GMR
The Original

POLY-Γ-GLUTAMIC ACID (Γ-PGA): AN EMERGING GREEN BIOSTIMULANT FOR SUSTAINABLE CROP PRODUCTION

Akshaya S[1] , Jeyakumar P[2*], Ravichandran V[3], Arul L[4], Kavino M[5]

[1, 2*,3] Department of Crop Physiology, Tamil Nadu Agricultural University, Coimbatore, 641003, India
[4]Department of Biotechnology, Centre for Plant Molecular Biology and Biotechnology, Tamil Nadu Agricultural University, Coimbatore, 641003, India
[5]Horticultural Research Station, Tamil Nadu Agricultural University, Coimbatore, 641003, India

ABSTRACT
Poly-γ-glutamic acid (γ-PGA) is a biodegradable, water-soluble biopolymer increasingly recognized for its diverse applications in sustainable agriculture. Synthesized predominantly by Bacillus species through microbial fermentation, and it possesses distinctive characteristics including exceptional water retention, strong ion-chelating ability, biodegradability, and environmental safety. At soil level, γ-PGA improves soil quality by enhancing aggregation, porosity, and water-holding capacity, while reducing nutrient depletion. At physiological level, it stimulates the Ca^{2+}/calmodulin (CaM) signalling pathway, accelerating nitrogen assimilation through enhanced activity of nitrate reductase and glutamine synthetase, thereby promoting chlorophyll biosynthesis, photosynthetic efficiency and root development. These combined effects improve fertilizer efficiency and reduce dependence on chemical inputs. Empirical research from cereals, vegetables, legumes, and horticultural crops demonstrates a continuous improvement in biomass accumulation, nutrient efficiency, and yield; for example, γ-PGA application increased rapeseed fresh weight by 7.6-9.3% and grain yield by 6.5-11.0% and has been reported to enhance nitrogen use efficiency and chlorophyll content in several species. γ-PGA also mitigates abiotic stresses including drought, salinity and heavy metal toxicity, supporting its value for climate-resilient cropping systems. Despite the positive results, challenges persist regarding production costs, field unpredictability, and the absence of long-term studies. Overall, γ-PGA represents a promising eco-friendly biostimulant for sustainable and climate-resilient agriculture.

KEYWORDS: γ-Polyglutamic acid; biostimulant; Ca^{2+}/calmodulin (CaM) signalling; nitrogen use efficiency; abiotic stress mitigation; climate-resilient farming

1. INTRODUCTION
Modern agriculture is heavily dependent on chemical fertilizers and pesticides to sustain high crop productivity [1,2]. In Intensive cropping systems worldwide and particularly across major economies in Asia, the application of inorganic fertilizers has significantly increased to ensure elevated yields [3,4]. By 2050, global agricultural production is projected to be 60% higher than in 2005-07, with fertilizer demand rising accordingly [5]. Although these inputs have significantly enhanced food production, excessive fertilizer application can result in diminished nutrient use efficiency, nitrogen leaching, nonpoint source pollution, soil deterioration, and potentially reduced yields [6,7]. Farmers frequently apply excessive fertilizer to optimize crop yield, which can diminish fertilizer efficacy, damage soil health, and elevate environmental issues. Consequently, identifying sustainable alternatives to excessive fertilizer usage is crucial for the long-term advancement of agriculture.

To address these problems, increasing attention is being directed towards improved fertilizer, controlled-release fertilizers, urease and nitrification inhibitors, and ecologically friendly fertilizer synergists. Poly-γ-glutamic acid (γ-PGA) is a novel biopolymer that has garnered interest for its capacity to regulate plant growth. γ-PGA is an isopolypeptide composed of glutamic acid monomers interconnected by amide bonds between the α-NH_2 and γ-COOH groups [13,14]. This forms a nylon-like structure that is resistant to proteolytic degradation. Its atypical molecular structure enables the creation of hydrogels with multi-networks architecture, capable of retaining water up to 5000 times their own weight. γ-PGA possesses numerous potential applications in food, medicine, cosmetics, wastewater treatment, and, more recently, agriculture (Fig.1) [10].

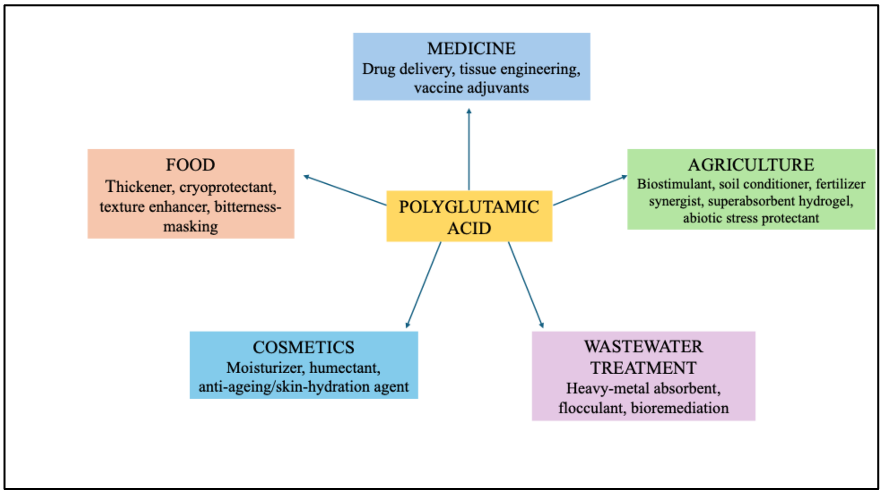

Fig. 1. Application of Poly-γ-glutamic acid (γ-PGA) in agriculture

Fig. 1. Major applications of polyglutamic acid (PGA) across different industrial and agricultural sectors. Polyglutamic acid serves as a versatile biodegradable biopolymer with broad applications in medicine, agriculture, food, cosmetics, and wastewater treatment. In medicine, it functions as a drug delivery carrier, tissue engineering scaffold, and vaccine adjuvant. In agriculture, PGA is used as a biostimulant, soil conditioner, fertilizer synergist, superabsorbent hydrogel, and abiotic stress protectant to improve crop productivity and resource use efficiency. In the food industry, it acts as a thickener, cryoprotectant, texture enhancer, and bitterness-masking agent. Cosmetic applications include its use as a moisturizer, humectant, and anti-aging/skin-hydration ingredient. In wastewater treatment, PGA is employed as a heavy-metal adsorbent, flocculant, and bioremediation agent due to its excellent metal-chelating and environmentally friendly properties.

This is due to its capacity to retain significant amounts of water, its biodegradable and edible nature, its strong complexation ability, its solubility in water, and its environmental benefits.

γ-PGA has gained popularity in sustainable agriculture. It has been recorded to enhance water and fertilizer conservation, reduce soil pollution, improve crop resilience to stress, stimulate root development, and extend the shelf life of agricultural products [11]. For instance, soil application of γ-PGA increased the fresh weight and grain yield of rapeseed by 7.57–9.26% and 6.46–10.98%, respectively [12].

Besides improving production, γ-PGA has been shown to influence plant physiological systems. γ-PGA accelerated nitrogen metabolism via activating the Ca^{2+}/calmodulin (CaM) signalling pathway, hence promoting plant growth [23]. γ-PGA fermentation broth, even in its unrefined state, significantly enhanced maize growth, soil moisture content, and microbial biomass [38]. Notably, although γ-PGA degrades in soil to glutamic acid which is a direct source of carbon and nitrogen to microorganisms. Numerous experimental investigations have demonstrated that γ-PGA is beneficial for agriculture; However, the available information remains fragmented across research focusing on crop yield, soil factors, stress physiology, and biotechnological production. This review consolidates existing knowledge on the effects of poly-γ-glutamic acid on agriculture, emphasizing (I) its chemical structure, and microbial production, (II) its physiological responses in plants centred on Ca^{2+}/calmodulin (CaM) mediated nitrogen metabolism, photosynthesis and root development, (III) its soil and rhizosphere effects, (IV) crop-specific responses and abiotic stress mitigation. This study identifies deficiencies in existing research and discusses potential future applications of γ-PGA in climate resilient and sustainable agriculture systems.

STRUCTURE AND PROPERTIES OF POLYGLUTAMIC ACID

Polyglutamic acid (PGA) is a naturally occurring anionic biopolymer composed of repetitive units of glutamic acid. γ-Polyglutamic acid (γ-PGA) has attracted considerable interest among its structural variants due to its unique physicochemical properties and broad applicability in agriculture, medicine, food processing, and environmental management. Numerous Bacillus species synthesize γ-PGA extracellularly [13]. It is extremely soluble in water, readily decomposes, is non-toxic, and possesses a great affinity for ion binding. These attributes render it particularly effective for long-term agricultural applications, such as a soil conditioner, fertilizer synergist, and plant growth enhancer.

The α-amino group and the γ-carboxyl group of D- and/or L-glutamic acid units are linked by amide bonds to create an isopeptide polymer known as γ-PGA. The γ-amide bond forms a backbone akin to nylon, imparting exceptional structural stability and conferring resistance to protease degradation [14]. The polymer may be D-PGA, L-PGA, or a DL-copolymer, contingent upon the specific microorganism involved and the fermentation circumstances. The polymer chain contains several free α-carboxyl groups, imparting γ-PGA significant hydrophilicity and polyanionic characteristics [15]. This facilitates the binding of metal ions and nutritional cations. This structural characteristic is crucial for agricultural applications as it aids in retaining nutrients and moisture in the soil.

The molecular weight (MW) of γ-PGA varies significantly, often ranging from 10^4 to 10^7 Da fluctuates according to microbial strain and fermentation parameters [16,17]. High-molecular-weight γ-PGA typically exhibits superior water absorption and viscosity, rendering it advantageous for hydrogel formation and soil enhancement. Conversely, low-molecular-weight γ-PGA has enhanced solubility, perhaps increasing its bioavailability and signalling effects inside plant systems. The molecular weight is influenced by factors such as pH, sources of carbon and nitrogen, levels of dissolved oxygen, and the genetic composition of the producing strain [18]. γ-PGA is environmentally benign and undergoes full degradation. Particular enzymes such as γ-glutamyl hydrolase and several microbial depolymerases present in soil ecosystems are capable of degrading it [19]. Upon the degradation of γ-PGA, it converts into glutamic acid, an amino acid utilized by plants and soil microorganisms as a nitrogen source. The biodegradability of γ-PGA distinguishes it from synthetic superabsorbent polymers, which can persist in soil and contribute to the accumulation of microplastics. The degradation products of γ-PGA do not produce detrimental residues, rendering it an excellent option for sustainable agricultural systems [20].

