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Nanopriming as a strategic tool to boost abiotic stress tolerance in wheat (*Triticum aestivum* L.)

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Abstract
Abiotic stresses such as extreme temperatures, drought, salinity, heavy metal toxicity and ultraviolet radiation significantly impact plant growth and development, causing major yield losses globally. In the face of climate change and soil degradation, these stresses are becoming increasingly detrimental, particularly to essential crops like wheat (*Triticum aestivum* L.). Wheat is a staple food for over one-third of the world population, supplying more calories and protein than any other cereal. It also serves a wide range of industrial purposes including use in animal feed, brewing, ethanol production and cosmetics. A rapidly evolving field, nanotechnology offers innovative solutions to modern agricultural challenges. One promising application is seed nanopriming which involves pre-treating seeds with nanoparticles. This technique enhances germination, seedling vigor, stress tolerance and ultimately crop yield. Nanoparticles smaller than 100 nm such as ZnO, SiO_2, Ag, Au and Cu are particularly effective. They can penetrate seed coats and plant tissues in turn accelerating early metabolic activity and triggering beneficial physiological and biochemical responses. In wheat, nanopriming overcomes stress induced disruptions to key functions such as photosynthesis, nutrient uptake and reproductive development. It reduces seed dormancy, improves germination rates and promotes stronger seedling growth. By inducing favorable molecular responses, the priming enhances the plant ability to tolerate recurring and moderate stress conditions. These internal changes also manifest as visible anatomical adaptations that support survival under adverse environments. Additionally, the priming contributes to micronutrient biofortification for improving the nutritional quality of wheat grains. This dual benefit of stress tolerance and enhanced nutrition not only increases productivity but also supports resource conservation. As a result, nanopriming presents a sustainable and effective strategy to strengthen wheat cultivation against mounting environmental pressures and growing food security concerns worldwide.

Keywords Abiotic stress, Nanopriming, Stress tolerance, *Triticum aestivum* L., Reactive oxygen species, Antioxidant enzymes

1 Introduction

Abiotic stresses negatively affect plant growth and development which causes major losses in crop yield worldwide [1]. These stresses include extreme temperatures, water deficiency, high salinity, heavy metal toxicity and ultraviolet radiation. It is estimated that abiotic stresses are responsible for more than 50% of global yield losses in major crops in which drought and heat stress alone accounting for nearly 40% of wheat production losses in several regions [2]. Developing crops with multi-stress tolerance has become increasingly crucial to mitigate the impacts of environmental fluctuations and to meet the rising food demands of a growing population, as multiple abiotic stresses often occur simultaneously in the field. This goal is feasible since land plants have already evolved broad defense mechanisms against abiotic stresses including protective structures like the cuticle and cellular components such as unsaturated fatty acids, reactive species scavengers, molecular chaperones and compatible solutes [3]. These defense responses are governed by a complex regulatory network that links upstream signaling molecules with downstream regulators, particularly transcription factors that control gene expression [4]. The major signaling molecules include stress hormones, reactive oxygen species (ROS), gasotransmitters, polyamines, phytochromes and calcium. However, stress conditions can result in failures of seed germination, loss of uniformity, disrupted cellular redox homeostasis and the over accumulation of ROS, in turn reducing productivity and threatening global food security [5].

Among the various crops, wheat (*Triticum aestivum* L.), a staple for over one-third of the global population, is highly susceptible to abiotic stress. Drought, heat, salinity and nutrient deficiencies are the most damaging factors affecting wheat cultivation and productivity, particularly under changing climatic conditions. Drought stress can cause 20–40% yield reductions, while combined drought and heat stress during flowering and grain filling stages may result in up to 60% yield loss due to impaired photosynthesis, pollen sterility and reduced grain weight [6]. Heat stress above the optimal temperature range (15–25 °C) leads to accelerated leaf senescence, protein denaturation and poor kernel development with 3–4% yield decline for every 1 °C temperature increase during the reproductive phase [7]. Salinity stress interferes with root water uptake and ion homeostasis leading to growth inhibition and chlorophyll degradation that affects over 20% of irrigated farmlands globally [8]. However, the heavy metal stress disturbs metabolic pathways, while nutrient deficiencies limit chlorophyll synthesis and enzyme activity thereby reducing photosynthetic efficiency [9].

Combined abiotic stresses exert even more severe impacts on wheat growth and yield than individual stresses. Simultaneous drought and heat stress amplify oxidative damage, disturb hormonal balance and reduce photosynthetic efficiency while the combination of salinity and nutrient deficiency leads to severe ionic and osmotic imbalances. These conditions collectively cause significant reductions in kernel number, biomass accumulation and overall productivity [10]. Moreover, the stresses increase the generation of ROS and damaging lipids, proteins and nucleic acids, ultimately reducing plant vigor and survival capacity. Despite natural defense mechanisms such as antioxidant enzyme activity and osmolyte accumulation, wheat tolerance often remains insufficient under prolonged or combined stress conditions [11].

Nowadays, nanotechnology is a fascinating and rapidly developing branch of research that has led to various innovations. In particular, it provides effective solutions to agriculture related challenges and contributes to achieving sustainable and secure food production (Fig. 1) [12]. Nanoparticles (NPs) are tiny materials with 1–100 nm in size and possessing unique physicochemical properties that differ significantly from their larger counterparts. For instance, they have a high surface area-to-volume ratio, strong

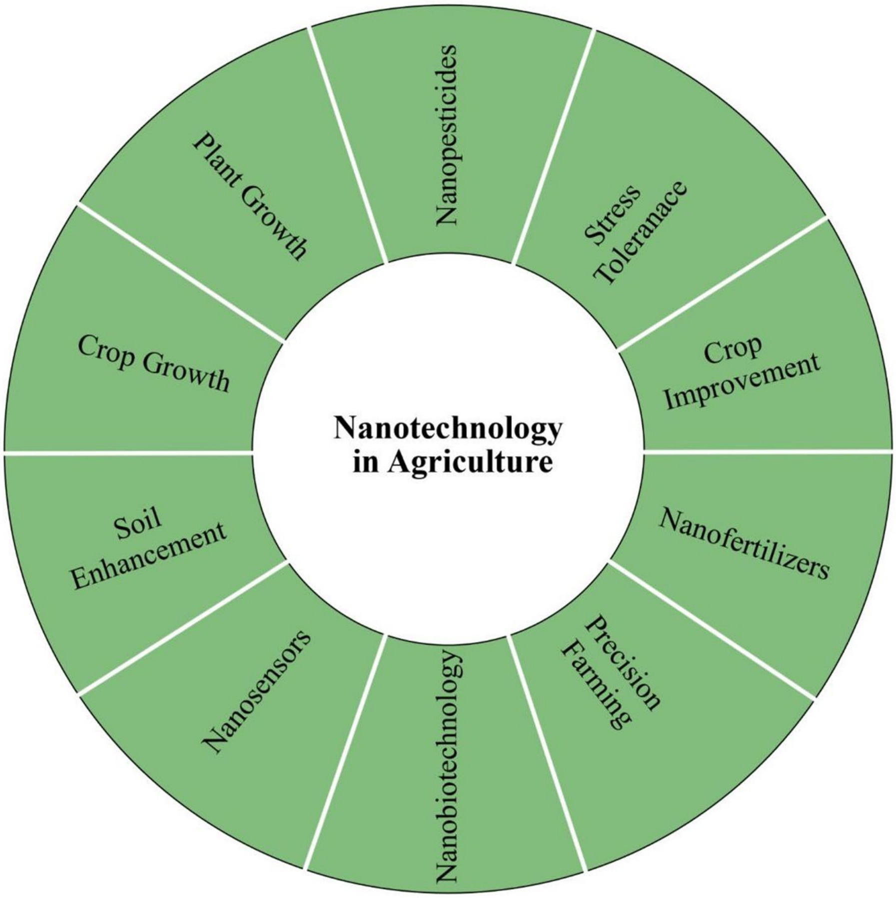

Fig. 1 The illustration highlights how nanotechnology and nanobiotechnology enhance agricultural productivity and sustainability. Nanoparticles and nanobioformulations improve nutrient delivery, pesticide efficiency and plant stress tolerance. They regulate ROS levels, strengthen antioxidant defenses and support key physiological responses. Nanosensors and nanobiosensors further enable real-time monitoring of soil and plant health for precision farming

adsorption potential and enhanced interaction efficiency owing to their small size [13]. Presently, nanotechnology is utilized in applications such as nanofertilizers and nanopesticides to improve nutrient delivery, growth and productivity while enhancing plant resistance to insect pests and microbial diseases [14]. Similarly, the pretreatment of seeds with NPs offers a promising approach to overcoming abiotic stress and enhancing plant tolerance [15]. This technique induces several metabolic and physiological responses in plants to better withstand stress conditions. Nanoparticle based priming benefits plant metabolism, enzyme regulation and phytohormone balance, ultimately improving growth, development and resilience under adverse environments [16]. Furthermore, the extremely small size and controlled release of NPs facilitate improved nutrient uptake to enhance seed germination, seedling vigor and yield quality [17].

