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Enhancing Drought Tolerance in Food Crops: Recent Non-genetic Engineering Strategies

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ABSTRACT: This review synthesizes recent advances in non-genetic engineering strategies to enhance crop drought tolerance, focusing on phytohormones, priming, bioaugmentation, non-phytohormone organic supplementation, and inorganic supplementation. Across these approaches, drought resilience is consistently improved through coordinated regulation of antioxidant defense, osmotic adjustment, photosynthetic stability, water-use efficiency, and stress-responsive gene networks. Phytohormone applications, particularly melatonin, brassinosteroids, and jasmonates, enhanced drought tolerance by reducing reactive oxygen species and lipid peroxidation while strengthening antioxidant systems. Melatonin increased ascorbate (16.35%) and glutathione (91.49%) contents in kiwifruit and elevated antioxidant enzyme activities by up to 10.35% to 110.41% in oat seedlings. Photosynthetic performance also improved substantially, with net photosynthesis in brassinosteroid-treated plants increasing from 2.01 to 6.1 μmol $CO_2/m^2/s^1$. Drought priming induced stress memory, improving hydraulic regulation and photosynthetic resilience, with recurrent priming increasing leaf water retention by 21.88% in tea plants. Bioaugmentation using arbuscular mycorrhizal fungi enhanced root volume by 172.11% in citrus and increased maize biomass by up to 1,189 to 2,062 g/plant under drought. Antioxidant enzyme activities were enhanced by up to 98.63%. Organic supplementation (e.g., seaweed extracts, fulvic acid, ethanol) improved leaf water content by ~50% and stomatal conductance by 46%, while inorganic amendments such as silicon and potassium increased yield by up to 55% and water-use efficiency by over 100% in some systems. Nanoparticles (ZnO, TiO_2, CeO_2) further improved drought tolerance but exhibited dose-dependent effects. Overall, integrated bioaugmentation and inorganic supplementation emerge as the most scalable strategies, while priming and phytohormones offer high mechanistic efficacy.

KEYWORDS: Arbuscular mycorrhizal fungi; bioaugmentation; organic supplementation; phytohormone; priming; seaweed extract; silicon

1. Introduction

Drought stress is widely recognized as one of the most severe constraints on global agricultural productivity, posing a direct threat to food security in both rainfed and irrigated systems. Increasing frequency, duration, and intensity of drought events, driven by climate change and

land-use pressures, have exacerbated yield instability in major food crops such as wheat, rice, maize, and legumes [1, 2]. For instance, global average yields for maize have decreased by roughly 11.6% and wheat by 9.2% due to drought and heat impacts. Furthermore, legumes face significant harvest instability, with documented drought-related losses averaging around 12.4% globally [3]. Unlike other abiotic stresses, drought affects plants at multiple organizational levels simultaneously, disrupting water relations, impairing photosynthetic efficiency, altering nutrient uptake, and inducing oxidative stress. These physiological disruptions collectively reduce biomass accumulation, reproductive success, and ultimately grain yield [4]. Given that agriculture must feed a growing global population under increasingly water-limited conditions, improving drought tolerance in crops has become a central objective of modern plant science and agronomic innovation.

Traditional approaches to improving drought tolerance have largely relied on genetic improvement strategies, including conventional breeding and, more recently, molecular breeding and genetic engineering [5, 6]. Conventional breeding has successfully produced drought-tolerant cultivars by selecting for favorable traits such as deeper root systems, improved stomatal regulation, and enhanced water-use efficiency. However, these approaches are often time-consuming, limited by genetic variability, and constrained by the complex polygenic nature of drought tolerance [7, 8]. The emergence of genetic engineering and genome editing tools, such as CRISPR/Cas systems, has enabled more precise manipulation of drought-responsive genes, including those involved in abscisic acid (ABA) signaling, osmolyte biosynthesis, and transcriptional regulation (e.g., DREB/CBF pathways) [9]. Despite their promise, these technologies face regulatory challenges, public acceptance issues, and limitations in translating laboratory success into field performance due to environmental variability and genotype–environment interactions.

In parallel with genetic approaches, a wide range of non-genetic engineering strategies has emerged as a practical and often faster alternative to enhance drought tolerance. These strategies do not modify the plant genome but instead modulate plant physiology, biochemistry, and stress signaling pathways through external applications or management interventions [10]. Among the most widely studied are plant growth regulators (PGRs), including phytohormones such as brassinosteroids (BRs), jasmonates (JA), auxins (IAA), and melatonin. These compounds regulate stomatal behavior, antioxidant defense systems, osmotic adjustment, and gene expression associated with stress responses [11]. Another important category of non-genetic strategies includes the application of biostimulants derived from natural sources, such as seaweed extracts, humic substances, protein hydrolysates, and microbial inoculants. These substances enhance plant resilience by stimulating root growth, improving nutrient uptake, and inducing systemic tolerance responses [12, 13]. In addition, mineral-based amendments, including nanoparticles such as silicon and zinc oxide, have attracted increasing attention for their ability to modulate reactive oxygen species (ROS), enhance antioxidant enzyme activities, and improve photosynthetic efficiency under drought conditions. These nanomaterials often function as “nano-primers,” activating stress defense mechanisms without altering the plant genome [14, 15].

Seed priming and stress priming techniques also represent effective non-genetic engineering approaches. These methods expose seeds or plants to mild stress or chemical treatments that “prime” physiological systems, enabling faster and stronger responses to subsequent drought exposure. Priming can enhance antioxidant capacity, improve hormonal

balance, and induce stress memory through epigenetic and metabolic adjustments [16, 17]. Furthermore, bioaugmentation of the rhizosphere through beneficial microbial inoculation has emerged as a powerful strategy to enhance drought tolerance. In particular, arbuscular mycorrhizal fungi (AMF) form symbiotic associations with plant roots, extending the effective root surface area and significantly improving water and nutrient acquisition under water-limited conditions [18]. AMF colonization has been shown to enhance soil–plant hydraulic conductivity, improve soil aggregation through glomalin production, and increase the uptake of phosphorus and micronutrients, all of which contribute to better plant performance under drought stress [19].

Despite the growing body of research on these individual approaches, existing literature remains fragmented and largely discipline-specific. Many reviews focus on individual compounds, isolated mechanisms, or specific crop species, without integrating findings into a unified framework to enhance non-genetic drought tolerance [20, 21]. For instance, Liu et al. [22] provide a useful synthesis of plant growth-promoting bacteria (PGPB)-mediated drought tolerance mechanisms across different crops, but it remains largely limited in scope by its exclusive focus on microbial interventions within the rhizosphere. Similarly, the review by Iqbal et al. [23] focuses on the role of phytohormones in enhancing drought tolerance in crops, primarily as mechanisms triggered by strategies such as bioaugmentation and exogenous chemical applications, without systematically presenting and evaluating these strategies. Farooq et al. [24] outline a wide range of plant responses to drought stress. Their review does not aim to present strategies to enhance drought tolerance in crops and the underlying mechanisms. The review by Ferioun et al. [25] has a crop-specific focus, concentrating primarily on barley and therefore providing limited insight into drought-tolerance strategies applicable across diverse food crops. While the review discusses drought impacts and the use of drought-tolerant genotypes and PGPB, it does not develop a broader framework for non-genetic engineering interventions in agricultural systems. Moreover, there is limited comparative analysis of the effectiveness, mechanisms, and practical applicability of different non-genetic strategies across physiological, biochemical, and molecular levels. This lack of synthesis makes it difficult to evaluate the relative advantages, limitations, and synergistic potential of different approaches in real agricultural systems.

The present review addresses this gap by providing a comprehensive and integrative analysis of non-genetic engineering strategies to enhance drought tolerance in food crops. Unlike previous reviews that have focused narrowly on specific treatments such as phytohormones or nanoparticles, this work systematically categorizes and compares multiple intervention strategies, including phytohormones, organic supplementation, inorganic supplementation, priming techniques, and bioaugmentation. The novelty of this review lies in its integrative perspective that bridges physiological, biochemical, and emerging molecular insights to explain how non-genetic interventions collectively enhance drought resilience. In addition, it highlights recent advances in nanotechnology and biostimulant research, which represent rapidly evolving frontiers in crop stress biology yet remain underrepresented within traditional drought-tolerance practices.

The primary aim of this review is to synthesize current knowledge on non-genetic engineering approaches and evaluate their mechanisms of action, effectiveness, and potential for field applications in major food crops. Specifically, it seeks to (i) classify major categories of non-genetic drought mitigation strategies, (ii) elucidate their physiological, biochemical, and

molecular mechanisms, (iii) compare their effectiveness across different crop systems where data are available, and (iv) identify knowledge gaps and future research directions for optimizing their integration into sustainable agricultural practices. By doing so, this review aims to provide insights to help researchers and agronomists better understand and deploy non-genetic strategies as part of integrated drought management systems.

2. Phytohormones

Recent advances in the use of phytohormones to enhance drought tolerance in crops have increasingly shifted from simple growth stimulation toward targeted modulation of stress-responsive physiological, biochemical, and molecular networks. Among the phytohormones and hormone-like compounds investigated, melatonin, BRs, JA, and their analogs have emerged as particularly effective in improving crop resilience under water deficit conditions [26, 27]. Current research trends emphasize the optimization of hormone concentration, timing, and application methods, together with the integration of transcriptomics and metabolomics to elucidate the regulatory pathways involved in drought adaptation. These studies collectively demonstrate that exogenous phytohormones not only alleviate drought-induced damage but also reprogram stress signaling, antioxidant metabolism, osmotic adjustment, and photosynthetic machinery to sustain crop productivity under limited water availability.

One of the major advances in this field is the recognition that phytohormones function as central regulators of ROS homeostasis and membrane stability during drought stress [28]. Water deficit commonly induces excessive ROS accumulation, resulting in oxidative damage, lipid peroxidation, chlorophyll degradation, and impaired photosynthesis [29]. Exogenous melatonin application has consistently been shown to mitigate oxidative stress through both enzymatic and non-enzymatic antioxidant systems. In wheat, melatonin treatments reduced H_2O_2 and malondialdehyde (MDA) accumulation while enhancing catalase (CAT) and peroxidase (POD) activities, resulting in improved shoot relative water content and survival under drought conditions [30]. Similar responses were observed in kiwifruit, where melatonin increased the contents of reduced ascorbate and glutathione by 16.35% and 91.49%, respectively, while maintaining higher ascorbate/dehydroascorbate and glutathione/glutathione disulfide ratios under drought stress [31]. Enhanced activities of enzymes associated with the ascorbate–glutathione cycle, including ascorbate peroxidase (APX), monodehydroascorbate reductase (MDAR), and dehydroascorbate reductase (DHAR), further strengthened ROS detoxification capacity. Likewise, in naked oat seedlings, melatonin pretreatment significantly reduced ROS accumulation while increasing superoxide dismutase (SOD), POD, CAT, and APX activities by 110.41%, 34.29%, 26.14%, and 10.35%, respectively, relative to drought-stressed plants [32]. These findings indicate that modern phytohormone-based strategies primarily function by reinforcing cellular antioxidant defense systems to maintain membrane integrity and metabolic stability during drought.

