



REVIEW ARTICLE

Biostimulants in groundnut (*Arachis hypogaea* L.) under abiotic stress: Mechanistic insights, field performance and practical constraints

A Gulshan¹, R Baskaran^{2*}, C Harisudan², P Boominathan³ & M Baskar⁴

¹Department of Agronomy, Agricultural College and Research Institute, Tamil Nadu Agricultural University, Coimbatore 641 003, Tamil Nadu, India

²Regional Research Station, Tamil Nadu Agricultural University, Vriddhachalam 606 001, Tamil Nadu, India

³Department of Crop Physiology, Agricultural College and Research Institute, Tamil Nadu Agricultural University, Coimbatore 641 003, Tamil Nadu, India

⁴Department of Soil Science and Agricultural Chemistry, Anbil Dharmalingam Agricultural College and Research Institute, Tamil Nadu Agricultural University, Tiruchirapalli 620 027, Tamil Nadu, India

*Correspondence email - baskaran.r@tnau.ac.in

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Abstract

Groundnut (*Arachis hypogaea* L.) is a globally vital legume whose yield and nutritional quality are severely threatened by escalating abiotic stresses, particularly drought, soil salinity and extreme temperatures. To mitigate these challenges sustainably and reduce reliance on synthetic agrochemicals, plant biostimulants have emerged as effective, eco-friendly inputs, including microbial inoculants such as plant growth-promoting rhizobacteria and arbuscular mycorrhizal fungi, as well as non-microbial products like chitosan, seaweed extracts, protein hydrolysates and humic substances. Groundnut productivity is highly vulnerable to these constraints; terminal drought can cause yield losses of up to 85 %, while salinity and nutrient deficiencies contribute to reductions exceeding 40–50 %. This review critically synthesises groundnut-specific mechanistic insights. It highlights how biostimulants preserve biological nitrogen fixation within unique crack-entry nodules and modulate phytohormone signalling under stress. Additionally, they enhance antioxidant defence systems and promote osmolyte accumulation to maintain cellular turgor. These mechanisms translate into measurable benefits, including improvements in relative water content and chlorophyll retention exceeding 50 % under severe drought, along with enhanced nodulation and biomass. Furthermore, targeted applications can bypass key physiological bottlenecks; nanoscale formulations improve calcium availability in the geocarposphere to enhance pod filling, while biopolymer-based inputs regulate ionic balance and improve yield by approximately 25–30 % under combined stress. Despite these promising outcomes, formulation stability, genotype-dependent responses and inconsistent field performance remain major constraints. Establishing a function-based, stage-specific deployment framework is therefore essential to ensure reliable use of biostimulants in climate-resilient groundnut production.

Keywords: abiotic stress tolerance; groundnut; osmotic and antioxidant regulation; plant biostimulants; symbiotic nitrogen fixation

Introduction

Groundnut (*Arachis hypogaea* L.) is a globally important leguminous oilseed crop cultivated across tropical and subtropical regions, valued for its high oil (40–60 %) and protein (20–30 %) content (1). According to FAOSTAT, 2024 groundnut is largely cultivated in India (5.65 m ha) followed by China (4.87 m ha) and China is the leading producer (19.6 million tonnes) followed by India (11.9 million tonnes). Despite its critical role in food security and rural economies, its productivity is highly vulnerable to abiotic stresses, particularly drought, salinity and temperature extremes (2). As groundnut is predominantly grown under rainfed conditions, terminal drought during flowering and pegging severely reduces pod yield and alters seed composition (3). In addition, salinity and heat stress disrupt osmotic balance, induce ion toxicity and enhance reactive oxygen species (ROS) production, ultimately impairing photosynthesis and nitrogenase activity in root nodules (4,5).

Conventional management practices rely heavily on synthetic fertilisers and agrochemicals; however, their excessive use has led to soil degradation, nutrient imbalances and declining microbial diversity, highlighting the need for sustainable alternatives (6). In this context, plant biostimulants (PBs) have emerged as promising eco-friendly inputs. These are defined as substances or microorganisms that enhance nutrient use efficiency, abiotic stress tolerance and crop quality irrespective of their nutrient content (7). Biostimulants include microbial inoculants such as plant growth-promoting rhizobacteria (PGPR) and arbuscular mycorrhizal fungi (AMF), as well as non-microbial products like humic substances, seaweed extracts and protein hydrolysates (8,9).

Although the general modes of action of biostimulants such as hormonal modulation and antioxidant regulation are well documented across crops, groundnut-specific analyses remain limited. Groundnut exhibits unique physiological traits, including geocarpy and specialised symbiosis with *Bradyrhizobium*, which

influence its stress responses (3, 10). Therefore, generalised interpretations from other crops often fail to capture these crop-specific mechanisms. Recent studies highlight such specificity, including chitosan-mediated regulation of ionic balance (enhanced potassium (K) and calcium (Ca) over sodium (Na)) under combined drought-alkali stress (11) and the role of osmolyte-producing PGPR (e.g., *Acinetobacter calcoaceticus*, *Bacillus amyloliquefaciens*) in protecting photosynthetic systems under drought by mitigating ROS-induced lipid peroxidation, as evidenced by reduced malondialdehyde (MDA) accumulation (12).

In this context, the present review provides a focused synthesis of biostimulant applications in groundnut. It integrates mechanistic insights with agronomic outcomes, emphasising their roles in ROS regulation, osmotic adjustment and maintenance of nodulation and biological nitrogen fixation (BNF) under abiotic stress. Additionally, practical challenges such as formulation stability, genotype-dependent responses and field-level inconsistencies are critically examined to facilitate the effective deployment of biostimulants in climate-resilient groundnut production systems.

Conceptual framework: From definition to functional relevance

A clear conceptual framework is essential for evaluating the role of PBs in alleviating abiotic stress in groundnut. Existing literature often relies on broad, crop-generalised classifications that overlook the unique physiological and symbiotic characteristics of leguminous crops such as groundnut. This limitation restricts a precise understanding of biostimulant-crop interactions under stress conditions.

To address this gap, a shift from conventional descriptive approaches toward a function-oriented framework is necessary. Accordingly, this section outlines the regulatory and functional definitions of biostimulants. It also highlights the limitations of current legislative perspectives. Furthermore, it emphasises the need for a function-based classification aligned with groundnut-specific physiological responses under abiotic stress.

Functional definition and regulatory context

The concept of PBs has evolved from input-based descriptions toward a function-oriented framework centered on physiological outcomes. A widely accepted definition describes biostimulants as substances or microorganisms that enhance nutrient use efficiency, abiotic stress tolerance and crop quality, irrespective of their nutrient content, distinguishing them from fertilisers and pesticides (7, 9, 13). This perspective has been formalised in the European Union under Regulation (EU) 2019/1009, which classifies biostimulants based on their capacity to stimulate plant nutrition processes independently of nutrient content, with emphasis on nutrient use efficiency, stress tolerance, crop quality and rhizosphere nutrient availability (8, 13, 14).

A fundamental principle in biostimulant science is that function outweighs composition. Unlike synthetic agrochemicals which possess defined active ingredients, biostimulants are complex systems comprising multiple bioactive compounds or living microorganisms whose efficacy arises from synergistic interactions (9, 15, 16). This principle is particularly relevant in groundnut, where productivity depends on efficient symbiotic nitrogen fixation. Under abiotic stress, nodule function is impaired due to disruption of the oxygen diffusion barrier and degradation of leghemoglobin, which regulates oxygen supply to nitrogenase. Consequently, assessing

biostimulants based on their ability to sustain nodule functionality, preserve leghemoglobin integrity and maintain oxygen balance provides a more physiologically meaningful framework than composition-based classification. Their efficacy arises from synergistic interactions among constituents rather than a single identifiable compound (15, 16).

