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REVIEW

Humic substances: their role in improving plant growth and resilience in sustainable agriculture

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Abstract

Background: Many concerns have been raised about the extensive use of agrochemicals and their impacts on environment and soil. Some serious issues include increased soil salinization, toxicity and decrease in soil microbial biodiversity. Biostimulants have emerged as a promising ecofriendly alternative to agrochemicals. Humic substances (HSs) are biostimulants with many beneficial effects in plants physiology and productivity.
Aims: This review aims to synthesize current evidence on the role of HSs in supporting sustainable agriculture that improves crop productivity while maintaining good soil health in changing environmental conditions.
Methods: Relevant studies related to HSs and their effects on soil fertility, plant growth, stress tolerance and hormonal regulation were collected from major scientific databases including Scopus, Web of Science, and Google Scholar. The main outcomes of these studies were extracted and analyzed to provide an overview of the available evidence.
Results: The literature shows that the integration of HSs into agricultural practices improves soil structure, increases water retention, maintains healthy microbial diversity and enhances plant productivity.
Conclusions: This review highlights the importance of using HSs in enhancing soil health and plant physiology. However, further studies are required to integrating new technologies and diversify HSs sources, plants species, and different environments.

Keywords: abiotic stress, crops, humic acids, humic substances.

Introduction

Increased food production is required to feed the rapidly growing human population, while maximizing resource use efficiency (RUE) and minimizing environmental impact on the ecosystem and human health (Rouphael and Colla, 2018; Punia et al., 2020a). The exponential growth of the global population has led to overconsumption of agricultural lands used for pasture, forage and food production (Mu et al., 2013). To solve this problem, it is crucial to enhance agricultural productivity while reducing the use of synthetic agrochemicals, such as fertilizers and hazardous pesticides (Calvo et al., 2014; Punia et al., 2020b). A promising strategy is to use biostimulants, which involve organic natural plants or microbial compounds to boost agricultural productivity. Over the years, biostimulants have proven their effectiveness in enhancing plant growth, development and nutrient use efficiency (NUE). In addition, they stimulate plant flowering, fruit setting, and crops productivity (Nardi et al., 2016; Rouphael et al., 2017; Yakhin et al., 2017; de Pascale et al., 2018; Quille et al., 2025). There is considerable confusion regarding the definition of "biostimulants". Various definitions have been proposed over time, many of these definitions aim to distinguish biostimulants from fertilizers, as well as from pesticides and biocontrol agents (du Jardin, 2015). In December 2018, the Farm Bill (Congress, 2018) introduced the first statutory language regarding plant

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Abbreviations: CK - cytokinin; FA - fulvic acids; GA - gibberellic acid; HAs - humic acids; HKT - high affinity potassium transporter; HSPs - heat shock proteins; HSs - humic substances; NUE - nutrient use efficiency; ROS - reactive oxygen species; RUE - resource use efficiency; SOS - salt overly sensitive.
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biostimulant, defining it as “a substance or microorganism that, when applied to seeds, plants, or the rhizosphere, stimulates natural processes to improve nutrient uptake, nutrient efficiency, tolerance to abiotic stress, or crop quality and yield”. This legal definition makes a significant step toward establishing a regulatory framework for reviewing and approving these biostimulants as well as having a consistent national labeling of these materials, which are currently regulated as fertilizers, soil inoculants, or soil amendments. The definition in the 2018 Farm Bill aligns with the one proposed by the European Union (European Biostimulants Industry Council, 2025).

There has been no specific standard classification for biostimulants, however, many researchers have proposed several categories for these substances based on their source and/or their mode of action (Calvo et al., 2014; du Jardin, 2015; Yakhin et al., 2017; Bulgari et al., 2019). One of these categories is humic substances which is discussed in this review.

Humic substances composition and properties

Humic substances (HSs) are naturally occurring heterogeneous mixtures of various organic compounds characterized by their high resistance to decomposition. They are generated from the deposition processes of animal and plant materials that are further metabolized by soil microorganisms (Rouphael and Colla, 2018).

HSs are classified based on their molecular weights and solubilities into humins (insoluble in water), humic acids (soluble in alkaline, pH 8 - 12) and fulvic acids (soluble in water) (Fig. 1*A*). HSs are highly dynamic, exhibiting association and dissociation into supra-molecular structures (Nardi et al., 2016). Their behavior and functionality in soil are strongly influenced by the interaction between organic substances, soil microbes, and plant roots. Thus, it is crucial to optimize these interactions when using HSs to enhance plant growth and yield, to achieve the desired outcomes. This explains their different effects on plant growth and yield under varying application conditions (Rose et al., 2014).

The molecular weight of HSs varies; it ranges between few hundred daltons (Da) to several hundred kilodaltons (kDa). Fulvic acids (FAs) are generally characterized by their low molecular weight compared to humic acids (HAs). The main reactive functional groups in HSs are carboxyl and hydroxyl which contribute to their various functional roles in plants and environments.

The chemical composition of HSs varies depending on their origins and the chemical processes that happened during humification. The main chemical components present in HSs are carbon (making up to 50 - 60% of their mass), hydrogen (3 - 7% of their mass), oxygen (forming 30 - 45% of their mass, mainly found in carboxylic, phenolic, and alcoholic groups), nitrogen (represents only 1 - 5% of their mass, mainly present in proteins, amino acids, and other nitrogen containing compounds), sulfur and phosphorus (present in very little quantities and usually associated with biomolecules such as lignin, nucleic acids, or microbial compounds) (Fig. 1*B*). In addition, they contain inorganic components including minerals and metals that are added to their structures during different processes such as adsorption, complexation and co-precipitation. Calcium (Ca^{2+}), magnesium (Mg^{2+}), potassium (K^{+}), iron (Fe^{2+}, Fe^{3+}), and aluminum (Al^{3+}) are examples of some metals that bind to carboxyl or phenolic groups in HSs (Nardi et al., 2021).

