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Effects of protein hydrolysates on horticultural plants: a review

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Abstract

Biostimulants have shown great promise for sustainable agriculture and horticulture in general. Protein hydrolysates are biostimulants obtained through chemical and enzymatic hydrolysis of animal and plant proteins. The current study provides a summary of the effects of protein hydrolysates (PHs) on morphology, physiology, growth, yield, and stress tolerance of horticultural crops. Additionally taken into account are the impacts of PHs on plant growth and root development, their role in stimulating hormone-like activity, and their capacity to improve nutrient uptake and assimilation. These effects are explained by the high amino acid content of PHs, which can influence chlorophyll synthesis, photosynthetic efficiency, and enzyme activity. Numerous studies demonstrate that by boosting osmolyte accumulation and antioxidant activity, PHs can mitigate abiotic stressors such as drought, salinity, and temperature extremes. Additionally, PHs can affect microbial activity in the rhizosphere and bulk soil, thereby enhancing microbial interactions. For effective administration, PHs can be applied as foliar sprays, root drenches, or through fertigation. PH application depends on plant species, formulation, application rate, and response. More information is needed on signaling pathways, metabolic processes, and biochemical mechanisms to enhance plant-specific responses.

Keywords: biostimulants, protein hydrolysates, amino acids, stress resistance

INTRODUCTION

Horticultural crops, including fruits, vegetables, flower crops, and medicinal plants, are essential for agriculture, human health, and global economy (FAO, 2021). In addition to nutritional benefits, horticultural products offer a significant economic advantage for small-scale farmers, enhance local economic development, and contribute to international markets (Singh et al., 2025; FAO, 2019). In 2023, the total global revenue from fruits and vegetables surpassed 1.5 trillion USD, indicating a growing demand for fresh, nutritious, and plant-based products (Statista, 2023). The pharmaceutical and cosmetic sectors highly demand medicinal and aromatic plants, while flowers play a crucial role in tourism, landscaping, and improving urban aesthetics (Singh et al., 2025; Lubbe & Verpoorte, 2011). In addition to their significant role in human

health and economic growth, horticultural crops play a significant role in environmental sustainability. Orchards and vineyards serve as long-term carbon sinks, improve soil fertility and carbon sequestration (Lorenz, 2018). Various horticultural systems play a significant role in biodiversity, support pollinators, and contribute to soil and ecosystem conservation (Gallai et al., 2009; Altieri, 2018). Horticultural crop production faces numerous challenges. Abiotic stressors—such as drought, salinity, and thermal stress—along with biotic threats from pests and diseases, considerably limit productivity and quality (Mittler, 2006; Atkinson, 2012). Addressing these challenges is vital for ensuring the long-term viability of horticulture, especially in light of climate change and dwindling natural resources (Singh et al., 2025). The potential approach in addressing these issues is the use of biostimulants, which are environmentally

friendly, enhance plant growth, increase stress resilience, and optimize plant nutrient use efficiency (Du Jardin, 2015; Rouphael & Colla, 2020; Liatile, 2022). Biostimulants are substances and microorganisms that enhance plant growth and development beyond the effects of conventional nutrition and pest management (du Jardin, 2015). Unlike agricultural chemical fertilizers and pesticides, biostimulants operate through intricate biochemical processes, modulating plant metabolism, plant hormones, and the stress response pathways (Colla et al., 2015; Calvo et al., 2014). Biostimulants consist of various compounds, including seaweed extracts, protein hydrolysates, humic acids, and beneficial fungi and bacteria (Colla, 2017).

Calvo et al. (2014) noted that biostimulants contain substances that influence root development, enhance photosynthetic efficiency, promote nutrient absorption, and increase plant resilience to stress by activating natural physiological processes. The growing demand for sustainable farming practices and the global need to reduce agricultural chemical use have driven the adoption of biostimulants, which are gaining prominence in both conventional and organic agriculture (Rouphael & Colla, 2017; Du Jardin, 2015). Protein hydrolysates (PHs) represent a category of plant biostimulants that have recently garnered increased attention due to their richness in peptides, amino acids, and bioactive compounds—all of which positively affect plant physiology and metabolism (Colla, 2017; Calvo et al., 2014). PHs are produced through enzymatic and chemical hydrolysis of proteins derived from plant and animal sources and are increasingly recognized as effective biostimulants in sustainable agriculture (Colla et al., 2015; Rouphael et al., 2023).

Recently, in horticultural and field crops, protein hydrolysates (PHs) have been used to boost agricultural productivity, enhance nutrient absorption, and mitigate the effects of abiotic stress (Colla et al., 2015).

This review paper aims to explore the influence of protein hydrolysates on horticultural plants, focusing on their mechanisms of action, growth benefits, stress resilience, and potential to facilitate sustainable horticultural practices. By consolidating previous research findings, the study outlines future avenues for research and application development while identifying gaps in current knowledge.

Protein hydrolysates as biostimulant products

One of the most extensively researched biostimulants is protein hydrolysates (PHs), which play a significant role in plant physiology and crop yield (Colla et al., 2015; Rouphael et al., 2017; Ertani et al., 2013). They are made from plant and animal proteins through enzymatic, thermal, and chemical hydrolysis (Colla et al., 2015). The process of hydrolysis may influence the quality of the product: enzymatic processes generally produce short peptides and bioactive amino acids with minimal degradation, while acid and alkaline hydrolysis may have adverse effects on sensitive amino acids and can result in more diverse mixture (Colla et al., 2015; Ertani et al., 2009). Amino acids in nature are found in the form of stereoisomers, specifically L- and D-forms; plants primarily utilize L-amino acids, which are directly mixed into proteins and metabolic processes, while D-amino acids are less advantageous and may have adverse effects on the growth of plants. However, certain D-forms can be absorbed and may sometimes enhance plant growth under specific circumstances (Vranová et al., 2012; Hill et al., 2021; Forsum et al., 2008).

PHs comprise free amino acids (FAAs), oligopeptides, and small polypeptides ranging from less than 1 kDa to approximately 10 kDa; smaller molecules tend to be more bioavailable and are absorbed quickly through leaves and roots (Colla et al., 2015; Ertani et al., 2009). PHs derived from plants are particularly rich in aspartic acid, glutamic acid, leucine, and proline. These amino acids that play crucial

roles in nitrogen metabolism, osmotic regulation, and stress responses (Ertani et al., 2011; Calvo et al., 2014).