Consequently, evaluating biostimulants based solely on chemical composition is inadequate. A functional or claims-based approach focusing on measurable plant responses such as improved root architecture, osmotic regulation, or stress tolerance is more appropriate (15–17). This is particularly relevant for groundnut, where productivity under stress depends on integrated physiological processes including geocarp and symbiotic nitrogen fixation, as well as sensitivity during critical development stages such as flowering, pegging and pod filling (3).

Limitations of regulatory variability

Despite increasing acceptance of functional definitions, regulatory fragmentation remains a major constraint. There is no global consensus on classification or regulation of biostimulants, leading to inconsistencies across regions (18–21). While the European Union has established a clear framework under Regulation (EU) 2019/1009, its Fertilising Products Regulation (FPR; applicable from July 2022) classifies biostimulants as “PFC 6 - Plant Biostimulants,” providing a function-based definition centered on the stimulation of plant nutrition processes independent of nutrient content. This framework is increasingly regarded as a global reference point and has influenced the adoption of similar terminology in other regions. However, countries such as the United States still operate within evolving or partially defined regulatory structures, resulting in continued ambiguity in classification and product claims (9, 22).

Such variability limits commercialisation and adoption by increasing regulatory costs and creating uncertainty for both researchers and farmers (19, 23). In groundnut-growing regions, particularly in developing countries, this often results in inconsistent product quality and unreliable field performance (24). Therefore, harmonised, function-based regulatory standards are essential for the effective integration of biostimulants into stress management strategies (19).

From classification to functional interpretation

Biostimulants have traditionally been classified based on their origin into microbial and non-microbial categories (8, 25).

Microbial biostimulants include living organisms such as PGPR, AMF and endophytic microorganisms, with commonly reported genera including *Pseudomonas*, *Bacillus*, *Azospirillum* and *Rhizobium* (26).

Non-microbial biostimulants comprise organic and inorganic substances such as humic and fulvic acids, protein hydrolysates, seaweed and botanical extracts, amino acids and biopolymers like chitosan (7, 27).

Shift toward function-based classification in groundnut

Although widely used, origin-based classification is largely descriptive and provides limited mechanistic insight. In groundnut, stress responses are highly specialised due to features such as geocarp, BNF and distinct nutrient dynamics in the pod zone. Consequently, generalised classifications fail to adequately explain biostimulant performance in this crop.

A function-based classification, aligned with specific physiological constraints, offers a more meaningful framework. Categorising biostimulants according to their mechanistic roles enables better interpretation of their agronomic relevance and field performance. Accordingly, in groundnut systems, biostimulants can be functionally grouped into three primary categories, while also encompassing emerging inputs such as silicon-based biostimulants and nano-biostimulants that provide targeted physiological and nutrient-delivery advantages.

Modulators of osmotic adjustment and cellular hydration

Under drought and salinity, groundnut experiences loss of cellular turgor, leading to stomatal closure and reduced photosynthesis (3). Biostimulants functioning as osmotic regulators mitigate these effects by enhancing osmolyte accumulation and cellular hydration.

Groundnut-specific studies demonstrate that halotolerant PGPR, such as *A. calcoaceticus* and *B. amyloliquefaciens*, induce the accumulation of key osmolytes including trehalose, glycine betaine, proline and salicylic acid, thereby stabilising membranes and reducing oxidative damage (12). Similarly, *Stenotrophomonas maltophilia* enhances tolerance to salinity by improving plant water status through osmoprotectant pathways (28). These biostimulants can thus be functionally categorised as regulators of cellular hydration.

Enhancers of symbiotic nitrogen fixation and nutrient homeostasis

Groundnut productivity depends heavily on BNF through its association with *Bradyrhizobium*. Abiotic stresses, particularly drought and heat, disrupt nodule function by limiting oxygen supply and inhibiting nitrogenase activity (29, 30).

Unlike cereals and most legumes, groundnut exhibits unique traits such as crack-entry nodulation and geocarpy, where pods develop underground and depend on direct soil Ca uptake. These distinct physiological and nutrient dynamics limit the direct transferability of findings from other crops, necessitating groundnut-specific evaluation of biostimulant responses.

Biostimulants that sustain this symbiosis act as regulators of nutrient homeostasis. For instance, humic substances and amino acid-based formulations enhance root growth and infection sites, facilitating rhizobial colonisation under stress (6, 31, 32). Additionally, chitosan has been shown to improve nutrient balance under combined drought-alkali stress by promoting K and magnesium (Mg) uptake while restricting Na⁺ accumulation, thereby maintaining ionic equilibrium and plant function (11, 33, 34).

Elicitors of antioxidant defence and reactive oxygen species scavenging

Abiotic stress in groundnut leads to excessive generation of ROS, causing oxidative damage to cellular structures (3, 13). Biostimulants mitigate this by enhancing antioxidant defence systems.

Both microbial and non-microbial biostimulants act as elicitors of antioxidant activity by upregulating key enzymes such as superoxide dismutase (SOD), catalase (CAT) and ascorbate peroxidase (APX). This results in reduced lipid peroxidation and improved protection of the photosynthetic apparatus under stress conditions (12).

Overall, a function-based classification provides a mechanistically relevant framework for understanding biostimulant action in groundnut. By targeting osmotic regulation, symbiotic nitrogen fixation and antioxidant defence, biostimulants can effectively address key physiological constraints and enhance stress resilience.

Functional classes of biostimulants in groundnut systems

Groundnut exhibits distinct physiological constraints under abiotic stress, including geocarpic reproduction, high Ca demand during pegging and sensitivity of symbiotic nitrogen fixation to drought. These crop-specific characteristics necessitate a mechanistic evaluation of biostimulants tailored to groundnut systems. Generic extrapolations from other crops are inadequate, as they fail to capture the complex interactions among the plant, its associated microbiome and the soil environment, particularly microbial functional traits such as 1-aminocyclopropane-1-carboxylate (ACC) deaminase activity (ethylene regulation), osmolyte production (cellular hydration) and exopolysaccharide (EPS) production (soil aggregation and stress buffering). Therefore, this section critically examines the functional roles of non-microbial, microbial and emerging biostimulants based on groundnut-specific evidence.

Non-microbial biostimulants

Non-microbial biostimulants comprise diverse organic compounds that regulate plant metabolism, root architecture and stress responses beyond simple nutrient supply.

Seaweed extracts

Seaweed extracts, rich in phytohormones and trace elements, play a significant role in regulating reproductive development and osmotic balance in groundnut. Application of *Kappaphycus alvarezii* extracts enhance seed yield and harvest index by promoting efficient partitioning of photosynthates toward developing pods (35–37). Their cytokinin-mediated effects accelerate flowering and peg development (37, 38). Under salinity stress, seaweed extracts mitigate ionic toxicity by enhancing proline accumulation, maintaining protein synthesis and improving uptake of essential nutrients such as K, Ca, Mg, zinc (Zn) and iron (Fe) (39, 40).

Humic substances

Humic and fulvic acids influence both soil properties and plant metabolism, particularly in degraded or calcareous soils. In groundnut, they stimulate key enzymes involved in carbon and N metabolism, thereby improving growth and nutrient assimilation (41–45). Under drought, humic acids enhance antioxidant activity and maintain cellular stability by regulating ROS through secondary metabolite synthesis (42, 46). Furthermore, humic substances mitigate drought-induced photosynthetic inhibition by maintaining stomatal conductance (g_s), thereby sustaining CO₂ availability and a higher photosynthetic rate (P_n) under water-deficit conditions. Additionally, their application improves root proliferation, increasing sites for rhizobial infection and enhancing nodulation, nitrogenase activity and nutrient accumulation (47–49).

