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Encapsulated plant growth regulators and associative microorganisms: nature-based solutions to mitigate the effects of climate change on plants

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Abstract

Over the past decades, the atmospheric CO₂ concentration and global average temperature have been increasing, and this trend is projected to soon become more severe. This scenario of climate change intensifies abiotic stress factors (such as drought, flooding, salinity, and ultraviolet radiation) that threaten forest and associated ecosystems as well as crop production. These factors can negatively affect plant growth and development with a consequent reduction in plant biomass accumulation and yield, in addition to increasing plant susceptibility to biotic stresses. Recently, biostimulants have become a hotspot as an effective and sustainable alternative to alleviate the negative effects of stresses on plants. However, the majority of biostimulants have poor stability under environmental conditions, which leads to premature degradation, shortening their biological activity. To solve these bottlenecks, micro- and nano-based formulations containing biostimulant molecules and/or microorganisms are gaining attention, as they demonstrate several advantages over their conventional formulations. In this review, we focus on the encapsulation of plant growth regulators and plant associative microorganisms as a strategy to boost their application for plant protection against abiotic stresses. We also address the potential limitations and challenges faced for the implementation of this technology, as well as possibilities regarding future research.

Keywords:

biostimulants; seed priming; nanobiotechnology; plant growth-promoting rhizobacteria; plant growth regulators; microencapsulation

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1. Introduction

In recent decades, extreme events that characterize climate change have become increasingly frequent and intense around the world. This climate change has severely affected all life forms, including plants (O'Neill et al., 2017). Several climate models have demonstrated that the climate regulates the growth rate and distribution of plants, which might be altered by the combination of elevated CO₂ concentration and global warming (Pugnaire et al., 2019). Currently, the global average carbon dioxide is over 400 ppm and this value is expected to double by the end of this century (Buis, 2019; Lüthi et al., 2008). In addition, the temperature on Earth has risen at an average rate of 0.1 – 0.4 °C per decade since 1981 (IPCC, 2021; NOAA, 2021).

Climate change intensifies the abiotic stress factors that act over plants, with alteration in precipitation patterns leading to more frequent drought and flooding events, extreme temperatures, high wind speeds, and altered intensity and spectrum of ultraviolet radiation. The severity of climatic events is strongly influenced by biogeographical characteristics as well as by land use (Espeland and Kettenring, 2018). For example, land degradation and inherent susceptibility of certain ecosystems to climate change might be worsened by uncontrolled urbanization, intensive cropping, deforestation, and overgrazing. In developing countries, at least one quarter of the problems attributed to climate-related disasters are related to agricultural activity (FAO, 2015). Progressive and permanent changes are expected to occur in natural habitats, which will negatively affect the associated ecosystems, overall biodiversity, and plant fitness (Chiabai et al., 2018). In addition, several abiotic stresses can occur at the same time in the environment, and the interactions among them determine their effects on plants. These stresses vary according to their duration, severity, and nature (Figure 1).

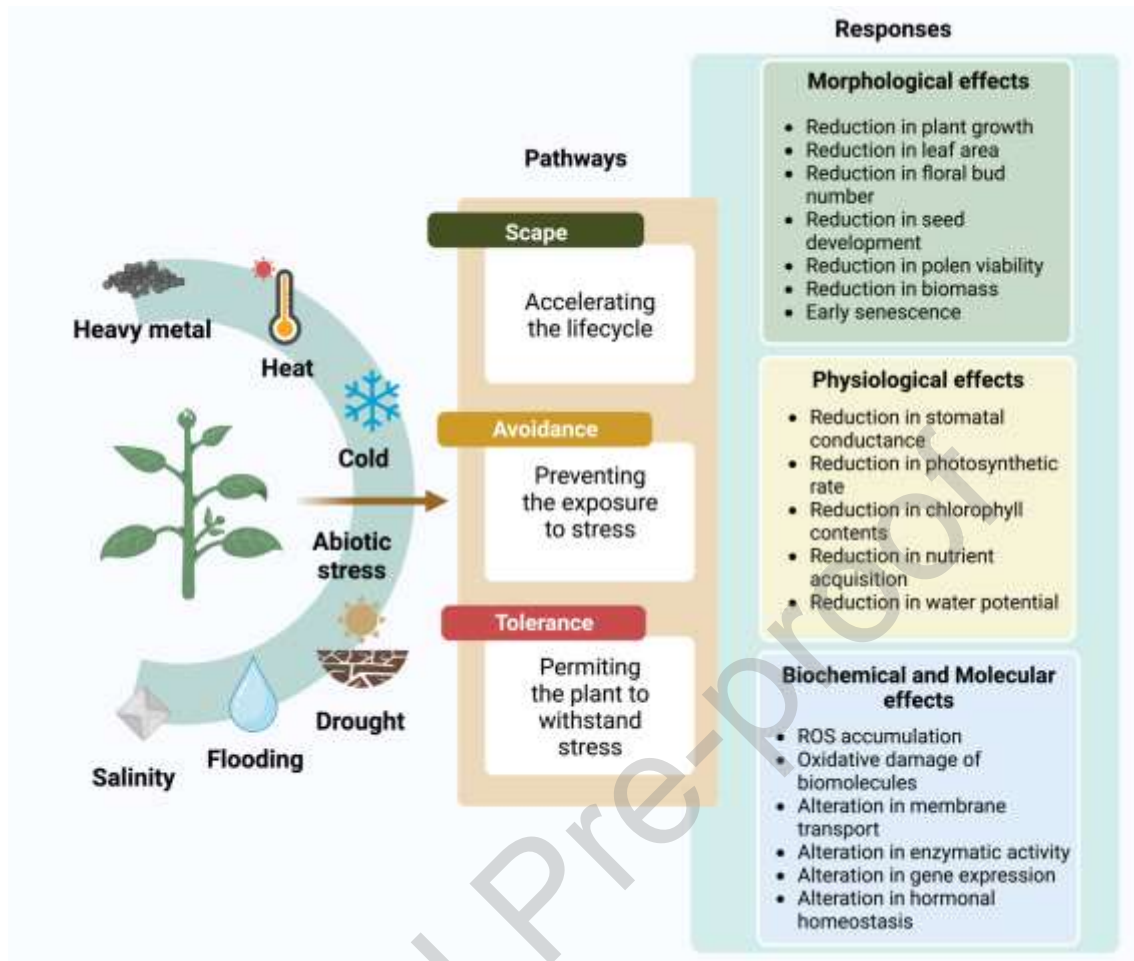


Figure 1: Effects of abiotic stress on plants. Plants under stress conditions can demonstrate different responses, which determine if they are resistant or susceptible to the stress. Plants under abiotic stress present changes at morphological, physiological, biochemical, and molecular levels in order to build an appropriate response to the stress condition. Created with BioRender.com

There are differences in the management of abiotic stress when dealing with plants of agricultural/forestry interest and native trees for ecosystem restoration. For the agronomical approach, the goal is to ensure that the plants are more resilient to climate change and at the same time have increased productivity. On the other hand, the ecological approach aims to maintain biodiversity and the associated ecosystems by promoting the survival of different plant species submitted to stresses of various characteristics. This approach is very important to establish tools and frameworks for ecosystem restoration programs around the world (Charrier et al., 2021; Chiabai et al., 2018).

Forests worldwide are key players in the mitigation of climate change, functioning as a sink that can compensate the emission of some greenhouse gases, and being responsible for approximately 46% of global terrestrial carbon flux. In addition, forests are key global regulators of atmospheric moisture and rainfall (Popkin, 2019). However, climate change has already negatively impacted many forest ecosystems around the world (e.g., by hampering plant growth rates, augmenting plant susceptibility to pests, altering species composition, and increasing the frequency of fire events), which reinforces the pressure that forests are under (Climate ADAPT, 2019). Implementation of reforestation programs with native tree seedlings is among the most effective approach for climate change mitigation. However, the number and quality of tree seedlings currently produced is not enough to meet reforestation demands. For example, it has been estimated that tree nurseries in the United States must double their seedling production to supply the reforestation programs across the country (Fargione et al., 2021).

Agriculture is the backbone of the economy of many countries (especially developing countries) and is highly dependent on the climate. During the last century, the crop yield has been increased by the use of high amounts of fertilizers and pesticides, as well as by genetic breeding and modification (Nowicka et al., 2018). However, these approaches are not sufficient to maximize agricultural production in face of climate change, which highlights the need for the development of innovative, sustainable strategies to minimize the effects of climate change on crops while decreasing side-effects on the ecosystem (Burgess et al., 2022).

Currently, several strategies are used to improve plant responses to stresses, such as chemical and biological priming. Priming is based on the preconditioning of the plant defense mechanisms against stresses, resulting in a faster, stronger, and more effective response against stresses. The use of biostimulants is increasing rapidly in agriculture since they show promise to increase crop productivity in a sustainable way (Rouphael and Colla, 2020). Biostimulants are defined as non-nutrient molecules or microorganisms, which have the ability to stimulate plant growth, yield, and plant fitness/health when applied at very low concentrations. Previous studies have shown that these compounds and/or microorganisms regulate different physiological processes, such as germination, photosynthesis, water balance, nutrient uptake and use, senescence, and the metabolism of plant growth regulators (Ahmad et al., 2022). There are several types of biostimulants, however, in the current review we will explore the

utilization of plant growth regulators and plant associative microorganisms for application in the cultivation of both crops and native trees (Lephatsi et al., 2022).

In spite of the known effects of the exogenous application of plant growth regulators to improve plant resistance to different stresses (Li et al., 2021), the premature loss of their biological activity due to environmental factors (such as UV radiation, temperature, humidity, and oxidative degradation) is one of the largest challenges for the agricultural applications of plant growth regulators (Pereira et al., 2019). Similarly, although several types of microorganisms have been proven to be effective for plant stress alleviation and growth promotion (Nephali et al., 2020), only a few formulations have reached the market, mainly due to the lack of reproducibility in the field of the results observed in laboratory and greenhouse conditions. This failure could be related to: i) loss of microorganism viability during the shelf storage or even during the treatment; ii) poor stability in the formulation or scarcity of methods to store the microorganisms without disrupting their microbial interactions; iii) incomplete or poor-quality formulation; iv) management practices (such as chemical inputs, fertilizers, tillage, etc.) that affect agricultural microbiomes through modifications of microbe-microbe and plant-microbe interactions; and v) competitiveness of the microorganism inoculated (Daisley et al., 2022; French et al., 2021; Vassilev et al., 2020).

