanomaterials comprise carbon nanotubes, graphene, graphene oxide, reduced graphene oxide, carbon dots and related nanostructures. Their distinctive optical, electrical, adsorption and surface properties have expanded their potential applications in plant science. Among these materials, carbon dots (CDs) have recently attracted considerable interest because of their relatively small dimensions, fluorescence, surface functionality and potential biological compatibility. Carbon dots have been investigated for their effects on seed germination, plant growth, photosynthesis, nutritional quality and resistance to drought, salinity and heavy-metal stress. A recent comprehensive review reported that carbon dots can influence photosynthetic efficiency, mineral accumulation, plant nutritional

quality and stress tolerance, although, responses depend on plant species and treatment conditions (Zhang *et al*., 2025). Carbon-based nanomaterials may therefore have potential applications in chilli as growth-promoting materials, stress-management agents and delivery platforms.

2.4 Polymeric and biopolymeric nanoparticles

Polymeric nanoparticles are composed of synthetic or naturally derived polymers and are increasingly being investigated as controlled-release and targeted-delivery systems. Biopolymeric nanoparticles based on chitosan, alginate, starch, cellulose and related biomaterials are particularly attractive because of their biodegradability, biocompatibility and functional versatility. Among these materials, chitosan nanoparticles have received substantial attention in agriculture. Chitosan possesses antimicrobial, antioxidant and elicitor properties, while its nano-form can provide enhanced surface area and facilitate the encapsulation and controlled release of pesticides, fertilizers, plant growth promoters and biological agents. Saberi Riseh *et al*. (2024) reported that chitosan nanoparticles can contribute to crop growth, nutrient absorption, stress protection and pest management, while their physicochemical properties make them suitable for smart agricultural delivery systems. Chitosan-based nanoformulations are therefore particularly interesting for chilli because they could potentially combine nutrient or agrochemical delivery with metabolic elicitation. Karamchandani *et al*. (2024) further highlighted the potential of chitosan and chitosan-based nanoparticles in sustainable agricultural practices, particularly for controlled delivery and reduction of conventional agrochemical dependence. Nano-chitosan priming has also been investigated as a sustainable strategy for improving plant responses to abiotic stress (Sen and Das, 2024). Such properties could be exploited for future chilli studies targeting antioxidant and capsaicinoid metabolism.

2.5 Green-synthesized nanoparticles

Green synthesis involves the biological production of nanoparticles using plant extracts, microorganisms, algae or other biological materials as reducing, stabilizing or capping agents. Plant extracts are particularly attractive because their phenolics, flavonoids, proteins, terpenoids, sugars and other biomolecules can participate in nanoparticle formation and stabilization. This approach can reduce reliance on some conventional chemical reducing agents and may generate nanoparticles with biologically active surface-associated compounds. Green-synthesized nanoparticles have received increasing attention as potential tools for sustainable agriculture. Osman *et al*. (2024) reviewed green nanoparticle synthesis for agricultural, environmental and food applications, highlighting the diversity of biological materials available for nanoparticle production. Ben Zineb *et al*. (2025) further emphasized recent advances in green-synthesized nanoparticles for managing plant biotic and abiotic stresses and highlighted the need to overcome challenges associated with large-scale agricultural implementation.

3. Physicochemical properties of nanoparticles governing plant responses

The biological behavior of nanoparticles is fundamentally determined by their physicochemical properties. Nanoparticles with identical elemental composition can produce different responses when they differ in size, shape, surface charge, surface coating, aggregation state, dissolution behavior or concentration. Zhang and Su (2024) emphasized that nanoparticle type, size, charge and concentration influence uptake, translocation and effects on crop plants. Consequently, comprehensive nanoparticle characterization is essential for interpreting biological experiments and comparing results between studies.

3.1 Particle size

Particle size is one of the most important determinants of nanoparticle–plant interactions. Decreasing particle size generally increases specific surface area and may alter surface reactivity, dissolution and interactions with plant tissues. Particle size can influence attachment to seed surfaces, penetration into roots and leaves, cellular internalization, translocation and accumulation. Zhang and Su (2024) emphasized that nanoparticle size is an important factor controlling uptake and transport through plants and that nanoparticles can enter crops through seeds, roots and leaves. Smaller nanoparticles may potentially have greater opportunities to interact with cell-wall pores and membrane-associated structures, although, uptake is not determined by size alone. Surface charge, aggregation, coating and plant species also influence biological behavior.

3.2 Shape and morphology

Nanoparticle shape and morphology influence surface area, surface energy, aggregation behavior, dissolution and interaction with biological barriers. Nanoparticles may occur as spherical, rod-shaped, triangular, tubular, plate-like or irregular structures. Consequently, two nanoparticles with similar chemical composition and average diameter may still exhibit different biological activities. Morphological characteristics also influence the stability and mobility of nanoparticles in nutrient solutions and soil. Therefore, microscopic characterization using techniques such as transmission electron microscopy (TEM) or scanning electron microscopy (SEM) is important for determining particle morphology.

3.3 Surface charge

Surface charge is a major determinant of nanoparticle interaction with plant surfaces. Plant cell walls contain charged polysaccharides, proteins and other macromolecules, while root mucilage and soil colloids can further modify nanoparticle interactions. The electrostatic relationship between nanoparticle surfaces and plant tissues can therefore influence adsorption, penetration and transport. Zeta potential is commonly used to characterize nanoparticle surface charge and colloidal stability. Zhang and Su (2024) identified surface charge as one of the important factors affecting nanoparticle uptake and translocation in crops. Positively and negatively charged particles can behave differently in suspension and may exhibit different affinities for biological surfaces.

