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Navigating complex agricultural challenges: harnessing microbial solutions for sustainable growth and resilience

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This study explores the potential of Cell-Free Supernatants (CFSs) derived from beneficial bacteria as a sustainable solution to enhance crop resilience in the face of environmental stress. In the context of climate change and soil salinity, CFSs emerge as a promising tool to mitigate crop losses and safeguard food security. By employing bioactive compounds extracted from microbial cultures, CFSs offer a reliable approach to support plant growth and fight abiotic stressors. The research emphasizes the effectiveness of CFSs in promoting seed germination and improving overall plant health, particularly under salinity stress. Additionally, it highlights the role of CFSs in enhancing nutrient absorption and improving plant defense mechanisms, contributing to agricultural sustainability. Despite technical limitations associated with microbial formulations, CFSs provide an alternative to conventional methods, presenting scalable and eco-friendly solutions. Among various production methods of the CFS, centrifugation only and centrifugation plus 0.22 µm filtration stand out due to their simplicity, and efficiency. However, the absence of field-level studies reveals a critical research gap, necessitating further evaluation of CFS performance under real agricultural conditions. Through collaborative research works and innovative application methods, CFSs hold the potential to transform modern agriculture, ensuring resilient crop production systems and global food security for generations to come.

KEYWORDS

cell-free supernatants, crop resilience, environmental stress, sustainable agriculture, microbial formulations, global food security

1 Introduction

Numerous agricultural systems have witnessed heightened crop productivity through the use of synthetic fertilizers, which effectively lowers costs and maximizes yields. However, environmentalists' express concerns that without action to mitigate fertilizer use, we risk creating an unsustainable situation in the long term, leading to an increased agricultural carbon footprint and elevated environmental compliance costs. These concerns have prompted a global shift towards more sustainable crop production approaches (Dhankher and Foyer, 2018; Pareek et al., 2020). In recent decades, bioactive natural products have been viewed as a positive approach, with the utilization of these eco-friendly compounds/materials in agriculture showing promise due to their low cost and potential for enhancing crop yield and quality. Biofertilizers, composed of active microbes, have emerged as cost-effective and eco-friendly alternatives to chemical-based fertilizers, being widely distributed in soil and capable of inducing specific desirable plant functions (Hug et al., 2020; Naamala and Smith, 2020).

Beneficial microbes, particularly Plant Growth-Promoting Rhizobacteria (PGPR), play essential roles in supporting plant growth, enhancing nutrient uptake, regulating phytohormone levels, and helping plants tolerate abiotic environmental stresses such as salinity, drought, and temperature fluctuations (Rai et al., 2020; Chauhan et al., 2021; Riaz et al., 2021; Khoshru et al., 2020; Parameswaran et al., 2021). However, the performance of live microbial biofertilizers in the field is often inconsistent due to variable environmental conditions (Rilling et al., 2019) and competition from other microbes already at the site of application.

Beneficial microbes, particularly Plant Growth-Promoting Rhizobacteria (PGPR) constitute sustainable crop production inputs able, among other things to help mitigate the effects of climate change related stresses and to enhance uptake of atmospheric CO_2 by plants (Khoshru et al., 2020; Rai et al., 2020; Chauhan et al., 2021; Parameswaran et al., 2021; Riaz et al., 2021). However, there is a need to make their effects as consistent and as large as possible (Rilling et al., 2019). Microbial biostimulants, especially PGPR cell-free supernatants (CFSs) and isolated metabolites from the CFSs, have recently gained attention as tools to help plants withstand abiotic and biotic stresses. Specifically, these substances offer novel opportunities to promote tolerance to adverse environmental conditions during critical crop growth stages (Pellegrini et al., 2020; Li et al., 2021).

Soil salinization is a prominent abiotic stress that hampers plant functions and disrupts crop growth and yield on a global scale. Salinity reduces the plant's water absorption capacity, creating drought-like conditions and impeding growth through osmotic stress. In addition, saline stress often leads to ion toxicity due to imbalances in cytosolic nutrients, mainly excess sodium (Na^+) and chloride (Cl^-) accumulation. Another consequence is the heightened synthesis and accumulation of reactive oxygen species (ROS) under salinity stress, causing oxidative stress, cellular damage, and ultimately cell death (Assaha et al., 2017; Isayenkov and Maathuis, 2019). Despite these challenges, plants have evolved an efficient network of ROS scavenging/detoxifying systems. This detoxification process involves nonenzymatic or enzymatic antioxidants (Pang and Wang, 2008). The ability of beneficial plant-associated bacteria from saline and arid environments to develop unique evolutionary adaptations with plants for coping with challenging conditions has gained significant attention (Etesami and Adl, 2020; Leontidou et al., 2020). For instance, Plant Growth-Promoting Rhizobacteria (PGPR) play crucial roles in scavenging ROS, enhancing enzymatic and nonenzymatic antioxidant activities during stress, and reducing ROS levels under abiotic stress conditions (Bharti and Barnawal, 2019; Kumar et al., 2020). Moreover, bioactive compounds produced by these beneficial microbes can stimulate crop production without the limitations faced by live microbial biofertilizers. These microbial-derived compounds are a diverse group of natural substances that contribute to the agricultural sector by enhancing resistance to biotic/abiotic stresses and acting as inter-organismal signals to improve symbioses with beneficial organisms (Naamala and Smith, 2021). Some studies highlight the positive effects of PGPR CFSs and isolated metabolites as biostimulants for enhancing plant health and growth under salinity stress (Naamala et al., 2022; Shah et al., 2022a). However, despite this evidence, considerably less attention has been directed towards utilizing PGPR-CFSs to develop eco-friendly bio-formulations for enhancing crop production under field conditions. These bioagents are designed to improve crop yield in actual fields. Despite the potential of PGPR-CFSs, using them in real-world field conditions hasn't been explored much. This calls for more in-depth research. This effort could uncover the full potential of these biostimulants and help advance sustainable farming by connecting lab discoveries with practical use.

1.1 Definition and characteristics of CFS and microbial metabolites

Plant Growth-Promoting Rhizobacteria (PGPR) CFSs refer to the extracellular liquids obtained after removing bacterial cells from a liquid culture—typically through centrifugation and filtration. These supernatants contain an array of microbial-derived compounds such as enzymes, phytohormones (like indole-3-acetic acid), volatile organic compounds, siderophores, and antibiotics, among others (Pellegrini et al., 2020; Naamala and Smith, 2021). CFSs can be derived from various PGPR genera, including *Bacillus*, *Pseudomonas*, *Devosia*, and *Rhizobium*, known for their efficacy in promoting plant growth and resilience.

The metabolites within these CFSs can be harvested during stationary or exponential growth phases, depending on the desired activity, and are usually concentrated or freeze-dried for agricultural applications. These bioactive metabolites are typically applied as seed treatments, foliar sprays, or soil amendments. The effective concentration varies depending on the crop species and environmental conditions, but studies often use dilutions ranging from 10% to 50% (v/v) or apply dry weights in the range of 50–200 mg L^{-1} (Naamala et al., 2022; Shah et al., 2022a; Monjezi et al., 2023).