The pronounced hydrophilicity of γ-PGA is attributed to its many carboxyl groups, which readily interact with water molecules via hydrogen bonding. PGA hydrogels can absorb water up to 5000 times their weight, contingent upon their crosslinking and environmental conditions [21]. This remarkable capacity to retain water enhances soil moisture levels, reduces irrigation requirements, and aids crops in managing drought stress. Its solubility in water facilitates uniform distribution in soil and effective integration with liquid fertilizers.

γ-PGA is non-toxic to humans, animals, and plants, and does not elicit immunological responses. It has been extensively utilized in food (such as the fermented soybean product "natto"), medicine, and cosmetics, indicating its safety [22]. Toxicological assessments indicate that γ-PGA does not accumulate in tissues and is metabolized into amino acids that are already endogenous to the organism. This safety characteristic renders it an excellent option for environmentally sustainable agricultural input.

STRUCTURAL VARIANCES OF POLYGLUTAMIC ACID

Polyglutamic acid (PGA) has two primary structural variants: α-polyglutamic acid (α-PGA) and γ-polyglutamic acid (γ-PGA) (Fig. 2). The distinction between them lies on the type of amide linkage that unites the glutamic acid monomers. Both varieties consist solely of glutamic acid residues; nevertheless, their bonding configurations impart distinct physical and chemical properties, biological stability, and applications. Although α-PGA and γ-PGA share the same glutamic acid building block, the position of the amide linkage gives them markedly different architectures and behaviour. In α-PGA the monomers are joined through the α-carboxyl group, producing a conventional peptide backbone that resembles ordinary proteins and is readily cleaved by common proteases. In γ-PGA the linkage is formed between the γ-carboxyl group of one residue and the α-amino group of the next, creating an isopeptide bond and leaving every α-carboxyl group free along the chain. This arrangement gives the molecule a nylon-like backbone that resists enzymatic and chemical degradation and accounts for its exceptional stability [14]. The presence of numerous free α-carboxyl groups makes γ-PGA strongly polyanionic and highly hydrophilic, enabling it to bind water, metal ions, and nutrient cations far more effectively than the α-linked form. These same groups allow the polymer to be tailored, for instance through cross-linking into hydrogels, which is why γ-PGA rather than α-PGA is favoured for agricultural and environmental applications [15].

A further source of structural variation lies in the stereochemistry of the glutamate units. Depending on the producing strain and its glutamate racemase activity, the chain may be assembled from D-, L-, or a mixture of D- and L-glutamate, yielding D-PGA, L-PGA, or a DL-copolymer [18]. The relative proportion of the two enantiomers, together with the chain length, governs the polymer's solubility, conformation, and physicochemical behaviour. This structural tunability, absent in the α-linked variant, underlies the versatility of γ-PGA and its suitability as a sustainable agricultural input [20].

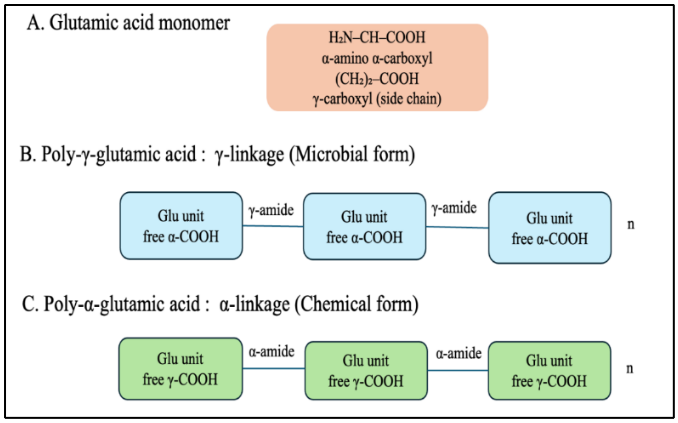

Fig. 2. Structural organization of glutamic acid and polyglutamic acid (PGA)

Fig. 2 Molecular structure of poly-γ-glutamic acid. (A) The glutamic acid monomer with its □-amino, □-carboxyl, and γ-carboxyl groups. (B) In γ-PGA, peptide bonds link the α-amino group of one residue to the carboxyl group of the next, leaving the α-carboxyl side groups free making it strongly water absorbing and able to bind nutrient cations. (C) Poly-α-glutamic acid joined through α-linkages.

PHYSIOLOGICAL RESPONSES OF PLANTS TO γ-PGA

γ-PGA exerts direct effects on plant physiology (Fig. 3). γ-PGA elevates the cytoplasmic free Ca^{2+} concentrations in plant cells and activates the Ca^{2+}/calmodulin (CaM) signalling pathways. When a CaM antagonist was applied, γ-PGA induced stimulation of nitrogen metabolism was suppressed, indicating that the response is Ca^{2+}/calmodulin (CaM) dependent [23]. This is mechanistically significant because Ca^{2+}/(CaM) acts as a second messenger that regulates the enzymes of nitrogen assimilation. In canonical pathway, nitrate absorbed by roots is reduced to nitrite by nitrate reductase (NR) and then to ammonium by nitrite reductase (NiR). The ammonium is subsequently assimilated into amino acids through the glutamine synthetase-glutamate synthase (GS-GOGAT) [24]. By raising cytoplasmic Ca^{2+} and activating CaM, γ-PGA enhances the activity of these assimilatory enzymes, accelerating the conversion of inorganic nitrogen to glutamine, glutamate, and downstream amino acids and proteins. Consistently, γ-PGA treated plants show decreased nitrate and free amino acid pools alongside increased soluble protein, reflecting more efficient assimilation rather than uptake [25].

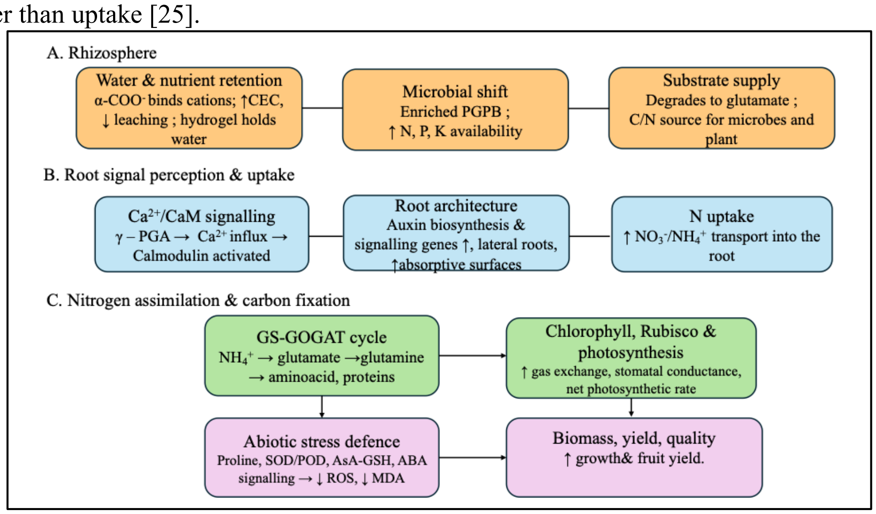

Fig. 3. Proposed mechanism of γ-polyglutamic acid (γ-PGA)-mediated enhancement of plant growth and stress tolerance.

Fig. 3 Mechanistic role of γ-PGA action in plants, organised by site of action. In the rhizosphere, γ-PGA improves water and nutrient retention, shifts the microbial community toward plant growth promoting taxa, and supplies carbon and nitrogen on degradation. At the root, it elevates cytoplasmic Ca2+ and activates calmodulin signalling, promotes auxin-mediated lateral root formation, and enhances nitrogen uptake. Absorbed nitrate is reduced by nitrate reductase and assimilated through the glutamine synthetase-glutamate synthase (GS-GOGAT) cycle into amino acids and protein, supporting chlorophyll and rubisco synthesis and raising photosynthetic rate. Parallel osmolyte, antioxidant defences and ABA signalling confer abiotic stress tolerance. These processes converge to increase biomass, yield, and quality

These improvements in nitrogen assimilation have a direct payoff for photosynthesis. Nitrogen and magnesium are both built into the chlorophyll molecule, and nitrogen is also the main building block of Rubisco and the photosynthetic machinery, so plants that assimilate nitrogen more efficiently can build more chlorophyll and fix carbon more effectively. In heat stressed Chinese cabbage, γ-PGA priming raised the chlorophyll content and improved gas exchange parameters while supporting better vegetative growth [26] and in maize, RNA-sequencing showed that photosynthesis related genes were upregulated alongside the higher chlorophyll content and photosynthetic rate [27]. γ-PGA also slows the breakdown of chlorophyll under stress, which keeps the photosynthetic apparatus functional for longer. Collectively, these effects enhanced the size and longevity of the plant photosynthetic capacity. Many of these physiological responses are underpinned by structural changes in the root system. γ-PGA has been shown to promote root elongation and to stimulate the formation of lateral roots, collectively expanding the surface area available for water and nutrient uptake. In maize, this effect was linked to the upregulation of genes involved in auxin biosynthesis and signalling, which coincided with a marked increase in lateral root number and a notable enrichment of plant growth promoting bacteria in the rhizosphere [28]. The mechanisms driving this response appear to involve both calcium signalling pathways and the improved moisture and nutrient conditions that γ-PGA generates in the root zone which boosted the greater root development.