In view of these bottlenecks in the application of biostimulants in agriculture and forest restoration, a promising alternative is their encapsulation (micro/nanoencapsulation) with different matrices (Jiménez-Arias et al., 2020), which is a widely used strategy for pesticide molecules (Bartolucci et al., 2022; Scott-Fordsmand et al., 2022). Through encapsulation it is possible to: i) create a favorable micro-environment for the molecule of interest and/or microorganism in order to reduce the loss of viability during storage and application; ii) reduce premature degradation of the molecule due to environmental factors as well as biodegradation by the microbiota after application; iii) provide sustained release of the molecule; and/or iv) help in the competition of the microorganisms with well-adapted native soil strains (Vassilev et al., 2020). In this review, we provide an overview of the micro/nanoencapsulation technique as a promising strategy for the improvement of biostimulant formulations, aimed at expanding their commercialization in the market. We also highlight the bottlenecks that should be addressed to achieve this goal.

2. Plant Growth Regulators

Climate change resulting from anthropogenic activities represents a major challenge for plant survival, since plants are sessile organisms that are prone to the effects of environmental fluctuations (EL Sabagh et al., 2022; Zeng et al., 2021). Allied to this, the excessive use of agrochemicals contributes to the contamination of natural soil resources and may further hinder plant growth and development (Fraceto et al., 2016; Pereira et al., 2019). The mitigation of climate change and environmental degradation is a great challenge for humans, in the sense of bringing sustainable solutions that seek to increase global food production while preserving the environment (Pereira et al., 2019; Zeng et al., 2021)

Among the active substances that can be used to promote plant resistance to stresses are plant growth regulators (PGRs), which are natural or synthetic substances, mostly applied at low concentrations, that are involved in the hormonal homeostasis and/or signaling network, therefore triggering plant growth, development, metabolic processes, and responses to stress (Iqbal et al., 2022; Pereira et al., 2019; Rademacher, 2015; Small and Degenhardt, 2018). Phytohormones themselves, their precursors and analogues can be used as PGRs. In addition, PGRs include substances that alter the biosynthesis, inactivation, translocation, or signaling pathway of plant hormones (Rademacher, 2015).

Phytohormones are substances present in plant metabolism, which act at low concentrations and regulate physiological processes involved in growth, development, and responses to the environment (Ordaz-Ortiz et al., 2015; Small and Degenhardt, 2018). They are separated into well-known groups according to their chemical structure and/or functions in plant physiology: auxins, cytokinins, gibberellins, abscisic acid, ethylene, brassinosteroids, salicylic acid, jasmonic acid, and strigolactones (Table 1, Figure 2) (Pereira et al., 2019; Small and Degenhardt, 2018). In addition to the classical phytohormones, other signaling molecules are known to modulate processes of plant physiology, such as nitric oxide (Lindermayr and Durner, 2018), hydrogen sulfide (Zhou et al., 2021), γ -aminobutyric acid (Khan et al., 2021), polyamines, and melatonin (Arnao and Hernández-Ruiz, 2019; Sabagh et al., 2021) (Table 1, Figure 2).

Table 1: Main signaling molecules found in plants (with their chemical nature) and the biological applications of some plant growth regulators (PGRs) related to them (natural compounds or synthetic analogues).

| <i>Type of signaling molecule</i> | <i>Chemical nature</i> | <i>Examples of related PGRs</i> | <i>Biological applications</i> |
|-----------------------------------|--|--|---|
| Auxins | Indolic acids | 2,4-dichlorophenoxyacetic acid (2,4-D), naphthalene-1-acetic acid (NAA), indole acetic acid (IAA), indole butyric acid (IBA) | (+) Growth (cell division and elongation), apical dominance, fruit development, root formation (-) Abscission At high concentrations: (+) Abscission (-) General growth (herbicidal effect) |
| Cytokinins | Adenine derivatives with an isoprene-derived side chain | Kinetin, zeatin, 6-benzylaminopurine (6BA), thidiazuron (TDZ), 2-isopentenyladenine (2iP) | (+) Shoot growth (cell division), development of lateral buds, sink strength (-) Senescence At high concentrations: (-) General growth (herbicidal effect) |
| Gibberellins | Tetracyclic diterpenoid carboxylic acids with the <i>ent</i> -gibberellan skeleton | GA ₁ , gibberellic acid (GA ₃) | (+) Longitudinal growth (cell division and expansion), floral induction (long-day plants), flower, seed and fruit development, seed germination |
| Abscisic acid (ABA) | Isoprenoid, synthesized from carotenoids | (<i>S</i>)-cis-ABA (active form), (<i>S</i>)-2-trans-ABA (Inactive, but interconvertible with the active cis form), (<i>R</i>)-cis-ABA (Inactive form in stomatal closure) | (+) Abiotic stress responses, seed maturation, dormancy of seeds and buds (-) General growth, seed germination |
| Ethylene | Gaseous simple olefin | Ethephon (Ethylene releaser) | (+) Senescence, abscission, ripening of climacteric fruits, formation of roots and root hairs, stress responses (-) General growth |
| Brassinosteroids | Steroidal lactones | 24-epibrassinolide (EBL), 28-homobrassinolide (HBL) | (+) General growth (cell division and expansion), seed germination, formation of lateral roots, stress responses At high concentrations: (-) General growth |
| Salicylic acid | Phenolic compound | Salicylic acid, 2,6-dichloroisonicotinic acid (INA), benzothiadiazole (BHT) | (+) Stress responses (-) Senescence |
| Jasmonic acid | Oxo monocarboxylic acid derived from cyclic fatty acids | n-Propyl dihydrojasmonate | (+) Stress responses, trichome and stamen development, senescence (-) General growth |
| Strigolactones | Terpenoid | Synthetic strigolactone | (+) Seed germination, secondary |

| | | | |
|-------------------------------------|---|---|--|
| | lactones, derived from carotenoids | (GR24) | growth, root hair growth, interaction with beneficial microorganisms |
| Nitric oxide (NO) | Gaseous nitrogen free radical | S-nitrosothiols, sodium nitroprusside | (-) Root and shoot ramification (+) Stress responses, seed germination, root and root hair formation |
| Hydrogen sulfide (H ₂ S) | Gaseous molecule | Sodium hydrosulfide (NaHS) | (-) Floral induction, senescence, fruit ripening (+) Seed germination, root development, flowering, photosynthesis |
| γ -Aminobutyric acid (GABA) | Non-proteogenic amino acid | Commercial formulation | (+) Root development, pollen tube development, regulation of cytosol pH and redox balance |
| Polyamines | Low-molecular-weight, ubiquitous polycationic compounds, with aliphatic nitrogenous bases | Putrescine (Put), Sperdimine (Spd) and Spermine (Spm) | (+) Cell division and differentiation, DNA and protein synthesis, reproductive development, fruit maturation (-) Senescence |
| Melatonin | Methoxylated indoleamine | <i>N</i> -acetyl-5-methoxytryptamine | (+) Antioxidant defense, root development, flowering, seed germination, photosynthesis (-) Senescence |

(+) refers to positive effects and (-) to negative effects.

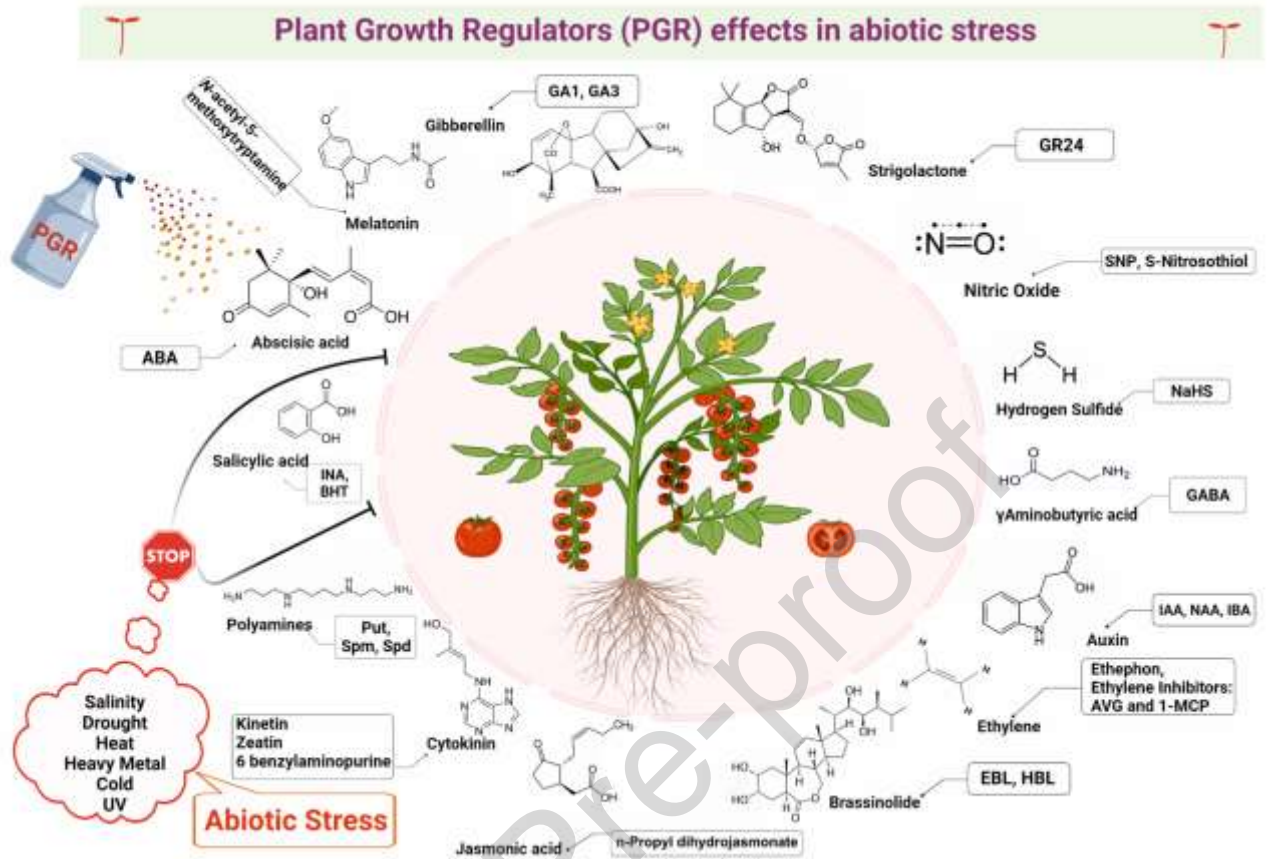


Figure 2: Main effects of plant growth regulators on plant growth, development, and responses to the environment. Main signaling molecules found in plants with the representation of their chemical structure and examples of some plant growth regulators related to them. The abbreviations are defined in Table 1.