These microbial products have been tested on various crops, including soybean, maize, canola, cassava, and pigeon pea, under different stress conditions like salinity, drought, and temperature extremes. The positive effects include enhanced seed germination, improved antioxidant enzyme activity, greater nutrient uptake, and increased biomass and yield (Buensanteai et al., 2013; Tewari et al., 2020; Monjezi et al., 2023). An overview of the bacterial strains' CFSs, their key metabolites, application methods, and corresponding crop responses is presented in Table 1.

TABLE 1 Summarizing the bacterial strains CFSs, their derived metabolites, modes of application, and crop responses.

PGPR strain	Source metabolite/ CFS	Crop	Stress condition	Application mode	Observed effects	Estimated change vs. control	Reference
Devosia sp. SL43	Cell-Free Supernatant (CFS)	Soybean	Salt stress	Seed priming	↑ Germination %, ↑ Seed vigor	19%, 318%	(Monjezi et al., 2023)
Bacillus amyloliquefaciens	CFS	Soybean, Corn	Salt stress	Seed priming	↑ Germination%, Radicle length	Soybean: +39–49%, Corn: +25–38%	(Naamala et al., 2022)
Bradyrhizobium sp. IC-4059	CFS + EPS	Pigeon pea	Field conditions	Seed + soil application	↑ Growth and nodulation:	Root (+30%), shoot (+20%), nodules (+100%)	(Tewari et al., 2020)
Devosia sp.	CFS	Canola, Soybean	Salt stress	Seed priming	↑ Germination%	Canola: 54%, soybean: 19%	(Shah et al., 2022a)
Bacillus sp. CaSUT007	CFS (extracellular proteins & hormones)	Cassava	Normal	Soil application	↑ Root/shoot length, ↑ Biomass	30%, 25%	(Buensanteai et al., 2013)
Bacillus vallismortis RHFS10	CFS	*In vitro*	Pathogen stress	–	↓ *Macrophomina phaseolina*, ↑ Disease resistance	90% more effective than chemical fingicide	(Castaldi et al., 2021)
Pseudomonas spp.	CFS/metabolites	Multiple crops	Biotic stress	Soil amendment	↑ Pathogen suppression, ↑ Growth promotion	Descriptive review	(Pellegrini et al., 2020)

↑, ↓ , indicate increase and decrease, respectively.

2 Intersecting pressures: climate change, agricultural stress, and population growth

Clear evidence shows that climate change is happening, bringing various effects such as higher temperatures, drought and rising sea levels. The levels of these changes to date indicate a faster warming of the Earth than initially thought. It's well-established that human activities are making this situation worse by releasing more greenhouse gases (GHGs), strengthening the greenhouse effect in the earth's atmosphere. This disturbance in the natural balance causes the atmosphere to trap more heat, leading to significant changes in the global climate system (Ahmad et al., 2010; Corwin, 2021).

The effects of climate change, especially on crops, have become more significant in recent times. Abiotic stresses, such as water shortages, temperature extremes, waterlogging, and soil salinity, pose challenges for modern crop production. These issues disrupt the growth of crops, affecting their reproductive phases and ultimately reducing the harvest index (the proportion of grain yield to total above-ground biomass) and overall crop yield. The damage depends on factors like the crop's development stage, when the stress occurs, and how severe it is (Onu et al., 2019; Raza et al., 2019). In real-world agriculture, multiple stressors come together, making the effects more complicated and harmful than isolated stresses. This complex stress situation highlights the challenges crops face under field conditions (Pandey et al., 2015).

At the same time, the growing human population is putting more pressure on arable land. This population increase adds to the challenges for agriculture, involving both living (biotic) and non-living (abiotic) stresses. For instance, farmers often try to boost productivity by using more chemical fertilizers, pesticides, irrigation, and machinery. Ironically, this intensified farming may increase vulnerability to various stress factors. The expected increase in disturbances caused by climate change will worsen both biotic and abiotic stresses, making it more difficult for agriculture and weakening industrialized farming systems (Xie et al., 2019). Considering these factors, there's an urgent need to rethink agricultural strategies. A more comprehensive and integrated approach is crucial, taking into account the combined challenges of climate change and population growth.

The strategic use of natural agricultural biostimulants presents a promising solution for achieving multiple agricultural and environmental goals. By improving soil health, reducing greenhouse gas emissions, and enhancing nutrient-use efficiency, biostimulants can play a crucial role in the transition towards more sustainable and resilient farming systems. These agricultural biostimulants, such as plant growth-promoting rhizobacteria (PGPR), CFSs, seaweed extracts, and bioflavonoids, have become more popular as an eco-friendly method, which can help achieve the goals of reducing greenhouse gas (GHG) emissions and lowering the carbon footprint. Additionally, they improve the efficiency of nutrient use in plants. Combining and applying these natural biostimulants can enhance soil quality and further reduce GHG emissions. This approach not only supports sustainable farming but also promotes healthier crop growth. By improving soil structure and increasing microbial activity, biostimulants can enhance nutrient availability, leading to better root development and increased plant resilience against diseases and environmental stresses. Moreover, the use of these biostimulants can reduce the need for synthetic fertilizers and pesticides, which are often associated with negative environmental impacts. Natural biostimulants can also be considered a great boost for restoring degraded soils, making them more fertile and productive over time, and leading to higher crop yields and better food security, particularly in regions where soil degradation is a significant issue. In addition to their environmental benefits, natural biostimulants can also contribute to the economic sustainability of farming. By reducing the dependence on chemical inputs, farmers can lower their production costs and increase their profitability. Furthermore, the use of biostimulants can open up new markets for organic and sustainably produced crops, meeting the growing consumer demand for environmentally-friendly products (Pandey et al., 2015; Pellegrini et al., 2020; Naamala et al., 2022; Shah et al., 2022a, 2022b; Zhao et al., 2023).

2.1 Understanding how plants deal with stress: impact on global agriculture

Plants, being stationary, can't move away from harsh conditions caused by either abiotic or biotic factors. Abiotic factors like extreme temperatures, drought, floods, heavy metals, UV radiation, and salinity stress weaken plants, making them more prone to diseases and pests. This vulnerability leads to significant drops in crop yields worldwide. Salinity, especially, is a major stressor limiting global agricultural productivity (Sahab et al., 2021). Salinity is a primary abiotic stress affecting agriculture, significantly hindering crop growth globally. Around 830 million ha of agricultural land worldwide are affected by salinity, especially in arid and semi-arid regions with limited rainfall and high evaporation rates (Sahab et al., 2021; Wang et al., 2021). In these salty soils, high salt levels cause a lack of water and essential nutrients for plants. This can happen naturally or be worsened by human activities like improper irrigation and excessive chemical fertilizer use (Raza et al., 2019; Çatav et al., 2021; Wang et al., 2021). High salt levels also negatively affect the soil ecosystem, impacting processes in plants, microorganisms, and other underground organisms (Sahab et al., 2021). Concerningly, soil salinization is increasing more than researchers predicted, indicating a need for caution as salinity-related challenges might spread to new regions (Macdonald et al., 2021). In recent years, efforts have increased to find ways to manage soil salinity. Most focus on improving soil properties and organic matter, with some looking into plant-level solutions. Combining different techniques for salt management is suggested for better results (Sahab et al., 2021). Considering the interconnected nature of how plants respond to various stresses, including salinity, has proven valuable for studying plant stress defense mechanisms. The advantage lies in consistently applying and controlling salt stress levels in various controlled environments, such as laboratories, growth chambers, greenhouses, and similar facilities (Shavrukov, 2013).