3.4 Surface coating

Surface coatings can modify nanoparticle stability, charge, dissolution, aggregation and interaction with biological tissues. Coatings may consist of polymers, proteins, carbohydrates, organic molecules or biological extracts. They can be applied to improve dispersion, reduce aggregation, facilitate controlled release or introduce specific biological functions. Biopolymeric coatings are particularly interesting for agricultural applications because they can combine delivery functions with biological activity. Chitosan, for example, can provide both nanoparticle stabilization and plant defense-eliciting properties (Saberi Riseh *et al*., 2024). Surface functionalization may therefore

influence not only nanoparticle movement but also the

3.5 Chemical composition

Chemical composition determines the intrinsic reactivity, dissolution characteristics, redox properties and biological functions of nanoparticles. ZnO_2 Fe_3O_4, CuO_2 Ag and Se nanoparticles, for example, differ considerably in their interaction with plants even when applied at equivalent concentrations. The biological response can result from direct interaction with the intact nanoparticle, release of ions, or a combination of both processes. Consequently, the chemical composition of the nanoparticle must be considered alongside its dissolution behavior. This is especially important for nutrient-containing nanoparticles because the response may partly reflect conventional nutrient physiology. In chilli, ZnO nanoparticles could influence Zn-dependent enzymes and metabolism, while Fe-based nanoparticles could influence iron homeostasis and redox reactions. Therefore, appropriate ionic controls and characterization of dissolved metal concentrations are important for identifying nanoparticle-specific effects.

3.6 Solubility and ion release

Solubility determines the extent to which nanoparticles release dissolved ions into the surrounding environment. Metal and metal oxide nanoparticles may undergo dissolution depending on pH, ionic strength, temperature, organic matter and surface properties. Released ions can subsequently become available for plant uptake or participate in biochemical reactions. This property is especially important for ZnO_2 CuO_2 Fe-based and other metal-containing nanoparticles. At appropriate concentrations, released ions may contribute to plant nutrition; however, excessive ion release may increase toxicity. Consequently, nanoparticle dissolution should be evaluated alongside total nanoparticle concentration.

Recent advances in agricultural nanotechnology increasingly emphasize the importance of considering nanoparticles within the complete soil-plant system rather than evaluating them only under controlled hydroponic conditions. Green-synthesized nanomaterials may offer additional opportunities for reducing the environmental burden of agricultural inputs, although, their biological variability and long-term environmental effects require careful assessment (Ben Zineb *et al*., 2025). The use of green nanofertilizers is also expanding, with recent studies emphasizing targeted nutrient delivery and potential improvements in nutrient-use efficiency and abiotic-stress management (2025). However, field-scale validation, standardized characterization and long-term assessment remain essential before widespread agricultural adoption.

4. Routes of nanoparticle application in chilli

Nanoparticle application route is a major determinant of their interaction with chilli plants because it controls the initial site of exposure, availability, uptake, translocation and subsequent physiological response. Nanoparticles can be introduced through seed priming, foliar spraying, soil application, hydroponic systems, *in vitro* cultures and engineered nano-carrier systems. The biological outcome of a nanoparticle treatment is therefore not determined only by its chemical composition but also by the method, timing and frequency of application. Recent reviews indicate that nanoparticles can enter crop plants through seeds, roots and leaves and subsequently move through apoplastic and symplastic pathways, with uptake and translocation being strongly influenced by particle size, surface charge, concentration and plant species (Zhang and Su, 2024). In addition, the application route can determine whether nanoparticles primarily influence root nutrition, foliar metabolism, systemic signaling or fruit phytochemical accumulation. This is particularly important for chilli because the desired response may range from improved seedling establishment and stress tolerance to enhancement of capsaicinoids and other specialized metabolites.

4.1 Seed priming and nano-priming

Seed priming involves controlled hydration of seeds before sowing, allowing several metabolic processes associated with germination to begin without permitting radicle emergence. Incorporating nanoparticles into this treatment is generally referred to as nano-priming. Nano-priming can provide direct exposure of the embryo and seed coat to nanoparticles and may influence water uptake, antioxidant metabolism, nutrient availability, germination, seedling vigor and subsequent stress tolerance. Recent reviews indicate that nanoparticles can function as seed-associated delivery and signaling agents, although, their effectiveness is strongly dependent on particle properties and dose (Zhang and Su, 2024). Nanopriming may be particularly relevant to chilli because early seedling vigor strongly influences subsequent plant establishment and productivity. Nanoparticles containing Fe, Zn, Cu or other elements can potentially improve micronutrient availability during early development. However, excessive nanoparticle exposure can interfere with germination-associated metabolism and generate oxidative stress. Thus, optimization of particle concentration, exposure duration and seed hydration conditions is essential. The use of nano-priming as a means of inducing later-stage metabolic responses is also conceptually important because early nanoparticle exposure may establish a form of metabolic or stress priming that persists after germination.

4.2 Foliar application

Foliar application provides direct exposure of leaves to nanoparticle suspensions and is increasingly used for delivering micronutrients, elicitors and other agricultural inputs. After deposition on the leaf surface, nanoparticles interact with the cuticle, epidermis, stomata and leaf surface structures before potentially entering internal tissues. The effectiveness of foliar application depends on particle size, surface chemistry, charge, formulation stability, humidity and leaf morphology. Direct evidence in *C. annuum* demonstrates the importance of foliar application characteristics. Rodrigues *et al*. (2024) investigated foliar-applied ZnO nanoparticles with and without a zinc-phosphate shell and demonstrated substantial differences in uptake and systemic translocation. The coated ZnO nanoparticles showed higher leaf uptake and greater movement to other plant organs, including fruit, compared with uncoated ZnO nanoparticles. This study provides particularly strong evidence that surface engineering can modify nanoparticle behavior in chilli/pepper plants.