Moreover, nanoparticle based biofortification represents a promising approach to enhance the nutritional quality of wheat grains while improving plant tolerance to abiotic stresses. Traditional biofortification strategies such as soil and foliar fertilization or genetic modification, often face challenges including nutrient loss, low bioavailability and environmental pollution [18]. Nanoparticles, owing to their nanoscale dimensions and high reactivity, enable controlled and targeted delivery of essential micronutrients such as zinc (Zn), iron (Fe), selenium (Se) and copper (Cu) directly to plant tissues. These NPs can penetrate root or foliar surfaces more efficiently, successively improving translocation to developing grains and enhancing nutrient content and bioavailability [19]. Similarly, nanobiofortification contributes to improved photosynthetic activity, antioxidant enzyme function and membrane stability that mitigate oxidative damage caused by drought, salinity or temperature stress. For instance, ZnO and Fe_3O_4 NPs have been shown to increase chlorophyll synthesis, grain protein content and enzymatic antioxidant capacity in wheat under stressful environments [20, 21]. Thus, nanoparticle assisted biofortification not only strengthens nutritional security but also complements stress resilience mechanisms, aligning with sustainable agricultural goals and the broader vision of climate smart crop production.

Wheat remains a vital staple crop that contributes more calories and protein to the human diet than any other cereal. Due to the presence of essential minerals, carbohydrates and dietary fiber, wheat production is crucial for global food security. Beyond human consumption, wheat serves as an important raw material for animal feed, brewing, ethanol production and cosmetics [22]. The wheat kernel is composed of three major parts, the bran, germ and endosperm, which together serve as a powerhouse of essential nutrients [23]. As global food demand continues to increase, the detrimental effects of abiotic stresses on wheat productivity emphasize the urgent need for developing resilient cultivars and adopting advanced strategies such as nanopriming. Therefore, the present review focuses on the significance of nanopriming in improving wheat seed germination, seedling growth and yield by modulating morphological, anatomical, physiological, biochemical and molecular processes that collectively enhance stress tolerance.

2 How do wheat plants cope with abiotic stress?

Plants encounter various abiotic stresses including extreme temperatures, water scarcity and high salinity which disrupt cellular functions and hinder growth and productivity. To combat the challenges, plants have developed diverse physiological mechanisms. Studying these responses offers valuable phenotypic insights that help uncover genetic mechanisms, supporting molecular breeding efforts aimed at enhancing stress tolerance [24]. Normally, the plants produce various compounds to tolerate stress conditions including 6-gingerol, salicylic acid (SA), indole-3-acetic acid (IAA), gibberellin A4 (GA4), abscisic acid (ABA), trans-cinnamic acid, sucrose, L-phenylalanine, L-tyrosine, succinic acid and nicotinic acid [25]. As food security becomes a growing concern, developing stress resistant crops has become a key priority in modern agriculture. This goal is supported by progress in understanding the physiological, biochemical and molecular mechanisms underlying plant responses such as signaling pathways, transcriptional regulation, structural adaptations and biochemical processes.

2.1 Phenotypic and physiological mechanisms

Wheat productivity is increasingly threatened by abiotic stresses which are becoming more frequent and persistent. These stresses induce osmotic imbalance and cellular damage, affecting wheat growth and yield across all developmental stages [26]. Wheat is highly vulnerable to osmotic stress during stages like germination, tillering, anthesis and grain filling. Germination delays caused by inadequate moisture reduce crop density and uniformity, while drought during reproductive stages decreases kernel number, disrupts physiological processes like photosynthesis and dry matter accumulation and shortens grain filling [27]. Drought sensitive varieties exhibit higher canopy temperatures and lower yields whereas tolerant cultivars maintain better fertility due to lower anther ABA levels. Terminal drought priming has shown promise in enhancing stress resilience by triggering protective metabolic pathways. Salt stress mimics drought by limiting leaf growth, tillering and kernel development. Damage to the flag leaf that essential for carbohydrate supply reduces photosynthesis and yield. At the cellular level, high salinity disrupts ion balance and leading to excessive Na^+ uptake, ROS production and impaired nutrient absorption [28]. It also affects nitrogen use efficiency and transpiration. Tolerant cultivars exhibit higher K^+/Na^+ selectivity, stable membranes and better physiological integrity. Salt and osmotic stress responses vary among wheat genotypes, with hexaploid wheat generally displaying better drought tolerance than diploid or tetraploid forms, although genetic variability plays a key role. Usually, wheat can withstand temperatures from − 17 °C to 47.5 °C, but extremes during critical phases like germination, anthesis and grain filling are detrimental. Cold stress impairs photosynthesis, damages cells, and reduces grain number and size, while gradual cold acclimation can enhance tolerance [29]. High temperatures negatively impact pollen quality, accelerate senescence, reduce photosynthesis and hinder grain development. According to recent studies, the yield losses can reach 3–4% per 1 °C rise above 15 °C during reproductive phases; however, the heat priming before sensitive stages can mitigate these effects [30].

2.2 Biochemical mechanisms

Wheat plants have developed various biochemical mechanisms to combat abiotic stresses with osmotic adjustment being an early and crucial response. This involves the accumulation of osmolytes such as proline, soluble sugars, glycine betaine (GB), gamma-aminobutyric acid (GABA) and polyamines which help maintain cell turgor, protect cellular structures and enhance stress tolerance [16]. Proline acts as a key stress marker which accumulates under drought and salinity, contributing to osmotic balance and antioxidant activity. Plants also adjust carbohydrate metabolism, accumulating compounds like glucose, fructose, trehalose and starch that support energy supply, osmotic regulation and ROS scavenging. GB improves stress tolerance in several crops, while GABA enhances photosynthetic efficiency, ion homeostasis and ROS detoxification. Polyamines aid in growth regulation and stress defense [31]. It is evident that abiotic stress induces excess ROS such as hydrogen peroxide and superoxide radicals which damage cells. To counteract this, plants activate antioxidant defense systems including enzymatic antioxidants (Superoxide Dismutase (SOD), Catalase (CAT), Ascorbate Peroxidase (APX), Glutathione Peroxidase (GPX), Peroxiredoxine (PRDX)) and non-enzymatic antioxidants in turn maintain cellular integrity and improve stress resilience [32].

2.3 Molecular mechanisms

In wheat, understanding the integration of salinity response mechanisms with developmental and environmental cues is critical for improving stress tolerance. The wheat gene *TaAOC1* which encodes an enzyme in the jasmonic acid (JA) biosynthetic pathway, is induced by high salinity [33]. Over expression of *TaAOC1* enhances salt tolerance but inhibits root growth, indicating a trade-off between stress adaptation and development. Together with *TaOPR1*, *TaAOC1* participates in the α-linolenic acid pathway, which not only generates JA but also engages with the abscisic acid (ABA) pathway. This crosstalk promotes expression of *MYC2*, a transcription factor involved in abiotic stress signaling [34]. Genetic variation in these key genes presents opportunities for molecular breeding aimed at improving salt tolerance. Another important gene, *TaBASS2*, plays a role in transporting pyruvic acid into chloroplasts, supporting the biosynthesis of ABA and other metabolites involved in stress signaling. Over expression of *TaBASS2* in wheat enhances salt tolerance and reduces oxidative stress, primarily by repressing *ABI4*, thereby linking plastid retrograde signaling with ABA signaling pathways [35].

