Journal of Plant Physiology 316 (2026) 154665

Contents lists available at ScienceDirect

Journal of Plant Physiology

journal homepage: www.elsevier.com/locate/jplph

Mechanistic insights into bio-based fertilisers, biostimulants, and novel delivery systems in plant physiology

Jacinta Santos, Marta Nunes da Silva, Carla S. Santos *

Universidade Católica Portuguesa, CBQF - Centro de Biotecnologia e Química Fina – Laboratório Associado, Escola Superior de Biotecnologia, Rua Diogo Botelho 1327, 4169-005, Porto, Portugal

ARTICLE INFO

Keywords:
Agricultural policy
Sustainable agriculture
Rhizosphere
Nanoparticles
Stress tolerance

ABSTRACT

The transition toward sustainable agriculture requires fertilisation strategies that improve nutrient use efficiency, enhance resilience to abiotic and biotic stress, and minimise environmental impacts. Bio-based fertilisers, biostimulants, and novel delivery systems have emerged as promising alternatives or complements to conventional agrochemicals, yet their physiological bases remain only partially understood. This review examines current knowledge on the mechanistic pathways through which these products act and identifies research gaps to enable predictive use in diverse cropping systems.

Evidence indicates that bio-based inputs influence plant performance by modulating nutrient uptake and assimilation, hormonal and redox signalling, stress perception and defence priming, and biomass allocation. Protein hydrolysates, humic substances, and seaweed extracts alter root morphology, ion transport, and stress signalling, while microbial inoculants such as rhizobia, phosphate-solubilising bacteria, and arbuscular mycorrhizal fungi provide nutrient mobilisation and immune priming. Novel delivery systems, including clays and encapsulation systems, extend these effects by improving the stability and targeted release of bioactive compounds. Despite these advances, the lack of standardised protocols, incomplete dose-response characterisation, and strong context dependence of plant responses remain major obstacles to reproducibility and scalability. Progress in this field requires a mechanistically anchored approach that links molecular events (such as transporter activation, hormone dynamics, and antioxidant activity) to agronomic outcomes under variable environments. Embedding mechanistic descriptors into both experimental design and regulatory frameworks could accelerate the translation of bio-based inputs into reliable tools for sustainable crop production, supported by environmental impact assessments.

1. Introduction

The global population currently surpasses 8 billion, and is projected to reach 9–10 billion by 2050 (Assylkhankyzy and Seitmagzimova, 2024; Chaudhary et al., 2022; United Nations Population Fund, 2023). Meeting the associated increase in food demand while preserving environmental integrity remains one of the defining challenges of modern agriculture. Despite advances in crop breeding, agronomy, and input management, food insecurity continues to affect 7.8–8.8 % of the global population (Food and Agriculture Organisation et al., 2025). To enhance yields and maintain crop quality, farmers have relied heavily on agrochemicals, including fertilisers, soil amendments, pesticides, herbicides, and plant growth regulators. The types and quantities vary with crop species, climate, and technological capacity (Devi et al., 2022; Jalal and Bondarenko, 2025) (see Table 1).

These inputs have significantly advanced productivity since the Green Revolution. However, their excessive and inefficient use poses well-documented environmental and human health risks, including nutrient leaching, eutrophication, biodiversity loss, and contamination of food chains (Brownlie et al., 2023; Brunelle et al., 2024; Fayiga and Nwoke, 2016). Such concerns have accelerated the search for bio-based and low-impact alternatives, such as biostimulants, biofertilisers, and novel delivery systems. These products aim to improve nutrient use efficiency (NUE), abiotic stress resilience, and crop quality while reducing dependency on synthetic inputs (du Jardin, 2015; Rouphael and Colla, 2020; Zhao et al., 2024).

These products act primarily by modulating plant physiological processes rather than supplying bulk nutrients. Documented

---

* Corresponding author.
E-mail address: cssantos@ucp.pt (C.S. Santos).

https://doi.org/10.1016/j.jplph.2025.154665
Received 11 September 2025; Received in revised form 25 November 2025; Accepted 27 November 2025

Table 1

Current biostimulants (BS), biofertilisers (BF) and novel delivery systems (NDS) actuation sites, physiological results and known constraints.

Product type	Example molecule(s)	Primary molecular/biochemical target	Physiological outcome	Constraints/limitations	References
(BS) Amino acid and protein hydrolysates	L-tryptophan, L-methionine, glutamic acid, signalling peptides	Phytohormone precursors (auxin, ethylene, and polyamines), stimulation of amino acid permeases (*AAP* family), expression of hormone responsive genes (*SAUR*, *AUX/IAA*, *ARF*); upregulation of cytokinin riboside 5′-monophosphate phosphoribohydrolase; modulation of nitrate reductase and glutamine synthase activity; regulation of MAPK cascades and SA pathways	Modulation of hormonal balance, improved root development, nitrogen assimilation, stress tolerance, enhanced photosynthesis, and higher yield	Lack of standardisation; overdosing can cause inhibitory effects or osmotic stress; composition depends on the origin and hydrolysis process	(Colla et al., 2015; Herrmann et al., 2024; Malécange et al., 2023; Pasković et al., 2024; Rouphael and Colla, 2020)
(BS) Humic/ fulvic acids	Humic acids extracts, leonardite-derived fulvics	Auxin signalling components (IAA mimicking), activation of plasma membrane H^+-ATPases; photosynthetic enzymes (RuBISCO, photosystem II, ATPase), upregulation of nutrient transporters (*PHT*, *LAX*, *PIN*, nitrate/ammonium transporters, *CsIRT1*)	Root elongation and lateral root formation, nutrient solubilisation and uptake, metabolic activation, and osmoregulation	Activity varies with soil pH and organic matter; solubility and chelation efficiency is environment dependent; heterogeneity of sources limits reproducibility	(Ampong et al., 2022; Antu et al., 2025; du Jardin, 2015; Nardi et al., 2017)
(BS) Secondary metabolites (phenolics)	Caffeic acid, ferulic acid, flavonoids, terpenoids, alkaloids	Antioxidant and redox signalling activation, root development, modulation of auxin transport proteins (*PIN* family), activation of MAPK, lignin synthesis, regulation of proline metabolism (proline dehydrogenase)	UV protection, ROS scavenging and stress tolerance, improved root growth, seed germination, modulation of rhizosphere microbiota	Highly variable across species and doses; excessive application can alter soil microbial balance and redox homeostasis	(Aina et al., 2022; Ampong et al., 2022; Antu et al., 2025; de Melo et al., 2016; du Jardin, 2015; Ghadirnezhad Shiade et al., 2024; Nardi et al., 2017; Sun et al., 2024; Wang et al., 2023)
(BS) Plant growth regulators	Gibberellic acid (GA), abscisic acid (ABA), salicylic acid (SA)	Hormone receptors (*GID1*, *PYR/PYL*, *NPR1*), flowering genes (*CsIPT1b* and *CsUGT85A2*), phenylpropanoid metabolism modulation, upregulation of RuBISCO, NADH, CXE and cytochrome P450	Control of germination and flowering, enhanced stress tolerance, antioxidant activity, and pathogen defence	Unstable under field conditions; regulatory restrictions on use; effective within a narrow dose range, excessive doses cause toxicity	Rouphael and Colla (2020)
(BS) Seaweeds and microalgae extracts	*Ascophyllum nodosum*, *Ecklonia maxima, Chlorella vulgaris*, *Spirulina platensis*	Cytokinin and auxin pathways, cell division regulation, root-shoot balance modulation, upregulation antioxidant enzymes (SOD, CAT, POD), activation of phenylpropanoid pathways, induction of ABA genes (cryoprotection and drought tolerance), expression of aquaporin genes, brassinosteroid synthesis, polysaccharide-mediated MAMP signalling	Improved stress tolerance and antioxidant capacity, delayed senescence, enhanced water relations, better yield quality	Batch-to-batch, species and extraction method variability; undefined active compounds limit reproducibility	(Ferreira et al., 2023; González-Pérez et al., 2022; Herrmann et al., 2024; Parmar et al., 2023)
(BS) Inorganic compounds	Al, Co, Na, Se, Si (amorphous forms)	Cell walls strengthening, osmotic regulation, crystal deposition for reducing transpiration, cofactors in enzymatic reactions, activation of phytohormone signalling (ABA, auxin), chelation of heavy metals	Thermotolerance, NUE improvement, heavy metal detoxification, antioxidant activity, drought tolerance	Risk of toxicity or metal accumulation; species and dose dependent	Rajesaheb et al. (2025)
(BF) Microbial inoculants	*Rhizobium* spp., *Azospirillum* spp., *Azotobacter* spp., *Bacillus* spp., *Trichoderma* spp., *Pseudomonas* spp., *Enterobacter* spp., AMF (*Rhizophagus irregularis, Funneliformis mosseae*, *Claroideoglomus etunicatum*, *Glomus* spp.), ECM fungi (*Pisolithus tinctorius*)	*Nod* genes and *nif* genes (nitrogenase); phosphatases, organic acids (*pho*, *pqq*, *gdh* families); phosphate transporters (*PHT*, *PSR*); siderophore-mediated Fe acquisition; ACC deaminase (ethylene regulation); VOC signalling; mycorrhiza-induced resistance (JA, ABA); H^+-ATPase activity; MAPK cascades	Biological N fixation, improved P and micronutrient uptake, altered root architecture, induced systemic resistance, improved antioxidant response, enhanced soil fertility, and pathogen protection	Field performance depends on soil physicochemical properties, native microbiota, and climate; high N and P fertilisation suppresses symbiosis and efficiency; unpredictable strain-host-environment interaction	(Bisht et al., 2025; Cruz et al., 2022, 2023; Dasgupta et al., 2023; Delaeter et al., 2024; Gupta et al., 2022; Herrmann et al., 2024; Ikram et al., 2025; Jones and Oburger, 2011; Liu et al., 2025; Panda, 2022; Rodríguez-Vázquez and Mesa-Marín, 2023; Wei et al., 2024)
(BS) Chelated micronutrients	Cu-EDTA, Fe-EDDHA, Fe-DTPA, Mn-EDTA, Mn-DTPA, Zn-EDTA	Metal transporters (*IRT1*, *ZIP* family), ferric reductase oxidases (*FRO2*), metal tolerance proteins (*MTP*)	Correction of deficiency symptoms, improved enzyme function, higher reproductive success, nutrients uptake, antioxidant response	Limited persistence in the soil; rick of metal leaching; high production cost	(Rahman et al., 2021)
(NDS) Nanoparticles,	ZnO-NPs, Fe_2O_3-NPs, Ag-NPs, Si-NPs, MgO-NPs, GO-NPs, Au-NPs, $Ca_3(PO_4)_2$-	Regulation of ion transporters (Zn–*ZIP*, Fe transporters, Ag via K^+ channels, Si	Enhanced NUE and bioavailability, chlorophyll and DNA synthesis,	Lack of standardised release and toxicity testing; environmental	(Balla et al., 2022; Fadiji et al., 2024; Hajihashemi and Kazemi, 2022; Kaboosi

(*continued on next page*)

Table 1 (*continued*)

Product type	Example molecule(s)	Primary molecular/biochemical target	Physiological outcome	Constraints/limitations	References
encapsulated, coats	NPs; encapsulated NPK, microorganisms, BVOCs, urea (chitosan, alginate, Si-based capsules)	downregulating *IRT1/NRAMP5*); MAPK and *SOS1* signalling; controlled release, enzyme-mediated and osmoregulatory mechanisms; stimulation of antioxidant enzymes (SOD, CAT, POD, APX, GR, PAL, GST); accumulation of metabolites (proline, sugars, proteins); alginate/chitosan as osmoregulators and carbon sources	osmolyte production, stress tolerance (salinity, drought, UVB, heat, heavy metals), immune priming (PAMP-triggered), improved plant growth and yield, prolonged microbial survival	dependent; possible nano-ecotoxicity; unclear regulation	et al., 2023; Kumari et al., 2023; Lopes et al., 2021, 2024; Moradi et al., 2024; Pinho et al., 2025; Rajesaheb et al., 2025; Shoukat et al., 2024; Singh et al., 2025)
(NDS) Hydrogel formulations	Chitosan, cellulose, starch hydrogels (cross-linked polymers)	Nutrient diffusion and active; crosslink density and swelling influencing release; stimulation of plant defence mechanisms	Water retention, reduced leaching and fertilisation frequency, soil aeration, stress tolerance, enhanced nutrient uptake, improved microbial carrier survival	Activity dependent of temperature, salinity and degradation rates; polymer residues accumulations in the soil; high production cost	(Ali et al., 2024; Chamorro et al., 2025; Fadiji et al., 2024; Mandal et al., 2025)

mechanisms include: enhanced root nutrient acquisition via regulation of membrane transporters (e.g., NRTs, AMTs, PHTs, K^+ channels) and rhizosphere pH adjustment by plasma membrane H^+-ATPases; hormonal modulation (auxin, abscisic acid, cytokinins, ethylene) and redox signalling involving reactive oxygen and nitrogen (N) species (ROS, NO); increased photosynthetic efficiency, osmotic adjustment, and activation of antioxidant defences under abiotic stress; and altered ionomic and metabolomic profiles, improving nutrient partitioning and accumulation of beneficial metabolites (Ikram et al., 2025; Irineu et al., 2023; Martínez-Lorente et al., 2024; Roche et al., 2024).

Emerging delivery technologies, such as clay-based carriers (smectites, palygorskite, halloysite), nanoparticles (NPs), encapsulation and coatings, further expand the toolbox by enabling controlled release of bioactives, stabilisation of microbial inoculants, and synchronisation of nutrient availability with plant demand (Kumar et al., 2018; Moradi et al., 2024; Rajesaheb et al., 2025).

Regulatory definitions vary between jurisdictions (e.g., EU Regulation (EU) 2019/1009 versus the US Plant Biostimulant Act 2022), leading to inconsistencies in product categorisation and research comparability (Ghorui et al., 2024; Malusá and Vassilev, 2014). Also, terminological boundaries between "*biofertilisers*" and "*biostimulants*" remain fluid in the literature. Microbial inoculants frequently act beyond nutrient mobilisation by influencing signalling and stress responses, thus overlapping with classical biostimulant functions (Santos et al., 2024). Conversely, several non-microbial products can indirectly affect soil microbial activity and nutrient availability (du Jardin, 2015; du Jardin et al., 2025). Herein, a pragmatic distinction aligned with EU Regulation (EU) 2019/1009: microbial products are discussed as biofertilisers, while non-microbial substances are treated as biostimulants. This framework facilitates clarity in mechanistic analysis, while recognising the functional overlap between categories.

This review focuses on the mechanistic basis for the action of bio-based fertilisers, biostimulants, and novel delivery systems in plants. We synthesise current evidence linking product classes to nutrient uptake, signalling pathways, stress responses, and ionomic shifts, and identify key research priorities to bridge the gap between agronomic performance and mechanistic understanding.

2. Physiological pathways and responses

Bio-based inputs exert their effects mainly by modulating physiological processes in plants rather than supplying bulk nutrients (Verma et al., 2024). Their reported impacts include improved nutrient uptake and assimilation, modulation of hormonal and redox signalling pathways, enhanced tolerance to abiotic and biotic stresses, and adjustments in biomass partitioning that influence yield and quality (Priya et al., 2023).