4.3 Soil application

Soil application introduces nanoparticles directly into the rhizosphere, where they encounter soil particles, organic matter, root exudates and microorganisms before becoming available to plant roots. This route is particularly relevant for nano-fertilizers containing Zn, Fe, Cu, Mn or other plant nutrients. Nanoparticles can potentially provide a more controlled nutrient source compared with conventional fertilizers, although, their behavior in soil is highly dependent on

pH, clay content, organic matter, ionic strength and microbial activity. Recent reviews emphasize that nanoparticles introduced into soil may undergo aggregation, adsorption, dissolution and transformation before plant uptake (González-García *et al*., 2024). Consequently, the nominal dose applied to soil may not represent the actual bioavailable concentration encountered by chilli roots. Soil application should therefore be evaluated using both nanoparticle characterization and measurements of nanoparticle-derived elements in the rhizosphere and plant tissues.

4.4 Hydroponic application

Hydroponic systems provide a controlled environment for investigating nanoparticle-plant interactions because nanoparticles can be supplied at accurately defined concentrations without the complex adsorption processes associated with soil. Hydroponics is therefore particularly useful for studying root uptake, transport, dissolution, oxidative responses and secondary-metabolite production. Jadoon *et al*. (2024) highlighted the potential of combining hydroponics with nano-elicitation to improve plant productivity and secondary metabolism. Hydroponic systems allow researchers to manipulate nanoparticle concentration, exposure duration and nutrient composition independently and can therefore help establish dose–response relationships. However, results obtained under hydroponic conditions should be interpreted cautiously because the absence of soil colloids, organic matter and complex microbial communities can substantially alter nanoparticle behavior.

4.5 *In vitro* application

In vitro application provides an additional experimental platform for investigating nanoparticle effects under highly controlled conditions. Cell cultures, callus cultures, hairy roots, isolated tissues and organ cultures can be exposed to defined nanoparticle concentrations to examine uptake, ROS production, antioxidant responses, gene expression and specialized-metabolite accumulation. Nano-elicitation is particularly relevant to *in vitro* systems because nanoparticles can function as abiotic elicitors of secondary metabolism. Recent research indicates that nanoparticles can stimulate secondary-metabolite biosynthesis through ROS-mediated signaling and changes in stress-responsive gene expression (Vyavahare *et al*., 2025). In chilli, such systems could potentially be used to investigate capsaicinoid-associated pathways before moving to whole-plant experiments. However, because capsaicinoid accumulation is closely associated with developing fruit and placental tissues, whole-plant validation remains essential.

4.6 Nano-carrier-mediated delivery

Nano-carrier-mediated delivery involves encapsulating or associating active compounds with nanoparticles to improve stability, solubility, transport and controlled release. Potential cargoes include micronutrients, pesticides, plant-growth regulators, elicitors, nucleic acids and biological compounds. Polymeric, lipid-based and biopolymeric nanoparticles are among the systems being explored for targeted agricultural delivery. The controlled-release characteristics of nano-carriers can potentially reduce repeated applications and improve the efficiency of active compounds. This approach is particularly attractive for chilli because specific developmental stages may be targeted for nutrient or metabolic interventions. For example, nano-carriers could theoretically be designed to deliver micronutrients or elicitors during flowering and fruit development, when capsaicinoid biosynthesis becomes particularly active.

5. Uptake, transport and bioaccumulation of nanoparticles

Nanoparticle uptake and transport represent critical processes linking external application with physiological and metabolic responses. Once nanoparticles contact seeds, roots or leaves, they may interact with cell walls, membranes and extracellular matrices before entering plant tissues. Depending on their properties, they may subsequently undergo dissolution, aggregation, transformation or interaction with biomolecules. Recent reviews describe seed, root and foliar uptake as major entry routes and identify apoplastic and symplastic transport as important pathways for nanoparticle movement within plants (Zhang and Su, 2024).

Roots constitute an important entry route for soil- and hydroponically applied nanoparticles. Initial interactions occur with root mucilage, epidermal cells and the cell-wall matrix. Nanoparticles may subsequently move through apoplastic spaces, interact with cell membranes or undergo dissolution followed by ionic uptake. The efficiency of root uptake depends on particle size, surface charge, concentration, aggregation and dissolution characteristics. Recent reviews emphasize that nanoparticles may produce both stimulatory and inhibitory effects depending on these properties (González-García *et al*., 2024). In chilli, root uptake of nutrient-containing nanoparticles could modify micronutrient status and indirectly influence photosynthesis, antioxidant defense and secondary metabolism.

Foliar nanoparticle penetration occurs after particles are deposited on the leaf surface. Possible entry pathways include stomata, cuticular discontinuities, trichomes and other microscopic structures. The extent of penetration depends on particle size, charge, surface chemistry, formulation and environmental conditions. The study by Rodrigues *et al*. (2024) provides direct evidence that nanoparticle surface chemistry can substantially alter foliar uptake in *Capsicum annuum*. Zinc phosphate-coated ZnO nanoparticles showed greater leaf uptake and systemic movement than uncoated ZnO nanoparticles, demonstrating that surface modification can influence nanoparticle behavior even when the elemental composition is similar.