Similarly, blue light responsive G-box binding factor (*TaGBF*1) that induced by salt exposure modulates salinity responses by promoting photomorphogenesis and increasing salt sensitivity rather than enhancing tolerance. This role is mediated by *ABI5* which is an ABA pathway regulator, indicating that its function in salt stress is more related to hormone signaling than light perception [36]. In wheat, ionic homeostasis is a major determinant of salt tolerance [37]. Bread wheat shows higher salt tolerance than tetraploid wheat due to its ability to maintain a favorable potassium (K^+)/Na^+ ratio in leaves, controlled by the *Kna1* gene on chromosome 4D. In addition, two major loci (Nax1, Nax2), identified from crosses between durum wheat and the Na^+ excluding diploid relative *Triticum monococcum*, are linked to class 1 *HKT* (High Affinity K^+ Transporter) genes that regulate Na^+ transport [38]. The loci, Nax1 and Nax2, play critical roles in sodium exclusion in wheat. Nax1, located on chromosome arm 2AL, co-segregates with *HKT*1;4-A2, a gene responsible for Na^+ unloading from the xylem in roots. Nax2, situated on chromosome 5AL, is syntenic with the genomic region containing Kna1, and *TmHKT*1;5-A has been identified as its putative candidate gene [39]. Field evaluations have demonstrated that *TmHKT*1;5-A effectively reduces Na^+ accumulation in leaves and enhances grain yield under saline conditions. In bread wheat, silencing of *TaHKT*1;5-D, the homoeolog of *TmHKT*1;5-A, results in elevated leaf Na^+ content, thereby confirming its essential role in Na^+ exclusion and salt tolerance [40].

Expression patterns of *HKT* genes exhibit considerable variation across wheat genotypes and environmental contexts. For instance, *TaHKT*1;5-D shows constitutively high expression in *Aegilops tauschii;* whereas in synthetic hexaploid wheat, the expression is inducible by salt stress. Conversely, in cultivars such as Bobwhite, JN177 and the introgression line SR3, *TaHKT*1;5-D expression is not strongly induced under salinity [41]. Regulation of *HKT* gene expression is further modulated by epigenetic mechanisms including DNA methylation. In *Arabidopsis thaliana*, *HKT*1 transcription is controlled by small RNAs and methylation, suggesting that similar epigenetic processes may influence *TaHK*T1;5 expression in wheat, particularly as transcript levels of *TaHKT*1;5-B1 and *TaHKT*1;5-B2 are significantly lower than those of *TaHKT*1;5-D [42].

Moreover, the transcription factors like *AtABI4* and *OsMYBc* are known to regulate *HKT* genes in *Arabidopsis* and rice; they might be used as targets for manipulating HKT expression in wheat. However, no upstream regulator for wheat *HKT* genes has been clearly identified, likely due to the complex hexaploid genome of wheat [43]. The development of salt tolerant wheat germplasm including lines derived from *T. monococcum* has enhanced the understanding of salt tolerance mechanisms, particularly ionic and ROS homeostasis [44]. Several salt responsive genes have been identified from this line and functionally analyzed in *Arabidopsis*, although further validation in wheat is required [45]. To accelerate gene discovery, researchers are now using integrative approaches like omics, QTL mapping and population genetics. The creation of EMS mutant libraries for both tetraploid and hexaploid wheat, combined with next generation sequencing and exome capture techniques, is enabling systematic identification and functional validation of salinity responsive genes. These resources are essential for advancing wheat breeding and improving crop resilience under saline conditions.

3 Nanopriming: a new strategy for inducing abiotic stress tolerance in wheat plants

Nanotechnology application in agriculture has increased in recent years to overcome the abiotic stresses in turn achieving the objective of sustainable food production around the world. A wide range of nanomaterials have been employed to develop strategies for delivery of bioactive substances aimed at increasing crop productivity and protection [46].

3.1 Biological process behind wheat seed germination

Germination is a vital physiological process involving biological and biochemical activities that lead to seedling development. In wheat, it determines seedling establishment and the efficient use of nutrients and water. This process is influenced by environmental factors like temperature, light, pH, water and soil moisture, as well as the seed physiological state. Successful germination depends on the seed response to these overlapping abiotic conditions and ultimately affects plant abundance, distribution and population size [47]. The germination process starts with water uptake by the dry dormant seed, leading to radicle emergence as the embryo axis elongates. This involves a sequence of physiological and biochemical processes such as energy transfer, nutrient absorption and enzyme activity [48]. Water uptake occurs in three phases including rapid initial imbibition, a plateau and a final increase tied to germination onset. Imbibition softens the seed coat, enabling radicle and shoot emergence by enhancing the key early processes include respiration, DNA repair, translation, cell expansion and division [49]. Germination involves two main physical stages including endosperm rupture and radicle protrusion. Enzymes that break down stored carbohydrates and lipids are crucial during this phase, and both temperature and water availability significantly influence these activities.Water is essential for seed germination as it hydrates protoplasm, supplies oxygen, softens the seed coat and increases permeability [50]. In wheat, water is crucial for imbibition and activates metabolic processes like enzyme function and nutrient mobilization. Water stress reduces germination rates by inhibiting enzyme activity, disrupting carbohydrate metabolism, lowering water potential, reducing potassium and calcium levels, and altering hormone balance; hence optimum quantity of water is necessary for proper seed germination [51]. Temperature greatly influences the duration and success of seed germination. Germination occurs within a temperature range minimum, optimum and maximum, with the optimum promoting the fastest and highest germination rate. Temperature responses can vary across germination stages due to process complexity and are affected by seed variety, quality and harvest timing [52]. Recent studies show temperature alters cellular energy states and enzyme activity. ATP production and protein synthesis peak at optimal temperatures and decline outside this range. Abnormal temperatures disrupt respiration and ROS balance, negatively affecting the antioxidant system and wheat seed germination [53]. Similarly, wheat seeds need optimum light and soil pH for successful germination, while above and below the optimum value negatively influencing the germination rate. In addition, the varying effects of different colours of light on wheat seed germination is also evident [54]. Beyond abiotic factors, seed size, sowing depth and seed disinfection can influence seed germination and seedling establishment.

3.2 Nanopriming in wheat seeds

Seed priming is a pre-sowing technique that induces physiological changes in seeds, enabling faster germination and enhancing plant resilience to abiotic and biotic stresses. Traditional priming methods include pre-soaking and coating, while advanced approaches involve treating seeds with various agents such as salt solutions (halopriming), water (hydropriming), osmotic agents (osmopriming), plant hormone solutions (hormonal priming), beneficial microbes (biopriming), magnetic fields (magneto-priming), solid carriers (matriconditioning) and NPs (nanopriming) [55]. These treatments reduce seed dormancy and improve germination rates, seedling growth, stress tolerance and crop yield, particularly in cereals. Among the methods, nanopriming using NPs smaller than 100 nm has shown superior potential for enhancing seed germination, seedling vigor and stress tolerance under moderate and recurring conditions [56]. It is considered a promising strategy for addressing dormancy issues and improving germination in crop species, making it beneficial for boosting the agricultural economy.

The plasma membrane, composed of a phospholipid bilayer with hydrophilic heads and hydrophobic tails, acts as a selective barrier regulating molecule entry into the cell [57]. Nanoparticles can enter plant cells through three proposed mechanisms. The first involves direct diffusion where small NPs passively cross the membrane, influenced by their size, charge, shape, composition and hydrophobicity. The second mechanism is endocytosis in which the cell actively engulfs NPs by enclosing them within its membrane. The third mechanism includes transmembrane proteins or channels that facilitate NP entry into cells [58]. Once inside, NPs are transported within the plant via foliar, shoot or root pathways through two main routes, apoplastic and symplastic. Apoplastic transport occurs through the extracellular matrix, cell walls and xylem vessels, allowing radial movement to the vascular system and upward translocation to aerial parts. In contrast, symplastic transport involves the movement of substances through plasmodesmata and sieve plates between adjacent cells [59]. In plants, NP uptake commonly occurs through roots, leaves and root hairs. Other possible entry routes include ion channels, stomata, cuticle membrane, vasculature, pit membranes, hydathodes, casparian strips and extracellular spaces [60]. In the root system, NPs can enter through the rhizodermis, root hairs, root tips and lateral roots (Fig. 2).