Role of humic substances in soil

The continuous use of the same land for planting every year has a negative impact on soil. In addition, climate change further affects soil properties by altering water availability (Horel et al., 2022). HSs come as a low-cost,

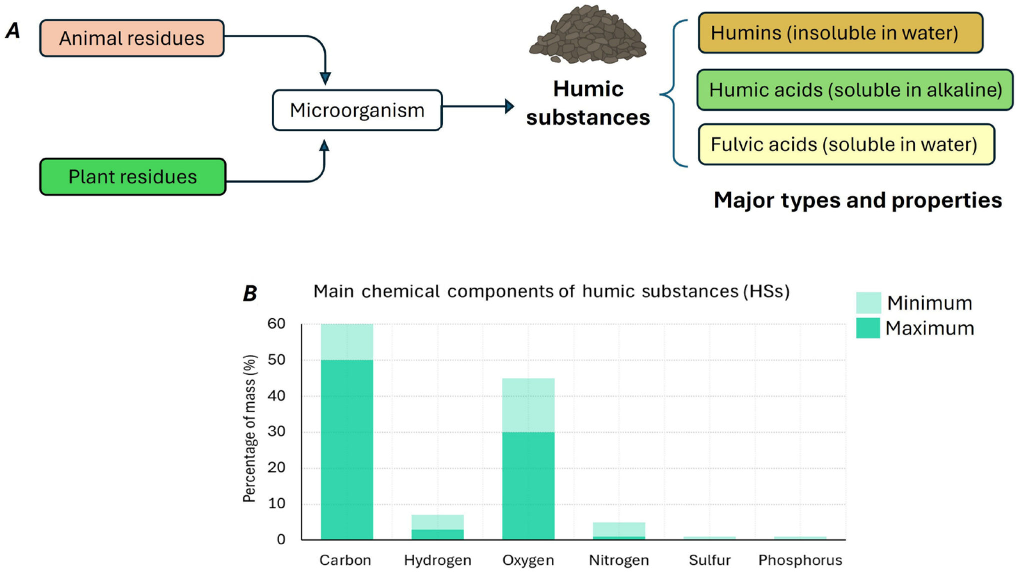

Fig. 1. Overview of humic substances. (*A*) Humic substances (HSs) sources, types, and properties. (*B*) Main chemical constituents of HSs according to Nardi et al. (2021).

natural approach to enhancing resilience of soil under these conditions. HSs enhance soil properties and plant–soil interactions through multiple mechanisms including improvements in soil physio-chemical properties as well as through the regulation of soil biological activities and rhizosphere properties (Nardi et al., 2021). Fig. 2 summarizes the beneficial effects of HSs in soil.

Improving soil physio-chemical properties: The high content of carboxyl, phenolic and quinone functional groups in humic substances provide them with colloidal properties and affordable cation-exchange capacity (CEC) (Nardi et al., 2016; 2021). These characteristics participate in the formation and stabilization of soil aggregates through the binding of minerals with organic residues to form polyvalent cation (Zydlik and Zydlik, 2020). As a result, soil structure and porosity are improved while susceptibility to erosion is reduced. This aggregation effect also enhances the water holding capacity of coarse-textured and degraded soil, thereby helping crops to survive both drought and intense rainfall (Antu et al., 2025).

HSs also help in reducing soil crusting and runoff by enhancing soil aggregation and altering the internal pore architecture. The resulting micro- and macropores within and between the aggregates improve water retention and allow more efficient movement of air and water through soil (Antu et al., 2025). HSs-based aggregation produces stronger and more stable soil structure and thereby minimizes soil surface crusting that happens in weak aggregates in non-HSs-treated soil. Overall, enhanced soil aggregation, aeration, and moisture retention contributes significantly to better soil conservation and resilience under climate change scenarios (Zydlik and Zydlik, 2020; Antu et al., 2025).

Several studies have shown that applying HAs to these lands can enhance the texture and structure of degraded soils (Olk et al., 2018; Yang et al., 2021). For instance, applying bentonite-HA to degraded sandy soil in maize field increased the stability of soil macro-aggregates, improved water holding capacity of soil and increased maize yield (Zhou et al., 2019). Additionally, HAs improved the structure of clay soil by forming chelates with cationic metals, which act as a bridge between HA and clay surfaces (Yamaguchi et al., 2004). Continuous addition of HAs to the soil of peanut plants significantly increased the peanut yield and quality by 78.29% over three years (Li et al., 2019). This positive effect is attributed to the enhanced physical and chemical properties of soil associated with enhanced nutrient contents and organic matter in soil liquid FA, both mineral-derived and plant-derived, improved nutrient availability and soil properties of albic black soil and accelerated the growth of maize plants as indicated by substantial increase in plant height, biomass, stem diameter, and grain weights (Kumar Sootahar et al., 2019). However, some studies found that applying HSs does not significantly affect soil aggregation. For example, two growing cycles of maize in soil supplemented with coal-derived HA did not affect soil aggregate stability (Mukherjee et al., 2014). This might be attributed to the amount of HA applied that was insufficient to induce changes in soil texture and structure. Other suggested reasons could be the soil pH and the source of HSs (Rose et al., 2014).

