








Review

Interaction between Humic Substances and Plant Hormones for Phosphorous Acquisition

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Abstract: Phosphorus (P) deficiency is a major constraint in highly weathered tropical soils. Although phosphorous rock reserves may last for several hundred years, there exists an urgent need to research efficient P management for sustainable agriculture. Plant hormones play an important role in regulating plant growth, development, and reproduction. Humic substances (HS) are not only considered an essential component of soil organic carbon (SOC), but also well known as a biostimulant which can perform phytohormone-like activities to induce nutrient uptake. This review paper presents an overview of the scientific outputs in the relationship between HS and plant hormones. Special attention will be paid to the interaction between HS and plant hormones for nutrient uptake under P-deficient conditions.

Keywords: fulvic acid; humic acid; abiotic stresses; biostimulants; organic matter

1. Introduction

Phosphorous (P) is an essential nutrient for all cellular processes of plant growth, including development and reproduction [1]. P is a crucial component of biomolecules, including adenosine triphosphate (ATP), nucleic acids and phospholipids. Mineral resources required for manufacturing P chemical fertilizer may last for 300–400 years [2]. However, world population is expected to grow from 7.3 billion inhabitants in 2015 to 9.7 billion by 2050 [3], placing these reserves and estimates under increased demand and uncertainty.

Additionally, more than 40% of the planet's soils are P-deficient [4]. Acid-weathered soils in subtropical and tropical regions such as Southern Africa [5] and Sub-Saharan Africa [6] are especially prone to deficiency and require higher P input due to P absorption by the mineral complex Al/Fe. Future sustainable agriculture therefore demands the optimization of P management and improved P use efficiency [5,7].

Part of this optimization requires a better understanding of plant physiological adaptation mechanisms under P deficiency, in interaction with both soil microorganisms and the soil itself [8]. Phytohormone signaling of P starvation is one of the main pathways which modulates plant response

to abiotic stress through cross-talk with other stress signaling pathways [9]. Plant hormones play a vital role in linking gene transcription to P starvation response mechanisms. Auxins (AUXs) [10], cytokinins (CKs) [11–13], gibberellin (GAs) [14], ethylene (ET) [15], abscisic acid (ABA) [16,17], and strigolactones (SLs) [18–20] are the main hormones which regulate the P starvation response.

Organic matter also forms an essential component in the P cycle and alters the efficiency of plant uptake by: (1) providing a source of organic P in soil [21], (2) enhancing the microbial activity of P-solubilizing microbes [22,23] (e.g., *Azospirillum*), (3) solubilizing fixated phosphate by increasing organic acid levels in soil [24], and (4) increasing P availability in soil by interlinking with complexes of humic substances (HS) and metal ions (Fe/Al) [25–27]. Additionally, the phytohormone-like activity of humic substances can act as a biostimulant. Typical plant morphological changes by HS include the elongation of lateral roots and increasing H⁺-ATPase activity in root tissue [28].

Current literature on the interaction between HS and nutrient deficiency has focused on Fe [29] and N [30]. However, little attention has been paid to the impact of HS on the P cycle or plant growth under P deficiency. In this work, we present an outline of the phytohormonal effect of humified organic matter on P uptake, with special attention paid to the P cycle.

2. Hormonal-Like Actions of Humic Substances

HS are complex and heterogeneous fractions of stable organic matter resulting from the transformation of plant and animal waste by microbial activities and chemical reactions [31]. HS fractions are operationally defined into humic acid (HA), fulvic acid (FA) and humin (HM) based on their respective solubility in acid/alkaline solutions [31]. HAs are high molecular-weight chemical structures formed by small molecules with weak bonds [32]. Their supramolecular arrangement supports HA-bioactivity properties by releasing bioactive compounds, such as phytohormones and derivatives phytohormonal compounds, which can then bind to plant cell receptors to stimulate plant growth and stress tolerance responses [33,34].