PGRs have wide applications in agriculture and horticulture, and recently in research seeking to improve ecological restoration techniques. They provide important benefits, such as improved plant growth and development, increased crop yield and quality, and the induction of resistance against biotic and abiotic stresses (Table 1) (Rademacher, 2015; Small and Degenhardt, 2018). In addition, PGRs have been used to alleviate heavy metal toxicity. For example, exogenous application of IAA was found to induce growth of tea seedlings (*Camellia sinensis*) in the presence of Cadmium (Cd) by regulation of physiological and biochemical reactions, which were responsible for alleviating the deleterious effect of this heavy metal (Zhang et al., 2020). Furthermore, GA₃, EBL, 6BA, ABA, salicylic acid, and jasmonic acid also alleviate heavy metal

toxicity in plants as well as increase their biomass production (Li et al., 2022; Rostami and Azhdarpoor, 2019).

A summary of the overall benefits of the PGRs most-commonly applied to mitigate the effects of abiotic stresses in plants is provided in Table 2. Other PGRs (*e.g.*, gibberellins, cytokinins, and auxins) are often applied to promote growth or modulate specific processes of plant development, but their use to induce stress responses has recently been raised, especially as priming agents (Bryksova et al., 2020; Dolui et al., 2022; Zhu et al., 2021).

Table 2: Main PGRs applied to mitigate the effects of abiotic stresses in plants.

| <i>PGR</i> | <i>Main types of abiotic stress</i> | <i>Principal responses</i> | <i>References</i> |
|--|---|---|--|
| Abscisic acid (ABA) | Salinity, cold, heat, and drought | Stomatal closure, enhanced root/shoot ratio, promotion of water uptake, induction of several acclimation proteins (<i>e.g.</i> , antioxidant response, chaperones, compatible osmolytes) | (Iqbal et al., 2022; Kosakivska et al., 2022; Rehman et al., 2022) |
| Ethylene inhibitors: Aminoethoxyvinylglycine (AVG) and 1-methylcyclopropene (1-MCP) | Cold, heat, and drought | Reduction of oxidative stress, delay of senescence | (Kazan, 2015; Poor et al., 2022; Rademacher, 2015) |
| Brassinosteroids: 24-epibrassinolide (EBL) and 28-homobrassinolide (HBL) | Salinity, cold, heat, and drought | Enhanced photosynthesis, chlorophyll and antioxidant contents | (Bhandari and Nailwal, 2020; Siddiqi and Husen, 2021) |
| Salicylic acid: Salicylic acid, 2,6-dichloroisonicotinic acid (INA) and benzothiadiazole (BHT) | Salinity, drought and metal | Enhanced photosynthesis, antioxidant defense, osmolyte production and improvement of water status | (Damalas and Koutroubas, 2022; Khan et al., 2015; Wani et al., 2017) |
| Jasmonic acid: n-Propyl dihydrojasmonate | Salinity, cold, drought, metal, and light | Induction of antioxidant defense, protection of the photosynthetic apparatus and stomatal closure | (Kazan, 2015; Kosakivska et al., 2022; Wang et al., 2020) |
| Strigolactones: Synthetic stringolactone (GR24) | Nutrient starvation, heat, cold, salinity, drought, and light | Regulation of root architecture and secondary growth, induction of antioxidant defense | (Bhoi et al., 2021; Mostofa et al., 2018) |
| Nitric oxide donors: S-nitrosothiols, sodium nitroprusside (SNP) | Salinity, drought, cold, heat, metal, and light | Induction of antioxidant defense, regulation of stomatal physiology, increase of | (do Carmo et al., 2021; Iqbal et al., 2022; Singhal et al., 2021) |

| | | | |
|---|--|---|---|
| | | photosynthetic efficiency, induction of root and root hair formation, and improvement of water status | |
| Hydrogen sulfide donor: Sodium hydrosulfide (NaHS) | Salinity, drought, metal, cold, and heat | Induction of antioxidant defense and osmolyte accumulation | (Huang et al., 2021; Z.-G. Li et al., 2021; Raza et al., 2021) |
| γ -Aminobutyric acid (GABA) | Salinity, drought, flooding, heat, cold, and metal | Induction of antioxidant defense, osmolyte accumulation and stomatal closure | (Rezaei-Chiyaneh et al., 2018; Shelp et al., 2021) |
| Polyamines: Putrescine (Put) Spermidine (Spd) Spermine (Spm) | Salinity, drought and metal | Induction of antioxidant defense, photosynthesis and osmolyte accumulation | (Chen et al., 2019; Khajuria et al., 2018; Spormann et al., 2021) |
| Melatonin: <i>N</i> -acetyl-5-methoxytryptamine | Salinity, drought, heat, and metal | Induction of antioxidant defense and photosynthesis, delay of senescence | (Khan et al., 2021; Rajora et al., 2022; Rehaman et al., 2021) |

The application of PGRs can be hindered due to the chemical characteristics of the molecules, such as the rapid degradation of these compounds when exposed to the light and temperatures found in the field, resulting in some loss of their biological activity (Pascoli et al., 2018; Seabra et al., 2015). For example, natural auxins, extracted directly from plants, degrade rapidly in the presence of light (George et al., 2007; Small and Degenhardt, 2018). In addition, nitric oxide donors are also susceptible to factors such as temperature, light, and pH, that lead to the rapid and excessive release of nitric oxide from donor molecules and the loss of beneficial effects (Seabra et al., 2015; Silveira et al., 2021).

Besides the rapid degradation, PGRs need to be applied in proper concentrations to stimulate the desired responses, because they can become phytotoxic at high concentrations, acting as herbicides and not as hormones or regulators (Pascoli et al., 2018). For example, gibberellins need to be applied at correct concentrations and timing to avoid detrimental effects on plant development (Dong et al., 2016). In addition, the function of hydrogen sulfide is directly dose dependent: at low concentrations it acts as a signaling molecule and at high concentrations as a toxin (Banerjee and Roychoudhury, 2021). Another relevant aspect is related to the low water solubility of some PGRs, which can make their application more difficult. Moreover, the high cost associated with their production and application generates a high demand for the development of

technologies for slow, controlled, and efficient PGR release systems (Oliveira et al., 2016; Pascoli et al., 2018; Pereira et al., 2019).

In this sense, the development of micro- and nanoparticles as carrier systems of bioactive substances is a promising strategy with the purpose of improving the biological action of molecules (Athanassiou et al., 2018; Fraceto et al., 2016; Pereira et al., 2019). The use of micro- and nanoparticles provides several advantages, including protection against premature degradation of the encapsulated molecules, reduction in photosensitivity and instability of the molecules, and the slow and controlled release of the active compounds, enhancing and prolonging their effects (Seabra et al., 2015; Silveira et al., 2021). The characteristics of micro- and nanoparticles allow reductions in the dosage and frequency of application of active compounds, as well as reducing the risk of contamination and harmful consequences for the organisms to which they are applied (Pereira et al., 2019).

3. Plant Associative Microorganisms

Soil is one of the richest habitats for a variety of living organisms and is also a “playground” for chemical reactions that ensure the normal functioning of ecosystems. The majority of soil bio-geochemical processes are driven by active soil microbiota (Bastida et al., 2016), which represents up to 5% of total microbial biomass (Blagodatskaya and Kuzyakov, 2013). Due to its richness in mineral resources, soil is a key element in the nutrition of land plants, and serves as a site for the plant-driven recruitment of microbiota, which leads to the establishment of interactions with plant associative microorganisms (PAMs, both fungi and bacteria).

Arbuscular mycorrhizal fungi (AMF) and *Trichoderma* ssp. are beneficial microorganisms, which have been known to establish mutualistic symbiotic interactions with different types of plants, including economically important crops (Szczalba et al., 2019). For this reason, a rising number of studies have focused on the utilization of these fungi as inoculants for increasing plant resistance to both abiotic and biotic stress (Begum et al., 2019). AMF can increase nutrient uptake by plants, such as phosphorus (P), increase photosynthesis, enhance osmotic adjustment in drought conditions, and improve soil properties (Begum et al., 2019). Likewise, *Trichoderma* ssp. improves plant growth and development by the production of PGRs, solubilization of soil nutrients, and enhancement of the uptake and translocation of less accessible minerals.

In addition, this fungal genus is widely used for the biological control of several economically important plant pathogens (Halifu et al., 2019; Sood et al., 2020).

The interest of the scientific community in plant-bacteria interactions first appeared in the 60-70s, when scientists were trying to understand the nature of the formation of grapevine galls caused by the bacterium *Agrobacterium tumefaciens* (Kado, 2014). The results of these and subsequent studies (Burr, 1978; Howie and Echandi, 1983; Klopper et al., 1980; Suslow and Schroth, 1982) have made it clear that the plant-associated microbiota (the phytomicrobiome) is more important in plant growth and development than previously thought and could be beneficial (mutualist), neutral (commensal), and unfavorable (detrimental) (Newton et al., 2010). In 1978, Klopper and Schroth introduced the concept of plant growth-promoting rhizobacteria (PGPR), which marked the beginning of a new era of study of bacterial symbiotic interactions and their biostimulating properties (Klopper and Schroth, 1978).

PGPR are mostly located in the rhizosphere, the 0.5–4 mm zone around the root that is under plant control (Braga et al., 2016), and is characterized by an increased content of organic nutrient-rich root exudates containing up to 10^{11} microbial cells per gram of root (Feng et al., 2021), which corresponds to 50–2000 $\mu\text{g C g}^{-1}$ soil (Fierer, 2017). Due to the fact that the plant rhizosphere is a very “competitive” habitat, microorganisms have developed specific mechanisms that allow them to occupy their microenvironmental niche. Thus, in the course of evolution, PGPR have acquired the ability to adjust their metabolic pathways to the needs of the “host organism” (and *vice versa*) in order to remain in their beneficial microenvironment (Ankati and Podile, 2019; Khatoon et al., 2020).