Specifically, these bio-based inputs can improve nutrient uptake and assimilation through the upregulation of nitrate and ammonium transporter genes (*NRTs*, *AMTs*), phosphate (*PHT*) transporters, and plasma membrane H^+-ATPases. Thus, increasing ion influx and driving rhizosphere acidification (Albornoz and Godoy, 2025; Ngosong et al., 2022). They can also impact nodulation activities and root architecture, improving growth, nutrient uptake and yield (Liu et al., 2025; Ngosong et al., 2022; Pooja et al., 2025).

Extracts from seaweeds, humic acids, and microbial elicitors modulate auxin, cytokinin, salicylic acid (SA), and jasmonic acid (JA) pathways, thereby influencing both growth and defence (Maciel-Rodríguez et al., 2025). These effects in hormonal signalling networks often converge with redox regulation, where shifts in antioxidant enzyme activity and ROS signalling integrate metabolic and developmental responses (Faria de Souza et al., 2025).

Many bio-based inputs contribute to improved abiotic stress tolerance by modulating stress signalling pathways. They often functioning as priming agents rather than direct stress mitigators, and can enhance signals from receptor-like kinase (RLK) and histidine kinases (HK), enabling downstream responses involving cytosolic calcium (Ca^{2+}), mitogen-activated protein kinase (MAPK) and late embryogenesis abundant (LEA) class genes (Johnson et al., 2023; Lephatsi et al., 2022). Certain bio-based inputs provide solutes such as proline or glycine betaine, that stabilise proteins and membranes under osmotic stress and modulate dehydrin and aquaporin genes to improve plants' water status and drought tolerance (Crespo-Barreiro et al., 2025). Others can also attenuate ethylene accumulation, alleviating growth inhibition under adverse conditions and aiding in the regulation of SA and JA signalling pathways (Feng et al., 2025).

The physiological improvements induced by bio-based inputs can ultimately translate into enhanced yield stability and quality attributes. Enhanced nutrient acquisition and abiotic stress tolerance modify carbon allocation patterns, often favouring reproductive over vegetative sinks (Rouphael and Colla, 2020). Inoculants that improve nutrient status and water-use efficiency can sustain photosynthetic performance during reproductive phases, thereby stabilising yield under adverse conditions (dos Reis et al., 2024; Nadarajah and Abdul Rahman, 2023). The effectiveness of bio-based inputs, however, is strongly modulated by environmental and edaphic factors. Soil pH regulates both microbial activity and nutrient solubility, while soil texture and organic matter influence the retention and diffusion of active compounds (Mitter et al., 2021). Climatic variability further shapes degradation rates and plant physiological demand, introducing strong genotype × environment interactions that remain insufficiently characterised (Baum et al., 2024). These factors interact in feedback loops, where each influence subsequent nutrient uptake and stress responses (Khoulati et al., 2025). Such complexity means that mechanistic effects observed under controlled conditions cannot be assumed to hold under variable field environments (Ullah et al., 2021). Hence, studies pinpoint particularly pronounced genotype × environment × management interactions in various crops' physiological responses to bio-based products, especially under abiotic stress regimes such as drought, heat, and elevated CO_2 (Janni et al., 2023; Machado et al., 2025).

Biostimulants derived from protein hydrolysates, humic substances, or seaweed extracts contain bioactive molecules that can influence root development, ion transport, and stress signalling (Matthews et al., 2025). Microbial inoculants, including rhizobia, phosphate-solubilising bacteria, and arbuscular mycorrhizal fungi, contribute to nutrient mobilisation and assimilation, while also acting as elicitors of systemic plant responses (Kurniawati et al., 2023). Novel delivery systems, ranging from clay minerals to encapsulation technologies, extend these effects by stabilising bioactive compounds, protecting sensitive microorganisms, and synchronising the release of nutrients or elicitors with plant demand (Nwankwo et al., 2025; Verma et al., 2024). Together, these product classes converge on a set of common physiological pathways (Fig. 1), which will be examined in greater mechanistic detail in the following section.

3. Agrochemical categories and emerging delivery technologies

3.1. Microbial biofertilisers

Microbial biofertilisers are formulations containing living beneficial microorganisms, both bacteria or fungi. They play a key role in nutrient cycling, soil fertility, plant health, and biotic and abiotic stress tolerance (Bisht et al., 2025). Their primary mechanisms of action involve direct nutrient acquisition, modulation of root physiology, and induction of

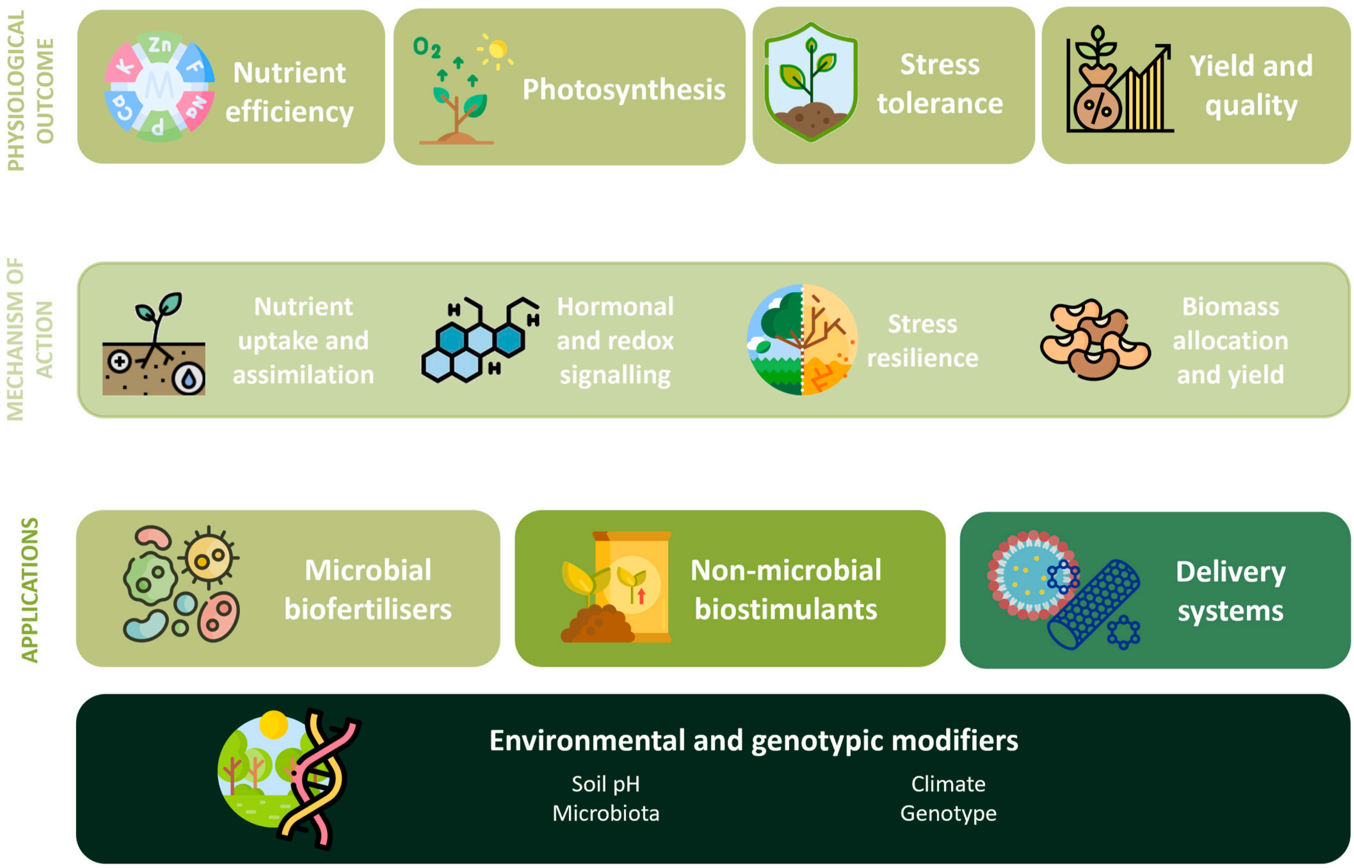

Fig. 1. Biostimulant-mediated processes influencing plant physiology. Applications of microbial biofertilisers, non-microbial biostimulants, and novel delivery systems are shaped by environmental and genotypic factors (soil pH, microbiota, climate and plant genotype). The resulting physiological outcomes as improved NUE, enhanced photosynthesis, greater abiotic stress tolerance and higher yield and quality. These effects are mediated by mechanisms involving nutrient uptake and assimilation, hormonal and redox signalling, stress resilience and biomass allocation.

plant signalling pathways (Bisht et al., 2025; Ikram et al., 2025; Irineu et al., 2023; Lephatsi et al., 2022).

Nitrogen-fixing bacteria, such as *Rhizobium* spp., establish symbiotic or associative interactions with their hosts (Lindström and Mousavi, 2020). Also, their free-living homologous, including *Azotobacter* spp. and *Azospirillum* spp. (Fukami et al., 2018; Martin del Campo et al., 2022), provide bioavailable N through the activity of nitrogenase enzymes encoded by *nif* genes (Alleman and Peters, 2023; Sharma et al., 2023). These associations frequently alter root system architecture through the production of auxins, leading to enhanced soil exploration and improved nutrient capture. Phosphate-solubilising microorganisms contribute to phosphorus (P) acquisition by excreting organic acids, phosphatases, and chelating compounds that mobilise insoluble soil P fractions (Bargaz et al., 2021; Bisht et al., 2025; Jones and Oburger, 2011; Liu et al., 2025). These processes are often accompanied by an upregulation of plant phosphate transporter genes, such as members of the *PHT* family and *PSR* (phosphate starvation response) transcription factors, thereby increasing uptake efficiency under phosphorus-limited conditions (Albornoz and Godoy, 2025; Bisht et al., 2025; Khan et al., 2023; Lephatsi et al., 2022).

Arbuscular mycorrhizal fungi (AMF), including *Rhizophagus irregularis*, *Funneliformis mosseae*, and *Claroideoglomus etunicatum* and *Glomus* spp., are obligate symbionts commonly associated with crops, whereas ectomycorrhizal (ECM) fungi, such as *Pisolithus tinctorius*, are mainly symbionts of trees and form a mantle structure in the intracellular spaces of the root (Panda, 2022). Both AMF and ECM extend the functional root system through extensive hyphal networks, enhancing the acquisition of low-mobility nutrients such as P and zinc (Zn), and regulating developmental processes (budding, flowering, and rooting) (Panda, 2022). Arbuscular mycorrhizal fungi play a key role in protecting plants from soil-borne diseases, along with providing abiotic stress tolerance, even under extreme conditions, and also share capacities with ECM (Panda, 2022). Fungal colonisation is further associated with altered phytohormone profiles, particularly with increases in JA and abscisic acid (ABA), and can elicit mycorrhiza-induced resistance through the production and exudation of antibiotics (Delaeter et al., 2024; Salomon et al., 2022).

In addition, several other bacterial genera, such as *Pseudomonas* spp., *Bacillus* spp., and *Enterobacter* spp., exhibit multifunctional traits that are relevant to plant nutrition and stress physiology. These include the production of siderophores that facilitate iron (Fe) mobilisation, the synthesis of 1-aminocyclopropane-1-carboxylate (ACC) deaminase that modulates ethylene levels under stress, and the emission of volatile organic compounds capable of influencing stomatal conductance and photosynthetic performance (Bisht et al., 2025; Dasgupta et al., 2023; Rawat et al., 2021; Sharma et al., 2013; Wei et al., 2024).

At the physiological level, microbial biofertiliser application can lead to increased expression of key nutrient transporter genes (Bisht et al., 2025; Pan and Cai, 2023), and elevated activity of plasma membrane H^+-ATPases that acidify the rhizosphere (Gupta et al., 2022; Rodríguez-Vázquez and Mesa-Marín, 2023). Under stress conditions, they enhance antioxidant enzyme activity, including superoxide dismutase (SOD), catalase, (CAT) and peroxidase (POD) (Cruz et al., 2022, 2023). These effects are often integrated into broader signalling cascades involving mitogen-activated protein kinases (MAPKs) and the regulation of reactive oxygen and nitrogen species homeostasis (Dasgupta et al., 2023). Nevertheless, the performance of microbial biofertilisers in field conditions is highly dependent on edaphic factors, climatic variability, and native microbial community composition. High rates of N and P fertilisation can suppress symbiotic establishment and reduce efficacy (Delaeter et al., 2024), emphasising the importance of aligning microbial inoculation strategies with context-specific agronomic practices.

3.2. Non-microbial biostimulants

Non-microbial biostimulants comprise a diverse group of substances of plant, algal, or animal origin, including humic and fulvic substances, protein hydrolysates, amino acids, phenolic compounds, and plant hormones, as well as whole algae or algal extracts (Ngosong et al., 2022). These products act primarily by modulating plant physiological processes rather than supplying substantial amounts of nutrients, thereby improving nutrient use efficiency, abiotic stress tolerance, and crop quality (du Jardin, 2015; Martínez-Lorente et al., 2024; Parmar et al., 2023).

Humic substances, derived from the decomposition of organic matter, possess a high tolerance to withstand microbial reactions, allowing for a long-lasting effect (Ampong et al., 2022; Antu et al., 2025), which influences nutrient acquisition. They are rich in phenolic and carboxylic groups, which dissociate to form free functional groups, and they can chelate metals in the soil (Ampong et al., 2022; de Melo et al., 2016). Their high-molecular-weight compounds stimulate the activation of the plasma membrane H^+-ATPases, leading to rhizosphere acidification and enhanced solubilisation of nutrients such as P and micronutrients. They also upregulate the expression of nitrate, ammonium, and iron (Fe) transporters genes (*ZMNrt1.1*, *ZMNrt2.1*, *BnNRT1.1*, *BnNRT2.1*, *CsIRT1*), thereby improving N uptake (Ampong et al., 2022; du Jardin, 2015; Nardi et al., 2017). In addition, humic fractions can alter root morphology and enhance lateral root formation via auxin and cytokinin activity (Antu et al., 2025). Because their solubility is dependent on pH, their performance may vary across soils (de Melo et al., 2016).

Protein hydrolysates (PHs) are obtained mainly by enzymatic hydrolysis and also by chemical hydrolysis or fermentation of plant or animal by products. They contain short peptides and free amino acids, with glutamic acid, glutamine, and proline often abundant (Malécange et al., 2023). Depending on the source and process, they may also contain carbohydrates, minerals, phenolic compounds, and trace phytohormones (Colla et al., 2015; Pasković et al., 2024). Applied to roots, protein hydrolysates can stimulate amino acid uptake via the amino acid permease family, including carriers of glutamate (Pasković et al., 2024). The released amino acids and short peptides act as precursors of metabolic intermediates and stress related metabolites, and they also function as signalling molecules (Monterisi et al., 2024). At low concentrations, PHs elicit auxin and gibberellin like responses, in part by increasing tryptophan availability and enhancing indole-3-acetic acid (IAA) related signalling (Colla et al., 2015; Malécange et al., 2023; Pasković et al., 2024). Root architecture is modified by the upregulation of cytokinin riboside 5′-monophosphate phosphoribohydrolase (Pasković et al., 2024). Exogenous amino acids can also modulate N assimilation by affecting the activity of key enzymes, such as nitrate reductase and glutamine synthetase, and stimulate antioxidant systems that mitigate oxidative stress (Colla et al., 2015; Pasković et al., 2024; Rouphael and Colla, 2020). In particular, oxidative stress mitigation is accompanied by transcriptional upregulation of key elements in the photosynthetic electron transport chain (Malécange et al., 2023; Pasković et al., 2024).