HSs can also influence soil pH, and their effects largely depend on the amount of carboxyl and phenolic functional groups. Nevertheless, studies investigating the impact of HSs on soil pH are limited and their findings have been inconsistent (Li et al., 2019; Laskosky et al., 2020; Ampong et al., 2022). For example, one study reported that the soil pH, measured during post-harvest analysis of barley soil, decreased with increasing HAs at concentrations ranging from 0 to 26.2 g/kg (Laskosky et al., 2020). In contrast, HAs application did not cause a significant change in soil pH in a three-year-continuous peanut cropping field experiment (Li et al., 2019). Similarly, HA application did not enhance the buffering capacity of a nutrient solution

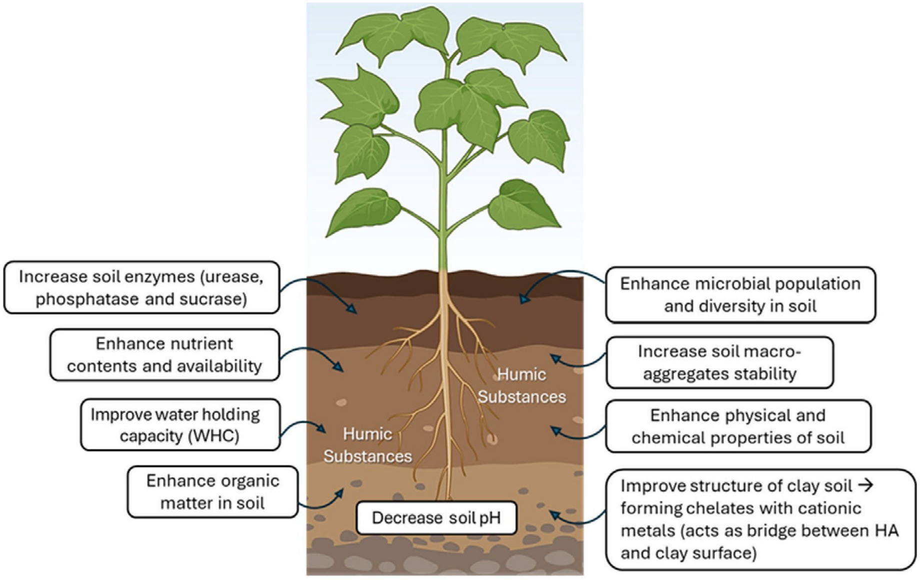

Fig. 2. Major effects of humic substances (HSs) in enhancing soil properties.

in hydroponic system used for wheat at initial pH of 3.5, likely due to low HA concentration used as reported by authors (Mackowiak et al., 2001). Collectively, these studies indicated that the effect of HAs on pH is highly dependent on experimental condition, plant species, and source of HA. Further studies are required to determine the optimal conditions for each HA source and specify their role in controlling soil pH (Ampong et al., 2022).

Effects on soil biology and rhizosphere: HSs have an important role in biological activities in the rhizosphere. Their presence in soil provides two major roles in maintaining and conserving microbial community in soil. First, they act as a stable source of organic matter that is essential as a long-term carbon and energy source for microorganisms. Second, through their contribution to soil aggregation, they provide favorable microhabitat that protect microbes from environmental extremes and predation (Jindo et al., 2020).

Several studies showed that HSs supplementation increases microbial population, activity, and diversity. For example, in a three-year field experiment on continuously cropped peanut, the activity of several enzymes such as urease, sucrase, and phosphatase was increased in HA treated soil indicating better microbial activity (Li et al., 2019). It also enhanced microbial diversity in soil as it increased Firmicutes bacteria and Basidiomycota and Mortierellomycota fungi while reducing pathogenic fungi such as Ascomycota (Li et al., 2019). A similar study found that applying vermicompost rich with HA significantly increased the activity of urease enzyme in the soil of pea plants (Maji et al., 2017). However, contrasting results were reported by Shen et al. (2020) where they found that incubating soil with coal derived HA inhibited the activity of urease enzyme, however, the microbial biomass was not determined in this study.

Urea hydrolysis by urease produced by soil microorganism converts urea into ammonium, which is an important form of nitrogen available for plant uptake. Some parts of ammonium are then converted into nitrate and gaseous nitrogen through nitrification and denitrification processes. This conversion is rapid and has been a major concern as it reduces NUE (de Pascale et al., 2018). Urea hydrolysis is accelerated by high nickel concentration in soil. Chelating nickel can help in decreasing urease activity (Tan et al., 2000). HSs through their chelating properties can form complex with nickel and thus slow down urease activity (Sible et al., 2021). Studies have reported contradictory results on the effect of HSs on urease activity. Coal-derived HSs reduced urea hydrolysis two times compared to control, however, this reduction was not maintained for a long time, as ammonium concentration was sharply decreased after day three, which reflects increase in nitrate level (Shen et al., 2020). Another study showed that HSs reduce the abundance of soil nitrifying microorganisms, leading to lower nitrification rate and thus higher ammonium concentration in soil (Dong et al., 2009). One study investigating the effect of HAs on urea hydrolysis and nitrification in the rhizosphere of barley plants reported that HA application increased urea hydrolysis while reducing the nitrification of ammonium to nitrate. The high ammonium that persists in soil resulted in increased CEC and reduced soil pH (Laskosky et al., 2020). Finally, it is important to take into consideration that different HAs used in different studies have different structure and chemical composition and are used in different concentration and application rates. Therefore, it will be critical to investigate the source of HSs and their application rate on the hydrolysis of urea and the subsequent nitrification and denitrification processes under defined growth conditions.

Effects of HSs on plant physiology

HSs have shown beneficial effects on plants growth, reproduction, quality and quantity of crop yield, and enhanced tolerance to many stresses (Fig. 3). Here are examples of some HSs applications in several types of plants.

HSs enhances plants root nutrition: Plants require several macro- and micronutrients to grow and function properly. These macronutrients include carbon, nitrogen, oxygen, phosphorus, magnesium and calcium, whereas micronutrients such as iron, manganese, copper, zinc, molybdenum and chlorine are also essential for plant development (Barker and Pilbeam, 2015). One of the key effects of HSs is the enhancement of root nutrition which happens *via* various mechanisms. One of these mechanisms is through enhancing root uptake of macro- and micronutrients, which occurs due to the elevated CEC of the soil containing the polyanionic HS, along with the increased availability of phosphorus by HSs (Canellas et al., 2002).

