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Review article

Effects of Phson Plant Metabolism and Development

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Abstract

Protein hydrolysates (PHs) are gaining increasing attention as sustainable biostimulants in agriculture due to their ability to improve plant performance under both optimal and stressful conditions. These compounds, derived from plant or animal proteins, contain a mixture of amino acids and peptides that influence numerous physiological and biochemical processes. Recent studies have shown that PHs play a regulatory role in primary metabolism by modulating enzyme activity and gene expression involved in nitrogen and carbon pathways. They also impact secondary metabolism, enhancing the biosynthesis of phenolics, flavonoids, and other compounds that contribute to stress tolerance and crop quality. In addition, PHs applied as seed treatments or foliar sprays have been reported to stimulate germination, improve seedling establishment, and promote nutrient uptake. Their beneficial effects extend to yield and quality traits, including increases in biomass, fruit set, phytochemical content, and reductions in nitrate accumulation in leafy vegetables. Overall, PHs represent promising biostimulant tools for sustainable crop production, combining growth promotion, improved nutrient use efficiency, and enhanced resilience to abiotic stresses.

Keywords: Protein Hydrolysates, Plant Metabolism, Bioactive Amino Acids and Peptides.

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INTRODUCTION

Protein hydrolysates (PHs) are complex mixtures of amino acids and peptides that function as bioactive compounds and have been associated with beneficial effects on both metabolism and overall organismal health (Shahidi & Zhong, 2008; Sharma et al., 2011). These peptides are typically embedded within intact proteins in an inactive state and are released upon hydrolysis (Meisel & Bockelmann, 1999). The choice of hydrolysis method depends largely on the protein source and its structural characteristics. Keratin-rich byproducts such as feathers, horns, and hair, which are known for their resistance to degradation, can be converted into hydrolysates through chemical (acidic or alkaline) or enzymatic processes, including those mediated by microbial keratinases. The resulting products are generally enriched in sulfur-containing amino acids and short bioactive peptides, which have been shown to promote primary plant metabolism, stimulate the biosynthesis of secondary metabolites, and improve tolerance to various abiotic stresses (Berechet et al., 2024; Gaidau et al., 2021; Li, 2022; Możejko & Bohacz, 2023; Pasupuleti et al., 2008).

Different hydrolysis strategies are applied to produce protein hydrolysates, and the choice of method strongly influences their composition and functionality. Acidic and alkaline hydrolysis typically employ high temperatures together with strong chemical reagents such as mineral acids or sodium/potassium hydroxide, leading to extensive cleavage of peptide bonds (Bouhamed & Kechaou, 2017; Colla, Nardi, et al., 2015; Gezgin et al., 2020; Hou et al., 2017). Each method offers specific advantages depending on the desired composition, functionality, and application of the resulting hydrolysates.

PHs have been shown to modulate plant metabolism, particularly by stimulating key processes such as nitrogen and carbon metabolism (Baglieri et al., 2014; Schiavon et al., 2008). These beneficial effects are often linked to an increase in enzymatic activities and a more efficient uptake of essential nutrients (Cerdán et al., 2008). Beyond their metabolic role, PHs contribute to improved plant performance under adverse conditions by enhancing stress tolerance mechanisms (Apone et al., 2010; Ertani et al., 2013). In addition, several studies have reported that PHs display functional properties relevant to human and animal health, including antioxidant, antimicrobial, and antihypertensive activities (Cicero et al., 2017; Je et al., 2005; Przybylski et al., 2016)

In this article, the metabolic effects of PHs on plants and their contributions to growth processes are discussed, focusing on the potential benefits and applications of these bioactive compounds in plant development.

Effect of PHson Plants

The effectiveness of PHs in plant-specific formulations largely depends on their ability to enter plant tissues. Both amino acids and small peptides present in hydrolysates can be absorbed through roots as well as leaves (Matsumiya & Kubo, 2011). At the same time, these compounds also represent a potential nutrient source for soil microorganisms. As a result, the proportion of amino acids and peptides available for plant uptake is influenced by microbial activity in the rhizosphere. Experimental studies have demonstrated that free amino acids in soil are rapidly metabolized, with reported half-lives ranging between one and six hours (Moe, 2013).