More extensively branched root architecture enhances the plants capacity to acquire nitrogen and water required to support carbon assimilation and photosynthetic activity. Overall, these observations suggests a self-reinforcing cycle, which is enhanced Ca^{2+}/(CaM) signalling accelerates nitrogen assimilation, which in turn supports greater chlorophyll synthesis and photosynthetic output. The consistent growth promoting effects of γ-PGA observed across diverse crop species can be attributed to the coordinated interaction of signalling, metabolic, and structural responses working synergistically (Table 1).

Table 1. Summary of the physiological mechanisms of γ-PGA action in plants

Signalling	Physiological effect	Key molecules	References
Surface perception & ROS relay	H_2O_2 burst at root surface; Ca^{2+} influx relayed root to leaf	RbohD, RbohF, H_2O_2, Ca^{2+}	[33]
Ca^{2+}/CaM signalling	Activation of nitrogen-assimilation enzymes	Ca^{2+}, calmodulin (CaM)	[23]
Nitrogen assimilation	Faster conversion of nitrate to amino acids and protein	NR, NiR, GS-GOGAT	[23,24]
Carbon–nitrogen metabolism	Higher soluble sugars; lower nitrate and free amino acids; improved N, P, K uptake	Glutamine synthetase, sugars	[25]
Photosynthesis	Increased chlorophyll and photosynthetic rate; delayed chlorophyll breakdown	Chlorophyll, Rubisco	[26,27]
Root development	Root elongation and lateral-root formation; larger uptake surface	Auxin biosynthesis & signalling	[28]

Hormonal cross-talk	Integrated growth and stress-defence response	Brassinolide, jasmonic acid, ABA	[52]

Signal perception and hormonal cross-talk

An important question is how a water-soluble polymer such as γ-PGA is perceived by the plant. Fluorescent-labelling studies indicate that γ-PGA does not enter the cytoplasm but instead attaches to the surface of the root protoplast, where it acts as an extracellular elicitor rather than a nutrient taken up directly [33]. At the root surface it triggers a burst of hydrogen peroxide (H_2O_2) by up-regulating the respiratory-burst oxidase genes RbohD and RbohF; the elicited H_2O_2 then drives an influx of Ca^{2+} into root cells, and this Ca^{2+} signal is transmitted through the stem to the leaves, where it provokes a second H_2O_2 burst that promotes growth and stress tolerance [33]. This H_2O_2–Ca^{2+} relay links the surface perception of γ-PGA to the Ca^{2+}/CaM-dependent activation of nitrogen metabolism. Beyond H_2O_2 and Ca^{2+}, γ-PGA engages several phytohormone pathways: it induces cross-talk among Ca^{2+}, H_2O_2, brassinolide, and jasmonic acid in leaves [52], and, under drought, promotes abscisic acid (ABA) biosynthesis and accumulation, the canonical signal for stomatal closure. This multi-hormone integration explains why the physiological effects of γ-PGA extend simultaneously to growth promotion and stress defence.

Carbon–nitrogen metabolism and nutrient distribution

The influence of γ-PGA on plant physiology extends beyond nitrogen assimilation to the coupled metabolism of carbon and the partitioning of nutrients. Isotope-labelling experiments using $^{13}C_1$-^{15}N-L-glutamic-acid-derived γ-PGA showed that about 26.5% of the γ-PGA-derived nitrogen is taken up as intact organic molecules within the first 24 h, with roughly 29.7% of the labelled nitrogen recovered in the plant and 59.4% remaining in the soil at harvest, and about 5.64% of total plant nitrogen ultimately derived from γ-PGA [25]. The same study demonstrated that γ-PGA simultaneously improved plant uptake of nitrogen, phosphorus, and potassium, strengthened root biomass and activity, and altered carbon–nitrogen metabolism, evidenced by higher soluble-sugar contents together with lower nitrate and free-amino-acid pools [25]. The decline in free amino acids and nitrate alongside rising soluble protein and sugars indicates that γ-PGA shifts the plant toward more efficient assimilation and carbon fixation rather than mere nutrient accumulation. Because γ-PGA behaves partly as a slow-release organic nitrogen source and partly as a signalling elicitor, its physiological benefit reflects both a nutritional and a regulatory contribution, a dual role that distinguishes it from conventional inorganic fertilizers.

The magnitude of these physiological responses is modulated by the molecular weight of γ-PGA. High-molecular-weight γ-PGA, with its greater water-holding and ion-binding capacity, acts predominantly through improvement of the root-zone environment, whereas low-molecular-weight γ-PGA is more readily mobile and is thought to enhance direct signalling and biostimulant effects within the plant.

STRESS TOLERANCE

γ-PGA enhances plant resilience to abiotic stresses through two complementary routes. The first is indirect, operating through the soil. Its water-holding and ion-binding capacity buffers the rhizosphere against drought, salinity and metal toxicity. The second is direct and physiological by accumulation of osmolytes, activation of antioxidant defences, and modulation of stress hormones. Recent transcriptomic and biochemical studies have confirmed γ-PGA as a biostimulant rather than a soil conditioner. The stress-reducing effects are especially significant in climate change scenarios, when climatic extremes progressively jeopardize crop productivity (Table 2).

Table 2. γ-PGA in Stress Tolerance

Stress type	Effect	Mechanism	References
Drought			
Maize	Higher dry weight, ABA, soluble sugar, proline, chlorophyll and photosynthetic rate under severe drought	Upregulation of ABA biosynthesis, signal transduction and photosynthesis genes; PGPB enriched in rhizosphere	[27]
Cotton	Proline, SOD and POD raised; MDA lowered	Osmotic adjustment and reduced membrane lipid peroxidation	[29]
Rice (seed priming)	Reduced ROS; higher soluble sugars and proline; improved germination	Priming of antioxidant and osmolyte metabolism before radicle emergence	[30]
Oilseed rape	ABA accumulation increased	Induction of ABA-biosynthesis genes	[31]

		driving stomatal closure	
Soil-mediated	Rhizosphere moisture retained; microbiota restructured under drought	Hydrogel water retention plus glutamate-driven shift to stress-tolerant taxa	[38, 41]
Temperature			
Rapeseed (cold)	SOD and CAT increased; fresh weight and chlorophyll raised	Ca^{2+}–H_2O_2 signalling crosstalk activating oxidative defence	[33, 52]
Chinese cabbage (heat)	Carotenoid biosynthesis, photosynthesis and antioxidant system enhanced	Transcriptional reprogramming of carotenoid and ROS-signalling pathways (RNA-Seq confirmed)	[26]
Salinity			
Wheat	SOD, POD and CAT increased; K^+ uptake raised, Na^+ uptake reduced	Antioxidant induction with restored K^+/Na^+ ratio	[50]
Maize	Osmotic, ionic and oxidative components of salt injury jointly reduced	Osmolyte accumulation, ion exclusion, and enrichment of salt-tolerant PGPB in the rhizosphere	[32]
Rapeseed	Proline accumulation, chlorophyll and fresh biomass increased	Osmotic adjustment sustaining photosynthetic capacity	[60]
Rice	K^+, Ca^{2+} and Mg^{2+} uptake enhanced; proline and soluble sugars raised	Improved osmotic adjustment and nutrient balance	[30, 32]
Heavy metals			
Cd and Pb (cucumber)	Metal uptake and bioavailability reduced; MDA lowered, proline and total antioxidant capacity raised	Carboxyl chelation shifts metals to complexed pools; chelation rates 27.26% (Pb), 14.28% (Cd)	[34]
Cd (wheat, rice, pepper)	Cd uptake and translocation reduced; growth and micronutrient status maintained	Modulation of ascorbate–glutathione metabolism alongside rhizosphere immobilisation	[35, 36, 37]
Cr (tobacco, cucumber)	Cr accumulation and bioavailability lowered; leaf metabolite profile and rhizosphere community partly restored	Chelation of Cr(III) and Cu(II); altered bacterial community assembly	[46, 49]

Drought and Temperature stress

Drought stress inhibits plant growth by reducing water availability, decreasing stomatal conductance, impairing photosynthesis, and inducing oxidative damage. PGA assists plants in managing drought stress by enhancing soil water retention and maintaining moisture in the rhizosphere. Due to its carboxyl groups that attract water, it functions as a hydrogel, retaining moisture in the root zone and reducing evaporation losses. γ-PGA enhanced soil water retention and improved maize growth under conditions of limited water availability [27,30]. In cotton, exogenous γ-PGA under drought raised proline content and the activities of superoxide (SOD) and peroxidase (POD), while lowering malondialdehyde (MDA), indicating stronger osmotic adjustment and reduced membrane lipid peroxidation [29]. In rice, γ-PGA treatment reduced reactive oxygen species accumulation and raised soluble sugar and proline levels [30]. In oilseed, γ-PGA promoted the expression of ABA-biosynthesis genes and increased ABA accumulation, the canonical drought signal that drives stomatal closure and the stress response cascade [31]. These mechanisms improved the soil water status and enhanced yield stability under conditions of water scarcity.

γ-PGA also buffers plant against thermal extremes. Under cold stress, γ-PGA improved the physiological status of rape seedlings by raising fresh weight and chlorophyll through calcium signalling[33]. Under heat stress, γ-PGA priming of Chinese cabbage enhanced thermos tolerance by promoting carotenoid biosynthesis, sustaining photosynthesis, and modulating ROS signalling, with RNA-Seq confirming the underlying transcriptional changes [26]. γ-PGA mitigates both cold and heat stress by priming of stress-defence pathways rather than a stress-specific effect.

Salinity and Heavy metal toxicity

Salt stress damages plant through osmotic stress, specific Na+/Cl- ion toxicity, and nutrient imbalance. At the soil level, the polyanionic γ-PGA backbone binds cation and by improving aggregation and porosity, helps leach excess salts and retain Ca2+ and Mg2+ in plant available form. In maize, γ-PGA improved salt resistance by simultaneously easing osmotic, ionic and oxidative stress, and by enriching salt tolerant plant growth promoting bacteria in the rhizosphere [32]. This dual action limiting Na+ at the root surface while improving the plants own osmotic and antioxidant capacity which allows treated plant to maintain root growth and nutrient uptake under moderate salinity.