Biostimulation effects of HS have been described in a wide range of plant species in both laboratory and field studies [35,36]. Plant response differs depending on the origin of HA, concentration, method of application and stage of plant development. Concomitantly, the effect of HS varies with plant species in terms of developmental pattern alteration resembling hormonal modulation such as increased germination rate, root elongation, shoot biomass, stem diameter, leaf area, and accelerated reproductive cycle [34,37–40]. This section will cover the relationship between HS application and biostimulation effects related to the main plant hormone classes.

2.1. Auxin (AUX)

The AUX-like effect is the most well-known phytohormonal behavior of HS and has been examined in the literature for over half a century [41]. Root elongation and lateral root emergence are recognized, as morphological impacts of HA [42,43]. This effect has been associated with the activation of the plasma membrane (PM) enzyme H⁺-ATPase by small molecules present in HA endowed with auxinic activity [42]. These small bioactive molecules in HS, such as IAA, access cell receptors to initiate cell signaling [33,44]. P-type ATPase enzymes promote H⁺ extrusion through PM, which acidifies the apoplast, and activates pH-sensitive enzymes which in turn loosen the cell-wall and strengthen cell-expansion associated with increased turgor pressure in coordination with vacuolar-type H⁺-ATPase anchored at the tonoplast membrane, depending on contact time between HS and plants [45]. The effects of HS on root morphology appear to mimic those produced by IAA [46,47]. This induction has been confirmed by using IAA inhibitors in plants treated with HA to block root development of maize [45]. Besides the direct-action of the P-ATPase domain, the induction of genes encoding some enzymes associated with secondary nutrient transporters (e.g., *ZmNrt2.1*, a nitrate transporter) have been considered as candidates for the AUX effect of HS [48]. Furthermore, Russel et al. [49] showed that the maximum stomatal aperture in the epidermal peel of pea (*Pisum sativum* L.) when induced by HA was similar to those treated with IAA (indole acetic acid) and appears to be mediated by phospholipase A2

(PLA2) and protein kinase C-like activity (PKC). Both enzymes are involved in the signal transduction pathway, leading to the response of plants to IAA [49].

2.2. Cytokinins (CK)

CK-like effects of HS have been examined since the 1980s [50]. Shoot growth can be positively influenced by HS soil content through different mechanisms in both roots and shoots, such as enhancement of PM ATPase related to the production of P-type ATPase gene isoforms. Regulation of these genes correlates with root-to-shoot mobility of CK and nitrate [38]. Several physiological effects mediated by HS in the roots are associated with cytokinin activity in the leaves [37]. CK is involved in the protection of photosynthetic machinery in plants under stress [51], and the physiologically active concentration of form isopentenyladenosine was found in HS as well as CK-like activity [52]. Physiologically active CK from HS in soil increased the weight of radish cotyledons and consequently increased leaf growth [52]. Despite an evident effect on the absorption of nutrients by winter rapeseed [53], low concentrations of this hormone were observed in black peat HA.

Application of HA to plant roots effects the expression of genes involved in shoot CK signaling pathways, promoting CK accumulation and a significant reduction in the root tissue [38]. Jannin and co-workers [53] reported interconnectivity between the differential distribution of CK in the root versus shoot, increased nutrient uptake, and enhanced shoot growth. HA provoked redistribution of CK from the root to aerial plant parts, which can alter the translocation of nutrients to regions of the plant with higher metabolic activity [54]. Thus, the CK action of HS on shoot growth is often associated with increases in plant nutrient concentrations.

2.3. Gibberellin (GA)

GA-like substances and activity in HS have been reported since the 1990s [55–57]. Typical effects of GAs are hypocotyl elongation, interruption of dormancy, promotion of flower and fruit development, and amylase induction. Similar effects have been observed with HS soil additions [57–60]. In addition to the GA-like impacts, HS has been found to up-regulate the metabolism of CKs and GAs by interacting with genes involved with these hormones [53].