Isotopic tracing experiments with ^{13}C-^{15}N-labeled amino acids in tomato, wheat, and grass have demonstrated that only a fraction of the compounds applied to the root zone—approximately 6% to 25%—is directly absorbed by plants, while the majority is utilized by soil microorganisms. The efficiency of amino acid uptake is not uniform; it is influenced by factors such as plant species and cultivar, soil characteristics, and the concentration of amino acids provided (Moe, 2013). More recent studies have confirmed and refined these findings. In tomato seedlings, glycine uptake dynamics were characterized under phosphorus and iron deficiency, showing condition-specific absorption rates (Trevisan et al., 2024). In *Arabidopsis thaliana*, isotopic tracing with dual-labeled ^{13}C-^{15}N glutamine provided accurate quantification of amino acid uptake at the root level (Svennerstam & Jämtgård, 2022). Similarly, in maize seedlings, treatment with PHs and humic substances under salinity stress enhanced amino acid profiles and demonstrated significant root uptake (Canellas et al., 2024). Together, these results demonstrate that root uptake of amino acids is quantifiable, environmentally dependent, and a widespread mechanism across different plant species.

Foliar application of PHs allows amino acids and peptides to be directly taken up by leaves, thereby avoiding competition with soil microorganisms. Evidence from bentgrass (*Agrostis stolonifera*) showed that when proline, glutamic acid, and glycine were applied to the foliage, about 52%, 51%, and 48% of the compounds were absorbed within eight hours (Stiegler et al., 2013). Similarly, in peach trees, the uptake of alanine, glutamic acid, glycine, and lysine through the leaves reached 14%, 10%, 25%, and 26%, respectively (Furuya & Umemiya, 2002).

These results suggest that foliar absorption of amino acids varies depending on factors such as plant species, amino acid structure, and environmental conditions. Generally, amino acids and peptides with lower molecular weights are absorbed more rapidly through the leaf surface. However, absorption is not solely determined by molecular weight; other properties such as polarity and charge also play a role. For instance, despite having similar molecular weights, arginine and lysine have been reported to exhibit higher foliar uptake efficiency compared to other amino acids, possibly due to their basic nature and interaction with leaf cuticle components (Colla, Nardi, et al., 2015).

Amino acids and peptides taken up via roots or leaves can be transported over long distances through cell-to-cell movement and by the xylem and phloem. Integral membrane protein systems such as the lysine–histidine transporter family, the proline transporter family, and the amino acid permease family play important roles in the direct uptake of amino acids by plant roots (Tegeder, 2012).

Within plants, amino acids and peptides serve as readily available organic nitrogen sources for protein synthesis and the production of other nitrogenous metabolites essential for growth (Rentsch et al., 2007). Beyond this nutritional role, they also act as signaling molecules: once taken up, they interact with receptors at the cell surface and initiate a cascade of biochemical and morpho-physiological responses (Ryan & Pearce, 2001). Microorganisms further contribute by releasing proteases that degrade proteins into small peptide fragments, some of which can act as plant growth regulators (Trouvelot et al., 2014). Evidence from studies at the University of Tuscia demonstrated that the application of plant-derived PHs to lettuce stimulated beneficial soil microorganisms, including nitrogen-fixing, phosphate-solubilizing, and indole-3-acetic acid–producing bacteria. Collectively, these findings indicate that PHs function as biostimulants not only through direct plant uptake but also by fostering microbe-mediated processes that enhance plant growth (Colla, Nardi, et al., 2015).

Effect of PHs on Primary Plant Metabolism

A substantial body of research indicates that PHs stimulate nitrogen metabolism and assimilation in plants (Baglieri et al., 2014; Calvo et al., 2014; Ertani et al., 2009; Ertani et al., 2013). Nitrogen assimilation represents a central process for plant growth and development, as inorganic nitrogen must first be reduced to ammonia before being incorporated into organic compounds (Crawford et al., 1993; Hoff et al., 1994). Ammonium is subsequently assimilated into amino acids such as glutamine, glutamate, asparagine, and aspartate, which play key roles as nitrogen transporters within plant tissues. Experimental work on maize (*Zea mays*) has shown that treatment with PHs enhances the activity of enzymes including NAD-dependent glutamate dehydrogenase, nitrate reductase, and malate dehydrogenase, all of which are associated with growth and stress adaptation (Maini, 2006). Moreover, applications of PHs to maize have been reported to modulate central metabolic pathways such as glycolysis and the tricarboxylic acid cycle (Ertani et al., 2009; Ertani et al., 2013).