Algal extracts, from macroalgae, such as *Ascophyllum nodosum* and *Fucus spiralis*, and from diverse microalgal species, e.g., *Coccomyxa onubensis*, *Chlorella vulgaris*, are complex mixtures containing phytohormones, sterols, vitamins, minerals, and N-containing compounds (Ferreira et al., 2023; Maciel-Rodríguez et al., 2025; Martins et al., 2024; Parmar et al., 2023). These constituents enhance photosynthetic performance, modulate hormonal balance, improve abiotic stress tolerance, and promote nutrient uptake by stimulating enzymatic activities, including dehydrogenases, RNase, acid and alkaline phosphatase, and nitrate reductase (Faria de Souza et al., 2025; Ferreira et al., 2023; González-Pérez et al., 2022). Phytohormones present in the mixtures promote faster plant growth, development, and metabolism regulation (González-Pérez et al., 2022). In addition, algal polysaccharides can act as microbial-associated molecular patterns (MAMPs), eliciting antioxidant responses that include the induction of ROS scavenging enzymes (González-Pérez et al., 2022). Microalgae are also used to recover nutrients in wastewater treatment stations, supporting the circular bioeconomy (Mau et al., 2021; Solovchenko et al., 2016).

Phenolic compounds, more specifically tannins, lignins, flavonoids, phenolic acids and terpenoids, from plant residues or algal biomass, have gained importance for their antioxidant capacity and free radical scavenging activity (Aina et al., 2022; Ghadirnezhad Shiade et al., 2024; Sun et al., 2024). Several phenolic classes enhance plant growth and soil fertility (Aina et al., 2022; Wang et al., 2023). They contribute to seed germination, protection against UV damage, and they induce enzymes important for seed nutrition and redox balance, including α-amylase, β-amylase, CAT, POD and proteases (Aina et al., 2022; Ghadirnezhad Shiade et al., 2024; Sun et al., 2024). Beyond UV protection, phenolic compounds support cell wall formation through stimulation of lignin biosynthesis, modulation of auxin signalling, and promotion of root growth (Aina et al., 2022; Ghadirnezhad Shiade et al., 2024). Under stress conditions, they modulate the proline cycle, including proline dehydrogenase and pyrroline-5-carboxylate synthase, supporting proline accumulation and osmotic adjustment (Aina et al., 2022).

Inorganic compounds are also used. They are considered as not essential, but generally beneficial to plants growth, such as aluminium (Al), cobalt (Co), sodium (Na), selenium (Se), silica (Si) and their amorphous forms (Nunes da Silva et al., 2022). Their function is mostly focused on strengthening cell walls, osmoregulation, reduction of transpiration via crystal deposits, thermotolerance, cofactors supply, NUE, antioxidant activity, heavy metals chelation and phytohormone synthesis and signalling (Rajesaheb et al., 2025).

The physiological outcomes of non-microbial biostimulant application are strongly context-dependent, influenced by factors such as soil pH, texture, and organic matter content, as well as plant developmental stage and prevailing stress conditions (Li et al., 2022). Typical responses include improved chlorophyll content, increased photosynthetic efficiency, and enhanced root growth, reflecting improved nutrient acquisition and allocation (Boutahiri et al., 2024; Ciriello et al., 2025; Herrmann et al., 2024; Roche et al., 2024). However, reproducibility of these effects remains a challenge, partly due to variability in product composition, extraction processes, and the lack of standardised experimental protocols (Herrmann et al., 2024). Application dose also plays a decisive role, as low concentrations tend to elicit positive effects, whereas higher concentrations may induce inhibitory responses (Aina et al., 2022). Moreover, secondary metabolites within these biostimulants can influence microbial communities associated with host plants, with potential implications for plant health and productivity (Ghadirnezhad Shiade et al., 2024).

3.3. Novel delivery systems

Novel delivery systems (NDS) for agrochemicals, largely represented by controlled-release fertilisers and stimulants (CRFs), provide more precise and targeted delivery compared to traditional applications. Materials with high surface areas, strong adhesion, permeability to water and nutrient, tuneable pore sizes, controlled degradability, and ion exchange capacities, such as silica, cellulose, iron oxide, hydroxyapatite, and lignin, are selected for adsorption, encapsulation, or intercalation of active ingredients (Moradi et al., 2024; Rajesaheb et al., 2025). These systems protect sensitive molecules from degradation, modulate their release kinetics, and improve their bioavailability. This enhances nutrient use efficiency and mitigates environmental losses, while reducing fertiliser use up to 30 % without compromising yield (Kumar et al., 2018; Moradi et al., 2024). Slow-release fertilisers (SRFs) release nutrients more gradually than conventional fertilisers but are not typically encapsulated like the CRFs (Fig. 2), and their release rates are strongly influenced by microbial activity, and on soil and environmental conditions, which makes precise nutrient delivery more challenging (Moradi et al., 2024).

Nanoparticles (NPs) offer advantages due to their high surface area, thermal stability and physiochemical properties, which allow lower nutrient doses to achieve greater delivery efficiency (Moradi et al., 2024; Rajesaheb et al., 2025; Yadav et al., 2023). Nanofertilisers (NFs), a class of NPs, include macronutrients, such as N, P, potassium (K), magnesium (Mg), calcium (Ca), and sulphur (S), and micronutrients like Fe, Zn, and copper (Cu), formulated as nanoscale particles. To be defined as NFs, formulations should have at least 50 % of the particles with dimensions below 100 nm, to provide a high surface-area-to-volume ratio boosting nutrient absorption, diffusion and uptake, while reducing nutrient losses up to 50–70 % compared to the conventional water-based fertilisers (Yadav et al., 2023). These compounds can also be incorporated in conventional fertilisers as nano-additives or as coatings, and in some formulations the particles are coated with microorganisms to prolong survival and interaction time (Elnahal et al., 2022; Karunakaran et al., 2024; Moradi et al., 2024; Rajesaheb et al., 2025).

Nanoparticle composition strongly influences plant responses. Chitosan-based NPs loaded with SA buffer cellular redox and stimulate antioxidant response, including POD, phenylalanine ammonia-lyase (PAL) and polyphenol oxidase, while promoting shoot and root growth and chlorophyll accumulation (Rajesaheb et al., 2025; Shoukat et al., 2024). Carbon-based NPs enhance seed germination and facilitate

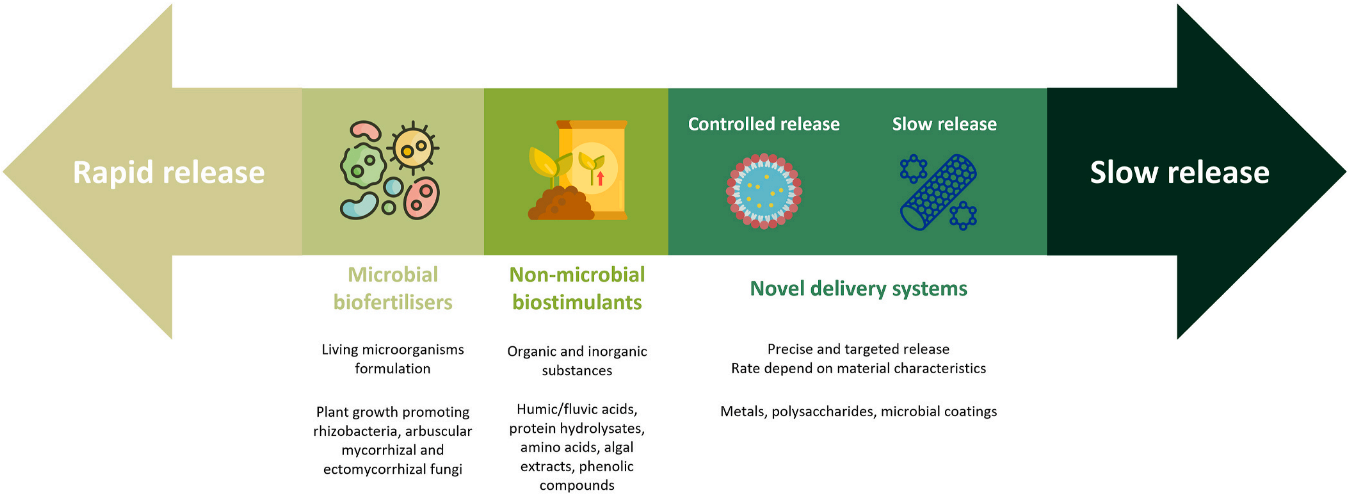

Fig. 2. Release dynamics of fertilising applications. Three main categories are microbial biosfertilisers, non-microbial biostimulants, and novel delivery systems, arranged from rapid to slow release. Microbial biofertilisers enable a rapid release of compounds through living microorganism formulations. Non-microbial biostimulants may exhibit intermediate or controlled release behaviour. Novel delivery systems enable a precise and targeted release rates that depend on the material characteristics, resulting in sustained to slow delivery.

delivery of DNA and small molecules (Aruna et al., 2025; Lopes et al., 2021), whereas silver-based (Ag-NPs) and Zn-NPs restore the ionic balance under salinity and drought stress (Faisal et al., 2024). In addition, zinc oxide NP (ZnO-NP) regulate *ZIP* transporters, while Ag-NPs mimic K^+ enabling passage through K^+ transport pathways (Shoukat et al., 2024). Silica-based (Si-NPs) improve photosynthetic efficiency, limit the uptake of heavy metals such as cadmium (Cd) via down-regulation of genes *IRT1* and *NRAMP5*, immobilise lead (Pb) and arsenic (As), and increase the activity of several antioxidant enzymes, such as SOD, CAT, glutathione reductase (GR), PAL, and the ascorbate-glutathione cycle. Copper-based NPs (Cu-NPs) act as biocides by enhancing polyphenol oxidase and PAL activity; Mg-NPs promote Mg uptake and photosynthesis; while Fe-NPs interact with Fe-regulated transporters, increasing the chlorophyll content and supporting DNA synthesis (Shoukat et al., 2024). Beyond these, polymeric NPs are being explored as carriers of micronutrient chelates, increasing plants growth and chlorophyll content, while modulating nutrient-specific molecular pathways (Pinho et al., 2025).

On the other hand, CRFs are designed to release nutrients in a controlled and gradual manner in accordance with the plant's developmental requirements. The nutrient granules are coated with water-resistant polymeric materials that release nutrients via diffusion and interactions with soil water (Moradi et al., 2024). Encapsulation strategies are also applied to microbial inoculants and pesticides. Most capsules are based on chitosan or alginate and can carry microbial cells, gases or metabolites (Fadiji et al., 2024; Wang et al., 2023). Encapsulation of bacterial volatile organic compounds (BVOCs) in alginate matrices enhances antioxidant responses under drought (e.g., higher CAT, glutathione S-transferases (GST), proline, protein and sugar accumulation), while promoting shoot and root growth (Lopes et al., 2024). The use of alginate in CRF matrices is supported by evidence that it functions both as an osmoregulator and a carbon source, similarly to chitosan. This dual role enhances nutrient release control and soil conditioning effects while providing biodegradable carbon that can support microbial activity (Balla et al., 2022). Under drought, encapsulated fungal inoculum induced antioxidant defences, including increases in carbohydrates, protein, proline, CAT, SOD, ascorbate peroxidase (APX), and POD, lower lipid peroxidation, and higher growth and yield (Kaboosi et al., 2023). Under salt stress, Si and chitosan capsules produced comparable responses (Hajihashemi and Kazemi, 2022), while urea capsules yielded similar outcomes under non stress conditions (Singh et al., 2025). Together, these convergent results across materials and contexts indicate that the capsule matrix itself, not only PGPR traits or the urea payload, shapes the plant response. In addition, capsules of Si reduce the effect of UVB damage (Hajihashemi and Kazemi, 2022).

Hydrogel formulations are surging as carriers due to their high-water absorption capacity, non-toxicity, stability after swelling and storage, and versatility (Ali et al., 2024; Chamorro et al., 2025). They can be made from natural polymers, like chitosan, cellulose and starch (Chamorro et al., 2025; Mandal et al., 2025), making them a sustainable alternative. These formulations can serve as carriers for microbial inoculants and nutrients, minimising nutrient washout, reduce fertilisation frequency and nutrient loses by leaching and runoff (Rodrigo and Munaweera, 2025). Their release mechanisms by diffusion and, in the case of polysaccharide hydrogels, by active transport (Ali et al., 2024), depend on water penetration, nutrient dissolution, and diffusion capacity of the polymer matrix, influenced by cross-linking density, swelling behaviour, and soil conditions (Mandal et al., 2025). Similarly to the encapsulation materials, some of the materials used in hydrogel formulations also promote plant defence mechanisms, like chitosan (Ali et al., 2024). However, the slow release and production costs are still a limitation (Fadiji et al., 2024; Mandal et al., 2025; Rodrigo and Munaweera, 2025).

4. Linking physiological mechanisms to agronomic performance

While the mechanistic evidence indicates that bio-inputs can enhance nutrient uptake, stress resilience, and yield formation, their effects in the field are strongly context-dependent. Responses are larger in dry climates and are favoured by neutral soil pH and low soil organic matter, with weaker effects on very high P soils, which points to clear targeting rules for practice (Schütz et al., 2018). Field evaluations generally report stronger and more reproducible agronomic gains than greenhouse assays, and applications made before planting or at early vegetative stages tend to produce larger yield responses than late applications (de Zutter et al., 2022; Pei et al., 2025). Mechanistically, the meta evidence attributes roughly one half of the benefits to stress alleviation, with the remainder split between direct pathogen suppression and improved nutrient availability, which helps explain why some trials show large physiological changes without proportional yield gains when stress is absent or mild (Li et al., 2022).

For example, across thirteen crops under rainfed management, AMF increased yields by 23 % on average, with gains linked to improved stress resistance and P capture (Wu et al., 2022). Inoculation with AMF also increased shoot biomass by 24.2 % and root biomass by 29.6 %, while delivering increased seed number and pods or fruits per plant (Wu et al., 2022). A more recent meta-analysis found that AMF inoculation increased plant biomass by 47 %, N concentration by 16 %, P concentration by 27 %, whole plant N uptake by 67 %, and whole plant P uptake by 105 %. Gains were larger for P than for N, and responses were stronger with single AMF species than with mixed AMF species, in laboratory trials than in field trials, and in legumes compared with other crops (Wu et al., 2024). Soilless and hydroponic systems can support these biological interactions, but colonisation is generally lower than in soil and strongly influenced by nutrient supply and system hydraulics (Othman et al., 2024). In comparative trials, AMF colonisation averaged 52.3 % in hydroponics versus 61.1 % in soil, with performance favoured by moderate phosphorus concentrations ($0.15–15.5\ \text{mg L}^{-1}$) but suppressed at higher levels ($40–75\ \text{mg L}^{-1}$) (Othman et al., 2024). Turbulence from air bubbling or continuous recirculation can further damage spores and hyphae, reducing colonisation success (Dasgan et al., 2022). Together, this argues for pilot trials to refine inoculation timing and placement and to validate sanitation protocols compatible with microbial persistence before attempting large scale deployment in high value protected cropping.