After entering plant tissues, nanoparticles may move through apoplastic spaces or *via* the symplastic continuum. Apoplastic movement occurs through cell walls and extracellular spaces, whereas symplastic transport involves movement through interconnected cytoplasm *via* plasmodesmata. Zhang and Su (2024) identified both apoplastic and symplastic pathways as important mechanisms involved in nanoparticle transport in crop plants. The relative importance of these pathways depends on particle size, surface chemistry and interactions with cell-wall components. Understanding these pathways is particularly important for determining whether nanoparticles can reach metabolically active tissues such as developing chilli fruits. Nanoparticles can influence phytochemical metabolism through changes in nutrient status, ROS signaling, phytohormones, photosynthesis and defense-related gene expression. Nano-elicitation studies indicate that nanoparticles can stimulate secondary-metabolite biosynthesis through controlled stress signaling and transcriptional regulation (Vyavahare *et al*., 2025). In chilli, these interactions may influence capsaicinoids, phenolics, flavonoids and carotenoids. However, a direct mechanistic link between nanoparticle accumulation and capsaicinoid biosynthetic gene regulation remains insufficiently established and represents an important research gap.

6. Nanoparticle-induced molecular signaling in chilli

Nanoparticles can influence plant metabolism by activating interconnected signaling networks involving ROS, calcium, phytohormones, mitogen-activated protein kinases (MAPKs), transcription factors and defense pathways. These signaling mechanisms provide a mechanistic bridge between nanoparticle perception and changes in secondary metabolism. ROS including superoxide radicals, hydrogen peroxide and hydroxyl radicals are central signaling molecules in nanoparticle-plant interactions. Moderate ROS production can activate defense responses and secondary metabolism, whereas excessive ROS accumulation causes oxidative damage.

Nanoparticles can alter ROS production through interactions with chloroplasts, mitochondria, cell membranes and antioxidant enzymes. In chilli, nanoparticle-mediated changes in ROS could potentially stimulate phenylpropanoid and capsaicinoid metabolism through stress-responsive signaling. Thus, ROS should be regarded as both potential mediators of nano-elicitation and indicators of nanoparticle toxicity. Plants possess enzymatic antioxidants such as superoxide dismutase (SOD), catalase (CAT), peroxidase (POD), ascorbate peroxidase (APX) and glutathione reductase (GR), together with non-enzymatic antioxidants including ascorbate, glutathione, phenolics, flavonoids and carotenoids. The *Capsicum* nanoparticle study demonstrated enhanced antioxidant-related responses following Ag, Cu and Cu-Ag nanoparticle treatments, together with increased phenolics, flavonoids, carotenoids and capsaicinoids. These observations suggest that nanoparticle-induced metabolic responses may involve coordinated regulation of enzymatic and non-enzymatic antioxidant systems. Calcium ions (Ca^{2+}) function as ubiquitous intracellular second messengers in plant responses to environmental stimuli. Nanoparticle exposure may alter membrane properties and ion fluxes, potentially modifying cytosolic Ca^{2+} concentrations. Changes in Ca^{2+} can activate calcium-dependent protein kinases, calmodulin and other downstream signaling components. These signals may subsequently regulate transcription factors involved in stress adaptation and specialized metabolism. Direct evidence connecting nanoparticle-induced Ca^{2+} signaling with capsaicinoid biosynthesis in chilli remains limited, making this an important area for future investigation.

Nanoparticle exposure can influence phytohormones such as salicylic acid, jasmonic acid, ethylene, abscisic acid, auxin and cytokinins. These hormones regulate growth, development and responses to environmental stress. Jasmonate, salicylate and ethylene signaling are particularly relevant to defense-associated secondary metabolism. Because capsaicinoid accumulation is developmentally and environmentally regulated, interactions between nanoparticle-induced hormonal changes and capsaicinoid pathways deserve greater attention. MAPK cascades provide important links between extracellular stimuli and nuclear gene regulation. A typical MAPK cascade involves sequential activation of MAPKKK, MAPKK and MAPK proteins, ultimately influencing transcription factors and stress-responsive genes.

7. Nanoparticle-mediated regulation of secondary metabolism

7.1 Nano-elicitation of secondary metabolism

Nanoparticles have emerged as important abiotic elicitors capable of modifying plant secondary metabolism through controlled cellular stress and signaling. Their nanoscale dimensions, high surface-area-to-volume ratio and tunable surface chemistry facilitate interactions with cell walls, membranes, organelles and signaling molecules. Recent research indicates that nanoparticles can stimulate reactive oxygen species (ROS), antioxidant responses, hormonal signaling and transcriptional regulation, ultimately redirecting metabolic flux toward phenolics, flavonoids, terpenoids, alkaloids and other specialized metabolites (Jadoon *et al*., 2024; Vyavahare *et al*., 2025). The magnitude of nano-elicitation is strongly dependent on nanoparticle composition, size, morphology, surface charge, concentration, exposure duration and plant developmental stage (Zhang and Su, 2024; Thiruvengadam *et al*., 2024).

7.2 Phenylpropanoid pathway

The phenylpropanoid pathway represents one of the most important metabolic routes affected by nanoparticle elicitation because it produces phenolic acids, flavonoids, lignin precursors and the vanillylamine moiety required for capsaicinoid biosynthesis. The pathway begins with phenylalanine and involves phenylalanine ammonia lyase (PAL), cinnamate 4-hydroxylase (C4H) and 4-coumarate-CoA ligase (4CL). Nanoparticle-induced ROS signaling may stimulate these enzymes and increase phenylpropanoid flux.

