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REVIEW

Research Progress on the Growth-Promoting Effect of Plant Biostimulants on Crops

Qi Lu[1,2], Longfei Jin[2], Cuiling Tong[3], Feng Liu[2], Bei Huang[2] and Dejian Zhang[1,2,*]

[1]College of Horticulture and Gardening, Hubei Key Laboratory of Waterlogging Disaster and Agricultural Use of Wetland, Yangtze University, Jingzhou, 434020, China

[2]Institute of Citrus Research, Zhejiang Academy of Agricultural Sciences, Taizhou, 318026, China

[3]Jingzhou Institute of Technology, Jingzhou, 434025, China

[*]Corresponding Author: Dejian Zhang. Email: zhangdejian0553@126.com

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ABSTRACT

A Plant Biostimulant is any substance or microorganism applied to plants to enhance nutrition efficiency, abiotic stress tolerance, and/or crop quality traits, regardless of its nutrient content. The application of Plant biostimulants (PBs) in production can reduce the application of traditional pesticides and chemical fertilizers and improve the quality and yield of crops, which is conducive to the sustainable development of agriculture. An in-depth understanding of the mechanism and effect of various PBs is very important for how to apply PBs reasonably and effectively in the practice of crop production. This paper summarizes the main classification of PBs; The growth promotion mechanism of PBs was analyzed from four aspects: improving soil physical and chemical properties, enhancing crop nutrient absorption capacity, photosynthesis capacity, and abiotic stress tolerance; At the same time, the effects of PBs application on seed germination, seedling vigor, crop yield, and quality were summarized; Finally, how to continue to explore and study the use and mechanism of PBs in the future is analyzed and prospected, to better guide the application of PBs in crop production in the future.

KEYWORDS

Plant biostimulants; growth promoting effect; crop production

1 Introduction

Plant biostimulants (PBs) refer to any substances (including microorganisms) that can improve plant nutritional efficiency, abiotic stress tolerance, and crop quality traits, and their effects are independent of their nutrient composition or content [1]. PBs are different from traditional fertilizers and pesticides, which directly provide nutrients to improve plant nutrition and alleviate stress. The effect of PBs on plant growth is indirect [2]. By stimulating the natural growth process of plants or improving the growth environment of plants, PBs can improve the ability of plants to absorb and utilize nutrients and their tolerance to abiotic stress [1]. At present, PBs have been widely used in crop production. It effectively reduces the application of chemical fertilizers and pesticides, reduces the damage to the soil environment, and maintains the yield and quality of crops [3]. It is of great significance to the sustainable development of agriculture. Therefore, PBs have a broad market prospect. According to the MarketsandMarkets report, the global market sales of PBs in 2019 were approximately $2.6 billion and are expected to exceed $4 billion in 2025 [4]. In this review, we summarized the classification, biodynamic mechanism, application effect, and future development direction of PBs, to promote the application of PBs in crop production.

2 Main Classification of Plant Biostimulants

2.1 Non-Microbial Plant Biostimulants

Non-microbial PBs mainly include humic substances, seaweed extracts, protein hydrolysates, other nitrogenous substances, chitin and its derivatives, and inorganic compounds with biological stimulatory effects [5]. Humic substances are a class of naturally occurring organic compounds derived from the decomposition and transformation of plant, animal, and microbial residues, which can generally be classified as humin, humic acid, and fulvic acid [6]. Seaweed extracts are naturally active substances extracted from seaweed, which are composed of many different components (including polysaccharides, minerals, phytohormones trace elements, and many other substances) [7]. Moreover, these components will change according to the type of seaweed and collection time as well as the extraction time and method of seaweed extract [8,9]. Protein hydrolysates are mixtures of peptides, oligopeptides, and amino acids formed by partial hydrolysis of various protein sources [10]. Other nitrogen-containing compounds include betaine, polyamines, and non-protein amino acids [1]. Chitin and its derivatives are also a common type of PBs. Chitin is mainly extracted from the shell of crustaceans and the cell wall of fungi. Chitin is insoluble in water and most organic solvents, whereas chitosan is the product of the deacetylation of chitin and has good solubility in acidic solutions [11]. Chitosan oligosaccharides are the products of continuous degradation of chitosan, which have smaller molecular weights, stronger bioactivity, and better water solubility, so they are more convenient to be applied and utilized by plants [12]. Thus, chitosan and chitosaccharides are the main forms of chitin, and its derivatives are used as PBs. The inorganic compounds used as PBs are composed of beneficial elements. Elements that promote plant growth, in addition to those necessary for the plant, are called beneficial elements [13].