Activity similar to GA has been detected in HA, and FA extracted from the O horizon of alpine soil. This activity has been attributed to aromatic components and amides in the analyzed fractions [61], as well as the neutral or basic pH of the extract [26]. Other studies have detected GA in leonardite HA [58] and forest soils [61]. The application of HA to grapes increased berry size, similar to results obtained when flowering plants received synthetic GAs [62].

2.4. Abscisic acid (ABA)

Another phytohormone present in HS, which influences plant hormonal signaling pathways is abscisic acid [37]. ABA is responsible for the production and regulation of H_2O_2 and Ca^{2+} , which control the opening and closing of stomata [63,64]. Additionally, HA-treated plants have displayed increased root hydraulic conductivity through regulating the expression of plasma membrane intrinsic protein (PIP) and tonoplast intrinsic aquaporin (TIP), both related to water flow [65].

Increased hydraulic conductivity mediated by aquaporins has been attributed to ABA accumulation in roots [66]. The use of inhibitors specific to ABA synthesis reduced hydraulic conductivity and root growth in cucumber [66]. However, the ABA-dependent pathway may also be related to other hormones. HAs can increase the concentration of ABA in roots, a process which is also dependent on IAA-NO-ET signaling [67].

2.5. Ethylene (ET)

Beneficial effects of HS have also been associated with ethylene-dependent signaling pathways. ET is a hormone involved in fruit ripening, as well as seed germination, cell expansion and flower senescence. However, high concentrations of ET can inhibit root growth [35]. HA applications to

cucumber were associated with increases in ET production and consequent root development [38,44]. Although HS-mediated effects on root morphology (mainly lateral root emission) involve IAA-ET crosstalk, other effects (primary root weight, root thickness, and the number of secondary roots) were not affected after the use of specific inhibitors for these hormones (PCIB for IAA; Cobalt II and STS for ethylene) [67].

ET is also involved in root hair development in response to environmental conditions [68]. Unlike other mentioned phytohormones, change in root architecture similar to the effect of ethylene is not observed with HS treatment, although ethylene concentration in root tissue increases by HS application [44,69].

3. HS Modulation of Primary Plant Metabolism

Farmers may benefit by applying HS to crops in both fields and greenhouses. Crop yield increases have been observed following HS application of different sources, concentrations, application forms and at various stages of plant development [36].

Regarding primary metabolism, HS application triggers alteration of plant gene expression and the content of chemical compounds [70] which are involved in different processes of plant physiology (e.g., Krebs cycle, metabolisms and photosynthesis) [71]. While it is generally agreed that HS increases photosynthetic pigment content [72,73], there is less consensus whether this translates into an increased rate of photosynthesis [74]. Interestingly, the inverse has also been observed as HS application increased net photosynthesis rate with no change in photosynthetic pigment concentration [75].

Furthermore, the positive effect on photosynthesis was shown to result from not only increased chlorophyll content but also increased Rubisco (ribulose-1,5-bisphosphate carboxylase/oxygenase) activity [76]. However, foliar application of HA on durum wheat affected neither photosynthesis nor stomatal conductance, while Rubisco activity and leaf protein content were higher than the control [77]. Overall, HS is not a silver bullet which holistically increases plant growth, grain yield and quality, and photosynthetic metabolism. However, some comprehensive studies [78] have shown increased wheat production on sandy soils with HA application, resulting from increases in plastid enzyme activities involved in photosynthesis, sucrose biosynthesis and starch accumulation.