PGPR directly promote plant growth by producing and secreting phytostimulatory hormonal substances, supplying readily available micro and macroelements (*e.g.*, iron (Fe^{3+}) via the production of siderophores), achieving biological nitrogen fixation (by regulation of *nif* genes in diazotrophs), and/or improving P solubilization (by converting insoluble forms of P to an accessible orthophosphate form) (Figure 3) (Hardoim et al., 2015; Kalayu, 2019; Vacheron et al., 2013). Interestingly, some siderophore-producing bacteria produce siderophores that are able to bind heavy metals that are similar in nature to Fe, resulting in induction of metal resistance (Rajkumar et al., 2010; Złoch et al., 2016). For example, *Streptomyces tenae* F4 produces a siderophore complex consisting of desferrioxamine B, desferrioxamine

E, and coelomelin that binds cadmium ions, thereby reducing its toxicity and improving phytoremediation (Dimkpa et al., 2009).

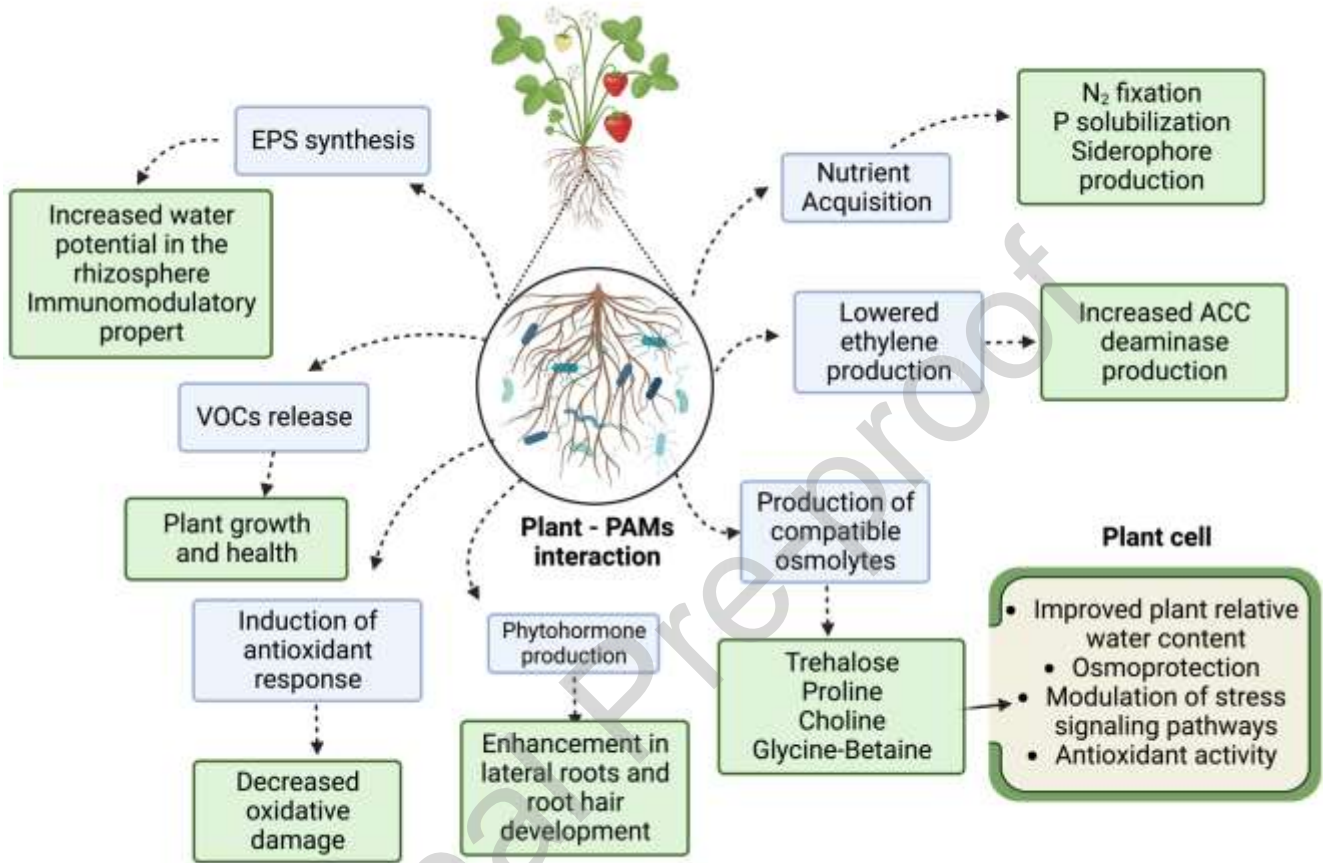


Figure 3: Main effects of plant associative microorganisms (PAMs) on plant growth, development, and responses to abiotic and biotic stressors. The direct effect of PAMs on plants are represented in blue boxes while the response to these effects is represented in green boxes. The schematic representation was adapted from (Sati et al., 2022) (<https://doi.org/10.1007/s42729-021-00724-5>). **EPS** – **exopolysaccharides**; **VOCs** – **volatile organic compounds**; **ACC deaminase** - **1-aminocyclopropane-1-carboxylate deaminase**; **N₂** – **nitrogen**; **P-** **phosphorus**. Created with biorender.com

Some PGPR produce, for example, indole-3-acetic acid (IAA, an auxin), thus modifying the architecture of the root system by increasing its branching and the formation of root absorbent hairs. Several strains of PGPR possess the enzyme 1 aminocyclopropane-1-carboxylate deaminase (ACC deaminase), which limits ethylene production in plants by cleaving its precursor molecule (1-aminocyclopropane-1-carboxylic acid, ACC) into ammonia and alpha keto butyrate (Krishnamoorthy et al.,

2022). This allows a reduction in the concentration of endogenous ethylene in the plant, with a positive effect on plant growth and stress alleviation (Hardoim et al., 2015; Vacheron et al., 2013).

In addition, many PGPRs are capable of forming biofilms by secreting exopolysaccharides (EPS), which serve as a buffer between bacteria and environmental fluctuations in moisture and temperature. The EPS produced in the rhizosphere form a sheath around the roots that help to retain water in the soil and create favorable conditions for plant-bacteria interactions (Dar et al., 2021). In addition, some PGPR are capable of producing volatile organic compounds (VOCs) that have a stimulating effect on plant growth (Ryu et al., 2003). All cited mechanisms are summarized in Figure 3 and Table 3.

Considering the beneficial effects of PAMs to plants, the efforts of scientists have been directed to the study of the practical application of certain strains in agriculture, aiming to increase crop yield. In the last two decades, 1,731 biofertilizer-related patents have been registered, which confirms the high interest in the use of green fertilizers and growth stimulants (Fatimi, 2022). This has led to the development of commercial bacterial formulations that have been tested in controlled conditions and shown positive effects on plant physiology in the field (Mofokeng et al., 2021). For example, the application of EM Bokashi 2-fi and EM-5 Sutociu (which are composed of beneficial bacteria and fungi) has a biostimulant and biocontrol effect in common bean plants (*Phaseolus vulgaris* L.) (Mofokeng et al., 2021; Roberti et al., 2015). In the same way, Compete Plus (composed of *Bacillus* spp., *Streptomyces griseoviridis* and *Trichoderma harzianum*) increased the yield and reduced disease by 20–23% and 20–32%, respectively in barley culture (Larkin, 2008). Another example of a successfully commercialized biostimulant is Soil-Life™ which, thanks to its rich and varied composition of *Lactobacillus*, *Actinomycetes*, yeast, and fungal strains, improves soil quality and crop growth, yield, and quality (Mofokeng et al., 2021).

Furthermore, inoculation with PGPR has been demonstrated to induce drought resistance in neotropical tree seedlings, thus emerging as a biotechnology to be used for tree seedling production (Tiepo et al., 2020, 2018). Thus, PGPR inoculation may provide an alternative to improve the resistance of these plants to abiotic stresses and increase the success of reforestation programs.

Despite the high potential of biofertilizers, they are still subject to the influence of external factors and require a special approach for storage and conservation to

prevent their destabilization. Careful selection of strain-specific carriers is needed in the preparation of commercial formulations to avoid loss of effectiveness. Nowadays a wide variety of carrier materials are available: natural (peat, lignite, coal, clay), synthetic (polyacrylamide), organic (charcoal, biochar, composts), or biopolymers (starch, sodium alginate) (Fasusi et al., 2021; Le Corre et al., 2010; Moradi Pour et al., 2022). Recent advances in biotechnology and nanoscience highlight the possibility of using microparticles as bacterial carriers, which can be applied to biofertilizers (Kumar et al., 2022). It has also been shown that nanomaterials are able to increase the biofertilizer potential of PGPR, as well as maintain bacterial viability (Safari et al., 2020).

Table 3. Role of PGPR in alleviating abiotic stress in different plant species.

| Bacterial species/ Strain | Exerted mechanisms | Plant species | Reference |
|--------------------------------------|---|--|-------------------------------|
| <i>Agrobacterium radiobacter</i> D14 | Heavy metal uptake | Poplar (<i>Populus deltoides</i> Marshall) | (Wang et al., 2011) |
| <i>Agrobacterium rubi</i> A-18 | N ₂ fixation, IAA, cytokinin and gibberellin production | Apple (<i>Malus domestica</i> Borkh.) | (Karakurt and Aslantas, 2010) |
| <i>Azomonas</i> sp. | Increased protein, proline, starch and water contents; improved photosynthesis and growth; decreased oxidative stress; drought resistance | <i>Trema micrantha</i> (L.) Blume (neotropical tree) | (Tiepo et al., 2018) |
| <i>Azospirillum brasilense</i> Ab-V5 | Increased protein, proline, starch and water contents; improved photosynthesis and growth; decreased oxidative stress; drought resistance | <i>Trema micrantha</i> (L.) Blume (neotropical tree) | (Tiepo et al., 2018) |
| <i>Azospirillum brasilense</i> Ab-V5 | Increased protein and starch contents; improved photosynthesis; decreased oxidative stress; drought resistance | <i>Cariniana estrellensis</i> (Raddi) Kuntze (neotropical tree) | (Tiepo et al., 2018) |
| <i>Azospirillum brasilense</i> Ab-V5 | Induction of antioxidant response and drought resistance | <i>Cariniana estrellensis</i> (Raddi) Kuntze and <i>Cecropia pachystachya</i> Trécul (neotropical trees) | (Tiepo et al., 2020) |