2.2 Microbial Plant Biostimulants

Microbial PBs have a great application prospect in the market. Some studies have shown that microbial PBs can help increase crop yield by 10%–40% [14]. They colonize the rhizosphere and plant body to improve the soil environment and plant nutrition, and even protect plants from the effects of pests and diseases [15]. Microbial PBs can be divided into beneficial bacteria and beneficial fungi. Plant growth-promoting bacteria (PGPB), as a representative of PBs in bacteria, can improve nutrient acquisition, growth, and development of plants, and improve the tolerance of plants to abiotic and biotic stresses. Over the years, researchers have isolated and studied a variety of PGPB strains as PBs, among which the most widely studied and used is plant growth-promoting rhizobacteria (PGPR) [16]. Fungi used as PBs mainly include mycorrhizal fungi, yeasts, and fungi of the genus Trichoderma. Mycorrhizal fungi can form mycorrhizae in symbiosis with plant roots to promote plant growth. Arbuscular mycorrhizal fungi (AMF) are the most widely studied and used mycorrhizal fungi. Yeasts and Trichoderma fungi are mainly used to improve plant resistance to biotic stress.

3 Mechanism of Action of Plant Biostimulants to Promote Crop Growth

3.1 Improve Soil Physicochemical Properties

Most PBs are directly applied to soil and have a certain improvement effect on the soil environment. Various PBs can chelate fixed nutrients and decompose mineralized nutrients due to the structural properties or biological activities of their components. Because of its various functional groups and colloidal properties, humus has a high affinity for inorganic and organic ions and many molecules in soil [17]. Therefore, humus can form complexes with metal cations and inorganic phosphorus in soil and improve soil aggregate structure, thereby fixing nutrients to reduce nutrient loss between soils and improving soil physicochemical properties [18–20]. Amino acids have strong chelation ability and can fix metal ions in soil. Amino acids can chelate Fe and other metal ions through their carboxyl groups, such as arginine, glycine, and histidine, to prevent Fe loss and promote Fe absorption by plants [21]. Algal extracts and protein hydrolysates are rich in amino acids. Therefore, these two PBs can also improve soil and improve nutrient availability in soil. Seaweed extracts also contain many kinds of polysaccharides (kelp polysaccharide, rock Ethan, alginic acid, etc.), among which alginic acid is a good chelator, and can form alginate after chelating with metal ions [22]. Alginate has gel properties, which can promote soil aggregate structure, and improve soil physicochemical properties [22]. Other polysaccharides are also important cementing agents, which are conducive to the formation of soil aggregate stability structure [23]. Chitosan is also a polysaccharide. Chitosan could enhance the aggregate structure and permeability of a variety of soils [24]. Chitosan also has very good chelation, and its amino functional group can form a complex with metal ions [25]. PGPR can produce substances that can dissolve minerals, including organic acids and various enzymes, which can improve the availability of elements such as phosphorus and potassium in the soil. In addition, PGPR can produce extracellular siderophores, which can not only complicate with iron ions in soil but also form complexes with other heavy metals, thereby improving the soil environment [26]. The secretion of PGPR and AMF also enhanced the activity of soil phosphatase and promoted the decomposition of organic phosphorus. The extra-root mycelial network formed by mycorrhizal fungi after infection of roots can participate in the formation of microaggregates and maintain the composition of soil aggregates [27]. Soil yeast also can decompose organic matter, dissolve phosphate, and promote soil aggregation [28].

PBs can not only increase the availability of soil nutrients and improve soil physical and chemical properties but also have a positive effect on soil microbial communities. Humus can increase the release of organic acids from the roots of crops such as maize, thereby promoting the activities of microorganisms in the soil, and thus promoting the construction of a good symbiotic relationship between crops and microorganisms [29,30]. Seaweed extracts can also promote the growth of a variety of microorganisms in soil and improve the abundance of soil microorganisms [22].