7.3 Flavonoid biosynthesis

Flavonoids are major antioxidant and defense metabolites synthesized downstream of phenylpropanoid metabolism. Nanoparticles may enhance flavonoid biosynthesis through ROS-mediated activation of PAL, C4H, 4CL, chalcone synthase (CHS) and chalcone isomerase (CHI). In *C. annuum*, Cu and Ag nanoparticle treatments produced substantial increases in total flavonoid content, particularly following seed priming (Mawale *et al*., 2024). Green-synthesized Ag nanoparticles also increased flavonoids together with carotenoids, phenolics and antioxidant activity in chilli seedlings (Mawale and Giridhar, 2024).

7.4 Phenolic acid biosynthesis

Phenolic acids, including chlorogenic, caffeic, ferulic and p-coumaric acids, contribute to antioxidant defense and plant stress adaptation. Recent metabolomic analysis of SeNP-treated *C. annuum* demonstrated dose- and tissue-dependent metabolic changes, including increased chlorogenic acid in shoots at an appropriate SeNP concentration. This observation provides direct evidence that selenium nano-elicitation can modify phenolic acid metabolism in chilli.

7.5 Carotenoid biosynthesis

Carotenoids are essential for photosynthesis, antioxidant protection and chilli fruit pigmentation. Their accumulation is particularly important during the transition from green to mature red fruit. Integrated metabolome and transcriptome analysis has demonstrated substantial genetic and metabolic variation in carotenoid accumulation among differently coloured peppers (Lv *et al*., 2023). More recently, developmental transcriptome-metabolome analysis demonstrated that fruit colour changes during later developmental stages are closely associated with changes in carotenoids and flavonoids (Zhang *et al*., 2025).

8. Molecular regulation of capsaicinoid biosynthesis

Capsaicinoids are characteristic vanillylamide metabolites of pungent *Capsicum* fruits. Capsaicin and dihydrocapsaicin generally represent the major components, whereas nordihydrocapsaicin, homocapsaicin and homodihydrocapsaicin contribute to the broader capsaicinoid profile. Their structural diversity is primarily determined by differences in the acyl-CoA substrates incorporated during the final condensation reaction.

Recent metabolomic research has demonstrated that capsaicinoid composition changes substantially during pepper fruit development. Zhang *et al*. (2025) identified 1,775 differentially accumulated metabolites across six fruit developmental stages and found that capsaicinoid accumulation was particularly associated with specific developmental transitions. These findings demonstrate that capsaicinoid production is a dynamic metabolic process rather than a constant trait. Capsaicinoid biosynthesis occurs predominantly in the fruit placenta and is strongly influenced by developmental stage. Zhang *et al*. (2025) identified the S3-S4 developmental period as particularly associated with capsaicinoid accumulation, while later stages were more strongly associated with fruit colour changes. This developmental regulation is highly relevant to nano-elicitation because the same nanoparticle may produce different metabolic responses depending on whether it is applied during vegetative growth, flowering, fruit initiation, fruit enlargement or ripening. Spatial metabolomic analysis published in 2026 further demonstrated that capsaicinoids exhibit localized and dynamic accumulation patterns within the placenta during fruit development (Yang *et al*., 2026). Such findings indicate that nanoparticle delivery should eventually be optimized according to both tissue and developmental stage. The phenylpropanoid branch provides the vanillylamine component of capsaicinoids. Phenylalanine is converted through PAL, C4H and 4CL-associated reactions to generate downstream intermediates that ultimately contribute to vanillylamine formation. Recent molecular evidence has established that transcription factors directly regulate several of these structural genes.

Cheng *et al*. (2025) demonstrated that CcMYB330 activates CcPAL transcription and positively regulates capsaicinoid biosynthesis. Conversely, Yu *et al*. (2024) demonstrated that the repressor transcription factor CcMYB4-12 negatively regulates CcPAL2 and thereby modulates both lignin and capsaicin biosynthesis. These contrasting regulatory mechanisms demonstrate that nanoparticle-induced signaling could potentially influence capsaicinoid production through transcriptional control of the phenylpropanoid branch. The second major branch of capsaicinoid biosynthesis supplies the acyl-CoA components required for different capsaicinoid molecules. Branched-chain amino acids contribute to precursor formation, followed by reactions involving fatty-acid elongation and acyl-CoA formation.

Recent multi-omics research in pungent *Capsicum* identified proteins involved in acyltransferase activity, 3-oxoacyl-ACP metabolism, 4CL activity and 3-ketoacyl-CoA synthase functions in highly pungent fruit tissues (Momo *et al*., 2025). These findings suggest that capsaicinoid accumulation depends on coordinated regulation of both phenylpropanoid and fatty-acid-associated metabolism. Nanoparticle-induced changes in nitrogen metabolism, amino-acid availability or fatty-acid metabolism could therefore theoretically affect this branch, although, direct nanoparticle evidence remains limited. Direct molecular evidence connecting nanoparticles with the capsaicinoid biosynthetic pathway remains an emerging research area. However, nanoparticles can alter ROS production, antioxidant activity, hormonal signaling and secondary metabolism, providing a plausible mechanism for indirect regulation (Jadoon *et al*., 2024; Vyavahare *et al*., 2025). Importantly, direct evidence is now emerging from *Capsicum* studies. Chitosan nanoparticles have been reported to increase capsaicinoid content in *Capsicum* fruits while also increasing phenolic and flavonoid accumulation (Mawale and Giridhar, 2024). A 2024 nano-encapsulated biostimulant study also demonstrated enhancement of capsaicin during early chilli fruit development together with improved flavonoid and ascorbic acid characteristics (2024).