Protein hydrolysates

Protein hydrolysates, consisting of amino acids and peptides, act as signalling molecules and osmoprotectants under water stress. In groundnut, their application under drought conditions preserves chlorophyll content, improves relative water content and maintains photosynthetic efficiency. Importantly, protein hydrolysates sustain nodule functionality by preventing leghemoglobin degradation, thereby preserving active N fixation under stress (50–52).

Microbial biostimulants

The rhizosphere and geocarposphere of groundnut harbor complex microbial communities that play a critical role in stress adaptation. Microbial biostimulants aim to enhance these interactions, although their effectiveness is strongly influenced by strain specificity and host

genotype.

Plant growth-promoting rhizobacteria

Recent groundnut-focused studies highlight specialised PGPR strains with enhanced stress-mitigating functions beyond conventional roles. For example, *S. maltophilia* improves membrane stability under salinity and N stress by modifying fatty acid composition (53). Similarly, strains such as *A. calcoaceticus* and *B. amyloliquefaciens* promote osmotic adjustment by enhancing osmotic regulation and cellular stability under stress (12).

However, PGPR performance is highly genotype dependent. While certain cultivars show significant improvements in growth, nodulation and yield, others exhibit limited responses; this emphasises the need for genotype-specific microbial formulations (28, 54, 55).

Rhizobium

Groundnut exhibits a promiscuous nodulation behaviour with diverse native *Bradyrhizobium* populations, often limiting the effectiveness of introduced inoculants (56). Abiotic stresses further impair nodulation and nitrogenase activity, resulting in reduced N fixation (28, 57). Co-inoculation strategies combining *Bradyrhizobium* with PGPR have shown improved outcomes, including enhanced nodulation, chlorophyll content and seed nutritional quality (58). The PGPR act as helper organisms by producing siderophores and ACC deaminase, which facilitate rhizobial infection and reduce stress-induced ethylene levels (59–61). Improved nodulation efficiency under such interactions supports sustained N availability, which is critical for peg penetration and subsequent pod filling, thereby linking belowground symbiosis with reproductive development in groundnut.

Arbuscular mycorrhizal fungi

Arbuscular mycorrhizal fungi (AMF) play a vital role in nutrient acquisition and stress tolerance in groundnut, particularly in nutrient-poor soils. While composition-based classification identifies AMF simply as microbial inoculants, a function-based perspective highlights their role in enhancing the uptake of immobile nutrients such as phosphorus (P) through extensive hyphal networks, which is essential for nodulation and energy metabolism (62, 63). Under drought conditions, AMF improve root hydraulic conductivity and plant water status (64). Additionally, they influence rhizosphere microbial composition, promoting beneficial communities that enhance tolerance to salinity and alkalinity (65). This distinction underscores the importance of evaluating biostimulants based on functional outcomes rather than their biological origin alone.

Emerging biostimulants

Emerging biostimulants focus on novel compounds and advanced delivery systems designed for targeted stress mitigation in groundnut. Unlike conventional biostimulants that rely on bulk molecular formulations or broad-spectrum organic matrices, these emerging technologies leverage unique physicochemical properties such as nanoscale reactivity, precise surface structures and large surface-area-to-volume ratios to enable highly targeted cellular penetration and precisely controlled nutrient delivery (66).

Chitosan

Chitosan, a biopolymer derived from chitin, has shown strong potential in managing combined abiotic stresses. Under drought-alkali conditions, it regulates nutrient homeostasis by enhancing the accumulation of N, K and Mg while restricting Na⁺ uptake, thereby

maintaining ionic balance and improving stress tolerance (11, 67, 68). This selective nutrient regulation enhances photosynthetic stability, irrigation water use efficiency and yield. Additionally, seed treatment with chitosan improves germination, reduces seed-borne diseases and accelerates flowering, contributing to increased pod yield (69).

Silicon

Silicon is increasingly recognised for its role in stress mitigation, particularly in sandy and heat-stressed soils with limited Ca and P availability. Foliar application of silicon improves transpiration efficiency, cellular stability and nutrient utilisation (70). Importantly, it enhances Ca and P use in the peg zone, reducing the incidence of empty pods and improving yield, seed weight and oil and protein content (71, 72).

Nano-inputs

Nanotechnology offers advanced delivery of nutrients and bioactive compounds through nanoparticles typically ranging from 1–100 nm, characterised by a high surface area-to-volume ratio that enhances reactivity, penetration and nutrient use efficiency. In groundnut, nano-formulations such as nano-Ca and nano-B, especially when combined with microbial inoculants, significantly improve growth, yield attributes and seed quality compared to conventional inputs (73, 66).

Evidence and uncertainty

Despite promising results, the large-scale application of emerging biostimulants remains constrained by uncertainties. Issues related to environmental safety, potential accumulation in edible plant parts and impacts on soil microbiota are not fully understood (66). Moreover, their effectiveness depends on precise formulation, application timing and soil conditions. Therefore, further research is required to optimise their safe and consistent use under field conditions.

Mechanistic basis of biostimulant action in groundnut

To enable targeted agronomic applications, it is essential to move beyond generalised concepts of “plant growth promotion” and examine the specific biochemical and molecular mechanisms induced by biostimulants. Groundnut possesses distinct physiological traits, including geocarpy, crack-entry nodulation and a high requirement for Ca in the pod zone, which influence its response to abiotic stress (3). Under conditions such as drought, salinity and temperature extremes, biostimulants modulate key physiological processes. This section examines major mechanisms, including hormonal regulation, root architecture modification, osmotic adjustment, antioxidant defence, nutrient homeostasis and rhizosphere interactions, in relation to stress mitigation in groundnut. A summary of key biochemical and oxidative stress biomarkers regulated by biostimulants in groundnut is presented in Table 1.

Hormonal regulation and growth coordination

Abiotic stress in groundnut disrupts hormonal balance, characterised by increased ethylene and abscisic acid (ABA) levels and reduced auxins (IAA) and cytokinins, leading to growth inhibition, premature senescence and peg abortion (76). Biostimulants modulate this phytohormonal imbalance to sustain growth and reproductive development under stress.