3 Plant responses to saline soil: exploring mechanisms and strategies

Soil salinization harms plants, disrupting their processes. How plants respond to salinity stress varies based on factors such as species, genotype, growth stage, and environmental conditions. Seedling emergence, a crucial phase, is vulnerable to salinity stress across crops (Naamala et al., 2022; Yaghoubian et al., 2022). While growth stage is a key determinant of stress sensitivity, the other factors—plant species, genotype, and environmental conditions—also play significant roles in shaping plant responses to salinity. Different species and genotypes exhibit variable salinity tolerance due to inherent physiological and biochemical traits. For instance, halophytes like *Suaeda fruticosa* exhibit superior ion compartmentalization and osmotic adjustment compared to glycophytes such as soybean (Shah et al., 2022b). Environmental factors, such as light intensity and temperature, modulate plant metabolism and antioxidant activity under salt stress, thereby influencing the degree of damage or tolerance. In this context, understanding species-specific and genotype-dependent mechanisms, alongside environment-driven modulation, is critical for targeted stress management strategies.

Moreover, although this manuscript emphasizes salinity stress as a case study, the effects of PGPR and their CFSs extend to other abiotic stressors, such as drought, extreme temperature, and heavy metal toxicity. PGPR-derived compounds help maintain water homeostasis during drought by increasing root growth and accumulation of osmoprotectants (Ayuso-Calles et al., 2021). Under cold stress, compounds like lipo-chitooligosaccharides (LCOs) enhance seed germination and early vigor, especially in canola (Schwinghamer et al., 2015). In heat stress conditions, thuricin 17 has been shown to boost biomass and root growth (Lyu et al., 2020). In the context of biotic stress, PGPR-CFSs also act as biocontrol agents, triggering systemic resistance and suppressing pathogens such as *Macrophomina phaseolina* (Castaldi et al., 2021). A more holistic exploration of these applications is needed, and future studies should expand beyond salinity to harness PGPR potential across diverse environmental challenges.

Challenges in seed germination due to heightened salinity are multi-dimensional. Salinity interferes with water absorption by seeds due to elevated osmotic potential, hindering germination. Harmful sodium and chloride ions in saline conditions add another layer of hindrance. These factors reduce seed germination rates under high salinity stress (de Leija et al., 2022; Huang et al., 2022; Shah et al., 2022a), as studied by Safdar et al. (2019). As plants grow beyond the vulnerable seedling stage, they develop greater resilience to salinity stress (Shah et al., 2022b). However, the speed of seed germination and seedling establishment is crucial for determining crop yield, especially with stress factors like salinity. Signs of salt stress might not be apparent later on, yet they can result in lower crop yields. This is because the adverse effects of salinity can impact the plant's growth from an early stage, causing reduced final yields (Sabagh et al., 2021). Moreover, seeds facing challenges due to salinity may allow weeds to grow alongside or even faster than the main crop, resulting in a significant decrease in the final harvest (Arce et al., 2009). Extended exposure to salt stress significantly impacts various physiological and biochemical aspects of plants, reducing essential characteristics like leaf area, leaf water content, and photosynthetic pigments. This hampers overall photosynthetic capacity, causing a decrease in yield. These outcomes result from a complex interplay of factors, including nutritional imbalances, osmotic stress, ion effects, oxidative stress, and impaired water uptake from the soil. The cell wall becomes a primary site of salt stress effects, leading to significant changes in its physical properties (Pang and Wang, 2008; Raza et al., 2019; Çatav et al., 2021; Corwin, 2021).

The decline in photosynthesis, a crucial process in plant metabolism, in response to salt stress, is accompanied by an accumulation of reactive oxygen species (ROS). The oxidative stress-induced elevation of ROS harms plant physiology, causing the breakdown of chloroplast structure and a decrease in photosynthetic pigments (Zhao et al., 2021). In response to salinity stress, plants undergo metabolic reprogramming to maintain cellular equilibrium, involving changes in the production of primary and secondary metabolites, including proteins, responding to varying degrees of salt stress (Athar et al., 2022). The physiological shifts from salt stress exposure have far-reaching implications for plant morphological traits, affecting features like leaf area. These effects lead to a reduction in both crop yield quantity and quality. This becomes evident in the context of total leaf area reduction, a consequence of changes in cell wall regulations and integrity, leaf turgor, and photosynthetic rates. These changes negatively impact other morphological traits, including plant height, stem diameter, and root growth. Various investigations have shown the adverse negative effect of soil salinity on agronomic traits in soybean, encompassing height, stem diameter, leaf size and shape, biomass accumulation, pod count, and seed yield (Phang et al., 2008; Yu et al., 2019; Otie et al., 2021; Hasanuzzaman et al., 2022).

4 Harnessing biostimulants for enhanced plant growth and sustainable agriculture

Over the past few decades, cultivating agriculture using environmentally sustainable farming systems has become a significant challenge in the agricultural sector. Recently, there has been considerable focus on various biological substances and microorganisms known as plant biostimulants. These agents are used in agriculture to improve plant health, growth, and nutritional vigor. Plant biostimulants include beneficial fungi and bacteria, algal extracts, inorganic compounds, protein hydrolysates, humic substances, fulvic acid, and chitosan. The global biostimulant market has been steadily growing due to the favorable and environmentally friendly nature of these products, in contrast to synthetic agrochemicals, as documented by Dong et al. (2020); Sangiorgio et al. (2020), and D'Addabbo et al. (2019). In natural ecosystems, the well-being of most cultivated and wild plants is closely connected to the microbial organisms in the soil. These microorganisms have the potential to support plant growth and development by influencing hormone production, enzyme activities, signaling pathways, and various other mechanisms. Together, these factors help plants deal with both living and non-living environmental challenges. By promoting stress tolerance and resilience in plants, these mechanisms support plant growth. Additionally, the microorganisms associated with plants also play a role in making essential nutrients available through the release of complex substances, as explained by Sahab et al. (2021). Therefore, the need to create biostimulants based on microbes to lessen the negative effects of environmental stresses and ensure global food security is a significant concern. In this context, a top priority involves understanding the detailed interactions between plant roots and soil microorganisms. Elucidating and improving these interactions are crucial, not just for making agricultural systems work better, but also for keeping the soil healthy. Sangiorgio et al. (2020) and Etesami and Adl (2020) have provided valuable insights into these processes. Despite the promising use of microbial biostimulants as a smart alternative to regular chemicals in farming, there are some limitations that need careful consideration. These include issues like lower effectiveness compared to chemical alternatives and being more sensitive to environmental factors. The fact that outcomes can vary considerably among crops and locations emphasizes the need for more research. Therefore, making microbial biostimulants work better and having consistent results require collaborative scientific efforts, as highlighted by Lyu et al. (2021) and Sangiorgio et al. (2020).