PHs have been shown to stimulate the activity of several key enzymes associated with both carbon and nitrogen metabolism. These include malate dehydrogenase, isocitrate dehydrogenase, and citrate synthase in carbon pathways, as well as nitrate reductase, nitrite reductase, glutamine synthetase, glutamate synthase, and aspartate aminotransferase in nitrogen assimilation (Planques et al., 2012; Schiavon et al., 2008). Beyond their impact on enzyme activity, PHs also influence the transcriptional regulation of genes encoding these enzymes (Ertani et al., 2013). For instance, experiments on maize demonstrated that application of an alfalfa-derived protein hydrolysate enhanced the activity of tricarboxylic acid cycle enzymes while simultaneously upregulating the corresponding gene transcripts (Schiavon et al., 2008).

PHs enriched with free amino acids can influence nitrogen dynamics in plants by limiting nitrate uptake in the roots. This effect is thought to result from enhanced amino acid transport into the phloem, which in turn reduces the rate of nitrate reduction. The extent of this inhibition varies depending on external nitrate levels as well as the composition and concentration of amino acids within the hydrolysate. For example, external application of glutamine was found to suppress the expression of genes encoding nitrate and ammonium transporters in barley (*Hordeum vulgare*) roots (Fan et al., 2006; Miller et al., 2008). Similarly, in pepper (*Capsicum annuum*), foliar application of an animal-derived protein hydrolysate supplemented with micronutrients decreased nitrate uptake and nitrogen assimilation in root tissues (Ruiz et al., 2000). These findings indicate that amino acids act as signaling and regulatory molecules in root nitrogen uptake.

Applications of PHs, whether to the foliage or the root zone, have been shown to stimulate the uptake of both macro- and micronutrients and to enhance plant water-use efficiency (Cerdán et al., 2008; Ertani et al., 2009; Halpern et al., 2015). These beneficial outcomes are generally explained by several complementary mechanisms, including increased microbial and enzymatic activity in the soil, improved solubility and mobility of micronutrients, modifications in root system architecture, and enhanced activity of nutrient-related enzymes (Cerdán et al., 2008; Colla et al., 2014; Ertani et al., 2009; Lucini et al., 2015):

Building on previous evidence, more recent studies have provided stronger confirmation that PHs act as regulators of primary metabolism in a wide range of plant species. In tomato plants, their application has been shown to accelerate recovery following drought stress by enhancing the accumulation of dipeptides and fatty acids, thereby modulating primary metabolic pathways and strengthening stress tolerance (Leporino et al., 2024). Similarly, in soybean, PHs were found to improve nitrogen metabolism, upregulate related gene expression, and significantly increase pod and seed yield (Engel et al., 2024). In tomato and lettuce, applications of PHs have been found to regulate primary metabolic processes under salinity stress by stimulating antioxidant enzyme activity, promoting the buildup of osmolytes, and inducing the expression of phenylalanine ammonia-lyase, ultimately contributing to improved stress adaptation. (Zuluaga et al., 2023). In *Arabidopsis* seedlings, seed priming treatments with PHs have been shown to enhance photosynthetic efficiency and regulate primary metabolic processes, thereby promoting growth and strengthening physiological resilience under salinity stress (Sorrentino et al., 2021).

Taken together, these studies provide compelling evidence that PHs act as key modulators of primary metabolism by simultaneously regulating enzymatic activity and gene expression, ultimately fostering plant growth, optimizing nutrient utilization, and strengthening resilience to abiotic stress.

Effect of PHs on Plant Secondary Metabolism

Secondary metabolism refers to the synthesis of organic compounds that are not directly involved in plant growth or primary developmental processes. These products, known as secondary metabolites, play crucial roles in enhancing plant defense against biotic and abiotic stresses and can also exert allelopathic effects on competing plant species. Beyond their ecological functions, secondary metabolites hold significant industrial value, with broad applications in areas such as textiles, cosmetics, and pharmaceuticals. (Tiring et al., 2021).