3.2 Promote Crop Root Growth and Nutrient Uptake

PBs can enhance the endogenous phytohormone content of crop roots to promote root growth. For example, the treatment of cucumber with humic acid can increase the auxin content in its roots [31]; the application of an animal protein hydrolysate to tomato significantly increased endogenous levels of auxin, cytokinin, and jasmonate [32]; the application of kelp extracts to cannabis resulted in an 8-fold increase in auxin content compared to the control [33]. In addition, many PBs also contain phytohormones or phytohormone-like substances that can stimulate root growth and lateral root development. For example, most seaweed extracts contain gibberellins, and protein hydrolysates contain auxin-like and gibberellin-like substances [34,35]. Some microbial PBs can directly produce phytohormones, for example, most PGPR can synthesize and release auxin as secondary metabolites [36]. PBs can not only promote crop root growth but also directly promote crop nutrient absorption. Some studies have shown that humus can induce and stimulate H^+-ATPase [37]. H^+-ATPase can provide energy for active transport of root cells, thus directly improving the ability of crop roots to acquire nutrients [38]. PBs, such as humus, amino acids, seaweed extracts, and PGPR, can affect the expression of genes and the activity of enzymes related to nutrient transport systems to promote nutrient acquisition [26,39–41]. In addition, most microbial PBs can not only affect the root system by synthesizing secretions but also form symbiotic relationships with roots. For example, commensal nitrogen-fixing bacteria can form a symbiotic relationship with roots to fix nitrogen from the air and provide it to crops, and mycorrhizal fungi can form mycorrhizae in symbiosis with crops to expand the absorption area of crop roots, thereby promoting nutrient absorption of crop roots [26,42].

3.3 Improve the Photosynthetic Efficiency of Crops

Various PBs can improve the photosynthetic efficiency of crops in a variety of ways. Humus can increase the chlorophyll content and leaf photosynthetic rate of crops such as fava beans and peanuts [43,44]. Several amino acid-based PBs have been shown to improve photosynthesis [45]. Seaweed extracts contain substances with cytokine-like activity, which can promote the division and proliferation of chloroplasts [7]. The application of seaweed extract to lettuce resulted in a decrease in the activity of cysteine proteases associated with aging and a significant increase in the expression of genes associated with promoting photosynthesis [46]. Therefore, seaweed extracts can enhance crop chlorophyll content by increasing chloroplast biogenesis, reducing chlorophyll degradation, and delaying chlorophyll senescence. Seaweed extracts, protein hydrolysates, chitosan, and many beneficial elements also enable crops to maintain a good PSII maximum light energy conversion efficiency under various stresses [47,48]. Chitosan can enhance the photosynthetic pigment content of most crops. Wheat seedlings were treated with chitosan and it was found that chitosan may reduce the breakdown of chlorophyll by inhibiting the transcription level of chlorophyllase and thus increase the content of chlorophyll [49]. Spraying chitosan oligosaccharides on leaves increased chlorophyll content and Rubisco activity, thereby accelerating the photosynthetic rate [50]. A beneficial element, titanium (Ti) has also been shown to have this function, and Ti can also induce the expression of crop LHCII-B gene, thereby increasing the content of light-harvesting Complex II (LHCII) in crops [51]. Cerium and lanthanum can not only increase the content of LHCII through the above effects but also promote light energy transfer between LHCII and Photosystem II (PSII) reaction centers [52,53]. In addition, the most beneficial elements can enhance photosynthesis by improving mesophyll conductance and stomatal conductance in crops [48]. Microbial PBs are also able to improve crop photosynthesis Both PGPR and AMF can promote the synthesis of cytokinin to increase chloroplast content, and enhance crop water use efficiency and stomatal conductance to enhance photosynthesis [36,54,55].

3.4 Enhance Crop Tolerance to Abiotic Stresses

Improving the abiotic stress tolerance of crops is one of the main functions of PBs. After suffering from abiotic stress, crops will metabolize different substances to reduce the impact of abiotic stress. PBs can promote and enhance the production and activity of these metabolites [5]. Environmental conditions such as drought and high salt can cause water stress on crops. Crops can produce and accumulate osmoregulatory substances, including inorganic ions such as NA^+, K^+, and Ga^+, and organic solutes such as proline, betaine, and soluble sugar to alleviate water stress [56]. Under abiotic stress conditions, crops can produce a large amount of reactive oxygen species to cause oxidative damage to crops. Crops themselves will produce antioxidant enzymes and non-enzymatic antioxidants to remove reactive oxygen species [57]. Multiple types of PBs can improve the content and activity of the above osmoregulatory substances and antioxidants to alleviate the damage caused by abiotic stress, and thus enhance the tolerance of crops to abiotic stress. For example, seaweed extracts could increase superoxide dismutase activity and proline content in rape under drought conditions [58], and humus increased the activities of superoxide dismutase, peroxidase and catalase and the content of proline in mung bean under both drought and salt stress [59], and inoculation of arbuscular mycorrhizal fungi enhanced the activities of superoxide dismutase, catalase, ascorbate peroxidase and glutathione peroxidase under abiotic stress in crops [60]. Chitin and chitosan could enhance the activities of superoxide dismutase, peroxidase, and catalase in tomatoes [61]. Protein hydrolysates also have this function. In addition, protein hydrolysates can increase the transcription level of genes encoding heat shock proteins and promote the synthesis of heat shock proteins [62]. Heat shock proteins are proteins that are rapidly synthesized by crops under high-temperature stress, and oxidative stress can also stimulate their synthesis. Like functional proteins such as osmoregulatory protein and late embryogenesis abundant protein, it can protect protein structure and enhance membrane stability under abiotic stress conditions [63]. Finally, we summarized the mechanism of action of PBs in Fig. 1.