Microbial biostimulants, particularly PGPR, enhance IAA production, promoting root proliferation and improving water

Table 1. Regulation of key biochemical and oxidative stress biomarkers by biostimulants in groundnut

Biostimulant agent	Stress condition	Antioxidant enzyme modulation (Upregulated)	Key osmolytes & metabolites (Accumulated)	Stress biomarkers (Downregulated)	References
Chitosan (Biopolymer, 500 mg L ⁻¹)	Combined drought and alkalinity	Modulates general antioxidant defence pathways	Selective partitioning of potassium (K ⁺) and magnesium (Mg ²⁺) to leaves for stomatal regulation and chlorophyll synthesis.	Root-to-shoot translocation of toxic sodium (Na ⁺) ions.	(11)
<i>Acinetobacter calcoaceticus</i> AC06 and <i>Bacillus amyloliquefaciens</i> BA01	Severe drought (40 % field capacity)	Catalase (CAT), ascorbate peroxidase (APX), superoxide dismutase (SOD)	Massive, localised synthesis of trehalose, salicylic acid, glycine betaine and proline.	Malondialdehyde (MDA) content, electrolyte leakage (EL).	(12)
Seaweed extract (<i>Kappaphycus alvarezii</i> , <i>Gracilaria edulis</i>)	Drought / heat stress	Peroxidase (POX), superoxide dismutase (SOD)	Endogenous cytokinins, proline and total soluble sugars.	Oxidative degradation of the photosynthetic apparatus (thylakoid membranes).	(34, 40)
<i>Stenotrophomonas maltophilia</i> BJ01	Salinity (100 mM NaCl) and nitrogen deficit	Superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX)	Total amino acids; specific increases in omega-7 and omega-6 (γ-Linolenic acid) monounsaturated fatty acids to maintain membrane fluidity.	Hydrogen peroxide (H ₂ O ₂), lipid peroxidation, chlorophyll degradation.	(53, 74)
Ascorbic acid (AsA) priming (50-100 mg L ⁻¹)	Heavy metal toxicity (Lead-Pb ²⁺)	Bolsters the ascorbate-glutathione cycle (SOD, POD, PPO)	Endogenous ascorbic acid, total soluble proteins.	H ₂ O ₂ and MDA accumulation in both root and shoot tissues.	(75)

acquisition under stress (12, 20). Beyond root effects, they act as elicitors of plant defence by modulating salicylic acid (SA) and jasmonic acid (JA) pathways, inducing tolerance to oxidative stress. The PGPR also contribute to membrane stabilisation by reducing lipid peroxidation and regulate stomatal function via ABA-mediated pathways, optimising water use without compromising carbon assimilation (12, 77). Similarly, seaweed extracts rich in cytokinins and IAA regulate reproductive development by enhancing flowering and assimilate partitioning, improving harvest index under limited moisture (35, 78). Their bioactive compounds further act as defence elicitors, reducing ROS accumulation and supporting stomatal regulation to maintain leaf hydration and photosynthetic stability under stress.

Regulation of stress-induced ethylene is also critical. Under drought and salinity, increased accumulation of its precursor (ACC) inhibits root growth and pod development. The PGPR possessing ACC deaminase reduce ethylene levels by degrading ACC, thereby facilitating root growth, peg elongation and pod expansion under stress (18, 77).

Root system architecture and nodulation

The groundnut root system performs dual functions: accessing soil moisture under drought and supporting BNF through *Bradyrhizobium* symbiosis. Biostimulants modify root system architecture to enhance both processes.

Humic substances and protein hydrolysates stimulate plasma membrane H⁺-ATPase activity, promoting cell wall loosening and lateral root proliferation (7, 42). In groundnut, this is particularly important as rhizobial infection occurs via “crack entry” at lateral root junctions, rather than via root hair curling (79). Increased lateral root formation therefore enhances nodulation efficiency.

Abiotic stress restricts oxygen diffusion into nodules, inhibiting nitrogenase activity and BNF (29). Co-inoculation with *Bradyrhizobium* and PGPR (e.g., *Bacillus* and *Pseudomonas*) helps maintain nodule function under stress. The PGPR act as helper organisms by producing IAA and siderophores, thereby enhancing both nutrient availability in the rhizosphere and nutrient uptake efficiency by the plant, while supporting nodule integrity and sustaining leghemoglobin levels for efficient oxygen regulation (59). This interaction ensures continued N assimilation during critical growth stages.

Osmotic adjustment and cellular stability

Drought and salinity reduce cellular turgor in groundnut, leading to stomatal closure and reduced photosynthesis. Biostimulants mitigate these effects by promoting osmotic adjustment through the accumulation of compatible solutes (osmolytes), which maintain cellular hydration without disrupting metabolism (80, 81).

Groundnut-specific studies demonstrate that halotolerant PGPR, such as *A. calcoaceticus* and *B. amyloliquefaciens*, enhance the accumulation of osmolytes including trehalose, proline and glycine betaine under severe stress (12). Trehalose plays a protective role by stabilising proteins and membranes during dehydration (82).

Non-microbial biostimulants, particularly protein hydrolysates, further support osmotic adjustment by supplying precursors for proline synthesis (52). Proline functions both as an osmotic regulator and as a stabiliser of key enzymes such as nitrogenase. Consequently, biostimulant-treated plants maintain higher relative water content (RWC) and reduced electrolyte leakage,

preserving cellular integrity under stress conditions.

Antioxidant defence and reactive oxygen species regulation

Biostimulants mitigate oxidative stress by enhancing both enzymatic and non-enzymatic antioxidant systems (83). Applications of seaweed extracts, humic substances and PGPR act as priming agents that upregulate key antioxidant enzymes such as SOD, CAT and APX. For instance, *S. maltophilia* increases the activity of these enzymes under salinity and nutrient stress, facilitating efficient detoxification of ROS (74).

Non-enzymatic antioxidants also play a critical role. Seed priming with ascorbic acid enhances the ascorbate-glutathione cycle, protecting the photosynthetic machinery under heavy metal stress (75). This results in sustained chlorophyll levels and reduced lipid peroxidation, as indicated by lower MDA accumulation in treated plants (84). Maintaining photosynthetic integrity is essential for supporting pod development in groundnut under stress. However, a major limitation is the lack of long-term field validation, as most evidence on ascorbic acid priming is derived from short-term, controlled studies on limited genotypes. Therefore, multi-season field trials across diverse genotypes are needed to confirm its effectiveness under complex, real-world conditions.

Nutrient-use efficiency and ionic balance

Groundnut exhibits unique nutritional dynamics due to geocarpy, where developing pods absorb Ca directly from the soil, as it is not translocated through the phloem. Under drought or alkaline conditions, reduced availability of Ca and P leads to poor pod development and increased seed abortion (66).

Biostimulants improve nutrient availability and uptake under such constraints. Nano-formulations of Ca and boron enhance nutrient delivery to the peg zone, improving pod filling and shelling percentage (66). Additionally, humic and fulvic acids increase nutrient accessibility by chelating micronutrients and enhancing P availability in calcareous soils (85).

Maintaining ionic balance is critical under combined drought-alkali stress. Chitosan application promotes selective nutrient uptake by restricting Na⁺ accumulation while enhancing K, N and Mg levels, thereby maintaining a favourable K⁺/Na⁺ ratio (11). This regulation supports osmotic balance, chlorophyll synthesis and water-use efficiency, improving stress tolerance and productivity (33, 86). However, its effectiveness can vary due to dose-response inconsistencies and interactions with soil type, particularly between sandy and clay soils.

Rhizosphere-mediated processes

The rhizosphere, particularly the geocarposphere, is a key site of biostimulant activity in groundnut. Abiotic stresses, such as drought and salinity degrade soil structure, reduce microbial diversity and hinder peg penetration (87).

Microbial biostimulants improve soil physical and biological properties. The PGPR (e.g., *Enterobacter*, *Bacillus* and *Pseudomonas*) produce EPS that promote soil aggregation, enhancing porosity and water retention (88, 89). This improves soil structure and facilitates peg penetration. Additionally, EPS-based biofilms formed on root surfaces can limit Na⁺ entry under saline conditions, contributing to stress tolerance (80).

Non-microbial inputs such as humic substances and biochar stimulate microbial activity by providing stable carbon sources. This

enhances enzymatic processes such as phosphatase and dehydrogenase activity, improving nutrient mineralisation (90, 91). The PGPR also release volatile organic compounds (VOCs) that induce systemic tolerance in groundnut, enhancing resilience to environmental stress (19).