| | | | |
|--|---|--|---------------------------------|
| <i>Bacillus subtilis</i> BRU16-Sr | Siderophore production | Alfalfa (<i>Medicago sativa</i> L.) | (Tamariz-Angeles et al., 2021) |
| <i>Bacillus subtilis</i> JS | VOC production | Necklace poplar (<i>Populus deltoides</i> Marshall) | (Jang et al., 2018) |
| <i>Bacillus cereus</i> VBE23 | EPS and ACC deaminase production; phosphate and zinc solubilization | Maize (<i>Zea mays</i> L.) | (Galeano et al., 2021) |
| <i>Bacillus methylotrophicus</i> PM19 | EPS, IAA and ACC deaminase production; salt stress resistance | Wheat (<i>Triticum aestivum</i> L.) | (Amna et al., 2019) |
| <i>Bacillus mycoides</i> T8 | Phytohormone production | Cherry (<i>Prunus cerasus</i> L.) | (Arikan and Pirlak, 2016) |
| <i>Bacillus safensis</i> FN13 | EPS and IAA production; heavy metal uptake | Field mustard (<i>Brassica campestris</i> L.) | (Nazli et al., 2020) |
| <i>Bacillus</i> sp. ZK | Induction of antioxidant response and drought resistance | <i>Cariniana estrellensis</i> (Raddi) Kuntze and <i>Cecropia pachystachya</i> Trécul (neotropical trees) | (Tiepo et al., 2020) |
| <i>Bacillus subtilis</i> OSU-142 | N ₂ fixation; IAA and cytokinin production; phosphate solubilization | Apple (<i>Malus domestica</i> Borkh.) | (Karlidag et al., 2007) |
| <i>Bacillus velezensis</i> D3 | EPS and ACC deaminase production | Maize (<i>Zea mays</i> L.) | (Nadeem et al., 2021) |
| <i>Bacillus subtilis</i> Rhiso SF48 | ACC deaminase production | Sunflower (<i>Helianthus annuus</i> L.) | (Brijesh Singh et al., 2019) |
| <i>Burkholderia multivorans</i> WS-FJ9 | Phosphate solubilization | Poplar (<i>Populus euramericana</i> Guinier) | (Li et al., 2013) |
| <i>Ensifer meliloti</i> Rm1021 | EPS production | Alfalfa (<i>Medicago sativa</i> L.) | (Primo et al., 2020) |
| <i>Enterobacter turicensis</i> RCT5 | EPS production; phosphate and potassium solubilization | Tomato (<i>Lycopersicon esculentum</i> Mill.) | (Aeron et al., 2021) |
| <i>Erwinia gerundensis</i> A4 | Nutrient acquisition | Almond (<i>Prunus dulcis</i> (Mill.) D.A.Webb) | (Saldierna Guzmán et al., 2021) |
| <i>Glutamicibacter</i> sp. YD01 | ACC deaminase, IAA production, salt stress resistance | Rice (<i>Oryza sativa</i> L.) | (Ji et al., 2020) |
| <i>Herbaspirillum</i> sp. YDSY8 | ACC deaminase production | Chinese peony (<i>Paeonia lactiflora</i> Pall.) | (Yuan et al., 2022) |
| <i>Microbacterium</i> | Heavy metal uptake | Rapeseed (<i>Brassica napus</i> L.) | (Ren et al., 2019) |

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| | | | |
|--|---|---|---------------------------|
| <i>Planomicrobium chinense</i> P1 | Phytohormone and HCN production | Wheat (<i>Triticum aestivum</i> L.) | (Khan and Bano, 2019) |
| <i>Pseudomonas frederiksbergensis</i> JW-SD2 | Phosphate solubilization | Poplar (<i>Populus euramericana</i> Guinier) | (Zeng et al., 2016) |
| <i>Pseudomonas oryzihabitans</i> AXSa06 | ACC deaminase, IAA and siderophore production; phosphate solubilization | Tomato (<i>Solanum lycopersicum</i> L.) | (Mellidou et al., 2021) |
| <i>Pseudomonas polymyxa</i> FB-50 | EPS production, salt stress resistance | <i>Acacia abyssinica</i> Benth. | (Getahun et al., 2020) |
| <i>Pseudomonas putida</i> RA | Modulation of stress-related plant miRNA | Chickpea (<i>Cicer arietinum</i> L.) | (Jatan et al., 2019) |
| <i>Pseudomonas putida</i> W619-TCE | TCE degradation | Poplar cuttings [<i>Populus deltoides</i> x (<i>trichocarpa</i> x <i>deltoides</i>) cv. Grimminge] | (Weyens et al., 2010) |
| <i>Pseudomonas</i> sp. SP3 | Siderophore production | Siberian crab apple (<i>Malus baccata</i> (L.) Borkh.) | (Gao et al., 2022) |
| <i>Rhizobium alamii</i> GBV030 | EPS production | Rapeseed (<i>Brassica napus</i> L.) | (Tulumello et al., 2021) |
| <i>Rhizobium favelukesii</i> LPU83 | EPS production | Alfalfa (<i>Medicago sativa</i> L.) | (Castellani et al., 2021) |
| <i>Rhizobium phaseoli</i> Mn-6 | EPS production | Maize (<i>Zea mays</i> L.) | (Dar et al., 2021) |
| <i>Rhodococcus qingshengii</i> RL1 | N ₂ fixation, phytohormone production | Rucola (<i>Eruca sativa</i> L.) | (Kuhl et al., 2021) |
| <i>Streptomyces</i> sp. SIIB-Zn-R8 | Siderophore production, heavy metal uptake | Black alder (<i>Alnus glutinosa</i> L.) | (Złoch et al., 2016) |

Abbreviations: ACC: 1-aminocyclopropane-1-carboxylate; EPS: exopolysaccharides; IAA: indole-3-acetic acid; HCN: hydrogen cyanide; TCE: trichloroethylene; VOCs: volatile organic compounds

4. Encapsulation strategy

As mentioned above, both PGRs and PAMs are susceptible to premature degradation/loss of viability when applied to the plants, which has encouraged the development of several types of formulations, including those using the encapsulation strategy. Encapsulation indicates the entrapment of molecules or microorganisms by chemical, mechanical, or physical methods using different types of matrices (wall material), resulting in particles with a wide range of sizes, which is dependent on the

technique used. Different wall materials that can be used to produce particles, such as natural and synthetic polymers, waxes, gums, fats, and carbohydrates (Rojas-Sánchez et al., 2022; Saberi Riseh et al., 2021).

It is important to evaluate the type of matrix material that will be used for the encapsulation and the methodological process, aiming at sustainable agriculture and forest restoration practices. Currently, there is a trend to choose methods that apply green processes (such as the use of biodegradable materials, biosurfactants, and low-energy consuming production processes, and the avoidance of hazardous materials), which are essential for products aiming at biostimulant effects (Jiménez-Arias et al., 2020). Biopolymers (*e.g.*, alginate, chitosan, cellulose, zein) have been used for nano- and microencapsulation processes due to characteristics such as biodegradability, biocompatibility, low toxicity, and promotion of circular economy. These biopolymers have many functional groups that can promote the nanoencapsulation of bioactive compounds (such as PGRs) or the microencapsulation of microorganisms, mainly by electrostatic interaction or the anti-solvent method.

One of the most commonly used biopolymers is chitosan, which is a polysaccharide with many applications due to its chemical, physical, and biological properties. Its structure has primary and secondary hydroxyl groups and the presence of amine groups (Islam et al., 2017) that allow electrostatic interactions with other biopolymers or salts (*e.g.*, alginate and tripolyphosphate), forming nanoparticles by ionotropic pre-gelation and ionic gelation (Korpayev et al., 2021; Valderrama N et al., 2020). Many studies have reported that chitosan *per se* has plant growth promotion and stress resistance induction effects (de Melo et al., 2019; Rv et al., 2018)

4.1. PGR nanoencapsulation

Despite the great potential of PGR applications in agriculture and forest restoration, two main challenges need to be overcome: the short shelf-life of these compounds and their low stability in the field, which compromise their biological activity (Jiménez-Arias et al., 2020). A good example is abscisic acid (ABA), which has a half-life of 24 min under sunlight; thus, the use of high doses of this PGR together with an anti-photolysis agent is required to improve its activity in the field (Yin et al., 2020a). To face these challenges, the nanoencapsulation of PGRs appears as an effective strategy to offer protection (during storage and after application) against premature degradation by processes such as hydrolysis and photolysis, improving the

shelf-life of PGR formulations and their biological activity under realistic conditions (Falsini et al., 2019a; Jiménez-Arias et al., 2020; Pascoli et al., 2018; Yin et al., 2020a). Moreover, nanoencapsulation promotes sustained release of the bioactive molecules over time, prolonging their action in plants, in addition to allowing targeted delivery of PGRs to plants of interest, with enhanced uptake and/or translocation of the molecules in the plants (Figure 4). Although in the last decade there has been an increase in the number of studies reporting the nanoencapsulation of PGRs (Table 4), the use of these systems for plant protection against stress conditions is still little explored, especially if compared to application of metallic nanoparticles.

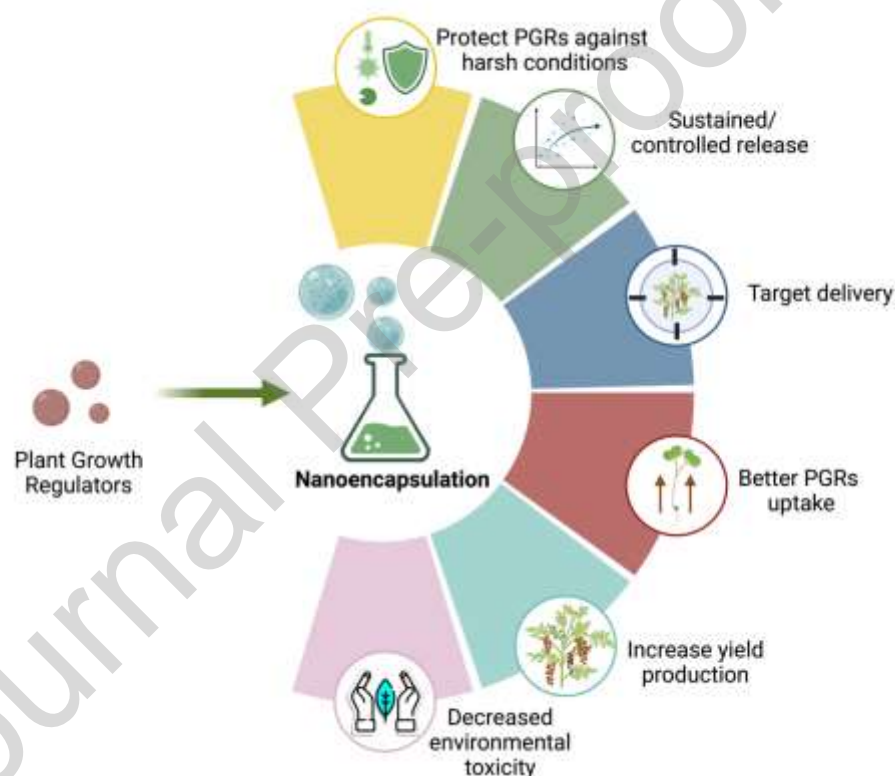


Figure 4: Nanoencapsulation as a strategy to improve the physicochemical stability and biological activity of PGRs. Created with BioRender.com

Chitosan/tripolyphosphate (TPP) nanoparticles are the most commonly used system for the encapsulation of hydrophilic PGRs, such as gibberellic acid, indole-3-butyric acid, indole-3-acetic acid, salicylic acid, and S-nitrosothiols (Table 4). The formation of nanoparticles results from the interaction of the protonated chitosan amino group with TPP anion (Korpayev et al., 2021; Anderson Espirito Santo Pereira et al., 2017; Valderrama N et al., 2020). Another methodology used for the formation of chitosan nanoparticles is the ionotropic pre-gelation: there is a pre-gelation process with a cation (*e.g.*, Ca^{2+}) that interacts with carboxylic groups forming an egg-box structure.