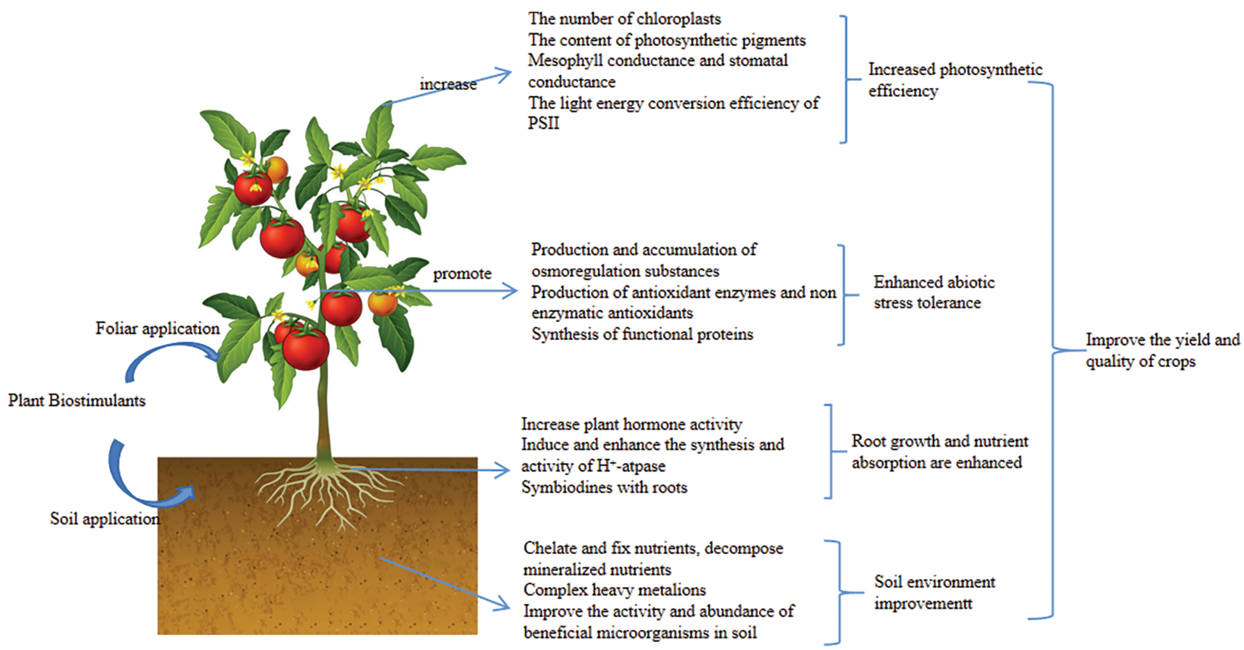

Figure 1: Schematic diagram of the mechanism of plant biostimulants promoting crop growth