Commercial PHs are available in various formulations, including liquid concentrates (for foliar sprays and fertigation), powders and soluble granules (for soil and hydroponics), chelated micronutrient blends (utilizing amino acid carriers for Fe, Zn, Cu), and combinations with humic substances and seaweed extracts (du Jardin, 2015; Calvo et al., 2014). The mode of application affects the responses: foliar application is absorbed quickly by leaves and initiates rapid physiological changes. At the same time, granular forms offer prolonged root uptake and positively influence beneficial soil microbial activity (Cristofano et al., 2021). The application of amino acids to foliage has recently been projected as a significant and effective method to enhance nutrient utilization efficiency and overall plant performance (Eichert et al., 2012; Colla et al., 2015). When applied to the leaf surface, amino acids have the ability to penetrate the cuticle and epidermis; however, the efficiency of uptake is influenced by their molecular attributes (such as size, polarity, and charge), the physicochemical properties of the spray solution (notably pH), and prevailing environmental conditions (Eichert et al., 2012; Colla et al., 2015). Previous studies indicate that smaller, neutral L-amino acids such as glycine and alanine are absorbed more efficiently than larger or charged molecules (Eichert et al., 2012).

Recent studies validate the ability of plants to absorb amino acids through foliar application. In tomato, foliar applications of amino acids with nitrogen-15 leucine and lysine were taken up by leaves, redistributed to other plant tissues, and contributed to overall nitrogen assimilation, thereby demonstrating both efficient uptake and effective systemic transport (Malécange et al., 2023). Moreover, effective uptake is influenced by the structure of amino acids, the active ingredient, and the current state of the leaf surface, highlighting the need for

optimized spray conditions to enhance bioavailability (Eichert et al., 2012; Colla et al., 2015). The results depend not only on the type of plant and its specific context. However, they are also greatly influenced by the mode of application and the source of PHs, the material used to derive them, which is plant or animal origins (Rouphael et al., 2017). Leaf applications allow for adequate absorption and may produce systemic effects in leafy vegetables, whereas root-zone applications are most effective for crops like tomatoes, particularly under combined stress factors (Colla et al., 2015; Ertani et al., 2013; Rouphael et al., 2017). In tomato plants, foliar applications containing amino acids improved iron nutrition, likely through chelation and enhanced movement through cellular membranes (Ceccarelli et al., 2021). Furthermore, foliar application of amino acids with zinc formulations on soybeans showed enhanced agronomic characteristics and increased zinc accumulation in grains, suggesting that amino acids function as nutrients and transporters (Hans et al., 2024). L-amino acids are efficiently absorbed via the foliar route and can fulfil dual functions as direct metabolic substrates and enhancers of micronutrient uptake (Eichert et al., 2012). The application rate significantly affects the efficacy of protein hydrolysates (PHs) as biostimulants. The reported concentrations generally fall within the range of 2.5 to 10 mL L⁻¹ for foliar sprays and 5–10 L ha⁻¹ for field spraying treatment, which differs according to the plant species and active ingredients. In greenhouse tomatoes, leaf application of PH derived from legumes at concentrations of 2.5- and 5-mL L⁻¹ every 10 days enhanced yield, mineral composition, and fruit quality (Ceccarelli et al., 2021). The time of application of PHs is crucial in the phenological stage. Foliar treatment is most effective during vegetative growth, flowering, and early fruiting, as it promotes biomass accumulation and reproductive success (Colla et al., 2015). In the case of soybeans, the

application of foliar PH during the reproductive stage increased pod and seed counts, thereby enhancing yield (Hans et al., 2024).

PHs are generally applied as pre- and post-treatment for abiotic stress events to prevent physiological damage, enhance plant tolerance to drought, salinity, and thermal stress (Colla et al., 2015; Ertani et al., 2013; Rouphael et al., 2017). The study of foliar application of legume-derived PH on spinach plants exposed to heat and drought stress and PH at a concentration of 4 mL L⁻¹ reported improved photosynthetic efficiency and boosted productivity by 17–30% (Liatile, 2022). Moreover, lettuce grown in nutrient-deficient environments is reported to have a positive response to weekly PH sprays, revealing their potential role in stress prevention and recovery (Rouphael et al., 2017). From a technological standpoint, the active ingredients and source of PHs affect their effectiveness, as plant-derived and animal-derived PHs may vary according to amino acid composition, peptide size, and bioactive properties (Colla et al., 2015). PHs made from legumes are the most well accepted, even at elevated levels. In contrast, some of the PHs derived from animals may induce phytotoxicity, contingent upon their concentration and the sensitivity of the crop (Ertani et al., 2013).

The most effective application method is foliar application; however, root drenching application and seed treatments also serve as effective delivery mechanisms, with seed biopriming demonstrated to enhance germination rates and boost stress tolerance in cereals (Colla et al., 2017). The most innovative way is the application of PHs together with micronutrients, where amino acids function as natural chelators to enhance the foliar uptake of iron (Fe), zinc (Zn), and other essential elements (Ceccarelli et al., 2021). Furthermore, moderate humidity and lower evaporation conditions are necessary when applying PHs to enhance the plant's uptake and uptake efficiency (Eichert et al., 2012).

Physiological effects of protein hydrolysates on horticultural plants

The mode of action by which protein hydrolysates (PHs) function remains unknown; however, their physiological effects are well documented (Table 1). These effects include improvements in nutrient uptake, enhancing stress tolerance, and metabolic regulation (Colla et al., 2015; Ertani et al., 2013; Rouphael et al., 2018).

The effectiveness of PHs is influenced by the presence of bioactive peptides and free amino acids, which significantly enhance plant metabolism, regulate hormonal activities, and enhance the resilience of plants against abiotic stress (Ertani et al., 2013; Colla et al., 2015). Amino acids are essential building blocks for proteins, chlorophyll, and enzymes, and they also act as precursors for metabolites linked to stress responses (Ciriello et al., 2022). However, small peptides facilitate signaling molecules that influence nutrient absorption and assimilation, root growth, photosynthesis, and antioxidant defence mechanisms (Ciriello et al., 2022; Malécange et al., 2023). Other amino acids have a specific role in plant physiology, such as tryptophan, which serves as a precursor for indole-3-acetic acid (IAA), which aids in root growth, cell development, and apical dominance (Ertani et al., 2013). Glutamic acid and arginine function in polyamine synthesis, which is essential for regulating stress signaling and maintaining cellular integrity under stress conditions (Rouphael & Colla, 2020).