Contamination of cadmium, lead, copper, zinc threatens both crop productivity and food safety, since these metals accumulate in plant tissue. Carboxyl groups form stable complexes with these metal cations, lowering their solubility and bioavailability and thereby reducing root uptake [34]. Beyond direct chelation, γ-PGA improves soil structure and microbial activity, which further immobilizes contaminants in the rhizosphere. Because the polymer itself biodegrades to glutamic acid, this remediation occurs without leaving a persistent synthetic residue.

Pepper grown on Cd-contaminated soil, γ-PGA application increased below and above ground biomass by 33.3% and 21 % respectively, improved root traits such as total length and surface area and shifted the balance of micronutrient uptake while limiting Cd accumulation [35]. In wheat under Cd stress γ-PGA reinforced tolerance by modulating the ascorbate-glutathione (AsA-GSH) cycle thereby protecting photosynthetic performance, lowering malondialdehyde content and electrolyte leakage and preserving plant height and biomass [36]. Cd-alleviating effects of γ-PGA have also been reported in rice [37]. Together, the chemical immobilization in the soil and the strengthened antioxidant defence within the plant reduces both uptake and toxicity of heavy metals.

EFFECTS OF γ-PGA ON EARLY ESTABLISHMENT

γ-PGA has been employed as seed coating agent, facilitating accelerated and more uniform germination. Its water absorbing capacity speeden and evens out seed germination, and in rice it raised the seedling vigour index and increased seedling dry weight, total sugars, free amino acid, and chlorophyll relative to control [30]. In maize, it increased emergence and seedling survival under drought [38].

Germination and the earliest stages of seedling development are among the most delicate phases of the plant life cycle, and plants are especially sensitive to abiotic stresses such as drought, salinity, and extreme temperatures during this window [55,56]. γ-PGA, a naturally derived and biodegradable biopolymer, has attracted attention as a biostimulant capable of enhancing seed vigour and early growth [57,58]. Its water-absorbing capacity promotes rapid and uniform hydration of the seed, a crucial first step in germination. In tobacco, γ-PGA accelerates germination by shortening germination time and enhancing the activity of key hydrolytic and antioxidant enzymes, including amylases, peroxidases, and catalases [59]. Elevated amylase and protease activity improves mobilization of stored seed reserves, while increased antioxidant enzyme activity mitigates oxidative stress during early development.

Beyond germination itself, γ-PGA strengthens the developing root system: in maize it increased seedling fresh weight and lateral root length, an effect linked to elevated auxin synthesis and signalling that drive root elongation and branching [28]. γ-PGA also enriches rhizosphere microbial communities, creating a more favourable environment for seedling growth. In rapeseed seedlings, γ-PGA has been shown to alleviate salt stress by promoting proline accumulation, raising chlorophyll content and fresh biomass accumulation, and thereby improving overall seedling health and stress resilience [60]. Taken together, these effects indicate that γ-PGA facilitates early plant establishment by improving water availability, enzyme activity, hormonal balance, and root development, effects that enhance seedling resilience, stress management, and ultimately crop yield.

EFFECTS OF γ-PGA ON SOIL STRUCTURE

γ-PGA influences agricultural soil through its polyanionic, high-molecular-weight structure and its many carboxyl groups, which interact with soil particles, water, nutrient ions, and microorganisms simultaneously (Fig. 4).A key physical benefit of γ-PGA is that its long polyanionic chain acts as a binding and hydrating agent (Table 3). It physically bridges clay, silt, and organic matter into macro aggregates, while its carboxyl groups form cation bridges with Ca2+ and Mg2+ that stabilize those aggregates against dispersion. Because aggregation, porosity, and water-holding are physically interdependent and this γ-PGA improves all three at once. In maize fields, γ-PGA fermentation broth increased aggregate stability and reduced bulk density, promoting macroaggregate formation and easing compaction [38]. A two year field trail in northwestern desert soils reported higher soil moisture retention and aggregate stability alongside improving improved cotton yield and nutrient uptake efficiency [39]. This aggregate structure creates a more favourable pore size distribution, improving aeration and reducing the risk of the anaerobic, denitrifying condition that waste nitrogen. Its hydrophilic carboxyl groups also hold large amount of water in hydrogel form up to several thousand times its own weight, depending on molecular weight and crosslinking which is especially valuable in sandy and drought prone soils where rapid drainage limits crop growth.

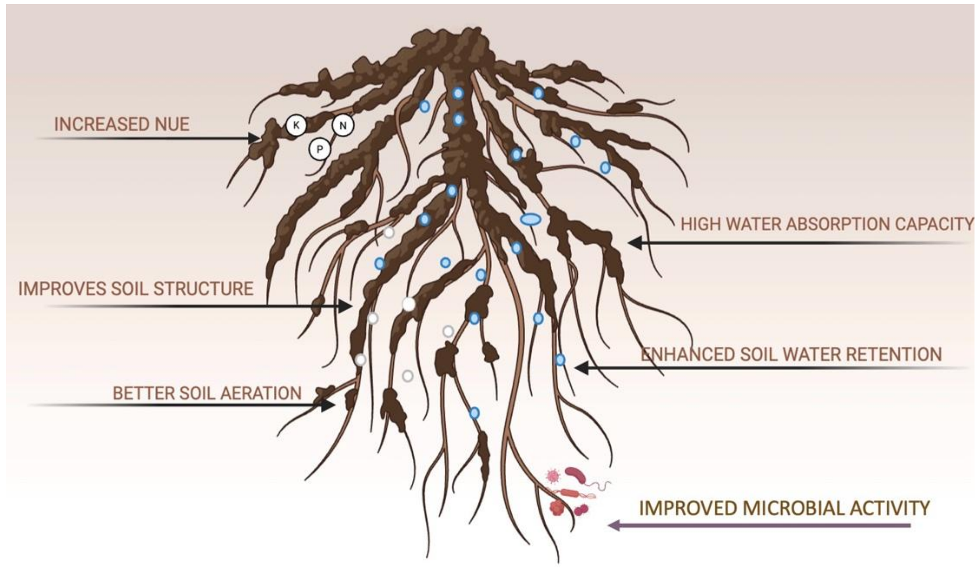

Fig. 4 Beneficial effects of γ-polyglutamic acid (γ-PGA) on the rhizosphere and plant growth. γ-PGA enhances soil water retention, improves soil structure and aeration, stimulates beneficial microbial activity, increases nutrient use efficiency (NUE), and promotes water and nutrient uptake through the root system, thereby supporting improved plant growth and stress resilience.

Table 3. γ-PGA as a soil conditioner: principal functions and mechanism

Function	Observed effect	Mechanism	References
Soil aggregation and structure	Larger, more water-stable aggregates; lower bulk density and higher porosity	Polymer bridging of clay, silt and organic particles; carboxylate–Ca2+/Mg2+ cation bridges	[38, 39, 47, 61]
Water retention	Higher field capacity and plant-available water	Hydration of side-chain carboxyl groups and hydrogel swelling	[45, 62, 63]
Water movement	Reduced infiltration rate and surface evaporation	Swollen polymer narrows conducting pores and lengthens the vapour path	[45, 63, 64, 67]
Nutrient retention	Greater NH4+ and K+ retention; higher available N and P	Carboxylate groups add exchange sites and raise CEC; cation chelation limits phosphate fixation	[25, 40, 67]
Nitrogen conservation	Lower nitrate leaching and NH3 volatilisation; improved nitrogen use efficiency	Electrostatic binding of NH4+ with transient microbial immobilisation	[43, 44, 65, 66]
Soil biological activity	Increased organic matter, enzyme activity and microbial biomass; beneficial taxa enriched	Degradation to glutamate supplies labile carbon and nitrogen to soil microorganisms	[38, 41, 42, 43, 46]
Saline, sodic and acidic soil amelioration	Reduced soluble Na+ and salinity; raised pH in acidic soils	Competitive Na+ binding and displacement; protonation of carboxylate groups consumes H+	[67, 68, 69]
Heavy-metal immobilisation	Lower bioavailable Cd, Pb and Cr and reduced uptake by crops	Free carboxyl groups chelate metal cations into stable complexes	[34, 46, 49]
Biodegradability	Fully mineralised in soil; no persistent synthetic residue	Cleavage by γ-glutamyl hydrolases and microbial depolymerases to glutamic acid	[34, 65]

EFFECTS OF γ-PGA ON NUTRIENT RETENTION AND FERTILIZER EFFICIENCY

γ-PGA's Carboxyl group bind cation for aggregation also make γ-PGA an effective nutrient retention agent (Table 4). By electrostatically holding $NH4^{+}$, K^{+}, $Ca2^{+}$, Mg^{2+} and by raising the soil cation exchange capacity, γ-PGA keeps nutrients in plant available forms within root zone and limits their loss to leaching and runoff. γ-PGA's capacity to chelate cations such as Ca^{2+}, Fe^{3+}, and Al^{3+}, which typically form insoluble phosphate and precipitate micronutrients complexes in calcareous or acidic, may enhance phosphorus, iron, zinc soluble and mobile in the rhizosphere. These properties make γ-PGA useful as a matrix or coating in controlled-release fertilizers. Its polymer network and moisture responsive hydrogel behaviour slow nitrogen leaching and γ-PGA coated formulations have outperformed uncoated fertilizers in nitrogen retention and use efficiency. Unlike petroleum derived coatings, γ-PGA biodegrades to glutamic acid, leaving no synthetic residue. At soil level, γ-PGA application reduced nitrogen loss and raised rapeseed fertilizer use efficiency and yield [40]. Field studies confirm these benefits: in wheat, γ-PGA applied with urea raised nitrogen use efficiency (NUE) by 11.3% and grain yield by 7.2% relative to urea alone [43], while in maize under mulched drip irrigation it cut cumulative ammonia volatilization by 8.4–19.4% and increased grain yield by 4.9–21.6%, with an optimal field rate near 70 kg/ha [44]. At the soil level, γ-PGA retains ammonium and reduces gaseous and leaching losses, and at the plant level it accelerates nitrogen assimilation through the Ca^{2+}/CaM pathway and the NR/GS-GOGAT enzymes.