4 Practical Application and Effect of Plant Biostimulant in Production

4.1 Application in Seed Germination and Seedling Cultivation

Higher germination rate, faster seedling emergence rate, good uniformity, and strong seedling growth activity are sought by people in production practice, and the application of PBs can help to achieve such goals. In Table 1, we enumerated the practical applications of various PBs in seed germination and seedling cultivation. The methods used by PBs to promote seed germination are mainly seed priming and seed coating. Seed priming is to allow seeds to absorb water under certain environmental conditions so that they start some important metabolic activities before germination in advance stop the whole process, and dry before the radicle breaks through the seed coat [64]. Seed coating refers to applying a layer of special film to the seed to form coated seeds. Coated seeds can normally absorb and germinate, and coating can slowly release active substances to promote germination and prevent stress [65]. Through these two treatments, PBs increased the activities of biological enzymes and enhanced the plant hormone response of seeds at the early germination stage, thereby increasing germination rate, germination speed, seedling vitality, and controlling seedling emergence time [66,67]. For example, glycine betaine treatment increased α-amylase activity in maize seedlings under both normal and low-temperature stress [68]. On the one hand, the enhancement of phytohormone response in seeds by PBs comes from the regulation of endogenous phytohormone content in seeds [69]. For example, soaking wheat seeds with polyamines under drought conditions can increase the endogenous auxin, abscisic acid, and gibberellin content of seeds. On the other hand, as mentioned above, some PBs contain phytohormones or substances with similar phytohormone activity to provide phytohormone stimulation to seeds.

Treatment of seeds with PBs also improved germination rate and seedling vitality by helping seeds cope with abiotic stresses. Abiotic stresses during seed germination mainly lead to osmotic stress and the accumulation of reactive oxygen species. The mechanism of action of PBs has been described in the previous section PBs regulate plant metabolism to cope with osmotic stress and the accumulation of reactive oxygen species, and also affect seeds. For example, Bacillus was used to soak priming maize seeds can not only increase the activities of superoxide dismutase, catalase, peroxidase, and ascorbic acid peroxidase in maize seeds to reduce the accumulation of reactive oxygen species, but also increase the content of proline to alleviate osmotic stress, and finally improve the emergence rate of maize seeds under salt stress [70], and the use of PBs with lignin derivatives as an active ingredient in soybean seeds can increase the content of non-protein thiol to reduce the content of hydrogen peroxide and alleviate heat stress, thereby improving seed germination rate [71].

In addition, for microbial PBs, the method of seed coating can also increase the colonization efficiency of beneficial microorganisms. For example, on maize, 4860 AMF per plant by soil inoculation and 273 AMF per plant by seed coating resulted in similar colonization rates [72,73].

Table 1: Effects of various plant biostimulants on seed germination and seedling development of crops

Active component	Crops	Stress	Improve indicators	Reference
Washed salt of humic acids	Rice (*Oryza sativa* L.)	No stress	Germination speed, germination rate, seedling vigor	[74]
Humus extracted from earthworm manure compost	Hemp (*Cannabis sativa* L.)	No stress	Growth of hypocotyl and radicle, concentration of chlorophyll in cotyledons	[75]
Humic acid	pumpkin (*Cucurbita pepo* L.)	Cadmium stress	Activities of SOD, POD, CAT, ICL, and MS, germination rate and vitality of seeds under Cadmium Stress	[76]
Humic acid	Barley (*Hordeum vulgare* L.)	Salt stress	The adverse effects of salt stress on barley seed germination, seedling growth, and leaf anatomy were improved	[77]
Brown algae	*Cleome gynandra* (*Cleome gynandra* L).	No stress	Germination rate, seedling biomass, chlorophyll content	[78]
Ascomycete algae	Sunflower (*Helianthus annuus* L.)	No stress	Germination rate, germination rate, seedling biomass	[79]
Centipede algae	Rice (*Oryza sativa* L.)	Salt stress	Pro content, SOD and POD activity, germination rate, seedling biomass	[80]
Ascomycete algae	Spinach (*Spinacia oleracea* L.)	Heat stress	Germination speed, germination rate, and seedling biomass reduced the content of hydrogen peroxide and MDA	[81]

(Continued)

Table 1 (continued)

Active component	Crops	Stress	Improve indicators	Reference
Capsules made from animal-derived protein hydrolysate	Cucumber (*Cucumis sativus* L.)	No stress	The germination rate, germination rate, and biomass of seedlings	[82]
Fish protein hydrolysate	Corn (*Zea mays* L.)	No stress	The weight and height of seedlings, CAT activity, and chlorophyll content	[83]
Polyamine	Wheat (*Triticum aestivum* L.)	Drought stress	Seed Endogenous IAA, Z, ABA, and GA, seed starch degradation, soluble sugar, germination rate	[69]
Betaine	Rice (*Oryza sativa* L.)	Heat stress	Germination rate and seed vigor, SOD, POD activity, Pro content, and gibberellin content, in addition to reduced abscisic acid and auxin content	[84]
Chitosan oligosaccharide	Barley (*Hordeum vulgare* L.)	No stress	The content of phenolic compounds and antioxidant capacity	[85]
Chitosan	Soybean (*Glycine max* (L.) Merr.)	No stress	Germination rate, seedling development	[86]
Chitosan	Platycodon grandflorus (*Platycodon grandiflorus* (Jacq.) A. DC.)	No stress	Germination rate, germination index, cotyl length, radicle length	[70]
Chitosan	Pepper (*Capsicum annuum* L.)	Low-temperature stress	Germination rate, germination speed, seedling length, and fresh weight	[87]
Selenium	Barley (*Hordeum vulgare* L.)	No stress	Length of roots and shoots, the number of roots, and germination percentage	[88]
Selenium	Turnip (*Brassica rapa* L).	Salt stress	Germination percentage, photosynthetic content, and seedling biomass production the expression levels of the antioxidant genes, including CAT, POD, SOD, and APX	[89]
Silicon	Tomato (*Solanum lycopersicum* L.)	Drought stress	Germination rate, total length and fresh weight of buds and seedlings, SOD, POD activity and Pro content,	[90]