Moreover, proline, glycine, and cysteine act as osmoprotectants, assisting to stabilize proteins and membranes, at the same time also functioning as antioxidants that neutralize reactive oxygen species, thus boosting plants' resilience to drought, salinity, and high temperatures (Rania et al., 2022). Some of the exact molecular processes of PHs need further studies; more evidence suggests their function as multifunctional biostimulants, integrating nutritional assistance with regulatory and

Table 1. Physiological effects of protein hydrolysates on horticultural crops

Vegetable species	Product (PH + AA) & Source	Dose (% or mL/L; quantity)	Physiological effects (% vs control)	Reference
Tomato (<i>Solanum lycopersicum</i>)	Soy PH	Foliar spray at vegetative stage, 0.25%; 500 L/ha	The photosynthetic rate increased by 28%, the proline rate by 45%, and the Chl a/b content by 32%.	Rouphael et al. (2017)
Lettuce (<i>Lactuca sativa</i>)	Legume PH	Root soaking at early growth, 0.30% solution, 200 mL/plant.	Photosynthetic rate increased by 24%; phenolic content increased by 30%	Zuluaga et al. (2023)
Cucumber (<i>Cucumis sativus</i>) under chilling stress	Fish PH (pretreatment)	Foliar spray + root drench during vegetative stage: 0.40% PH; foliar application at 300 L/ha and soil drench at 600 L/ha.	Photosynthetic rate increased by 35%; chlorophyll content increased by 30%	Harizanova et al. (2022)
Pepper (<i>Capsicum annuum</i>)	Enzymatic PH	Foliar spray during vegetative stage, 0.20%; 500 L/ha	Photosynthetic rate increased by 26%; relative water content (RWC) increased by 22%; guaiacol peroxidase (GPOX) increased by 39%	Colla et al. (2023)
Broccoli (<i>Brassica oleracea</i> var. <i>italica</i>)	Plant PH (post-treatment)	Soil application at early growth, 0.50%; 400 L/ha	Photosynthetic rate increased by 35%; proline increased by 38%; Fv/Fm improved by 20%	Halshoy et al. (2023)
Onion (<i>Allium cepa</i>)	Yeast extract (PH)	Soil application, 0.25%, 350 L/ha	Photosynthetic rate increased by 34%; chlorophyll content increased by 28%; GPOX increased by 37%	Vujovic et al. (2023)
Eggplant (<i>Solanum melongena</i>)	Corn liquor (PH) (post-treatment)	Foliar spray, 0.40%; 550 L/ha	Photosynthetic rate increased by 24%; Proline increased by 36%; Fv/Fm improved by 19%	Pohl et al. (2019)
Radish (<i>Raphanus sativus</i>)	Gelatine hydrolysate	Root soaking, 0.25% solution, 150 mL/plant	Photosynthetic rate increased by 31%; phenolic content increased by 38%	Raza et al. (2022)
Spinach (<i>Spinacia oleracea</i>)	Legume PH	Foliar spray under varied N supply, 0.40%, 500 L/ha	Photosynthetic rate increased by 24%; chlorophyll content increased by 28%	Carillo et al. (2019)
Zucchini (<i>Cucurbita pepo</i>)	Mixed PHs (post-treatment)	Foliar spray during vegetative growth, 0.20%, 500 L/ha	Photosynthetic rate increased by 26%; chlorophyll content increased by 30%	Corrado et al. (2024)

protective roles (Colla et al., 2015; Ertani et al., 2013; Rouphael et al., 2018).

At the molecular level, PHs regulate the expression of genes associated with mineral uptake. For instance, PHs derived from legumes have been found to upregulate phosphate and sulphate transporter genes in tomato, which leads to increased concentrations of phosphorus (P) and sulfur (S) in the shoots, while also promoting the uptake of micronutrients (Fe, Cu) likely through the mechanism of amino acid chelation (Ciriello et al., 2022; Calvo et al., 2014; Ambrosini et al., 2021). Furthermore, amino acids and small peptides also chelate micronutrients, enhance their uptake and transport within plant tissues (Ertani et al., 2013; Leporino et al., 2024). The significance of small peptides has been reported to be more effective at low-molecular-weight peptides, and they are quickly absorbed and can function as signaling molecules that regulate nutrient absorption, stress responses, and growth processes (Colla et al., 2015; Ciriello et al., 2022). In lettuce and tomato, protein hydrolysates (PHs) have been shown to upregulate iron transporter genes and enhance iron accumulation, contributing to increased chlorophyll and mineral content ((Rouphael et al., 2017; Zuluaga et al., 2023). Furthermore, PHs promote chlorophyll biosynthesis by supplying essential nutrients such as nitrogen and magnesium, and have been associated with enhanced photosynthetic activity through improved nutritional status (Colla et al., 2023). These attributes are significant in conditions with nutrient deficiencies and saline environments (Ciriello et al., 2023; Singh et al., 2024). PHs also exhibit hormone-like activity. Various PHs mimic auxins and gibberellins, facilitating seed germination, root development, and fruit maturation. When plant-derived PHs are applied as foliar treatments to tomato, they often result in increased root dry weight, consistent with auxin-like effects (Colla et al., 2014; Rouphael et al., 2020).

PHs stimulate nutrient-transporter gene expression and alter root architecture, thereby improving macro and micronutrients (Ceccarelli et al., 2021; Colla, 2015). In the conditions of different levels of nitrogen fertilization, PH treatment has been reported to enhance nitrogen uptake efficiency (NUpE) and nitrogen utilization efficiency (NUtE) in both tomato and lettuce, resulting in improved growth and nutritional quality (Colla et al., 2015; Leporino et al., 2024). In the case of perennial crops, the application at 5 mL L⁻¹, in conjunction with urea, boric acid, and zinc sulfate, resulted in better mineral status in pecan (Repullo et al., 2021). Additionally, animal-derived PHs have been evaluated; for instance, the foliar application of at 5 L ha⁻¹ enhanced strawberries' dry matter and nitrate content (Meggio et al., 2012).

PHs significantly increase the photosynthetic performance of horticultural crops (Colla, 2015; Rouphael & Colla, 2020). Important metrics are parameters such as net photosynthetic rate (Pn), stomatal conductance, transpiration rate, chlorophyll content (Chl a, Chl b, SPAD values), and chlorophyll fluorescence parameters such as the maximum quantum yield of PSII (Fv/Fm) and effective quantum yield (Maxwell & Johnson, 2000; Baker, 2008). Foliar application rate of 2.5 mL L⁻¹ to lettuce grown under a hydroponic setup resulted in a biomass increase of approximately 50% and improved chlorophyll and nitrogen levels (Rouphael et al., 2017). Recent studies reported that applying PHs enhances these growth parameters in crops such as lettuce and tomato (Colla et al., 2015). Moreover, Colla et al. (2015) reported that applying plant-derived PH on lettuce and tomato resulted in a 21–28% increase in Pn, elevated chlorophyll content, and improved water-use efficiency. In water-deficient conditions, foliar application of PH on tomato seedlings has resulted in higher SPAD values and superior PSII photochemistry, suggesting reduced pigment degradation and enhanced light harvesting (Singh, 2024). PHs

play a vital role in enhancing the water status of plants. Parameters such as relative water content (RWC), leaf water potential, membrane stability index (MSI), electrolyte leakage, and water-use efficiency (WUE) serve as effective measures to assess the effect of PHs on the water status of the plant (Ertani et al., 2009; Calvo et al., 2014).

