

Insight on the impacts of brassinosteroid- and seaweed-based biostimulants on glyphosate-resistant commercial crop growth, yield and soil microorganisms: A scoping review

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Abstract. Globally, compliance with the chemical regulations on the use of herbicides, particularly glyphosate, remains a challenge. Glyphosate controls various broadleaf, annual, and perennial grasses in the agricultural and non-agricultural sectors. Although glyphosate targets weeds, it can also influence non-target soil microorganisms and high-value plants through early-season broadcast, pre-plant application, or indirectly via foliar application by droplets falling to the ground. In plants, glyphosate impacts various physiological and physiochemical processes, inhibits auxin transport, and enhances auxin oxidation in plants. Hence, biostimulants serve as a gateway in alleviating such problems. Biostimulants are agricultural products manufactured from natural materials that contain active compounds, which stimulate growth when applied in minute volumes under different growth conditions. In the past, a major focus was directed toward biostimulants' effects on commercial crops under abiotic stress conditions such as drought, heat, and salinity. However, less emphasis has been placed on the stress caused by herbicide applications. Therefore, this review focuses on future studies to explore brassinosteroid and seaweed-based biostimulants' impact on glyphosate-resistant commercial crop growth and soil microorganisms. Conclusions and recommendations could be reached using the pool of research material, which consists of research articles, reviews, book chapters, theses, research short communications, and industrial short communications from at least the last ten years.

Key words: Botanical-extracts, herbicides, phytohormones, plant-based biostimulants, soil organisms, weeds.

INTRODUCTION

Globally, commercial crops are important crops despite their production fluctuations caused by environmental and anthropogenic factors, and this could be noted a lot in South Africa as highlighted by Heyl (2017). However, weeds continue to be a massive obstruction in agriculture. A majority of commercial crops are highly vulnerable

to weeds in the first 6–8 weeks after crop emergence; hence, weed growth regulation is recommended during this period (Heyl, 2017). This results from weed-crop competition for essential resources such as water, light and nutrients that cause yield losses varying from 21–53% (Safdar et al., 2016).

Herbicides reduce commercial crop yield losses caused by weed competition in the agricultural sector. Of all commercially available herbicides, glyphosate remains the most widely used for controlling weeds (Dalazen et al., 2020). It is less labour intensive, cheap, simple to apply, effective and saves time compared to other herbicides, mechanical (hand weeding/hoeing) and biological control. However, the increased adoption rate of glyphosate resulted in the production of glyphosate-resistant commercial crops (Dalazen et al., 2020).

In South Africa, roundup-ready commercial grain crops like maize (*Zea mays* L.) were introduced around 2002 with an adoption rate of 30%, which escalated to roughly 50% in 2010/2011 (ACBI, 2017). According to Benbrook (2016), glyphosate is available in more than 130 countries, and the total global glyphosate active ingredient applied has increased from 67 million kg in 1995 to 826 million kg in 2014. The widespread use of glyphosate has increased dramatically in South Africa, from 12 million kg in 2005 to 20 million kg in 2012 (ACBI, 2017). Furthermore, import records from the United Nations deemed South Africa as a major importer of glyphosate between 2006 and 2012, with an increase of 177% (James, 2016).

Consequently, the increased use of glyphosate has resulted in certain weeds developing resistance against glyphosate (Dalazen et al., 2020). According to Bonny (2016), herbicides do not cause resistance, but how they are used causes weeds to develop resistance, such as rehashed use of a similar herbicide (same method of activity) on a similar weed. Nevertheless, herbicide stress intensity greatly hinders plant growth and microbial activity by negatively affecting the morphological, physiological and metabolic aspects (including secondary metabolism) (Velini et al., 2010).