Phosphorus is an essential macronutrient required for plant growth and development; however, it is predominantly present in forms that are less soluble, which limits its availability to plants. Thus, when phosphorus is applied to the soil as fertilizer, only small fractions are directly available for plant uptake, while the majority is transformed into insoluble mineral forms in the soil (van der Salm et al., 2017). HSs due to the presence of several oxygen-based functional groups in their structure, can create a slightly acidic soil environment. This acidity can enhance the availability of certain macronutrients, such as phosphorus by increasing their solubility (Yang and Antonietti, 2020; Jung et al., 2021). In addition, HSs indirectly protect phosphate from fixation through the formation of organo-mineral complexes and by decreasing the activity of Al^{3+} and Fe^{3+} in acidic soil through complexation. They can also enhance phosphorus availability by promoting its desorption from iron and aluminum oxides by competing for sorption sites. They also inhibit the precipitation of insoluble calcium phosphate and thereby increasing the available phosphorus (Rouphael and Colla, 2018; Gerke, 2021).

Nitrogen is a key nutrient for plant growth, plays central role in the biosynthesis of amino acids, proteins, chlorophyll, and nucleic acids. HSs enhances nitrogen uptake by several mechanisms. One mechanism is through

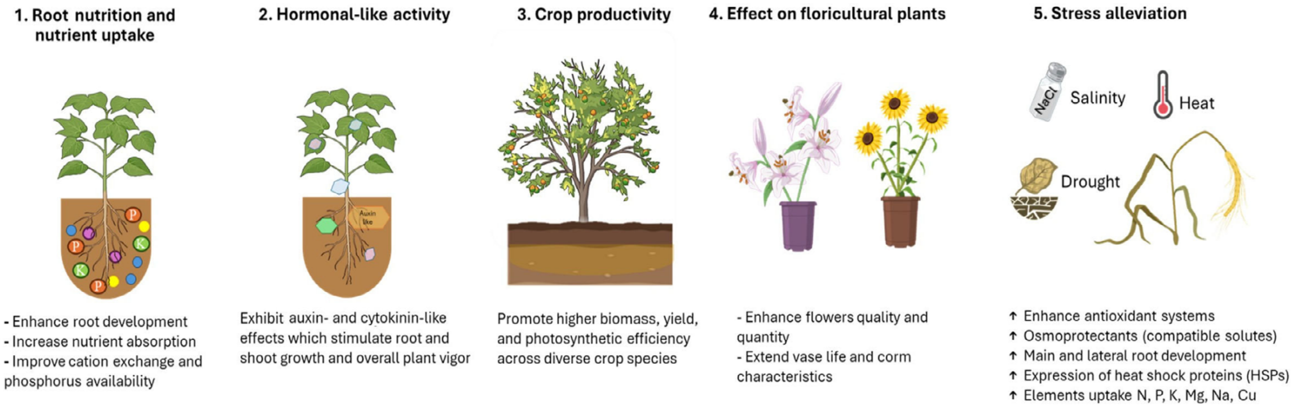

Fig. 3. Major applications of humic substances (HSs) in crops and horticulture for enhancing their growth and resilience.

decreasing rhizosphere pH and stimulating H^+/NO^{3-} symport activity thereby enhancing nitrate uptake by plant roots (Nardi et al., 2021). Another mechanism is by upregulating the expression of nitrate transporters (Zanin et al., 2018). The expression of genes encoding accessory proteins for nitrate transport such as dual *affinity nitrate transporter* (*NRT1.1*) and *high affinity nitrate transporter* (*NRT2.1* and *NRT2.2*), was upregulated in a hydroponic experiment used in growing maize seedling with peat-derived HSs (Quaggiotti, 2004; Zanin et al., 2018). In the same study, HSs upregulated the expression of key enzymes involved in nitrogen assimilation including nitrate reductase (NR), glutamine synthetase (GS), and glutamine oxoglutarate aminotransferase (GOGAT) (Zanin et al., 2018).

Iron is an essential micronutrient, plays a significant role in plant growth and root development. In soil, iron predominantly exists as Fe^{3+} (ferric), while plants mainly absorb it in the Fe^{2+} (ferrous) form. HSs facilitate the reduction of Fe^{3+} to Fe^{2+} through electron donation from redox-active functional groups. A study on rice found that HSs (both HA and FA) in combination with iron $FeSO_4$ at 0.25% enhance nutrient uptake and dry weight yield under greenhouse conditions (Gerke, 2021).

Another mechanism is through activating plasma membrane H^+-ATPases which transform the free energy released from ATP hydrolysis into a transmembrane electrochemical potential utilized for the uptake of nitrate and other nutrients. In addition to nutrient uptake, proton pumping by plasma membrane ATPases also facilitates organ growth by increasing cell wall loosening and cell enlargement (Canellas et al., 2002; Jindo et al., 2012). Humic substances (both HA and FAs) enhance nutrient uptake and dry weight yield in rice plants (Eshwar et al., 2017).

Hormone like activity: The beneficial effects of HSs can be attributed to their hormone-like activity, specifically through certain HS compounds that exhibit cytokinin (CK) activity and auxin or gibberellin (GA)-like effects (Dobbss et al., 2010; Nardi et al., 2018). While the exact mechanism by which HSs mediate hormonal function is still unclear, HSs might contain functional groups recognized by receptors and signaling compounds within plant hormonal pathways (du Jardin, 2015).

Many studies have reported that HSs induce root phenotype similar to those caused by auxin, including enhanced main roots length and initiation and proliferation of lateral roots. For instance, HS isolated from vegetables enhanced main and lateral root proliferation and modified root architecture (Canellas and Olivares, 2014). This auxin-like effect is further supported by the identification of auxin-like structures within the organic fractions of HSs derived from earthworm compost. These structures stimulated root growth in maize (*Zea mays*) seedlings and increased the number of lateral root emergence sites (Canellas et al., 2002). Notably, the auxin-like activity of HSs in promoting lateral root initiation has been demonstrated in *Arabidopsis thaliana* through genetic and molecular studies. These findings were further supported by expression of the early auxin-responsive *IAA19* gene (Trevisan et al., 2011).