For example, the biopolymers alginate or polyglutamic can be used to interact with chitosan amine groups by electrostatic interaction, resulting in micro/nanoparticles (Pereira et al., 2017). These methodologies follow the precepts of green chemistry, since no solvents or surfactants are used for nanoparticle stabilization. Moreover, biopolymers are biodegradable, biocompatible, and may induce synergetic effects with PGRs on plants (Malerba and Cerana, 2019; Rv et al., 2018).

In a field study, Pereira et al. (2019) showed that seed priming with chitosan nanoparticles improved tomato plant development and yield. It is noteworthy that gibberellic acid-loaded chitosan/TPP and alginate/chitosan nanoparticles increased tomato production by around 4-fold, to a higher extent than the non-encapsulated PGR. However, this system has not yet been tested for induction of plant stress resistance (Pereira et al., 2019).

In contrast, various reports have demonstrated that the encapsulation of S-nitrosothiols into chitosan/TPP nanoparticles potentiates the protective effect of nitric oxide (NO) in plants submitted to different types of abiotic stresses (Table 4). Despite the well-known involvement of NO as a signaling molecule in the induction of stress responses, the application of NO donors (as S-nitrosothiols) has been hampered by the relative instability of these molecules (Seabra et al., 2014). Nanoencapsulation has recently been demonstrated to be an efficient strategy to increase the half-life of S-nitrosothiols and promote more sustained NO release, enhancing the protective effects of NO on stressed plants (Table 4). Studies carried out with crop and tree species highlighted the potential applications of NO-releasing chitosan nanoparticles for increasing agricultural production and tree seedling survival in a scenario of climate change (Seabra et al., 2022).

Another trend for the development of nanocarriers is the use of lignin. This biopolymer has different characteristics according to the extraction method, yielding more hydrophobicity or hydrophilicity. The physico-chemical characteristics of lignin may also result in UV protection, and antioxidant and antimicrobial activities (Chauhan, 2020; Pereira et al., 2022).

Falsini et al. (2019) used the solvent/co-solvent methodology for the encapsulation of gibberellic acid into lignin nanoparticles. In this process, an organic solvent (acetone) and a high energy input (sonication) are required for the nanoparticle formation (Falsini et al., 2019b). The nanoparticles were absorbed by rocket and tomato seeds, increasing the germination and root development. Yin et al. (2020) developed

lignin nanoparticles for the encapsulation of ABA by the electrostatic adsorption method. This system protected the PGR against photolysis and was more efficient than the free ABA in inducing drought resistance in rice and Arabidopsis plants (Yin et al., 2020b).

Another strategy is the development of stimuli-responsive nanoparticles. Mesoporous silica nanoparticles have been developed as carrier systems for ABA and salicylic acid (Sun et al., 2018; Yi et al., 2015). This system involved many process steps for functionalization of the nanoparticle surface with decanethiol groups, that work as a gate for the PGR release in the presence of glutathione. Stressed plants usually have overproduction of glutathione, triggering the release of the PGRs involved in the induction of stress resistance (Sun et al., 2018; Yi et al., 2015).

In the study performed by Sun et al. (2018), the ability of ABA-loaded silica nanoparticles to aid drought resistance and reduction in water loss was evaluated in *Arabidopsis thaliana* plants. After 14 days of drought stress, plants treated with nanoencapsulated ABA showed better resistance to water deficit, and an increased number of flowering seedlings and seedling greening rates when compared to plants treated with non-encapsulated ABA. In addition, prolonged expression of the ABA inducible marker gene *AtGALK2* was observed when plants were treated with nanoencapsulated ABA (Sun et al., 2018).

Kumaraswamy et al. (2019) functionalized/coated chitosan nanoparticles with salicylic acid. The results demonstrated that the nanoparticles improved plant resistance to abiotic stress and showed antifungal activity against *Fusarium verticillioides*, that causes a disease responsible for 40-100% of yield loss in maize. Moreover, the nanoformulation improved the germination and production of maize plants and increased the antioxidant activity and induced lignin deposition, avoiding further infection by microorganisms (Kumaraswamy et al., 2019).

Recently, the priming technology has been considered as a promising strategy to increase plant resistance to abiotic and biotic stress. In addition, application of nanocarriers as a smart delivery system could increase the efficiency of the priming agent and reduce overall chemical usage (Ioannou et al., 2020; Wang et al., 2016). For instance, Gohari et al. (2022) reported that seedling priming treatment with melatonin-coated chitosan nanoparticles on spearmint (*Mentha spicata* L.) under salinity stress not only increased the plant defense system against salinity stress (by increasing proline content, enzymatic antioxidant activities, and essential oil content) but also decreased

the effective concentration of melatonin compared to solo melatonin treatment (Gohari et al., 2022).

Table 4: Nanoencapsulated plant growth regulators (PGRs) and their biological effects in plants.

| <i>Type of nanoparticle</i> | <i>PGR</i> | <i>Methodology</i> | <i>Biological effects</i> | <i>Reference</i> |
|--|--|--|--|-------------------------------|
| Chitosan/ tripolyphosphate and chitosan/alginate | Gibberellic acid | Iontropic pre-gelation and ionic gelation method | (+) Seedling development, leaf area and photosynthetic pigments in common bean seedlings (<i>Phaseolus vulgaris</i> L.) | (Pereira et al., 2017) |
| Chitosan/polyglutamic | Gibberellic acid | Iontropic pre-gelation | (+) Development and vigor of common bean seedlings (<i>Phaseolus vulgaris</i> L.) | (Pereira et al., 2017) |
| Chitosan/ tripolyphosphate and chitosan/alginate | Gibberellic acid | Iontropic pre-gelation and ionic gelation method | (+) Plant development, yield and fruit weight in tomato plants (<i>Solanum lycopersicum</i> L.) | (Pereira et al., 2019) |
| Alginate/chitosan | Indole-3-acetic acid | Iontropic pre-gelation | (+) Growth and chlorophyll content of tomato plants (<i>Solanum lycopersicum</i> L.) | (Andrade Ayala et al., 2020) |
| Chitosan/tripolyphosphate | Salicylic acid | Ionic gelation | (+) Protection against fungal infection, antioxidant enzyme activity and yield of maize plants (<i>Zea mays</i> L.) | (Kumaraswamy et al., 2019) |
| Chitosan/tripolyphosphate | S-nitroso-mercaptosuccinic acid (NO donor) | Ionic gelation | (+) Protection of maize plants (<i>Zea mays</i> L.) against salt stress | (Oliveira et al., 2016) |
| Chitosan/tripolyphosphate | S-nitroso-mercaptosuccinic | Ionic gelation | (+) Growth of <i>Heliocarpus popayanensis</i> Kunth | (Lopes-Oliveira et al., 2019) |

| | | | | |
|--|---|-------------------------------------|--|---------------------------|
| | acid (NO donor) | | seedlings under full sun | |
| Chitosan/tripolyphosphate | S-nitrosoglutathione (NO donor) | Ionic gelation | (+) Protection of sugarcane plants (<i>Saccharum</i> spp.) against water deficit | (Silveira et al., 2019) |
| Chitosan/tripolyphosphate | S-nitroso-mercaptopuccinic acid (NO donor) | Ionic gelation | (+) Protection of <i>Heliocarpus popayanensis</i> Kunth seedlings against water deficit | (do Carmo et al., 2021) |
| Chitosan/tripolyphosphate | S-nitrosoglutathione, S-nitroso-N-acetylcysteine, S-nitroso-mercaptopuccinic acid (NO donors) | Ionic gelation | (+) Recovery of sugarcane plants (<i>Saccharum</i> spp.) after water deficit | (Silveira et al., 2021) |
| Chitosan/tripolyphosphate | S-nitroso-mercaptopuccinic acid (NO donor) | Ionic gelation | (+) Protection of soybean plants (<i>Glycine max</i> (L.) Merr.) against high copper levels in the soil | (Gomes et al., 2022) |
| Chitosan/tripolyphosphate | Methyl jasmonate | Ionic gelation | (+) Elicitation of phenolics and flavonoids in rice (<i>Oryza sativa</i> L.) cell cultures | (Arya et al., 2022) |
| Chitosan and silver | Indole-3-acetic acid and indole-3-butyric acid | Ionic gelation and reduction method | (+) Root development of apple microcuttings (<i>Malus domestica</i> Borkh.) | (Korpayev et al., 2021) |
| Mesoporous silica nanoparticles/chitosan | Melatonin | Ionic gelation | (+) Photosynthetic efficiency and antioxidant enzyme activities; (-) Cadmium concentration in rice leaves (<i>Oryza sativa</i> L.) | (Chen et al., 2022) |
| Zinc | Indole-3-acetic acid and indole-3-butyric | Surface coating (hydrogen | (+) Root development of pear microcuttings (<i>Pyrus elaeagrifolia</i> Pall | (Karakeçili et al., 2019) |

| | | | | |
|--|--|------------------------------------|---|--------------------------------|
| | acid | bonding) | and <i>Pyrus communis</i> L.) | |
| Zinc | Indole-3-acetic acid and indole-3-butyric acid | Surface coating (hydrogen bonding) | (+) Root development in apple micro cuttings (<i>Malus domestica</i> Borkh.) | (Alizadeh and Dumanoglu, 2022) |
| Silica nanoparticles | Absciscic acid | Not mentioned | (+) Protection of <i>Arabidopsis thaliana</i> (L.) Heynh. against drought stress | (Sun et al., 2018) |
| Silica nanoparticles | Salicylic acid | Not mentioned | (+) Expression of defense genes in <i>Arabidopsis thaliana</i> (L.) Heynh. | (Yi et al., 2015) |
| Lignin | Gibberellic acid | Solvent/co-solvent method | (+) Development and biomass of rucola (<i>Eruca vesicaria</i> (L.) Cav.) and tomato (<i>Solanum lycopersicum</i> L.) seedlings | (Falsini et al., 2019a) |
| Alkali lignin/cetyltrimethylammonium bromide | Absciscic acid | Electrostatic adsorption | (+) Protection of <i>Arabidopsis thaliana</i> (L.) Heynh. plants against water deficit (-) Germination of rice (<i>Oryza sativa</i> L.) and <i>Arabidopsis thaliana</i> (L.) Heynh. seeds | (Yin et al., 2020a) |
| Chitosan/tripolyphosphate | Melatonin | Ionic gelation | (+) Morphophysiological attributes and secondary metabolite content in spearmint (<i>Mentha spicata</i> L.) under salinity stress | (Gohari et al., 2022) |