Since farmers often use higher concentrations than recommended to kill weeds, this negatively affects both susceptible and tolerant commercial crops and soil microorganisms. Injuries caused by glyphosate to resistant crops are due to the by-product aminomethylphosphonic acid (AMPA) (Viirlaid et al., 2015). Additionally, AMPA negatively influences chlorophyll biosynthesis and reduces plant growth (Dalazen et al., 2020). On the other hand, glyphosate significantly reduces photosynthesis, mineral nutrition, and plant-microorganism relations (Gomes et al., 2014). Hence, this review study explored the impact of brassinosteroid (BR)- and seaweed-based biostimulants on glyphosate-resistant commercial crop growth and soil microorganisms.

MATERIALS AND METHODS

This review article was developed by examining studies on the impact of biostimulants on glyphosate-resistant commercial growth and soil microorganisms treated with glyphosate worldwide and cascading to South African studies. As a result, the authors carried out a desktop and literature study from 2014 to 2024 as described by Holcombe (2023), where a scoping review approach (Fusar-Poli et al., 2020) was adopted with an emphasis on commercial crops, biostimulants and glyphosate. As

described by Fusar-Poli et al. (2020), the databases used for this study were Google Scholar and ResearchGate, using the search words:

‘Herbicides and commercial crops or herbicides and agronomic crops or weedkiller and commercial crops or weedkiller and agronomic crops’; ‘Glyphosate and commercial crops or glyphosate and agronomic crops’; ‘Glyphosate and glyphosate-resistant crops’; ‘Herbicides and biostimulants or herbicides and plant growth regulators or herbicides and phytohormones or herbicides and seaweed-extract or herbicides and brassinosteroids’; ‘Glyphosate and biostimulants or glyphosate and plant growth regulators or glyphosate and phytohormones or glyphosate and seaweed-extract or glyphosate and brassinosteroids’.

The authors used a ten-year exclusion criterion, where the research material constituted research articles, reviews, book chapters, theses, short research communications, and short industrial communications. All materials included in this review were not selected on a strict quality assessment for inclusion or exclusion other than the ten-year exclusion criterion. Therefore, there should be no presumption that the evidence examined was comprehensive (Fusar-Poli et al., 2020). All material reviewed was analyzed and discussed based on the primary objective, with the conclusion leading to the recommended future studies to lay a foundation for the sustainable agricultural production systems strategy using Br-based biostimulants and seaweed-based biostimulants on glyphosate-resistant commercial crops globally.

RESULTS AND DISCUSSION

Herbicide-tolerant (HT) commercial crops, especially those tolerant to glyphosate, are grown worldwide because they are profitable and simplify weed management by reducing herbicide application but still preventing yield loss induced by weeds (Bonny, 2016; Dalazen et al., 2020). However, overusing the same herbicide has led to resistant weeds, which in turn has increased herbicide usage again (Bonny, 2016). This caused a shift from selective herbicides towards broad-spectrum glyphosate, causing changes in cultural practices, which might increase the risk of herbicide resistance in weeds.

Glyphosate [*N*-(phosphonomethyl) glycine] is a post-emergence, non-selective, organophosphorus herbicide that is mainly foliar-applied and translocated via the plant phloem (Singh et al., 2020). Glyphosate controls various broadleaf, annual and perennial grasses such as fleabane, crabgrass, morning glory, and sedges both in the agricultural and non-agricultural sectors. It controls weeds in cotton, maize, soya beans, canola, sugar beets, and alfalfa fields (Green, 2018). Some trade names include Roundup, Ultramax, Clear-up, and Clear all.

Henri Martin, a chemist from Cilag pharmaceutical company, was the first person to synthesize glyphosate in 1950, but it was not tested or patented for herbicide use (Tauhata et al., 2020). Nonetheless 1970, E. Franz, a chemist from Monsanto, synthesized, tested, and patented glyphosate for herbicide use and named it Roundup. As a result, Monsanto introduced glyphosate isopropyl ammonium and glyphosate sesquisodium, while ICI agrochemicals from Spain introduced trimethylsulfonium in 1989. In South Africa, the first formulation of glyphosate (360 g L⁻¹) of an acid equivalent of isopropylamine salt of *N*-(phosphonomethyl) glycine] was registered in 1975 for controlling weeds in sugarcane (Nguyen, 2018).