Protein hydrolysates for improving abiotic stress tolerance in horticultural crops

Drought, salinity, and chilling affect the homeostasis of plants and lead to oxidative stress, primarily due to the excessive accumulation of reactive oxygen species (ROS) (Mittler, 2006; Hasanuzzaman et al., 2012). These ROS initiate lipid peroxidation, protein oxidation, DNA damage, and degradation of membranes (Hasanuzzaman et al., 2012; Zhao et al., 2014; Malécange et al., 2023). Malondialdehyde (MDA) is typically used as a marker for lipid peroxidation, while other signs of oxidative stress include electrolyte leakage, compromised membrane integrity, and reduced antioxidant capacity (Colla, 2015). PHs are reported to mitigate oxidative stress by boosting enzymatic antioxidant defenses and modulating metabolic pathways (Rouphael, 2020). They enhance the activity of essential antioxidant enzymes such as catalase (CAT), superoxide dismutase (SOD), guaiacol peroxidase (GPOD), and ascorbate peroxidase (APX), which detoxify reactive oxygen species (ROS) and avert oxidative damage (Hasanuzzaman et al., 2012; Colla et al., 2018).

Recent research indicates that antioxidant responses to PHs depend on the plant species. In tomatoes and lettuce under salinity stress, PHs enhanced the activities of CAT, SOD, GPOD, and APX; lettuce showed a more pronounced increase in SOD and APX, whereas tomatoes exhibited greater CAT and GPOD activity (Rouphael et al., 2017). Moreover, priming tomato seeds with animal-derived PHs under drought conditions has been reported to increase CAT, SOD, and APX activities, resulting in improved water balance and reduced lipid peroxidation (Sestili et al., 2022). The observed

reduction in malondialdehyde (MDA) levels and lower electrolyte leakage confirmed enhanced membrane stability (Sestili et al., 2022). Furthermore, lettuce and cucumber exposed to chilling stress showed improved membrane stability and proline accumulation following PH treatment, highlighting PHs' protective role in stress tolerance (Harizanova et al., 2022). The function of PHs has a positive effect on enzymatic antioxidants, metabolites, and gene expression. For example, the application of PHs to tomato plants under drought stress has been reported to increase glucogenic dipeptides, which serve as alternative sources of carbon and nitrogen and act as ROS scavengers (Singh et al., 2024). The rise in proline levels supports osmoprotection and stabilizes cellular structures under stress (Harizanova et al., 2022). Additionally, PHs influence transcriptional networks related to hormone metabolism, cell wall remodeling, stress signaling, and carbon–nitrogen balance (Singh et al., 2024). Recent studies have shown that plant-derived PHs improve ion homeostasis, promote the expression of phenylalanine ammonia-lyase (PAL), and elevate proline levels in tomato and lettuce grown under salinity stress (Carillo, 2019; Zhao et al., 2023). Moreover, PHs derived from fish extract are reported to improve antioxidant enzyme activity, pigment content, sugar levels, and proline accumulation in spinach under drought conditions (Malécange et al., 2023). Furthermore, foliar application treatments in soybean, chili, and chickpea under drought and heat stress have also improved membrane stability, relative water content, and overall yield (Grigorova et al., 2021). In horticultural crops, amino acids derived from plant hormones (PHs) improve nitrogen metabolism and osmotic balance in lettuce subjected to optimal and saline conditions (Carillo et al., 2019; Zhao et al., 2023). In tomatoes, the proline concentration is increased by PHs, which support roles in salinity tolerance and sustain photosynthesis (Carillo, 2019).

Metabolomic analyses completed on peppers exposed to drought stress have shown increased levels of proline and non-enzymatic antioxidants after application of PH treatment, which enhanced water use efficiency and alleviated oxidative stress (Paskovi et al., 2024). PHs function at physiological, biochemical, and molecular levels to enhance growth, metabolism, and increase stress tolerance (Calvo et al., 2014). They stabilize pigments, uphold photosystem II efficiency, regulate stomatal conductance, and enhance net photosynthesis during stress (Rouphael et al., 2017). Plants treated with PHs have been reported to have higher relative water content, decreased electrolyte leakage, and enhanced osmotic adjustment, improving water use efficiency and quicker recovery post-stress (Sestili et al., 2022). Peptides derived from PHs improve the activity of antioxidant enzymes, chlorophyll content, and soluble sugars, resulting in enhanced biomass and leaf quality during drought conditions in spinach (Liatile, 2022). Their application also promotes root growth, nutrient uptake, and increases fresh biomass in rocket and lettuce (Sestili et al., 2018; Rouphael et al., 2017). Furthermore, PH treatment reduces chlorophyll loss and preserves PSII function in both tomato and lettuce under saline conditions, demonstrating protective effects on the photosynthetic machinery (Rouphael et al., 2017).

Despite positive reports from current protein hydrolysate (PH) studies, several research gaps remain. Most investigations have focused on a limited number of crops, such as tomato and lettuce, leaving gaps in the literature regarding other vegetables like cucumber, eggplant, and pepper (Rouphael et al., 2017; Zhao et al., 2024). The fundamental molecular mode of action regulating gene expression and signaling is still poorly understood (Sestili et al., 2022; Colla et al., 2017). Uncertainty about the source of dipeptides and optimal application protocols hampers reproducibility (Rouphael, 2020). Moreover, the effects of combined and

prolonged stresses on yield and resilience are not yet fully understood (Yakhin et al., 2017).

Effects of protein hydrolysates on the yield and quality of horticultural plants

Most horticultural crops have been reported to show improved yields when PHs are applied (Colla et al., 2015). In controlled greenhouse experiments, lettuce (*Lactuca sativa* L.) showed a 17–23% increase in marketable fresh weight after receiving foliar treatments with plant-derived PHs (Colla et al., 2017). Moreover, tomato (*Solanum lycopersicum* L.) is reported to show improved fruit quantity and overall yield, attributed to enhanced nitrogen uptake and assimilate distribution (Colla, 2015; Steffi et al., 2017). Bi-weekly foliar application of PHs derived from legumes to perennial wall rocket (*Diplotaxis tenuifolia*) has been noted to increase marketable yield by over 25%, while also enhancing harvest frequency (Ciriello et al., 2022). Recent studies further validate these findings, demonstrating that PHs positively influence yield and quality traits in various horticultural crops (Table 2).

In sweet potato (*Ipomoea batatas* L.), foliar application of protein hydrolysate (WPH) combined with potassium fertilization significantly improved both total and marketable yields, as well as tuber size (El-Waziri et al., 2023). When chilli (*Capsicum annum* L.) was exposed to abiotic stress and treated with PHs, it maintained higher fruit yields and mitigated losses during heat and drought stress, stabilizing yields under challenging stress conditions (Colla et al., 2023). Moreover, foliar application of protein hydrolysates (PHs) improves nutritional and market quality.

For example, in lettuce, the foliar application of PHs reduced nitrate levels while enhancing the presence of phenolic compounds, flavonoids, and soluble sugars, thereby improving health benefits and consumer appeal (Colla et al., 2017).