The agronomic benefits of γ-PGA have been documented across cereals, vegetables, industrial, oilseed, and plantation crops, with the optimal form and dose depending on whether the polymer is used as a foliar biostimulant or a soil conditioner. Reported strategies span low-rate foliar sprays of the order of tens of mg L^{-1}, soil-amendment rates from a few mg kg^{-1} of soil up to about 0.1% (w/w), and field application rates of the order of tens of kg ha^{-1}.In cereals, the response is driven mainly by improved nitrogen economy and soil moisture: γ-PGA applied with urea raised nitrogen use efficiency by 11.3% and grain yield by 7.2% in wheat [43], and in maize under mulched drip irrigation it reduced ammonia volatilization by 8.4–19.4% and increased grain yield by 4.9–21.6% at an optimal field rate near 70 kg ha^{-1} [44].

In vegetables, effective doses are considerably lower. Foliar priming of Chinese cabbage with γ-PGA at 20 mg L^{-1} (daily sprays for five days) was sufficient to improve growth and heat tolerance [26]. In cucumber, γ-PGA acts chiefly as a bio-chelator of heavy metals: under Cd and Pb stress it reduced metal uptake and oxidative damage in a dose-dependent manner, with in-vitro chelating rates of 27.26% for Pb and 14.28% for Cd [34], while under Cr and Cu stress it lowered metal content in plant tissue by 67.45–86.77% (Cr) and 94.67–98.21% (Cu) and raised fruit biomass by 13.5% and 25.3%, respectively [49].In industrial and oilseed crops, soil-scale application predominates. A two-year field trial in the barren desertified soils of Northwest China showed that γ-PGA improved water-stable aggregation and nitrogen and phosphorus uptake efficiency, with the highest water–fertilizer productivity and net profit obtained at about 65 kg ha^{-1} [39], and in oilseed rape soil application increased fresh weight and grain yield [12].In plantation crops, γ-PGA has been evaluated for heavy-metal remediation: in tobacco grown on Cr-contaminated soil (202 mg kg^{-1} Cr), a low rate of 5 mg kg^{-1} markedly increased root and shoot biomass and reduced tissue Cr content by about 18.1% (root) and 13.0% (shoot), with parallel improvements in leaf metabolite profiles and the soil microbial community [46]. Across these studies, γ-PGA consistently improved yield, nutrient-use efficiency, and stress tolerance, confirming its versatility as an agricultural input while underscoring that effective dose and delivery differ markedly between foliar and soil applications.

Table 4 Role of γ-PGA in Nutrient Use Efficiency (NUE) and as Fertilizer Synergist

Aspect	Reported Effects	Mechanism of Action	References
Nutrient retention	Reduced nutrient leaching; improved nutrient availability in root zone	Chelation and adsorption via carboxyl and amino groups; improved soil aggregation	[40]
Soil structure improvement	Enhanced water holding capacity; improved N and P availability	Increased aggregation, porosity, and moisture retention	[39,45]
Nitrogen use efficiency (NUE)	Increased N accumulation and utilization; enhanced dry matter in reproductive organs	Enhanced urease, sucrose, and catalase activities; increased microbial N	[43]
Controlled-release fertilizer	Regulated and sustained urea release	γ-PGA-coated urea synchronizes nutrient release with crop demand	[44]
Cation exchange	Increased ammonical nitrogen retention	Anionic polymer with multiple carboxyl groups enhances NH_4^+ retention	[40]
Drought mitigation in nutrient uptake	Improved N, P, Ca, Mg availability under water deficit	Chelation and biostimulant activity; improved SOM and nutrient transformation	[41]
Phosphorus bioavailability	Reduced fixation; increased soluble P	Chelation of Ca^{2+}, Fe^{3+}, Al^{3+}; improved rhizosphere dynamics	[39]

Soil microbial community and the rhizosphere

As γ-PGA degrades in soil to glutamic acid, it supplies a readily usable carbon and nitrogen source to microorganisms, and its reshapes the soil microbial community. Adding γ-PGA fermentation broth markedly increases soil bacterial diversity and biomass while reducing the relative abundance of pathogenic fungi. In maize rhizosphere , it enriched plant growth promoting genera such as Bacillus, Pseudomonas, and Burkholderia [38]. Integrated metagenomic and metabolomic analysis under drought showed that γ-PGA restructured the soil microbiota towards carbon, nitrogen, and phosphorus cycling, with amino acid and vitamin metabolism pathways significantly enriched [41]. In sandy soil, γ-PGA at a 4% rate improved soil quality and regulated the alfalfa rhizosphere community [9] and in degraded urban land it raised the abundance of Proteobacteria and Actinobacteria across wheat growth stages [42]. Notably the application method influenced more strongly than the application rate [40]. Consistent with this, γ-PGA has been reported to enhance soybean nodulation and biological nitrogen fixation by improving rhizosphere conditions and stimulating beneficial microbes, increasing plant biomass [47,48].This microbial restructuring not only favours nutrient cycling and growth-promoting taxa and suppressing pathogen, γ-PGA links its physical and chemical effects on the soil to the plant growth. Most of this evidence comes from short term pot or single season trails, and long term, field scale study of repeated γ-PGA application for microbial community stability remains insufficiently characterized.

Increased water retention capacity

One of the most remarkable attributes of γ-PGA is its exceptional water retention capacity (Table 5). The polymer has several hydrophilic carboxyl groups that readily associate with water molecules. γ-PGA can absorb water in hydrogel form, potentially up to several thousand times its weight, contingent upon its molecular weight and degree of crosslinking [38].

The incorporation of γ-PGA into soil enhances its water retention capacity, reduces evaporation rates, and increases water availability for plants. This effect is particularly beneficial in sandy soils and regions prone to drought, where rapid drainage and evaporation hinder crop growth. Soils treated with γ-PGA fermentation broth exhibited significantly higher water content and microbial biomass compared to untreated soils [39]. Increased soil moisture facilitates nutrient absorption by the roots and sustains metabolic activity, even under conditions of limited water availability. Improved water retention results in reduced watering frequency, hence conserving water in agriculture.

Table 5. Effects of γ-PGA on Water Use Efficiency (WUE)

Parameter	Observed Effects	Mechanism	References
Soil water parameters (Wheat, NW China)	Increased θs (6.3–11.5%), field capacity (8.4–15.3%), plant available water (5.1–12.5%)	Improved soil pore structure and moisture retention	[39]
Sandy soil improvement	Increased θs, field capacity, permanent wilting point; optimal at 1.2% (w/w)	Reduced large pores (2–15 µm); increased small pores (0.2–2 µm)	[45]
Alternate wet–dry cycles	Improved soil structure and retention at 0.8% PGA	Enhanced aggregation and moisture stabilization	[39]
Reduced evaporation & percolation	Enhanced WUE and yield	Biodegradable superabsorbent polymer properties	[45]
Water deficit + P fertilization	Increased WUE and yield	Accelerated water uptake; maintained osmotic balance	[39]

γ-PGA APPLICATION METHODS

The mode of γ-PGA delivery determines both the effective concentration and the dominant mechanism of action. Three application methods used are seed treatment, foliar spraying, and soil amendment each operating in a distinct concentration regime and eliciting a different physiological response.

Seed Treatment (Priming)

Used at germination and early establishment, γ-PGA acts as a nutri-priming and biostimulant agent, improving seedling vigour, root architecture, and drought resilience.Seed priming with γ-PGA improved the germination performance of rice under drought-simulated soil conditions across eleven indica and japonica varieties, and was particularly effective in the most drought-susceptible indica varieties, acting as a source of glutamic acid for GABA-mediated stress tolerance and nitrogen mobilization in germinating seeds [30]. In maize, treating seedlings with a 50 mg L^{-1} γ-PGA solution for seven days increased root fresh weight, with lateral root number rising by 71.87% relative to control, driven by up-regulation of auxin-biosynthesis and auxin-signalling genes [28]. Complementary work with glutamic acid, the monomer released on γ-PGA degradation, showed that seed priming at 0.5 mmol L^{-1} gave the most consistent gains in maize seedling vigour (epicotyl and root growth, biomass, chlorophyll) while lowering H_2O_2 and malondialdehyde and raising SOD and peroxidase activity, indicating reduced oxidative damage [51].

Foliar Application

As a foliar spray, γ-PGA operates at low concentrations (mg L^{-1}) as a signalling biostimulant, accelerating nitrogen metabolism and priming stress-defence pathways rather than acting as a bulk nutrient source [8]. In Chinese cabbage, foliar priming with γ-PGA at 20 mg L^{-1} applied as daily sprays for five days before heat stress increased plant dry weight by 39.39%, total chlorophyll by 23.12%, and carotenoid content by 24.00% relative to control, while lowering malondialdehyde, electrolyte leakage, and superoxide anion and raising SOD, CAT, APX, and POD activity [26]. In oilseed rape, exogenous foliar application of γ-PGA enhanced leaf stress defence by inducing cross-talk among Ca^{2+}, H_2O_2, brassinolide, and jasmonic acid signalling [52]. The underlying nitrogen-metabolism mechanism was established in Chinese cabbage, where γ-PGA accelerated nitrogen assimilation through the Ca^{2+}/calmodulin (CaM) signalling pathway, linking foliar γ-PGA directly to enhanced nitrogen use and growth [23].

Soil Application

Incorporated into soil, γ-PGA functions as a fertilizer synergist and soil conditioner at field level, improving nitrogen retention, soil structure, microbial activity, water-use efficiency, and yield. In a two-year winter wheat field trial, γ-PGA applied at 40, 80, 120, and 160 kg ha^{-1} increased grain yield by 7.62–14.67% and water-use efficiency by 4.75–9.80%, with soil ammonium-nitrogen rising by 8.67–38.20% and urease, phosphatase, and sucrase activities all increasing; yield gains slowed once the rate exceeded 80 kg ha^{-1} [53]. In cotton grown under film drip irrigation in the sandy soils of southern Xinjiang, γ-PGA improved water-use efficiency, yield, and fibre quality, with the greatest benefit at an application rate of 80 kg ha^{-1} [54]. In the barren desertified soils of Northwest China, γ-PGA improved water-stable aggregation and nitrogen and phosphorus uptake efficiency, with the highest water-fertilizer productivity and net profit achieved at 65 kg ha^{-1} [39].