Although glyphosate targets weeds, it can also influence non-target soil microorganisms and high-value plants through early-season broadcast, pre-plant application, or indirectly via foliar application by droplets falling to the ground (Singh et al., 2020). Glyphosate inhibits the biosynthesis of aromatic amino acids in plants and soil microorganisms by inhibiting the synthesis of 5-enolpyruvylshikimate-3-phosphate in the shikimic acid pathway (Sardrood & Goltapeh, 2018).

This may result in minor to severe toxicity symptoms in soil microorganisms like increased or decreased microbial activity and disease resistance. This effect is highly favoured by soil microorganisms' involvement in nutrient cycling and availability, long-term soil sustainability, biogeochemical processes, and resistance to perturbation (Prashar et al., 2014; Malynovska et al., 2024). In plants, glyphosate impacts various physiological and physiochemical processes, such as reducing photosynthesis rate, degrading chlorophyll, inhibiting auxin transport and enhancing plant auxin oxidation (Dalazen et al., 2020; Singh et al., 2020). Hence, biostimulants serve as a gateway in alleviating such problems.

Biostimulants are agricultural products manufactured from natural materials that contain active compounds, which stimulate growth when applied in minute volumes under different growth conditions (Malik et al., 2021). These products can be foliar applied or soil drenched and sometimes administered as seed treatments. Various kinds of biostimulants are available in the global market. However, no formal classification is regulated by any government, including the European Union and the United States of America. 'Despite that, scientists, stakeholders and regulators recognize some of the major biostimulant categories into several groups namely, humic substances, seaweed extracts, botanicals, protein hydrolysates and other nitrogen-containing compounds, chitosan and other biopolymers, beneficial fungi, inorganic compounds and beneficial bacteria' (Calvo et al., 2014; Du Jardin, 2015; Halpern et al., 2015). Only seaweed and extracts containing BR as active compounds were investigated for this research.

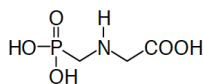
In crops, biostimulants increased plants' photosynthetic efficacy, sugar production, natural fruit set, and plant size (Zulfiqar et al., 2019). They also significantly increased plant growth under drought stress, temporary anaerobic conditions in the rhizosphere and extreme heat conditions due to the production of antioxidants by plants (Hasanuzzaman et al., 2021). However, biostimulant effects on soil microorganisms have been positive and negative (Pascual et al., 2021). For instance, when humic acid was the sole carbon source, it hindered soil microbial activity. Meanwhile, aromatic amino acids cause a partial or reversal of glyphosate effects on soil bacterial cultures (Chernikova et al., 2023).

Chemical and physical properties of glyphosate

Herbicides are categorised into various groups based mainly on chemical, physical and toxicological properties, utilization, and behaviour in plants and soils (Table 1). Thus, glyphosate is categorised under the family glycine with an HRAC and WSSA code 9. This herbicide inhibits the enzyme enolpyruvyl shikimate phosphate synthase (EPSPS) in the shikimic acid pathway and does not share chemical and physiological similarities with other herbicides. Similarly, a few other herbicides are unclassified, such as gluphosinate, bendioxide and oxadiazon.