Another important trend is the enhancement of photosynthetic performance and water-use efficiency through hormonal regulation. Drought stress typically suppresses stomatal conductance, transpiration, chlorophyll synthesis, and carbon assimilation, thereby reducing biomass accumulation and yield [33]. Exogenous phytohormones have demonstrated substantial capacity to maintain photosynthetic activity under these adverse conditions. Melatonin-treated wheat plants exhibited increases of 11.52–17.30% in plant height and approximately 35–38% in seed weight per panicle under drought stress, indicating improved

assimilate production and reproductive performance [30]. In coffee seedlings, 300 μM melatonin maintained higher photosynthetic rate, stomatal conductance, and carboxylation efficiency during water deficit and facilitated rapid recovery after rehydration [34]. Similarly, the BR analog DI-31 markedly improved photosynthetic efficiency in drought-stressed lulo plants, increasing net photosynthesis from 2.01 to 6.1 μmol CO_2 m^{-2} s^{-1} and intrinsic water-use efficiency from 61.5 to 131.3 μmol CO_2 mmol H_2O^{-1} at an application rate of 8 mL/L [35]. Improvements in chlorophyll fluorescence parameters, including increases in Fv/Fm (variable fluorescence-to-maximum fluorescence ratio) and photochemical quenching, accompanied by simultaneous reductions in non-photochemical quenching, further indicate that phytohormones protect PSII from drought-induced photoinhibition [34−36]. These physiological improvements collectively contribute to enhanced biomass production, leaf expansion, and yield stability under water-limited conditions.

Recent studies also highlight the role of phytohormones in osmotic regulation and carbon metabolism. Maintenance of cellular water balance is a crucial component of drought tolerance, and phytohormone treatments frequently enhance osmolyte accumulation, root growth, and carbohydrate redistribution. In *Brassica rapa*, exogenous BR and JA significantly increased soluble sugars, glycine betaine, anthocyanins, and relative water content under drought stress, while simultaneously stimulating root elongation and water-use efficiency [37]. In coffee, melatonin promoted the accumulation of sucrose and total soluble sugars in roots during drought, suggesting enhanced carbon allocation to the root system to improve water uptake and survival [34]. Likewise, DI-31-treated lulo plants showed substantial increases in relative water content and equivalent water thickness, reflecting improved water retention and osmotic adjustment [35]. Such responses indicate that phytohormones contribute to drought adaptation not only by protecting cellular structures but also by optimizing resource allocation and maintaining plant water relations.

At the molecular level, transcriptomic and gene expression analyses have significantly advanced the understanding of hormone-mediated drought tolerance mechanisms [38]. Modern research increasingly integrates RNA-seq approaches to identify drought-responsive genes, signaling pathways, and transcription factors regulated by phytohormones. In wheat, melatonin induced the differential expression of 2796 genes under drought stress, with enrichment in pathways related to protein phosphorylation, hormone signaling, phenylpropanoid biosynthesis, starch and sucrose metabolism, and cutin/suberin/wax biosynthesis [30]. Importantly, melatonin influenced JA-related signaling and activated transcription factors such as MYB, NAC, WRKY, AP2/ERF, bZIP, bHLH, and HSF, which are known regulators of stress adaptation. In kiwifruit, melatonin upregulated antioxidant- and carotenoid-related genes, including *APX*, *DHAR*, *PSY*, *PDS*, *LYC*, *ZDS*, *CAT1*, and *CAT6* [31]. Similarly, drought-stressed oat seedlings treated with melatonin exhibited enhanced MAPK signaling and increased expression of stress-responsive transcription factors, including WRKY1 and MYB [32]. These findings demonstrate that phytohormones function as signaling molecules capable of orchestrating broad transcriptional reprogramming to improve drought resilience.

A further emerging trend is the use of hormone combinations and optimized dosage strategies to maximize stress tolerance. Studies consistently show that hormonal effects are dose-dependent, with moderate concentrations often producing the greatest benefits. For example, 300 μM melatonin was more effective than 500 μM in improving drought tolerance in coffee seedlings, suggesting that excessive concentrations may disrupt metabolic balance

[34]. Similarly, the strongest drought-tolerance responses in lulo plants occurred at 4–8 mL/L DI-31, whereas lower concentrations produced smaller effects [35]. Combined applications of BR and JA in *Brassica rapa* also generated synergistic responses, particularly in antioxidant activity and osmotic adjustment, indicating that multi-hormone strategies may enhance stress tolerance more effectively than single-hormone treatments [37]. This reflects a broader shift toward integrated hormonal regulation approaches that target multiple stress-response pathways simultaneously.

Overall, recent developments demonstrate that phytohormones represent highly promising non-genetic engineering tools for enhancing drought tolerance in crops. Their effectiveness is associated with coordinated improvements in antioxidant defense, osmotic adjustment, photosynthetic efficiency, nutrient metabolism, root development, and stress-responsive gene regulation. Advances in omics technologies are further revealing the complex signaling networks underlying these responses, paving the way for precision hormone-based strategies in climate-resilient agriculture. Table 1 summarizes the applications of phytohormones to enhance drought tolerance in food crops.

Table 1. Enhancing Drought-Tolerance in Food Crops Through the Use of Phytohormones.

Plant species/System	Treatment	Experimental conditions & key drought effects	Effects of exogenous treatment	Ref.
Wheat (*Triticum aestivum*) varieties (Chinese Spring, Shi4185, Hanxuan10, Chang6878)	Melatonin (50–1000 μM; optimum 100 μM)	PEG6000 hydroponic and soil drought experiments; drought reduced growth, survival, and water status and increased ROS and MDA	100 μM melatonin improved growth, yield (grain traits +9.5–38.3%), survival, and water status; reduced H_2O_2/MDA; enhanced CAT/POD and regulated 4400 differentially expressed genes (DEGs) associated with JA signaling, osmotic adjustment, and stress responses	[30]
Kiwifruit seedlings	Melatonin (100 μM)	Drought with/without melatonin pretreatment; relative water content declined from 80.23% to 56.40%, with increased H_2O_2 and MDA	Maintained higher water content (76.71%), reduced H_2O_2/MDA, increased the contents of reduced ascorbate and glutathione, enhanced antioxidant enzymes and carotenoids, and reduced transcriptional disruption	[31]
Coffee (*Coffea arabica*) seedlings	Melatonin (300 and 500 μM)	Water deficit followed by rehydration; drought reduced water potential, photosynthesis, chlorophyll, and growth	300 μM improved water status, biomass, gas exchange, sugars, APX and ascorbate, while reducing MDA and improving post-drought recovery; 500 μM was less effective	[34]
Apple ('Naganofuji No.2')	Melatonin (100 μM, soil application)	60-day controlled drought; growth parameters decreased by 22.9–40.2%	Reduced electrolyte leakage and H_2O_2; increased photosynthesis (2.34-fold), nutrient uptake (5.3–29.2%), and N-metabolism enzyme activities	[36]
Naked oat (*Avena nuda*) seedlings	Melatonin (100 μM pretreatment)	PEG6000-induced hydroponic drought; H_2O_2 and $O_2^{\bullet-}$ increased by 208.98% and 257.32%, respectively	Improved growth, reduced ROS (~13.7%), enhanced SOD, POD, CAT and APX activities, and strongly upregulated *Aspk11* (+29.45-fold)	[32]
Brassica rapa genotypes	BR (0.01 μM), JA (10 μM), BR+JA	Controlled drought; photosynthesis, water content, and protein declined by 86–89%, 52–58%, and 77–79%, respectively	BR/JA, particularly combined treatment, improved root growth, water status, pigments, osmolytes, and antioxidant activity while reducing ROS and membrane damage	[37]
Lulo (*Solanum quitoense*) seedlings	BR analog DI-31 (1–8 mL/L)	Pot water-deficit conditions; drought reduced water status, photosynthesis, pigments, and biomass and increased MDA	DI-31 (4–8 mL L^{-1}) improved water content (46.3–54.7%), biomass, photosynthesis, water-use efficiency and Fv/Fm; reduced MDA and increased drought tolerance index to 69%	[35]

3. Priming

Recent advances in drought priming research have demonstrated that controlled pre-exposure to abiotic stress or signaling agents can substantially enhance drought tolerance in crops by inducing long-lasting physiological, biochemical, metabolic, and molecular "stress memory." Unlike conventional drought management approaches that primarily focus on mitigating damage after stress onset, priming strategies prepare plants for future water deficits through adaptive reprogramming of cellular processes [39]. Current trends increasingly emphasize recurrent drought priming, metabolic priming, and nanopriming approaches, integrated with transcriptomics, metabolomics, and gene regulatory analyses to elucidate the mechanisms underlying acquired drought tolerance. These developments position priming as a promising non-genetic engineering strategy for climate-resilient agriculture.

One of the major emerging trends in drought priming is the concept of stress memory, whereby repeated mild drought exposure induces long-term acclimation that improves plant performance during subsequent severe stress events. Recurrent drought cycles have been shown to enhance hydraulic regulation, water conservation, and photosynthetic resilience in multiple crops. In coffee, repeated drought priming enabled plants to maintain higher predawn leaf water potential, reduced disruption of leaf hydraulic conductivity, and improved net CO_2 assimilation under water deficit compared with plants experiencing a single drought episode [40]. Similarly, repeated drought exposure in tea plants increased leaf water retention capacity by 21.88% relative to non-primed drought-stressed plants while alleviating declines in chlorophyll fluorescence and photosynthetic pigments [41]. These findings indicate that drought priming enhances the capacity of plants to sustain water balance and protect photosynthetic systems during subsequent stress episodes.

Physiological acclimation induced by priming is closely associated with structural and morphological adjustments that improve water conservation. Recent studies have shown that primed plants frequently develop enhanced cuticular barriers, altered stomatal behavior, and improved root–shoot hydraulic coordination [40−42] (Figure 1). In potato, drought acclimation cycles reduced leaf wilting and induced thicker cuticular layers and more open stomata during stress, thereby improving water-use regulation under drought conditions. Genotype-dependent responses were also evident, as drought-resistant genotypes exhibited greater stem water content and faster post-stress recovery, highlighting the importance of hydraulic buffering and tissue water storage in priming-induced tolerance [43]. Such acclimatory responses suggest that priming not only modifies short-term stress responses but also induces persistent structural adaptations that enhance drought resilience.

A major advance in priming research is the identification of extensive metabolic reprogramming associated with acquired drought tolerance. Primed plants commonly accumulate compatible solutes, osmoprotectants, amino acids, flavonoids, and antioxidant metabolites that stabilize cellular structures and maintain osmotic balance under water deficit (Figure 1). Repeated drought priming in coffee promoted the accumulation of amino acids, tricarboxylic acid (TCA) cycle intermediates, glycerol, galactose, myo-inositol, proline, phenylalanine, cinnamic acid, and caffeate, all of which are associated with osmotic adjustment and antioxidant defense [40]. Likewise, drought-primed tea plants showed increased levels of amino acids, flavonoids, theaflavins, alkaloids, organic acids, and L-theanine, reflecting broad metabolic adaptation to repeated stress exposure [41]. These metabolic adjustments enhance

cellular osmoprotection, stabilize proteins and membranes, and improve ROS scavenging capacity during drought.