4.1. Cereals

In maize, seed or early vegetative inoculation with *Azospirillum brasilense* increased root volume by about 12 %, 4.3 % N leaf concentration, 5.4 % grain yield, and 3.6 % of N in grains. The highest inoculation efficiency was achieved when applications were timed to the V2 to V3 stages, with seed inoculation outperforming in furrow or foliar applications across environments (Barbosa et al., 2022). In parallel, phosphate solubilising bacteria reduced the need for mineral P in maize and increased soil P availability when applied around the V7 stage, translating into better growth with less fertiliser (Beltran-Medina et al., 2023). In acidic soils, pairing biofilm forming biofertilisers with organic ameliorants supports not only soil fertility, but also maize height and grain yield while cutting mineral NP use by about 40 % with no yield penalty (Ambarita et al., 2025). In barley and wheat, the mycorrhizal pathway contributes to total above-ground Zn, improving yield and spike traits particularly under low to moderate Zn supply, under greenhouse conditions. At higher Zn availability, additional benefits diminish but have no negative effects on grain P. These processes appear to be mediated by genes from the *ZIP* transporter family, including *ZIP13* (Coccina et al., 2019; Watts-Williams and Cavagnaro, 2018).

These biological inputs mesh with NPK management and conservation practices in ways that matter on farm. For instance, in long-term no-till maize, *Azospirillum*-based programs increased yield stability and produced multi-season net returns near US$ 409 per hectare. Similarly, integrating *A. brasilense* into N management raised operating profit by about 10.5 % across field trials, illustrating that agronomy and economics move together when timing and dose are tuned (Caires et al., 2021; Galindo et al., 2022). Wheat shows a similar pattern, where inoculation with *Bradyrhizobium* sp. together with *A. brasilense* favoured grain yield, plant N uptake and complemented top dress N without changing fertiliser recovery, a result that supports moderate reductions in mineral N when co-inoculation is used judiciously (Galindo et al., 2022). Beyond yellow and white maize, purple maize maintained key performance indicators with less 30 kg N per hectare when *Azospirillum* was used, reinforcing the substitution potential in low input systems (Condori et al., 2024). Meta analysis in African cereals further indicates that adequate P management together with *Rhizobium* strains inoculation, leads to the highest grain yields (Kanomanyanga et al., 2021). In turn, nanofertiliser use in rice increased grain yield, improved photosynthetic performance and also strengthened tolerance to environmental stress and disease pressure (Kumar et al., 2023).

4.2. Legumes

A continent-wide synthesis in African indigenous soils reported that rhizobial inoculation significantly increased legume yields, although the extent of the benefits observed varied between microbial strain and crop species, with cowpea having the largest average yield gain at 61.7 % and groundnut the smallest at 19.8 % (Buernor et al., 2022). A recent meta-analysis estimated average yield gains of around 40 % and seed protein increases of 11 %, which aligns with the nitrogen fixation mechanism (Sufar et al., 2024). However, the authors caution that results were confounded by experiment design, fertiliser regime, legume species, and country context, and many studies lacked measures of variation, limiting rigorous, weighted meta-analyses (Sufar et al., 2024).

It becomes clear that practical parameters matter. For example, for common bean, it is recommended using at least 10 g of *Rhizobium* inoculant per kg of seed to secure consistent nodulation and yield advantages against mineral N alone (dos Santos Sousa et al., 2022). On average, *Rhizobium* inoculation was 12.3 % less efficient than mineral N fertilisation. Yet, when meta-analysis results were stratified by season, soil management, and soil properties, *Rhizobium* inoculation outperformed mineral N fertilisation when common beans were grown in the dry season, under no tillage, and in soils with high organic matter, with a likely positive impact on yield. The efficiency gap also narrowed in clay textured, eutrophic soils with low to neutral acidity and adequate P availability (dos Santos Sousa et al., 2022). In addition, co-inoculation with PGPB, such as N_2-fixing rhizobia and *Bacillus*, tends to amplify benefits in soybean, cowpea, and common bean by improving nodulation and early vigour (Kaschuk et al., 2022). While co-inoculation generally enhanced symbiotic function, raising nitrogenase activity in chickpea, common bean, and pigeon pea in pots, and in faba bean and lentil in the field, it decreased activity in lentil from a single data point and in mung bean in pots, and had no effect in other legumes. Plant N tended to increase with co-inoculation in chickpea, common bean, faba bean, mung bean, pigeon pea, and soybean, although field studies reported decreases for soybean and cowpea. In addition, P uptake rose in chickpea, lentil, and urad bean, and vegetative growth was usually promoted, with larger roots in chickpea, faba bean, groundnut, lentil, and soybean, smaller roots in common bean, and reduced shoot size only in cowpea. Yield effects were mostly positive for chickpea, cowpea, faba bean, lentil, mung bean, and soybean, but lentil grown in pots showed a negative response (Kaschuk et al., 2022). In field trials, biochar increased legume productivity by 21.2 %, with shifts in the soil N pool (total N, nitrate N, ammonium N) and greater plant N uptake emerging as the primary drivers (Zhang et al., 2022). Taken together, despite small contradictions across studies, biofertilisers are estimated to increase legume yield, with common bean in particular gaining at least 54 % (Pei et al., 2025).

Responses can be further enhanced by integrating nanofertilisers. Under greenhouse conditions, a molybdenum (Mo) NP formulation increased total green bean biomass by 41.6 % relative to a Mo chelate and by 36.84 % relative to molybdate, while also improving nutrient use efficiency (Muñoz-Márquez et al., 2024). Similarly, in a field experiment, combining ZnO, MnO_2 and MoO_3 NP increased vegetative growth, fertility, photosynthetic capacity, and yield (Salama et al., 2022). However, optimal application timing and dose remain crop specific. For example, in field-grown lentil, a moderate ZnO-NP rate of 2.5 ppm maximised yield when sowing on favourable dates such as October, whereas a higher rate of 5 ppm had a buffer effect in sowing stress with only marginal additional yield (Ali et al., 2025).

4.3. Horticultural crops

In horticultural crops, both biofertilisers and biostimulants demonstrate agronomically meaningful effects on nutrient management, yield, and quality. For instance, in floating soilless basil culture, bacterial, mycorrhizal, and microalgal biofertilisers improved yield, leaf area, mineral nutrition and antioxidant profile, relative to mineral controls at matched nutrient strength (Dasgan et al., 2022). Bacteria delivered the highest total yield and leaf area and, together with mycorrhiza, increased dry matter and total soluble solids. Mycorrhiza also maximised canopy development by promoting lateral branching without stem thickening. All treatments enhanced uptake of N, P, K, Ca, Mg, Fe, Mn, Zn, and Cu and reduced leaf nitrate at the final harvest, most notably with microalgae and mycorrhiza, while bacteria increased phenols by 17.7 % and flavonoids by 35.3 %, outcomes relevant to leafy green quality standards (Dasgan et al., 2022).

In broccoli and lettuce under field conditions, a consortium containing *Bacillus megaterium* and *Pseudomonas fluorescens* sustained yield and mineral accumulation with only ½ to ⅓ of the usual chemical fertiliser, indicating real substitution potential when biologicals are paired with reduced mineral inputs (Demir et al., 2023). In broccoli, *Bacillus* spp. enriched minerals, head vitamin C and shoot fresh weight. *Arthrobacter* spp. outperformed it belowground, increasing root dry weight by 47 % and giving the longest roots, while microalgae and amino acids led for shoot dry matter (Altuntaş, 2018). Higher vermicompost rates paired with the best planting material, in a pot experiment, also increased broccoli growth, photosynthetic capacity and quality traits, including vitamin C, alongside greener, sweeter heads at harvest, highlighting that organic amendments and biobased products can be combined to tune both yield and quality (Hasan et al., 2024).

In greenhouse grown strawberries under organic management, a plant derived protein hydrolysate increased leaf CO_2 assimilation by 34.5 % and fruit yield per unit area by 13.5 %, alongside a broader mineral improvement, including nitrate and magnesium (Ciriello et al., 2025). In contrast, a seaweed extract raised fruit antioxidant activity by 17.4 %, illustrating divergent yet complementary modes of action that can be selected according to quality targets (Ciriello et al., 2025). In Chinese cabbage under controlled conditions, a liquid biofertiliser made from livestock manure and *Chlorella fusca* increased chlorophylls, carotenoids, and N and P assimilation, with transcriptomics indicating upregulated photosynthetic and nutrient assimilation pathways (Le et al., 2025). However, per unit antioxidant concentrations declined, likely due to dilution by rapid biomass accumulation (Le et al., 2025), a trade-off that should be factored into dose, harvest timing, and quality targets.

Even so, with biofertilisers, harvest quality often matches or exceeds conventional benchmarks. In tomato grown under field conditions, compost-based fertility programs increased vitamin C, flavonoids, total phenolics, DPPH radical scavenging activity, and FRAP antioxidant capacity, while maintaining sensory attributes comparable to mineral fertilisation across several cultivars (Teshome et al., 2025). By contrast, chemical fertilisation primarily enhanced β-carotene and lycopene across different growing seasons, which should be accounted for when setting quality targets, choosing cultivars, and defining processing end uses (Teshome et al., 2025). In celery, pre harvest vermicompost and biofertiliser improved shelf life and quality, limiting colour change, weight loss, titratable acidity decline, pH rise, and total soluble solids drift during 4 weeks at 0–2 °C. They also increased vitamin C, total phenolics, and antioxidant activity. Overall, these organic programs, under greenhouse conditions, matched or outperformed higher mineral N regimes and performed on par with the low urea rate, indicating quality gains with reduced synthetic N inputs (Babalar et al., 2023). Under the similar conditions, probiotic microorganisms also increased carotenoids and antioxidants in carrot without raising nitrate accumulation, a desirable quality profile for fresh market roots (Gavelienė et al., 2021). Probiotics improved carrot size and quality in organic and nonorganic systems, with root weight increasing by 18 %, length up to 98 %, monosaccharides by at least 18 %, ascorbic acid up to 15 %, and antioxidant activity up to 20 % (Gavelienė et al., 2021). Together, these results indicate that probiotic programs can be applied across organic and conventional systems to raise marketable yield and enhance nutritional quality while keeping nitrate within standards.

In field-grown okra, nano urea combined with ZnO or TiO_2 raised yield, fruit size, and nutritional quality, and strengthened market traits, achieving these gains with only 75 % of the recommended conventional fertiliser (Razauddin et al., 2025). In a pot experiment with tomato, Fe nanofertilisers increased photosynthetic pigments and carotenoids in leaves (Morfín-Gutiérrez et al., 2025). Mixed nanofertiliser formulations enhanced plant height, stem diameter, root length, leaf mineral content, and fruit quality relative to commercial fertiliser. Protein, fibre, Fe, Zn, and K were also increased, although ash and protein remained below the untreated control (Rahman et al., 2021). Co-application of commercial fertiliser with a nanofertiliser increased antioxidant properties and raised nutrient use efficiency, total production, and the benefit to cost ratio by 26.08, 26.04, and 25.38 %, respectively (Rahman et al., 2021). Finally, a 25 % nano composite NPK significantly promoted growth, yield, and harvest of pot-grown *Capsicum annuum* compared with both the control and conventional fertiliser treatments (Abdel-Aziz et al., 2021).

4.4. Fibre and medicinal crops

Fibre crops present additional constraints that highlight where biofertilisers work and where irrigation quality can suppress gains. In severely salinised cotton soils, phosphate-solubilising bacteria that release organic acids such as lactic and tartaric acid and the phytohormone IAA increased yield up to 15.5 %, improved nutrient availability, and shifted the rhizosphere toward beneficial taxa such as *Acidobacteria*, *Bacteroidetes*, and *Verrucobacteria* (Ding et al., 2024; Wang et al., 2025). Compared with conventional fertilisation, biofertilisers lowered soil specific gravity, improved water and salt distribution, reduced plant sodium uptake, and alleviated salt stress under fresh water and brackish water irrigation. They also elevated urease and invertase activities, increased microbial biomass carbon and nitrogen, promoted crop nutrient uptake, and raised plant N accumulation (Ding et al., 2024). Efficacy was weaker under saltwater irrigation, underscoring that water quality is a decisive parameter for achieving biofertiliser benefits (Ding et al., 2024). In a semi-field experiment, seed coating with the entomopathogenic fungus *Beauveria bassiana* delivered a dual benefit, boosting vegetative vigour leaf number, plant height, stem diameter, fresh and dry biomass, and total chlorophyll and simultaneously suppressing *Aphis gossypii* from week five (Mantzoukas et al., 2023). This positions beneficial fungal coatings as biofertiliser compatible crop protection tools that couple growth promotion with pest pressure reduction in intensive cotton systems.

In hemp, biofertiliser efficacy hinges on water quality, substrate, and the target product. For instance, in an open-field experiment, legume protein hydrolysate was effective in buffering saline irrigation, restoring growth and N uptake and steering phytocannabinoids under higher salinity, indicating a dual role in nutrient acquisition and stress physiology modulation (Formisano et al., 2024). On the other hand, in an outdoor pot experiment, organic amendments coupled with seaweed extracts expanded root length density and root nitrogen, supporting biomass oriented and nutrient efficient systems (Kosmidis et al., 2023).

Microbial consortia based on *Bacillus* spp. also seem to enhance both productivity and secondary metabolism, but their effect depends on the growing substrate, with coco fibre favouring metabolite enrichment and potting soil favouring biomass accumulation and higher leaf chlorophyll across stages (Lyu et al., 2025). Amino acid supplementation acts as a targeted nutritional signal that reconfigures the ionome and the terpene and cannabinoid space, but its benefit is contingent on fertigation strategy. Across recirculating and drain to waste hydroponics, amino acids increased N and S but lowered Ca and Fe in tissues, reduced cannabinolic acid in flowers by 44 %, increased monoterpenes and showed a strong interaction between amino acid signalling and nutrient cycling (Malík et al., 2022). This favours quality and yield under recirculation and aroma focus under drain to waste at the cost of cannabinoid output. Other complex biostimulant cocktails, such as, a molasses, *Aloe vera*, and fish hydrolysate blend, delivered in hydroponics can also modulate seed nutraceutical potential even when bulk antioxidant readouts are unchanged. Shifted seed phytochemistry toward compounds with higher predicted bioavailability and antioxidant capability, with increases or upward trends in pantothenic acid, rosmanol, tributyrin, and biochemical and bioassay indicators of induced defense related pathways (Wise et al., 2025).

Despite generally positive agronomic responses to biofertilisers, predictive rules linking climate, soil pH, soil organic matter, available phosphorus, and application timing to realized field performance are still missing, which hampers targeting and slows adoption (Ghimirey et al., 2025). Signals from beneficial fungi and bacteria that are strong in controlled studies often attenuate in farmers' fields, and guidance on species selection, the use of single strains versus consortia, and how biomass gains translate into nutrient uptake and yield remains incomplete (Liu et al., 2023). In particular, in hydroponic and other soilless systems, the biological operating envelope is poorly defined, since colonisation windows, solution phosphorus set points, and hydraulic constraints are not standardised, making scale up uncertain. Importantly, genotype by microbe by management interactions also remain largely unmapped, so strains, doses, and timings are frequently misaligned with crop phenology and local soils, which blunts efficacy (Ali et al., 2025). Furthermore, protocols for co-inoculation and NDS are not yet settled, and crop and soil specific limits for the safe substitution of mineral N and P are missing, complicating nutrient budgets and risk management. Nevertheless, falling costs in phenotyping technologies, more robust models powered by machine learning (Kaur et al., 2024; Zhao et al., 2024), and tighter integration of multi season field trials (Nguyen et al., 2017), remote sensing (de Souza et al., 2022), and digital twins can deliver site specific decision rules and dose timing windows. Embedding these rules in simple advisory tools and benchmarking them against life cycle and economic outcomes should translate promise into reliable, scalable practice.