The auxin-like signaling effects of HSs is primarily mediated by H^+-ATPase which is activated by indole-3-acetic acid (IAA) that is present in small quantity in some HSs (Canellas et al., 2002; Zandonadi et al., 2010). However, the auxin-like effects are not always associated with IAA content in HS and the auxin-responsive genes such as *IAA5* and *IAA9* are not always modified by HS. This suggests that further compounds, other than IAA, control root development (Nardi et al., 2021). Nitric oxide (NO) appears to be a key intermediator in HS-induced auxin like effects. Studies found that plants treated with either HA or NO stimulated lateral root emergence in a similar manner, even in the presence of auxin inhibitors. This indicates that these effects are mediated by HA and NO. Both treatments also increased H^+-ATPase activity by three times (Zandonadi et al., 2010).

Another auxin-like effect of HS is enhancing stomatal opening. HS isolated from earthworm exhibited auxin-like activity by inducing stomatal opening in epidermal peel of pea (*Pisum sativum* L.) leaves in a manner similar to IAA. The application of specific phospholipid lipase A2 (PLA2) inhibitor blocked stomatal opening indicating that this response is mediated by PLA2 (Russell et al., 2006).

Cytokinin (CK)-like activity is another recognized property of HSs that contribute to shoot growth and nutrient distribution (Mora et al., 2010). They influence plant growth through the stimulation of plasma membrane H^+-ATPase activity and through the regulation of gene expression association with CK signaling (Rathor et al., 2024). Several CK like physiological responses in the shoot, are linked with high HSs in soil. A recent study on wheat showed that the HSs treatment induce changes in both auxin and CK pathways. The expression of several genes involved in auxin- (such as tryptophan aminotransferase) and CK-related pathways were upregulated in HS-treated seedlings (Rathor et al., 2024). Supporting this, a study demonstrated that the physiologically active form of CKs, isopentenyladenosine (IPA), is present in various HSs including lignohumates, leonardite (oxidized form of lignite) and earthworm faeces with highest concentration detected in earthworm faeces. The IPA enhanced shoot growth in radish plants and increased chlorophyll and protein content as well as ATP sulfurylase activities in maize plants, thereby confirming CK-like activity of HSs (Pizzeghello et al., 2013). In addition, a study on cucumber plants found that HSs influences the distribution of CKs within plants by facilitating their transport from root to shoot leading to increased accumulation of several active CKs in the shoot along with low levels in roots. This redistribution is associated with enhanced H^+-ATPase activity and improved nutrient uptake and enhanced shoot growth (Mora et al., 2010).

Gibberellic acid (GA)-like activity in HS has been reported in several research. Typical effects of GAs include hypocotyl elongation, breaking dormancy, accelerating flower and fruit development. Effects like GA have been reported in HS supplemented soil (Pizzeghello et al., 2001; Ertani et al., 2009; Nakasha et al., 2014; Savy et al., 2017). In addition to the GA-like effects, HS also participate in activating the metabolism of CKs and GAs by interacting with genes involved in these metabolic pathways (Ertani et al., 2009). The GA-like activity of HA and FA obtained from alpine soil were attributed to several aromatic and amides components present in these HSs (Pizzeghello et al., 2001). HA treated grapes showed increased berry size, an effect similar to that obtained by treating flowering plants with synthetic gas (Ferrara and Brunetti, 2008; 2010).

Humic substances in crops: HAs can be applied either as foliar spray or directly to the soil. When HAs are applied as foliar spray, they are readily absorbed by leaves and stimulate enzymes involved in various biological processes. For instance, they enhance photosynthetic rate and thus increase the production of various pigments involved in plant resistance to biotic and abiotic stresses. Additionally, they promote plant growth and productivity while extending the shelf life of fruits (Abourayya et al., 2020; Moura et al., 2023). Soil application of plant-derived FAs (liquid and solid) and mineral-derived liquid FAs improved the physicochemical and biological properties of different types of soils with different textures including Aridisols, Vertisols, and Mollisols soil. There was a significant increase in the heavy fraction carbon (10 - 60%), light fraction carbon (30 - 60%), nitrogen (30 - 70%), and potassium (20 - 45%) in all soil types tested, with high increase in phosphorus content by 80 - 90% in Aridisols and Vertisols. In addition, plant-derived (liquid and solid) and mineral-derived liquid improved wheat growth traits including plant height, biomass, grain weight, and spike grain weight associated with improved nutrient uptake in Mollisols and Aridisols soils, respectively (Kumar, 2020). HSs have been applied to various vegetables such as lettuce, broccoli and cauliflower (Hernandez et al., 2015; Hawall et al., 2018; Rachid et al., 2020). Foliar application of HSs to these vegetables accelerated their development by reducing their production cycle without affecting the quality of the plants. Foliar application of potassium humate to the leaves of the lettuce increased the leaves number per plant, reduced carbohydrate levels, increased protein content and increased the activities of some enzymes such as nitrate reductase and phenylalanine ammonia lyase (Hernandez et al., 2015).

Dziugieł and Wadas (2020) performed a three-year experiment where they spray potato plants with leonardite (12% HA and 6% FA) twice (first was during leaf development stage and they repeated the application one week later). The results showed that there was an increase in the average weight of tubers while the total number of tubers per plant did not increase. Multiple studies have demonstrated positive effects of HSs on oilseed plants. Foliar applications of HA at bud stage, and FA combined with NPK fertilizers at floral stage improved the nutrient content in seeds of sunflower (*Helianthus annuus* L.) (Thakur et al., 2017). In another study on sunflower plants, Shindhe et al. (2020) demonstrated that applying HA (4 ppm) at 40 and 60 days after sowing improved many traits including plant height, number of leaves, leaf area, percentage of filled achenes, harvest index, number of seeds per plant and total yields. For all these parameters, HA outperformed control. In a flax crop (*Linum usitatissimum* L.) applying HA (15 mg/L) to leaves at 45 and 60 days after sowing, increased plant growth indices such as plant height, root and shoot fresh and dry mass, percentage of total dissolved solids, polysaccharide contents, total phenols, seeds number, oil content and yield percentage (Bakry et al., 2013). The beneficial effect of HSs was also tested on medicinal plants, for example potassium humate increased the ability of turmeric (*Curcuma longa* L.) to absorb sulfur (Baskar and Sankaran, 2004). Potassium humate was also found to increase the vegetative growth of fennel (*Foeniculum vulgare* Mill.) (El-Sawy et al., 2021).