The proposed mechanism can therefore be represented as:

Nanoparticle exposure → ROS/Ca^{2+} signaling → hormonal/MAPK signaling → transcription-factor activation → phenylpropanoid and branched-chain fatty-acid pathways → precursor availability → capsaicinoid biosynthesis.

At present, this should be considered a mechanistic model rather than an established nanoparticle-specific pathway.

9. Effects of individual nanoparticles on capsaicinoids

ZnO nanoparticles are among the most important nano-enabled micronutrient formulations because zinc participates in enzyme activation, protein metabolism, photosynthesis, membrane stability and transcriptional regulation. In chilli, biogenic ZnO NPs have demonstrated significant physiological and biochemical effects under salinity. Adnan *et al*. (2025) reported increased growth, chlorophyll and phenolic responses together with reduced oxidative damage following ZnO NP application. Similarly, Guzel Deger *et al*. (2025) demonstrated that both green-synthesized and chemically synthesized ZnO NPs modified drought responses in *C. annuum*. These responses provide a possible basis for maintaining precursor availability for secondary metabolism under stress. However, direct evidence for consistent increases in mature-fruit capsaicin and dihydrocapsaicin remains limited.

Selenium nanoparticles are increasingly recognized as nano-biostimulants capable of modifying antioxidant metabolism, stress tolerance and specialized metabolism. The recent SeNP metabolomics study in *C. annuum* demonstrated dose- and tissue-dependent metabolic changes, including increased chlorogenic acid in shoots at an appropriate treatment concentration. Iron nanoparticles may influence secondary metabolism by improving iron availability, chloroplast function, photosynthetic activity and redox homeostasis. Green-synthesized nanofertilizer research has emphasized the potential of iron-based nanoparticles for improving plant nutrition and abiotic-stress tolerance (Ben Zineb *et al*., 2025). Copper nanoparticles have dual nutritional and elicitation functions because copper is an essential micronutrient but can generate oxidative stress at excessive concentrations. Mawale *et al*. (2024) demonstrated that Cu nanoparticles influenced growth, chlorophyll, carotenoids, phenolics, flavonoids and antioxidant enzyme activity in *C. annuum*.

These effects suggest that Cu NPs can modify the biochemical environment associated with secondary metabolism. Controlled ROS production could potentially activate phenylpropanoid-related pathways and influence capsaicinoid precursor availability.

Nevertheless, fruit-stage experiments measuring individual capsaicinoids are required to establish this relationship. Silver nanoparticles can function as strong elicitors because they influence ROS generation, antioxidant defense and stress-responsive metabolism. Green-synthesized Ag nanoparticles produced from biological sources increased germination, chlorophyll, carotenoids, phenolics, flavonoids and antioxidant capacity in *C. annuum* seedlings (Mawale and Giridhar, 2024).

10. Nanoparticle effects on major chilli phytochemicals

10.1 Capsaicinoids

Capsaicinoids represent one of the most important quality attributes of chilli fruits and are highly responsive to changes in plant metabolic status. Nanoparticle-mediated elicitation can influence capsaicinoid accumulation by modifying reactive oxygen species (ROS), antioxidant metabolism and defense-related secondary metabolic pathways. In *Capsicum* spp., chitosan-based nanoparticles, including chitosan-silver and chitosan-copper formulations, significantly enhanced total capsaicinoid accumulation, with increases of approximately 125-142% reported under optimized treatments (Mawale and Giridhar, 2024). These responses indicate that nanoparticle treatments may stimulate defense-associated metabolic pathways that contribute to capsaicinoid biosynthesis. Nano-encapsulated microbial and botanical biostimulants have also been shown to influence capsaicin accumulation during chilli fruit development. Treatment enhanced capsaicin content particularly during the early stages of fruit development, suggesting that nano-enabled delivery systems can modify the timing and intensity of phytochemical accumulation (Matthews *et al*., 2025).

10.2 Carotenoids

Carotenoids contribute substantially to the characteristic colour, nutritional value and antioxidant capacity of chilli fruits. Nanoparticle treatments can alter carotenoid metabolism through changes in oxidative signalling, photosynthetic activity and precursor availability. Chitosan-based nanoparticles increased carotenoid accumulation in *Capsicum* plants by approximately 20–30%, together with improvements in chlorophyll and antioxidant characteristics (Mawale and Giridhar, 2024). Such responses suggest that nanoparticle-mediated stimulation of primary metabolism may support the biosynthesis and accumulation of carotenoid pigments.

10.3 Phenolic compounds

Phenolic compounds are among the most responsive secondary metabolites to nanoparticle-induced elicitation. Nanoparticles can generate controlled oxidative signals that activate defense-related biochemical pathways and consequently enhance phenolic biosynthesis. In *Capsicum*, chitosan-based nanoparticles increased total phenolic content by approximately 20-45%, demonstrating that nanoparticle treatment can stimulate phenylpropanoid-associated metabolism (Mawale and Giridhar, 2024). More broadly, nanoparticle-assisted elicitation has been proposed as an effective strategy for stimulating plant secondary metabolites through ROS-mediated signalling and activation of defense responses (Vyavahare *et al*., 2025).

10.4 Flavonoids

Flavonoid accumulation is closely associated with plant antioxidant defense and phenylpropanoid metabolism. Chitosan, chitosan–silver and chitosan–copper nanoparticles markedly increased total flavonoid concentrations in *Capsicum*, with reported increases of approximately 40-125% depending on nanoparticle composition and application regime (Mawale and Giridhar, 2024). Therefore, nanoparticle treatment may function as an elicitation stimulus capable of redirecting carbon flux toward flavonoid biosynthesis.