At the time of seed priming, there is the controlled water uptake to activate metabolic processes without initiating radicle protrusion. This controlled hydration extends the lag phase while delaying the log phase of germination. According to the recent studies, NPs can enter seeds via the intercellular spaces of parenchymatous tissue, reaching cotyledons [61]. Moreover, NPs adhering to the seed coat trigger the production of ROS, which in turn initiate multiple downstream signaling pathways. In addition, the environmental factors influence NP behavior in soil. High ionic strength can cause rapid aggregation of NPs, reducing their availability. Conversely, organic macromolecules like humic acid, fulvic acid, citric acid and extracellular polymeric substances can stabilize

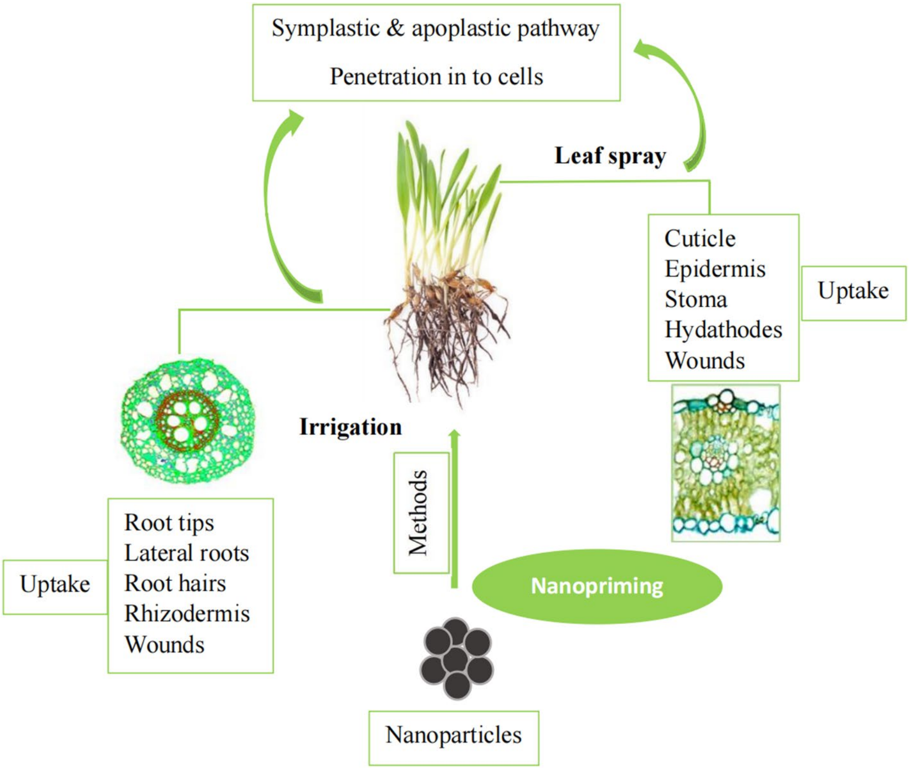

Fig. 2 Uptake and cellular entry pathways of NPs in plants. The figure shows how NPs enter plants through foliar spraying and irrigation. After leaf application, NPs penetrate through stomata, cuticular pores or micro-cracks to reach the apoplast. When applied through irrigation, NPs are absorbed by roots via epidermal cells and root hairs. Inside the plant, NPs move through two main routes: the apoplastic pathway, traveling along cell walls and intercellular spaces, and the symplastic pathway, entering cells through membrane transport, endocytosis or plasmodesmata. These pathways enable NP movement to different tissues and organelles that influencing plant physiological and stress response processes

NPs and reduce their sedimentation. Oftenly, low molecular weight organic acids in root exudates such as citrate and malate, can also complex with metal ions like Fe and Cu, enhancing mineral solubility and promoting uptake by plants or associated microorganisms [62].

3.3 Nanopriming induced abiotic stress tolerance in wheat plants

Under abiotic stress, the application of various NPs is a unique and cost effective method for improving seed germination and subsequent plant growth in wheat by activating plant physiological processes and giving resistance to diverse stressors (Table 1). Seed priming with NPs promotes electron exchange and enhances surface reaction capabilities related to plant cell and tissue components [63]. Due to their nanoscale size and high reactivity, particles such as zinc oxide (ZnO), silver (Ag), silicon dioxide (SiO_2), and Cu and Au based NPs can penetrate seed coats and trigger biochemical processes that promote faster and more uniform germination [64]. Zinc oxide nanoparticles (ZnO NPs) boost chlorophyll production and root development, while silver nanoparticles (AgNPs) offer antimicrobial protection. Similarly, silicon and iron nanoparticles enhance stress tolerance and nutrient availability. When delivered in nanoparticle form, copper nanoparticles (CuNPs) can enhance seed germination by increasing antioxidant enzyme activity, reducing oxidative stress and improving water absorption. They also

Table 1 Summary of nanopriming effects on wheat under abiotic Stress. The table presents an overview of how different nanoparticles influence wheat seed germination, physiological responses and overall stress tolerance

Nanoparticle type	Mode of action	Stress alleviated	Key outcomes
ZnO NPs	Enhanced nutrient uptake due to small particle size and large surface area [33] Controlled Zn release improves enzyme activity, antioxidant defense and osmolyte accumulation [67]	Drought and salinity stress	Improved germination, seed vigor, shoot and root growth, chlorophyll content, antioxidant enzyme activity, phenolic content, proline accumulation and nutrient uptake [66] Reduced lipid peroxidation and Na^+ toxicity [69] Enhanced photosynthetic efficiency and yield [69]
SiO_2 NPs	Strengthen cell wall and membranes [74] Regulate photosynthetic machinery and antioxidant system [76] Reduce metal toxicity and oxidative damage [77]	Drought and heavy metal stress	Improved germination, root/shoot length, chlorophyll content, PSII/PSI stability, electron transport rate and antioxidant activity [76] Decreased Cd accumulation in shoots, roots and grains [77] Enhanced drought tolerance and growth performance [76]
AgNPs	Act as nanopesticides and regulators of water balance and phytohormones [81] Enhance photosynthetic and antioxidant responses [38]	Drought and salinity stress	Increased germination rate, biomass, chlorophyll content, photosynthetic efficiency and stomatal conductance [80] Improved grain yield and drought tolerance [38] Mitigated salt induced growth inhibition [80]
CuNPs	Participate in redox and electron transport reactions [87] Stimulate enzymatic activation and protein synthesis linked to stress resistance [87]	Drought and general oxidative stress	Promoted early germination, increased germination rate and vigor [86] Activated stress responsive proteins and enzymes [87] Improved plant growth and stress resilience [83]
AuNPs	Modulate photosynthetic pigments and gene expression (*COR*, *PSA*, *RuBisCo*, *Wcor*15) [91] Enhance antioxidant and ion balance mechanisms [90]	Cold and salinity stress	Increased chlorophyll and sucrose content, K^+/Na^+ ratio, nitrogen uptake and photosynthetic gene expression [89] Improved cold and salt tolerance [91] Reduced ROS/RNS accumulation [90]

exhibit strong antimicrobial properties, protecting seeds from fungal or bacterial infections during germination. Gold nanoparticles (AuNPs) can enhance seed germination by stimulating cellular respiration and accelerating metabolic processes in the early stages [65]. It may also improve membrane permeability and water uptake that leading to faster germination. When used in appropriate concentrations, NPs can significantly improve germination rates and seedling vigor, offering a sustainable and innovative approach to wheat productivity (Table 1).

3.3.1 ZnO nanopriming

ZnO nanopriming is sustainable and cost effective with small particle size and larger surface area that resulting in enhanced nutrient absorption by plants, and increasing overall output with minimal environmental impact. The regulated release and higher absorption of zinc from NPs may improve nutrient delivery, in turn lowering the fertilizer application and contributing to better seedling growth and yield [33]. Similarly, ZnO NPs priming in wheat cultivar H-I 1544 shows beneficial effect on seed germination efficiency and seed vigour index compared to unprimed and hydroprimed seeds [57]. In addition, wheat nanopriming with ZnO NPs enhances shoot height and increased overall plant physiology including growth under salinity stress [66].