In fruits, fertilizing pomegranate (*Punica granatum* L.) with HA (2 and 5 mg/L), in addition to other supplements including kaolin, calcium, and boron reduced fruit cracking and increased the weight of fruits (Ghanbarpour et al., 2019). Spraying guava (*Psidium guajava* L.) with potassium humate (0, 2, and 4 mg/L) enhanced the growth of guava plants as evidenced by increases in plant height, stem diameter, number of lateral shoots and number of leaves per seedling (Ibrahim and Al-Sereh, 2019). The yield of several fruit trees (as indicated by kg/tree) increased after treating them with HA. Table 1 shows some fruit and the concentration and frequency of adding as described by different research.

HSs in floricultural plants: HSs are also beneficial to floricultural plants as they enhance their growth and yield. For instance, HA isolated from leonardite rock material, when used as 2 mL/L and mixed with NPK (17:17:17), improved the growth, flowers quality and quantity, vase life, and corm characteristics of gladiolus flowers (Ahmad et al., 2013). FA and HA (40 mg/kg) significantly enhanced plant growth and flower numbers of *Impatiens walleriana* flowers (Esringü et al., 2015). When HA was applied at relatively low concentration (500 mg/L), it improved some postharvest traits, such as increased flower numbers and extended the vase life for cultivated flowers. At higher concentration (1 000 mg/L) it promoted root growth and significantly increased the levels of nitrogen, phosphorus, potassium, calcium, magnesium, iron, and zinc in the leaves and scapes of Gerbera flowers (Nikbakht et al., 2008). Another study by Yazdani et al. (2014) found that HA and FA (50 mg/L of FA), improved root structure, nutrient uptake and increased number of flowers by up to 72%. They also extended the vase life by about 8 days of Gerbera flowers.

HA, when used along with silver nanoparticles and *Aloe vera* treatment, contributed to extending the vase life of flowers, enhancing vase solution uptake, increasing flowers diameter and relative fresh weight while increasing carbohydrates, chlorophyl, and phenols in the leaves and petals. They also contribute to decreasing bacterial count in vase solution and thereby extend vase life of flowers of a standard carnation flower (*Dianthus caryophyllus* cv. Dover) (El-Attar and Sakr, 2022). In another study, Arafa et al. (2024) found that HSs when used alone or in combination with sucrose and citric acid enhance chlorophyl and carbohydrates biosynthesis and thereby contribute to increasing longevity and quality in Calla lilies flowers. In lilies, HA improved quality parameters including flower stem length, fresh weight and the number of buds and leaves. These enhancements are attributed to mineral and growth regulators present in HA which promote biomass and overall health (Ataklı et al., 2021). A study reported that spraying plants with HA at concentration of 1 000 mg/mL significantly improved plant growth, flowering capacity, nutrient and chlorophyl content in Ivy geranium (*Pelargonium peltatum*) plants under saline and saline conditions (Elhindi et al., 2023).

While HSs improve longevity in floricultural plants, it also improves metabolic yield in medicinal plants such as Safron. In the recent study by Feizi et al. (2025), HA irrigation (3 kg/ha) combined with foliar application of copper (Cu) resulted in a substantial increase in flower number, stigma weight, leaf length, and phytochemical profile in Safron (*Crocus sativus* L.).

Collectively, these studies demonstrated that HSs have beneficial effects in enhancing several quality characteristics of flower plants, which happens through different mechanisms including enhancing nutrient uptake, changing root architecture and activating pathways in carbohydrates and chlorophyll biosynthesis. However, it is crucial to take into consideration the specific need and characteristics of different flower species and the effectiveness of HSs vary depending on the type of flower and conditions under which they were applied.

HSs in stress alleviation: Plants encompass various biotic and abiotic stresses such as salinity, drought,

Table 1. Summary of humic acid foliar application rates and timing in different fruit crops.

Fruit crop	Application dose timing/Frequency	Effect on plants	Reference
Mango (*Mangifera indica* L.)	0.1, 0.2, and 0.3% sprayed at stage of flower bud initiation	Increase total fruit weight and yield	Ngullie et al. (2014)
Mango (*Mangifera indica* L.)	0.15, 0.3 and 0.45% applied three times, before and once during flowering	Increase yield and significantly enhance fruit quality	El-Hoseiny et al. (2020)
Peach (*Prunus persica* L.)	0.25 and 0.5% after fruiting, repeated 4 times at an interval of 15 days	Yield increased by ~30%, improved fruit quality (fruit weight, sugar) and increase nutrient content in leaves	Abd El-Razek et al. (2012)
Sugar apple (*Annona squamosa* L.)	1 and 1.5%	Fruit yield increased to 15.5 kg/plant, fruit weight to 175 g/fruit and size increased to 7 cm/fruit, increase fruit quality and extend shelf life (6.5 days)	Sindha et al. (2018)
Cashew apple (*Anacardium occidentale* L.)	0.5% repeated three times in the stages before and after vegetative flushing and during fruiting	Increase yield per tree	Dhanasekaran et al. (2018)
Kiwi fruit (*Actinidia deliciosa* A. Chev.)	0.1 and 0.2%, sprayed three times, before anthesis, after fruiting, and at the fruit development stage	Enhance yield and morphology under salinity stress, increase leaf area, and relative water content	Mahmoudi et al. (2014)
Strawberry (*Fragaria* × *ananassa*)	Commercial *Humi Brown Gold* (contains 12% humic acid) applied at concentration 0.5% applied before flowering, during bud stage, during bloom, and after flowering	Significant increase in fruit weight, enhanced total soluble sugar content, reduced bacterial infection	Zydlik and Zydlik (2023)