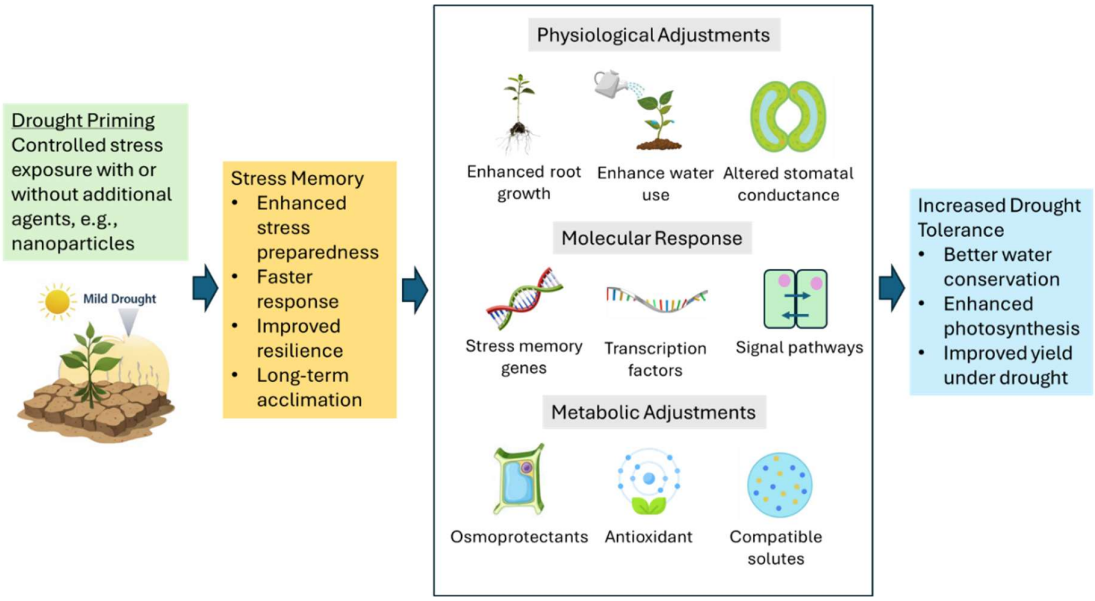

Figure 1. Mechanisms of Drought Priming for Drought Tolerance Enhancement in Crops.

Among the metabolic pathways identified, flavonoid biosynthesis has emerged as a particularly important mechanism underlying priming-induced drought tolerance. Recent work in tea plants demonstrated that moderate drought priming specifically activated flavonoid biosynthesis pathways, leading to enhanced drought adaptation through transcriptional and metabolic reprogramming [44]. Functional analyses confirmed that flavonoid accumulation contributed directly to drought tolerance, while transcription factors CsYABBY1 and CsMYB114 acted synergistically to activate flavonoid biosynthesis genes, including *CsCHS*, *CsCHI*, *CsFLS*, *CsDFR*, *CsANS*, and *CsANR*. This coordinated transcriptional regulation redirected metabolic flux toward flavonoid production, strengthening antioxidant defense and stress acclimation [44]. These findings highlight a broader trend in priming research toward identifying key regulatory hubs that mediate acquired drought tolerance through secondary metabolism.

The enhancement of antioxidant defense systems is another central mechanism underlying drought priming. Water deficit commonly induces excessive ROS accumulation, leading to oxidative damage, membrane lipid peroxidation, and photosynthetic impairment. Priming strategies frequently induce a controlled ROS burst during the priming phase, which subsequently activates antioxidant defense pathways and improves ROS homeostasis during later stress exposure. In wheat, silver nanoparticle (AgNP) priming triggered a rapid but transient ROS increase accompanied by 1.5–2.5-fold increases in CAT and POD activities shortly after treatment [42]. During subsequent drought stress, ROS accumulation and MDA levels were significantly lower in primed plants than in untreated controls, indicating enhanced oxidative stress mitigation. Similar antioxidant acclimation was observed in drought-primed coffee and tea plants, where activities of enzymes such as SOD, APX, glutathione reductase, and catalase were enhanced or more effectively regulated under repeated drought exposure

[40,41]. Collectively, these studies suggest that priming strengthens antioxidant preparedness, enabling plants to better manage oxidative stress during drought.

At the molecular level, drought priming is increasingly recognized as a transcriptionally regulated process involving stress memory genes, signaling pathways, and transcription factor networks (Figure 1). Transcriptomic analyses have revealed that repeated drought exposure induces extensive reprogramming of genes associated with photosynthesis, hormone signaling, carbohydrate metabolism, amino acid biosynthesis, and phenylpropanoid pathways [40, 41, 45]. In tea plants, weighted gene co-expression network analysis identified AP2/ERF, MYB, NAC, WRKY, and bHLH transcription factors as central regulators of drought memory and metabolic adaptation [41]. Similarly, repeated drought cycles in coffee induced stronger expression of drought-responsive genes, such as RD29B and RD22, than single drought events, supporting the concept of transcriptional memory [40]. The identification of transcriptional regulators such as CsYABBY1 and CsMYB114 further demonstrates that priming-induced tolerance involves coordinated gene regulatory networks that modulate both primary and secondary metabolism.

Recent developments also indicate a growing interest in integrating nanopriming technologies with conventional drought priming approaches. Nanopriming with low nanoparticle concentrations has emerged as a novel strategy to enhance drought tolerance by controlled activation of stress signaling pathways. In wheat, low-dose AgNP priming of the foliar at the third leaf stage improved leaf water potential, photosynthetic efficiency, and shoot and root biomass, ultimately increasing grain yield by approximately 12% under drought conditions [42]. Importantly, the responses were concentration-dependent, as higher nanoparticle concentrations caused chlorophyll degradation, PSII inhibition, and growth suppression. This highlights the importance of optimizing priming intensity and dosage to maximize beneficial stress acclimation while avoiding toxicity.

Additionally, seed priming has emerged as a practical and cost-effective strategy to enhance drought tolerance by inducing stress-adaptive responses prior to crop establishment. Recent studies show that seed priming with osmotic agents, micronutrients, antioxidants, and nanoparticles improves water relations, antioxidant defense, and stress memory mechanisms [46−49]. In wheat, $CaCl_2$ osmopriming increased leaf area by 9–43%, tissue water status by 2–47%, osmolyte accumulation by 6–48%, and grain yield by 14–79% under drought conditions [46]. Nanopriming with ZnO nanoparticles further enhanced drought tolerance by increasing POD activity by up to 289.9%, phenolic content by 1139.6%, and lipid peroxidation inhibition by 433% in drought-stressed wheat seedlings [47]. Similarly, selenium seed priming improved photosynthetic rate by 28.8%, stomatal conductance by 35.3%, relative water content by 14.6%, and grain yield by 36.0% in drought-stressed quinoa [48]. In wheat, salicylic acid priming increased germination by 62%, improved relative water content by 64%, reduced malondialdehyde accumulation by 22%, and enhanced antioxidant enzyme activities under PEG-induced drought stress [49]. These findings highlight seed priming as a scalable approach for improving crop resilience through enhanced physiological preparedness, antioxidant capacity, and stress acclimation.

Current research demonstrates that drought priming enhances crop resilience through integrated physiological, biochemical, metabolic, and molecular mechanisms. Advances in omics technologies have substantially improved understanding of drought memory, transcriptional regulation, antioxidant acclimation, and metabolic reprogramming associated

with priming-induced tolerance. These findings underscore the potential of priming as an effective and sustainable non-genetic engineering strategy for improving crop performance under increasingly frequent and severe drought conditions.

4. Bioaugmentation

Recent advances in bioaugmentation have positioned beneficial rhizosphere microorganisms as one of the most promising non-genetic engineering strategies for enhancing drought tolerance in food crops [50, 51]. Current research trends increasingly emphasize the use of multifunctional microbial consortia, particularly AMF, PGPB, endophytic fungi, and rhizosphere microbiome engineering, to improve plant resilience under water-limited conditions. Unlike conventional single-trait approaches, modern bioaugmentation strategies aim to simultaneously regulate water uptake, nutrient acquisition, oxidative stress mitigation, osmotic adjustment, and stress-responsive signaling pathways [50]. Increasing attention has also been directed toward combining microbial inoculants with organic amendments such as vermicompost, as well as exploiting drought-adapted native microbial communities and microbiome network engineering to enhance plant adaptation under increasingly erratic climatic conditions [52−54].

One of the dominant trends is the extensive application of AMF to improve drought resilience through enhanced root hydraulic conductivity, nutrient uptake, and maintenance of plant water relations. AMF colonization consistently improves root architecture, including root length, diameter, surface area, and root volume, thereby increasing the soil exploration capacity of crops under drought [55]. In trifoliate orange, AMF inoculation increased root volume by 172.11% under drought stress, while substantially improving leaf relative water content and water potential [56, 57]. Similarly, AMF-treated tomato plants under water deficit exhibited an increase in biomass from 1,189 to 2,062 g/plant, along with improved stomatal conductance and water-use efficiency [52]. Enhanced hydraulic regulation is strongly associated with the modulation of aquaporins and membrane transport systems. For example, AMF inoculation upregulated aquaporin genes such as *PtTIP1;3* and *PtTIP4;1* in trifoliate orange roots, facilitating improved water transport under drought conditions [57]. In olive, native AMF improved root hydraulic conductivity through coordinated regulation and phosphorylation of aquaporins, including PIP1;2 and TIP1;2, thereby enhancing drought adaptation [58].

Another major advance involves integrating AMF with PGPB or organic biofertilizers to achieve synergistic drought-mitigation effects. Combined inoculation strategies frequently outperform single inoculants by simultaneously improving nutrient cycling, root growth, and antioxidant defense. In walnut seedlings, the combination of AMF and PGPB significantly enhanced root length, fresh biomass, nutrient acquisition, and chlorophyll content under drought stress compared with either treatment alone [59]. Likewise, the combined application of AMF and vermicompost in quinoa substantially improved photosynthetic efficiency, leaf water potential, osmolyte accumulation, and post-harvest soil fertility while reducing oxidative damage markers such as H_2O_2 and malondialdehyde [53]. These findings demonstrate a growing trend toward integrated microbiome-based soil management systems that simultaneously target plant physiology and soil ecosystem function.

Bioaugmentation also exerts profound effects on photosynthetic performance and carbon metabolism under drought stress. AMF and endophytic inoculants frequently maintain higher chlorophyll contents, stomatal conductance, PSII efficiency, and carbon assimilation under

water deficit. In maize, AMF inoculation partially restored photosynthetic rate, transpiration, and chlorophyll fluorescence under severe drought while increasing chlorophyll pigments by up to 88.67% [60]. Similar improvements were observed in sesame, where AMF enhanced irrigation water productivity by 22–71% under severe drought conditions [61]. Enhanced photosynthetic performance is often associated with better nutrient acquisition, particularly phosphorus, nitrogen, and potassium, which are critical for photosynthetic enzymes and osmotic regulation. AMF inoculation increased phosphorus uptake in tomato from 0.5 to 1.3 g/plant under water deficit conditions [52], while quinoa soils treated with AMF and vermicompost showed phosphorus increases exceeding 1,100% after harvest [53].

At the biochemical level, microbial bioaugmentation primarily enhances drought tolerance through modulation of antioxidant defense systems and osmotic adjustment. Drought stress typically induces excessive ROS accumulation, leading to lipid peroxidation, membrane instability, and cellular damage [4]. Beneficial microorganisms alleviate oxidative stress by enhancing antioxidant enzyme activities including SOD, CAT, POD, glutathione reductase, and APX. In maize, AMF inoculation increased SOD, CAT, POD, APX, and glutathione reductase activities by up to 98.63%, 73.61%, 92.47%, 75.00%, and 54.22%, respectively, while reducing H_2O_2 and lipid peroxidation by nearly 50% [60]. Similar antioxidant enhancement was observed in trifoliate orange, where AMF upregulated antioxidant-related genes, such as *PtMn-SOD* and *PtCAT1*, by more than 400–600% under drought stress [56]. Concurrently, microbial inoculation promotes the accumulation of compatible osmolytes, including proline, soluble sugars, amino acids, glycine betaine, and phenolics, which stabilize proteins, membranes, and cellular osmotic balance under dehydration conditions.