(Continued)

Table 1 (continued)

Active component	Crops	Stress	Improve indicators	Reference
Lanthanum	Rice (*Oryza sativa* L.)	Salt stress	Seed germination rate, seed vigor, chlorophyll contents, and root length	[91]
Trichoderma harzianum	Wheat (*Triticum aestivum* L.)	No stress	Germination rate, underground shoot length and biomass, POD activity germination rate, underground shoot length and biomass, POD activity	[92]
Trichoderma viride	Soybean (*Glycine max* (L.) Merr.)	No stress	Germination rate, total root length, and total root surface area	[93]
Trichoderma harzianum and *Bacillus subtilis*	Canola (*Brassica napus* L.)	Salt stress	Germination rate and seedling vigor index, root length	[94]
MGW9 Bacillus	Maize (*Zea mays* L.)	Salt stress	Germination rate, germination potential. The total length and dry and fresh weight of buds, chlorophyll content, pro content, soluble sugar content, root activity, SOD, CAT, PODand APX activity of seedlings reduced MDA content	[70]

Note: SOD: superoxide dismutase; POD: peroxidase; Cat: catalase; ICL: isocitrate lyase; MS: malate synthase; Pro: proline; MDA: malondialdehyde; IAA: auxin; Z: Zeatin; ABA: abscisic acid; GA: gibberellin; APX: ascorbic acid peroxidase.

4.2 Applications in Increasing Crop Yields

Improving crop yield and quality is the main purpose and effect of PBs application in production. In Table 2, we list the practical applications of various PBs in improving crop yield and quality. PBs increased crop yield through the mechanisms described above (improved nutrient uptake capacity and photosynthetic efficiency). For example, the Application of PBs with free amino acids as the main active ingredient in soybean at the leaf development and the beginning of flowering increased soybean yield by 25% and pod and seed number by 32% [95]. Abiotic stress can inhibit plant growth and reduce crop yield. The application of PBs can alleviate stress and improve crop yield. For example, under salt stress at a concentration of 80mM, the growth of tomato was significantly inhibited, and the yield decreased by 33% compared with the normal condition. However, after the application of seaweed extract, the salt stress could be alleviated and the yield of tomato was maintained at the normal level [96].

Table 2: Effects of various plant biostimulants on crop yield and quality

Active component	Crops	Stress	Improve indicators	Reference
Fulvic acid	Tomato (*Solanum lycopersicum* L.)	No stress	Total yield (35%), Number of fruits (44.4%), Phenylalanine, Valine, Methionine, Citric acid and Malic acid (5500%, 5600%, 61%, 211% and 42%), Content of Mg, Ca and Zn (55.9%, 31.4% and 43.1%)	[97]

(Continued)

Table 2 (continued)