10.5 Ascorbic acid

Ascorbic acid is an important antioxidant and nutritional constituent of chilli fruits. Nano-enabled biostimulant delivery has demonstrated potential for improving ascorbic acid accumulation during fruit development. Matthews *et al*. (2025) reported enhanced ascorbic acid concentrations in chilli fruits following application of nano-encapsulated microbial and botanical biostimulants, indicating that nanoformulations can influence nutritional quality in addition to growth and yield.

10.6 Tocopherols

Tocopherols participate in the protection of cellular membranes against oxidative damage and are closely connected with plant antioxidant metabolism. Although, direct evidence for nanoparticle-induced changes in tocopherol concentrations in chilli remains comparatively limited, nanoparticle treatments have been shown to modify oxidative stress and antioxidant systems in plants. Consequently, changes in tocopherol metabolism may represent an important component of the broader antioxidant response to nano-elicitation (Vyavahare *et al*., 2025).

10.7 Glutathione

Glutathione is a central component of the cellular redox system and contributes to detoxification and maintenance of oxidative homeostasis. Nanoparticle exposure can modify ROS generation and antioxidant responses, thereby potentially altering glutathione metabolism. The response is strongly dependent on nanoparticle composition, concentration and physicochemical characteristics, emphasizing the importance of dose-dependent nano-elicitation rather than assuming a universally stimulatory effect (Thiruvengadam *et al*., 2024).

10.8 Volatile compounds

Volatile metabolites contribute to chilli aroma, flavour and ecological interactions. Nanoparticle-induced changes in primary metabolism, oxidative signalling and secondary metabolic pathways may consequently affect volatile compound production. However, direct investigations of nanoparticle-mediated changes in chilli volatile profiles remain limited, highlighting an important research gap for future metabolomics-based studies (Vyavahare *et al*., 2025).

11. Nanoparticles and chilli fruit quality

Nanoparticle treatments can influence fruit development through improved nutrient utilization, photosynthetic performance and metabolic activity. Nano-enabled biostimulants have demonstrated positive effects on chilli growth and fruit quality, suggesting that controlled delivery of bioactive compounds may improve both vegetative performance and reproductive development (Matthews *et al*., 2025). Yield responses to nanoparticles are generally associated with improved nutrient acquisition, photosynthetic efficiency, stress tolerance and reproductive performance. Nanofertilizer technologies have been proposed as an approach for improving nutrient-use

efficiency and crop productivity, although, the magnitude of the response depends on nanoparticle composition, dose, application route and environmental conditions (Mehta *et al*., 2024; Wang *et al*., 2025). Fruit colour is determined largely by carotenoid accumulation and pigment transformation during ripening. Nano-encapsulated biostimulant treatment has been reported to modify colour-related characteristics of chilli fruits, demonstrating that nano-enabled treatments can influence postharvest quality attributes in addition to yield (Matthews *et al*., 2025).

Capsaicinoid concentration is a critical quality characteristic of chilli and is influenced by developmental stage, genotype and environmental conditions. Chitosan-based nanoparticles significantly increased total capsaicinoid accumulation in *Capsicum*, demonstrating the potential of nanoparticle-mediated elicitation to enhance pungency-related phytochemicals (Mawale and Giridhar, 2024). Nano-encapsulated biostimulants have likewise been associated with increased capsaicin accumulation during early fruit development (Matthews *et al*., 2025). Phenolics and flavonoids contribute strongly to the antioxidant potential and functional nutritional quality of chilli. Chitosan-based nanoparticles substantially increased both phenolic and flavonoid concentrations in *Capsicum*, with the response varying according to nanoparticle formulation and concentration (Mawale and Giridhar, 2024). More generally, nanoparticle-assisted elicitation can activate defense-related secondary metabolism and promote accumulation of bioactive compounds (Vyavahare *et al*., 2025).

12. Omics approaches to understand nanoparticle-induced metabolic changes

Transcriptomics provides a powerful approach for identifying genes and regulatory networks associated with nanoparticle-induced metabolic responses. Nanomaterials can modify the expression of genes associated with antioxidant defense, hormone signalling, nutrient transport, stress responses and secondary metabolism. Recent reviews emphasize that transcriptomic analysis is particularly valuable for understanding how nanoparticles influence plant abiotic stress tolerance at the molecular level (Chen *et al*., 2024). Proteomics complements transcriptomics by determining whether nanoparticle-induced transcriptional changes result in corresponding changes in protein abundance and function. Analysis of proteins involved in antioxidant defense, photosynthesis, metabolism and stress signalling can provide mechanistic information that cannot be obtained from physiological measurements alone. Integration of transcriptomic and proteomic datasets is therefore important for establishing functional links between nanoparticle exposure and metabolic regulation (Bhat *et al*., 2025). Metabolomics is particularly important for this review because capsaicinoids, phenolics, flavonoids, carotenoids and other phytochemicals represent the final products of complex metabolic networks. Selenium nanoparticle treatment of *C. annuum* seedlings produced differential shoot and root metabolic responses, including changes in sugars, fatty acids, terpenes, phytosterols, phenolics, ascorbate and other metabolites. Such findings demonstrate the value of non-targeted metabolomics for identifying previously unrecognized metabolic responses to nanoparticles. Ionomics can be used to characterize changes in the elemental composition of plants following nanoparticle exposure. This approach is particularly relevant for Zn, Fe, Cu, Mn and Se nanoparticles because nanoparticle-derived elements may participate in nutrient metabolism, antioxidant defense and stress adaptation. Understanding nanoparticle uptake and translocation is therefore essential for interpreting changes in elemental profiles and phytochemical accumulation (Zhang and Su, 2024).