PHs have been shown to activate secondary metabolic pathways in plants, strengthening defense responses and thereby increasing tolerance to abiotic stresses such as salinity, drought, temperature fluctuations, and oxidative stress (Apone et al., 2010; Ertani et al., 2013; Kauffman et al., 2007). For instance, in *Arabidopsis thaliana* (mouse-ear cress), application of a mixture containing free amino acids, peptides, and sugars led to the upregulation of genes associated with oxidative stress responses (Apone et al., 2010).

In maize seedlings subjected to salinity stress under hydroponic culture, the application of a plant-derived protein hydrolysate was shown to stimulate flavonoid biosynthesis and accumulation (Ertani et al., 2013). This enhancement in flavonoid levels is closely linked to the activity of phenylalanine ammonia-lyase (PAL), a key enzyme in the phenylpropanoid pathway. The PAL-encoding gene is known to be highly responsive to a broad spectrum of abiotic and biotic stresses across different plant species (Huang et al., 2018) and can be activated by several classes of biostimulants (Ertani et al., 2011; Schiavon et al., 2008).

Proline is a key amino acid involved in osmotic adjustment during stress conditions (Bayat et al., 2014), Beyond this function, it promotes the accumulation of phenolic compounds by activating the proline-linked pentose phosphate pathway, which subsequently drives both the shikimate and phenylpropanoid pathways (Shetty & McCue, 2003). Evidence from a metabolomic study on lettuce exposed to salinity stress showed that treatment with a plant-derived protein hydrolysate enhanced the synthesis of secondary metabolites such as terpenes and glucosinolates. These metabolites act as modulators of signaling cascades that trigger plant defense responses, thereby improving salt tolerance in lettuce (Lucini et al., 2015).

Resveratrol is a phytoalexin-type secondary metabolite that accumulates in high concentrations in grapevine (*Vitis vinifera*) leaves and berry skins, where it plays an important role in disease resistance (Keskin et al., 2009). Foliar application of casein- and soybean-derived PHs has been shown to regulate the expression of stilbene synthase, a key enzyme in the resveratrol biosynthetic pathway, leading to elevated resveratrol levels in grapevine leaves. The increased accumulation of this compound activates defense mechanisms against *Plasmopara viticola*, the pathogen responsible for downy mildew. These findings suggest that PHs of casein and soybean origin could contribute to sustainable viticulture by reducing dependence on fungicides. (Lachhab et al., 2014).

PHs have been increasingly recognized not only for their effects on primary metabolism but also for their significant influence on secondary metabolism in plants. These compounds regulate the biosynthesis of phenolics, flavonoids, anthocyanins, and other secondary metabolites, thereby strengthening plant defense mechanisms and improving product quality. For example, in grapevines, the soil application of a plant-derived PHs was reported to selectively accelerate secondary metabolic processes associated with ripening (Peli et al., 2025). From a broader perspective, a comprehensive review highlighted the biostimulant properties of PHs, emphasizing their ability to enhance the accumulation of secondary metabolites, particularly phenolic compounds, thereby improving both stress tolerance and the nutritional value of crops (Malécange et al., 2023).

In tomato, the combined use of a protein hydrolysate with a seaweed extract was reported to reshape the metabolomic profile of plants subjected to salinity stress, resulting in pronounced alterations in both secondary metabolite production and phytohormone levels (Zhang et al., 2023). Likewise, in strawberry, foliar treatment with maize-derived PHs led to substantial increases in ascorbic acid, anthocyanins, and phenolic compounds, thereby enhancing both the nutritional value and functional quality of the fruits (Mancuso et al., 2025). In addition, a study on Brassicaceae microgreens demonstrated that priming with PHs not only improved growth and yield but also significantly enhanced traits related to secondary metabolism, such as antioxidant capacity (Ciriello et al., 2023). Finally, recent studies have further emphasized that PHs regulate plant secondary metabolism by promoting the synthesis of antioxidant defense compounds. For instance, plant hydrolysate application in tomato under salt stress reprogrammed metabolic pathways, enhancing secondary metabolites and phytohormone profiles (Zhang et al., 2023), while a comprehensive review highlighted their broader role in improving stress tolerance and quality parameters (Pasković et al., 2024)

Taken together, these findings clearly indicate that PHs act as strong modulators of secondary metabolism, playing a crucial role in enhancing both plant physiological resilience and product quality.