5 Utilization of plant growth-promoting bacteria as biotechnological tools for alleviating abiotic stress in plants

The use of plant growth-promoting bacteria (PGPB) involves various types of bacteria that can independently team up with plants in specific ways. Those found around the roots are called plant growth-promoting rhizobacteria (PGPR) (Sansinenea, 2019). These bacteria are good at living on and in plant roots and in the nearby soil, helping plants grow better. The ways they help can vary depending on the specific plant they're working with. Importantly, the substances produced by these helpful bacteria not only boost plant growth by increasing nutrient availability or changing plant hormone levels but also have the potential to influence the entire plant's genetic activity (Rai et al., 2020). Traditional agriculture has often relied on using lots of chemicals to make crops grow more, but this can cause considerable environmental harm, as indicated by Ramakrishna et al. (2019).

Alternatively, using naturally occurring plant growth-promoting bacteria (PGPR) is an eco-friendlier approach. It not only helps plants grow better but also improves the health of the soil. This happens because these bacteria produce different substances that make important changes in the soil around the plant, like its pH, structure, and nutrient levels. So, this method has the potential to make agriculture more sustainable in the long run (Hu et al., 2018; Ramakrishna et al., 2019; Naamala and Smith, 2020). In addition, the microbiome, acting like the 'second genome' of plants, has a big effect on how plant genes work. It does this by releasing signal molecules that affect the host plant, making a significant impact on the plant's health and overall condition, including responses to stress factors. So, understanding and controlling the activities of the microbiota, especially the ones that help cultivated crops, can be very useful (Turner et al., 2013; Arif et al., 2020).

It's well-established that microbes closely linked with plant roots play a key role in boosting plant resilience to environmental stress. This helps in enhancing growth, yield, and nutrient absorption, especially when conditions are tough. This idea is supported by the research of Leontidou et al. (2020); Etesami and Adl (2020); Singh et al. (2019), and Mhatre et al. (2019). The microbial community around plant roots is known for its various contributions in diminishing the negative effects of salinity-induced stress. By regulating and adapting plant growth and development, these microbes help plants survive and thrive. So, using halo-tolerant PGPR on the intended plant species is a practical way to lessen the negative impacts of salinity-related challenges on plant growth, as explained by Leontidou et al. (2020). In simple terms, microbes that help plants grow in salty soils have various ways of doing it. They can directly improve plant growth under saline conditions, possibly by making growth-promoting hormones like auxins, cytokinins, and gibberellins. They might also reduce the levels of ethylene, a substance that hinders plant growth. PGPR's role in managing hormone levels, particularly reducing ethylene and its negative impact on plant growth in salty conditions, is a crucial part of how they work. At the same time, some helpful microbes boost bacterial auxin production or increase the plant's own auxin levels. This helps the main root grow longer and creates more lateral roots. Balancing ethylene and auxin in this way helps plants efficiently absorb water, ions, and nutrients when dealing with saline conditions (Spaepen and Vanderleyden, 2011; Zerrouk et al., 2016; Iqbal et al., 2017; Kumar et al., 2020; Eichmann et al., 2021; Park et al., 2021).

In saline soil, plants encounter a primary challenge known as osmotic stress, which disrupts water balance and stomatal gas exchange, consequently impeding the rate of photosynthesis. Addressing this issue strategically involves facilitating osmotic adjustment through the accumulation of water-soluble molecules. Halo-tolerant Plant Growth-Promoting Rhizobacteria (PGPRs) have the capacity to contribute to this mechanism by synthesizing compatible solutes or osmoprotectants, such as proline and glycine betaine. The synthesis and accumulation of these stress protectants enable plants to navigate the deleterious impacts of salinity-induced stress on growth, as corroborated by Ahmed et al. (2021); Ayuso-Calles et al. (2021); Nawaz et al. (2020), and Kumar et al. (2020). Furthermore, the adverse effects of soil salinity extend to the overproduction of reactive oxygen species (ROS), resulting in oxidative damage to vital biomolecules and even to cellular demise. Nonetheless, selectively chosen microbes exhibit the capacity to stimulate various antioxidant defense enzymes, including peroxidases, catalases, superoxide dismutases, glutathione reductases, and glutathione S-transferases. This orchestrated enhancement of antioxidant defense systems effectively counters the toxic effects of ROS in stressful environments, as underscored by Leontidou et al. (2020); Otlewska et al. (2020), and Gapińska et al. (2008).

5.1 Technical preparation and application methods for PGPR and their cell-free supernatants

Plant Growth-Promoting Rhizobacteria (PGPR) are typically isolated from rhizospheric soils or plant tissues and cultured in nutrient-rich media such as Luria-Bertani (LB) broth, Nutrient Broth (NB), Tryptic Soy Broth (TSB), or Yeast Mannitol Broth (YMB), depending on the bacterial species. The incubation temperature ranges from 28°C to 32°C, and the cultures are typically grown for 24–72 hours under shaking conditions (120–180 rpm) to achieve high cell density ($OD_{600} \approx 1.0$). Commonly used PGPR genera include *Bacillus, Pseudomonas, Azospirillum, Devosia, Rhizobium, and Bradyrhizobium* (Naamala and Smith, 2020; Basu et al., 2021).

PGPR are applied to crops via various methods, including seed coating, soil drenching, foliar sprays, or root dips. Application rates vary with method and strain but typically range from 10^7 to 10^9 CFU mL^{-1} for inoculation. These microbes have been widely studied in crops like soybean, maize, canola, wheat, tomato, cassava, and rice, among others.

To obtain CFSs, bacterial cultures are centrifuged at 8,000–12,000 rpm for 10–20 minutes at 4°C to pellet cells. The supernatant is then filtered (usually with 0.22 µm filters) to remove residual cells. In some protocols, cell lysis techniques like ultrasonication, freeze-thaw cycles, or enzymatic treatment are applied to release intracellular metabolites before filtration (Naamala et al., 2022; Shah et al., 2022a).

CFSs are rich in bioactive metabolites, including phytohormones (e.g., indole-3-acetic acid), volatiles, siderophores, enzymes, antimicrobial peptides, and lipo-chitooligosaccharides (LCOs). These components help enhance nutrient uptake, stress tolerance, and pathogen resistance in plants. The supernatants are either used fresh or preserved through freeze-drying, spray drying, or cold storage (4°C) with stabilizers to prolong shelf-life (Pellegrini et al., 2020). An integrated overview of the biochemical and physiological mechanisms triggered by CFS in plants is illustrated in Figure 1.