Drought stress negatively impacts all stages of plant growth by disturbing physiological and metabolic activities leading to dehydration, oxidative damage and impairment of vital biomolecular functions. To compensate the negative effects, zinc plays a crucial role in enzyme activity, cell membrane integrity, seed development and stress resistance [67]. Under drought stress, the antioxidant activities and nutrient contents of wheat boost when ZnO NPs applied. It is clear in wheat varieties, Zincole-16 and Ujala-16, in which better performance under drought stress conditions were observed in response to ZnO NPs priming [68]. ZnO seed priming in these seedlings alleviates drought induced stress at 80% and 60% field capacity by enhancing antioxidant enzyme activities, phenolic content, H_2O_2 scavenging, lipid peroxidation inhibition, and levels of free amino acids and soluble carbohydrates. In Ujala-16 and Zincol-16, drought stress negatively impacts on all traits, while ZnO NPs at 120 ppm, significantly enhance root and shoot lengths, biomass, chlorophyll content, antioxidant activity, proline levels and essential nutrient uptake with Zincol-16 performing better than Ujala-16 [69].

ZnO nano priming can reduce salt induced toxicity in wheat plants especially salt induced changes in growth, photosynthetic pigments, photosynthetic efficiency and leaf ultrastructure. The priming also causes distinct alterations in the electrophoretic profiles of shoot proteins [70]. Pre-treating wheat seeds with ZnO NPs substantially enhances germination rate and grain production while attenuating the detrimental effects of salt stress [71]. Photosynthesis associated ZnO NPs seed priming in wheat plants reduces the saline stress mediated degradation of leaf ultrastructures by lowering Na^+ induced alterations in the electrophoretic profile of shoot proteins, eventually improving chlorophyll synthesis and photosynthetic efficiency [72]. The stability of photosynthetic pigments in response to the exogenous application of ZnO NPs improves the net photosynthetic rate by limiting the oxidative damage caused by abiotic stress such as salinity or heavy metal ion accumulation in wheat [73].

3.3.2 SiO_2 nanopriming

Silicon dioxide nanoparticles (SiO_2 NPs) are recognized as important components in promoting plant growth and development. They play a crucial role in enhancing plant survival by strengthening cellular structures and regulating various physiological and metabolic pathways particularly under abiotic stress conditions. Due to their biocompatibility and multifaceted functions, the NPs have demonstrated significant potential for applications in agriculture and environmental management [74]. The exogenous application of SiO_2 NPs has been shown to effectively mitigate heavy metal toxicity in wheat plants [75]. Biocompatible NPs are commonly employed as nanopriming agents to enhance seed germination in rabi crops such as wheat, pea and mustard. Nanopriming with nanosilica or gibberellic acid (GA_3) loaded nanosilica markedly improves germination percentage, shoot and root elongation, seedling biomass and vigor indices I and II. The influence of the nanopriming on photosynthetic performance is particularly notable in drought sensitive wheat cultivar HI-1544 under drought conditions. Drought stress typically reduces the quantum yield and electron transport rates of both photosystems II and I in unprimed plants [76]. In contrast, nanoprimed plants exhibit only minimal declines indicating enhanced tolerance. Furthermore, the energy dissipation parameters increase sharply in unprimed drought stressed plants, reflecting stress induced photoprotective responses, whereas these parameters remain comparatively stable in nanoprimed plants. Similarly, limitations in the donor and acceptor sides of PSI and inhibition of P700 redox kinetics observed under drought stress are largely mitigated by SiO_2 nanopriming. In addition to improving photosynthetic performance, SiO_2 NPs exert beneficial effects on wheat growth and chlorophyll content by reducing oxidative stress and promoting antioxidant enzyme activity. The NP treatment also decreases cadmium accumulation in wheat, while increasing silicon concentrations within plant tissues [77].

3.3.3 Ag nanopriming

Silver nanoparticles (AgNPs) play a pivotal role in modern agriculture due to their multifunctional properties that contribute to enhanced crop productivity. They act as efficient nanopesticides, enabling targeted delivery of active compounds to plants while minimizing unwanted pesticide dispersion and environmental contamination [78]. The exposure of crops to Ag^{2+} containing NPs has been reported to enhance physiological processes by improving germination rate, biomass accumulation and the synthesis of key phytoconstituents [79]. Seed priming with AgNPs has shown promising results in improving wheat tolerance to drought stress. Under the nanopriming, root length exhibits a positive correlation with various drought stress related parameters indicating its central role in enhancing germination and seedling vigor under water limited conditions. Both hydropriming and nanopriming with AgNPs contribute significantly to the plant drought stress responses [38].

The beneficial role of green synthesized AgNPs in improving drought tolerance and yield performance of wheat under different osmotic potentials has been well documented. Treatment with 10 mg L^{-1} AgNPs markedly enhances chlorophyll stability index (CSI), leaf succulence (LS) and leaf potassium content (LK), thereby improving drought tolerance. AgNPs application also promotes stomatal conductance and morphological traits under stress conditions. Since the tillering phase of wheat is particularly susceptible to water deficit, AgNPs confer significant protective effects during this stage, as demonstrated by Sarwar et al. [80]. Although drought stress substantially reduces photosynthetic activity and grain yield per spike, AgNP treatment effectively mitigates these negative impacts. Notably, wheat plants treated with AgNPs produce approximately 22% and 17% more grains per plant under moderate and severe drought respectively, compared with untreated drought stressed plants [38].

In addition to drought tolerance, AgNP seed priming enhances salinity tolerance in wheat. This treatment improves seed germination, seedling establishment, chlorophyll content and photosynthetic efficiency along with regulating endogenous phytohormone balance. These physiological and biochemical adjustments reflect enhanced salinity adaptation induced by AgNPs. Furthermore, AgNP priming alleviates the inhibitory effects of salinity on grain germination and early growth by promoting key metabolic processes and improving water uptake as evidenced by significant increases in germination percentage (GP), shoot length, and other growth parameters [81]. Low dose AgNP priming further elevates the fresh weight of shoots and roots while reducing proline and total soluble carbohydrate accumulation under salt stressed conditions, suggesting improved osmotic adjustment and metabolic balance [82].

3.3.4 Cu based nanopriming

Cu is an essential structural component of many enzymes involved in cellular redox and electron transfer reactions in plants, making it a vital micronutrient capable of boosting growth and development. Recognising this essential fact, CuNPs have recently been developed and examined for their ability to stimulate growth, improve development and disease management in plants [83, 84]. Synthesis of CuNPs has gained popularity due to its availability. The readily accessible nature of copper has made it a more desirable material and shares qualities with other pricey noble metals such as silver and gold. Moreover, CuNPs have been shown to exhibit antibacterial properties against a variety of bacteria and fungi [85]. Wheat seeds primed with 0.16% CuNPs under normal conditions display early germination and the best germination rate compared to all other seeds under control and stress environments [86]. Yasmeen et al. [87] investigated the physiological effects of CuNPs on wheat seeds, found that 25 ppm of NPs activated between 25 and 121 proteins involved in seed germination. As a result, there was an increase in the production of additional chemicals involved in protein and enzyme activation. As therefore, significant physiological support for the association of seed germination and resistance to stress factors has been obtained.

3.3.5 Au based nanopriming

Gold nanomaterials (AuNMs) are one type of metallic nanoparticle that has been widely used due to their distinct physical and chemical features. The introduction of AuNPs into agricultural processes holds promise for long-term and effective crop production as nanotechnology transforms modern agriculture. Gold nanoparticles, due to their distinct physicochemical features, have shown major potential in plant and soil health conditioning [88]. AuNPs have been widely used in this field in recent years which can be generated quickly. When used at microdoses, the particles are typically non-toxic to plants, animals and humans, while it mostly benefits plants. Nowadays, it has recently received a lot of interest as compounds with the potential to improve crop environmental tolerance. In wheat, AuNPs influence growth processes, increase the concentration of photosynthetic pigments and soluble sugars in leaves, and elevate the expression of *COR* and *PSA* genes [89]. The nanopriming seeds not only affect wheat plant metabolism under control conditions, but also cause a variety of extra adaptive modifications during cold hardening. The effect of biosynthesised particles on wheat plants during salt stress improves the K^+/Na^+ ratio, chlorophyll concentration, defence systems, nitrogen absorption, stomatal dynamics and growth characteristics under salt stress conditions. Moreover, the treatment with AuNPs under salt stress prevents the excessive accumulation of oxidative stress indicators including reactive oxygen/nitrogen species [90]. Treatment with AuNPs in cold sustainable wheat genotype Zlata increases resistance to low temperatures after cold hardening. The treatment increases the intensity of growth processes, the quantity of photosynthetic pigments, sucrose in leaves and the expression of encoded *RuBisCo* and *Wcor*15 genes [91].