Nanoparticle-induced responses may extend beyond transcriptional regulation to epigenetic mechanisms, including DNA methylation, histone modification and small-RNA-mediated regulation. Recent evidence indicates that nanomaterials can influence plant stress tolerance through epigenetic regulation, suggesting that nanoparticle-induced metabolic changes may persist beyond immediate physiological responses (Chen *et al*., 2024). The integration of transcriptomics, proteomics, metabolomics, ionomics and epigenomics offers a systems-level framework for understanding nanoparticle-mediated metabolic regulation. Such integration can connect nanoparticle uptake and transformation with molecular signalling, gene expression, protein activity and final phytochemical accumulation. Importantly, nanoparticle transformation within plant tissues can alter their biological effects, making characterization of nanoparticle transformations essential when interpreting multi-omics datasets (Wei *et al*., 2024). Bhat *et al*. (2025) similarly emphasized the importance of omics-based approaches for resolving nanoparticle-induced stress adaptation and potential toxicity at multiple biological levels. Thus, future chilli research should combine multi-omics datasets with nanoparticle characterization, dose-response analysis and fruit developmental-stage information to establish a mechanistic model of capsaicinoid and secondary-metabolite regulation.

13. Future prospects

The application of nanoparticles for modulating capsaicinoids and secondary metabolism in chilli represents an emerging research frontier with considerable potential for precision phytochemical management. Future investigations should move beyond simple comparisons of nanoparticle treatments and focus on establishing clear nanoparticle–plant–metabolite relationships. The effectiveness of nanoparticles is strongly influenced by particle size, morphology, surface chemistry, coating, concentration, application route and plant developmental stage; therefore, standardized characterization and dose-response experiments are essential for reproducible results. Multi-omics approaches represent another major opportunity. Transcriptomics, proteomics, metabolomics, ionomics and epigenomics should be integrated to establish relationships between nanoparticle uptake, ROS and Ca^{2+} signaling, hormonal responses, gene regulation, enzyme activity and final metabolite accumulation. The 2025 SeNP study in *C. annuum* demonstrated that non-targeted metabolomics can reveal dose- and tissue-specific alterations in primary and secondary metabolism, while also emphasizing the need for combined transcriptomic and metabolomic approaches. Future research should also examine genotype × nanoparticle interactions because chilli cultivars differ substantially in pungency, fruit colour, metabolic composition, nutrient-use efficiency and stress tolerance. Screening diverse pungent and non-pungent *Capsicum* genotypes could identify varieties with superior responsiveness to specific nanoparticles.

Another important direction is the development of green-synthesized, biodegradable and targeted nanoformulations. Such systems could combine nutrient delivery, stress priming and phytochemical enhancement while minimizing unnecessary nanoparticle accumulation. Smart nano-carriers capable of controlled release in response to pH, ROS, enzymes or environmental conditions may further improve application efficiency. Recent reviews emphasize that safer

nanoparticle design, biodegradable materials and targeted delivery will be important for sustainable agricultural deployment. Field validation is essential because most nanoelicitation studies remain laboratory-, hydroponic- or greenhouse-based. Long-term multilocation experiments should evaluate yield, capsaicinoids, carotenoids, phenolics, flavonoids, vitamin C, antioxidant capacity, nutritional quality and economic returns simultaneously. Effects under realistic combinations of drought, heat, salinity and nutrient stress should also be investigated.

14. Conclusion

Nanoparticle-mediated modulation of chilli phytochemistry represents a promising intersection between nanotechnology, plant physiology, molecular biology and sustainable crop production. Nanoparticles can influence plant growth, nutrient acquisition, ROS signaling, antioxidant defense, hormonal regulation and secondary metabolism, thereby creating opportunities to improve the biochemical and nutritional quality of *C. annuum*. Recent studies demonstrate that ZnO, Se, Cu, Ag, TiO, and other nanoparticles can modify physiological and metabolic responses in chilli, although, the magnitude and direction of these effects depend strongly on nanoparticle characteristics, concentration, application method, genotype and environmental conditions (Vyavahare *et al*., 2025). The potential for nanoparticles to enhance capsaicinoids, phenolics, flavonoids, carotenoids, ascorbic acid and antioxidant capacity is particularly significant because these metabolites determine many of the functional, nutritional and commercial attributes of chilli. However, direct evidence for consistent nanoparticle-induced enhancement of capsaicin and dihydrocapsaicin remains less developed than evidence for broader antioxidant and secondary-metabolic responses. Therefore, nanoparticle effects on capsaicinoid biosynthesis should be investigated through integrated biochemical, molecular and omics approaches rather than inferred solely from general phytochemical enhancement. Thus, nano-enabled manipulation of chilli phytochemistry should be viewed as a precision approach rather than a universal input technology. Future progress will depend on optimized formulations, standardized methodologies, genotype-specific responses, multi-omics integration, field validation and rigorous food-safety and environmental assessment. With these advances, nanoparticles could become valuable tools for developing high-quality, stress-resilient and phytochemically enriched chilli production systems, provided that their agricultural benefits are demonstrated alongside responsible environmental and food-safety management.

Availability of data and material

All data are provided within the manuscript.

Authorship contribution statement

M. Kabilan and K. Sundharaiya: Supervision, academic oversight and overall monitoring of the research work; **R.V. Sundarrajan and T. Anitha:** Conceptualization, supervision, critical review and overall guidance of the manuscript; **Adnan A. Khan:** Critical review, validation of scientific content and final approval of the manuscript.

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Conflict of interest

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