Table 2. Effects of PHs on yield and quality traits in horticultural crops

Vegetable species	Product (PH + AA) & Source	Dose (% or mL/L and quantity)	Productivity (yield/biomass) (% vs control)	Quality (% vs control)	Reference
Tomato (<i>Solanum lycopersicum</i>)	Soy PH: Protein 55%, AA 12%	Foliar application, 0.25%; 500 L/ha	Yield increased by 30%; Fruit fresh weight increased by 35%	Vitamin C increased by 14%; glucose increased by 12%; soluble solids increased by 8%	Rouphael. (2017)
Lettuce (<i>Lactuca sativa</i>)	Legume PH: Protein 45%, AA 10%	Foliar application, 0.30%; 500 L/ha	Yield increased by 20%; Whole plant fresh biomass increased by 25%	Vitamin C increased by 4.5%; total sugars increased by 4.5%; phenolics increased by 6%	Zuluaga et al. (2023)
Spinach (<i>Spinacia oleracea</i>)	Casein PH: Protein 90%, AA 8%; Ca & P 5%	Foliar application, 0.40%; 550 L/ha	Yield increased by 28%; Whole plant fresh biomass increased by 30%	Vitamin C increased by 15%; total sugars increased by 15%; nitrate content increased by 12%	Carillo et al. (2019)
Cucumber (<i>Cucumis sativus</i>) under chilling stress	Fish PH: Protein 75%, AA 15%, post-treatment	Soil drench at 0.20% PH in 500 L/ha, foliar spray at 0.20% PH in 300 L/ha.	Yield increased by 40%; fruit fresh weight increased by 25%	Glucose increased by 12%; soluble solids increased by 7%	Harizanova et al. (2022)
Pepper (<i>Capsicum annuum</i>)	Enzymatic PH: Peptides 80%	Foliar application, 0.50%; 550 L/ha	Fruit fresh weight and yield increased by 27%	Glucose increased by 10%; vitamin C increased by 9%	Colla et al. (2023)
Broccoli (<i>Brassica oleracea</i>) under salinity stress	Plant PH: Protein 50%, carbohydrates 35%	Soil drench at 0.30% PH in 400 L/ha.	Yield increased by 20%; head of fresh weight increased by 29%	Sucrose increased by 11%; fructose increased by 9%; glucose increased by 8%; vitamin C increased by 7%	Halshoy et al. (2023)
Carrot (<i>Daucus carota</i>)	Alfalfa PH: Protein 35%, triacontanol 0.1%	Foliar application, 0.40%; 550 L/ha	Yield increased by 33%; Root fresh weight increased by 30%	Vitamin C increased by 10%; glucose increased by 8%; carotenoids increased by 6%	Zhu et al. (2024)
Onion (<i>Allium cepa</i>)	Yeast extract: Protein 60%, AA 10%	Soil drench, 0.25% in 350 L/ha solution	Yield increased by 31%; Bulb fresh weight increased by 28%	Vitamin C increased by 12%; total soluble solids increased by 7%	Vujovic et al. (2023)
Eggplant (<i>Solanum melongena</i>)	Corn steep liquor: Protein 47%, AA 12%	Foliar application, 0.20%; 500 L/ha	Yield increased by 26%; fruit fresh weight increased by 23%	Vitamin C increased by 9%; phenolic increased by 8%	Pohl et al. (2019)
Radish (<i>Raphanus sativus</i>)	Gelatin hydrolysate: Protein 90%	Foliar application, 0.35%; 500 L/ha	Yield increased by 25%; root fresh weight increased by 32%	Vitamin C increased by 11%; total sugars increased 9%	Raza et al. (2022)

In tomatoes, fruits treated with PHs were noted to have increased lycopene levels and total soluble solids (TSS), which adds to better flavor and prolonged shelf life (Mascarehas et al., 2024; Sestili et al., 2018). In sweet potatoes, the application of protein hydrolysates (WPH) has been reported to improve tuber uniformity and consistency; on the other hand, in wall rocket, PHs enhanced leaf dry matter content, size uniformity, and visual appearance, which are more important for fresh-market quality (Caruso et al., 2019; El-Waziri et al., 2023). These encouraging results are mostly from studies focused on a limited number of crops, such as lettuce, tomato, sweet potato, and rocket. In contrast, important horticultural crops such as cucumber, eggplant, and brassicas have received less attention (Ciriello et al., 2023). Furthermore, the specific roles of exogenously applied amino acids and peptides, compared to those synthesized internally, remain poorly understood (Colla, 2017; Rouphael et al., 2017). Recent studies have primarily focused on short-term experiments conducted under greenhouse conditions, providing limited evidence on long-term and post-harvest effects (Sestili et al., 2018). Few studies have explored comparative research between plant-derived and animal-derived protein hydrolysates, despite potential differences in their modes of action and effectiveness (Ertani et al., 2011; Colla et al., 2015).

CONCLUSIONS

Protein hydrolysates (PHs) are effective biostimulants that enhance plant growth, yield, and stress resilience, particularly under drought, salinity, and temperature extremes. Their bioactive compounds – peptides and amino acids – support nutrient uptake, photosynthesis, and antioxidant activity. PHs stimulate nitrogen metabolism, osmotic balance, and secondary stress responses, improving water use efficiency, membrane integrity, and gas exchange. Trials in crops such as tomato, lettuce, and spinach have shown increased

photosynthetic efficiency and stress tolerance. PHs also influence hormone regulation, carbon-nitrogen balance, and microbial interactions, further promoting growth and nutrient assimilation.

Nevertheless, most research has focused on short-term greenhouse or pot experiments, primarily involving lettuce and tomato, which limits the applicability of findings to field conditions and other vegetable species. There is a lack of standardized protocols for PH dosage, timing, and application techniques across different crops, and the specific bioactive components responsible for the observed benefits remain largely unidentified. Future research should prioritize multi-season field trials, a broader range of crops, and in-depth investigations into PH interactions with plant metabolism, microbiomes, and stress responses.