Glycolysis is the preferential pathway of energy for plant respiration. Additionally, a significant proportion of carbon entering the plant glycolytic pathway and tricarboxylic acid cycle is not oxidized to CO₂ but is utilized in the biosynthesis of numerous compounds, including those of secondary metabolism. A previous study [79] observed the effects of different HS applications on enzymatic activities involved in the glycolytic and respiratory processes of maize seedlings—activities of responsible enzymes for primary metabolism were increased by HS treatment. Canellas et al. [75] observed a sharp reduction (approximately 50% compared to control seedlings) of the free carbohydrate content in leaves of maize treated with HA, indicating an apparent carbon skeleton demand for N assimilation. In fact, the total amino acid content was increased in fresh maize leaf tissue treated with HA, as well as activity of the main enzymes responsible for N assimilation, e.g., nitrate reductase (NR) and glutamine synthetase (GS) [75]. The effect of HS on N assimilation and metabolism has been reviewed [30]. HS enhances nitrate uptake and assimilation, resulting in increased nitrate reductase (NR), glutamate dehydrogenase (GDH) and glutamine synthetase (GS) activities. Interactions between HS and the enzymes of the N assimilation pathway in maize were described in a gene expression study at the transcriptional level [30]. The work of Trevisan et al. [80] was similar to previous studies and indicated that HS application increased both the plant metabolic pathways of glycolysis and the Krebs cycle. Moreover, Jannin and colleagues [53] observed increased N and sulfate uptake in *Brassica napus* and increased transcription of genes related to N and S metabolism. In both transcriptional studies with different plants (*Arabidopsis* and *Brassica*), roughly half of the relevant genes were down-regulated after HA treatment. This result is consistent with the first proteome studies reported by Carletti et al. [81] in maize seedlings treated with HA. Down-regulation of plasma membrane proteins was further observed in additional proteome studies involving different seedlings. For example, Roomi et al. [70] reported

up-regulation of enzymes in the glycolytic pathway, as well as regulation of ribosomal protein which indicated a stimulating effect of HS on energetic metabolism. They also observed down-regulation of 30 cytoplasmic enzymes, the transcription of which are regulated by several hormones (e.g., AUXs, CKs, and ABA).

4. P Uptake by HS Application Due to Phytohormonal Activity

The impact of HS on P uptake has been researched previously. Nearly all studies indicate that HS treatment increases P levels in plant tissue [27,82–84]. Underlying mechanisms include the multiple functions of HS as: (1) a chelator, making P more available in soil solution [27,84,85], and (2) a stimulator of root PM-ATPase (referred to as an “auxin-like effect”), which alters root growth and architecture [33,80]. In the latter mechanism, other hormones, ET [44], nitric oxide (NO) [45,86] and ABA [39,87] are mediated by HA. Shah and colleagues [88] describe three growth-triggering pathways which involve the link between HS treatment, gene expression of the aforementioned hormones, and NO modulation.

Following soil uptake, nutrients in root tissues move toward aerial plant parts. CKs play a vital role in regulating root-shoot translocation. Mora and colleagues [38] studied the enhancement of shoot growth following HA treatment in association with CK by comparing mineral content between the root and aerial plant parts. P content in shoots was significantly increased after four hours of HA treatment, along with a gradual reduction of all macronutrients in root tissue. In addition to CK as a regulator of root-shoot nutrient distribution, ABA also regulates shoot growth by altering root hydraulic conductivity. Several studies by Olaetxea et al. [39,66,87,89] revealed that high shoot growth resulted from increased ABA concentration in root following HA treatment, consequently enhancing root hydraulic conductivity.

5. Effect of HS on Secondary Metabolism under Abiotic Stress Conditions

Interlinking nutrient and energy availability is fundamental to drive cell proliferation [90]. This process requires checkpoints which either halt or permit cell growth when nutrients and energy are limited or sufficient.

The target of rapamycin (TOR) kinase is as a sensor of cell nutrient levels. This enzyme complex is upregulated at a high level of cytosolic amino acid and sugar concentration, allowing for cell growth [90]. In conditions of cell starvation, the TOR complex functions as an off-switch restraining growth and therefore forms a connection between environmental information and plant metabolism [91]. Canellas and colleagues [92] reported no evidence of a direct relationship between the differential expression of TOR and metabolite levels (amino acids, sugars, or organic acids) in the shoot or root tissues in plants treated with HA. Likely, HS disturbs the perception of cell nutrient status on maize seedlings producing a high level of TOR transcription, probably caused by enhanced auxin activity when amino acids and sugars were in low levels, changing the signaling pathway involved in nutrient sensing.