As demonstrated in the table 5, some inorganic nanoparticles, such as zinc and silica, have been used to delivery PGR to plants. These nanoparticles offer significant advantages over organic nanoparticles, like smaller size, higher stability, controlled tunability, higher uptake, trigger release, optical properties and easier trackability in the environment (Poon and Patel, 2020). However, some limitations are also associated

with the utilization of these kind of materials. For example, most inorganic systems have a lower loading capacity when compared to organic nanoparticles. From an environmental point of view, it is still unknown how fast these systems are degraded in the environment, which can lead to environmental damage if used on a large scale (Bundschuh et al., 2018). Furthermore, little is known about the biomagnification and accumulation of these materials in plant tissues and the possible exposure of humans and non-target organisms to these nanomaterials via trophic transfer (Lead et al., 2018).

4.2. PAM microencapsulation

As discussed in this review, PAMs can be very efficient to improve plant health and growth under normal and/or stressed conditions, with minimal environmental damage. In recent decades, PAMs have been widely studied in the agricultural sector and some commercial formulations have been launched on the market. However, this approach may not promote the expected benefits in the agricultural sector, since crop productivity is highly influenced by the properties of the inoculated PAM. PAM efficacy can be affected by its own survival in the soil, environmental factors (such as temperature, pH, light, and moisture), the interactions established between the inoculated PAM and the indigenous soil microbiota, and the effectiveness of the establishment of the plant-PAM interaction (Campos et al., 2014; Rossi et al., 2021; Saberi Riseh et al., 2022; Saberi-Riseh et al., 2021). In addition, the involved mechanisms of action are very broad when evaluating the PAM diversity, specificity of each strain, and interaction with the host organism (Poudel et al., 2021). Taken together, these drawbacks hinder the widely and efficient application of PAMs in the agricultural and forest restoration sectors.

In this way, strategies are required that are able to decrease the fast decline of the microorganism population by increasing the microorganism survival in both storage conditions and after the inoculation process. An approach that has proven to be efficient in overcoming the challenges for more efficient application of PAMs in agriculture is microencapsulation (Figure 5) (Strobel et al., 2018). In addition to preserving the viability of microbial cells during the storage period, microencapsulation can improve the survival of PAMs in the soil and provide sustained release of the cells, thus achieving long-term effects (Table 5).

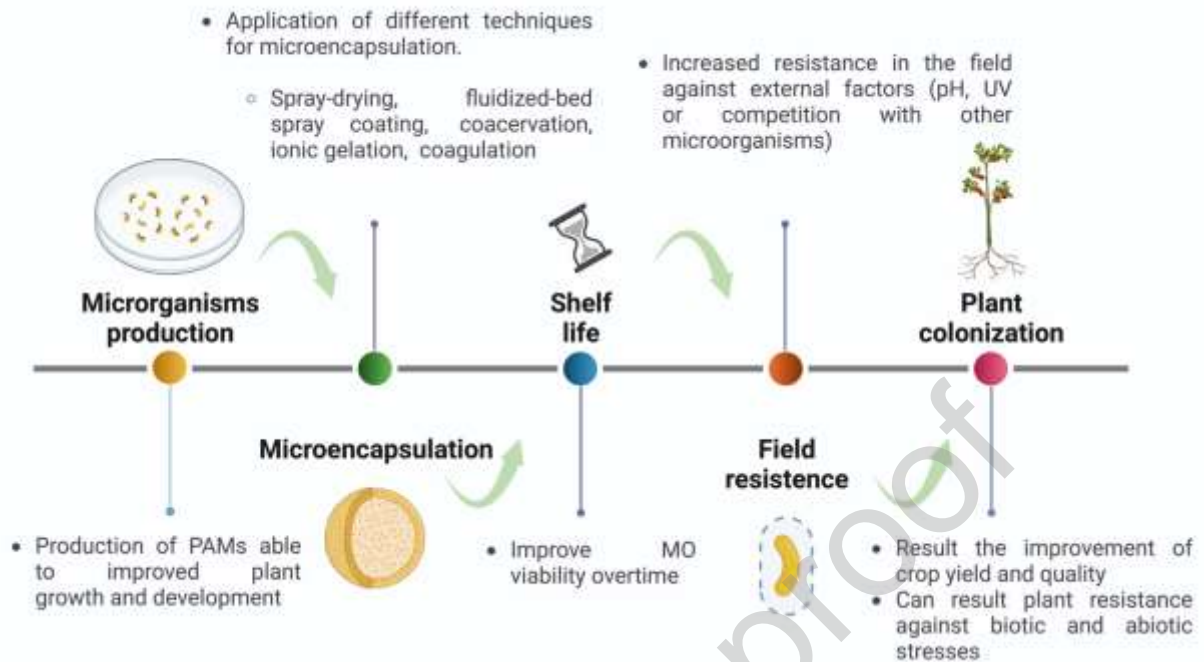


Figure 5: Advantages of microencapsulation of PAMs for agricultural application. Through encapsulation it is possible to increase the shelf-life, improve the field viability, and improve the biological activity and resistance to abiotic stress due to better plant colonization.

There are currently liquid (cell suspensions in water, oils, or emulsions) and powder (wettable powders, dust, and granules) formulations of PAMs (Saberi-Riseh et al., 2021). However, these formulations must be optimized for storage and maintenance of microorganism viability in field conditions. In this case, microencapsulation results in the formation of a physical barrier, as a shield that protects PAMs against environmental factors that could reduce their viability during storage or in the field. The capsule wall can be developed with different matrices (gelatin, alginate, chitosan xanthan gum, gellan gum, among others) that vary in size and structure, defining the microorganism release profile, the wall degradation, and the formulation shelf-life, as well as the adherence to the seeds in the case of seed treatments (Bosnea et al., 2014; Saberi-Riseh and Moradi-Pour, 2021). Inorganic wall materials, especially metal-based ones are not good candidates for PAMs encapsulation, since these materials are recognized as antimicrobial agents. In addition, it was also demonstrated that metal oxide particles (micro/nanoparticles) of copper and zinc oxide were able to affect negatively the soil microbiota as well as accumulate in both monocotyledonous (*Zea mays*) and dicotyledonous (*Crocus sativus*) plants species (Kim et al., 2013). It is

fundamental that the matrix used for microencapsulation is not toxic for the target microorganism, is prone to degradation by soil microbiome, and protects against abiotic and biotic factors that could reduce the viability of PAM cells, thus allowing more efficient colonization of the plant roots by the target PAM (Hii et al., 2021; Saberi Riseh et al., 2022)

Different methodologies have been used for PAM encapsulation, such as spray-drying, spray-chilling/cooling, lyophilization, fluidized bed, extrusion, emulsification, coacervation, and ionic, inverse, and thermal gelation (Saberi Riseh et al., 2022; Schoebitz and López Belchí, 2016; Vejan et al., 2019). Perez et al. (2018) prepared macrobeads for the encapsulation of *Azospirillum brasilense* Az39 and *Pseudomonas fluorescens* ZME4, singly or in combination (10^{10} CFU mL⁻¹ for both microorganisms). The microorganism viability remained high over time, showing 10^9 CFU g⁻¹ for *A. brasilense* and 10^8 CFU g⁻¹ of *P. fluorescens* after 12 months (Perez et al., 2018).

Spray-drying has been used for the microencapsulation of many microorganisms (Azaroual et al., 2021; Kawakita et al., 2021a; Saberi-Riseh and Moradi-Pour, 2021). In this case, it is necessary to evaluate the condition for drying (inlet and outlet temperature, flow, spray rate, and blow) in order to improve microorganism survival and powder yield (Azaroual et al., 2021; Kawakita et al., 2021a). Kawakita et al. (2021) evaluated two techniques for drying and encapsulating the bacterium *Collimonas arenae* Cal3 into alginate microcapsules, observing that spray-drying improved cell viability by 10-fold more than fluidized-bed spray coating (Kawakita et al., 2021a). In addition, Strobel et al. (2018) reported that encapsulating *Methylobacterium radiotolerans* by spray-drying using alginate as matrix resulted in no significant loss in cell viability after one year of storage. However, the effects of the developed formulation on plants were not tested (Kawakita et al., 2021b; Strobel et al., 2018).

In contrast, Saberi-Riseh et al. (2021) used the spray-drying technique and gellan gun and chitosan as matrices for the encapsulation of *Streptomyces fulvissimus* Uts22, aiming at the promotion of plant development and biological control. After the spray-drying process, the microorganism showed high survival rates (keeping 10^{10} CFU g⁻¹), that reduced but still maintained high levels after 60 days of storage (10^8 CFU g⁻¹). This bacterial strain produced several compounds (e.g., indole-3-acetic acid, 2,3-butanediol, N-alkylate and benzylamines), that improved wheat development (Saberi Riseh et al., 2021). However, the authors did not test the potential use of this formulation for plant stress alleviation.