heavy metals, and extreme temperatures. These stresses adversely affect plant growth, reproduction, and yield and causes overproduction of reactive oxygen species (ROS), resulting in cellular damage (Kumar, 2020). To combat these oxidative stresses, plants accumulate antioxidant compounds such as ascorbate, glutathione and tocopherol. They also activate enzymatic antioxidants such as superoxide dismutases (SOD), ascorbate peroxidases (APX), catalases, and peroxiredoxins (Mittler et al., 2004). HSs enhance antioxidant systems, including both enzymatic and non-enzymatic, helping plants scavenging excess ROS and thereby reducing the potential cellular damage. This supports plant cells in maintaining proper metabolic functions during stress (Asif et al., 2023). It was shown that HAs increase the accumulation of ascorbic acid which is associated with increased expression of superoxide dismutase, catalase, and NADPH-oxidase in wheat plants exposed to abiotic stress (Ozfidan-Konakci et al., 2018).

Osmoprotectants or compatible solutes, such as glycine betaine and proline, are often known as a primary strategy to protect plants and enhance their resistance to environmental conditions such as low temperature, salinity, drought, and oxidative stress (Wani et al., 2013). The application of HSs has been shown to increase the synthesis of these compatible solutes in plants (du Jardin, 2015).

In salinity stress, HSs enhance salinity stress tolerance by affecting sodium transporters. One study by Khaleda et al. (2017) found that HA was able to revert the phenotypes of *salt overly sensitive 1* (*SOS1*) mutant and *high affinity potassium transporter 1* (*HKT1*) overexpressor plants subjected to high salinity, indicating that HA act by activating *SOS1* signaling. Furthermore, HA increased the abundance of HKT1 protein in the root stele supporting its role in regulating ion homeostasis under salt (Khaleda et al., 2017). HA derived from vericompost increased salinity stress tolerance in maize and tomato by upregulating key genes involved in salinity stress tolerance including *SOS1*, *SOS3*, *basic leucine zipper 17* (*bZIP17*), *nicotianamine synthase* (*NAS66*), *SNRK1*, and *SnRK2.2* (Souza et al., 2021). HS improved salinity tolerance in bean (*Phaseolus vulgaris)* by reducing reactive oxygen species (ROS) and electrolyte leakage and increasing proline levels under salinity stress (Aydin et al., 2012). Similar effects were observed in rice (*Oryza sativa*), HA alleviated salinity tolerance by improving ion homeostasis, increasing the activity of several antioxidant enzymes and reducing MDA levels, and maintaining membrane integrity under high salinity conditions (Abu-Ria et al., 2023). Soil and foliar applications of HS enhance salinity stress tolerance in sorghum by improving phytohormones, osmoprotectants, and antioxidant systems in treated plants compared to untreated ones (Desoky et al., 2018). Another study found that treating beans (*Phaseolus vulgaris* L.) with HAs at high salinity (120 mM NaCl), enhanced proline levels and membrane integrity and thus improved tolerance to high salinity (Aydin et al., 2012). In wheat (*Triticum durum*), HA improved the uptake of several elements N, P, K, Mg, Na, Cu, and Zn in under saline stress when applied directly to soil as solid HAs (1g/kg) or sprayed (foliar spray 0.1%) (Asik et al., 2009). Another study on durum wheat showed that foliar spray of HA improved plant yield, spike fertility, total protein content and the activity of Rubisco compared to untreated controls (Delfine et al., 2005).

These studies collectively indicate that HSs alleviate salinity tolerance by modulating the SOS signaling pathway, regulating Na^+ compartmentalization via HKT1, adjusting osmotic potential by accumulating osmolytes, activating antioxidant defense mechanism and maintaining membrane integrity. However, the specific bioactive component underlying these effects requires further investigations.

In drought stress, HSs enhance drought tolerance through multiple physiological and biochemical pathways. One of these mechanisms is through the activation of antioxidant defense system and osmotic adjustments. The activity of key antioxidant enzymes including SOD and peroxidase (POD) was increased in rice and maize treated with HS compared with untreated plants under drought stress (Cordeiro et al., 2011; García et al., 2016). In addition, HA treated maize exhibit enhanced drought tolerance associated with increased accumulation of osmoprotectants including soluble sugar, trehalose, proline, and betaine which contribute to osmotic adjustment. Furthermore, HS treatment elevates IAA content accompanied by upregulations in the expression of auxin responsive genes including *Gretchen 3* (*GH3*) and *Aux/IAA* indicating the role of auxin regulation in HS-mediated drought tolerance (Chen et al., 2022). Another study showed that treating millet with HA (100 and 200 mg/L) mitigates drought stress by increasing proline, total soluble protein, and antioxidant enzymes including SOD and POD (Shen et al., 2020). Similar results were reported in rapeseed plants where HA treatment significantly reduced MDA accumulation and maintained membrane integrity under drought stress (Lotfi et al., 2015).