Drought stress may decrease photosynthetic rate, however this effect was shown to be mitigated in sugarcane plants treated with HA [93]. Lofti and colleagues [94] found that the application of HA improved net photosynthesis of rapeseed plants under water stress via increasing the rate of gas exchange and electron transport flux. Russel and colleagues [49] proposed that HS application to pea resulted in higher net photosynthesis by increasing the stomatal opening of epidermal peels through activation of phospholipase A2. This effect was also observed in IAA treated plants.

Phenolic compounds, along with other secondary metabolites, can protect plants against certain stresses [95]. For example, the phenylpropanoid pathway is a well-known generator of secondary metabolites related to nutrient deficiency [96]. The interaction of HS with the phenylpropanoid pathway has been reported in previous works [70,97,98]. Schiavon et al. [99] showed that HA not only increases phenol content but also induces phenylalanine ammonia-lyase activity, an enzyme involved in the phenylpropanoid pathway at the level of gene expression. The authors highlight the similarity

to other studies in which phenylpropanoid synthesis was enhanced at the transcriptional level by fungal elicitors and hormones. This enzyme acts as a catalyser in the biosynthesis of phenolics by converting phenylalanine to trans-cinnamic acid. High levels of cinnamic acids derivatives as well as shikimic acid in sugarcane and maize tissues were found in metabolomic studies in plants treated with HAs [100,101].

Plant physiological fitness is primarily governed by hormonal balance and antioxidant defense systems [102]. In this context, reactive oxygen species (ROS) are essential for the regulation of metabolism under stress [103]. The typical plant response to different abiotic stresses is the induction of oxidation through the production of ROS [104]. For example, during nutrient starvation (e.g., P deficiency), ROS serves as a cellular signaling molecule to modulate hormone signaling and biotic stress responses [105]. ROS interacts with lipids, proteins, and nucleic acids, resulting in lipid peroxidation, protein denaturation, and DNA mutation, respectively [106]. Enzymatic antioxidants such as superoxide dismutase (SOD), catalase (CAT) and glutathione peroxidase (GPX) minimize the concentration of cell hydrogen peroxide and superoxide. The induction of these antioxidants' enzymes by HS have been previously reported [37,65,93,107,108]. Additional authors have recently indicated the increasing relevancy of the ROS signaling pathway in conditions of plant stress, either dependent or independent of a hormone signaling pathway [37,70,109].

Phenotypic adaptations are a consequence of molecular and cellular changes that begin after the onset of stress, information of which is relayed via signal transduction pathways [110]. Although abiotic stress responses are often specific, signaling pathways leading to the response display considerable overlap. Figure 1 briefly describes the general sequence of stress perception and physiological response. Cell membrane receptors perceive abiotic stress cues which trigger a complex response, amplified and transmitted by secondary messengers. Messengers triggered by HAs includes a pulse of cytosolic Ca^{2+} , ROS and free H^+ [37,47]. For example, most abiotic stresses elicit rises in cytosolic free calcium levels ($[Ca^{2+}]_{cyt}$) and involve protein phosphatases and kinases. Increased cell Ca^{2+} ion uptake via plasma membrane Ca^{2+} channels have been observed, resulting in brief Ca^{2+} cytosolic waves [47]. These authors also noted the enhancement of Ca-transporter and calcium-dependent protein kinase (CDPK) activity at the transcriptional level. Protein kinases are important components of cell signal transduction [111].

Plant protein kinases regulate multiple processes [112], shown in Figure 1 adapted from Mahajan and Tuteja [113], including those of hormone and stress response [114]. Calcium-dependent protein kinase (CDPK) was the first protein kinase reported to be modulated by HAs, studied by Ramos [47]. Furthermore, Canellas and colleagues [112] observed a high transcriptional level of mitogen-activated protein kinases (MAPKs) induced by HAs. MAPKs are protein kinases enzymatically activated by abiotic stress [115]. Following stress perception, secondary messengers switch intracellular signal transduction cascades and promote gene activation by kinase and phosphatase activities.