4 Responses of nanoprimed wheat plants grown under abiotic stresses

In recent years, nanopriming has shown promising potential in enhancing stress tolerance in wheat. When exposed to abiotic stresses, nanoprimed wheat plants exhibit improved physiological and biochemical responses such as enhanced germination, better root-shoot growth and increased antioxidant defense. These responses contribute to greater resilience and stable yield under challenging environmental conditions.

4.1 Morphological changes

Under abiotic stress conditions, NPs induce significant morphological changes in wheat plants that enhance adaptability and performance. Treatment with NPs such as zinc oxide, silicon or iron oxide improves plant height, root length, leaf area and overall biomass even under drought, salinity or heat stress. These particles help to maintain turgor pressure, support sustained cell expansion and delay stress induced senescence, resulting in healthier and more vigorous plants. Enhanced root system architecture including increased root density and branching, allows for better water and nutrient acquisition [30]. Additionally, the improved shoot growth and leaf retention contribute to higher photosynthetic efficiency and yield stability which make NPs effective tools for mitigating the negative impacts of abiotic stress on wheat morphology [69].

4.2 Anatomical changes

Application of NPs can lead to improved root and shoot anatomy including increased root length, thicker epidermis and enhanced vascular tissue development which facilitate better water and nutrient uptake [92]. In leaves, NPs help to maintain chloroplast structure, increase mesophyll thickness and preserve stomatal integrity, thereby sustaining photosynthetic activity under stress. Strengthening of cell walls and enhanced lignification are also observed which improve structural stability and reduce water loss [93]. These anatomical modifications induced by the particles help wheat plants mitigate the adverse effects of drought, salinity and other stresses, ultimately supporting better growth and productivity.

4.3 Physiological and biochemical changes

Nanoparticles induce a range of beneficial physiological changes in wheat plants under abiotic stress conditions that improve the stress tolerance and productivity. Zinc oxide, silicon and selenium NPs enhance water use efficiency, maintain relative water content and stabilize cell membrane integrity in turn reducing the damaging effects of drought and salinity. Nanoprimed wheat plants generally show improved germination rates, better root and shoot growth and enhanced stress tolerance compared to nonprimed plants. They also boost photosynthetic performance by preserving chlorophyll content and improving stomatal conductance by increasing the activity of various enzymes [33, 94].

The environmental stresses disrupt normal biochemical processes in wheat plants, often leading to oxidative stress due to the overproduction of ROS [95]. The imbalance between ROS production and the plant ability to detoxify them results in damage to cellular components including lipids, proteins and nucleic acids. As a result, the activation of various biochemical pathways becomes essential for plant survival under such conditions [96]. Nanopriming has emerged as a promising strategy to enhance the biochemical resilience of wheat under abiotic stress. Nanoparticles in low concentrations stimulate early metabolic activity and induce a state of preparedness in wheat seedlings allowing them to mount a faster and stronger biochemical response when exposed to stress [97]. One of the key biochemical responses observed in nanoprimed wheat under stress is the enhanced activity of antioxidant enzymes. Enzymes such as SOD, CAT and APX are significantly upregulated, helping to scavenge excess ROS and protect cells from oxidative damage [31]. In addition to enzymatic antioxidants, the levels

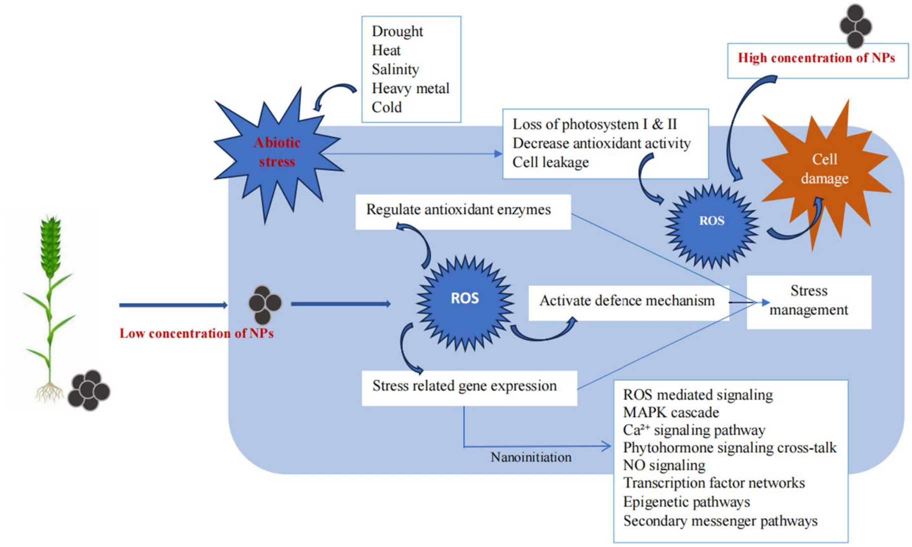

Fig. 3 Schematic representation of nanoparticle mediated stress response pathways in plants.The figure illustrates how different NPs trigger key molecular and physiological responses that enhance stress tolerance in plants. Upon exposure, specific NPs interact with root and leaf tissues, leading to controlled generation of ROS that act as signaling molecules. These signals activate antioxidant defense pathways. In addition, NPs upregulate the expression of key transcription factors which govern downstream stress responsive genes related to ion homeostasis, osmoprotection and detoxification. Collectively, these integrated NP mediated pathways improve plant resilience under abiotic stresses such as salinity, drought, heavy metal toxicity and cold

of non-enzymatic antioxidants such as proline, ascorbic acid and glutathione are also elevated. Proline acts not only as an osmoprotectant but also stabilizes proteins and membranes under stress conditions. Increased levels of these antioxidants contribute to maintaining cellular redox balance and minimizing damage to vital biomolecules [98]. Furthermore, nanoprimed wheat plants under abiotic stress often exhibit altered levels of stress related metabolites. For instance, the enhanced accumulation of soluble sugars, proteins and phenolic compounds is frequently observed. These compounds play roles in osmotic adjustment, enzyme protection and defense against oxidative damage. Nanopriming may also influence the expression of stress responsive genes involved in signal transduction and secondary metabolite biosynthesis, thus contributing to an integrated biochemical response that supports plant adaptation [99].

5 Molecular signaling pathways behind nanoinitiation

Nanoinitiation in plants is the process by which nanomaterials trigger cellular and molecular signaling events that lead to various physiological, biochemical and genetic responses. However, their interactions with plant systems are complex and involve a series of molecular signaling pathways [100]. When nanomaterials enter the plant system through roots, leaves or seed coating, they interact with the cell wall, plasma membrane and intracellular organelles. Depending on their size, charge, composition and surface chemistry, NPs may penetrate cells or remain adsorbed on the cell surface. This interaction acts as a stimulus to trigger signal transduction cascades that resemble responses to abiotic stress or beneficial elicitation (Fig. 3) [101].

5.1 ROS mediated signaling

When NPs are absorbed by plants through roots, leaves or other tissues, they interact with the cell wall, plasma membrane and intracellular organelles which triggering a series of molecular events [19]. These interactions can cause electron transport disturbances in chloroplasts and mitochondria, membrane depolarization and activation of NADPH oxidases on the plasma membrane leading to the production of ROS such as superoxide anion ($O_2\cdot^-$), hydrogen peroxide (H_2O_2) and hydroxyl radicals ($\cdot OH$) [102]. The accumulation of ROS serves as an early signaling cue rather than a mere indicator of stress. The ROS molecules act as secondary messengers that initiate multiple downstream signaling pathways. They activate receptor like kinases (RLKs) and mitogen activated protein kinase (MAPK) cascades which transmit signals to the nucleus [103]. Concurrently, ROS induce changes in cytosolic calcium (Ca^{2+}) concentration; further amplifying the signal through Ca^{2+} binding proteins such as calmodulin (CaM) and calcium dependent protein kinases (CDPKs). These pathways collectively activate redox sensitive transcription factors including *WRKY*, *NAC*, *MYB* and *bZIP*, which regulate the transcription of genes responsible for antioxidant defense, metabolic adjustments and stress adaptation. As a feedback mechanism, antioxidant enzymes like SOD, CAT and APX are upregulated to maintain redox homeostasis and prevent oxidative damage [104].