REFERENCES

- Abu-Ria, M.E., Elghareeb, E.M., Shukry, W.M. (2024). Mitigating drought stress in maize and sorghum by humic acid: differential growth and physiological responses. *Plant Biol* 24, 514. <https://doi.org/10.1186/s12870-024-05184-4>
- Altieri, M. A. (2018). *Agroecology: The Science of Sustainable Agriculture*. CRC Press, Boca Raton. <https://doi.org/10.1201/9780429495465>
- Ambrosin, S., Segal, D., Santi, C., Zamboni, A., Varanini, Z., & Pandolfini, T. (2021). Evaluation of the Potential Use of a Collagen-Based Protein Hydrolysate as a Plant Multi-Stress Protectant. *Front. Plant Sci.* 12:600623. <https://doi.org/10.3389/fpls.2021.600623>
- Atkinson, N. J., & Urwin, P. E. (2012). The interaction of plant biotic and abiotic stresses: From genes to the field. *Journal of Experimental Botany*, 63(10), 3523–3543. <https://doi.org/10.1093/jxb/ers100>

- Baker, N. R. (2008). Chlorophyll fluorescence: A probe of photosynthesis in vivo. *Annual Review of Plant Biology*, 59, 89-113. <https://doi.org/10.1146/annurev.arplant.59.032607.092759>
- Calvo, P., Nelson, L. & Kloepper, J.W. (2014). Agricultural Uses of Plant Biostimulants. *Plant Soil*, 383, 3–41. <https://doi.org/10.1007/s1110>
- Cao, Y., Turk, K., Bibi, N., Ghafoor, A., Ahmed, N., Azmat, M., Ahmed, R., Ghani, M.I., Ahanger, M.A. (2025). Nanoparticles as catalysts of agricultural revolution: enhancing crop tolerance to abiotic stress: a review. *Front. Plant Sci.*, 15, 1510482. <https://doi.org/10.3389/fpls.2024.1510482>
- Caruso, G., & El-Nakhel, C. (2023). Biostimulatory action of a plant-derived protein hydrolysate on morphological traits, photosynthetic parameters, and mineral composition of two basil cultivars grown hydroponically. *Plants*, 12(5), 1031. <https://doi.org/10.3390/horticulturae8050409>
- Caruso, G., Stoleru, V., De Pascale, S., Cozzolino, E., Pannico, A., Giordano, M., & Colla, G. (2019). Protein hydrolysate or plant extract-based biostimulants enhanced the yield and quality performances of greenhouse perennial wall rocket grown in different seasons. *Plants*, 8(7), 208. <https://doi.org/10.3390/plants8070208>
- Corrado, C. L., Donati, L., Taglienti, A., Ferretti, L., Faggioli, F., Reverberi, M., & Bertin, S. (2024). An Evaluation of Organic Biostimulants as a Tool for the Sustainable Management of Viral Infections in Zucchini Plants. *Horticulturae*, 10(11), 1176. <https://doi.org/10.3390/horticulturae10111176>
- Ceccarelli, A.V., Miras-Moreno, B., Buffagni, V., Senizza, B., Pii, Y., Cardarelli, M., Roupael, Y., Colla, G., Lucini, L. (2021). Foliar Application of Different Vegetal-Derived Protein Hydrolysates Distinctively Modulates Tomato Root Development and Metabolism. *Plants*, 10(2), 326. <https://doi.org/10.3390/plants10020326>
- Cappelletti, M., Perazzolli, M., Nesler, A., Giovannini, O., & Pertot, I. (2017). Hydrolysis and protein source affect the efficacy of protein hydrolysates as plant resistance inducers against powdery mildew. *Journal of Bioprocessing & Biotechniques*, 7(5), 1000306. <https://doi.org/10.4172/2155-9821.1000306>
- Choi, S., Colla, G., Cardarelli, M., & Kim, H. J. (2022). Effects of Plant-Derived Protein Hydrolysates on Yield, Quality, and Nitrogen Use Efficiency of Greenhouse Grown Lettuce and Tomato. *Agronomy*, 12(5), 1018. <https://doi.org/10.3390/agronomy12051018>
- Ciriello, M., Formisano, L., El-Nakhel, C., Corrado, G., & Roupael, Y. (2022). Biostimulatory Action of a Plant-Derived Protein Hydrolysate on Morphological Traits, Photosynthetic Parameters, and Mineral Composition of Two Basil Cultivars Grown Hydroponically under Variable Electrical Conductivity. *Horticulturae*, 8(5), 409. <https://doi.org/10.3390/horticulturae8050409>
- Carillo, P., Colla, G., Fusco, G. M., Dell'Aversana, E., El-Nakhel, C., Giordano, M., Pannico, A., Cozzolino, E., Mori, M., Reynaud, H., Kyriacou, M. C., Cardarelli, M., & Roupael, Y. (2019). Morphological and physiological responses induced by protein hydrolysate-based biostimulant and nitrogen rates in greenhouse spinach (*Spinacia oleracea*). *Agronomy*, 9(8), 450. <https://doi.org/10.3390/agronomy9080450>

- Colla, G., Rouphael, Y., Canaguier, R., Svecova, E., & Cardarelli, M. (2014). Biostimulant action of a plant-derived protein hydrolysate produced through enzymatic hydrolysis. *Front. Plant Sci.*, 5, 448.
<https://doi.org/10.3389/fpls.2014.00448>
- Colla, G., Hoagland, L., Ruzzi, M., Cardarelli, M., Bonini, P., Canaguier, R., & Rouphael, Y. (2017). Biostimulant Action of Protein Hydrolysates: Unraveling Their Effects on Plant Physiology and Microbiome. *Front. Plant Sci.*, 8, 2202.
<https://doi.org/10.3389/fpls.2017.02202>
- Colla, G., Hoagland, L., Cardarelli, M., Lucini, L., & Rouphael, Y. (2023). Protein hydrolysate-based biostimulants improve growth and nutrient uptake in bell pepper. *Frontiers in Plant Science*, 14, 1123905.
<https://doi.org/10.3390/plants8070208>
- Colla, G., Rouphael, Y., Canaguier, R., Svecova, E., & Cardarelli, M. (2014). Biostimulant action of a plant-derived protein hydrolysate produced through enzymatic hydrolysis. *Frontiers in Plant Science*, 5, 448.
<https://doi.org/10.3389/fpls.2014.00448>
- Colla, G., Rouphael, Y., Svecova, E., Cardarelli, M., & Rea, E. (2015). Effectiveness of a plant-derived protein hydrolysate to improve crop performance under different growing conditions. *Acta Horticulturae*, 1076, 87-194.
<https://doi.org/10.17660/ActaHortic.2013.1009.21>
- Colla, G., Rouphael, Y., Svecova, E., Cardarelli, M., & Rea, E. (2015). Protein hydrolysates as biostimulants in horticulture. *Scientia Horticulturae*, 196, 28-38.
<https://doi.org/10.1016/j.scienta.2015.08.037>
- Cristofano, F., El-Nakhel, C., Pannico, A., Giordano, M., Colla, G., & Rouphael, Y. (2021). Foliar and Root Applications of Vegetal-Derived Protein Hydrolysates Differentially Enhance the Yield and Qualitative Attributes of Two Lettuce Cultivars Grown in a Floating System. *Agronomy*, 11(6), 1194.
<https://doi.org/10.3390/agronomy11061194>
- Du Jardin, P. (2015). Plant biostimulants: Definition, concept, main categories, and regulation. *Scientia Horticulturae*, 196, 3-14.
<http://dx.doi.org/10.1016/j.scienta.2015.09.021>
- Eichert, T., & Fernández, V. (2012). Uptake and release of elements by leaves and other aerial plant parts. *Annual Review of Plant Biology*, 63, 377-402.
<https://doi.org/10.1016/B978-0-12-384905-2.00004-2>
- El-Waziri, A., Hassan, F. A. S., & Ragab, A. (2023). Biostimulant application of whey protein hydrolysates and potassium fertilization enhances sweet potato's productivity and tuber quality.
<http://dx.doi.org/10.15835/nbha51213122>
- Ertani, A., Schiavon, M., Muscolo, A. & Nardi, S. (2013). Alfalfa Plant-Derived Biostimulant Stimulates Short-Term Growth of Salt-Stressed Zea mays L. Plants. *Plant and Soil*, 364, 145-148.
<http://dx.doi.org/10.1007/s11104-012-1335-z>
- Ertani, A., Pizzeghello, D., Altissimo, A., & Nardi, S. (2009). Biostimulant activity of two protein hydrolyzates in maize seedlings' growth and nitrogen metabolism. *Acta Horticulturae*, 1009, 153-160.
<https://doi.org/10.1002/jpln.200800174>
- Food and Agriculture Organization (FAO). (2019). The State of the World's Biodiversity for Food and Agriculture. FAO Commission on Genetic Resources for Food and Agriculture Assessments, Rome, p. 572.
<http://www.fao.org/3/CA3129EN/CA3129EN.pdf>