Germination and Seedling Development

A range of technological approaches has been developed to improve sowing efficiency and ensure successful seedling establishment under diverse environmental conditions. Among these are seed conditioning, priming, and coating techniques. Coating seeds with hydrophilic and water-retentive substances can provide young seedlings with protection against pests, pathogens, fungal infections, and low temperatures (Gorim & Asch, 2012). Furthermore, seed coatings may serve as carriers for additional components such as macro- and micronutrients (Farooq et al., 2012), herbicides (Rushing et al., 2013), growth regulators (Halmer, 2004), and beneficial microorganisms (Colla, Rouphael, et al., 2015).

Earlier studies suggested that seed coatings might impair germination by limiting water uptake and gas exchange; however, these concerns were primarily based on older evidence and have since been reconsidered in light of recent advances in coating materials and technologies (Hill, 1999; Muecke, 1988).

In recent years, the potential use of biostimulant compounds in seed coating formulations has received increasing attention. For instance, coating broccoli (*Brassica oleracea*) seeds with soy flour, an inexpensive source of protein hydrolysates, resulted in enhanced stem and root development compared to uncoated seeds. Greenhouse trials from the same study provided more comprehensive evidence: seedlings emerging from seeds coated with 30%, 40%, and 50% soy flour showed significantly greater fresh and dry biomass, taller shoots, larger leaf areas, higher SPAD (Soil Plant Analysis Development) index values, and increased total nitrogen content relative to controls. These benefits were attributed to improved nitrogen uptake, assimilation, and transport, along with the stimulation of key enzymes involved in nitrogen metabolism (Amirkhani et al., 2016). Furthermore, when a plant-derived protein hydrolysate rich in soluble peptides and amino acids was applied to maize (*Zea mays*) coleoptiles, accelerated elongation was observed. This response was associated with the hydrolysate's tryptophan content, which contributes to indole-3-acetic acid biosynthesis and exerts auxin-like activity through the generation of bioactive peptides (Colla et al., 2014).

Gibberellins are well-established plant hormones that act as key regulators of cell elongation and play a central role in processes such as the induction of α-amylase activity during germination (Parrado et al., 2008). Interestingly, experiments with gibberellin-deficient dwarf pea (*Pisum sativum*) demonstrated that treatment with the commercial plant-derived protein hydrolysate *Trainer* increased shoot length by approximately 33% across all tested concentrations. These findings indicate that PHs can mimic gibberellin-like functions, supporting shoot elongation and growth even under conditions of hormonal deficiency (Colla et al., 2014).

The growth-promoting effects of animal-derived protein formulations have also been documented. For instance, experiments in cucumber (*Cucumis sativus*) demonstrated that placing gelatin capsules in proximity to seeds enhanced plant performance, leading to higher fresh and dry biomass, expanded leaf area, and increased nitrogen concentration in the tissues. These improvements were associated with the modulation of nitrogen transporter gene expression and activation of the xenobiotic detoxification pathway. Such evidence highlights the potential of animal-derived proteins to act as effective biostimulants during germination and early seedling development (Gaidau et al., 2013).

Similar findings have been reported for plant-derived PHs under optimal growing conditions. For example, in soybean (*Glycine max*), seed and foliar applications improved nitrogen metabolism and significantly increased pod and seed yield under non-stress conditions (Engel et al., 2024). Likewise, seed priming with vegetal PHs in lettuce (*Lactuca sativa*) markedly enhanced germination rates and seedling growth, particularly at low concentrations and short priming durations, even in the absence of stress factors (Saadatian et al., 2025). In addition, multi-species trials demonstrated that both plant- and animal-derived PHs promoted growth and positively shaped the rhizosphere microbiota, further confirming their biostimulant activity under non-stress environments (Costa et al., 2024).