Recent studies also highlight a shift toward rhizosphere microbiome engineering and microbial network optimization. Advanced metagenomic and transcriptomic analyses have revealed that drought-resistant crop genotypes recruit more diverse and functionally specialized microbial communities than drought-sensitive cultivars [54]. Drought-resistant wheat cultivars were shown to possess more complex microbial interaction networks enriched in carbon cycling and energy metabolism pathways, contributing to improved stress resilience. Moreover, inoculation with beneficial fungi such as *Mortierella alpina* activated drought-responsive genes, including *CIPK9* and *PP2C30*, demonstrating the capacity of rhizosphere microorganisms to directly modulate host stress signaling pathways [54]. These findings indicate that future bioaugmentation strategies may increasingly focus on microbiome selection, synthetic microbial communities, and precision manipulation of rhizosphere ecological networks rather than reliance on single microbial species.

Emerging evidence also underscores the importance of endophytic fungi isolated from extreme environments as novel drought-mitigation agents. Antarctic fungal endophytes inoculated into blueberry improved photosynthetic performance, water potential, fruit quality, antioxidant capacity, and membrane stability under drought conditions [62]. Such extremophile-associated microbes represent an important frontier in climate-resilient agriculture because they possess unique stress-adaptive metabolic traits that can be transferred to host plants.

Collectively, current advances demonstrate that bioaugmentation enhances drought tolerance through coordinated physiological, biochemical, molecular, and ecological mechanisms involving improved water acquisition, nutrient metabolism, ROS detoxification, hormonal regulation, osmotic adjustment, aquaporin-mediated transport, and rhizosphere

microbiome restructuring. The integration of multifunctional microbial consortia, native drought-adapted microbiomes, and soil health management strategies is increasingly recognized as a sustainable and highly promising approach for improving food crop productivity under intensifying global drought conditions. A summary of bioaugmentation strategies is shown in Table 2.

Table 2. Bioaugmentation Strategies to Enhance Drought Tolerance in Food Crops.

Crop/System	Treatment	Drought effects & main benefits	Quantitative outcomes	Ref.
Tomato	AMF inoculation under three irrigation levels	Water deficit reduced biomass and nutrient uptake; AMF improved biomass, P uptake, PSII efficiency, stomatal conductance, and water-use efficiency	Biomass increased from 1,189 to 2,062 g plant^{-1}; P uptake increased from 0.5 to 1.3 g plant^{-1} under drought	[52]
Maize (*Zea mays*)	*Glomus versiforme* inoculation under moderate/severe drought	Severe drought reduced growth and biomass; AMF enhanced growth, photosynthesis, chlorophyll, antioxidant defense, osmolytes, and nutrient uptake	Biomass +75.73%; SOD +98.63%, POD +92.47%, CAT +73.61%; H_2O_2 −46.83%	[60]
Walnut seedlings	AMF + PGPB	Drought impaired growth and root development; inoculation improved growth, chlorophyll, nutrient uptake, osmolytes, and antioxidant activity	Highest fresh weight (FW): 360 g with *G. etunicatum* + PGPB; POD reached 6.50 absorbance min^{-1} mg protein^{-1}	[59]
Quinoa	AMF + vermicompost under drought	Drought reduced colonization, biomass, photosynthesis, and yield; treatment improved water status, chlorophyll, antioxidant defense, osmolytes, and soil fertility	H_2O_2 −∼60%; MDA −∼65%; soil P +∼1185%	[53]
Olive (*Olea europaea*)	Native AMF from contrasting soils	Drought reduced leaf biomass, chlorophyll, and growth; AMF improved hydraulic conductivity, aquaporin regulation, photosynthesis, and nutrient uptake	Significant increase in root hydraulic conductivity and maintenance of chlorophyll under drought	[58]
Trifoliate orange	*Funneliformis mosseae* inoculation	Drought reduced root colonization and gas exchange; AMF enhanced root morphology, photosynthesis, H^+-ATPase activity, and N metabolism	Root volume +172.11%; photosynthetic rate +141.15%; *PtAHA2* upregulated 20.92-fold	[55]
Trifoliate orange	*Funneliformis mosseae* inoculation	Drought reduced biomass, chlorophyll, and antioxidant balance; AMF improved biomass, water status, root traits, antioxidant enzymes, and gene expression	Biomass +48.6%; *PtMn-SOD* +611.8%; $O_2^{\bullet-}$ −40.2%	[56]
Trifoliate orange	*Funneliformis mosseae* inoculation	Drought reduced growth and water status; AMF enhanced biomass, water relations, ABA accumulation, and aquaporin expression	Leaf biomass +72.34%; *PtTIP4;1* upregulated 124.67%	[57]
Tomato	*Funneliformis mosseae* and *Rhizophagus intraradices*	Water stress reduced water status and photosynthesis; AMF delayed drought effects, improved intrinsic water use, and reduced ABA and oxidative stress	Proline ~30.5 µmol g^{-1} FW in AMF plants vs. ~18.6 in controls	[63]
Sesame	*Rhizophagus intraradices* and *Funneliformis mosseae*	Drought reduced nutrient uptake and yield; AMF improved nutrient acquisition, grain yield, oil content, and irrigation water productivity	Irrigation water productivity increased by 22–71% under severe drought	[61]
Wheat rhizosphere microbiome	Metagenomics and fungal inoculation	Drought-sensitive wheat had less diverse microbiomes; resistant cultivars showed more complex microbial networks and stronger carbon cycling	*Mortierella alpina* activated drought-responsive *CIPK9* and *PP2C30* genes	[54]
Maize	AMF inoculation under drought	Drought reduced biomass and chlorophyll; AMF improved growth, antioxidant activity, soil fertility, and microbial network stability	Biomass +42.7%; soil organic matter +71.8%	[64]
Blueberry	Antarctic fungal endophytes	Drought reduced photosynthesis and fruit quality; endophytes improved water status, PSII efficiency, fruit quality, and antioxidant capacity	Fruit weight increased from 1.1 to 3.1 g; soluble solids/titratable acidity ratio increased from 50.2 to 75.0	[62]

5. Non-phytohormone Organic Supplementation

Recent advances in non-phytohormone organic supplementation have shifted from the traditional use of simple osmoprotectants toward multifunctional biostimulants and metabolically active organic compounds that can reprogram drought responses at physiological, biochemical, transcriptomic, and rhizosphere levels. Emerging strategies increasingly integrate natural organic acids, seaweed-derived biostimulants, flavonoids, phenolic metabolites, carbon-based signaling compounds, nanoparticle-formulated biopolymers, and plant-derived antioxidant extracts to enhance drought resilience in food crops while minimizing the growth penalties commonly associated with severe water deficit [65]. Unlike conventional phytohormone application, these compounds act indirectly by modulating endogenous signaling pathways, antioxidant systems, osmotic adjustment, membrane stabilization, and metabolic plasticity, thereby providing broader and more sustained stress acclimation.

One of the most prominent trends involves the use of natural biostimulants derived from humic substances and marine macroalgae. Fulvic acid (FA), a low-molecular-weight humic fraction with high bioactivity, has emerged as a potent regulator of drought-responsive metabolism [66]. Transcriptomic and metabolomic analyses in tea plants demonstrated that FA treatment substantially reprogrammed antioxidant and secondary metabolic pathways under drought stress, particularly through enhancement of ascorbate metabolism, glutathione metabolism, and flavonoid biosynthesis [67]. Coordinated upregulation of genes such as *GME*, *AO*, *ALDH*, *GST*, *G6PDH*, *CHS*, and *F3H*, together with accumulation of flavonoids including kaempferol, quercetin, and myricetin, indicates that FA strengthens ROS detoxification capacity through both enzymatic and non-enzymatic antioxidant systems [67]. These findings highlight a broader mechanistic trend in drought biostimulation whereby exogenous organic compounds trigger integrated antioxidant-metabolic networks rather than isolated defense responses. Enhanced flavonoid biosynthesis is particularly important because flavonoids function simultaneously as ROS scavengers, membrane stabilizers, UV protectants, and signaling molecules involved in stress adaptation.

Seaweed-derived biostimulants, especially extracts from *Ascophyllum nodosum*, represent another rapidly advancing area of drought mitigation research. These extracts contain complex mixtures of polysaccharides, phenolics, betaines, amino acids, and organic compounds that collectively improve water management and stress signaling [68]. In soybean, *Ascophyllum nodosum* extract (ANE) markedly enhanced drought resilience by maintaining approximately 50% higher leaf water content and 46% greater stomatal conductance under drought conditions, while also improving post-stress recovery [69]. Molecular analyses further revealed activation of both ABA-dependent and ABA-independent drought pathways, including upregulation of *GmDREB1B*, *GmRD22*, *GmERD1*, and aquaporin gene *GmPIP1b*. The simultaneous activation of stress-responsive transcription factors, water transport systems, and photoprotective genes such as *FIB1a* demonstrates that seaweed biostimulants function as complex signaling modulators rather than simple nutrient supplements [69]. Similar responses were observed with Acadian® seaweed extract, which improved stomatal regulation, leaf cooling, and thermal homeostasis under drought stress [70]. Treated soybean plants maintained lower leaf temperatures and higher turgor stability during water deficit, indicating sustained

transpiration control and improved hydraulic regulation. These responses suggest that seaweed extracts enhance drought tolerance partly by preserving stomatal responsiveness and evaporative cooling capacity, thereby delaying the transition from moderate stress to irreversible dehydration.

Another important development is the increasing use of naturally occurring low-molecular-weight carbon compounds as drought-protective metabolites. Acetic acid (AA) and ethanol have attracted considerable attention as metabolic priming agents that activate endogenous drought signaling pathways [71, 72]. Exogenous AA treatment enhanced drought tolerance in apple by stimulating ABA- and JA-mediated MAPK signaling pathways and inducing genes involved in ABA and JA biosynthesis, including 9-cis-epoxycarotenoid dioxygenase, lipoxygenase, allene oxide synthase, and allene oxide cyclase. Transcriptomic analyses further revealed enrichment of pathways related to secondary metabolism, stress signaling, and hormonal crosstalk, indicating that AA induces broad stress acclimation networks rather than isolated hormonal responses [71]. Ethanol supplementation similarly enhanced drought tolerance in *Arabidopsis*, wheat, and rice through coordinated regulation of stomatal closure, ABA signaling, and metabolic reprogramming [72]. Ethanol-treated plants exhibited delayed water loss, elevated leaf temperature indicative of controlled stomatal closure, and significant accumulation of compatible solutes, including proline, sucrose, glucose-6-phosphate, glycerol, and myoinositol. Stable isotope labeling further demonstrated incorporation of ethanol-derived carbon into sugars and stress-associated metabolites through gluconeogenesis. Importantly, ethanol-mediated tolerance depended on conversion to AA, linking carbon metabolism directly with drought signaling pathways [72]. Compared with direct AA application, ethanol caused less growth inhibition, highlighting its potential as a more agronomically practical drought protectant.