Overall, biostimulants enhance rhizosphere functionality by improving soil structure, microbial activity and nutrient availability, thereby supporting groundnut growth under stress conditions.

Molecular mechanisms and signalling networks

To transition PBs from empirical tools to precision inputs, their molecular mechanisms must be clearly understood. Rather than passive absorption, biostimulants initiate receptor-mediated signalling cascades. For example, chitosan interacts with plasma membrane-localised pattern recognition receptors (PRRs), triggering oxidative bursts (H₂O₂ accumulation) and Ca²⁺ influx, which activate mitogen-activated protein kinase (MAPK) signalling pathways (13, 92). These cascades regulate key transcription factors such as DREB, NAC and WRKY, leading to the expression of stress-responsive genes involved in osmotic regulation, aquaporin activity and cellular protection (12, 19). Simultaneously, biostimulants modulate hormonal crosstalk among ABA, SA and JA pathways, balancing stress tolerance with continued growth. In groundnut, this integrated signalling framework enables coordinated responses that enhance resilience without compromising productivity.

Beyond immediate signalling, biostimulants also induce longer-term stress adaptation through epigenetic regulation and rhizosphere-mediated ion homeostasis. Applications of microbial consortia and organic extracts influence DNA methylation, histone modifications and small RNA activity, establishing a primed state that enhances future stress responses (78, 81). Concurrently, rhizosphere interactions regulate ion transport systems rather than acting solely through physical barriers. Microbial and humic-based biostimulants modulate key transporters such as HKT1, SOS1 and NHX, facilitating Na⁺ exclusion, retrieval and vacuolar sequestration under salinity stress (93). These coordinated molecular and rhizosphere processes provide a mechanistic basis for sustained stress tolerance, although their dynamics in groundnut under field conditions remain insufficiently characterised.

Stress-specific performance of biostimulants in groundnut

Understanding the performance of biostimulants under specific stress conditions is essential for targeted agronomic application. Groundnut responses to abiotic stress are shaped by its unique physiological characteristics (3). This section synthesises groundnut-specific responses to biostimulants under drought, salinity, heat and combined stress conditions.

Drought stress

Agronomic responses

Increased soil hardness under drought restricts peg penetration, resulting in poor pod set and seed abortion (29). Biostimulants alleviate these constraints by improving growth and yield attributes. Application of protein hydrolysates under simulated drought conditions enhances plant growth, root development and pod number (52). Similarly, foliar application of metformin improves seed yield, 100-seed weight and irrigation water use efficiency under limited irrigation (93). Microbial biostimulants, particularly PGPR such as *A. calcoaceticus* and *B. amyloliquefaciens*, significantly increase biomass under drought stress (12, 59).

Physiological responses

The PGPR improve water retention and membrane stability under drought, resulting in enhanced stress tolerance and biomass accumulation (12). Protein hydrolysates help maintain photosynthetic performance under stress conditions. Importantly, they support sustained N fixation under stress (52).

Critical synthesis

Effective drought mitigation in groundnut requires more than simply general osmoprotection. Biostimulants must simultaneously maintain plant water status and sustain symbiotic N fixation. Evidence indicates that biostimulants combining osmotic regulation with preservation of nodule function are most effective, ensuring continued carbon and N supply for pod development under water-limited conditions (3, 12, 52).

Salinity stress

Ionic balance

Groundnut, being a glycophyte, is highly sensitive to salinity, which disrupts osmotic balance and causes ion toxicity by limiting the uptake of essential nutrients such as K^+ , Ca^{2+} and Mg^{2+} (40, 74). Maintaining high K^+/Na^+ and Ca^{2+}/Na^+ ratio is therefore critical for tolerance. Biostimulants enhance ionic regulation by restricting Na^+ accumulation and promoting essential nutrient uptake, which is reflected in improved g_s , P_n and transpiration rate (E) under stress conditions. For instance, halotolerant PGPR such as *Brachy bacterium saurashtrense* and *Brevibacterium casei* improve K^+ and Ca^{2+} accumulation under saline conditions (94), while seaweed extracts reduce Na^+ uptake while sustaining macro- and micronutrient absorption in groundnut cultivars under salinity stress (40).

Growth responses

Salinity reduces growth, induces chlorosis and impairs nodulation. Microbial biostimulants such as *S. maltophilia* enhance plant growth by maintaining photosynthetic pigments, promoting hormone production and increasing amino acid content (74). Non-microbial inputs, including potassium silicate, humate and amino acid formulations, improve plant height, branching and pod yield in saline soils (85). Seedbed application of seaweed extracts further enhances germination and biomass through osmotic regulation (40).

Critical synthesis

In groundnut, salinity tolerance depends primarily on ionic regulation rather than general antioxidant responses. Since pods absorb Ca^{2+} directly from the soil, high Na^+ levels severely disrupt pod development (3). Effective biostimulants function by selectively enhancing K^+ and Ca^{2+} uptake while limiting Na^+ interference, thereby maintaining ion balance in the geocarposphere (85, 94). Thus, evaluation of biostimulants under salinity should prioritise their ability to regulate ion dynamics, supported by physiological indicators such as PSII efficiency (Fv/Fm) and chlorophyll fluorescence, rather than relying solely on vegetative growth parameters.

Heat stress and combined stress

Reproductive failure under heat stress

Temperatures above 32–35 °C severely affect groundnut reproduction by reducing pollen viability, inhibiting peg elongation and disrupting carbon partitioning, ultimately lowering yield and harvest index (3). Application of biostimulants such as potassium silicate helps mitigate these effects by improving cellular stability,

regulating transpiration and enhancing nutrient utilisation, particularly Ca and P required for pod development. This results in improved seed weight, pod yield and seed quality under heat stress (71).

Combined stress effects

Groundnut often experiences multiple stresses simultaneously, such as drought-heat or drought-alkali conditions. These combined stresses intensify physiological damage, leading to reduced relative water content and increased cellular injury, while also disrupting source-sink relationships by limiting photosynthetic assimilate production and its translocation to developing pods (95). Biostimulants play a crucial role in mitigating these effects by stabilising metabolic processes and enhancing stress tolerance.

Under drought-alkali stress, chitosan application improves nutrient homeostasis by promoting the accumulation of key elements such as N, K and Mg while compensating for reduced availability of other nutrients (11). This selective regulation supports stomatal function and chlorophyll synthesis, maintaining photosynthetic efficiency and yield under adverse conditions.

Critical synthesis

Combined stresses impose complex physiological constraints that cannot be addressed through single-stress approaches. In groundnut, the interaction between drought and heat creates conflicting demands between water conservation and canopy cooling (3). Effective biostimulants mitigate such challenges by maintaining nutrient balance and cellular stability, particularly through the regulation of K^+ and Mg^{2+} . Future research should prioritise field-based evaluations under combined stress conditions to identify strategies that protect reproductive development and sustain productivity (11).

Class-specific trade-offs and performance patterns (Revised and condensed)

Effective integration of biostimulants in groundnut systems requires evaluation beyond isolated outcomes, as no single product provides universal stress tolerance. In addition to growth and yield parameters, reproductive indicators such as pollen viability (%), stigma receptivity and fertilisation rate are critical for assessing stress impacts and biostimulant effectiveness. This section critically examines the performance, specificity and limitations of major biostimulants, highlighting their strengths and practical constraints under field conditions.

Seaweed extracts

Seaweed extracts (SWE), derived from species such as *Kappaphycus alvarezii* and *Ascophyllum nodosum*, contain phytohormones, polysaccharides and trace elements that influence plant growth (36, 96).