Stress-responsive gene expression through either ABA-dependent or ABA-independent pathways activates physiological and metabolic responses. Generally, stress-responsive genes can be classified as two types: (i) functional genes encoding essential enzymes and metabolic proteins which directly protect cells from stresses and (ii) genes encoding various regulatory proteins, including transcription factors which regulate stress response via signal transduction and gene expression [116]. Transcription factors (TFs) are proteins that act together with other transcriptional regulators, including chromatin remodelling/modifying proteins, to enhance or obstruct RNA polymerase access to the DNA template [116]. These TFs interact with cis-elements in the promoter regions of several stress-related genes, thus conferring abiotic stress tolerance. High expression of ABA-responsive genes has been found in maize seedlings treated with HAs, mainly regulated by bZIP TFs, which interact with ABA-responsive elements (ABREs) [112]. WRKY TFs are a class of DNA-binding proteins involved in plant defence [117], including activation of secondary metabolism [118]. For example, WRKY23 was shown to regulate root growth [119], with the involvement in local biosynthesis of polyphenols responsible for the regulation of endogenous AUX transport.

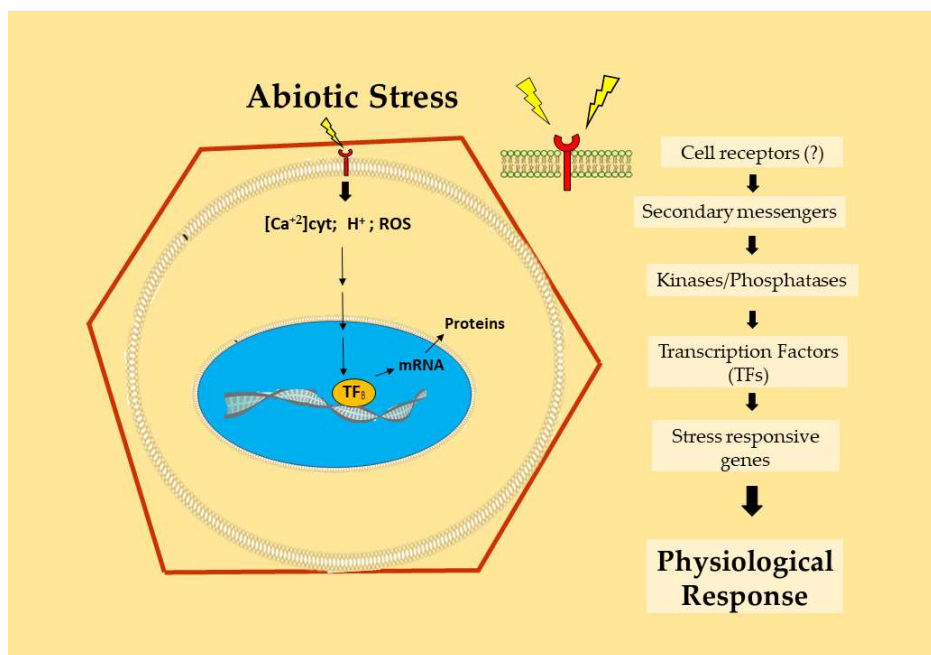


Figure 1. Scheme of generic signal transduction pathway and gene expression in response to abiotic stress signaling, adapted from Mahajan and Tuteja [113].

Moreover, expression of WRKY33 in maize was altered by different abiotic stresses [120], including nutrient deficiency [121]. WRKY TFs were involved in regulating a phosphate starvation response, including the promotion of high-affinity inorganic P (Pi) transporters and lateral root emergence. HAs induced differential expression of high-affinity Pi transporters [122] even at high Pi concentration and with changes in P speciation. The activation of high-affinity Pi transporters by WRKY45 TFs for phosphate acquisition has been reported [123]. Given that the transcriptional level of WRKY TFs was changed by HA treatment in maize root tissues [112], there is likely an interaction between WRKY and HS for initiation of a P deficiency response.