Plant-derived antioxidant supplements and natural phenolic compounds have also emerged as effective drought-mitigation tools. Vitexin, a flavonoid compound, substantially improved wheat drought tolerance through enhancement of antioxidant defense, osmotic adjustment, and stress-responsive signaling pathways [73]. Vitexin treatment increased shoot fresh weight by 75%, root dry weight by 97%, relative water content by 51.9%, and survival rate from 40% to 76% under drought conditions. These physiological improvements were associated with reduced accumulation of H_2O_2, O_2^-, and MDA, alongside enhanced activities of CAT, POD, and SOD. Transcriptomic analyses revealed significant regulation of genes associated with MAPK signaling, flavonoid biosynthesis, fatty acid metabolism, and membrane stabilization, including CHI, PAL, CYP75B1, and lipoxygenase-related genes [73]. The enrichment of flavonoid and phenylpropanoid pathways suggests that vitexin not only functions as a direct antioxidant but also amplifies endogenous secondary metabolic defenses against oxidative and membrane damage.

Similarly, plant-derived biostimulants rich in antioxidants and vitamins have shown substantial potential in improving drought resilience. Foliar application of moringa seed extract and α-tocopherol significantly alleviated drought-induced physiological impairment in maize hybrids grown under water-limited conditions [74]. Drought stress caused major reductions in chlorophyll content, stomatal conductance, photosynthetic efficiency, and grain yield, while simultaneously increasing oxidative stress indicators such as MDA and electrolyte leakage. Application of moringa extract improved chlorophyll content by 18.3%, net photosynthetic rate by 17.8%, membrane stability index by 15.2%, and grain yield by 9.7%, while enhancing

antioxidant enzyme activity and crop water productivity. α-Tocopherol produced similar protective effects through membrane stabilization and ROS scavenging [74]. These findings reinforce the growing recognition that exogenous antioxidants can maintain photosynthetic integrity and membrane functionality under drought stress, thereby sustaining productivity even under severe water limitation.

Nanostructured organic supplements represent another frontier in drought tolerance enhancement. Chitosan nanoparticles (CHNPs) have gained attention because nanoscale delivery improves stability, penetration efficiency, and sustained bioactivity. In tomato, CHNPs strongly amplified drought-responsive gene expression, including major increases in *HsfA1a*, *SlAREB1*, and *LeNCED1* expression under drought conditions [75]. These genes are closely associated with ABA biosynthesis, transcriptional regulation, and stress adaptation, indicating that CHNPs function as potent elicitors of molecular stress signaling. The concentration-dependent enhancement of drought-responsive transcription suggests that nanobiostimulants may provide precise control over stress acclimation pathways while minimizing phytotoxicity [75].

Recent studies also indicate that some organic compounds confer drought tolerance indirectly through rhizosphere microbiome modulation. A notable example is 4-methylumbelliferone (4-MU), a coumarin-related metabolite that accumulated preferentially in drought-tolerant *Malus sieversii* rootstocks under water deficit [76]. Exogenous 4-MU significantly improved drought tolerance by increasing biomass, water-use efficiency, photosynthetic performance, and root development under prolonged drought. Beyond direct physiological effects, 4-MU reshaped rhizosphere microbial communities by enriching beneficial taxa such as *Pseudomonas*, *Bacillus*, *Streptomyces*, and *Trichoderma*. Soil sterilization experiments further confirmed that microbial recruitment contributed substantially to drought mitigation, indicating that certain organic supplements function partly as rhizosphere signaling molecules that engineer beneficial plant–microbe interactions [76]. This represents an emerging paradigm in drought management in which organic metabolites act simultaneously as plant protectants and microbiome modulators.

From an agronomic perspective, the performance of these organic supplements has been highly promising across diverse crop species, including soybean, wheat, maize, rice, apple, tea, and tomato. Improvements commonly include enhanced biomass accumulation, greater water-use efficiency, improved photosynthetic performance, reduced oxidative damage, and increased yield stability under drought conditions. Importantly, many treatments also improved post-drought recovery, indicating enhanced resilience rather than merely temporary stress avoidance. Current trends, therefore, suggest a transition toward multifunctional organic biostimulants that integrate metabolic priming, antioxidant reinforcement, hydraulic regulation, and microbiome-mediated stress mitigation. Future advances will likely focus on optimizing dosage, formulation, delivery systems, and crop specificity while integrating transcriptomics, metabolomics, and microbiome analyses to develop precision biostimulant strategies for climate-resilient agriculture. Table 3 summarizes studies on non-phytohormone organic supplementation to enhance drought tolerance in food crops.

Table 3. Summary of Non-Phytohormone Organic Supplementation for Drought-Tolerance Enhancement in Food Crops.

Plant species/System	Treatment	Experimental conditions	Key drought mitigation effects	Molecular/mechanistic findings	Ref.
Tea plant	FA, 0.1 g/L	Drought stress for 4 and 8 days; transcriptomics and metabolomics analyses	Enhanced antioxidant defense and drought tolerance through improved ascorbate, glutathione, and flavonoid metabolism	30,702 genes and 892 metabolites identified; 604 and 3331 DEGs at 4 and 8 days; regulated *GME*, *AO*, *ALDH*, *GST*, *G6PDH*, *CHS*, *F3H*, and flavonoid pathways	[67]
Soybean	*Ascophyllum nodosum* extract (ANE, 7.0 mL/L)	Controlled growth chamber; drought induced by withholding irrigation	Reduced wilting; ~50% higher water content and 46% greater stomatal conductance; antioxidant activity increased during drought and recovery	Upregulated ABA/stress-related genes including *GmCYP707A1a*, *GmCYP707A3b*, *GmRD22*, *GmDREB1B*, *GmERD1*, and *GmPIP1b*	[69]
Soybean	*Ascophyllum nodosum* extract (Acadian®)	5-day stress–recovery drought trial with thermal imaging	Delayed wilting, maintained lower leaf temperature, accelerated recovery, and maintained higher leaf turgor (43.52% vs. 23.31%)	Improved stomatal regulation, transpiration, and leaf thermal regulation under drought	[70]
Tomato	Chitosan nanoparticles (CHNPs; 60 and 90 ppm)	Greenhouse drought experiment with 10 days of irrigation withholding	Enhanced drought-responsive gene expression in a concentration-dependent manner	Increased *HsfA1a* (16.0–17.27-fold), *SlAREB1* (60.00–62.72-fold), and *LeNCED1* (20.16–27.2-fold)	[75]
Apple	Acetic acid (AA)	Control, AA, drought, and drought + AA treatments	Maintained higher chlorophyll and carotenoid contents and improved drought tolerance	Increased ABA, JA, and methyl jasmonate; activated MAPK and hormone signaling and regulated *NCED*, *AOS*, *AOC*, *LOX*, and *OPR*	[71]
Maize hybrids	Moringa seed extract and α-tocopherol	Three irrigation regimes (100%, 75%, and 50% evapotranspiration) in sandy soil	Improved chlorophyll (+18.3%), photosynthesis (+17.8%), water status (+9.4%), membrane stability (+15.2%), and grain yield (+9.7%); reduced oxidative damage	Increased antioxidant activity, including SOD (+18.1%), and improved crop water productivity by up to 11.1%	[74]
Apple rootstocks (*Malus sieversii* and M9-T337)	4-Methylumbelliferone (4-MU; 125 or 500 μM)	Greenhouse, hydroponic, transcriptomic, metabolomic, and microbial analyses under drought	Improved growth, biomass, water status, photosynthesis, water-use efficiency, and root-to-shoot ratio	Regulated 1273 drought-responsive genes and enriched beneficial *Pseudomonas*, *Bacillus*, *Streptomyces*, and *Trichoderma*	[76]
Arabidopsis, wheat, rice	Ethanol (5–20 mM in *Arabidopsis*; 50–100 mM in cereals)	Drought stress with metabolomic and transcriptomic analyses	Enhanced stomatal closure, delayed water loss, maintained shoot water content, and improved drought survival	Activated ABA-dependent/independent pathways, gluconeogenesis, and osmolyte accumulation; conversion to acetic acid was required for tolerance	[72]
Wheat	Vitexin (50 μM)	Hydroponic PEG-induced drought experiment	Increased shoot FW (+75%), shoot dry weight (DW) (+35.5%), root DW (+97%), water content (+51.9%), and survival (40%→76%); reduced ROS and MDA	1785 DEGs identified; MAPK, flavonoid, phenylpropanoid, fatty acid, and hormone pathways were enriched; regulated *CHI*, *FNSII*, *CYP75B1*, *PAL*, *Ein3*, and lipoxygenase genes	[73]

6. Inorganic Supplementation

Recent advances in inorganic supplementation have demonstrated substantial potential for improving drought tolerance in food crops through integrated regulation of plant water relations, redox homeostasis, osmotic adjustment, nutrient acquisition, photosynthetic stability, and stress-responsive molecular signaling [77]. Current trends emphasize the use of beneficial mineral nutrients and nanomaterials, particularly silicon (Si), potassium (K), selenium (Se), titanium dioxide nanoparticles (TiO_2 NPs), zinc oxide nanoparticles (ZnO NPs), and cerium oxide nanoparticles (CeO_2 NPs), either alone or in combination with biological amendments such as AMF, to enhance crop resilience under water-limited conditions. Unlike phytohormonal interventions, these inorganic supplements primarily function through structural reinforcement, ion homeostasis, ROS detoxification, membrane stabilization, and modulation of drought-responsive genes and signaling networks, thereby providing a multifaceted strategy for sustaining productivity under increasingly frequent drought episodes [77]. Among inorganic supplements, Si has emerged as one of the most extensively studied drought-mitigating agents due to its ability to improve water-use efficiency, strengthen cell wall architecture, maintain membrane integrity, and stimulate antioxidant defenses (Figure 2).

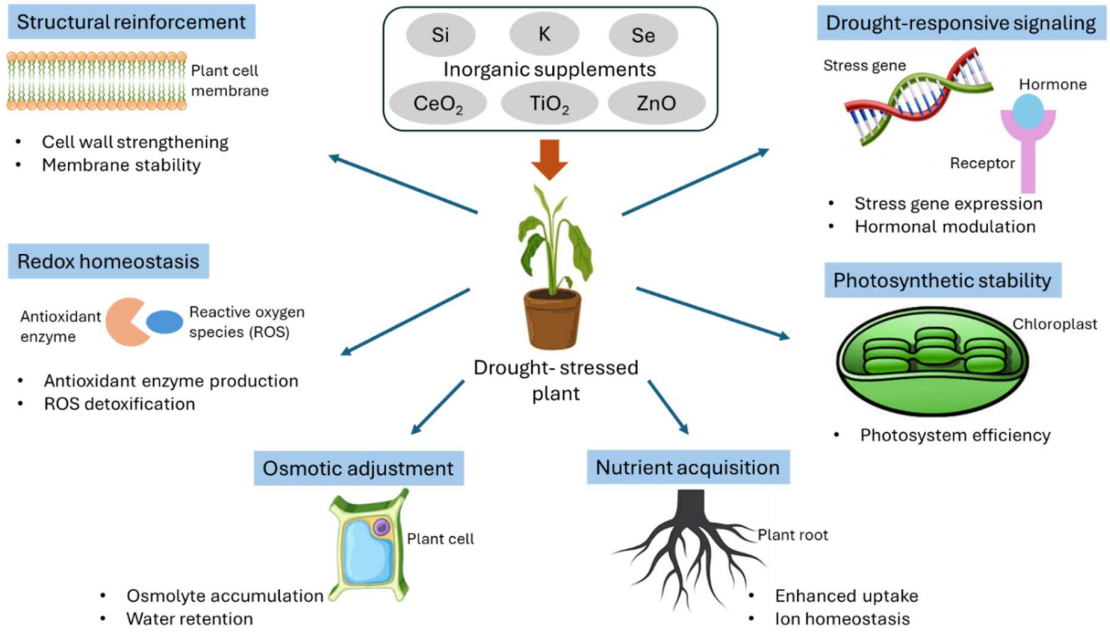

Figure 2. Drought Tolerance Pathways Through Inorganic Supplementation.