Strength (early-stage effectiveness): The SWE primarily enhance early plant vigour by supplying cytokinins that promote flowering and accelerate pegging in groundnut (35). Seedbed application also improves germination and seedling establishment under mild salinity, reducing early stand loss (40). In addition, SWE contribute to membrane thermostability and regulate transpiration, helping maintain cellular integrity and water balance under stress conditions.

Limitation (reduced efficacy under severe stress): The effectiveness of SWE declines under high stress intensity. While beneficial under moderate salinity, their capacity to mitigate damage is limited under severe conditions (≥ 150 mM sodium chloride (NaCl)), where

reductions in growth, chlorophyll and protein content persist (40). Thus, SWE act mainly as stress mitigators during early or moderate stress rather than providing sustained protection under extreme conditions.

Humic substances

Humic and fulvic acids are stable organic compounds that improve soil conditions and plant growth, particularly in sandy and calcareous soils (42).

Strength (soil-root synergy): Humic substances enhance soil cation exchange capacity, improve availability of nutrients such as P and K and chelate micronutrients (Fe, Zn) (85, 97). They also stimulate root growth through auxin-like activity and activation of H⁺-ATPase, promoting lateral root development. In groundnut, this expanded root system supports effective *Bradyrhizobium* colonisation and sustains N fixation under suboptimal soil conditions (42).

Limitation (slow response): A key limitation of humic substances is their delayed action. Their effectiveness depends on gradual integration into the soil and stimulation of microbial activity (97, 98). Consequently, they are less effective under sudden stress events and are better suited for pre-sowing or basal application rather than immediate stress mitigation.

Protein hydrolysates

Protein hydrolysates (PHs), composed of amino acids and small peptides, act as readily available signalling molecules and metabolic precursors under stress conditions (81, 99).

Strength (rapid metabolic support): Protein hydrolysates (PHs) provide immediate physiological relief by supplying osmoprotectants directly, reducing the energy required for their synthesis. In groundnut, their application under drought stabilises relative water content, preserves chlorophyll and maintains active root nodules. They also enhance antioxidant activity, limiting oxidative damage (52, 95, 99, 100).

Limitation (short-lived effect): The effects of PHs are transient due to rapid assimilation and degradation of amino acids. Sustained protection under prolonged stress requires repeated applications, increasing input costs and limiting practicality in field practicality. Compared to other biostimulants, PHs offer rapid physiological responses but lower durability, whereas inputs such as humic substances and microbial inoculants provide more sustained, though slower or variable effects.

Microbial biostimulants

Microbial biostimulants, including PGPR, *Bradyrhizobium* and AMF, function by establishing symbiotic interactions within the groundnut rhizosphere to enhance stress tolerance (6, 59).

Strength (sustained biological activity): When effectively established, microbial inoculants provide long-term benefits through continuous production of bioactive compounds such as EPS, osmolytes and ACC deaminase, which regulate stress ethylene and improve plant resilience (12, 53). These interactions enhance nutrient acquisition increase microbial biomass carbon (MBC) as an indicator of improved soil biological activity and sustain biological N fixation under stress conditions (91).

Limitation (variability and ecological constraints): The performance of microbial biostimulants is highly variable and influenced by host genotype and soil environment. Groundnut cultivars differ significantly in their responsiveness to microbial inoculation, with some showing strong positive effects while others exhibit minimal or

inconsistent responses (28). Additionally, introduced microbes often face competition from native microbiota and may fail to establish under harsh soil conditions, limiting their reliability in field applications.

Emerging biostimulants

Emerging biostimulants in groundnut systems include chitosan, silicon and nano-fertilisers such as nano-Ca and nano-Zn (66, 69).

Strength (targeted stress mitigation): These inputs provide highly specific solutions to groundnut constraints. Nano-ca improves Ca availability in the peg zone, reducing empty pod formation under stress (66). Chitosan enhances ionic balance by promoting K⁺ and Mg²⁺ accumulation while restricting Na⁺ uptake through complexation and ion-binding interactions, whereas chelation-based processes facilitate improved nutrient availability and mobility, thereby improving stress tolerance and water-use efficiency (11).

Limitation (uncertainty and regulatory challenges): Despite their potential, these technologies face limitations related to environmental safety, cost and regulatory approval. The long-term effects of nano-inputs on soil microbiota and potential accumulation in edible parts remain uncertain (75). Additionally, chitosan and silicon require precise dosing, as improper application can reduce effectiveness or cause phytotoxicity, necessitating further field validation.

Translating mechanisms into practice: Deployment matrix

Although biostimulants show strong potential for mitigating abiotic stress in groundnut, their field performance is often inconsistent due to improper alignment between application strategy and crop physiology. Groundnut's unique traits and cultivation in marginal soils, require precise deployment approaches (3, 42). Effective use of biostimulants therefore depends on appropriate formulation, targeted delivery and optimal timing to ensure interaction with key plant zones such as roots, nodules and the geocarposphere. In addition, certain biostimulants, particularly protein hydrolysates, exert signalling effects through bioactive peptides that modulate gene expression and enhance stress-responsive pathways. A schematic representation of stage-specific biostimulant deployment strategies in groundnut under abiotic stress is illustrated in Fig. 1.

Formulation and bioavailability

Stability

The effectiveness of biostimulants depends on formulation stability under field conditions. Microbial biostimulants, such as PGPR and *Bradyrhizobium*, often face reduced viability due to high temperature and desiccation in groundnut-growing regions. Liquid formulations are particularly vulnerable to environmental stress, leading to rapid microbial loss. In contrast, carrier-based formulations using materials such as biochar or peat improve microbial survival by providing protection and a supportive microenvironment. Additionally, spore-forming bacteria (e.g., *Bacillus*) offer greater resilience and longer shelf life compared to non-spore-forming strains.

Delivery constraints

For non-microbial biostimulants, bioavailability is a key limitation. In groundnut, nutrient delivery is complicated by geocarpy, as pods require direct uptake of Ca from the soil. Conventional fertilisers often become unavailable under alkaline or dry conditions. Nano-formulations improve delivery efficiency by enhancing penetration and reactivity, while encapsulation technologies such as alginate