Beyond their effects under optimal conditions, PHs have also been shown to promote seedling development under various abiotic stress conditions. In tomato (*Solanum lycopersicum*), seed priming with PHs enhanced drought tolerance by improving osmotic adjustment, boosting antioxidant enzyme activities, and increasing germination success (Wang et al., 2022). In cotton (*Gossypium hirsutum*), protein hydrolysate priming improved photosynthetic capacity and physiological performance under salinity stress (Zhen-yu et al., 2025). Similarly, soybean seeds treated with biostimulants exhibited improved germination and early seedling growth under both low- and high-temperature stress conditions (Sivarathri et al., 2025). Furthermore, pumpkin seed-derived PHs were shown to alleviate salinity stress in common bean (*Phaseolus vulgaris*) seedlings by enhancing antioxidant enzyme activities and restoring ion homeostasis (Sitohy et al., 2020).

Collectively, the evidence indicates that PHs function as effective biostimulants by promoting seedling establishment under optimal conditions while simultaneously enhancing

Role of PHs in Enhancing Vegetative Growth, Flowering Dynamics, and Crop Yield

PHs are recognized for stimulating vegetative growth and enhancing macro- and micronutrient uptake, ultimately improving productivity in horticultural crops (Halpern et al., 2015). For example, application of an animal-derived PH to papaya (*Carica papaya*) increased the number of marketable fruits by 22%, an effect attributed to improved fruit set (Morales-Payan & Stall, 2003). Greenhouse studies have shown that plant-derived PHs enhance yield, fruit quality, and nitrogen use efficiency in lettuce (*Lactuca sativa*) and tomato (*Solanum lycopersicum*) (Choi et al., 2022). In sweet potato (*Ipomoea batatas*), combining whey PHs with potassium fertilization significantly boosted tuber productivity and quality (Elwaziri et al., 2023). Under organic cultivation, both animal- and plant-based PHs markedly improved rosemary (*Rosmarinus officinalis*) yield while differentially influencing chemical composition, highlighting their potential as effective biostimulants in aromatic plants (Farruggia et al., 2025).

However, PH effects are not universally positive. Field trials on spinach (*Spinacia oleracea*) and endive (*Cichorium endivia*) showed no significant yield improvements compared with controls (Gajc-Wolska et al., 2012; Kunicki et al., 2010). By contrast, feather-derived PHs applied to papaya, both as soil amendments and foliar sprays, advanced harvest by 28 days and improved reproductive performance, increasing clusters per inflorescence, fruits per cluster, and average cluster weight by 10%, 24%, and 26%, respectively (Morales-Payan & Stall, 2003). These findings underscore both the agronomic benefits of PHs in promoting earliness and yield and their potential to valorize poultry by-products while reducing reliance on chemical fertilizers. In flowering crops, animal- and plant-derived PHs shortened the production cycle of *L.A. lilies* and improved leaf area, bud diameter, and root development relative to controls (De Lucia & Vecchietti, 2012). Collectively, these results indicate that PHs can enhance productivity and quality in certain crops, particularly ornamentals, though their effectiveness remains species- and context-dependent.

PHs containing amino acids and peptide fragments also increase plant biomass. This increase is attributed to the stimulated photosynthetic mechanism resulting from higher nitrogen content in the leaves and the synthesis of photosynthates. Application of a commercially produced protein hydrolysate to tomato (*Solanum lycopersicum*) plants increased root and shoot biomass, chlorophyll content, and leaf nitrogen content by 20%, 27%, 15%, and 21%, respectively. Moreover, the protein hydrolysate promoted strong root development in tomato plants, enhancing nitrogen uptake and its efficient utilization (Colla et al., 2014).

The observed enhancement in leaf chlorophyll concentration and nitrogen assimilation has been linked to the auxin-like activity of PHs (Nardi et al., 2009). Evidence for this hormonal effect has also been demonstrated in decapitated tomato plants, where the application of PHs promoted adventitious root formation, further confirming their role in mimicking auxin activity (Colla et al., 2014).