5.2 MAPK cascade

The MAPK cascade is one of the most important intracellular signaling mechanisms in plants, playing a crucial role in converting extracellular stimuli such as nanoparticles, pathogens, hormones and abiotic stress into specific cellular responses. It functions as a three tiered phosphorylation pathway that amplifies and transduces signals to regulate gene expression and physiological adaptation [105]. The cascade begins when plants perceive external stimuli through receptor like kinases (RLKs) or membrane bound receptors. Upon NPs exposure or other stress signals, these receptors activate the first component of the cascade, MAP kinase kinase kinase (MAPKKK or MEKK). The activated MAPKKK phosphorylates and activates the second kinase, MAP kinase kinase (MAPKK or MKK), which in turn phosphorylates the third component, MAP kinase (MAPK or MPK) [106]. The activated MAPKs then translocate into the nucleus where they phosphorylate specific transcription factors such as *WRKY*, *MYB*, *ERF* and *bZIP*. These transcription factors regulate the expression of downstream stress responsive and defense related genes including those involved in antioxidant defense, hormone biosynthesis and metabolic regulation [107]. Additionally, MAPK signaling is closely integrated with ROS and Ca^{2+} signaling pathways. The ROS generated by nanoparticle interaction or stress act as upstream activators of MAPK cascades, while changes in cytosolic Ca^{2+} levels further modulate MAPKKK activity through calcium dependent protein kinases (CDPKs) [108].

5.3 Calcium (Ca^{2+}) signaling pathway

Calcium serves as a universal secondary messenger in plant cells, playing a key role in translating external stimuli into physiological and molecular responses. During NP absorption, plants experience various physical and chemical interactions that disturb cellular equilibrium, leading to the activation of the Ca^{2+} signaling pathway [109]. When NPs are absorbed through roots or foliar surfaces, they interact with the plasma membrane, cell wall and apoplastic spaces, often causing mild oxidative stress or membrane depolarization. This interaction stimulates plasma membrane bound Ca^{2+} channels and vacuolar Ca^{2+} transporters, resulting in a rapid influx of Ca^{2+} ions into the cytosol from extracellular or intracellular stores such as the vacuole and endoplasmic reticulum [110]. The transient rise in cytosolic Ca^{2+} concentration acts as an early molecular signal which is sensed by Ca^{2+} binding proteins like calmodulin (CaM), calcium dependent protein kinases (CDPKs) and calcineurin B like proteins (CBLs). These Ca^{2+} sensors decode the signal based on the amplitude, frequency and duration of Ca^{2+} spikes. Activated CaM, CDPKs and CBL-CIPK complexes subsequently phosphorylate target proteins, enzymes and transcription factors involved in stress response, metabolism and gene regulation [111]. For instance, these proteins can modulate the activity of MAPK cascades, ROS generating enzymes and antioxidant defense genes. This integration of Ca^{2+} and ROS signaling ensures precise control over plant defense and growth regulation [112]. Ultimately, the Ca^{2+} signaling pathway initiated by NP absorption allows plants to sense and adapt to nano-induced stimuli, regulating cellular homeostasis, enhancing stress tolerance and promoting metabolic adjustments. The reversible nature of Ca^{2+} flux and its tight regulation make the pathway an essential component of the plant molecular response to nanomaterials.

5.4 Phytohormone signaling cross-talk

Phytohormones are key chemical messengers that regulate plant growth, development and stress responses. When plants absorb NPs through roots or leaves, these nanomaterials can alter hormone biosynthesis, transport, perception and signaling leading to hormonal cross-talk. This cross communication enables plants to integrate nano-induced signals into coordinated physiological and molecular responses [113]. Upon nanoparticle entry, plants experience changes in cellular redox status, ion homeostasis and ROS levels. These alterations influence the biosynthetic enzymes and signaling components of major hormones such as auxins (IAA), abscisic acid (ABA), salicylic acid (SA), jasmonic acid (JA), gibberellins (GA), cytokinins (CK) and ethylene (ET) [114]. Nanoparticles like TiO_2 and ZnO enhance auxin signaling by upregulating *AUX/IAA* and *ARF* genes, leading to improved root growth and cell elongation. Similarly, ROS generated during nanoparticle exposure stimulate ABA and SA pathways which help to regulate stomatal movement and activate stress defense genes. These hormone pathways do not act independently but interact synergistically or antagonistically, forming a dynamic signaling network [115]. ABA-SA-JA interactions modulate defense responses under nanoinduced oxidative stress, while auxin-cytokinin balance determines root and shoot development. Nanoparticles can also affect the expression and activity of hormone receptors and transcription factors, thereby influencing downstream gene expression patterns and metabolic adjustments [116]. Through such intricate hormonal cross-talk, the plants integrate signals from multiple pathways to maintain homeostasis, optimize growth and enhance tolerance to nanoparticle induced stress. Thus, nanoparticle absorption triggers a finely tuned hormonal network that translates molecular cues into adaptive physiological outcomes.

5.5 Nitric oxide (NO) signaling

Nitric oxide is a small, gaseous signaling molecule that plays a crucial role in regulating plant growth, development and stress responses. During NP absorption, plants often exhibit altered cellular redox balance and ion fluxes, which stimulate NO biosynthesis and trigger downstream signaling events. This NO mediated signaling acts in coordination with ROS and phytohormones to regulate defense, metabolism and gene expression [117]. When NPs enter plant tissues, they interact with the plasma membrane and intracellular organelles, leading to ROS production and activation of nitric oxide synthase (NOS) like enzymes or nitrate reductase (NR) pathways responsible for NO generation. The transient accumulation of NO acts as a secondary messenger, mediating post translational modifications such as S-nitrosylation and tyrosine nitration of proteins, thereby modulating the activity and function. NO also interacts synergistically with ROS to form signaling molecules like peroxynitrite ($ONOO^-$) which influence cellular redox status and activate stress related pathways. These redox changes further stimulate MAPK cascades, leading to the phosphorylation of transcription factors that regulate genes involved in antioxidant defense, ion transport and stress tolerance [118]. Moreover, NO signaling cross-talks with phytohormonal pathways, particularly ABA, SA and JA, coordinating responses to abiotic and biotic stresses induced by NP exposure. This integration ensures fine regulation of stomatal behavior, defense gene activation and metabolic adaptation.

5.6 Gene expression and transcription factor networks

Nanoparticle absorption in plants initiates a wide range of molecular and genetic responses that modify gene expression and activate complex transcription factor (TF) networks. These changes allow plants to perceive and adapt to the stress or stimuli induced by nanomaterials, ultimately influencing growth, metabolism and defense mechanisms [119]. When NPs are absorbed through roots or leaves, they interact with cellular membranes and organelles, leading to the generation of ROS, NO and fluctuations in cytosolic calcium (Ca^{2+}). These signaling molecules activate various intracellular pathways such as MAPK cascade and CDPKs, which serve as key intermediates in transmitting signals to the nucleus [120]. Inside the nucleus, these pathways stimulate the activation or repression of transcription factors that regulate stress and growth related genes. Major transcription factor families include *WRKY*, *NAC*, *MYB*, *bZIP*, *ERF* and *AP*2 in which *WRKY* and *NAC* regulate genes associated with defense, senescence and oxidative stress management [121]. *MYB* and *bZIP* control secondary metabolism and antioxidant enzyme expression. *ERF* and *AP*2 are linked to ethylene signaling and stress adaptation. These transcription factors bind to specific promoter regions, modulating the transcription of genes encoding antioxidant enzymes (SOD, CAT, APX), heat shock proteins, transporters and metabolic enzymes [122]. In addition, NPs can induce epigenetic modifications such as DNA methylation and histone acetylation which further alter gene expression patterns that leading to long term physiological adjustments.