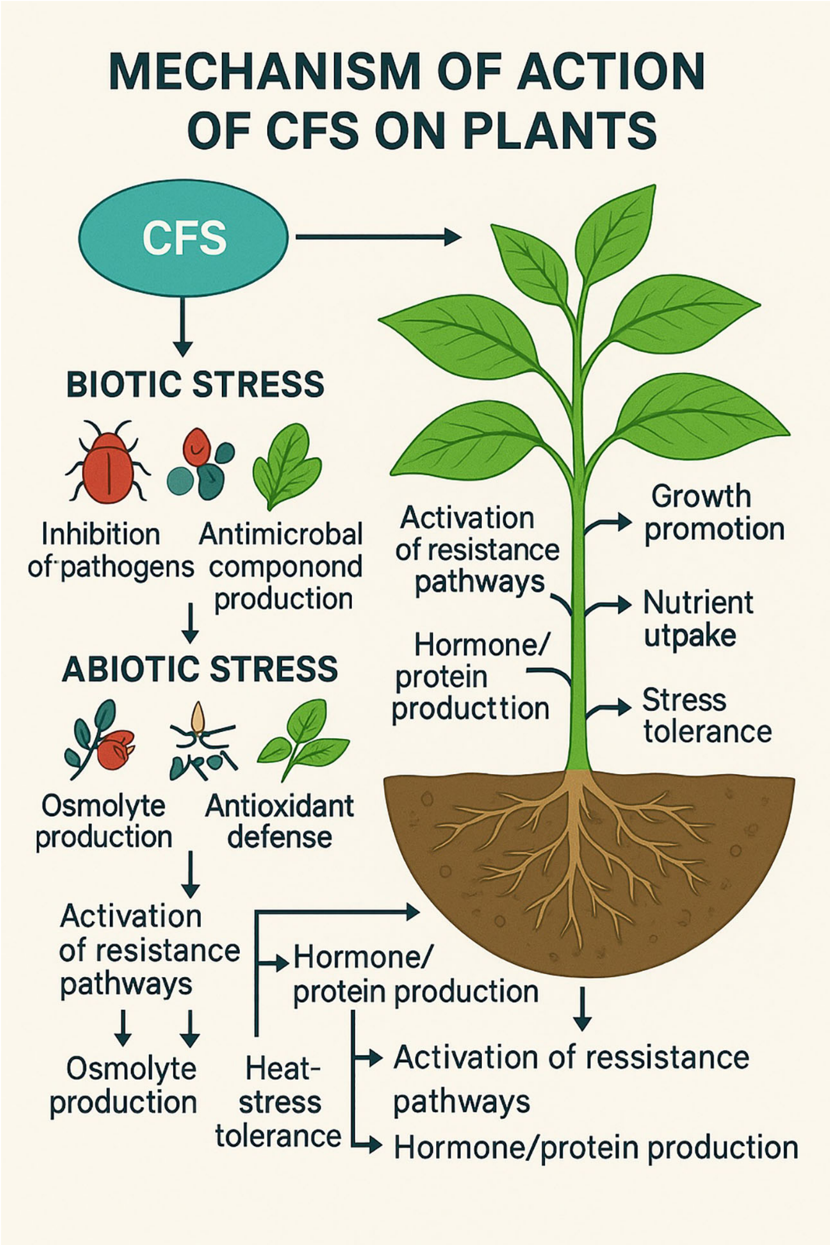

FIGURE 1
Mechanisms by which cell-free supernatants enhance plant performance under biotic and abiotic stress conditions.

For field use, CFSs can be applied via seed priming, soil application, or foliar spray, typically at concentrations ranging from 5% to 50% (v/v) or 50 to 200 mg L^{-1}, depending on the crop, growth stage, and environmental conditions. CFS treatments have shown strong performance under salinity, drought, heat, and pathogen pressure, especially in soybean, maize, and canola (Tewari et al., 2020; Monjezi et al., 2023).

This practical knowledge is vital for translating lab-scale benefits of PGPR and their metabolites into field-applicable bioformulations, helping ensure consistency and effectiveness in diverse agricultural systems. A comparison of various methods used for the production of CFSs is provided in Table 2, outlining their respective advantages, constraints, and potential applications in agricultural settings.

6 Field applications of CFSs: emerging evidence and future prospects

Although the majority of studies on CFSs have been conducted under laboratory and greenhouse conditions—where CFSs have demonstrated beneficial effects on seed germination, plant growth, and stress tolerance—recent research has begun to provide evidence of their efficacy under field conditions. For example, the application of a biosurfactant-rich CFS from Bacillus subtilis significantly reduced black scurf disease incidence in potato by 50% in a field setting (Hussain and Khan, 2020). Similarly, concentrated metabolites derived from Rhizobium tropici and *Bradyrhizobium*

TABLE 2 Comparative summary of commonly used methods for the preparation of CFSs from plant growth-promoting rhizobacteria, highlighting their advantages, limitations, and suggested applications.

CFS production method	Advantages	Limitations	Suggested applications	Reference
Centrifugation only	Simple, fast, scalable method for large volumes	May retain residual cells or cell debris	Quick preparation for field use	(Alori et al., 2025)
Centrifugation + 0.22 µm filtration	Produces highly purified CFS; removes all microbial cells and debris	Requires more time, sterile equipment, higher cost	Laboratory assays, formulation development	(Subramanian et al., 2021)
Heat or pH shock treatments	Stimulates bacterial secretion of bioactives under stress conditions	Risk of denaturation or altered activity of metabolites	Experimental screening, stress-responsiveness studies	(Chaiharn and Lumyong, 2011)
Solvent extraction/precipitation	Can isolate specific metabolites selectively	Involves chemicals; potential loss of bioactivity	Targeted metabolite profiling	(Santoyo et al., 2016)
Lyophilization (freeze-drying)	Enables long-term storage; preserves activity	Requires freeze-dryer; may need reconstitution	Storage and transport of CFSs	(Sornsenee et al., 2021)

diazoefficiens enhanced grain yields of maize and soybean in multi-location field trials (Marks et al., 2013). Furthermore, a combinational bioformulation comprising Bradyrhizobium cells, its CFS, and exopolysaccharides led to significant improvements in pigeon pea growth and nodulation under field conditions (Tewari et al., 2020). These findings highlight the promising potential of CFS-based products in real-world agricultural systems. However, to fully realize this potential, further well-replicated and crop-specific field trials are needed to assess the consistency, scalability, and economic viability of CFS applications across diverse agroecological zones.

7 Comparative analysis of microbial inoculants and extracellular bioactive compounds: evaluating pros and cons

The utilization of beneficial microorganisms to enhance plant growth and alleviate environmental stresses has garnered significant attention in agricultural research. However, despite substantial evidence highlighting the potential of microbe-based fertilizers and growth enhancers, their practical application on commercial farms faces several limitations. These constraints lead to inconsistencies in plant responses to microbial interventions, especially in the presence of unpredictable and adverse environmental conditions in croplands. Therefore, addressing these challenges is crucial to achieving consistent and reliable outcomes when implementing live beneficial microbes in real-world field conditions, which encompass diverse soils, crops, and climatic nuances (Rilling et al., 2019; Naamala and Smith, 2020; Tewari et al., 2020). The effectiveness of plant growth-promoting rhizobacteria (PGPR) in soil inoculations can face challenges due to various factors, particularly soil properties influencing microbial colonization and the expression of their biocontrol mechanisms. Abiotic features, including soil pH, texture, moisture content, temperature, oxygen levels, and nutrient availability, intricately affect PGPR colonization and the display of their beneficial traits. Temperature plays a crucial role as it influences microbial growth rates and enzymatic activities, impacting the diversity of biostimulants produced by PGPR. Soil moisture content is another crucial determinant, shaping microbial growth dynamics and functional diversity. Changes in soil water content can hinder successful PGPR inoculation; insufficient water can limit microbial growth, while excess moisture can create anaerobic conditions, hampering PGPR activities (Clark et al., 2009; Borowik and Wyszkowska, 2016; Liu et al., 2025). Additionally, soil pH significantly influences the composition and diversity of beneficial soil microorganisms. Even slight deviations from the optimal pH range can cause shifts in microbial biostimulant composition, potentially undermining the benefits of microbial inoculants for plant production (Kaur et al., 2019; Wang et al., 2022).