Due to the use of different protein sources and methods in the protein hydrolysis process, hydrolysates contain peptide fragments with various molecular weights. This variation in the molecular weight of peptide fragments alters the application dose and biological effects of PHs on plants. In a related study, various peptide fragments from animal-derived PHs were foliar-applied at different doses to potted kiwi (*Actinidia deliciosa*) plants. The results showed that low molecular weight peptides (1–3 kDa) promoted stem and root growth at low concentrations, whereas higher molecular weight peptides (3–10 kDa and >10 kDa) increased stem growth only at high concentrations (Lucchi et al., 2001). Gibberellins are plant hormones responsible for stem elongation. PHs also exhibit gibberellin-like activity. PHs applied to gibberellin-deficient dwarf pea plants promoted stem elongation (Cavani & Ciavatta, 2007). These findings indicate that low molecular weight amino acids and peptides are readily absorbed by plants, act as signaling molecules within the plant, and stimulate endogenous phytohormone biosynthesis (Colla et al., 2014). Most recently, foliar treatment with a vegetal protein hydrolysate was reported to aid tomato plants in recovering from recurrent drought stress. The application improved morphological traits, including total biomass and leaf area, and, according to metabolomic analyses, stimulated the accumulation of dipeptides, fatty acids, and phenolic compounds. These findings highlight the dual role of PHs in promoting both morphological recovery and metabolic reprogramming under repeated stress conditions. (Leporino et al., 2024).

In recent years, phytochemicals naturally present in fruits and vegetables have gained considerable attention from scientists, nutrition experts, and producers because of their beneficial impacts on human health (Gruda, 2009; Khanam et al., 2012). These bioactive compounds act as natural antioxidants, helping to prevent or mitigate the progression of chronic diseases such as cardiovascular disorders, arthritis, stroke, and inflammatory bowel conditions (Oude Griep et al., 2011; Slavin & Lloyd, 2012). The levels and profiles of these phytochemicals are influenced by multiple factors, including plant genotype, environmental conditions, and agronomic practices (Rouphael et al., 2012; Rouphael et al., 2010). Research has demonstrated that protein hydrolysate applications can modulate both primary and secondary metabolism, thereby stimulating the synthesis and accumulation of antioxidant phytochemicals such as carotenoids, polyphenols, and flavonoids (Ertani et al., 2014). For example, chicken feather-derived PHs, which are rich in amino acids, peptides, and minerals, significantly increased phenolic, flavonoid, and antioxidant contents in banana plants (Gurav & Jadhav, 2013). Likewise, plant-derived PHs enhanced quality-related parameters in red grapes (Vitis vinifera var.), improving color expression and anthocyanin accumulation. These improvements have been associated with the upregulation of genes involved in the phenylalanine ammonia-lyase pathway, a key route in secondary metabolism (Parrado et al., 2007).

In winter wheat, foliar application of PHs in combination with herbal extracts further enhanced seedling growth and biochemical performance. The treatment significantly increased shoot elongation, chlorophyll content, and antioxidant enzyme activities, and partly exerted antimicrobial effects that contributed to improved yield potential (Gendaszewska et al., 2025).

The nitrate content within plants varies according to their genetic makeup, species, cultivation conditions, plant organs, environmental factors, and agricultural practices applied. The nitrate levels in vegetables depend on the amount of nitrate absorbed from the soil via roots and the endogenous activity of nitrate reductase enzymes (Ayaz & Yurttagül, 2006). Excessive use of nitrate fertilizers applied to soil to increase agricultural yield, along with nitrate residues released into the environment from industrial activities, leads to nitrate contamination in cultivated plants. Both pre-sowing and subsequent applications of artificial fertilizers containing sodium, potassium, and ammonium nitrates, as well as industrial nitrate residues dispersed into the environment, contribute to nitrate accumulation in crop plants (Warman & Havard, 1998). Excessive nitrate fertilization to increase yield per unit area results in nitrate accumulation, especially in root and shoot tissues. Thus, in plants such as spinach and lettuce, more than 10% of dry matter content can consist of nitrate (Ayaz & Yurttagül, 2006). From a public health perspective, there is a close relationship between nitrate intake through vegetables and stomach cancer (Özdestan & Üren, 2010). It has been reported that foliar application of animal-derived PHs to pepper plants reduces nitrate uptake in roots (Ruiz et al., 2000).

Recent studies have further substantiated the role of PHs in reducing nitrate accumulation in vegetables while improving yield and quality. For instance, in perennial wall rocket (*Diplotaxis tenuifolia*), protein hydrolysate application under different environmental conditions significantly decreased leaf nitrate content, while simultaneously improving productivity and crop quality (Tallarita et al., 2025). Similarly, in basil (*Ocimum basilicum*), foliar application of a vegetal protein hydrolysate enhanced aromatic profile and antioxidant activity, including significant increases in total phenolics and monoterpene compounds, thereby improving overall crop quality even under reduced nutrient supply (Ciriello et al., 2022). These findings indicate that PHs not only act as growth- and yield-promoting biostimulants but also contribute to food safety and nutritional quality by lowering nitrate accumulation and enhancing the phytochemical composition of leafy vegetables.