Active component	Crops	Stress	Improve indicators	Reference
Humic acid	Cowpea (*Vigna unguiculata* (L.) Walp.)	No stress	SPAD (23.7%), Total chlorophyll content (89.5%), Number of pods per plant (111.4%), Number of seeds per pod (20%), Seed weight (83.5%), Content of Ga, Cu, Fe, K, Mg, Mn, P and Zn in seeds (18.8%, 45.7%, 12.2%, 2.9%, 32.5%, 204.5%, 9.9%, 70.1%)	[98]
Humic acid	Wheat (*Triticum aestivum* L.)	No stress	Chlorophylls a and b (22.8%), Leaf relative water content (12.3%), Membrane stability index (17.0%), Total dry weight (249.2%), Leaf area (480%), Volume of root (84.3%), Number of fruit (81.7), Weight of fruit (13.1%), Total yield (120.4%)	[99]
Humic acid	Wheat (*Triticum aestivum* L.)	Water stress	Content of N, P, K, Ga, Fe, Mn, Zn and Cu, Anthocyanin content (24.0%), Leaf chlorophyll fluorescence ratio, Fv/Fm (105.1), Plant height (9.6%), Number of bolls per plant (25.4%), Lint yield (15.7%), Lint yield (13.6%), Fiber strength (7.5%)	[100]
Red algae	Soybean (*Glycine max* (L.) Merr.)	No stress	Plant height (16.8%), Number of pods per plant (63.5%), Number of grains per pod (46.3%), Content of N, P and K (35.9%, 61.2% and 48.7%)	[101]
Brown seaweed	Carrot (*Daucus carota var.* sativa Hoffm.)	No stress	Total yield (42.2%), Chlorophyll a (28.6%), Chlorophyll b (60.0%), Carotenoid (20.7%), Phenols (59.7%), Flavonoids (31.4%), Anthocyanins (25%), N, P, K, Fe, Zn and Mn content in roots (23.1%, 20%, 9.1%, 40.7%, 17.4%, 26.3%)	[102]
Ascomycete algae	Onion (*Allium cepa* L.)	No stress	Plant height (15.4%), Leaf number (12.3%), Bulb fresh weight (31.8%), Chlorophyll (37%), Leaf protein (58.6%), Bulb protein (40%)	[103]
Ascomycete algae	Edible amaranth (*Amaranthus tricolor* L.)	Salt stress	Stem length and diameter, root length, leaf number, fresh and dry weight of leaves, stems, and roots (23.4%, 11.8%, 37.8%, 21.8%, 31.2%, 41.5%, 55.5%, 41.5%, 50.5%, and 63.9%), Plant carbohydrate (20.6%)	[104]

(Continued)

Table 2 (continued)

Active component	Crops	Stress	Improve indicators	Reference
Amino acid	Soybean (*Glycine max* (L.) Merr.)	No stress	Total yield (25%), Number of pods and seeds (32%), Plant height (38%), Phenol content (34%), Flavone content (74%)	[95]
Polypeptide	Wheat (*Triticum aestivum* L.)	No stress	Flag leaf area (20.2%), Total chlorophyll (5.2%), Number of grain per ear (8.9%), Grain weight per panicle (17.5%), Thousand seed weight (15.3%), Panicle number per hill (6.1%), Grain yield (11.0%), Grain protein content (12.4%), Grain N uptake (25.1%), Total N uptake (17.9%)	[105]
Polypeptide	Lettuce (*Lactuca sativa var. ramosa* Hort.)	Salt stress	Shoot dry weight (18.2%), Root dry weight (66.7%), Total root length (67.2%), Total root surface (76.2%), N content (8.1%), P content (20.6)	[106]
Polyamine	Rice (*Oryza sativa* L.)	Drought stress	Plant height (30.8%), Tiller number (29.4%), SPAD (13.8%), Panicle length (27.9%), Grain number (27.9%), Thousand grain weight (20.9%), Yield (60.6%)	[107]
Chitosan	*Pinellia ternata* (*Pinellia ternata* (Thunb.) Breit)	No stress	Leaf area (23.0%), Plant height (26.2%), Seed weight per 667 m^2 (98.1%), Medcinal material weight per 667 m^2 (100.1%), Total yield (99.9%)	[108]
Chitosan	Tomato (*Solanum lycopersicum* L.)	No stress	Total yield (3.7%), Fruit number (18.1%), Flavanones (40.5%)	[109]
Chitosan	Navel orange (*Citrus sinensis* Osb. var. Brasliliensis Tanaka)	No stress	Twig length (8.3%), number of leaves per twig (5.9%), Average leaf area (16.6%), Total chlorophyll (26.0%), Total sugar (10.3%), Total free amino acids (45.7%), Contents of N, P, K and Ga (13.3%, 20%, 66.7% and 35%)	[110]
Chitosan	Okra (*Abelmoschus esculentus* L. Moench)	No stress	Plant height (29.1%), leaf number (28.4%), Total chlorophyll (5.0%), Number of fruits per plant (36.2%), Total yield (48.7%)	[111]
Selenium	Buckwheat (*Fagopyrum esculentum* Moench)	No stress	Plant height (18.2%), Stem diameter (6.4%), Flower cluster number per plant (43.4%), Grains number per plant (44.4%)	[112]

(Continued)

Table 2 (continued)