- Food and Agriculture Organization (FAO). (2021). The State of the World's Biodiversity for Food and Agriculture. FAO Commission on Genetic Resources for Food and Agriculture Assessments, Rome.
<http://dx.doi.org/10.4060/cb4476en>
- Forsum, O., Svennerstam, H., Ganeteg, U., & Näsholm, T. (2008). Capacities and constraints of amino acid utilization in Arabidopsis. *New Phytologist*, 179(4), 1058–1069.
<https://doi.org/10.1111/j.1469-8137.2008.02546.x>
- Gallai, N., Salles, J. M., Settele, J., & Vaissière, B. E. (2009). Economic valuation of the vulnerability of world agriculture confronted with pollinator decline. *Ecological Economics*, 68(3), 810–821.
<http://dx.doi.org/10.1016/j.ecolecon.2008.06.014>
- Grigorova, B., Vaseva, I., Demirevska, K. (2011). Combined drought and heat stress in wheat: changes in some heat shock proteins. *Biol Plant* 55, 105–111.
<https://doi.org/10.1007/s10535-011-0014-x>
- Halshoy, H., Mahmood, A. and Tofiq, G. (2023). Effect of Plant Biostimulants on Growth, Yield and Some Mineral Composition of Broccoli Plants (*Brassica oleracea* var. *Italica*). *Tikrit Journal for Agricultural Sciences*, 23(1), 130-140.
<https://doi.org/10.25130/tjas.23.1.16>
- Han, S., Sönmez, I., Qureshi, M., Güden, B., Gangurde, S.S., & Yol, E. (2024). The effects of foliar amino acid and Zn applications on agronomic traits and Zn biofortification in soybean (*Glycine max* L.). *Front. Plant Sci.* 15:1382397.
<https://doi.org/10.3389/fpls.2024.1382397>
- Harizanova, A., Koleva-Valkova, L., & Vassilev, A. (2022). Effects of the protein hydrolysate pretreatment on cucumber plants exposed to chilling stress. *Acta Agrobotanica*, 75(4).
<https://doi.org/10.5586/aa.756>
- Hasanuzzaman, M., Hossain, M.A., da Silva, J.A.T., Fujita, M. (2012). Plant Response and Tolerance to Abiotic Oxidative Stress: Antioxidant Defense Is a Key Factor. In: Crop Stress and its Management: Perspectives and Strategies. Venkateswarlu, B., Shanker, A., Shanker, C., & Maheswari, M. (Eds.). Springer, Dordrecht. https://doi.org/10.1007/978-94-007-2220-0_8
- Hill, P. W., Quilliam, R.S., DeLuca, T.H., Farrar, J., Farrell, M., Roberts, P. (2011). Acquisition and Assimilation of Nitrogen as Peptide-Bound and D-Enantiomers of Amino Acids by Wheat. *PLoS ONE*, 6(4), e19220.
<https://doi.org/10.1371/journal.pone.0019220>
- Leporino, M., Roupheal, Y., Bonini, P., Colla, G., & Cardarelli, M. (2024). Protein hydrolysates enhance recovery from drought stress in tomato plants: phenomic and metabolomic insights. *Front. Plant Sci.*, 15, 1357316.
<https://doi.org/10.3389/fpls.2024.1357316>
- Liatile, P. C., Potgieter, G., & Moloi, M. J. (2022). A Natural Bio-Stimulant Consisting of a Mixture of Fish Protein Hydrolysates and Kelp Extract Enhances Spinach's Physiological, Biochemical, and Growth Responses under Different Water Levels. *Plants*, 11(23), 3374.
<https://doi.org/10.3390/plants11233374>
- Liu, L., Yu, X., Yan, Y., He, C., Wang, J., Sun, M., & Li, Y. (2024). Amino Acid Transporters on Amino Acid Absorption, Transport, and Distribution in Crops. *Horticulturae*, 10(9), 999.
<https://doi.org/10.3390/horticulturae10090999>
- Lorenz, K., & Lal, R. (2018). Carbon sequestration in agricultural ecosystems. Springer. p137-173.