Little scientific work has been reported on the direct impact of HS on plant growth under low P conditions. A previous study [84] found that low-molecular HA functioned to increase the concentration of ATP and glucose-6-phosphate in plant cells under low Pi conditions. Graber and colleagues [124] demonstrated increased root hair growth by application of HS extracted from biochar under low Pi condition, implying that the activation of ET and AUX may be enhanced by HS. However, the modulation of P acquisition is not limited to signalling pathways of only ET and AUX [19]. For a better understanding of biochemical and physiological responses associated with P starvation, more research is needed regarding how HS relates to crosstalk between plant hormones and other secondary metabolism mechanisms at multiple levels.

6. Interaction between HS and P-Solubilizing Microorganisms

HS is pivotal in the physical, chemical, and biological attributes of soils which in turn can modulate soil microbial community structure and activity. In plants treated with HS, changes of root anatomy and physiology related to phytohormonal actions are also able to influence rhizosphere microbial community composition [23,34,125,126]. Thus, microorganisms involved with the P cycle are directly or indirectly affected by HS action in the plant–soil system.

Microorganisms involved in P-dynamics of soil/rhizosphere niches are comprised of two groups, based on their distinct strategies to enhance plant P availability. The first group includes mineralizing microorganisms which produce nuclease enzymes, phospholipases, and phytases which hydrolyse P-organic compounds. In particular, phytase has great importance in the mineralization process, as 50% of the soil organic P is in the form of phytate (Na-IHP) [127]. After hydrolysis, the resulting

phosphomonoesters are further hydrolysed by phosphatase enzymes, releasing soluble phosphorus and other chelated minerals [128].

The second group is comprised of phosphorus solubilizing microorganisms (PSM) [129–131] which convert sources of inorganic P in mineral lattice complexes into soluble orthophosphate ions (H_2PO_4 and HPO_4) [132]. Most mineral P content in soils are in a form unavailable for plant uptake, especially in highly weathered soils [133]. PSM act on these unavailable P sources by proton extrusion and releases metabolites, including low-molecular-weight organic acids [134–136]. Although less efficient, other mechanisms are also reported to solubilize Pi such as by the production of hydroxyl ions and CO_2 , production of inorganic acids (such as sulfuric, nitric, and carbonic acids) and chelating substances [137,138].

Although different microbial species are reported as PSM, those which can survive as soil saprophytes and show exceptional ability to colonize the rhizosphere are often considered the best candidates for plants as P-nutrition enhancers. For fungi, studies have shown potential for Pi solubilizing activity in the genera *Aspergillus* and *Penicillium* [139,140]. In bacteria, several studies have indicated the potential for solubilization in the genera *Pseudomonas*, *Serratia*, *Paraburkholderia*, *Bacillus*, *Rhizobium*, *Azospirillum*, *Enterobacter*, and *Paenibacillus* [141–143]. Most of these species are also able to access organic P forms, indicating their crucial role in the P cycle of soils.

There is a complex relationship between HS and P-bioavailability mediated by soil microbes. Soil organic matter itself represents a source of P, and bioactive fractions such as HAs can trigger changes on root architecture and biochemistry, for example by stimulating proton pump activity across plant cell plasma membranes as well as root exudation [47,144]. Consequently, increased root exudation of carbon can stimulate growth in the rhizosphere microbial community, with the enhanced production of AUX and AUX-like compounds leading to an amplification of the positive interaction.

Coordinated interaction between HS and rhizosphere microbiota involving the central component of the auxinic hormonal pathway has been reported [23]. HS affected the formation of lateral roots and root hair length and density, consequently increasing the release of root exudates. Among these exudates were precursor compounds of IAA and other AUX-like compounds including the amino acid L-Tryptophan. L-Tryptophan acts as a precursor for the biosynthesis of IAA in plants and microbes, therefore increasing IAA content in the rhizosphere resulting in localized acidification and the release of Pi into the rhizosphere soil solution [145].