5. Knowledge gaps and research priorities

5.1. Ecosystem services and environmental benefits

Biofertilisation is broadly associated with higher soil organic carbon, with effect size shaped by climate, soil, and management, which supports its inclusion in whole farm carbon building strategies (Just et al., 2024). Manufacturing emissions for bacteria based biofertilisers are 9.8–23.2 times lower than nitrogen fertilisers such as urea, ammonium nitrate, and ammonium phosphate, and are broadly comparable to potassium and phosphorus fertilisers (Mulya et al., 2024). Most manufacturing emissions, 64 %, arise from electricity use to run bioreactors, mixers, and filling lines, which can be curtailed by cleaner energy sources, such as on site solar (Mulya et al., 2024). Reported benchmarks indicate very large advantages versus organic fertilisers, up to 10 666 times lower emissions, and roughly 10 times lower than microalgae based biofertilisers, while bacteria based products can displace N fertilisers and thereby cut sector wide emissions (Mulya et al., 2024). Across life cycle assessments, biofertilisers often show lower burdens than mineral dominated baselines when process energy and transport are optimised, though results depend on functional unit, system boundary, and allocation, underscoring the need for consistent methods when comparing scenarios (Álvarez-González et al., 2025; Bouhzam et al., 2025; Mulya et al., 2024).

At the product level, anaerobic digestates tend to have the highest average impacts, especially when manure is used as the functional unit, whereas composting routes are lower on average (Bouhzam et al., 2025; Orlandella and Fiore, 2025). Fish hydrolysate carries the greatest acidification burden, with K as the main driver of that impact, while compost tea is the most water intensive and shows the highest eutrophication and land use per tonne of N (Bouhzam et al., 2025). By contrast, biochar is consistently least impactful for acidification, eutrophication, land use, and water use across N, P, and K, and low biology compost, high biology compost, and insect frass also perform well across categories (Bouhzam et al., 2025). Microalgal biofertilisers show a distinct trade-off, higher freshwater eutrophication that could be mitigated by better nutrient removal at wastewater treatment, yet they are economically competitive, being about 30 % cheaper than inorganic fertilisers (Álvarez-González et al., 2025). Thermochemical routes that yield biochar or ash derived fertilisers generally post the lowest average impacts among technology families when set against digestates and composting, reinforcing their value in low footprint nutrient strategies (Orlandella and Fiore, 2025).

5.2. *Policy and regulatory context*

The regulatory landscape for bio-based fertilisers, biostimulants, and related products is heterogeneous, with significant implications for research design, product claims, and international trade. Within the European Union, Regulation (EU) 2019/1009 establishes harmonised rules for placing fertilising products on the market, defining plant biostimulants as materials that *"stimulate plant nutrition processes independently of the product's nutrient content"* and recognising a limited number of microbial taxa (*Rhizobium* sp., *Azotobacter* sp., *Azospirillum* sp., and AMF) (Buss et al., 2025; du Jardin et al., 2025; Ghorui et al., 2024). Microbial genera with well-documented physiological effects, such as *Pseudomonas* sp., *Bacillus* sp. and other genera, remain excluded under this definition, restricting the range of microorganisms eligible for biostimulant labelling (Buss et al., 2025). If they cannot be commercialised, it is not possible to know the effects on a large scale and how effective they could be.

Non-microbial products, including humic substances, seaweed extracts, and amino acids, are also regulated under this framework, which specifies microbiological and heavy metal limits. Complementary CEN (European Committee for Standardisation) technical specifications address methods for quality control to be branded as CE made, including microbial enumeration and molecular characterisation (du Jardin et al., 2025; Salomon et al., 2022). In parallel, other EU legislation governs the use of animal by-products (e.g., manure under the Nitrates Directive) and sewage sludge (Directive 86/278/EEC), as well as maximum residue levels for pesticides (Regulation (EC) No. 396/2005) and contaminants in food (Regulation (EU) 2023/915).

Globally, definitions and regulatory scopes vary. The United States Plant Biostimulant Act adopts a broader definition, encompassing both microbial and non-microbial products, and explicitly excludes biostimulants from the category of plant regulators (du Jardin et al., 2025). India's Fertiliser (Control) Order 1985 provides detailed microbial composition and viability criteria for biofertilisers, including mycorrhizal inoculants (Ghorui et al., 2024; Malusá and Vassilev, 2014). International standardisation efforts, such as ISO/TC 134, aim to harmonise terminology and testing methods but have yet to achieve universal adoption (Ghorui et al., 2024).

The emergence of novel delivery methods like NPs and CRFs, new frameworks and directives, have to be thought towards regulation and standardisation. Despite a CEN attempt to categorise CRFs and SRFs, it does not specify which one is not standardise methods to determine the nutrient release (Singh et al., 2025). On the other hand, ISO developed terminology and definitions for nanomaterials (ISO/TS 80004–1:2023) in a general manner (Kumari et al., 2023). Supposedly, Regulation (EU) 2019/1009 could also be applied since they are fertilisers (Kumari et al., 2023), despite not being written about them specifically. Additionally, it will be necessary to have other laws to indicate which products are used for the matrix, since microplastics and metals are the most commonly used for coating and surface (Saurabh et al., 2024; Singh et al., 2025). In addition, regulations like Regulation (EC) 1107/2009, which establish restrictions and goals for placing plant protection products on the market, including regulations for trials, should be created (Kumari et al., 2023). Otherwise, hinders the evaluation of the products in normal conditions.

These discrepancies affect product categorisation, experimental comparability, and market access. From a research perspective, they underscore the need to report product composition and mode of action in mechanistic terms, enabling physiological evidence to be interpreted consistently regardless of jurisdiction.

6. Conclusions

Bio-based fertilisers, biostimulants, and novel delivery systems represent a rapidly expanding frontier in crop management, but their integration into plant physiology remains incomplete. Most studies report positive outcomes, yet their mechanisms of action are still inconsistently described. Without this mechanistic precision, agronomic responses remain unpredictable and difficult to scale across environments and genotypes.

The next phase of research must therefore focus in integrative analysis, including molecular markers, ionomics, metabolomics, and flux analyses, to establish causal links between input application and crop function. Equally important is the recognition that plant responses are embedded in complex soil-microbe-climate interactions, demanding systems-level approaches that combine physiology with soil ecology, modelling, and materials science. Also, the sustainability promise of bio-based inputs cannot rest solely on physiological efficacy. Their environmental footprint, persistence in soils, and contribution to circular economy goals remain poorly quantified. Integrating LCA studies with mechanistic plant experiments will provide a more holistic framework to evaluate both agronomic potential and environmental trade-offs. Finally, regulatory frameworks should evolve to incorporate mechanistic descriptors and sustainability metrics, ensuring that claims are supported by reproducible physiological evidence and aligned with environmental goals.

CRediT authorship contribution statement

Jacinta Santos: Writing – original draft, Visualization, Data curation. **Marta Nunes da Silva:** Writing – review & editing, Data curation, Conceptualization. **Carla S. Santos:** Writing – review & editing, Supervision, Project administration, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

This work was supported by FCT (Portugal) through the project LAND [grant 10.54499/2022.06252.PTDC], and CEECIND [grant 10.54499/2022.01903.CEECIND/CP1745/CT0002 to C.S.S.; and grant 2023.06124.CEECIND/CP2855/CT0008 to M.N.S.]. The authors would like to thank the scientific collaboration under the FCT project UIDB/50016/2025.

Data availability

No external data is used for this paper or generated for this paper. Reports of other authors have been cited appropriately.

References

Abdel-Aziz, H.M.M., Soliman, M.I., Abo Al-Saoud, A.M., El-Sherbeny, G.A., 2021. Waste-derived NPK nanofertilizer enhances growth and productivity of *Capsicum annuum* L. Plants 10, 1144. https://doi.org/10.3390/plants10061144.

Aina, O., Bakare, O.O., Daniel, A.I., Gokul, A., Beukes, D.R., Fadaka, A.O., Keyster, M., Klein, A., 2022. Seaweed-derived phenolic compounds in growth promotion and stress alleviation in plants. Life 12, 1548. https://doi.org/10.3390/life12101548.

Albornoz, F., Godoy, L., 2025. Modulation of root nitrogen uptake mechanisms mediated by beneficial soil microorganisms. Plants 14, 2729. https://doi.org/10.3390/PLANTS14172729.

Ali, K., Asad, Z., Agbna, G.H.D., Saud, A., Khan, A., Zaidi, S.J., 2024. Progress and innovations in hydrogels for sustainable agriculture. Agronomy 14, 2815. https://doi.org/10.3390/AGRONOMY14122815.

Ali, M.A., Kordrostami, M., Javar, F.M., Rahimi, M., 2025. Effects of planting date and zinc oxide nano fertilizer on growth and yield of lentil (*Lens culinaris* L.) in two agroecological zones. BMC Plant Biol. 25, 1114. https://doi.org/10.1186/s12870-025-07187-1.

Alleman, A.B., Peters, J.W., 2023. Mechanisms for generating low potential electrons across the metabolic diversity of nitrogen-fixing bacteria. Appl. Environ. Microbiol. 89. https://doi.org/10.1128/aem.00378-23.

Altuntaş, Ö., 2018. A comparative study on the effects of different conventional, organic and bio-fertilizers on broccoli yield and quality. Appl. Ecol. Environ. Res. 16, 1595–1608. https://doi.org/10.15666/aeer/1602_15951608.

Álvarez-González, A., Castro, I.M.P., Ortiz, A., Díez-Montero, R., Passos, F., Garfí, M., Uggetti, E., 2025. Environmental and economic benefits of using microalgae grown in wastewater as biofertilizer for lettuce cultivation. Bioresour. Technol. 424, 132230. https://doi.org/10.1016/j.biortech.2025.132230.

Ambarita, D.D.M., Jingga, A., Fitriatin, B.N., Simarmata, T., 2025. Synergistic effect of biofilm-forming biofertilizers and ameliorants for enhancing fertilizer efficiency and maize agronomic traits on acidic soils. J. Ecol. Eng. 26, 171–184. https://doi.org/10.12911/22998993/203137.

Ampong, K., Thilakaranthna, M.S., Gorim, L.Y., 2022. Understanding the role of humic acids on crop performance and soil health. Front. Agron. 4. https://doi.org/10.3389/fagro.2022.848621.

Antu, U.B., Roy, T.K., Kulsum, T.I., Mitu, P.R., Ismail, Z., Arifin, M., Datta, M., Hossain, S. A., Islam, MdS., Mahiddin, N.A., Al Bakky, A., Hossin, S., Islam, S., Idris, A.M., 2025. Role of humic acid for climate change adaptation measures to boost up sustainable agriculture and soil health: a potential review. Int. J. Biol. Macromol. 313, 144043. https://doi.org/10.1016/j.ijbiomac.2025.144043.

Aruna, M., Nagabhooshanam, N., Kumar, R., Chahar, M., Sudhakar, T., Murthy, N.B.C.S. N., Maranan, R., Murali, M., Sathiyamurthy, S., 2025. Carbon-based nanofertilizers from marine biowaste: innovations, applications, and sustainable nanoengineering strategies. J. Environ. Chem. Eng. 13, 118880. https://doi.org/10.1016/j.jece.2025.118880.

Assylkhankyzy, A., Seitmagzimova, G., 2024. Advanced technologies of potash fertiliser production from promising raw materials. Open Chem. Eng. J. 18. https://doi.org/10.2174/0118741231330310240906080722.

Babalar, M., Daneshvar, H., Díaz-Pérez, J.C., Nambeesan, S., Tabrizi, L., Delshad, M., 2023. Effects of organic and chemical nitrogen fertilization and postharvest treatments on the visual and nutritional quality of fresh-cut celery (*Apium graveolens* L.) during storage. Food Sci. Nutr. 11, 320–333. https://doi.org/10.1002/fsn3.3063.

Balla, A., Silini, A., Cherif-Silini, H., Chenari Bouket, A., Alenezi, F.N., Belbahri, L., 2022. Recent advances in encapsulation techniques of plant growth-promoting microorganisms and their prospects in the sustainable agriculture. Appl. Sci. 12, 9020. https://doi.org/10.3390/app12189020.

Barbosa, J.Z., Roberto, L. de A., Hungria, M., Corrêa, R.S., Magri, E., Correia, T.D., 2022. Meta-analysis of maize responses to *Azospirillum brasilense* inoculation in Brazil: benefits and lessons to improve inoculation efficiency. Appl. Soil Ecol. 170, 104276. https://doi.org/10.1016/J.APSOIL.2021.104276.

Bargaz, A., Elhaissoufi, W., Khourchi, S., Benmrid, B., Borden, K.A., Rchiad, Z., 2021. Benefits of phosphate solubilizing bacteria on belowground crop performance for improved crop acquisition of phosphorus. Microbiol. Res. 252, 126842. https://doi.org/10.1016/j.micres.2021.126842.

Baum, M.E., Sawyer, J.E., Castellano, M.J., Archontoulis, S.V., 2024. Ranking genotype, environment, management effects on the optimum nitrogen rate for maize: a cropping system modeling analysis. Agron. J. 116, 1775–1791. https://doi.org/10.1002/agj2.21596.

Beltran-Medina, I., Romero-Perdomo, F., Molano-Chavez, Lady, Gutiérrez, A.Y., Silva, A. M.M., Estrada-Bonilla, G., 2023. Inoculation of phosphate-solubilizing bacteria improves soil phosphorus mobilization and maize productivity. Nutrient Cycl. Agroecosyst. 126, 21–34. https://doi.org/10.1007/s10705-023-10268-y.

Bisht, N., Singh, T., Ansari, MohdM., Chauhan, P.S., 2025. Harnessing plant-rhizobacteria alliances for nutrient homeostasis in depleting soilscape: shifting paradigms beyond chemical fertilizers. Pedosphere. https://doi.org/10.1016/j.pedsph.2025.07.015.

Bouhzam, I., Azarkamand, S., Puig, R., Bala, A., Fullana-i-Palmer, P., Sazdovski, I., Mazurenko, B., Mir, S., Sani, MdN.H., Lopes, I.G., Maievska, T., Raksha, N., Savchuk, O., Ghaley, B.B., Yong, J.W.H., Tonkha, O., 2025. Assessing environmental impacts of various biofertilizers in Europe: a step toward circular economy transition. Sustain. Prod. Consum. 56, 460–476. https://doi.org/10.1016/j.spc.2025.04.012.

Boutahiri, S., Benrkia, R., Tembeni, B., Idowu, O.E., Olatunji, O.J., 2024. Effect of biostimulants on the chemical profile of food crops under normal and abiotic stress conditions. Curr. Plant Biol. 40, 100410. https://doi.org/10.1016/J.CPB.2024.100410.

Brownlie, W.J., Sutton, M.A., Cordell, D., Reay, D.S., Heal, K.V., Withers, P.J.A., Vanderbeck, I., Spears, B.M., 2023. Phosphorus price spikes: a wake-up call for phosphorus resilience. Front. Sustain. Food Syst. 7. https://doi.org/10.3389/fsufs.2023.1088776.

Brunelle, T., Chakir, R., Carpentier, A., Dorin, B., Goll, D., Guilpart, N., Maggi, F., Makowski, D., Nesme, T., Roosen, J., Tang, F.H.M., 2024. Reducing chemical inputs in agriculture requires a system change. Commun. Earth Environ. 5, 369. https://doi.org/10.1038/s43247-024-01533-1.