Another mechanism is through enhancing photosynthesis. One of the key metabolic pathways in plants is photosynthesis, which is adversely affected by biotic and abiotic stresses (Ansari et al., 2019). HSs have been shown to be excellent in maintaining photosynthesis during stress. HS improved the total chlorophyl content and photosynthesis efficiency and reduced transpiration under drought stress (Lotfi et al., 2018). Treating rapeseed plants with HS during drought stress enhanced photosystem II (PSII) activity, stomatal conductance, and gas exchange (Lotfi et al., 2018). The increase in the concentration of photosynthetic pigment is one of the indicators of photosynthesis fitness, however, it is not always correlated with it. Some studies found that HSs enhanced net photosynthesis without changing the content of photosynthetic pigment and vice versa (Delfine et al., 2005; Ertani et al., 2009; Zanin et al., 2018). For instance, peat HA application resulted in increasing in photosynthesis rate without changing the counteraction of chlorophyl in maize treated seedlings. The number of chloroplasts per cell was significantly increased by HA treatment as seen by confocal microscopy compared to untreated plants (Zanin et al., 2018). Recent study on soyabean (*Glycine max*) reported similar results, where HS increased chlorophyll content without any significant change in photosynthesis rate under drought stress (Matuszak-Slamani et al., 2022). Of note, the measurements of chlorophyll content in most of these studies were conducted using the soil plant analysis development (SPAD) which is less accurate than conventional biochemical methods.

Carbon fixation is an important process for plant, and it is affected by several abiotic stresses. Under drought stress, HA treatment increases the activity of Rubisco and thus enhances carbon fixation. Phosphoribulokinase (PRK) is another key enzyme in carbon fixation pathway, and it has been shown that its activity was enhanced by HA under drought conditions (Chen et al., 2022). These studies suggest that HS enhances drought tolerance by improving photosynthesis and activation enzymes involved in carbon fixation beside activating antioxidant machinery and increasing stomatal conductance.

HSs have been also found to mediate high temperature stress tolerance (Abdellatif et al., 2017; Cha et al., 2020; Qin and Leskovar, 2020). Recent study found heat stress tolerance and fruit yield of tomato plants under heat stress was improved with HA treatment. The enhanced tolerance was associated with high accumulation of essential amino acids and antioxidant enzymes and reduced MDA levels (Cha et al., 2020). Similar study demonstrated that treating pepper, tomato, lettuce, and watermelon with leonardite derived HA improved both heat and drought stress tolerance compared with control plants (Qin and Leskovar, 2020). The improved heat stress tolerance in *Arabidopsis* was associated with high expression levels of several heat shock proteins including HSP101, HSP23.6, HSP17.6, and HSP101 (Cha et al., 2020).

Collectively, these findings indicate that HSs enhances heat stress tolerance by regulating gene expression of HSP and increasing activity of antioxidant enzymes. However, the exact functional group or bioactive component responsible in modulating these mechanisms remain unclear.

Although the exact molecular function of HAs is still not completely understood, there have been some research attempts to understand the molecular function. Cha et al. (2020) found that wild-type *Arabidopsis* grown with HA exhibited higher heat tolerance compared to plants grown without HA and it enhanced the transcriptional expression of several heat shock proteins (HSPs) promoting heat stress tolerance in *Arabidopsis*.

Heavy metal toxicity causes irreversible damage to plants. Heavy metals disrupt many physiological, biochemical, and metabolic pathways (Khanna et al., 2019; Kohli et al., 2019). Lead (Pb) and cadmium (Cd) are two examples of very damaging heavy metals. Plant exposure to Pb stimulates more ROS production leading to oxidative stress and lipid peroxidation. Pb damages nucleic acid and affects cell division (Singh et al., 2010). Even at low concentrations, Pb can alter membrane permeability, impair enzyme function, and interfere with mitosis (Zulfiqar et al., 2019). Cadmium (Cd) severely damages chloroplast structure and function and inhibits photosynthesis (Muhammad et al., 2021).

HSs represent an effective and sustainable strategy for mitigating heavy metal toxicity (Singh et al. 2022). They confer heavy metal tolerance by reducing their bioavailability; either by changing the physicochemical properties of the soil or by direct interaction with heavy metals to form insoluble complexes, thereby limiting their uptake by plant roots (Khan et al. 2017; Chen et al. 2019; Shen et al. 2020; Li et al. 2021). Recent studies showed that HS can form humic–heavy metal complex. For example, HS reduce Cd accumulation in wheat plants grown in Cd-contaminated soil compared with untreated plants due to formation of Cd–humic complex in soil (Rashid et al., 2020).

HA treatment reduced Cd accumulation in rice grains, it was reduced by 25 - 35% (Li et al., 2023). In this study, the application of mineral based potassium humate reduced Cd accumulation in brown rice while enhancing photosynthesis performance and antioxidant enzymes activity. In another study involving rice and wheat, HA application reduced Cd availability in Cd contaminated soil, and decreased Cd accumulation in the shoot, roots, and grains compared to untreated plants (Zia-ur-Rehman et al., 2023).

Zhou et al. (2018) demonstrated that HA application in rape (*Brassica campestris*) enhanced heavy metal tolerance by increasing grape yield while significantly decreasing the bioavailability of Cd and Pb. Likewise, HA increased Cd tolerance in strawberries as indicated by enhancing shoot biomass and yield associated with higher photosynthesis and improved relative water content and enhanced membrane stability (Dogan et al., 2022).

Wang et al. (2019) found that applying FA solutions mitigates Cd stress in lettuce by reducing Cd accumulation in roots and shoots while enhancing shoot and root growth, lowering ROS levels and increasing antioxidant enzyme activity (ascorbic peroxidase and catalase).

Conclusions

In conclusion, HSs have great potential as plant biostimulants for solving challenges facing agriculture. These compounds contribute significantly and sustainably in enhancing crop productivity and quality by improving nutrient uptake and use, enhancing plant tolerance to various stresses and regulating hormone signaling. Various studies across different crops have shown benefits of HS application, including increased yield and enhanced crop quality with minimum impact on the environment. To fully recognize the potential of HSs in agriculture and environment, standardized guidelines for formulation and application should be considered. These would ensure consistent efficiency and sustainability and contribute to a more resilient food production system. Although there have been significant advances in understanding their roles in plant physiology and ecological processes, major knowledge gaps persist, particularly in the molecular mechanisms by which HSs modulate plant responses. Furthermore, the variability of HS bioactivity under different environmental conditions remains poorly characterized. Bridging these gaps is essential in harnessing the full potential of HSs in agriculture.

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