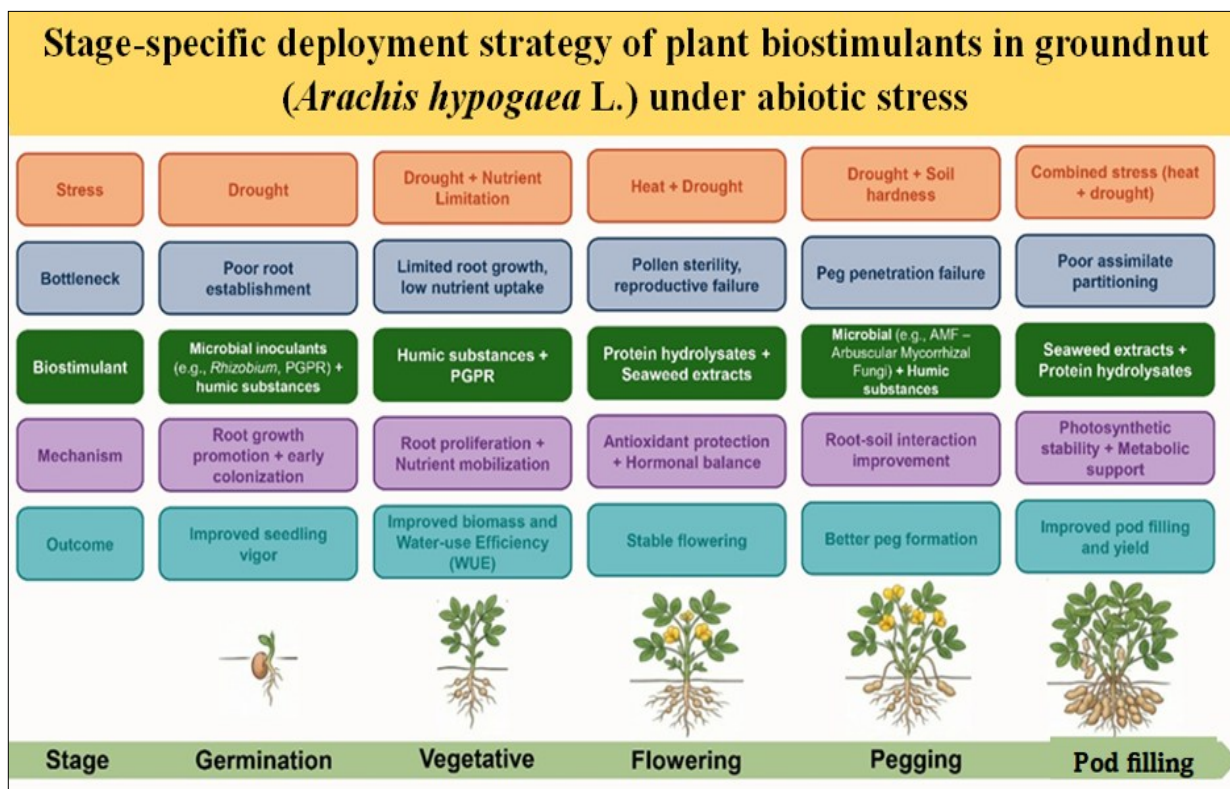


Fig. 1. Stage-specific deployment strategy of plant biostimulants in groundnut under abiotic stress. PGPR: plant growth-promoting rhizobacteria.

matrices and polymer coatings enable controlled release and improved stability of bioactive compounds. For example, nano-Ca and nano-B applications can bypass nutrient limitations in the soil and directly improve nutrient availability in the peg zone, reducing pod abortion under stress (66).

Delivery pathways

The effectiveness of biostimulants in groundnut depends strongly on the mode of application, which determines the targeted physiological response.

Seed application

Seed-applied biostimulants also improve early growth traits, although responses may vary among genotypes. Additionally, PGPR inoculation at the seed stage establishes a beneficial rhizosphere microbiome that supports early stress adaptation, with effectiveness influenced by microbial germination rate and survival under field conditions (12).

Soil application

Soil application targets rhizosphere processes and is critical for root development, nodulation and pod formation. Biostimulants such as humic substances and microbial consortia improve soil structure, enhance root proliferation and support crack-entry nodulation in groundnut (42). Arbuscular mycorrhizal fungi further enhance nutrient and water uptake, particularly P (66). Importantly, soil application is essential for Ca availability in the peg zone, as foliar Ca is ineffective due to phloem immobility. The success of microbial inoculants under this method also depends on sporulation efficiency and persistence in the soil environment.

Foliar application

Foliar application provides rapid physiological correction during stress by bypassing soil constraints. For instance, chitosan application under drought-alkali stress improves nutrient balance by enhancing K and Mg accumulation while limiting Na uptake (11).

Similarly, foliar biostimulants such as metformin improve water-use efficiency and maintain chlorophyll under reduced irrigation (93). Seaweed extracts applied to foliage also promote reproductive development through hormonal regulation (35).

Phenological timing

The effectiveness of biostimulants in groundnut depends on precise alignment with crop developmental stages and stress periods. Mistimed application can significantly reduce their agronomic value.

Stage-specific application

Groundnut is most sensitive to stress during reproductive stages, particularly flowering, pegging and pod filling (3). Heat stress during flowering reduces pollen viability, while drought during pegging restricts gynophore development. Targeted application during these stages is therefore essential. For example, foliar silicon applied at flowering improves heat tolerance and supports reproductive success (71), while protein hydrolysates applied during pod filling supply metabolic precursors that sustain seed development (52). In contrast, early application may promote excessive vegetative growth at the expense of yield.

Stress windows

Biostimulant application must also consider whether stress management is preventive or corrective. Microbial inoculants and humic substances require early application to establish in the soil and root system before stress onset (12). In contrast, foliar applications of fast-acting compounds such as amino acids or protein hydrolysates are more effective as corrective measures during acute stress, rapidly restoring osmotic balance and limiting oxidative damage (52).

Overall, effective deployment requires integrating early-stage soil-based applications with timely foliar interventions during critical stress periods.

Integrative framework for stress-specific biostimulant use

To improve field-level consistency, biostimulant application in groundnut must move beyond generalised approaches toward a mechanistic, stress-specific framework. This section focuses on integrating physiological constraints with underlying mechanisms to explain how targeted interventions improve agronomic outcomes.

Terminal drought during reproductive stages

Terminal drought during flowering-pegging represents a critical yield-limiting phase in groundnut, as reduced cellular turgor restricts peg elongation and soil penetration, while concurrent inhibition of nitrogenase activity suppresses BNF (29). This results in impaired source-sink relationships, limiting assimilate translocation to developing pods. Mechanistically, effective biostimulant interventions operate through enhanced osmotic adjustment and stabilisation of nodule function, enabling maintenance of cellular hydration and sustained nitrogen metabolism under water deficit conditions (12, 52). In addition, preservation of membrane integrity and photosynthetic capacity supports continued carbon assimilation during stress. These coordinated responses ultimately improve peg penetration, pod set and yield stability under drought conditions, particularly when early root-zone establishment is combined with timely foliar correction during peak stress periods (3, 52).

Salinity stress during early establishment

Salinity stress during early establishment imposes both osmotic and ionic constraints, limiting root growth, nodulation and early biomass accumulation in groundnut (40, 74). Elevated Na^+ concentrations disrupt K^+ and Ca^{2+} uptake, impairing enzymatic activity, membrane stability and overall metabolic function. Mechanistically, effective interventions focus on restoring ionic homeostasis through selective ion transport, including Na^+ exclusion, K^+ retention and Ca^{2+} stabilisation, alongside improvement of root architecture and rhizosphere conditions (85, 94). These processes are often mediated through regulation of membrane transport systems and enhanced nutrient acquisition efficiency, which collectively support early plant establishment. Importantly, early-stage resilience is critical, as initial stress exposure has cascading effects on subsequent growth, nodulation efficiency and reproductive success (40). Thus, targeting salinity stress during establishment provides a strategic opportunity to stabilise crop performance under marginal soil conditions.

Heat and combined stresses during pod filling

Heat stress ($> 35^\circ\text{C}$), often occurring in combination with drought or alkalinity, severely disrupts reproductive development during pod filling in groundnut by impairing carbon partitioning, reducing pollen viability and limiting Ca availability in the developing peg zone (3, 66). These stresses intensify source-sink imbalances and increase the incidence of seed abortion (“pops”). Mechanistically, effective mitigation requires stabilisation of cellular membranes, regulation of transpiration and maintenance of ionic balance under combined stress conditions. Improved stomatal regulation and protection of the photosynthetic apparatus help sustain assimilate production, while enhanced Ca availability in the geocarposphere supports proper pod development. Additionally, regulation of ion homeostasis under combined drought-alkali stress prevents toxicity and preserves metabolic activity (11, 71). Together, these mechanisms contribute to improved seed filling, pod retention and overall yield stability under high-temperature stress environments.