Buernor, A.B., Kabiru, M.R., Bechtaoui, N., Jibrin, J.M., Asante, M., Bouraqqadi, A., Dahhani, S., Ouhdouch, Y., Hafidi, M., Jemo, M., 2022. Grain legume yield responses to rhizobia inoculants and phosphorus supplementation under Ghana soils: a meta-synthesis. Front. Plant Sci. 13. https://doi.org/10.3389/fpls.2022.877433.

Buss, W., Belt, K., Hein, Z., Putri, A., Zhu, S., Suwandari, H., Bentley, A.R., 2025. Hurdles to overcome to achieve biostimulant-driven, low chemical input crop production. Plants People Planet 1–9. https://doi.org/10.1002/ppp3.70030.

Caires, E.F., Bini, A.R., Barão, L.F.C., Haliski, A., Duart, V.M., Ricardo, K. da S., 2021. Seed inoculation with *Azospirillum brasilense* and nitrogen fertilization for no-till cereal production. Agron. J. 113, 560–576. https://doi.org/10.1002/agj2.20488.

Chamorro, A.F., Palencia, M., Combatt, E.M., 2025. Starch hydrogels for slow and controlled-release fertilizers: a review. Polymers 17, 1117. https://doi.org/10.3390/POLYM17081117.

Chaudhary, P., Singh, S., Chaudhary, A., Sharma, A., Kumar, G., 2022. Overview of biofertilizers in crop production and stress management for sustainable agriculture. Front. Plant Sci. 13. https://doi.org/10.3389/fpls.2022.930340.

Ciriello, M., Pannico, A., Rouphael, Y., Basile, B., 2025. Enhancing yield, physiological, and quality traits of strawberry cultivated under organic management by applying different non-microbial biostimulants. Plants 14, 712. https://doi.org/10.3390/PLANTS14050712/S1.

Coccina, A., Cavagnaro, T.R., Pellegrino, E., Ercoli, L., McLaughlin, M.J., Watts-Williams, S.J., 2019. The mycorrhizal pathway of zinc uptake contributes to zinc accumulation in barley and wheat grain. BMC Plant Biol. 19, 133. https://doi.org/10.1186/s12870-019-1741-y.

Colla, G., Nardi, S., Cardarelli, M., Ertani, A., Lucini, L., Canaguier, R., Rouphael, Y., 2015. Protein hydrolysates as biostimulants in horticulture. Sci. Hortic. 196, 28–38. https://doi.org/10.1016/j.scienta.2015.08.037.

Condori, T., Alarcón, S., Huasasquiche, L., García-Blásquez, C., Padilla-Castro, C., Velásquez, J., Solórzano, R., 2024. Inoculation with *Azospirillum brasilense* as a strategy to reduce nitrogen fertilization in cultivating purple maize (*Zea mays* L.) in the inter-andean valleys of Peru. Microorganisms 12, 2107. https://doi.org/10.3390/microorganisms12102107.

Crespo-Barreiro, A., Mazuecos-Aguilera, I., Anta-Fernández, F., Cara-Jiménez, J., González-Andrés, F., 2025. Enhancing drought resistance in olive trees: understanding the synergistic effects of the combination of PGPR and biochar. J. Plant Growth Regul. 44, 4383–4395. https://doi.org/10.1007/S00344-025-11693-9.

Cruz, C., Cardoso, P., Santos, J., Matos, D., Figueira, E., 2022. Bioprospecting soil bacteria from arid zones to increase plant tolerance to drought: growth and biochemical status of maize inoculated with plant growth-promoting bacteria isolated from Sal island. Cape Verde. Plants 11, 2912. https://doi.org/10.3390/PLANTS11212912/S1.

Cruz, C., Cardoso, P., Santos, J., Matos, D., Sá, C., Figueira, E., 2023. Application of plant growth-promoting bacteria from Cape Verde to increase maize tolerance to salinity. Antioxidants 12, 488. https://doi.org/10.3390/antiox12020488.

Dasgan, H.Y., Aldiyab, A., Elgudayem, F., Ikiz, B., Gruda, N.S., 2022. Effect of biofertilizers on leaf yield, nitrate amount, mineral content and antioxidants of basil (*Ocimum basilicum* L.) in a floating culture. Sci. Rep. 12, 20917. https://doi.org/10.1038/s41598-022-24799-x.

Dasgupta, D., Paul, A., Acharya, K., Minkina, T., Mandzhieva, S., Gorovtsov, A.V., Chakraborty, N., Keswani, C., 2023. Bioinoculant mediated regulation of signalling cascades in various stress responses in plants. Heliyon 9, e12953. https://doi.org/10.1016/j.heliyon.2023.e12953.

de Melo, B.A.G., Motta, F.L., Santana, M.H.A., 2016. Humic acids: structural properties and multiple functionalities for novel technological developments. Mater. Sci. Eng. C Mater. Biol. Appl. 62, 967–974. https://doi.org/10.1016/j.msec.2015.12.001.

de Souza, A.E.S., Barbosa Júnior, M.R., de Almeida Moreira, B.R., da Silva, R.P., Lemos, L.B., 2022. UAV multispectral data: a reliable approach for managing phosphate-solubilizing bacteria in common bean. Agronomy 12, 2284. https://doi.org/10.3390/agronomy12102284.

de Zutter, N., Ameye, M., Bekaert, B., Verwaeren, J., De Gelder, L., Audenaert, K., 2022. Uncovering new insights and misconceptions on the effectiveness of phosphate solubilizing rhizobacteria in plants: a meta-analysis. Front. Plant Sci. 13, 858804. https://doi.org/10.3389/fpls.2022.858804.

Delaeter, M., Magnin-Robert, M., Randoux, B., Lounès-Hadj Sahraoui, A., 2024. Arbuscular mycorrhizal fungi as biostimulant and biocontrol agents: a review. Microorganisms 12, 1281. https://doi.org/10.3390/MICROORGANISMS12071281.

Demir, H., Sönmez, İ., Uçan, U., Akgün, İ.H., 2023. Biofertilizers improve the plant growth, yield, and mineral concentration of lettuce and broccoli. Agronomy 13, 2031. https://doi.org/10.3390/agronomy13082031.

Devi, P.I., Manjula, M., Bhavani, R.V., 2022. Agrochemicals, environment, and human health. Annu. Rev. Environ. Resour. 47, 399–421. https://doi.org/10.1146/annurev-environ-120920-111015.

Ding, B., Cao, H., Bai, Y., Guo, S., Zhang, J., He, Z., Wang, B., Jia, Z., Liu, H., 2024. Effect of biofertilizer addition on soil physicochemical properties, biological properties, and cotton yield under water irrigation with different salinity levels in Xinjiang, China. Field Crops Res. 308, 109300. https://doi.org/10.1016/j.fcr.2024.109300.

dos Reis, G.A., Martínez-Burgos, W.J., Pozzan, R., Pastrana Puche, Y., Ocán-Torres, D., de Queiroz Fonseca Mota, P., Rodrigues, C., Lima Serra, J., Scapini, T., Karp, S.G., Soccol, C.R., 2024. Comprehensive review of microbial inoculants: agricultural applications, technology trends in patents, and regulatory frameworks. Sustainability 16, 8720. https://doi.org/10.3390/SU16198720.

dos Santos Sousa, W., Soratto, R.P., Peixoto, D.S., Campos, T.S., da Silva, M.B., Souza, A. G.V., Teixeira, I.R., Gitari, H.I., 2022. Effects of *Rhizobium* inoculum compared with mineral nitrogen fertilizer on nodulation and seed yield of common bean. A meta-analysis. Agron. Sustain. Dev. 42, 52. https://doi.org/10.1007/s13593-022-00784-6.

du Jardin, P., 2015. Plant biostimulants: definition, concept, main categories and regulation. Sci. Hortic. 196, 3–14. https://doi.org/10.1016/J.SCIENTA.2015.09.021.

du Jardin, P., Brown, P.H., DeJong, T.M., Cassán, F., Ferrante, A., Fotopoulos, V., Manganaris, G.A., Carillo, P., 2025. Unlocking the black box of plant biostimulants. Sci. Hortic. 350, 114281. https://doi.org/10.1016/j.scienta.2025.114281.

Elnahal, A.S.M., El-Saadony, M.T., Saad, A.M., Desoky, E.-S.M., El-Tahan, A.M., Rady, M. M., AbuQamar, S.F., El-Tarabily, K.A., 2022. The use of microbial inoculants for biological control, plant growth promotion, and sustainable agriculture: a review. Eur. J. Plant Pathol. 162, 759–792. https://doi.org/10.1007/s10658-021-02393-7.

Fadiji, A.E., Xiong, C., Egidi, E., Singh, B.K., 2024. Formulation challenges associated with microbial biofertilizers in sustainable agriculture and paths forward. J. Sustain. Agric. Environ. 3, e70006. https://doi.org/10.1002/sae2.70006.

Faisal, M., Faizan, M., Alatar, A.A., 2024. Metallic allies in drought resilience: unveiling the influence of silver and zinc oxide nanoparticles on enhancing tomato (*Solanum lycopersicum*) resistance through oxidative stress regulation. Plant Physiol. Biochem. 212, 108722. https://doi.org/10.1016/j.plaphy.2024.108722.

Faria de Souza, A.F., Calderín García, A., Nivaldo de Oliveira Sátiro, J., Ribeiro de Lima, B., Silvestre Fernandes, M., Louro Berbara, R.L., Azevedo Santos, L., 2025. Humic acid regulates root growth through ROS-dependent pathway and hormone signaling in rice. J. Agric. Food Chem. 73. https://doi.org/10.1021/acs.jafc.5c06288.

Fayiga, A.O., Nwoke, O.C., 2016. Phosphate rock: origin, importance, environmental impacts, and future roles. Environ. Rev. 24, 403–415. https://doi.org/10.1139/er-2016-0003.

Feng, B., Wang, E., Zhang, Y., Xu, L., Xue, Y., Chen, Y., 2025. Short-term fertilization with the nitrogen-fixing bacterium (NFB) *Kosakonia radicincitans* GXGL-4A agent can modify the transcriptome expression profiling of cucumber (*Cucumis sativus* L.) root. Microorganisms 13, 506. https://doi.org/10.3390/MICROORGANISMS13030506/S1.

Ferreira, A., Bastos, C.R.V., Marques-dos-Santos, C., Acién-Fernandez, F.G., Gouveia, L., 2023. Algaeculture for agriculture: from past to future. Front. Agron. 5, 1064041. https://doi.org/10.3389/fagro.2023.1064041.

Food and Agriculture Organisation, 2025. International fund for agricultural development, United Nations international children's emergency fund, world food programme, world health organisation. The State of Food Security and Nutrition in the World 2025, 2025th Ed, the State of the World. FAO, IFAD; UNICEF; WFP; WHO, Rome. https://doi.org/10.4060/cd6008en.

Formisano, C., Fiorentino, N., Di Mola, I., Iaccarino, N., Gargiulo, E., Chianese, G., 2024. Effect of saline irrigation and plant-based biostimulant application on fiber hemp (*Cannabis sativa* L.) growth and phytocannabinoid composition. Front. Plant Sci. 15, 1293184. https://doi.org/10.3389/fpls.2024.1293184.

Fukami, J., Cerezini, P., Hungria, M., 2018. *Azospirillum*: benefits that go far beyond biological nitrogen fixation. AMB Express 8, 73. https://doi.org/10.1186/s13568-018-0608-1.

Galindo, F.S., Pagliari, P.H., da Silva, E.C., Silva, V.M., Fernandes, G.C., Rodrigues, W.L., Céu, E.G.O., de Lima, B.H., Jalal, A., Muraoka, T., Buzetti, S., Lavres, J., Teixeira Filho, M.C.M., 2022. Co-Inoculation with *Azospirillum brasilense* and *bradyrhizobium* sp. enhances nitrogen uptake and yield in field-grown cowpea and did not change N-Fertilizer recovery. Plants 11, 1847. https://doi.org/10.3390/plants11141847.

Gavelienė, V., Šocik, B., Jankovska-Bortkevič, E., Jurkonienė, S., 2021. Plant microbial biostimulants as a promising tool to enhance the productivity and quality of carrot root crops. Microorganisms 9, 1850. https://doi.org/10.3390/microorganisms9091850.

Ghadirnezhad Shiade, S.R., Zand-Silakhoor, A., Fathi, A., Rahimi, R., Minkina, T., Rajput, V.D., Zulfiqar, U., Chaudhary, T., 2024. Plant metabolites and signaling pathways in response to biotic and abiotic stresses: exploring bio stimulant applications. Plant Stress 12, 100454. https://doi.org/10.1016/j.stress.2024.100454.

Ghimirey, V., Chaurasia, J., Dhungana, R., Poudel, B., 2025. Organic fertilizers and their efficacy on soil characteristics, growth and yield of cauliflower (*Brassica oleraceae* var. *botrytis*) in sandy loam soil of Nepal. Front. Soil Sci. 5, 1556283. https://doi.org/10.3389/fsoil.2025.1556283.

Ghorui, M., Chowdhury, S., Balu, P., Burla, S., 2024. Arbuscular mycorrhizal inoculants and its regulatory landscape. Heliyon 10, e30359. https://doi.org/10.1016/j.heliyon.2024.e30359.

González-Pérez, B.K., Rivas-Castillo, A.M., Valdez-Calderón, A., Gayosso-Morales, M.A., 2022. Microalgae as biostimulants: a new approach in agriculture. World J. Microbiol. Biotechnol. 38, 4. https://doi.org/10.1007/s11274-021-03192-2.

Gupta, A., Mishra, R., Rai, S., Bano, A., Pathak, N., Fujita, M., Kumar, M., Hasanuzzaman, M., 2022. Mechanistic insights of plant growth promoting bacteria mediated drought and salt stress tolerance in plants for sustainable agriculture. Int. J. Mol. Sci. 23, 3741. https://doi.org/10.3390/ijms23073741.

Hajihashemi, S., Kazemi, S., 2022. The potential of foliar application of nano-chitosan-encapsulated nano-silicon donor in amelioration the adverse effect of salinity in the wheat plant. BMC Plant Biol. 22, 148. https://doi.org/10.1186/s12870-022-03531-x.

Hasan, M.J., Khatun, K., Mostarin, T., Karishma, K.C., Nadim, M.K.A., Chowdhury, S.M. A., 2024. Influence of vermicompost and biofertilizer on growth, head yield and quality of broccoli (*Brassica oleracea* L. var. *italica*). Agric. Sci. Technol. 16, 54–62. https://doi.org/10.15547/ast.2024.01.006.

Herrmann, M.N., Griffin, L.G., John, R., Mosquera-Rodríguez, S.F., Nkebiwe, P.M., Chen, X., Yang, H., Müller, T., 2024. Limitations of soil-applied non-microbial and microbial biostimulants in enhancing soil P turnover and recycled P fertilizer utilization - a study with and without plants. Front. Plant Sci. 15, 1465537. https://doi.org/10.3389/FPLS.2024.1465537.

Ikram, M., Khalid, B., Batool, M., Ullah, M., Zitong, J., Rauf, A., Rao, M.J., Rehman, H.U., Kuai, J., Xu, Z., Zhao, J., Wang, J., Zhou, G., Wang, B., 2025. Secondary metabolites as biostimulants in salt stressed plants: mechanisms of oxidative defense and signal transduction. Plant Stress 16, 100891. https://doi.org/10.1016/J.STRESS.2025.100891.