Moreover, the performance of PGPR is influenced by biological constraints, with specific root-secreted compounds regulating interactions with various biotic and abiotic components of the environment. The nature and magnitude of these root-secreted compounds vary with soil properties, nutrient availability, plant age, and physiological state. These compounds act as mediators of plant-microbe associations, ultimately affecting the efficacy of microbial inoculants (Bais et al., 2006). Technical challenges also pose significant hurdles in the application of PGPR. As living formulations, these biofertilizers require precise storage conditions at appropriate temperatures and durations to maintain viability. Ensuring the survival of these microbes during production, distribution, and storage is crucial, as the shelf-life of microbial inoculants is often shorter than that of chemical fertilizers, leading to potential financial losses (Ngampimol and Kunathigan, 2008; Brar et al., 2012; Arriel-Elias et al., 2018; Basu et al., 2021).

In response to these limitations, the use of CFSs derived from beneficial bacteria has emerged as a promising approach. These extracellular bioactive compounds offer an innovative solution that addresses various challenges associated with PGPR application.

Extracted from broth cultures through various techniques, these compounds can provide alternative methods for enhancing crop production and addressing the variability of environmental conditions. Importantly, CFS technologies avoid reliance on specific microbial strains, potentially yielding more consistent results, especially under varying conditions imposed by climate change (Naamala and Smith, 2020; 2021). In conclusion, the implementation of microbial inoculants and extracellular bioactive compounds involves a complex interplay of factors that determine their efficacy and viability within agricultural contexts. Overcoming the challenges posed by environmental variability, soil properties, and technical constraints requires a comprehensive understanding of these factors. Innovative approaches such as CFSs hold promise in mitigating the limitations associated with microbial interventions in modern agriculture.

While CFSs have emerged as a promising alternative to live microbial inoculants, their use is not without limitations. One key disadvantage is the short-lived nature of their effects, as CFSs lack the ability to replicate and sustain long-term interactions in the rhizosphere, unlike live PGPR which can colonize and adapt dynamically to their environment (Naamala and Smith, 2021). This can result in a limited duration of biostimulatory or biocontrol activity, necessitating repeated applications or complementary strategies such as slow-release formulations.

Furthermore, although CFSs eliminate certain challenges associated with microbial viability, their activity is still influenced by soil physicochemical properties, including pH, texture, organic matter content, moisture levels, and temperature. These factors can affect metabolite stability, diffusion rates, and interaction with root exudates, ultimately shaping their efficacy (Pellegrini et al., 2020; Castaldi et al., 2021). For instance, high soil pH or excessive clay content may bind or degrade bioactive compounds, while extreme moisture fluctuations can alter the bioavailability of applied metabolites, similarly to how they impact PGPR colonization.

Therefore, the claim that CFSs are categorically "better" than PGPR inoculants under stress-prone field conditions must be viewed contextually, rather than universally. In some environments, particularly where soil microbial competition, shelf-life concerns, or colonization failures hinder PGPR efficacy, CFSs may offer practical advantages. However, under conditions where sustained, root-associated activity is critical, traditional PGPR inoculation may remain superior. A combined or integrated approach—such as co-application of live PGPR with their CFSs or encapsulated metabolites—could provide synergistic benefits, offering both immediate and prolonged effects while buffering environmental variability. A comparative overview of PGPR and their CFSs regarding application requirements, risks, and modes of action is illustrated in Figure 2.

However, despite the promising attributes of PGPR-derived CFSs, several challenges remain that may limit their large-scale agricultural application. For instance, bioactive metabolites within CFSs are prone to degradation in soil due to microbial activity, UV radiation, and abiotic factors, potentially reducing their efficacy (Yakhin et al., 2017; Woo and Pepe, 2018). Moreover, the composition and concentration of metabolites can vary depending on microbial strain, growth phase, and medium conditions, complicating standardization (Vurukonda et al., 2016). From a practical perspective, large-scale production and formulation of stable and cost-effective CFS-based biostimulants also remains a bottleneck (Berg et al., 2020). These limitations underscore the need for further research to optimize formulations, evaluate long-term field performance, and assess the economic viability of CFS applications.

8 Cell-free supernatants as biostimulants and biocontrol agents: a promising path for agricultural enhancement

The search for sustainable ways to boost plant growth has led to interest in organic biostimulants. These compounds provide a practical way to strengthen plant development, whether applied to seeds, young plants in the soil, or through sprays on leaves. The recent emergence of Cell-Free Supernatants from plant growth-promoting rhizobacteria (PGPR-CFSs) is a new approach with the potential to offer many benefits to plants. Plants recognize and respond to these CFSs, which act as facilitators for resource acquisition, protection against pathogens, and triggers for growth mechanisms related to the specific microorganism involved (Naamala and Smith, 2020; Monjezi et al., 2023). Microbes produce compounds that, while not always necessary for direct growth, can work in a stimulus-response system. Various stimuli, both well-known and less understood, trigger the activation of hidden gene clusters in microorganisms, resulting in the creation of useful compounds. This collection includes antibiotics, pigments, growth hormones, and signaling molecules between organisms, all positively linked to the production of valuable secondary metabolites (Singh et al., 2019; Naamala and Smith, 2021). Furthermore, CFSs not only aid in plant growth and health but also help maintain populations of PGPR, including rhizobia, by promoting the growth of the host plants on which these microorganisms rely (Tewari et al., 2020).

8.1 CFSs in mitigating abiotic stress

Research findings emphasize the potential of compounds derived from bacteria in enhancing plant growth across various stages of development, from seed germination to crop maturation. This is especially relevant in challenging conditions, such as salinity stress. Studies demonstrate the germination-promoting abilities of different microbial CFSs under salt stress. For instance, cell-free supernatants from salt-tolerant *Bacillus* strains have proven effective in improving corn germination and seedling growth under salinity stress (Naamala et al., 2022; Yaghoubian et al., 2022). Similarly, the combined application of flavonoids and cell-free supernatants from *Devosai* sp. has been observed to boost canola and soybean seed germination, particularly in high salt stress conditions (Shah et al., 2022a).