A controlled hydroponic experiment on pak choi (*Brassica chinensis*) examined how substituting part of the nitrate-nitrogen supply with amino acids would affect plant growth and nitrate accumulation. In this study, 20% of the nitrate-N in the nutrient solution was replaced with 20 different amino acids (Hua-Jing et al., 2007). Results showed that seedlings treated with cysteine, glycine, histidine, and arginine accumulated less nitrate in their tissues than the untreated controls. Conversely, supplementation with asparagine and glutamine not only enhanced nitrogen concentrations but also significantly raised phosphorus levels in the sprouts. Based on these findings, the authors suggested that asparagine and glutamine could serve as alternative nitrogen sources, reducing nitrate buildup while simultaneously improving mineral nutrition and overall product quality.

The ability of amino acids to lower nitrate accumulation in plants has been associated with their regulatory influence on key enzymes involved in nitrogen metabolism. Specifically, enzymes such as nitrate reductase, nitrite reductase, glutamine synthetase, glutamate synthase, and aspartate aminotransferase play central roles in these processes, and their activities can be modulated by amino acid availability. (Calvo et al., 2014; Liu & Lee, 2012; Liu et al., 2007).

The role of amino acids in lowering nitrate accumulation within plants has been associated with their ability to regulate key enzymes involved in nitrate metabolism, such as nitrate reductase, nitrite reductase, glutamine synthetase, glutamate synthase, and aspartate aminotransferase. Recent studies further support this connection. For instance, in hydroponically grown lettuce, supplementation with selected amino acids (e.g., tryptophan, glycine, methionine) enhanced nitrate reductase activity and significantly reduced nitrate accumulation in leaves (Khan et al., 2025). Similarly, phosphorus deficiency in soybean induced substantial alterations in amino acid composition across leaves, roots, and nodules, thereby triggering a reprogramming of nitrogen metabolism; these changes involved 26 amino acids participating in 37 metabolic pathways (Yao & Liu, 2025). Likewise, the application of amino acid-based biostimulants has been shown to stimulate nitrogen assimilation, promote root development, and reduce nitrate accumulation in plant tissues, thereby improving overall nutrient efficiency and growth performance (Atero-Calvo et al., 2025). Similar findings in tobacco identified glutamate, aspartate, and phenylalanine pathways as critical regulators of nitrogen distribution and nitrate metabolism across different organs (Li et al., 2025). Collectively, these results emphasize that amino acids not only act as direct nitrogen sources but also function as regulators of nitrate metabolism, thereby contributing to improved nutrient efficiency and plant performance.

CONCLUSION

This review has comprehensively addressed the regulatory effects of PHs on metabolic processes and their growth-promoting impact on plants. It has been demonstrated that protein hydrolysates, due to their amino acid and peptide content readily absorbed by both roots and leaves, stimulating nitrogen and carbon metabolism in plants, supporting these fundamental processes.

Upon application to plants, these compounds enhance enzyme activities, thereby improving nitrogen assimilation, energy metabolism, and other primary metabolic pathways, ultimately optimizing plant growth and development. Furthermore, PHs have shown potential in enhancing stress tolerance and increasing crop productivity.

Particularly, studies on the uptake and transport of amino acids within plants reveal that these molecules serve not only as nutrient sources but also function as signaling molecules. Through their interaction with microorganisms and their function as natural biostimulants, PHs represent a sustainable and environmentally friendly approach to improving agricultural practices.

In conclusion, PHs constitute a powerful tool to increase agricultural productivity and improve plant adaptation to environmental stresses. Future research should focus on a more comprehensive evaluation of these bioactive compounds across diverse plant species and optimization of their application methods.

Author Contrubitions

MA has written the manuscript and ID and SD have revised the manuscript. All authors contributed to the article and approved the submitted version.

Conflict of Interest

The authors declare no conflict of interest, financial or otherwise.

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