Si-mediated drought tolerance is increasingly linked to synergistic interactions with AMF, highlighting a trend toward integrated bioinorganic approaches [15]. In rice, combined application of monosilicic acid and AMF substantially improved drought resilience by increasing shoot dry matter by 28% and grain yield by 37–55% under moderate to severe water deficit compared with untreated controls [78]. These synergistic effects are associated with improved nutrient uptake, enhanced root hydraulic conductivity, and greater photosynthetic stability. Si supplementation also enhances osmotic adjustment and antioxidant metabolism, reducing drought-induced oxidative damage through increased activities of SOD, CAT, APX, and POD while limiting lipid peroxidation and ROS accumulation [78]. Nano-Si formulations represent a particularly important advancement because of their higher surface area, improved

penetration efficiency, and stronger physiological activity compared with bulk silicon. In *Lallemantia iberica*, nano-Si increased biomass by 100%, water-use efficiency by 107%, and PSII efficiency by 70.9% under drought stress, while simultaneously enhancing phenolics, flavonoids, and antioxidant capacity (by 44–64%) [79]. These responses indicate that nano-silicon not only preserves primary metabolism but also stimulates secondary metabolite biosynthesis linked to stress protection.

K supplementation constitutes another major strategy for drought mitigation because of its central role in stomatal regulation, osmotic balance, enzyme activation, and maintenance of photosynthetic processes [80] (Figure 2). K-mediated drought tolerance is strongly associated with improved cellular hydration, reduced ROS accumulation, and enhanced antioxidant defense systems. In sesame, K application restored relative water content and chlorophyll levels while markedly enhancing osmolyte accumulation, including proline, soluble sugars, amino acids, and proteins, under drought stress [81]. K also reduced hydrogen peroxide and malondialdehyde accumulation and stimulated the activities of SOD, CAT, APX, and glutathione reductase, thereby demonstrating its role in maintaining redox equilibrium. Correlation analyses further revealed close associations between K-enhanced antioxidant activity, osmotic regulation, and delayed leaf senescence [81]. Foliar potassium nitrate (KNO_3) supplementation has similarly shown effectiveness under combined drought and heat stress, improving growth recovery, chlorophyll retention, stomatal conductance, and nutrient acquisition while modulating endogenous hormonal balance [82]. Importantly, KNO_3 treatment reduced ABA accumulation while increasing growth-promoting hormones such as IAA, gibberellic acid, and cytokinins, indicating that inorganic supplementation can indirectly influence hormonal signaling without acting as an exogenous phytohormone itself.

Nanotechnology-based inorganic supplementation has become one of the fastest-growing trends in drought management research because nanoparticles possess unique physicochemical properties that enhance uptake efficiency and biological activity [83]. TiO_2 NPs have demonstrated significant capacity to preserve photosynthetic machinery and antioxidant metabolism under drought conditions. In sweet corn, foliar application of 50 mg L^{-1} TiO_2 NPs improved relative water content, chlorophyll fluorescence, osmolyte accumulation, and antioxidant enzyme activities (Figure 2) while partially restoring grain yield and harvest index under deficit irrigation [84]. However, the findings also highlight the importance of dosage optimization, as excessive nanoparticle concentrations (100 mg L^{-1}) produced detrimental effects, likely due to nanoparticle-induced oxidative stress or metabolic disruption. This dose-dependent response is increasingly recognized as a critical consideration in nano-enabled drought mitigation strategies.

Similarly, ZnO NPs have shown strong potential in enhancing drought tolerance through coordinated physiological, biochemical, and molecular regulation. ZnO NPs improve chlorophyll synthesis, protein metabolism, amino acid accumulation, antioxidant activity, and osmotic adjustment while simultaneously inducing drought-responsive gene expression [85] (Figure 2). In wheat, ZnO NP application increased the expression of stress-related genes, including *Wdhn13*, *CAT1*, *DREB2*, and *P5CS*, by up to threefold under severe drought stress [86]. These molecular responses were accompanied by enhanced accumulation of proline, soluble sugars, proteins, and antioxidant enzymes, together with reduced lipid peroxidation. The activation of *DREB2* and *P5CS* suggests that ZnO NPs stimulate both transcriptional

drought signaling and osmoprotectant biosynthesis pathways, thereby integrating metabolic and gene-regulatory drought responses.

Rare-earth nanomaterials such as CeO_2 NPs represent another emerging frontier in inorganic drought mitigation. CeO_2 NPs possess intrinsic redox cycling capacity between Ce^{3+} and Ce^{4+} states, enabling direct scavenging of ROS [87]. In apple, foliar CeO_2 NP application enhanced photosynthetic performance, chlorophyll fluorescence, osmolyte accumulation, antioxidant activity, and drought-responsive transcription factor expression under severe drought conditions (Figure 2) [88]. Upregulation of *DREB1A* and *DREB1E* indicated activation of transcriptional stress signaling pathways, while increased ABA and IAA levels suggested improved coordination between stress adaptation and growth maintenance. CeO_2 NPs also substantially reduced electrolyte leakage, hydrogen peroxide, and malondialdehyde accumulation, highlighting their effectiveness in preserving membrane stability and minimizing oxidative injury. These findings demonstrate that nanoceria acts not only as a nutrient supplement but also as a nanozyme-like antioxidant system capable of directly modulating plant redox status.

Se supplementation has likewise gained increasing attention because of its dual role in antioxidant defense and nutrient homeostasis. Foliar Se application in sunflower significantly enhanced antioxidant enzyme activities, osmolyte accumulation, phenolic and flavonoid biosynthesis, and ion balance under drought stress (Figure 2) [89]. Se reduced hydrogen peroxide accumulation by approximately 21% while increasing SOD activity by more than 150%, thereby substantially improving growth performance under water deficit conditions. The enhanced accumulation of ascorbic acid, anthocyanins, flavonoids, and total phenolics further indicates that Se stimulates both enzymatic and non-enzymatic antioxidant systems. Moreover, selenium improved root ion homeostasis by increasing Ca^{2+}, K^+, and Na^+ accumulation, suggesting enhanced membrane transport and nutrient regulation under drought conditions [89].

Collectively, the latest advances indicate that inorganic supplementation enhances drought tolerance through several interconnected mechanisms. Physiologically, these supplements improve stomatal regulation, water retention, photosynthetic efficiency, chlorophyll stability, and water-use efficiency. Biochemically, they strengthen antioxidant defense systems, reduce ROS accumulation and membrane lipid peroxidation, stimulate osmolyte biosynthesis, and enhance secondary metabolite accumulation. At the molecular level, inorganic supplements increasingly appear to regulate stress-responsive transcription factors, osmoprotectant biosynthesis genes, antioxidant-related genes, aquaporins, and hormone-signaling pathways, including ABA-dependent drought signaling networks. Emerging evidence also demonstrates that inorganic supplements influence rhizosphere interactions and microbial recruitment, particularly when integrated with AMF or other beneficial microorganisms, thereby extending their effects beyond plant tissues to the broader soil–plant system.

A notable emerging trend is the convergence of nanotechnology, nutrient engineering, and microbial symbiosis into integrated drought management platforms. Nano-enabled delivery systems provide enhanced bioavailability and targeted stress protection, while combinations of inorganic supplements with AMF or other beneficial microbes generate synergistic improvements in nutrient acquisition, water transport, and metabolic resilience. These integrated approaches are increasingly viewed as promising climate-smart agricultural

strategies capable of sustaining crop productivity under escalating drought pressures associated with climate change.

7. Convergence of Non-genetic Strategies for Drought Tolerance

Despite differences in their primary modes of action, phytohormones, priming, bioaugmentation, organic supplementation, and inorganic supplementation converge on interconnected physiological, biochemical, and molecular responses that enhance drought tolerance. At the physiological level, all five strategies can improve plant water status, stomatal regulation, root development, photosynthetic stability, and water-use efficiency. Phytohormones directly modulate stress signaling and stomatal/photosynthetic responses [30, 34, 35], whereas priming establishes physiological and structural stress memory that improves hydraulic regulation and subsequent photosynthetic performance [40, 41]. Bioaugmentation enhances root development, hydraulic conductivity, and water acquisition through AMF- and microbe-mediated effects [52, 56−58], while organic and inorganic supplements improve water retention, stomatal regulation, and photosynthetic stability through metabolic, nutritional, and structural mechanisms [69, 70, 78, 81].

At the biochemical level, these strategies show particularly strong convergence in ROS homeostasis, antioxidant defense, and osmotic adjustment. Melatonin and other phytohormones enhance SOD, CAT, POD, and APX activities and strengthen the ascorbate–glutathione system [30−32]. Priming establishes antioxidant preparedness through controlled ROS signaling and subsequent enhancement of antioxidant capacity [40−42]. Beneficial microorganisms similarly increase antioxidant enzymes while promoting accumulation of compatible solutes such as proline and soluble sugars [53, 60]. Organic compounds and biostimulants stimulate enzymatic and non-enzymatic antioxidants, including flavonoids and phenolics [67, 73, 74], whereas Si, K, Se and metal-oxide nanoparticles reinforce antioxidant systems, osmotic regulation and membrane stability [78, 81, 84−89]. Thus, ROS detoxification and osmotic protection represent major biochemical convergence points among otherwise distinct interventions.

At the molecular level, the strategies converge through stress-responsive transcription factors, MAPK signaling, ABA and JA pathways, antioxidant genes, aquaporins, and metabolic reprogramming. Phytohormones can activate MYB, NAC, WRKY, AP2/ERF and other transcription-factor networks [30−32], while priming establishes transcriptional memory involving AP2/ERF, MYB, NAC, WRKY and bHLH regulators [40, 41, 44]. Microbial inoculation can modulate aquaporins and drought-responsive genes such as *CIPK9* and *PP2C30* [54, 57], whereas organic supplements activate ABA/JA signaling, MAPK pathways and drought-responsive genes such as *DREB*, *RD22* and *AREB* [69, 71, 75]. Inorganic supplements likewise regulate genes involved in drought signaling, osmolyte synthesis and antioxidant defense, including *DREB2*, *P5CS* and *CAT1* [86, 88]. These molecular responses ultimately feed back into common physiological outcomes—better water acquisition and retention, protection of photosynthetic machinery, reduced oxidative damage, and improved growth and yield under water deficit. A useful conceptual summary is provided in Figure 3. This convergence also explains why integrated strategies such as AMF + Si, AMF + organic amendments, or priming + micronutrients can potentially produce stronger responses than individual treatments: they simultaneously activate complementary components of the same broader drought-adaptation network [53, 59, 78].