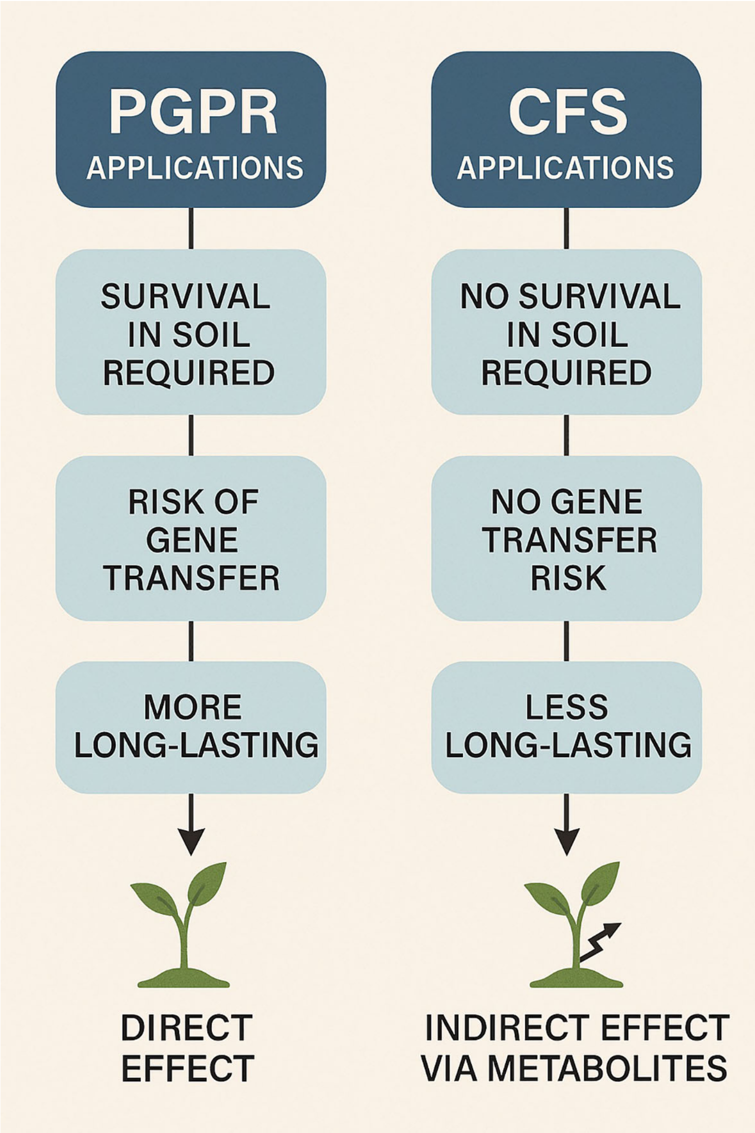

FIGURE 2
A visual comparison between PGPR and CFS-based applications, highlighting differences in survival, biosafety, durability, and mode of action.

Metabolites produced by rhizobial cells positively impact the growth and grain yield of maize and soybean plants (Marks et al., 2013). Tewari et al. (2020) explain the effectiveness of a treatment involving *Bradyrhizobium* sp. IC-4059, its cell-free culture supernatant, and exopolysaccharides (EPS) in promoting pigeon pea growth, not only in initial stages but also throughout later plant development. Buensanteai et al. (2013) demonstrated the growth-enhancing impact of phytohormones and extracellular proteins in the CFS of *Bacillus* sp. strain CaSUT007 broth cultures, leading to significant increases in cassava root and shoot lengths, as well as biomass production. In a recent study by Monjezi et al. (2023), the efficacy of CFS derived from a *Devosia* strain was further confirmed. Specifically, the CFS from *Devosia* sp. strain SL43 was investigated for its potential to improve soybean (*Glycine max* L.) seed vigor index and final germination, mitigating the detrimental impacts of salt stress. These findings highlight the significant positive effects of microbe-based CFS, emphasizing its ability to alleviate stress on plants and provide valuable insights into how microbial-derived compounds can be potent tools for enhancing plant resilience and productivity, especially in challenging environmental conditions.

Two significant signal compounds, lipo-chitooligosaccharides (LCOs) and thuricin 17, have emerged as better characterized players in influencing plant responses to various environmental stresses. These compounds have garnered attention for their potential to enhance plant resilience to stressful conditions. LCOs, acting as inter-organismal signals during the establishment of the legume-rhizobia nitrogen-fixing symbiosis, display remarkable abilities. They not only induce the formation of nitrogen-fixing nodules in leguminous host plants but also orchestrate a cascade of responses that contribute to plant adaptability to changing conditions. Similarly, thuricin 17 plays a potent role, enriching the spectrum of plant responses to a range of abiotic stressors (John

McIver et al., 2007; Lee et al., 2009; Gough and Cullimore, 2011; Schwinghamer et al., 2015; Tanaka et al., 2015; Subramanian et al., 2016; Nazari and Smith, 2020). As observed in the study of Lyu et al. (2020), thuricin 17 acts as a constitutive agent, enhancing the plant stress resilience. Schwinghamer et al. (2016) validated these findings, demonstrating the tangible consequences of thuricin 17 and LCOs in saline and temperature stress conditions. Their research highlighted positive outcomes, leading to increased biomass production and the robust establishment of root systems, with clear implications for overall plant vitality. In a parallel revelation, the influential impact of LCOs became evident as they significantly influenced the rate and uniformity of canola seed germination under stressfully low temperature conditions—a crucial attribute for successful early spring sowing, initial crop establishment and agricultural productivity (Schwinghamer et al., 2015). These diverse signal compounds contribute depth to the narrative of plant growth, acting as conductors of intricate biochemical symphonies that fortify the plant's physiological resilience against adversities. Their power to shape plant development and direct adaptive biochemical mechanisms offers an enticing avenue for scientific exploration and practical implementation in steering agricultural landscapes toward prosperity and sustainability. As we illuminate the complex details of these signal compounds, driven by their role in sculpting plant responses and adaptation, we embark on a promising path toward enhancing agricultural resilience to a wide range of stresses including those associated with climate change, nurturing productivity, and improving nutritional yields—while maintaining the integrity of our environment.

8.2 CFSs as biocontrol agents against pathogens

In addition to their effects on abiotic stress, CFSs have shown promise as biocontrol agents in combating plant pathogens. Ecological pressures stemming from excessive chemical pesticide usage to enhance plant growth under biotic stress conditions have underscored the urgency of substituting them with biopesticides. The utilization of CFSs in agriculture presents a promising avenue as a biocontrol agent against pathogens. Bacteria sourced from both domestic and undomesticated plants emerge as pivotal reservoirs of potential bioagents, owing to their varied adaptive mechanisms developed for endophytic survival (Miljaković et al., 2020; Oleńska et al., 2020). Castaldi et al. (2021) examined spore-forming bacteria from a salt-pan rhizobacterium for traits aiding plant growth and combating the plant pathogen *Macophomina phaseolina*. *Bacillus vallismortis* strain RHFS10 displayed potent antifungal effects, and its cell-free supernatants were effective at significantly lower inhibitory concentrations than a commercial fungicide, suggesting it as a promising, eco-friendly option for controlling the plant-harming fungus *M. phaseolina*. For example, numerous studies have highlighted the role of pathogen-antagonistic *Pseudomonas* types in disease reduction in soil. In this context, some studies found a connection between the quantity of *Pseudomonas* cells per gram of soil and the soil's disease-fighting capacity. They also discovered that diverse *Pseudomonas* strains, including those in varying environments, can generate compounds with varying effects on plant pathogens. A novel approach employing CFSs in the laboratory could aid in producing and applying the most effective compounds against pathogens, considering different environmental and soil conditions (Bhattacharjee et al., 2023; Khatri et al., 2023; Peng et al., 2023; Ranjan et al., 2023). A conceptual overview of how PGPR and their metabolites influence plant stress responses and agricultural sustainability is provided in Figure 3.