For liquid formulations, bioencapsulation by coacervation has been a trend, because of many advantages in comparison to other methodologies, such as the ease of the process, the use of biopolymers, low temperature, and no use of organic solvents (Silva et al., 2019). Coacervation involves the electrostatic reaction between polymers with opposite charge with their consequent neutralization, yielding the polymer rich-phase named the coacervate complex (Bosnea et al., 2014; Yeo et al., 2005). This complex can improve the viability of the microorganisms in liquid medium (Qi et al., n.d.). Amiet-Charpentier et al. (1998) used this methodology to encapsulate rhizobacteria in gelatin-polyphosphate polymer, followed by a drying process using rotary agitator and silica. The authors reported that the microbial cell concentration decreased after the process from $\sim 5 \times 10^9$ CFU g⁻¹ oil suspension to $\sim 10^4$ CFU g⁻¹ dry particles, suggesting that the microparticle wall worked as an oxygen barrier, responsible for the bacteria death (Amiet-Charpentier et al., 1998).

Table 5: Impact of the microencapsulation of plant associative microorganisms (PAMs) on their viability. When tested, their biological effects on plants are also shown.

| <i>Type of microparticle</i> | <i>Microorganism</i> | <i>Methodology</i> | <i>Biological effects</i> | <i>Reference</i> |
|------------------------------|---|--|--|-----------------------------|
| Gellan gun and chitosan | <i>Streptomyces fulvissimus</i> Uts22 | Spray-drying | (+) PAM viability, biological control of <i>Gaeumannomyces graminis</i> , biomass accumulation of wheat plants | (Hii et al., 2021) |
| Alginate and maltodextrin | N ₂ -fixing bacteria (Alphaproteobacteria, Betaproteobacteria, Gammaproteobacteria, and Bacteroidetes) | Spray-drying | (+) PAM viability | (Campos et al., 2014) |
| Alginate | <i>Collimonas arenae</i> Cal3 | Spray-drying and fluidized-bed spray coating | (+) PAM viability | (Kawakita et al., 2021b) |
| Gellan gun and chitosan | <i>Streptomyces fulvissimus</i> Uts22 | Spray-drying | (+) PAM viability | (Saberi-Riseh et al., 2021) |
| Alginate | <i>Methylobacterium</i> | Spray-drying | (+) PAM viability | (Strobel et al., |

| | | | | |
|--|---|--------------------------------------|---|----------------------------------|
| | <i>radiotolerans</i> | | | 2018) |
| Gelatin–polyphosphate polymer | <i>Pseudomonas fluorescens-putida</i> | Coacervation | (+) PAM viability | (Amiet-Charpentier et al., 1998) |
| Chitosan | <i>Azospirillum brasilense</i> Az39 and <i>Pseudomonas fluorescens</i> ZME4 | Ionic gelation | (+) PAM viability | (Perez et al., 2018) |
| Alginate | <i>Trichoderma harzianum</i> | Ionic gelation | (+) Protection of the microorganism against ultraviolet radiation, soil microbiome | (Maruyama et al., 2020) |
| Carboxymethyl cellulose and cellulose nanocrystals | <i>Trichoderma harzianum</i> | Coagulation | (+) PAM viability | (Brondi et al., 2022) |
| N-hydroxysuccinimide - modified poly(γ -glutamic acid) | <i>Pseudomonas stutzeri</i> NRCB010 | Coating by electrostatic interaction | (+) PAM viability, protection against ultraviolet radiation, development of tomato plants (<i>Solanum lycopersicum</i> L.) | (Yang et al., 2021) |

As observed for PGR encapsulation, the evaluation of the effects of microencapsulated PAMs on plants grown under stress conditions has been little explored. Most published works have evaluated the impacts of encapsulation on the survival of the microorganism, seeking to increase its viability and survival during storage and use in the field (Table 5). In one of the few studies using plants submitted to abiotic stress, Wu et al. (2014) evaluated the ability of *Klebsiella oxytoca* Rs-5 encapsulated in alginate microparticles to promote growth and the colonization of cotton plants grown in saline soil. After 28 days of inoculation, the root colonization with bacterial cells was 100-fold higher in plants treated with encapsulated bacteria when compared to non-encapsulated plants. Bacterial encapsulation did not improve seed germination when compared to non-encapsulated bacteria, but was more effective in the induction of physiological responses to salt stress, such as the accumulation of proline, soluble sugars, and chlorophyll *a* and the alleviation of oxidative stress (Wu et al., 2014). Despite these positive results (Wu et al., 2014), further studies are still

needed to evaluate the potential of microencapsulated PAMs as a sustainable tool to mitigate the effects of abiotic stresses (Campos et al., 2022; do Espirito Santo Pereira et al., 2021; Manzoor et al., 2022).

However, the association between nanoparticles and PGR and microparticles and PGPR are poorly studied and not well understood. In addition, it is well known that the intrinsic properties of the micro/nanoparticles, the type of material used, their concentration and mode of application in the plants, as well as the duration of stress are able to change the response to the stressor. It is also important to keep in mind that the plant characteristics, species, stage of development, and medium used also affect the biological response of the micro/nano-based solutions.

The use of micro-nanoencapsulation for PGRs or microorganisms has great potential aimed at agricultural applications. This system may be developed by a green process, respecting and following many Sustainable Development Goals (SDGs), resulting in sustainable management for agriculture. Moreover, improving plant development and tolerance against biotic and abiotic stress, increases production and food safety. At the same time, the application of this system can reduce the amounts of pesticides and fertilizers applied in the field, protecting and softening the agricultural impact on the environment.

In order to make the application of micro/nanotechnology in association with PGR and PGPR more comprehensive for the development of an agricultural system that is resilient to biotic and abiotic stresses, as well as environmentally sustainable, studies should focus on understanding the mechanisms of action of these materials, taking into consideration i) the different plant species (for agronomic or ecological applications), ii) the life-cycle and stage of development of the plant; iii) the type of material used in the encapsulation, iv) application method, v) concentration used, vi) type and duration of the stressing agent; and vii) studies in relevant environments (greenhouse) and the field.

Furthermore, it is worth mentioning that, although not much studied, the combination of the two approaches presented in this review (PGR and PGPR) are promising strategies to be used together in mitigating the effects of climate change on plants.

5. Conclusions and looking forward

As demonstrated in the present review, biostimulant formulations, represented here by PGRs and PAMs, have the potential to revolutionize agronomic and ecological

approaches, generating beneficial effects on plant resilience to biotic and abiotic stresses, survival, and productivity of different types of plants. Although the potential of biostimulants is well documented in the literature, and has grown exponentially in recent years, the validation and commercialization of biostimulant formulations are still at an early stage when compared to synthetic pesticide formulations. In addition, it is worth mentioning that the vast majority of published studies are focused on species of agricultural interest, while the contribution of PGRs and PAMs for non-fruit trees or reforestation has not yet been deeply studied.

There are substantial differences in stress management taking into account species of agronomic and ecological interest, such as: *i*) lifespan (agricultural plants have a shorter lifespan than tree species); *ii*) the concentration of the biostimulating agent necessary to have the necessary biological effect, which tends to be species-specific; *iii*) CO₂ storage efficiency, since trees have more wood, and this is where most of the carbon is absorbed in terms of plant mass; *iv*) expected biological response, plants of agricultural interest are expected to have increased production even under stress situations while plant seedlings of ecological interest are expected to survive stress even if it costs them a momentary stop in their growth). In addition, the exploration of local biodiversity, through the prospection of microorganisms that are able to survive under stress conditions, is a promising strategy for the acclimation of different types of plants to climate change. Furthermore, the use of microorganisms from local biodiversity reduces the risks to the environment.

In this context, studies carried out to date are limited to the analysis of the desired biological effect, while studies on how these biostimulants affect/regulate cellular metabolism are insufficient. In addition, many studies focus on only one specific plant species, which makes the dataset insufficient to assess the real potential of the studied agent to become a potential commercial formulation. Moreover, many of the studies carried out apply extremely severe stress conditions and for a relatively short period of time, which are feasible in controlled environments (laboratory and greenhouses) but rarely encountered in environmental conditions.

Regarding micro-nanoencapsulation technology, there is no doubt that this is an effective tool to overcome the challenges associated with biostimulant formulations. Different types of polymeric matrices have demonstrated positive effects both in the stabilization of biostimulants and a direct effect on different plants studied, which makes these materials promising components of biostimulant formulations. However, it

is known that micro and nanoparticulate systems can positively and/or negatively affect the metabolism of different types of microorganisms, and concerns about the adverse effects of these materials on the environment, ecosystem, food safety, and human health have arisen and should be addressed.

Future studies involving the complex interactions between plant-microorganism-delivery systems and the ecosystem must be carefully evaluated, since different factors are involved and can affect this process, such as: *i)* the plant species and environmental interactions; *ii)* the presence or absence of stress; *iii)* the microorganism and/or PGR used; and *iv)* the physicochemical properties of the encapsulating agent. Taking these parameters into account, it will be possible to establish the effectiveness of the systems at the molecular level and, consequently, establish an optimal concentration to obtain the desired biological effect. In addition, it is important to emphasize that these studies must be conducted under field conditions in order to better understand and validate previous results obtained in controlled environments.

Last but not least, the academic community, regulatory bodies, and industries in the sector must join efforts in order to develop guidelines that ensure the development, application, and effective environmental tracking of these biostimulants based on micro-nanotechnology, in order to allow their effective use, without becoming possible agents of contamination and/or environmental degradation. In addition, the development of education programs to raise awareness of the general population, as well as of the farmers who will apply the technology, are fundamental to reduce the uncertainties associated with the use of this technology.

As shown in this review, PGR nanoencapsulation and plant-associated microorganism PAM encapsulation are promising tools to promote different beneficial changes at the biochemical, morphological, physiological, and molecular levels in plants, and it is possible to assume that commonly used synthetic molecules in agriculture are currently not able to promote this broad spectrum of changes. In this way, the use of these biostimulants proved to be an alternative with great potential in mitigating abiotic stress in plants of agricultural interest, as well as native tree species used in reforestation programs. We can also conclude that the field of biostimulant formulations based on micro-nanotechnology is highly aligned with the United Nations Development Goals and could contribute to accelerating the achievement of these goals.

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Ethics declaration

The authors declare no conflict of interest.

CRedit roles: **EVRC** – Conceptualization, editing & review; **AESP** – Conceptualization, writing and figure drawing; **IA** – Write original draft; **GCC** – Write original draft; **GG** – Write original draft; **CS** – Supervision and review; **LFF** – Supervision, review and editing; **HCO** – Conceptualization and review.

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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.

Highlights

- Biostimulants can promote plant resilience to abiotic stress
- Biostimulants improve plant health with minimal environmental damage
- Micro/nanoparticles can boost biostimulant application in agriculture
- Nano-based biostimulants aiming sustainable agriculture
- Nature-based micro/nanoformulations generate high crop yields

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