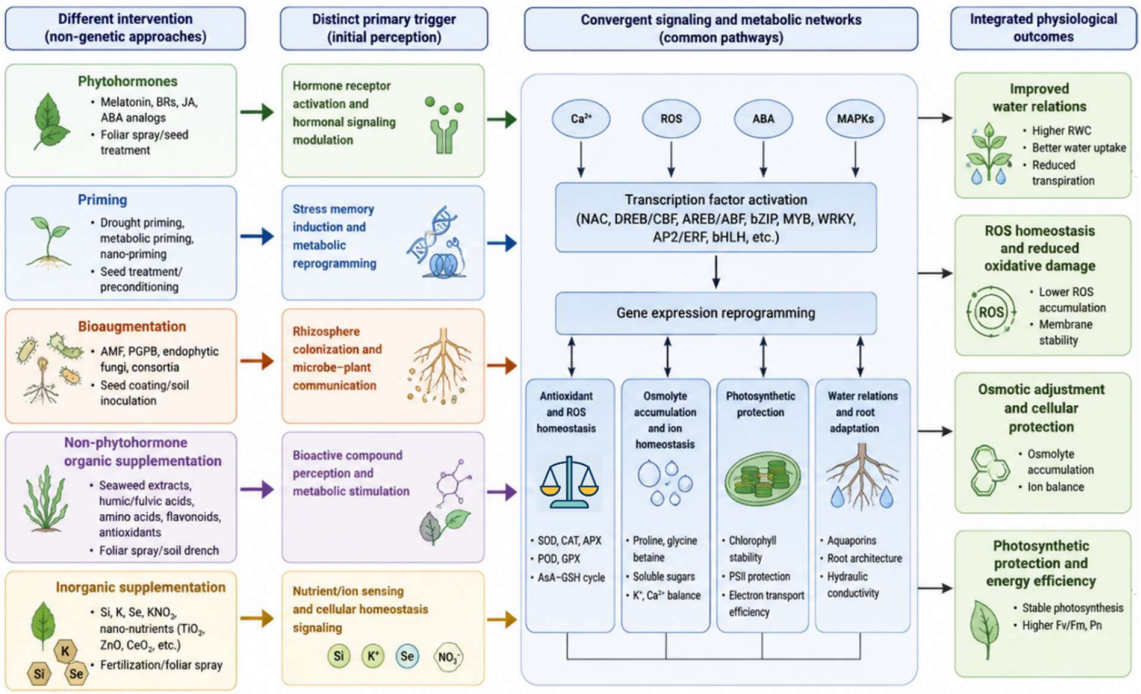

Figure 3. Conceptual Summary of Non-Genetic Strategies for Drought Tolerance. (Note: RWC = Relative water content; Pn = Net photosynthetic rate)

8. Comparative Feasibility of Drought-tolerance Enhancing Strategies

Among the non-genetic engineering approaches for enhancing drought tolerance in crops, phytohormones, priming, bioaugmentation, non-phytohormone organic supplementation, and inorganic supplementation differ substantially in their agronomic feasibility, mechanistic breadth, cost-effectiveness, scalability, environmental sustainability, and consistency of field performance. This review indicates that while all five strategies can significantly improve drought resilience, their practical feasibility for large-scale agricultural deployment varies according to crop system, environmental conditions, infrastructure requirements, and the degree of mechanistic complexity involved. Importantly, emerging technologies such as nanoparticles, nano-enabled biostimulants, and engineered microbial formulations may provide greater efficacy or delivery precision, but their advantages must be evaluated against potential phytotoxicity, environmental accumulation, ecological effects, regulatory uncertainty, and economic feasibility [90]. Thus, technological novelty should not be equated with agricultural readiness.

Bioaugmentation currently appears to be one of the most feasible long-term strategies for sustainable drought management because it integrates plant physiological protection with improvements in soil health, nutrient cycling, and rhizosphere resilience [91]. AMF, PGPB, and endophytic fungi enhance drought tolerance through multiple interconnected mechanisms, including improved root hydraulic conductivity, aquaporin regulation, nutrient acquisition, osmotic adjustment, antioxidant defense, and microbiome restructuring [52−54]. Compared with exogenous chemical applications, microbial inoculants generally require fewer repeated inputs because successful colonization can provide relatively persistent effects throughout the crop cycle [92]. In addition, bioaugmentation improves soil fertility and microbial diversity, making it highly compatible with regenerative and climate-smart agricultural systems. The integration of AMF with vermicompost or multifunctional microbial consortia further increases

feasibility because it simultaneously enhances drought tolerance and soil ecosystem functions [53]. However, despite its sustainability advantages, bioaugmentation also faces several limitations. Microbial establishment and effectiveness are highly dependent on soil physicochemical conditions, competition from native microbiota, temperature, and moisture regimes [92]. Field performance can therefore be inconsistent across environments, particularly in degraded soils or under intensive agricultural practices involving pesticides and high fertilizer inputs [91]. Large-scale production, storage stability, and shelf-life of microbial inoculants also remain important logistical constraints [93]. For emerging synthetic or multifunctional microbial consortia, additional evaluation is needed to determine their persistence, effects on native microbial communities, potential ecological displacement, and long-term soil ecosystem consequences [94]. Nevertheless, among the strategies reviewed, bioaugmentation likely offers the best balance between sustainability, environmental safety, long-term resilience, and multifunctional agronomic benefits.

Inorganic supplementation represents another highly feasible strategy because mineral nutrients and inorganic compounds are already widely integrated into conventional agricultural management systems. Si, K, Se, and KNO_3 are particularly attractive because they are relatively inexpensive, agronomically familiar, and readily applicable through existing fertilization or foliar spraying infrastructure. Their mechanisms are also broad and robust, involving osmotic regulation, stomatal control, antioxidant defense, membrane stabilization, nutrient homeostasis, and drought-responsive gene regulation [78, 81, 82]. Si supplementation is especially promising because it combines structural reinforcement with physiological protection and has consistently improved biomass, water-use efficiency, and yield stability under drought [15]. K-based approaches are similarly feasible because K fertilization is already a standard agronomic practice, enabling rapid integration into existing production systems without major technological modifications [80]. Inorganic supplementation also generally produces relatively rapid and reproducible responses across diverse crops and environments.

The feasibility of nanomaterial-based inorganic supplementation, however, is more complex. TiO_2, ZnO, and CeO_2 NPs demonstrate strong physiological and molecular benefits, including activation of antioxidant systems, osmolyte accumulation, and drought-responsive transcription factors such as DREB2 and P5CS [86, 88]. Nevertheless, large-scale application requires a broader risk–benefit assessment than conventional mineral supplementation. Nanoparticle concentration, particle size, surface properties, and application route can influence phytotoxicity, uptake, translocation, and biological activity [90, 95]. Excessive concentrations may induce oxidative stress, interfere with photosynthesis, or inhibit growth, as observed for TiO_2 NPs in sweet corn [84]. Moreover, repeated application could result in nanoparticle accumulation in soils or plant tissues and potentially alter soil microbial communities, nutrient cycling, or non-target organisms [96]. Their environmental fate and potential transfer through soil–water systems therefore require long-term field assessment. Economic feasibility is also uncertain because nanoparticle synthesis, formulation, quality control, and application may be more expensive than conventional mineral inputs, while regulatory requirements for nano-enabled agricultural products remain less established. Consequently, while nano-enabled inorganic supplementation represents a technologically advanced and highly effective strategy, its immediate field-scale feasibility is lower than that of conventional Si or K supplementation. Overall, conventional inorganic supplementation

currently ranks among the most feasible near-term strategies because of its scalability, compatibility with existing agricultural systems, and relatively predictable performance.

Non-phytohormone organic supplementation also demonstrates strong feasibility, particularly because many organic biostimulants are biodegradable, environmentally safer, and compatible with sustainable agriculture frameworks. Seaweed extracts, FA, ethanol, AA, flavonoids, and antioxidant-rich plant extracts improve drought tolerance through antioxidant enhancement, metabolic reprogramming, osmotic adjustment, and rhizosphere modulation [67, 71, 73, 97]. Seaweed-derived biostimulants are especially feasible because they are already commercially available and widely used in horticulture and high-value crops. Their multifunctional composition allows simultaneous regulation of hydraulic balance, ABA signaling, aquaporins, and antioxidant metabolism [68−70]. Ethanol and AA also offer practical advantages due to their low cost and ease of application, although growth inhibition at high concentrations may limit their operational window. Organic supplementation is additionally attractive because many compounds indirectly stimulate endogenous signaling pathways rather than imposing direct hormonal perturbations, potentially reducing risks of developmental imbalance.

However, the effectiveness of organic supplements can be highly dependent on dosage, crop specificity, formulation stability, and environmental conditions. Many natural biostimulants also exhibit compositional variability depending on extraction methods and source materials, potentially affecting reproducibility under field conditions [98, 99]. Furthermore, repeated foliar applications may increase labor and operational costs in large-scale cereal production systems. Emerging nano-formulated organic biostimulants, such as chitosan nanoparticles, may improve stability, uptake, and delivery efficiency, but their greater biological activity also warrants careful assessment of concentration-dependent phytotoxicity and environmental persistence [75]. Potential accumulation of nano-formulations in soil, effects on beneficial microorganisms and non-target organisms, and degradation products should be considered before repeated field application. Economic assessments should also determine whether increased efficacy offsets the additional cost of nano-formulation and specialized production. Despite these limitations, non-phytohormone organic supplementation remains highly feasible for integrated drought management, especially in sustainable and high-value agricultural systems where environmental compatibility and post-stress recovery are prioritized.

Phytohormone-based strategies exhibit exceptionally strong mechanistic effectiveness but somewhat lower large-scale feasibility than microbial- or nutrient-based approaches. Melatonin, BRs, JA, and hormone analogs strongly enhance drought tolerance through transcriptional reprogramming, antioxidant regulation, osmotic adjustment, and photosynthetic stabilization [30, 34, 35]. Their ability to directly regulate stress signaling pathways and transcription factors such as MYB, NAC, WRKY, AP2/ERF, and bZIP gives them a uniquely powerful capacity to coordinate whole-plant drought responses at physiological and molecular levels [30]. Phytohormones also frequently improve both drought tolerance and post-stress recovery, which is particularly important under fluctuating climate conditions.

Despite these advantages, phytohormone feasibility is constrained by several practical issues. Hormonal responses are often highly dose-sensitive, species-specific, and developmentally dependent, requiring precise optimization of concentration, timing, and delivery methods. Excessive or poorly timed hormone application may disrupt growth,

reproductive development, or source–sink relationships [100]. Production costs of certain phytohormones and synthetic analogs may also limit the economic feasibility of large-scale staple crop production [101]. Furthermore, phytohormone treatments generally provide transient effects and often require repeated application during stress periods [102]. Long-term environmental fate, persistence, potential effects on non-target plants and soil organisms, and residue considerations should also be incorporated into field-scale assessments, particularly for repeated application of synthetic hormone analogs. While highly effective in controlled environments and high-value crops, widespread field-scale deployment in low-input systems may therefore be more challenging than mineral supplementation or bioaugmentation approaches.

Priming represents one of the most conceptually attractive and environmentally sustainable strategies because it induces endogenous stress memory without continuous chemical input. Recurrent drought priming, metabolic priming, and nanopriming improve drought resilience through hydraulic acclimation, antioxidant preparedness, metabolic reprogramming, and transcriptional memory involving AP2/ERF, NAC, WRKY, and MYB regulatory networks [40, 41]. Priming is particularly appealing because relatively mild preconditioning can generate long-lasting tolerance with reduced resource input compared with repeated exogenous treatments. In theory, priming may therefore offer substantial sustainability advantages for climate-resilient agriculture.