Several studies have explored the AUX-producing interaction of HS and PSM [146] for use in soil fertility and plant development. In vermicomposting research [147], there was an observed increase of phosphatase activity and P availability in parallel with increased HS content in the growth substrate. HS also has an interesting protective effect against P-fixation in mineral soil fractions. With soybean plants in a controlled environment [141], HS application combined with P-solubilizing bacteria increased soil pH and plant-available P, concomitantly reducing exchangeable Al.

A combination of PSM and HS resulted in increased grain yield in maize and barley, a result of greater available P release and increased absorption of nutrients by plants [148,149]. Benefits from the combined use of PSM plus HS were also demonstrated in another maize experiment [22], in which treated plants had higher root and shoot biomass in relation to control plants. However, no increase in P concentration was observed, suggesting greater P use efficiency in plants treated with the combination of HS and PSM.

Despite the evidence of the effect of HS on PSM activity and consequent plant growth promotion, differing Pi solubilization results are obtained in vitro compared to those from field conditions [148,150]. Therefore, further study on the interaction mechanisms between HS and microorganisms is required.

7. Interaction between HS and Mycorrhizal Fungi for P Uptake

Combining microorganisms with organic matter maintains soil fertility and can result in a beneficial symbiosis for plants. Organic matter allows for the development of soil biota, responsible for nutrient mineralization and therefore, plant bioavailability [151]. In this sense, combining HS and ecto-

and endomycorrhizal fungi positively affect plant growth and development [151]. The most studied plant symbiotic interactions are with arbuscular mycorrhizal fungi (AMF) and ectomycorrhizal fungi (EMF). These interactions are mediated by a bi-directional transfer of nutrients [152] and differentially influence the dynamics of organic matter in ecosystems [153].

Several studies have reported that inoculation of AMF-type endomycorrhiza with HS increased plant growth and yield [154,155]. In non-inoculated plants, P is directly absorbed by nutrient transporters located in the root epidermis and cortex. When plants are inoculated with AMF, P is absorbed by hyphae/mycelia via nutrient transporters and subsequently translocated to fungal structures located inside the cortical cells of the roots [152,156]. These intracellular structures are called arbuscules and formed by hyphae differentiation. Arbuscules, in turn, exhibit a highly branched structure modulated by root exudation of strigolactones, a class of plant hormones [152].

Maize treated with HS and inoculated with heterogamous AMF *Dentiscutata* displayed an increased P content of 12% [151]. Remarkable absorption of P was also observed in lettuce treated with HS and *Rhizophagus irregularis* [157] and in lettuce treated with HA inoculated with AMF *Rhizophagus irregularis* and *Funneliformis mosseae* [158]. A similar result was observed [159] when treating tomato with *Rhizophagus clarus* with HS. P levels were also doubled in *Lippia alba* following inoculation with AMF [160] in combination with HS and P (200 mg) addition to the soil.

EMF, in association with the surface of tree roots, can access most of the P compartmentalized in HOM in forest soils [161,162]. These fungi are found mainly in temperate conditions and mobilize P from the soil based on the following steps: (1) soil import, (2) storage on the soil hyphen margin, (3) distribution in the mycelium, and (4) vacuolar export at the fungus–plant interface [163]. Additionally, phytases and phosphatases can be used by EMFs to solubilize organic forms of P [164].

8. Conclusions

The present work provides information on the role of HS for P uptake and outlines the strong association of HS with plant hormones at different levels including morphological effects (e.g., root elongation). Under conditions of abiotic stress such as P starvation, HS interacts not only with plant hormones signaling pathways in secondary metabolism systems such as by increasing expression of ABA-responsive genes and TOR transcription related to “AUX-like activity”, but also with other pathways including those of ROS and phenylpropanoids. In addition, the synergetic effect between HS and different types of microorganisms which strengthens phosphorous uptake by modulating root architecture is beneficial for P management. Further investigation should be conducted to reveal the function of HS on P uptake and crosstalk mechanisms between phytohormonal signaling pathways together with other plant functions, and to understand the interaction of HS with microorganisms. Novel plant hormones, including strigolactones and melatonin, should also be considered for future research on P uptake.

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