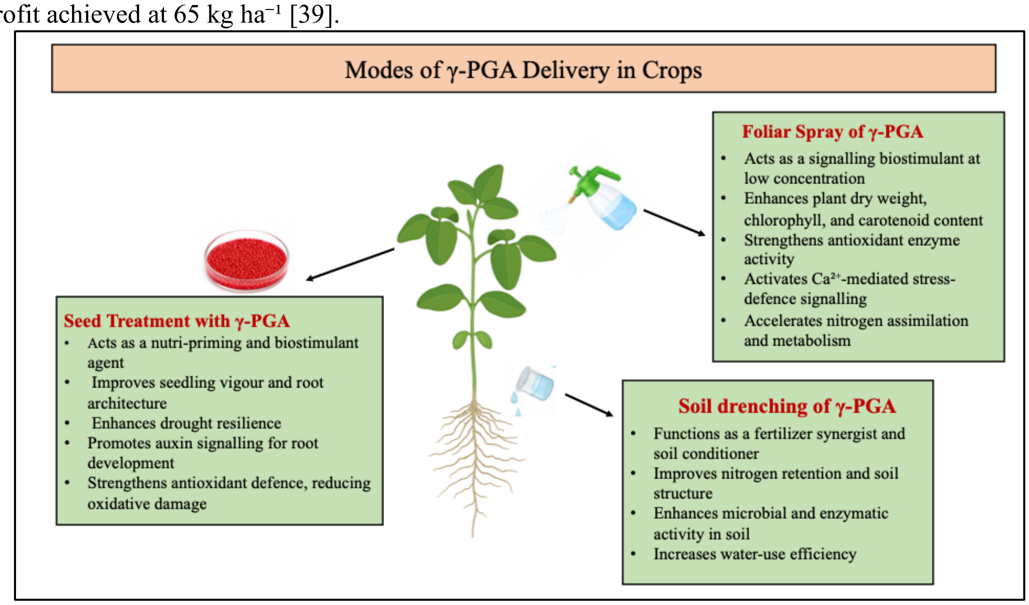

Fig. 5. Modes of γ-poly-glutamic acid (γ-PGA) delivery in crops and their associated physiological responses. γ-PGA can be applied through three complementary routes

Fig. 5 Modes of γ-poly-glutamic acid (γ-PGA) delivery in crops and their associated physiological responses. γ-PGA can be applied through three complementary routes: (i) seed treatment, where γ-PGA acts as a nutri-priming and biostimulant agent that improves seedling vigour and root architecture, enhances drought resilience, promotes auxin-mediated root development, and strengthens antioxidant defence against oxidative damage; (ii) foliar spray, where γ-PGA functions as a low-concentration signalling biostimulant that increases plant dry weight, chlorophyll and carotenoid content, boosts antioxidant enzyme activity, activates Ca^{2+}-mediated stress-defence signalling, and accelerates nitrogen assimilation and metabolism; and (iii) soil drenching, where γ-PGA serves as a fertilizer synergist and soil conditioner that improves nitrogen retention and soil structure, enhances microbial and enzymatic activity, and increases water-use efficiency. Together, these application modes highlight the multifunctional role of γ-PGA in promoting plant growth, stress tolerance, and soil health at different stages and tissues of crop development

ENVIRONMENTAL IMPACT

One of the key advantages of γ-PGA is that it is environmentally friendly. By improving the fertilizer use efficiency, it reduces the quantity of chemical fertilizer needed to achieve a given yield, and so curtails the nitrogen and phosphorus losses through leaching, volatilization, runoff, denitrification that drive eutrophication, ammonia emission, and groundwater nitrate contamination. The same aggregation and water-retention effects that benefit soil structure also limit nutrient runoff and erosion, reducing nonpoint-source pollution[39,45]. Crucially, γ-PGA is fully biodegradable. Soil microorganisms break it down to glutamic acid, a naturally occurring amino acid that is assimilated by plants and microbes. This distinguishes it sharply from synthetic superabsorbent polymers and petroleum based coated fertilizers, which can persists in soil and contribute to microplastic accumulation which is a growing concern for agricultural soils. Its long history of safe use in foods such as fermented soybean (natto) further supports its toxicological safety for humans, animals, and plants. Together these properties align γ-PGA with the goals of sustainable and climate-smart agriculture which is more efficient water and nutrient use, low chemical inputs, enhanced soil biological activity, and greater crop resilience under stress.

CONCLUSION

γ-Polyglutamic acid is a biodegradable, microbially produced biopolymer with broad and increasingly well documented value in agriculture. It improves soil structure, water retention, and nutrient retention, promotes root development, nitrogen assimilation, and photosynthesis through $Ca2+$/CaM linked physiological pathway and enhances crop tolerance to drought, salinity, temperature extremes and heavy metals. These effects translate into measurable agronomic gains. In cereals, grain yield and nitrogen use efficiency improvements of roughly 7-22% and substantial yield and quality responses in vegetables, legumes, and horticultural crops achieved while reducing fertilizer loss and pollution, leaving no persistent synthetic residue because the polymer degrades to glutamic acid. Its principal limitations are cost, variable field performance, and shortage of longterm data. With continued progress in lowcost production, stable formulation, mechanistic understanding and field validation, γ-PGA is well positioned to become a practical biostimulant cum biopolymer for climate-resilient agriculture.

FUNDING

No additional grants to carry out or direct this particular research were obtained.

DISCLOSURE STATEMENT

This article does not contain any studies with human participants performed by any of the authors.

CONFLICT OF INTEREST

The authors declare that they have no conflicts of interest.

REFERENCES

1. Basu, A., Prasad, P., Das, S.N., Kalam, S., Sayyed, R.Z., Reddy, M.S., and El Enshasy, H., Plant growth promoting rhizobacteria (PGPR) as green bioinoculants: Recent developments, constraints, and prospects, Sustainability, 2021, vol. 13, no. 3, p. 1140. https://doi.org/10.3390/su13031140
2. Hossain, M.E., Shahrukh, S., and Hossain, S.A., Chemical fertilizers and pesticides: Impacts on soil degradation, groundwater, and human health in Bangladesh, in Environmental Degradation: Challenges and Strategies for Mitigation, Cham: Springer, 2022, pp. 63–92. https://doi.org/10.1007/978-3-030-95542-7_4
3. Zhang, M., Yao, Y., Tian, Y., Ceng, K., Zhao, M., Zhao, M., and Yin, B., Increasing yield and N use efficiency with organic fertilizer in Chinese intensive rice cropping systems, Field Crops Res., 2018, vol. 227, pp. 102–109. https://doi.org/10.1016/j.fcr.2018.08.010
4. Ju, X.T., Kou, C.L., Christie, P., Dou, Z.X., and Zhang, F.S., Changes in the soil environment from excessive application of fertilizers and manures to two contrasting intensive cropping systems on the North China Plain, Environ. Pollut., 2007, vol. 145, no. 2, pp. 497–506. https://doi.org/10.1016/j.envpol.2006.04.017
5. Skorupka, M. and Nosalewicz, A., Ammonia volatilization from fertilizer urea—a new challenge for agriculture and industry in view of growing global demand for food and energy crops, Agriculture, 2021, vol. 11, no. 9, p. 822. https://doi.org/10.3390/agriculture11090822
6. Alexandratos, N. and Bruinsma, J., World Agriculture Towards 2030/2050: The 2012 Revision, ESA Working Paper No. 12-03, Rome: FAO, 2012.
7. Lim, J., Fernández, C.A., Lee, S.W., and Hatzell, M.C., Ammonia and nitric acid demands for fertilizer use in 2050, ACS Energy Lett., 2021, vol. 6, no. 10, pp. 3676–3685. https://doi.org/10.1021/acsenergylett.1c01614
8. Wang, Y., Guo, Z., Zhang, S., Li, F., and Han, Y., Foliar application of γ-polyglutamic acid enhances growth, yield, and rhizosphere microbiota of summer maize under varied water regimes, Agronomy, 2025, vol. 15, no. 3, p. 754. https://doi.org/10.3390/agronomy15030754
9. Guo, Z., Wang, J., Chen, T., Zhang, H., Hou, X., and Li, J., Effects of γ-polyglutamic acid supplementation on alfalfa growth and rhizosphere soil microorganisms in sandy soil, Sci. Rep., 2024, vol. 14, no. 1, p. 6440. https://doi.org/10.1038/s41598-024-57197-6
10. Wei, Q., Zhang, M., Gou, J., Hu, H., He, C., Lu, Z., and Liu, L., Effect of polyglutamic acid–enhanced fertilizer on the biological effect and fertilizer utilization of open-air eggplant in the yellow soil area of Guizhou, J. Henan Agric. Sci., 2022, vol. 51, no. 5, p. 53. https://doi.org/10.15933/j.cnki.1004-3268.2022.05.006