However, among the approaches discussed, priming may currently have the lowest large-scale operational feasibility for commercial agriculture. Effective priming often requires precise timing, carefully controlled stress exposure, and accurate prediction of future drought events. Variability in environmental conditions can make it difficult to standardize priming intensity across large agricultural systems. In addition, some priming effects are genotype-dependent and may diminish under prolonged or unpredictable stress conditions [17]. Nanopriming approaches using AgNPs also face the same regulatory and environmental concerns associated with nanoparticle-based inorganic supplementation [103]. In particular, repeated exposure to AgNPs or other nanomaterials requires assessment of phytotoxicity, nanoparticle persistence and accumulation in soil, effects on beneficial rhizosphere microorganisms and earthworms, and potential transfer into edible plant tissues. The economic advantage of nanopriming will also depend on whether improved yield protection justifies the cost of nanoparticle synthesis, formulation, and application. Consequently, although priming demonstrates exceptional mechanistic sophistication and strong experimental performance, its practical implementation at a broad field scale remains more difficult than direct supplementation or microbial inoculation strategies.

Overall, the most feasible strategies for near-term agricultural deployment are likely integrated bioaugmentation and conventional inorganic supplementation, particularly combinations involving AMF, Si, K, and organic soil amendments. These approaches provide several advantages simultaneously: relatively low cost, compatibility with existing agricultural practices, environmental sustainability, broad-spectrum physiological protection, and relatively consistent field performance. Integrated systems combining AMF with Si or K supplementation appear especially promising because they simultaneously improve root hydraulic conductivity, nutrient uptake, osmotic regulation, antioxidant defense, and rhizosphere stability while minimizing dependence on repeated high-cost chemical inputs. Non-phytohormone organic biostimulants, especially seaweed extracts and fulvic acid, also

represent highly feasible complementary tools for sustainable and high-value crop systems. A summary of the feasibility comparison is presented in Table 4.

Table 4. Comparative Assessment of Non-Genetic Strategies for Enhancing Drought Tolerance in Food Crops.

Strategy	Principal mechanisms of action	Major advantages & limitations	Indicative TRL	Scalability & field applicability
Phytohormones	Stress signaling; ROS detoxification; antioxidant activation; osmotic adjustment; stomatal and root regulation; ABA/JA/BR pathways	Advantages: Rapid response, low doses, multiple stress pathways, flexible application. Limitations: Strong dose dependence, crop/genotype specificity, repeated application, variable field consistency	5–7	High with standardized formulations; broadly applicable to cereals, horticultural, and perennial crops through foliar or soil application
Priming	Stress memory; controlled ROS signaling; metabolic reprogramming; antioxidant preparedness; osmolyte accumulation	Advantages: Pre-stress protection, low cost, potentially persistent effects, easy seed integration. Limitations: Dose/timing/genotype dependence, variable stress-memory persistence, nanopriming toxicity concerns	6–7 conventional; 4–6 nano	Very high for seed priming; particularly suitable for large-scale cereal and rainfed crop production
Bioaugmentation	AMF/PGPB/endophyte colonization; root development; nutrient/water uptake; antioxidant and hormonal regulation; microbiome restructuring	Advantages: Improves plant–soil interactions, multifunctional and potentially persistent. Limitations: Variable colonization, soil/climate/genotype effects, formulation and storage challenges	5–7 established inoculants; 3–5 synthetic microbiomes	Moderate–high; suitable for soil/root systems through seed coating, soil application, or fertigation
Organic supplementation	Antioxidant reinforcement; osmotic adjustment; metabolic priming; hormonal signaling; rhizosphere recruitment	Advantages: Multifunctional, biodegradable options, established biostimulants, supports recovery. Limitations: Variable composition/efficacy, dose specificity, standardization and nanomaterial safety issues	5–7 established products; 3–5 novel/nano products	High for standardized products; suitable for intensive horticulture, perennial crops, and foliar/soil biostimulant systems
Inorganic supplementation	Ion/osmotic regulation; stomatal control; antioxidant defense; photosynthetic protection; hormone interactions	Advantages: Combines nutrition and stress protection; compatible with fertilizer systems. Limitations: Dose-dependent toxicity, nutrient-status effects, nanoparticle fate and safety concerns	6–8 conventional; 4–6 nano	High for conventional and moderate for nano formulations; applicable where fertilizer infrastructure exists, especially in cereal and horticultural systems
Integrated strategies (e.g., AMF + Si; priming + micronutrients)	Combined regulation of water/nutrient uptake, ROS, osmotic balance, hormones, and rhizosphere processes	Advantages: Potentially stronger and more stable effects through multiple mechanisms. Limitations: Greater complexity, possible synergistic/antagonistic interactions, optimization requirements, and cost	4–6	Moderate–high; suitable for intensive/high-value systems and promising for cereals as protocols become standardized

Note: TRL indicates the maturity of a technology from TRL 1 (basic principles observed) to TRL 9 (fully demonstrated and commercially proven in an operational environment). In general, TRL 3 represents experimental proof of concept; TRL 4 laboratory validation; TRL 5 validation in a relevant environment; TRL 6 demonstration in a relevant environment; TRL 7 field-scale or operational demonstration; TRL 8 a complete and qualified system; and TRL 9 proven commercial application. The TRL ranges reported in this table are indicative estimates based on the level of laboratory, greenhouse, field, and commercial validation and may vary depending on the specific material, formulation, crop and application technology.

9. Field-scale Implementation and Translational Challenges

Despite substantial evidence that non-genetic strategies can improve drought tolerance, most studies summarized in this review were conducted under greenhouse, hydroponic, pot, or otherwise controlled conditions, where drought intensity, timing, soil properties, and treatment application can be precisely regulated. This controlled setting provides valuable mechanistic insights into drought tolerance under induced drought conditions, which may not be readily accessible or sustained under field environments. However, it may overestimate treatment consistency under heterogeneous agricultural conditions. Field environments introduce substantial variability in soil texture, nutrient availability, temperature, microbial communities, rainfall patterns, drought timing, crop genotype, and management practices, all of which can influence treatment efficacy [104]. This issue is particularly important for bioaugmentation, where microbial establishment and performance are strongly dependent on soil and indigenous microbiota [52−54, 58], and for phytohormones and biostimulants, where responses can vary with dose, genotype and environmental conditions [30, 34, 35, 67].

Cost-effectiveness and scalability are additional barriers to field deployment. Seed priming and conventional mineral supplementation are comparatively attractive because they can be incorporated into existing seed-treatment and fertilization infrastructure, whereas repeated foliar application of hormones, biostimulants or nanoparticles may increase labor, formulation and application costs. Bioaugmentation additionally requires reliable inoculant production, storage, transport and field delivery, with microbial survival and colonization remaining important constraints [52−54]. Integrated treatments may provide greater drought protection but also increase operational complexity and input costs. Consequently, future research should evaluate economic returns per unit input, rather than relying solely on physiological or yield responses observed under experimental conditions.

The persistence of treatment effects also requires greater attention. Priming can generate physiological, metabolic, and transcriptional memory, but the duration and stability of these effects under repeated or unpredictable drought cycles remain uncertain [40, 41]. Similarly, the persistence of microbial inoculants depends on their ability to establish and remain functionally active within native soil communities [54, 58]. For phytohormones and many organic biostimulants, effects may be relatively transient and therefore require appropriately timed applications [30, 34, 69]. Long-term field trials are consequently needed to determine whether treatment benefits persist throughout the production cycle and across multiple drought events.

Farmer adoption will depend not only on biological efficacy but also on compatibility with existing agricultural practices. Technologies requiring specialized equipment, frequent applications, complex dosage regimes, or substantial changes in farm management may face greater adoption barriers than seed treatments or inputs that can be integrated into existing fertilization and irrigation schedules [105]. Demonstrating consistent yield benefits, economic profitability, ease of application, and compatibility with local farming systems will therefore be critical for technology transfer.

Finally, regulatory and environmental considerations become increasingly important as these technologies move toward large-scale deployment. Conventional nutrients and established biostimulants generally have clearer agricultural use pathways, whereas nanoparticle-based treatments require further assessment of environmental persistence, accumulation, non-target effects and potential movement through soil–water systems [75, 83−86]. Similarly, microbial consortia and synthetic microbiomes require evaluation of

ecological compatibility, persistence and effects on native microbial communities [53,54]. Regulatory requirements may therefore differ substantially among phytohormones, microbial inoculants, organic biostimulants and nano-enabled materials.

10. Conclusions

In conclusion, recent advances in non-genetic engineering strategies demonstrate substantial potential for improving drought tolerance and sustaining crop productivity under increasingly severe climate conditions. Across the approaches reviewed, including phytohormones, priming, bioaugmentation, non-phytohormone organic supplementation, and inorganic supplementation, drought mitigation is consistently associated with coordinated regulation of antioxidant defense, osmotic adjustment, photosynthetic stability, water-use efficiency, nutrient acquisition, and stress-responsive molecular signaling. Modern studies further show that these strategies do not function through isolated mechanisms but instead induce integrated physiological, biochemical, transcriptomic, and rhizosphere-level adaptations that collectively enhance plant resilience. Among the approaches evaluated, bioaugmentation and conventional inorganic supplementation currently appear the most feasible for near-term field deployment because of their scalability, relatively low cost, compatibility with existing agricultural systems, and multifunctional benefits for both plants and soil ecosystems. Organic biostimulants and phytohormones also show considerable promise, particularly for high-value crops and sustainable agricultural systems, while priming offers a highly sustainable strategy through induction of stress memory and long-term acclimation. From a practical perspective, the findings of this review support the development of integrated drought-management systems rather than reliance on single interventions. Combining AMF or beneficial microbial consortia with Si, K, seaweed extracts, FA, or carefully optimized phytohormone treatments may provide synergistic improvements in hydraulic regulation, antioxidant protection, nutrient uptake, and rhizosphere stability. Such integrated approaches could enhance crop productivity while reducing dependence on excessive irrigation and agrochemical inputs, thereby supporting climate-smart and regenerative agriculture. Future research should prioritize the translation of promising strategies into robust, field-ready drought-management systems. Key priorities include long-term, multi-location field trials to validate treatment consistency, yield stability, persistence, and economic feasibility across diverse soils, genotypes, and climatic conditions; systematic evaluation of multi-strategy combinations, particularly bioaugmentation with organic biostimulants or mineral supplements, to identify synergistic effects; and integration of transcriptomics, metabolomics, phenomics, and microbiome profiling to resolve the mechanisms underlying treatment responses. Microbiome engineering should advance toward stable, crop- and soil-specific microbial consortia, while artificial intelligence and machine-learning approaches could optimize treatment dosage, timing, combinations, and delivery according to environmental and crop-specific conditions. Research should also develop climate-specific management protocols for recurrent drought, terminal drought, and combined drought–heat stress. For emerging technologies, particularly nanoparticles and advanced biostimulants, future studies should simultaneously assess phytotoxicity, environmental persistence and accumulation, non-target ecological effects, food-safety risks, and economic feasibility to ensure that improved drought tolerance is achieved without compromising environmental sustainability or farm-level viability.

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Competing Interest

The author declares that there are no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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