Irineu, L.E.S., Soares, C. de P., Soares, T.S., Almeida, F.A. de, Almeida-Silva, F., Gazara, R.K., Meneses, C.H.S.G., Canellas, L.P., Silveira, V., Venancio, T.M., Olivares, F.L., 2023. Multiomic approaches reveal hormonal modulation and nitrogen uptake and assimilation in the initial growth of maize inoculated with *Herbaspirillum seropedicae*. Plants 12, 48. https://doi.org/10.3390/PLANTS12010048/S1.

Jalal, M.A.F., Bondarenko, S., 2025. Agrochemicals: definition and regulation. In: Jalal, M.A.F., Bondarenko, S. (Eds.), Radiochemical Analysis of Agrochemicals. Springer, Cham, pp. 1–50. https://doi.org/10.1007/978-3-031-80080-1_1.

Janni, M., Maestri, E., Gullì, M., Marmiroli, M., Marmiroli, N., 2023. Plant responses to climate change, how global warming may impact on food security: a critical review. Front. Plant Sci. 14, 1297569. https://doi.org/10.3389/FPLS.2023.1297569.

Johnson, R., Joel, J.M., Puthur, J.T., 2023. Biostimulants: the futuristic sustainable approach for alleviating crop productivity and abiotic stress tolerance. J. Plant Growth Regul. 43, 659–674. https://doi.org/10.1007/S00344-023-11144-3.

Jones, D.L., Oburger, E., 2011. Solubilization of phosphorus by soil microorganisms. In: Bünemann, E., Oberson, A., Frossard, E. (Eds.), Phosphorus in Action, Soil Biology. Springer, Berlin, Berlin, Heidelberg, pp. 169–198. https://doi.org/10.1007/978-3-642-15271-9_7.

Just, B.S., Marks, E.A.N., Roquer-Beni, L., Llenas, L., Ponsà, S., Vilaplana, R., 2024. Biofertilization increases soil organic carbon concentrations: results of a meta-analysis. Int. J. Agric. Sustain. 22, 2361578. https://doi.org/10.1080/14735903.2024.2361578.

Kaboosi, E., Rahimi, A., Abdoli, M., Ghabooli, M., 2023. Comparison of Serendipita indica inoculums and a commercial biofertilizer effects on physiological characteristics and antioxidant capacity of maize under drought stress. J. Soil Sci. Plant Nutr. 23, 900–911. https://doi.org/10.1007/s42729-022-01091-5.

Kanomanyanga, J., Jiao, X., Mudare, S., Mabasa, S., Tang, L., 2021. Meta-analysis of the effects of Rhizobia inoculants and phosphorus fertilizer on soybean nodulation in Africa. Afr. J. Plant Sci. 15, 206–224. https://doi.org/10.5897/AJPS2021.2168.

Karunakaran, A., Fathima, Y., Singh, P., Beniwal, R., Singh, J., Ramakrishna, W., 2024. Next-generation biofertilizers: nanoparticle-coated plant growth-promoting bacteria biofertilizers for enhancing nutrient uptake and wheat growth. Agriculture 14, 517. https://doi.org/10.3390/AGRICULTURE14040517.

Kaschuk, G., Auler, A.C., Vieira, C.E., Dakora, F.D., Jaiswal, S.K., da Cruz, S.P., 2022. Coinoculation impact on plant growth promotion: a review and meta-analysis on coinoculation of rhizobia and plant growth-promoting bacilli in grain legumes. Braz. J. Microbiol. 53, 2027–2037. https://doi.org/10.1007/s42770-022-00800-7.

Kaur, G., Rana, P., Walia Kaur, H., Dwibedi, V., 2024. The role of machine learning in biofertilizer industry: from data anlytics to predictive modelling. In: Kaur, S., Dwibedi, V., Sahu, P.K. (Eds.), Metabolomics, Proteomics and Gene Editing Approaches in Biofertilizer Industry. Springer, Singapore, pp. 141–155. https://doi.org/10.1007/978-981-97-2910-4.

Khan, F., Siddique, A.B., Shabala, S., Zhou, M., Zhao, C., 2023. Phosphorus plays key roles in regulating plants' physiological responses to abiotic stresses. Plants 12, 2861. https://doi.org/10.3390/plants12152861.

Khoulati, A., Ouahhoud, S., Taibi, M., Ezrari, S., Mamri, S., Merah, O., Hakkou, A., Addi, M., Maleb, A., Saalaoui, E., 2025. Harnessing biostimulants for sustainable agriculture: innovations, challenges, and future prospects. Discov. Agric. 3, 1–28. https://doi.org/10.1007/S44279-025-00177-9.

Kosmidis, S., Stavapoulos, P., Kakabouki, I., Papastylianou, P., Roussis, I., Mavroeidis, A., Beslemes, D., Bilalis, D., 2023. Combined effect of biocompost and biostimulant on root characteristics of *Cannabis sativa* L. Bull. Univ. Agric. Sci. Vet. Med. Cluj-Napoca Hortic. 80, 47–53. https://doi.org/10.15835/buasvmcn-hort:2022.0038.

Kumar, Amarjeet, Kumar, Ajeet, Patel, H., 2018. Role of microbes in phosphorus availability and acquisition by plants. Int. J. Curr. Microbiol. Appl. Sci. 7, 1344–1347. https://doi.org/10.20546/ijcmas.2018.705.161.

Kumar, Saurabh, Biswas, S.K., Lal, K., Kumar, Shivam, Shukla, A., Kumar, Anoop, Singh, S., Shivam, Kumar Ankit, Kumar, R., 2023. Green synthesis of nanoparticles from leaves of *Cannabis sativa* L. and its effect on seed germination, seedling mortality and wilt incidence of tomato caused by *Fusarium oxysporum* f. sp. *lycopersici* (Sacc.) Snyder & Hansen. Biol. Forum Int. J. 15, 850–855.

Kumari, R., Suman, K., Karmakar, S., Mishra, V., Lakra, S.G., Saurav, G.K., Mahto, B.K., 2023. Regulation and safety measures for nanotechnology-based agri-products. Front. Genome, fifth ed., 1200987 https://doi.org/10.3389/fgeed.2023.1200987

Kurniawati, A., Toth, G., Ylivainio, K., Toth, Z., 2023. Opportunities and challenges of bio-based fertilizers utilization for improving soil health. Org. Agric. For. 13, 335–350. https://doi.org/10.1007/S13165-023-00432-7.

Le, T.Y.L., Lee, J., Shim, S.-Y., Jung, J., Kim, S.-R., Hong, S.-H., Lee, M.-G., Hwang, S.-G., 2025. Effects of liquid bio-fertilizer on plant growth, antioxidant activity, and soil bacterial community during cultivation of Chinese cabbage (*Brassica rapa* L. ssp. *pekinensis*). Microorganisms 13, 1036. https://doi.org/10.3390/microorganisms13051036.

Lephatsi, M., Nephali, L., Meyer, V., Piater, L.A., Buthelezi, N., Dubery, I.A., Opperman, H., Brand, M., Huyser, J., Tugizimana, F., 2022. Molecular mechanisms associated with microbial biostimulant-mediated growth enhancement, priming and drought stress tolerance in maize plants. Sci. Rep. 12, 1–18. https://doi.org/10.1038/s41598-022-14570-7.

Li, J., Van Gerrewey, T., Geelen, D., 2022. A meta-analysis of biostimulant yield effectiveness in field trials. Front. Plant Sci. 13. https://doi.org/10.3389/fpls.2022.836702.

Lindström, K., Mousavi, S.A., 2020. Effectiveness of nitrogen fixation in rhizobia. Microb. Biotechnol. 13, 1314–1335. https://doi.org/10.1111/1751-7915.13517.

Liu, R., Li, C., Zhang, Y., Liu, C., Xue, J., Zheng, Y., 2025. Enhanced biological nitrogen fixation and nodulation in alfalfa through the synergistic interactions between *Sinorhizobium meliloti* and *Priestia aryabhattai*. World J. Microbiol. Biotechnol. 41, 1–14. https://doi.org/10.1007/S11274-025-04394-8.

Liu, X., Mei, S., Salles, J.F., 2023. Inoculated microbial consortia perform better than single strains in living soil: a meta-analysis. Appl. Soil Ecol. 190, 105011. https://doi.org/10.1016/j.apsoil.2023.105011.

Lopes, T., Costa, P., Cardoso, P., Figueira, E., 2024. Bacterial volatile organic compounds as a strategy to increase drought tolerance in maize (*Zea mays* L.): influence on plant biochemistry. Plants 13, 2456. https://doi.org/10.3390/PLANTS13172456.

Lopes, T., Cruz, C., Cardoso, P., Pinto, R., Marques, P.A.A.P., Figueira, E., 2021. A multifactorial approach to untangle Graphene Oxide (GO) nanosheets effects on plants: plant growth-promoting bacteria inoculation, bacterial survival, and drought. Nanomaterials 11, 771. https://doi.org/10.3390/NANO11030771.

Lyu, D., Ruan, E.D., Backer, R., Gagné-Bourque, F., Smith, D.L., 2025. Changes in morpho-physiological traits and phytochemical composition of *Cannabis sativa* L. treated with microbial biostimulants across different substrates. Ind. Crops Prod. 224, 120377. https://doi.org/10.1016/j.indcrop.2024.120377.

Machado, J., Fernandes, A.P.G., Bokor, B., Vaculík, M., Kostoláni, D., Kokavcová, A., Heuvelink, E., Vasconcelos, M.W., Carvalho, S.M.P., 2025. Tomato responses to nitrogen, drought and combined stresses: shared and specific effects on vascular plant anatomy, nutrient partitioning and amino acids profile. Plant Physiol. Biochem. 221, 109649. https://doi.org/10.1016/j.plaphy.2025.109649.

Maciel-Rodríguez, M., Moreno-Valencia, F.D., Plascencia-Espinosa, M., 2025. The role of plant growth-promoting bacteria in soil restoration: a strategy to promote agricultural sustainability. Microorganisms 13, 1799. https://doi.org/10.3390/MICROORGANISMS13081799.

Malécange, M., Sergheraert, R., Teulat, B., Mounier, E., Lothier, J., Sakr, S., 2023. Biostimulant properties of protein hydrolysates: recent advances and future challenges. Int. J. Mol. Sci. 24, 9714. https://doi.org/10.3390/ijms24119714.

Malík, M., Velechovský, J., Praus, L., Janatová, A., Kahánková, Z., Klouček, P., Tlustoš, P., 2022. Amino acid supplementation as a biostimulant in medical cannabis (*Cannabis sativa* L.) plant nutrition. Front. Plant Sci. 13, 868350. https://doi.org/10.3389/fpls.2022.868350.

Malusá, E., Vassilev, N., 2014. A contribution to set a legal framework for biofertilisers. Appl. Microbiol. Biotechnol. 98, 6599–6607. https://doi.org/10.1007/s00253-014-5828-y.

Mandal, M., Singh Lodhi, R., Chourasia, S., Das, S., Das, P., 2025. A review on sustainable slow-release N, P, K fertilizer hydrogels for smart agriculture. ChemPlusChem 90, e202400643. https://doi.org/10.1002/CPLU.202400643.

Mantzoukas, S., Papantzikos, V., Katsogiannou, S., Papanikou, A., Koukidis, C., Servis, D., Eliopoulos, P., Patakioutas, G., 2023. Biostimulant and bioinsecticidal effect of coating cotton seeds with endophytic *Beauveria bassiana* in semi-field conditions. Microorganisms 11, 2050. https://doi.org/10.3390/microorganisms11082050.

Martin del Campo, J.S., Rigsbee, J., Bueno Batista, M., Mus, F., Rubio, L.M., Einsle, O., Peters, J.W., Dixon, R., Dean, D.R., dos Santos, P.C., 2022. Overview of physiological, biochemical, and regulatory aspects of nitrogen fixation in *Azotobacter vinelandii*. Crit. Rev. Biochem. Mol. Biol. 57, 492–538. https://doi.org/10.1080/10409238.2023.2181309.

Martínez-Lorente, S.E., Martí-Guillén, J.M., Pedreño, M.Á., Almagro, L., Sabater-Jara, A. B., 2024. Higher plant-derived biostimulants: mechanisms of action and their role in mitigating plant abiotic stress. Antioxidants 13, 318. https://doi.org/10.3390/ANTIOX13030318.

Martins, V.F.R., Coelho, M., Machado, M., Costa, E., Gomes, A.M., Poças, F., Sperotto, R. A., Rosa-Martinez, E., Vasconcelos, M., Pintado, M.E., Morais, R.M.S.C., Morais, A.M. M.B., 2024. Integrated valorization of *Fucus spiralis* alga: polysaccharides and bioactives for edible films and residues as biostimulants. Foods 13, 2938. https://doi.org/10.3390/foods13182938.

Matthews, S., Siddiqui, Y., Ali, A., 2025. Unleashing the power of bio-stimulants for enhanced crop growth, productivity, and quality: a comprehensive review. J. Plant Nutr. 48, 703–725. https://doi.org/10.1080/01904167.2024.2412736.

Mau, L., Kant, J., Walker, R., Kuchendorf, C.M., Schrey, S.D., Roessner, U., Watt, M., 2021. Wheat can access phosphorus from algal biomass as quickly and continuously as from mineral fertilizer. Front. Plant Sci. 12, 631314. https://doi.org/10.3389/fpls.2021.631314.

Mitter, E.K., Tosi, M., Obregón, D., Dunfield, K.E., Germida, J.J., 2021. Rethinking crop nutrition in times of modern microbiology: innovative biofertilizer technologies. Front. Sustain. Food Syst. 5, 606815. https://doi.org/10.3389/FSUFS.2021.606815.

Monterisi, S., Garcia-Perez, P., Buffagni, V., Zuluaga, M.Y.A., Ciriello, M., Formisano, L., El-Nakhel, C., Cardarelli, M., Colla, G., Rouphael, Y., Cristofano, F., Cesco, S., Lucini, L., Pii, Y., 2024. Unravelling the biostimulant activity of a protein hydrolysate in lettuce plants under optimal and low N availability: a multi-omics approach. Physiol. Plant. 176, e14357. https://doi.org/10.1111/ppl.14357.

Moradi, S., Babapoor, A., Ghanbarlou, S., Kalashgarani, M.Y., Salahshoori, I., Seyfaee, A., 2024. Toward a new generation of fertilizers with the approach of controlled-release fertilizers: a review. J. Coat. Technol. Res. 21, 31–54. https://doi.org/10.1007/s11998-023-00817-z.

Morfín-Gutiérrez, A., García-Cerda, L.A., González-García, Y., Juárez-Maldonado, A., 2025. Synthesis of Fe_3O_4@MCM-48 as nano fertilizer for growth stimulation in tomato plants. Plants 14, 405. https://doi.org/10.3390/plants14030405.

Mulya, K.S., Tan, J.P., Yeat, S.P., Yeat, C.N.C., Woon, K.S., 2024. Biofertilizers for sustainable agriculture: a life cycle assessment of upstream manufacturing to carbon reduction. Chem. Eng. Trans. 113, 187–192. https://doi.org/10.3303/CET24113032.

Muñoz-Márquez, E., Soto-Parra, J.M., Pérez-Leal, R., Sanchez, E., 2024. New nitrogen use efficiency indices for biomass formation and productivity in green beans under foliar fertilization with molybdenum nanofertilizer. Nitrogen 5, 667–687. https://doi.org/10.3390/nitrogen5030044.

Nadarajah, K., Abdul Rahman, N.S.N., 2023. The microbial connection to sustainable agriculture. Plants 12, 2307. https://doi.org/10.3390/PLANTS12122307.