11. Gardner, J.M. and Troy, F.A., Chemistry and biosynthesis of the poly(γ-D-glutamyl) capsule in Bacillus licheniformis. Activation, racemization, and polymerization of glutamic acid by a membranous polyglutamyl synthetase complex, J. Biol. Chem., 1979, vol. 254, no. 14, pp. 6262–6269. https://doi.org/10.1016/S0021-9258(18)50357-4
12. Joyce, J., Cook, J., Chabot, D., Hepler, R., Shoop, W., Xu, Q., Stambaugh, T., Aste-Amezaga, M., Wang, S., Indrawati, L., and Bruner, M., Immunogenicity and protective efficacy of Bacillus anthracis poly-γ-D-glutamic acid capsule covalently coupled to a protein carrier using a novel triazine-based conjugation strategy, J. Biol. Chem., 2006, vol. 281, no. 8, pp. 4831–4843. https://doi.org/10.1074/jbc.M509432200
13. Ogunleye, A., Bhat, A., Irorere, V.U., Hill, D., Williams, C., and Radecka, I., Poly-γ-glutamic acid: Production, properties and applications, Microbiology, 2015, vol. 161, no. 1, pp. 1–17. https://doi.org/10.1099/mic.0.081448-0
14. Ho, G.H., Ho, T.I., Hsieh, K.H., Su, Y.C., Lin, P.Y., Yang, J., Yang, K.H., and Yang, S.C., γ-Polyglutamic acid produced by Bacillus subtilis (Natto): Structural characteristics, chemical properties and biological functionalities, J. Chin. Chem. Soc., 2006, vol. 53, no. 6, pp. 1363–1384. https://doi.org/10.1002/jccs.200600182
15. Wang, L.L., Chen, J.T., Wang, L.F., Wu, S., Zhang, G.Z., Yu, H.Q., Ye, X.D., and Shi, Q.S., Conformations and molecular interactions of poly-γ-glutamic acid as a soluble microbial product in aqueous solutions, Sci. Rep., 2017, vol. 7, no. 1, p. 12787. https://doi.org/10.1038/s41598-017-13152-2
16. Shi, F., Xu, Z., and Cen, P., Microbial production of natural poly amino acid, Sci. China Ser. B Chem., 2007, vol. 50, no. 3, pp. 291–303. https://doi.org/10.1007/s11426-007-0061-5
17. Feng, J., Gao, W., Gu, Y., Zhang, W., Cao, M., Song, C., Zhang, P., Sun, M., Yang, C., and Wang, S., Functions of poly-γ-glutamic acid (γ-PGA) degradation genes in γ-PGA synthesis and cell morphology maintenance, Appl. Microbiol. Biotechnol., 2014, vol. 98, no. 14, pp. 6397–6407. https://doi.org/10.1007/s00253-014-5729-0
18. Parati, M., Khalil, I., Tchuenbou-Magaia, F., Adamus, G., Mendrek, B., Hill, R., and Radecka, I., Building a circular economy around poly(D/L-γ-glutamic acid)—a smart microbial biopolymer, Biotechnol. Adv., 2022, vol. 61, p. 108049. https://doi.org/10.1016/j.biotechadv.2022.108049
19. Choi, H.J., Yang, R., and Kunioka, M., Synthesis and characterization of pH-sensitive and biodegradable hydrogels prepared by γ-irradiation using microbial poly(γ-glutamic acid) and poly(ε-lysine), J. Appl. Polym. Sci., 1995, vol. 58, no. 4, pp. 807–814. https://doi.org/10.1002/app.1995.070580414
20. Ashiuchi, M., Microbial production and chemical transformation of poly-γ-glutamate, Microb. Biotechnol., 2013, vol. 6, no. 6, pp. 664–674. https://doi.org/10.1111/1751-7915.12072
21. Ko, Y.H. and Gross, R.A., Effects of glucose and glycerol on γ-poly(glutamic acid) formation by Bacillus licheniformis ATCC 9945a, Biotechnol. Bioeng., 1998, vol. 57, no. 4, pp. 430–437. https://doi.org/10.1002/(SICI)1097-0290(19980220)57:4<430::AID-BIT6>3.0.CO;2-N
22. Mohanraj, R., Gnanamangai, B.M., Ramesh, K., Priya, P., Srisunmathi, R., Poornima, S., Ponmurugan, P., and Robinson, J.P., Optimized production of gamma poly glutamic acid (γ-PGA) using sago, Biocatal. Agric. Biotechnol., 2019, vol. 22, p. 101413. https://doi.org/10.1016/j.bcab.2019.101413
23. Xu, Z., Lei, P., Feng, X., Xu, X., Liang, J., Chi, B., and Xu, H., Calcium involved in the poly(γ-glutamic acid)-mediated promotion of Chinese cabbage nitrogen metabolism, Plant Physiol. Biochem., 2014, vol. 80, pp. 144–152. https://doi.org/10.1016/j.plaphy.2014.03.036
24. Miflin, B.J. and Habash, D.Z., The role of glutamine synthetase and glutamate dehydrogenase in nitrogen assimilation and possibilities for improvement in the nitrogen utilization of crops, J. Exp. Bot., 2002, vol. 53, no. 370, pp. 979–987. https://doi.org/10.1093/jxb/53.370.979
25. Zhang, L., Yang, X., Gao, D., Wang, L., Li, J., Wei, Z., and Shi, Y., Effects of poly-γ-glutamic acid (γ-PGA) on plant growth and its distribution in a controlled plant-soil system, Sci. Rep., 2017, vol. 7, no. 1, p. 6090. https://doi.org/10.1038/s41598-017-06248-2
26. Quan, J., Zheng, W., Wu, M., Shen, Z., Tan, J., Li, Z., Zhu, B., Hong, S.B., Zhao, Y., Zhu, Z., and Zang, Y., Glutamic acid and poly-γ-glutamic acid enhanced the heat resistance of Chinese cabbage (Brassica rapa L.) by promoting carotenoid biosynthesis, photosynthesis, and the antioxidant system, Int. J. Mol. Sci., 2022, vol. 23, no. 19, p. 11671. https://doi.org/10.3390/ijms231911671
27. Ma, H., Li, P., Liu, X., Li, C., Zhang, S., Wang, X., and Tao, X., Poly-γ-glutamic acid enhanced the drought resistance of maize by improving photosynthesis and affecting the rhizosphere microbial community, BMC Plant Biol., 2022, vol. 22, no. 1, p. 11. https://doi.org/10.1186/s12870-021-03392-w
28. Ma, H., Li, P., Xiao, N., Xia, T., et al., Poly-γ-glutamic acid promoted maize root development by affecting auxin signaling pathway and the abundance and diversity of rhizosphere microbial community, BMC Plant Biol., 2022, vol. 22, p. 521. https://doi.org/10.1186/s12870-022-03908-y
29. Wang, Z., Zhang, X., Liusui, Y., Fu, W., Han, A., Zhao, D., Yue, J., Tu, Y., Zhang, J., and Guo, Y., Unveiling the molecular mechanisms of γ-polyglutamic acid-mediated drought tolerance in cotton through transcriptomic and physiological analyses, BMC Plant Biol., 2025, vol. 25, no. 1, p. 392. https://doi.org/10.1186/s12870-025-06406-z

30. Dueñas, C., Jr., Calvio, C., Slamet-Loedin, I.H., Susanto, U., and Macovei, A., Seed priming with poly-gamma-glutamic acid (γ-PGA) improves rice germination performance under drought conditions, Agriculture, 2024, vol. 14, no. 6, p. 926. https://doi.org/10.3390/agriculture14060926
31. Li, W., Xu, G., Zhang, J., et al., Poly-γ-glutamic acid induces system tolerance to drought stress by promoting abscisic acid accumulation in Brassica napus L., Sci. Rep., 2020, vol. 10, p. 6212. https://doi.org/10.1038/s41598-020-63040-5
32. Ma, H., Xiao, N., Liu, Y., Liu, J., Li, P., Deng, X., Wei, J., Li, P., and Xia, T., Poly-γ-glutamic acid could enhance the salt resistance of maize by collectively increasing the osmotic, ion, and oxidative stress resistance and enriching the salt-tolerant PGPBs in rhizosphere soil, Plant Soil, 2025. https://doi.org/10.1007/s11104-025-07643-9
33. Lei, P., Pang, X., Feng, X., Li, S., Chi, B., Wang, R., Xu, Z., and Xu, H., The microbe-secreted isopeptide poly-γ-glutamic acid induces stress tolerance in Brassica napus L. seedlings by activating crosstalk between H_2O_2 and Ca^{2+}, Sci. Rep., 2017, vol. 7, p. 41618. https://doi.org/10.1038/srep41618
34. Pang, X., Lei, P., Feng, X., Xu, Z., Xu, H., and Liu, K., Poly-γ-glutamic acid, a bio-chelator, alleviates the toxicity of Cd and Pb in the soil and promotes the establishment of healthy Cucumis sativus L. seedling, Environ. Sci. Pollut. Res., 2018, vol. 25, no. 20, pp. 19975–19988. https://doi.org/10.1007/s11356-018-1890-9
35. Yang, Q., Yang, Y., Li, X., Xu, Z., Peng, H., and Wang, J., γ-Polyglutamic acid enhances growth by facilitating micronutrients and mitigating cadmium in pepper, SSRN preprint, posted 25 November 2025, 18 pp. (preprint — replace with the peer-reviewed version once published; add the SSRN abstract ID or DOI)
36. Wu, L., Zhang, Q., and Lu, N., Poly-glutamic acid reinforces wheat cadmium tolerance by modulating ascorbic acid and glutathione metabolism, Plant Soil Environ., 2024, vol. 70, no. 8, pp. 483–491. https://doi.org/10.17221/154/2024-PSE
37. Kotabin, N., Tahara, Y., Issakul, K., and Chunhachart, O., Potential of γ-polyglutamic acid for cadmium toxicity alleviation in rice, Int. J. Biol. Food Vet. Agric. Eng., 2015, vol. 9, no. 8, pp. 915–919.
38. Yin, A., Jia, Y., Qiu, T., Gao, M., Cheng, S., Wang, X., and Sun, Y., Poly-γ-glutamic acid improves the drought resistance of maize seedlings by adjusting the soil moisture and microbial community structure, Appl. Soil Ecol., 2018, vol. 129, pp. 128–135. https://doi.org/10.1016/j.apsoil.2018.04.014
39. Liang, J. and Shi, W., Poly-γ-glutamic acid improves water-stable aggregates, nitrogen and phosphorus uptake efficiency, water-fertilizer productivity, and economic benefit in barren desertified soils of Northwest China, Agric. Water Manage., 2021, vol. 245, p. 106551. https://doi.org/10.1016/j.agwat.2020.106551
40. Xu, Z., Lei, P., Feng, X., Xu, X., Xu, H., Yang, H., and Tang, W., Effect of poly(γ-glutamic acid) on microbial community and nitrogen pools of soil, Acta Agric. Scand. B Soil Plant Sci., 2013, vol. 63, no. 8, pp. 657–668. https://doi.org/10.1080/09064710.2013.849752
41. Hong, L., Wei, L., Guo, F., Liu, J., Tang, S., Yang, H., Yao, R., Guo, X., and Yang, C., Unveiling the regulatory mechanism of poly-γ-glutamic acid on soil characteristics under drought stress through integrated metagenomics and metabolomics analysis, Front. Microbiol., 2024, vol. 15, p. 1387223. https://doi.org/10.3389/fmicb.2024.1387223
42. Shiheng, T., Fanglan, G., Yong, X., Qingyi, S., Fugui, X., Yao, R., Juan, D., Can, C., Boyuan, X., and Wei, L., Effects of γ-PGA application on soil physical and chemical properties, rhizosphere microbial community structure and metabolic function of urban abandoned land, Front. Microbiol., 2025, vol. 16, p. 1534505. https://doi.org/10.3389/fmicb.2025.1534505
43. Xu, Z., Wan, C., Xu, X., Feng, X., and Xu, H., Effect of poly(γ-glutamic acid) on wheat productivity, nitrogen use efficiency and soil microbes, J. Soil Sci. Plant Nutr., 2013, vol. 13, no. 3, pp. 744–755. https://doi.org/10.4067/S0718-95162013005000059
44. Zhai, Z., Shi, W., Liu, L., and Jing, B., Poly-γ-glutamic acid enhances corn nitrogen use efficiency and yield by decreasing gaseous nitrogen loss and increasing mineral nitrogen accumulation, Soil Tillage Res., 2025, vol. 249, p. 106480. https://doi.org/10.1016/j.still.2025.106480
45. Guo, J., Shi, W., Wen, L., Shi, X., and Li, J., Effects of a super-absorbent polymer derived from poly-γ-glutamic acid on water infiltration, field water capacity, soil evaporation, and soil water-stable aggregates, Arch. Agron. Soil Sci., 2020, vol. 66, no. 12, pp. 1627–1638. https://doi.org/10.1080/03650340.2019.1686137
46. Zhu, Q., et al., γ-Polyglutamic acid alleviates chromium toxicity in tobacco plants: physiological regulation and microbial mechanism, Ecotoxicol. Environ. Saf., 2026, vol. 289, p. 119756. https://doi.org/10.1016/j.ecoenv.2026.119756
47. Jing, B., Shi, W., Liu, L., et al., Poly-γ-glutamic acid application promoted nutrient uptake and productivity of soybean by improving soil properties, Soil Sci. Soc. Am. J., 2025, vol. 89, no. 1, p. e70164. https://doi.org/10.1002/saj2.70164
48. Jing, B., Shi, W., Liu, L., et al., Poly-γ-glutamic acid enhanced the yield and photosynthesis of soybeans by adjusting soil aggregates and water distribution, J. Sci. Food Agric., 2024, vol. 104, no. 9, pp. 5367–5377. https://doi.org/10.1002/jsfa.13520