5.7 Epigenetic and secondary messenger pathways

Nanoparticle absorption in plants triggers a cascade of molecular responses that influencing both epigenetic regulation and secondary messenger pathways. These mechanisms play vital roles in fine tuning gene expression, maintaining cellular homeostasis and facilitating adaptive responses to nanoinduced stimuli. When NPs enter plant cells through roots or leaves, they cause oxidative and ionic imbalances, leading to the production of ROS, NO and alterations in calcium (Ca^{2+}) fluxes. These molecules function as secondary messengers to transmit signals from the cell surface to the nucleus. The interaction among the messengers activates downstream kinases such as MAPKs and CDPKs which regulate transcription factors and stress responsive gene expression. This signaling cross-talk forms the basis of rapid cellular communication and defense activation during NP exposure [123]. Concurrently, NPs can induce epigenetic modifications to cause more stable and heritable changes in gene activity. These include DNA methylation, histone modifications and changes in chromatin structure which collectively influence transcriptional accessibility [124]. Nanoparticles may also affect small RNAs in turn altering post transcriptional regulation of stress and metabolism related genes. Such epigenetic reprogramming enables plants to remember previous nanoinduced stresses, providing a form of molecular priming or acquired tolerance [125]. Together, the secondary messenger networks provide rapid signal transduction while epigenetic mechanisms ensure long term adaptation and stability of gene expression. The integration of these pathways allows plants to coordinate immediate responses and sustained resilience under NP exposure, balancing growth, defense and environmental adaptation.

6 Role of nanopriming on yield and nutritional value

Nanopriming plays a significant role in enhancing the yield and nutritional value of wheat by improving germination, early seedling vigor and stress resilience. It facilitates better water uptake, accelerates metabolic activity and promotes uniform emergence, resulting in stronger root and shoot growth [126]. Nanoparticles such as zinc oxide, iron oxide and nanosilicon improve nutrient uptake and photosynthetic efficiency that leads to increased biomass, spike formation and grain weight [127]. Additionally, nanopriming enriches wheat grains with essential micronutrients including zinc, iron and selenium, improves protein content and enhances antioxidant activity, thereby contributing to both higher yield and improved grain quality under optimal and stress conditions.

7 Nanopriming for seed protection

Nanopriming offers an effective strategy for seed protection in wheat by enhancing resistance against seed borne pathogens and improving tolerance to abiotic stresses during early growth stages. The application of NPs such as silver, copper oxide or zinc oxide during seed priming imparts antimicrobial properties that inhibit the growth of fungal and bacterial pathogens, thus reducing seed decay and improving seedling survival [128]. Additionally, nanoprimed seeds exhibit enhanced antioxidant enzyme activity, better membrane stability and improved stress responsive signaling which collectively strengthen the plant defense mechanisms [129]. This protective effect not only ensures healthier germination but also contributes to robust plant establishment and subsequent yield stability.

8 Biofortification

Biofortification of wheat using NPs is an advanced and sustainable approach to enhance the nutritional quality of wheat grains by improving the uptake, transport and accumulation of essential micronutrients such as Fe, Zn, Se and Cu. Nanoparticles act as efficient nutrient delivery systems due to their small size, high surface area and controlled release properties which significantly increase nutrient bioavailability in plants [130]. When NPs such as ZnO, Fe_2O_3, Se or nanochelated fertilizers are applied to soil or as foliar sprays, they are absorbed by plant roots or leaves and translocated through the xylem and phloem [131]. Once inside plant tissues, NPs slowly release ions which participate in various metabolic and signaling pathways to enhance enzyme activity, chlorophyll synthesis and grain filling processes. At the molecular level, nanoparticle absorption triggers ROS, calcium and MAPK signaling pathways which modulate gene expression related to metal transporters and storage proteins, thereby facilitating the efficient deposition of nutrients in grains [18].

The process improves the nutritional quality of food crops by increasing their content of essential micronutrients like Fe, Zn, Se and Cu [132]. In recent years, nanotechnology has emerged as a powerful tool to enhance the efficiency of biofortification through the use of NPs. These ultra-small particles possess unique physicochemical properties such as a high surface area, enhanced reactivity and controlled release capacity which make them ideal for improving nutrient delivery and uptake in plants [133]. Usually, NPs act as novel nutrient carriers that improve the solubility, stability and bioavailability of micronutrients within soil-plant systems. When used alone or in combination with traditional fertilizers, NPs facilitate precise and efficient nutrient management [134]. Nowadays, the NPs in biofortification include ZnO, Fe_2O_3, CuO, TiO_2 and SiO_2, which can be applied to crops through soil amendment, foliar spraying or seed priming. Moreover, NP mediated method has been shown to effectively enrich staple crops such as wheat, rice, maize and legumes with vital micronutrients, thereby addressing widespread mineral deficiencies in human populations [135].

The mechanism by which NPs mediated biofortification involves several interrelated processes. Firstly, the particles increase nutrient availability by gradually dissolving in soil or on plant surfaces, providing a controlled and sustained release of nutrients [136]. Their small size allows to remain suspended for longer periods and interact more effectively with plant root surfaces. Once absorbed, NPs can enter root cells through pores, ion channels or endocytosis and are translocated through the xylem and phloem to various plant organs including edible parts like grains, leaves and fruits [137]. When applied as foliar sprays, NPs can also penetrate the cuticle and stomata of leaves, allowing direct nutrient absorption even under nutrient deficient soil conditions. Inside plant cells, they stimulate enzymatic and metabolic activities related to photosynthesis, respiration and nutrient metabolism [138]. The NPs can also influence the expression of genes responsible for nutrient transport and storage, leading to enhanced accumulation of micronutrients in edible plant parts. Additionally, it may interact with secondary messengers such as NO, ROS and Ca^{2+} which regulate signaling pathways involved in nutrient assimilation and stress responses [139].

The use of NPs in biofortification offers multiple benefits for agriculture and nutrition. One major advantage is enhanced nutrient use efficiency as the particles provide a slow and steady nutrient release, reducing losses from leaching or volatilization [140]. Their ability to deliver nutrients in a targeted and controlled manner ensures that specific plant parts receive optimal nutrient concentrations. Nanobiofortification also improves overall crop yield and quality by enhancing photosynthetic activity and physiological performance [141]. Environmentally, the approach promotes sustainability, since lower fertilizer inputs reduce soil and water contamination. Furthermore, NPs can enhance plant tolerance to various stresses such as drought, salinity and pathogen attacks, leading to more stable crop production under changing environmental conditions [142]. Due to the compatibility with various agricultural technologies, nanoformulations can be integrated with biofertilizers or genetic biofortification methods to produce synergistic effects [143].

9 Sustainable agriculture

Nanoparticles play a vital role in promoting sustainable agriculture in wheat by enhancing productivity, improving resource use efficiency and minimizing environmental impact. Their application in the form of nanofertilizers ensures targeted and controlled nutrient delivery, reducing fertilizer losses and increasing nutrient uptake by wheat plants [140]. Nanoparticles also support plant health by enhancing resistance to biotic and abiotic stresses including pathogens, drought and salinity, thereby reducing the need for chemical pesticides and promoting eco-friendly cultivation [144]. Additionally, they contribute to soil health preservation by minimizing leaching and runoff that ensuring long term fertility. Through improved germination, better stress tolerance and micronutrient biofortification, NPs help to achieve higher yields and nutritional quality while conserving resources in turn making wheat production more resilient and sustainable.

10 Conclusion

Being a staple food crop, wheat requires careful consideration of cultivation practices to ensure sustainable production. However, various abiotic stresses pose significant challenges to wheat growth and yield. To address these issues, nanopriming has emerged as a promising solution. Nanoparticles have the ability to penetrate plant tissues and influence multiple biological pathways. This interaction can lead to modifications in the morphological, anatomical, physiological, biochemical and molecular responses in plants that enhances the stress tolerance. Thus, nanopriming offers an effective strategy to mitigate stress related problems in wheat cultivation contributing to improved productivity and resilience.

Abbreviations

NPs	Nanoparticles
SOD	Superoxide dismutase
CAT	Catalase
APX	Ascorbate peroxidase
GPX	Glutathione peroxidase
PRDX	Peroxiredoxine
GB	Glycine betaine
GABA	Gamma-aminobutyric acid
GA	Gibberellins
CK	Cytokinins
ET	Ethylene
ABA	Abscisic acid
SA	Salicylic acid
EMS	Ethyl methanesulphonate
RLKs	Receptor like kinases
CaM	Calmodulin
CDPKs	Calcium dependent protein kinases
MAPK	Mitogen activated protein kinase
JA	Jasmonic acid
IAA	Indole-3-acetic acid
ROS	Reactive oxygen species
CSI	Chlorophyll stability index
LS	Leaf succulence

LK	Leaf potassium content
CBLs	Calcineurin B like proteins

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Author contributions

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Declarations

Ethics approval and consent to participate

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