Nardi, S., Ertani, A., Francioso, O., 2017. Soil–root cross-talking: the role of humic substances. J. Plant Nutr. Soil Sci. 180, 5–13. https://doi.org/10.1002/jpln.201600348.

Ngosong, C., Tatah, B.N., Olougou, M.N.E., Suh, C., Nkongho, R.N., Ngone, M.A., Achiri, D.T., Tchakounté, G.V.T., Ruppel, S., 2022. Inoculating plant growth-promoting bacteria and arbuscular mycorrhiza fungi modulates rhizosphere acid phosphatase and nodulation activities and enhance the productivity of soybean (*Glycine max*). Front. Plant Sci. 13, 934339. https://doi.org/10.3389/FPLS.2022.934339.

Nguyen, T.H., Phan, T.C., Choudhury, A.T.M.A., Rose, M.T., Deaker, R.J., Kennedy, I.R., 2017. BioGro: a plant growth-promoting biofertilizer validated by 15 years' research from laboratory selection to rice farmer's fields of the mekong Delta. In: Singh, J.S., Seneviratne, G. (Eds.), Agro-Environmental Sustainability. Springer, Cham, pp. 237–254. https://doi.org/10.1007/978-3-319-49724-2_11.

Nunes da Silva, M., Machado, J., Osorio, J., Duarte, R., Santos, C.S., 2022. Non-essential elements and their role in sustainable agriculture. Agronomy 12, 888. https://doi.org/10.3390/agronomy12040888.

Nwankwo, C.E.I., Okeke, E.S., Umeoguaju, F.U., Ejeromedoghene, O., Adedipe, D.T., Ezeorba, T.P.C., 2025. Addressing emerging contaminants in agriculture affecting plant–soil interaction: a review on bio-based and nano-enhanced strategies for soil health and global food security (GFS). Discov. Toxicol. 2, 1–30. https://doi.org/10.1007/S44339-025-00018-W.

Orlandella, I., Fiore, S., 2025. Life cycle assessment of the production of biofertilizers from agricultural waste. Sustainability 17, 421. https://doi.org/10.3390/su17020421.

Othman, Y.A., Alananbeh, K.M., Tahat, M.M., 2024. Can arbuscular mycorrhizal fungi enhance crop productivity and quality in hydroponics? A meta-analysis. Sustainability 16, 3662. https://doi.org/10.3390/su16093662.

Pan, L., Cai, B., 2023. Phosphate-solubilizing bacteria: advances in their physiology, molecular mechanisms and microbial community effects. Microorganisms 11, 2904. https://doi.org/10.3390/microorganisms11122904.

Panda, A., 2022. Fungal biofertilizer: an alternative for sustainable agriculture. In: Shukla, A.C. (Ed.), Applied Mycology, Fungal Biology. Springer, Cham, pp. 287–346. https://doi.org/10.1007/978-3-030-90649-8_14.

Parmar, P., Kumar, R., Neha, Y., Srivatsan, V., 2023. Microalgae as next generation plant growth additives: functions, applications, challenges and circular bioeconomy based solutions. Front. Plant Sci. 14. https://doi.org/10.3389/fpls.2023.1073546.

Pasković, I., Popović, L., Pongrac, P., Polić Pasković, M., Kos, T., Jovanov, P., Franić, M., 2024. Protein hydrolysates - production, effects on plant metabolism, and use in agriculture. Horticulturae 10, 1041. https://doi.org/10.3390/horticulturae10101041.

Pei, B., Liu, T., Xue, Z., Cao, J., Zhang, Y., Yu, M., Liu, E., Xing, J., Wang, F., Ren, X., Zhang, Z., 2025. Effects of biofertilizer on yield and quality of crops and properties of soil under field conditions in China: a meta-analysis. Agriculture 15, 1066. https://doi.org/10.3390/agriculture15101066.

Pinho, S., Santos, C., Moniz, T., Granja, A., Sarraguça, M., Reis, S., Rangel, M., Vasconcelos, M., 2025. Novel polymeric nanoparticles as nanofertilisers for alkaline iron-deficient conditions. Plant Soil 1–21. https://doi.org/10.1007/S11104-025-07462-Y.

Pooja, P., Tallapragada, S., Saini, S., Punia, S., Janaagal, M., Kumar, V., Lamba, A., 2025. Exploring the potential of arbuscular mycorrhizal fungi as biofertilizers to enhance growth, nutrient acquisition and yield in chickpea genotypes under salinity stress. J. Soil Sci. Plant Nutr. 1–16. https://doi.org/10.1007/S42729-025-02497-7.

Priya, A.K., Alagumalai, A., Balaji, D., Song, H., 2023. Bio-based agricultural products: a sustainable alternative to agrochemicals for promoting a circular economy. RSC Sustain. 1, 746–762. https://doi.org/10.1039/D3SU00075C.

Rahman, MdH., Hasan, MdN., Nigar, S., Ma, F., Aly Saad Aly, M., Khan, MdZ.H., 2021. Synthesis and characterization of a mixed nanofertilizer influencing the nutrient use efficiency, productivity, and nutritive value of tomato fruits. ACS Omega 6, 27112–27120. https://doi.org/10.1021/acsomega.1c03727.

Rajesaheb, K.S., Subramanian, S., Boominathan, P., Thenmozhi, S., Gnanachitra, M., 2025. Bio-stimulant in improving crop yield and soil health. Commun. Soil Sci. Plant Anal. 56, 458–493. https://doi.org/10.1080/00103624.2024.2416925.

Rawat, P., Das, S., Shankhdhar, D., Shankhdhar, S.C., 2021. Phosphate-solubilizing microorganisms: mechanism and their role in phosphate solubilization and uptake. J. Soil Sci. Plant Nutr. 21, 49–68. https://doi.org/10.1007/s42729-020-00342-7.

Razauddin, Maji, S., Kumar, S., Yadav, G.C., Meena, R.C., Verma, S., 2025. The efficacy of nano fertilizer on yield and physico-chemical quality of okra fruit. J. Adv. Biol. Biotechnol. 28, 967–981. https://doi.org/10.9734/jabb/2025/v28i32155.

Roche, D., Rickson, J.R., Pawlett, M., 2024. Moving towards a mechanistic understanding of biostimulant impacts on soil properties and processes: a semi-systematic review. Front. Agron. 6, 1271672. https://doi.org/10.3389/FAGRO.2024.1271672.

Rodrigo, L., Munaweera, I., 2025. Employing sustainable agriculture practices using eco-friendly and advanced hydrogels. RSC Adv. 15, 21212–21228. https://doi.org/10.1039/D5RA03035H.

Rodríguez-Vázquez, R., Mesa-Marín, J., 2023. Plant responses to plant growth promoting bacteria: insights from proteomics. J. Plant Physiol. 287, 154031. https://doi.org/10.1016/j.jplph.2023.154031.

Rouphael, Y., Colla, G., 2020. Editorial: biostimulants in agriculture. Front. Plant Sci. 11. https://doi.org/10.3389/fpls.2020.00040.

Salama, D.M., Abd El-Aziz, M.E., Shaaban, E.A., Osman, S.A., Abd El-Wahed, M.S., 2022. The impact of nanofertilizer on agro-morphological criteria, yield, and genomic stability of common bean (*Phaseolus vulgaris* L.). Sci. Rep. 12, 18552. https://doi.org/10.1038/s41598-022-21834-9.

Salomon, M.J., Watts-Williams, S.J., McLaughlin, M.J., Bücking, H., Singh, B.K., Hutter, I., Schneider, C., Martin, F.M., Vosatka, M., Guo, L., Ezawa, T., Saito, M., Declerck, S., Zhu, Y.-G., Bowles, T., Abbott, L.K., Smith, F.A., Cavagnaro, T.R., van der Heijden, M.G.A., 2022. Establishing a quality management framework for commercial inoculants containing arbuscular mycorrhizal fungi. iScience 25, 104636. https://doi.org/10.1016/j.isci.2022.104636.

Santos, F., Melkani, S., Oliveira-Paiva, C., Bini, D., Pavuluri, K., Gatiboni, L., Mahmud, A., Torres, M., McLamore, E., Bhadha, J.H., 2024. Biofertilizer use in the United States: definition, regulation, and prospects. Appl. Microbiol. Biotechnol. 108, 511. https://doi.org/10.1007/s00253-024-13347-4.

Saurabh, K., Prakash, V., Dubey, A.K., Ghosh, S., Kumari, A., Sundaram, P.K., Jeet, P., Sarkar, B., Upadhyaya, A., Das, A., Kumar, S., Makarana, G., Kumar, U., Kumar, A., Singh, R.R., 2024. Enhancing sustainability in agriculture with nanofertilizers. Discov. Appl. Sci. 6, 559. https://doi.org/10.1007/s42452-024-06267-5.

Schütz, L., Gattinger, A., Meier, M., Müller, A., Boller, T., Mäder, P., Mathimaran, N., 2018. Improving crop yield and nutrient use efficiency via biofertilization - a global meta-analysis. Front. Plant Sci. 8, 2204. https://doi.org/10.3389/fpls.2017.02204.

Sharma, P., Sangwan, S., Kaur, H., Patra, A., Anamika, Mehta, S., 2023. Diversity and evolution of nitrogen fixing bacteria. In: Singh, N.K., Chattopadhyay, A., Lichtfouse, E. (Eds.), Sustainable Agriculture Reviews 60, Sustainable Agriculture Reviews. Springer, Cham, pp. 95–120. https://doi.org/10.1007/978-3-031-24181-9_5.

Sharma, S.B., Sayyed, R.Z., Trivedi, M.H., Gobi, T.A., 2013. Phosphate solubilizing microbes: sustainable approach for managing phosphorus deficiency in agricultural soils. SpringerPlus 2, 587. https://doi.org/10.1186/2193-1801-2-587.

Shoukat, A., Pitann, B., Zafar, M.M., Farooq, M.A., Haroon, M., Nawaz, A., Wahab, S.W., Saqib, Z.A., 2024. Nanotechnology for climate change mitigation: enhancing plant resilience under stress environments. J. Plant Nutr. Soil Sci. 187, 604–620. https://doi.org/10.1002/jpln.202300295.

Singh, K., Singh, R., Nwosu, N.J., Omara, P., Sharma, L., Dunn, B.L., Singh, H., 2025. Optimizing nutrient delivery in agronomic crops: a review of enhanced efficiency fertilizers. J. Plant Nutr. Soil Sci. 188, 570–584. https://doi.org/10.1002/jpln.12010.

Solovchenko, A., Verschoor, A.M., Jablonowski, N.D., Nedbal, L., 2016. Phosphorus from wastewater to crops: an alternative path involving microalgae. Biotechnol. Adv. 34, 550–564. https://doi.org/10.1016/j.biotechadv.2016.01.002.

Sufar, E.K., Hasanaliyeva, G., Wang, J., Bilsborrow, P., Rempelos, L., Volakakis, N., Baranski, M., Leifert, C., 2024. Effect of *rhizobium* seed inoculation on grain legume yield and protein content – a systematic review and meta-analysis. https://doi.org/10.20944/preprints202404.0344.v1.

Sun, W., Shahrajabian, M.H., Kuang, Y., Wang, N., 2024. Amino acids biostimulants and protein hydrolysates in agricultural sciences. Plants 13, 210. https://doi.org/10.3390/plants13020210.

Teshome, K., Aklilu, S., Zewdu, A., 2025. Impact of fertilization on antioxidant activity, microbiological quality, and sensory attributes of tomato (*Solanum lycopersicum* L.) cultivated in Ethiopia's central rift valley. Food Sci. Nutr. 13, e70609. https://doi.org/10.1002/fsn3.70609.

Ullah, A., Bano, A., Khan, N., 2021. Climate change and salinity effects on crops and chemical communication between plants and plant growth-promoting microorganisms under stress. Front. Sustain. Food Syst. 5, 618092. https://doi.org/10.3389/FSUFS.2021.618092.

United Nations Population Fund, 2023. State of world population 2023 - 8 billion lives, infinite possibilities: the case for rights and choices. State of World Population, 2023rd ed,. United Nations.

Verma, S.K., Kumar, P., Mishra, A., Khare, R., Singh, D., 2024. Green nanotechnology: illuminating the effects of bio-based nanoparticles on plant physiology. Biotechnol. Sustain. Mater. 1, 1–24. https://doi.org/10.1186/S44316-024-00001-2.

Wang, R., Liu, S., Ma, Z., 2023. Recent development of versatile polyphenol platforms in fertilizers and pesticides. J. Agric. Food Chem. 71, 9599–9608. https://doi.org/10.1021/acs.jafc.3c01952.

Wang, T., Sun, Y., Huang, H., Li, Z., Fan, H., Pan, X., Wang, Y., Cao, Y., Wang, K., Yang, L., 2025. The effect of selected phosphate-solubilizing bacteria on the growth of cotton plants in salinized farmlands. Microorganisms 13, 1075. https://doi.org/10.3390/microorganisms13051075.

Watts-Williams, S.J., Cavagnaro, T.R., 2018. Arbuscular mycorrhizal fungi increase grain zinc concentration and modify the expression of root *ZIP* transporter genes in a modern barley (*Hordeum vulgare*) cultivar. Plant Sci. 274, 163–170. https://doi.org/10.1016/j.plantsci.2018.05.015.

Wei, X., Xie, B., Wan, C., Song, R., Zhong, W., Xin, S., Song, K., 2024. Enhancing soil health and plant growth through microbial fertilizers: mechanisms, benefits, and sustainable agricultural practices. Agronomy 14, 609. https://doi.org/10.3390/agronomy14030609.

Wise, K., Selby-Pham, S., Selby-Pham, J., 2025. Modulation of antioxidant and anti-inflammatory metabolites in hemp (*Cannabis sativa*) seed via a biostimulant complex of molasses, Aloe vera extract, and fish hydrolysate. N. Z. J. Crop Hortic. Sci. 53, 3149–3162. https://doi.org/10.1080/01140671.2025.2519571.

Wu, S., Shi, Z., Chen, X., Gao, J., Wang, X., 2022. Arbuscular mycorrhizal fungi increase crop yields by improving biomass under rainfed condition: a meta-analysis. PeerJ 10, e12861. https://doi.org/10.7717/peerj.12861.

Wu, Y., Chen, C., Wang, G., 2024. Inoculation with arbuscular mycorrhizal fungi improves plant biomass and nitrogen and phosphorus nutrients: a meta-analysis. BMC Plant Biol. 24, 960. https://doi.org/10.1186/s12870-024-05638-9.

Yadav, A., Yadav, K., Abd-Elsalam, K., 2023. Nanofertilizers: types, delivery and advantages in agricultural sustainability. Agrochemicals 2, 296–336. https://doi.org/10.3390/agrochemicals2020019.

Zhang, L., Wu, Z., Zhou, J., Zhou, L., Lu, Y., Xiang, Y., Zhang, R., Deng, Q., Wu, W., 2022. Meta-analysis of the response of the productivity of different crops to parameters and processes in soil nitrogen cycle under biochar addition. Agronomy 12, 1857. https://doi.org/10.3390/agronomy12081857.

Zhao, G., Zhu, X., Zheng, G., Meng, G., Dong, Z., Baek, J.H., Jeon, C.O., Yao, Y., Xuan, Y.H., Zhang, J., Jia, B., 2024. Development of biofertilizers for sustainable agriculture over four decades (1980–2022). Geogr. Sustain. 5, 19–28. https://doi.org/10.1016/j.geosus.2023.09.006.