Active component	Crops	Stress	Improve indicators	Reference
Lanthanum	Rice (*Oryza sativa* L.)	No stress	Fresh weight (12.8%), Dry weight (19.4%), Plant height (27.1%), Stem diameter (8.6%), Grain number per panicle (6.5%), Total yield (13.4%)	[113]
Cerium	Sorghum (*Sorghum bicolor* (L.) Moench)	Drought stress	Leaf carbon assimilation rates (38.0%), Pollen germination (31.6%), Seed yield per plant (31.0%)	[114]
Silicon	Barley (*Hordeum vulgare* L.)	Salt stress	Shoot fresh weight (21.7%), Shoot dry weight (49.0%), Root dry weight (36.3%), Root length (25.3%), Total chlorophyll (12.0%), Total soluble proteins (28.5%)	[115]
Rhizobia	Groundnut (*Arachis hypogaea* L.)	No stress	Aboveground biomass (9.8%), N and P contents (103.9% and 29.0%), Number of pods per plant (9.5%), Total yield (42.4%)	[116]
Arbuscular mycorrhizal fungi	Maize (*Zea mays* L.)	No stress	Plant height (10.2%), Stem diameter (30.8%), Leaf area (5.9%), Shoot dry weight (26.4%), Root dry weight (40.9%), Total yield (83.1%)	[117]
Arbuscular mycorrhizal fungi	Soybean (*Glycine max* (L.) Merr.)	High-temperature stress	Leaf area (30.5%), Plant height (34.1%), Root length (41.0%), Shoot dry weight (20.3%), Root dry weight (44.0%), Total chlorophyll (24.3%)	[118]
Bacillus	Wheat (*Tritium aestivum* L.)	Salt stress	Plant lengths (29.45%), Biomass (33.23%), Carotenoids (45.53%), Anthocyanin (32.51%), Ascorbic acid (41.53%), Total soluble proteins (59.21%), Total chlorophyll contents (49.65%), Peroxidase activity (31.76%)	[119]

Note: SOD: superoxide dismutase; APX: ascorbic acid peroxidase; GR: glutathione reductase; POD: peroxidase; CAT: catalase; Pro: proline.

4.3 Application in Improving Crop Quality

PBs can not only improve crop yield but also improve various qualities of crops. The improvement of crop quality by PBs is mainly reflected in the harvest, that is, PBs are applied during the growing stage of crops to improve various quality indicators of crops. For example, the use of protein hydrolysate in tomatoes can increase the soluble solids, potassium, calcium, magnesium, lycopene, and total ascorbic acid content of tomatoes by 10.7%, 10.5%, 10.7%, 28.3%, 34.9%, and 35.8%, respectively [120]. In addition, PBs can also be applied to improve the quality of crops after harvest, that is, spraying the fruits before harvest or soaking and smearing the fruits after harvest to maintain or improve the quality of crops and prolong the storage time. For example, when stored at 0°C for 60 days, the rot rate of grapes coated with chitosan was reduced by 21.62%, the weight loss rate was reduced by 3.30%, and the content of soluble solids and Vc lost was reduced by 1.54% and 1.43 mg/100g, respectively, compared with grapes without anything applied [121].

5 Future Directions

The green and sustainable development of agriculture has formed an irreversible trend in the world. People pay more and more attention to the quality and safety of crops, and the development momentum of the PBs industry will be more and more fierce. Therefore, more research and theoretical support are needed for the use of each PB. Future studies on the use and mechanism of PBs can be further explored in the following three aspects.

All kinds of PBs, especially non-microbial PBs, have complex components, and the enhancement of a trait may be the result of single or multiple components in PBs. However, most of the current studies only focus on the effect of overall PBs on plants, and the specific active substances that can trigger plant reactions are not clear. Future studies need to further extract the active substances that may play a role in PBs and verify their effect.

At present, the mechanism of PBs needs to be further studied. The physiological and molecular mechanisms by which PBs regulate biological metabolism remain unclear. In the future, experimental methods such as omics and biotechnology can be used to excavate the plant growth key genes regulated by PBs and analyze the molecular regulatory network of PBs to clarify the action mechanism of PBs.

At present, the combination of different PBs is more and more widely used in practice, especially microbial PBs combined with non-microbial PBs. There are often synergistic and additive effects between different PBs. Studying the effects and reaction mechanisms of multiple PB mixtures can better increase the practical benefits of PBs. This research is likely to become a hot spot for PBS-related research in the future.

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