Conclusion of the framework

Effective biostimulant use in groundnut requires a targeted, mechanism-based approach rather than generalised application. Aligning specific biostimulants with crop growth stage and stress type is essential for consistent performance. Integrating early-stage soil-based applications with timely foliar interventions provides a practical strategy for improving stress resilience and productivity under variable field conditions. A structured framework linking stress constraints, phenological stages, mechanistic responses and agronomic outcomes is summarised in Table 2.

Knowledge gaps and research priorities

Despite advances in biostimulant research, their consistent integration into groundnut production remains limited due to key empirical and mechanistic gaps.

Product variability

Biostimulants, particularly non-microbial types, exhibit high compositional variability influenced by source material and processing methods, leading to inconsistent functional outcomes (9, 15). This lack of standardisation limits the identification of specific bioactive compounds responsible for stress mitigation and hinders the development of optimised, crop-specific formulations. Additionally, their effectiveness is influenced by soil physicochemical factors, including adsorption-desorption dynamics in alkaline soils and soil moisture-dependent nutrient diffusion, which further affect bioavailability and field performance.

Field inconsistency

Biostimulant performance often varies between controlled conditions and field environments due to complex genotype $\times$ environment $\times$ treatment interactions. In groundnut, responses differ among cultivars and microbial inoculants frequently fail to establish due to competition with native microbiota and adverse soil conditions (28, 57).

Mechanistic gaps

Critical gaps include the regulation of BNF under stress, particularly through crack-entry nodulation and the role of biostimulants in modifying root exudates and rhizosphere interactions (3, 6, 95). Additionally, mechanisms governing Ca uptake in developing pods under stress conditions require further investigation.

Future directions

Future research should emphasise multi-stress field studies supported by integrated multi-omics approaches to better understand biostimulant mechanisms (19). This includes transcriptomics to identify stress-responsive gene expression, metabolomics to profile osmolytes and antioxidant compounds, proteomics to assess stress-related enzymes and nitrogenase-associated proteins and microbiome profiling to evaluate shifts in rhizosphere microbial communities. Development of genotype-specific microbial consortia and advanced delivery systems, including nanotechnology, may further enhance effectiveness (6, 66). Integration of high-throughput phenotyping tools will also be essential for evaluating field performance and improving precision in biostimulant application (3, 90).

Conclusion

Climate-driven abiotic stresses, including drought, heat and

Table 2. Stress-specific biostimulant selection matrix for groundnut cultivation

Field scenario	Dominant constraint	Effective biostimulant class	Functional role in groundnut	Recommended application	Key limitation /constraint	References
Terminal drought (Flowering-pegging)	Loss of turgor, peg abortion, biological nitrogen fixation (BNF) inhibition	PGPR + Protein hydrolysates	Exogenous osmolyte production (trehalose, proline); osmotic protection of nodules and nitrogenase enzyme	Seed treatment + foliar spray	Requires precise timing; free amino acids have short-lived metabolic efficacy	(52)
Early-stage salinity stress (Seedling establishment)	Na ⁺ toxicity, osmotic shock, poor germination	Halotolerant PGPR + seaweed extracts (SWE)	Early root stimulation via cytokinins; biofilm-mediated ion exclusion at the root-soil interface	Seedbed + Soil application	SWE efficacy drops precipitously under extreme salinity (>150 mM NaCl)	(40, 74)
Heat stress (Reproduction)	Pollen sterility, gynophore (peg) failure, elevated canopy temperature	Silicon (K-silicate) + seaweed extracts	Regulation of canopy transpiration; hormonal balance to accelerate floral initiation	Foliar spray	Narrow optimal dose range; highly dependent on precise phenological timing	(35, 71)
Combined drought + alkalinity	Catastrophic nutrient lock-up, complex ionic imbalance	Biopolymers (Chitosan)	Reorganises nutrient homeostasis (selective ↑K, Mg; ↓Na accumulation); maximises irrigation water use efficiency (IWUE)	Foliar spray	Risk of phytotoxicity if applied beyond optimal concentration thresholds	(11)
Nutrient-poor sandy or calcareous soils	Low P/Ca availability, mechanical resistance, weak nodulation	Humic substances (HS) + AMF	Stimulates lateral root expansion (H ⁺ -ATPase activity); enhances P mobilisation and provides more "crack-entry" sites for BNF	Soil application (Basal/fertigation)	Slow prophylactic response; ineffective for acute, rapid-onset stress events	(42, 66)
Heavy metal contamination (Lead - Pb ²⁺)	Oxidative chloroplast degradation, severe ROS accumulation	Organic acids (Ascorbic acid)	Bolsters the ascorbate-glutathione cycle; scavenges ROS to preserve photosynthetic pigments	Seed priming	Long-term soil-metal interactions and plant hyper-accumulation remain uncharacterized	(75)
Calcareous saline soils (Combined stress)	Salt-induced oxidative damage, restricted macronutrient uptake	Potassium humate / silicate + amino acids	Counteracts oxidative damage; restores K ⁺ transport and branching under high pH and salinity	Foliar spray	Field efficacy is strongly dictated by the baseline chemical properties of the soil matrix	(85)
Pod filling stage (Calcium deficiency)	Phloem-immobility prevents Ca transport to subterranean pods, causing "pops"	Nano-calcium (nano-Ca), nano-Boron	High reactivity/penetration enables direct Ca and B delivery to develop subterranean pods	Soil / targeted geocarposphere application	Regulatory hurdles and ecological uncertainties regarding soil microbiome toxicity	(74-66)

PGPR: plant growth-promoting rhizobacteria; NaCl: sodium chloride; K: potassium; Mg: magnesium; Na: sodium; Ca: calcium; B: boron; AMF: arbuscular mycorrhizal fungi; BNF: biological nitrogen fixation; ROS: reactive oxygen species.

salinity, pose significant challenges to groundnut productivity and quality. Plant biostimulants (PBs) offer a promising approach to enhance stress tolerance; however, they should be viewed as physiological modulators rather than substitutes for conventional agronomic practices. The PBs function by regulating key processes such as osmotic adjustment, antioxidant defence and maintenance of biological nitrogen fixation (BNF), thereby improving plant resilience under stress.

Effective utilisation of PBs requires context-specific deployment aligned with crop physiology and stress conditions. Given the unique traits of groundnut, including geocarp and dependence on soil-derived calcium, appropriate selection of biostimulant type, application method and timing is essential. Moreover, variability in field performance due to genotype $\times$ environment $\times$ treatment interactions necessitate tailored recommendations rather than generalised use.

Integrating biostimulants into groundnut production systems can improve nutrient-use efficiency, sustain nitrogen fixation and reduce dependence on synthetic inputs, contributing to more sustainable agriculture. These benefits are mediated through key mechanisms including enhanced ROS detoxification via antioxidant enzymes (superoxide dismutase (SOD), catalase (CAT) and ascorbate peroxidase (APX)), improved osmotic regulation through accumulation of compatible solutes such as proline and glycine betaine and protection of nitrogenase activity within nodules under stress. Progress depends on linking mechanistic understanding with precise field application strategies to improve reliability of biostimulants under variable climatic conditions.

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Authors' contributions

The first draft of the manuscript was written by AG. RB provided guidance for overall correction and improvement. CH, PB and MB assisted with literature collection and formatting. All authors have read and approved the final manuscript.

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Declaration of generative AI and AI-assisted technologies in the writing process

During the preparation of this work the authors used Grammarly to correct the grammar and maintain the academic tone of the manuscript. After using this tool, the authors reviewed and edited the content as needed and take full responsibility for the content of the publication.

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