9 Conclusions

Dealing with climate change, agricultural stress, and a growing population requires a comprehensive approach. Climate change, with its rapidly developing and human-made conditions, causes problems like water scarcity and unpredictable temperatures, affecting crops. Meanwhile, the increasing global human population puts more pressure on essential resources, making these challenges more complex. While trying to boost agricultural productivity is an important goal, intensification of standard methods may have unintended consequences and trade-offs for the environment. Considering the complex interplay of factors, it is important to have a clear strategy that addresses multiple priorities. This involves adopting coordinated approaches to tackle the adverse effects of climate change and adjusting agricultural practices to meet evolving conditions. This comprehensive strategy aims to navigate the challenges posed by climate change, ensure food security, and sustainably manage resources amid population growth. Furthermore, plants face challenges, especially from non-living factors like extreme temperatures and soil salinity, complicating modern agriculture.

The increasing prevalence of soil salinity emphasizes the urgent need to address this challenge, which often surpasses, in severity, even the most advanced predictive models. Research efforts are therefore focused on developing versatile strategies, including innovative soil improvement techniques tailored to mitigate the extensive impacts of soil salinity. The story of sustainable and regenerative farming gets better with the increasing importance of plant biostimulants. Together, substances and microorganisms work to support plant health and encourage growth, all while aligning with the goal of preserving the environment. The organized progress and careful use of microbial-based biostimulants have the potential to contribute to global food security. However, the road ahead is filled with challenges that highlight the need for dedicated research efforts and a deep understanding of the complex relationships between plants and the various soil microorganisms.

Through collaborative scientific efforts, the improvement of biostimulant effectiveness and the cultivation of positive farming approaches global food security might be able to be maintained or increased in the face of climate change. In this a complex and detailed context, the idea of using plant growth-promoting bacteria (PGPB) emerges as a powerful approach to boost both plant growth

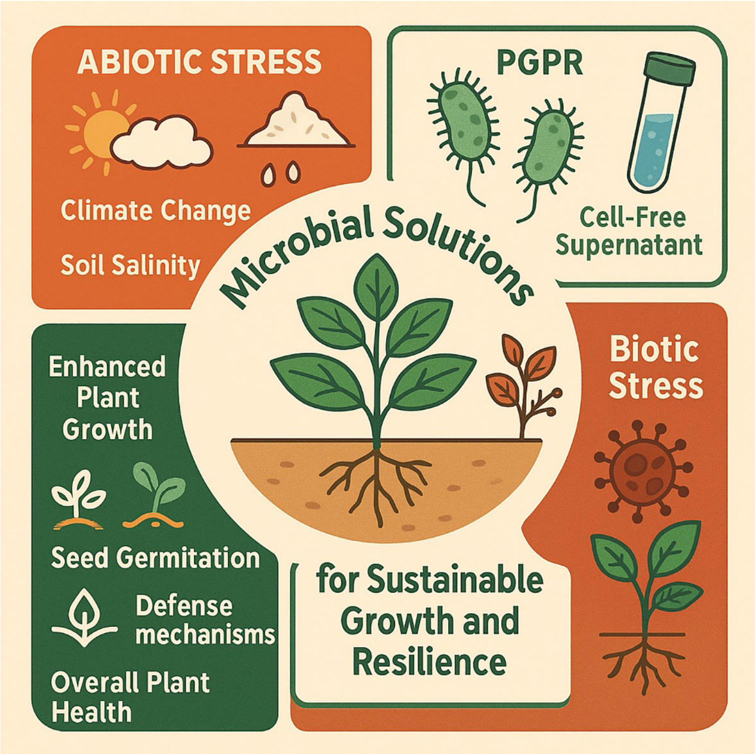

FIGURE 3
Conceptual representation of microbial-based solutions in sustainable agriculture. The schematic illustrates how plant growth-promoting rhizobacteria (PGPR) and their CFSs contribute to plant resilience by mitigating abiotic stresses (such as salinity, drought, temperature extremes) and biotic stresses (such as pathogen attacks). Beneficial microbial metabolites enhance seed germination, root development, nutrient uptake, and systemic resistance, promoting sustainable crop growth under challenging environmental conditions.

and the inherent resilience in agricultural systems. Among these helpful bacteria, PGPR play a key role, strategically positioned in the root area to coordinate various growth-enhancing mechanisms. This includes a symphony of actions, such as adjusting nutrient accessibility and working in harmony with the subtle regulation of gene expression in plants. Unlike traditional chemical methods, using PGPR strategically has the potential to increase yields and improve soil fertility. At the same time, these microorganisms influence the nearby rhizosphere environment, signaling a significant shift in modern agricultural practices. The significant impact of the microbiome in influencing gene expression highlights the depth of the symbiotic partnership that has the potential to reshape current agricultural approaches. The vital role played by PGPR in alleviating the harmful effects of stresses showcases their diverse capabilities. This involves coordinating growth processes that result in the production of stress-reducing substances, effectively counteracting oxidative stress and providing plants with an improved survival strategy in the face of adversity. Hence, the potential of using PGPR as a sustainable agricultural strategy seems very bright, outlining a path that is set to enhance crop production while carefully maintaining the overall ecological balance.

The use of beneficial microorganisms to enhance plant growth and mitigate environmental stress presents a promising avenue for sustainable agriculture. Among these, microbial CFSs have emerged as an innovative solution, offering many of the benefits of live microbes while overcoming limitations related to survival, colonization, and environmental variability. However, the practical implementation of these microbial strategies—whether using PGPR or their derived metabolites—requires careful consideration of local soil conditions, including pH, moisture, temperature, and nutrient availability. The complex interplay between plant, microbe, and environment necessitates a deep and nuanced understanding to achieve consistent results. While laboratory and greenhouse studies have reported encouraging effects of CFSs under abiotic stresses such as salinity and drought, their real-world application remains limited. This lack of field-based validation highlights a critical gap in the literature. To bridge this divide, future efforts must prioritize optimizing CFS production, formulation, and delivery systems, alongside conducting robust, replicated field trials. Ultimately, with continued interdisciplinary research and scientific collaboration, microbial biostimulants hold immense potential to transform agriculture by enhancing crop resilience, improving soil health, and contributing meaningfully to global food security.

Author contributions

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Conflict of interest

Author RL was employed by the company SeaPurAgro Inc.

The remaining authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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