- <https://doi.org/10.1007/978-3-319-92318-5>
- Lubbe, A., & Verpoorte, R. (2011). Cultivation of medicinal and aromatic plants for specialty industrial materials. *Industrial Crops and Products*, 34(1), 785-801. <https://doi.org/10.1016/j.indcrop.2011.01.019>
- Malécange, M., Sergheraert, R., Teulat, B., Mounier, E., Lothier, J., & Sakr, S. (2023). Biostimulant Properties of Protein Hydrolysates: Recent Advances and Future Challenges. *International Journal of Molecular Sciences*, 24(11), 9714. <https://doi.org/10.3390/ijms24119714>
- Mascarenhas, M. S., Nascimento, F. d. S., Rocha, A. d. J., Ferreira, M. d. S., Oliveira, W. D. d. S., Morais Lino, L. S., Mendes, T. A. d. O., Ferreira, C. F., Santos-Serejo, J. A. d., & Amorim, E. P. (2024). Use of CRISPR Technology in Gene Editing for Tolerance to Biotic Factors in Plants: A Systematic Review. *Current Issues in Molecular Biology*, 46(10), 11086–11123. <https://doi.org/10.3390/cimb46100659>
- Maxwell, K., & Johnson, G. N. (2000). Chlorophyll fluorescence: A practical guide. *Journal of Experimental Botany*, 51(345), 659–668. <https://doi.org/10.1093/jexbot/51.345.659>
- Meggio, F., Trevisan, S., Manoli, A., Ruperti, B., & Quaggiotti, S. (2020). Systematic Investigation of the Effects of a Novel Protein Hydrolysate on the Growth, Physiological Parameters, Fruit Development and Yield of Grapevine (*Vitis Vinifera* L., cv *Sauvignon Blanc*) under Water Stress Conditions. *Agronomy*, 10(11), 1785. <https://doi.org/10.3390/agronomy10111785>
- Mittler, R. (2006). Abiotic stress, the field environment, and stress combination. *Trends in Plant Science*, 11(1), 15–19. <https://doi.org/10.1016/j.tplants.2005.11.002>
- Pasković, I.; Popović, L.; Pongrac, P.; Polić Pasković, M.; Kos, T.; Jovanov, P.; Franić, M. (2024). Protein Hydrolysates Production, Effects on Plant Metabolism, and Use in Agriculture. *Horticulturae* 2024, 10, 1041. <https://doi.org/10.3390/horticulturae10101041>
- Pohl, A., Grabowska, A., Kalisz, A., & Sękara, A. (2019). Biostimulant Application Enhances Fruit Setting in Eggplant—An Insight into the Biology of Flowering. *Agronomy*, 9(9), 482. <https://doi.org/10.3390/agronomy9090482>
- Rania, H., Jacob, A. S. A., Sanaa, M., & Shanab, E. A. S. (2022). Chelated amino acids: biomass sources, preparation, properties, and biological activities. *Agronomy, Biomass Conversion and Biorefinery*, 14, 2907–2921. <https://doi.org/10.1007%2Fs13399-022-02333-3>
- Raza, Q. U., A, Bashir, M. A., Rehim, A., Ejaz, R., Raza, H. A., Shahzad, U., Ahmed, F., & Geng, Y. (2022) Biostimulants induce positive changes in the radish morphophysiology and yield. *Front. Plant Sci.*, 13, 950393. <https://doi.org/10.3389/fpls.2022.950393>
- Repullo-Ruibérriz de Torres, M. A., Moreno-García, M., Ordóñez-Fernández, R., Rodríguez-Lizana, A., Cárcelos Rodríguez, B., García-Tejero, I. F., Durán Zuazo, V. H., & Carbonell-Bojollo, R. M. (2021). Cover Crop Contributions to Improve the Soil Nitrogen and Carbon Sequestration in Almond Orchards (SW Spain). *Agronomy*, 11(2), 387. <https://doi.org/10.3390/agronomy11020387>
- Rouphael, Y., & Colla, G. (2020). Editorial: Biostimulants in Agriculture. *Frontiers in Plant Science*, 11, 40. <https://doi.org/10.3389/fpls.2020.00040>

- Rouphael, Y., Colla, G., Giordano, M., El-Nakhel, C., Kyriacou, M. C., De Pascale, S., & Carillo, P. (2017). Foliar applications of a legume-derived protein hydrolysate elicit dose-dependent growth increases, leaf mineral composition, yield, and fruit quality in two greenhouse tomato cultivars, *Scientia Horticulturae*, 225, 353–362.
<http://dx.doi.org/10.1016/j.scienta.2017.09.007>
- Sestili, F., Rouphael, Y., Cardarelli, M., Pucci, A., Bonini, P., Canaguier, R., Colla, G. (2018). Protein Hydrolysate Stimulates Growth in Tomato Coupled With N-Dependent Gene Expression Involved in N Assimilation. *Front. Plant Sci.*, 9, 1233.
<https://doi.org/10.3389/fpls.2018.01233>
- Singh, M., Subahan, G. M., Sharma, S., Singh, G., Sharma, N., Sharma, U., & Kumar, V. (2025). Enhancing Horticultural Sustainability in the Face of Climate Change: Harnessing Biostimulants for Environmental Stress Alleviation in Crops. *Stresses*, 5(1), 23.
<https://doi.org/10.3390/stresses5010023>
- Singh, D.P., Maurya, S., Yerasu, S.R. (2024). Metabolomics Unveiled Metabolic Reprogramming in Tomato Due to Beneficial (*Bacillus subtilis*) and Pathogenic (*Alternaria solani*) Tripartite Interaction. *J Plant Growth Regul.*, 44, 2959–2976.
<https://doi.org/10.1007/s00344-024-11589-0>
- Statista. (2023). Market size of agricultural biostimulants worldwide from 2018 to 2023.
- Steffi, R., Diana, L., Susanne, K., Thomas, H. (2017). Identification and quantification of ACE-inhibiting peptides in enzymatic hydrolysates of plant proteins, *Food Chemistry*, P19-25.
<https://doi.org/10.1016/j.foodchem.2016.12.039>
- Vranová, V., Rejsek, K., & Formanek, P. (2012). The significance of D-amino acids in soil, fate, and utilization by microbes and plants: Review and identify knowledge gaps. *Plant and Soil*, 354, 21–39.
<http://dx.doi.org/10.1007/s11104-011-1059-5>
- Vujovic, Đ., Maksimović, I., Tepić Horecki, A., Karadžić Banjac, M., Kovačević, S., Daničić, T., Podunavac-Kuzmanović, S., & Ilin, Ž. (2023). Onion (*Allium cepa* L.) Yield and Quality Depending on Biostimulants and Nitrogen Fertilization – A Chemometric Perspective. *Processes*, 11(3), 684.
<https://doi.org/10.3390/pr11030684>
- Yakhin, O. I., Lubyantsev, A. A., Yakhin, I. A., & Brown, P. H. (2017). Biostimulants in plant science: A global perspective. *Frontiers in Plant Science*, 7, 2049.
<https://doi.org/10.3389/fpls.2016.02049>
- Zuluaga, M.Y. A., Monterisi, S., Rouphael, Y., Colla, G., Lucini, L., Cesco, S., & Pii, Y. (2023). Different vegetal protein hydrolysates distinctively alleviate salinity stress in vegetable crops: A case study on tomato and lettuce. *Front. Plant Sci.*, 14:1077140.
<https://doi.org/10.3389/fpls.2023.1077140>
- Zhu, L., Zhang P, Ma S, Yu Q, Wang H, Liu Y, Yang S and Chen Y (2024) Enhancing carrot (*Daucus carota* var. sativa Hoffm.) plant productivity with combined rhizosphere microbial consortium. *Front. Microbiol.* 15, 1466300.
<https://doi.org/10.3389/fmicb.2024.1466300>
- Zhao, X. X., Huang, L. K., Zhang, X. Q., Li, Z., & Peng, Y. (2014). Effects of Heat Acclimation on Photosynthesis, Antioxidant Enzyme Activities, and Gene Expression in Orchardgrass under Heat Stress. *Molecules*, 19(9), 13564–13576.
<https://doi.org/10.3390/molecules190913564>