49. Wen, H., et al., Poly-γ-glutamic acid chelates chromium(III) and copper(II), alleviating their toxicity in cucumber and affecting rhizosphere bacterial community assembly, Environ. Pollut., 2025, vol. 364, part 1, p. 125332. https://doi.org/10.1016/j.envpol.2024.125332
50. Guo, Z., Yang, N., Zhu, C., and Gan, L., Exogenously applied poly-γ-glutamic acid alleviates salt stress in wheat seedlings by modulating ion balance and the antioxidant system, Environ. Sci. Pollut. Res., 2017, vol. 24, no. 7, pp. 6592–6598. https://doi.org/10.1007/s11356-016-8295-4
51. Marques, E.R.F., Drachenberg, E., Fogaça, K.M.S., and Gorni, P.H., Glutamic acid seed priming enhances seedling growth through metabolic and antioxidant modulation in maize (Zea mays L.), Rev. Bras. Eng. Biossistemas, 2026, vol. 20, art. 1373. https://doi.org/10.18011/bioeng.2026.v20.1373
52. Xu, Z., Lei, P., Pang, X., Li, H., Feng, X., and Xu, H., Exogenous application of poly-γ-glutamic acid enhances stress defense in Brassica napus L. seedlings by inducing cross-talks between Ca^{2+}, H_2O_2, brassinolide, and jasmonic acid in leaves, Plant Physiol. Biochem., 2017, vol. 118, pp. 460–470. https://doi.org/10.1016/j.plaphy.2017.07.015
53. Guo, J., Zhang, J., Zhang, K., Li, S., and Zhang, Y., Effect of γ-PGA and γ-PGA SAP on soil microenvironment and the yield of winter wheat, PLOS ONE, 2023, vol. 18, no. 7, p. e0288299. https://doi.org/10.1371/journal.pone.0288299
54. Liang, J., Shi, W., He, Z., Pang, L., and Zhang, Y., Effects of poly-γ-glutamic acid on water use efficiency, cotton yield, and fiber quality in the sandy soil of southern Xinjiang, China, Agric. Water Manage., 2019, vol. 218, pp. 48–59. https://doi.org/10.1016/j.agwat.2019.03.009
55. Bewley, J.D., and Black, M., Seeds: Physiology of Development and Germination, Springer Science & Business Media, 2013. https://doi.org/10.1007/978-1-4899-1002-8_1
56. Finch-Savage, W.E., and Bassel, G.W., Seed vigour and crop establishment: Extending performance beyond adaptation, J. Exp. Bot., 2016, vol. 67, no. 3, pp. 567–591. https://doi.org/10.1093/jxb/erv490
57. Ashiuchi, M., Nawa, C., Kamei, T., Song, J.J., Hong, S.P., and Sung, M.H., Physiological and biochemical characteristics of poly-γ-glutamate synthetase complex of Bacillus subtilis, Eur. J. Biochem., 2001, vol. 268, pp. 5321–5328. https://doi.org/10.1046/j.0014-2956.2001.02475.x
58. Bajaj, I., and Singhal, R., Poly(glutamic acid)—An emerging biopolymer of commercial interest, Bioresour. Technol., 2011, vol. 102, no. 10, pp. 5551–5561. https://doi.org/10.1016/j.biortech.2011.02.047
59. Wang, J., Liu, Z., Wang, Y., Cheng, W., and Mou, H., Production of a water-soluble fertilizer containing amino acids by solid-state fermentation of soybean meal and evaluation of its efficacy on rapeseed growth, J. Biotechnol., 2014, vol. 187, pp. 34–42. https://doi.org/10.1016/j.jbiotec.2014.07.015
60. Lei, P., Xu, Z., Liang, J., Luo, X., Zhang, Y., Feng, X., and Xu, H., Poly(γ-glutamic acid) enhanced tolerance to salt stress by promoting proline accumulation in Brassica napus L., Plant Growth Regul., 2016, vol. 78, no. 2, pp. 233–241. https://doi.org/10.1007/s10725-015-0088-0
61. Liu, L., Shi, W., Liang, J., Yuan, Y., and Hao, Q., Soil macropore characteristics and aggregate stability with poly-γ-glutamic acid amendment under wetting–drying cycles, Eur. J. Soil Sci., 2023, vol. 74, no. 3, p. e13361. https://doi.org/10.1111/ejss.13361
62. Liu, L., Shi, W., Liang, J., et al., Poly-γ-glutamic acid application rate effects on hydraulic properties of sandy soil under wetting–drying cycles conditions, Soil Sci. Soc. Am. J., 2022, vol. 86, no. 4, pp. 904–917. https://doi.org/10.1002/saj2.20398
63. Guo, J., Shi, W., Li, J., and Zhai, Z., Effects of poly-γ-glutamic acid and poly-γ-glutamic acid super absorbent polymer on the sandy loam soil hydro-physical properties, PLOS ONE, 2021, vol. 16, no. 1, p. e0245365. https://doi.org/10.1371/journal.pone.0245365
64. Fu, Y., Wang, S., Gao, S., Wang, S., Gao, Z., and He, Z., Effect of a superabsorbent polymer (poly-gamma-glutamic acid) on water and salt transport in saline soils under the influence of multiple factors, Polymers, 2022, vol. 14, no. 19, p. 4056. https://doi.org/10.3390/polym14194056
65. Zhang, L., et al., Effects of poly-γ-glutamic acid on soil nitrogen and carbon leaching and CO_2 fluxes in a sandy clay loam soil, Can. J. Soil Sci., 2017, vol. 97, no. 3, pp. 319–328. https://doi.org/10.1139/cjss-2016-0127
66. Liu, L. and Shi, W., Poly-γ-glutamic acid affects NH_3 volatilization, soil nitrogen content, and soybean seedling growth, Water Supply, 2023, vol. 23, no. 10, pp. 4242–4251. https://doi.org/10.2166/ws.2023.228
67. Liu, P., Chen, L., Alhaj Hamoud, Y., Zheng, J., Chang, T., Ali, J., Huang, H., and Shaghaleh, H., Ameliorative effect of poly-γ-glutamic acid biopreparation on coastal saline soil, Heliyon, 2024, vol. 10, no. 17, p. e36762. https://doi.org/10.1016/j.heliyon.2024.e36762
68. Chen, L., Su, W., Xiao, J., Zhang, C., Zheng, J., and Zhang, F., Poly-γ-glutamic acid bioproduct improves the coastal saline soil mainly by assisting nitrogen conservation during salt-leaching process, Environ. Sci. Pollut. Res., 2021, vol. 28, no. 7, pp. 8606–8614. https://doi.org/10.1007/s11356-020-11244-7
69. Kang, F., Lv, Q., Fan, J., Zhang, Y., Song, Y., Ren, X., and Hu, S., Ameliorative effect of calcium poly(aspartic acid) (PASP-Ca) and calcium poly-γ-glutamic acid (γ-PGA-Ca) on soil acidity in different horizons, Environ. Sci. Pollut. Res., 2023, vol. 30, no. 30, pp. 75681–75693. https://doi.org/10.1007/s11356-023-27713-8