Table 1. Properties of glyphosate

Properties	
Physical State	White solid
Density	1.74 g mL ⁻¹
Structural formula	C ₃ H ₈ NO ₅ P
Molecular formula	Glyphosate acid
Molecular weight	169.07 g mole ⁻¹
Melting point	200 °C
Solubility	Water 15.700 mg L ⁻¹ (pH 7, 25°C); 11.600 mg L ⁻¹ (pH 2.5, 25 °C)
Corrosiveness	Corrosive to iron and galvanized steel.
Sorption	Promptly and tightly absorbed into the soil
Persistence	Moderately persistent with 47 days field half-life



Glyphosate absorption and translocation

Since glyphosate is a post-emergence herbicide, it is mainly absorbed through the plant surface, passing through the leaf cuticle (Li et al., 2018). According to Singh et al. (2020), leaf uptake of glyphosate varies from species to species due to differences in plant susceptibility. Most importantly, glyphosate uptake occurs through diffusion, which is the movement of solutes from high- concentration zones to low- concentration regions. As a result, glyphosate moves from plant leaves via the phloem through metabolic tissues that act as sucrose sinks (Konlan et al., 2019). This is a symplastic translocation through the vascular endodermis with accumulation in underground tissues, immature leaves and meristem. However, weeds like morning glory and quack grass have apoplastic translocation (Benbrook, 2016). Literature has suggested little or no apoplastic translocation in various plant studies.

Glyphosate mode of action

Glyphosate inhibits 5-enolpyruvylshikimate-3-phosphate synthase that produces enolpyruvyl Shikimate-3-phosphate (EPSP) from shikimate-3-phosphate and phosphoenolpyruvate in the shikimic acid pathway, which is in plant plastids. The shikimic acid pathway is the fundamental transition in the biosynthesis of essential amino acids (Sardrood & Goltapeh, 2018). Amino acids serve as fundamental building blocks of proteins and play a role in various plant functions, such as structural, metabolic and transport processes (Corsetti et al., 2024). The initial process of aromatic acid biosynthesis begins with condensing erythrose-4-phosphate with phosphoenolpyruvyl (PEP). The former is a product of the pentose phosphate respiratory pathway, and the latter is a product of glycolysis. A 7-carbon sugar forms from the initial condensation process, which is then cyclized and reduced to produce shikimate. Finally, chorismate forms from shikimate and branches to the formation of phenylalanine, tyrosine and tryptophan (Parthasarathy et al., 2018). Furthermore, aldolase catalyzes the condensation of erythrose-4-phosphate with PEP. In addition, three amino acids (phenylalanine, tyrosine, and tryptophan) hinder aldolase. Phenylalanine and tyrosine impede the conversion of chorismate into prephenate, while tryptophan hinders the conversion of chorismate into anthranilate (Heap, 2024). These amino acids play crucial roles in other aspects of plant development. In the conversion of shikimate to 3-enolpyruvylshikimate-5-phosphate, glyphosate inhibits the EPSP enzyme. It forms an allosteric interaction by binding with EPSP outside the active site, resulting in the active site being unavailable to PEP (Parthasarathy et al., 2018). Hence, glyphosate is the EPSP enzyme inhibitor.

Plants treated with glyphosate usually die within 1–3 weeks because they cannot synthesize aromatic amino acids and their derivatives, such as protein (Duke, 2021). Hence, they die of protein starvation. In addition, tyrosine deficiencies result in a lack of antioxidants, electron carriers, and defence compounds under stress (Schenck & Maeda, 2018). In addition, a lack of structural support, water transport, and physical barriers might result in plants dying when treated with glyphosate because of phenylalanine deficiencies (Lushchak et al., 2018).

Glyphosate adsorption and degradation

Glyphosate strongly binds to soil particles making the herbicide immobile in soil profiles. Hence, because of small soil pores, glyphosate has a low leaching ability (324–900 mL g⁻¹), especially in silty clay loam and loamy sand soils. In addition, hydrous oxides such as iron and aluminium oxide adsorb glyphosate, and this adsorption is also dependent on the number of free sorption sites in the soil, soil pH levels, and transpires through binding with the phosphonic acid moiety (Torres, 2019). Furthermore, glyphosate becomes available for plant uptake at a soil pH above seven and is adsorbed to the soil at a pH below six (De Gerónimo & Aparicio, 2022). However, soil phosphorus deficiencies make the adsorption ability reversible, ultimately leading to glyphosate desorption.

Moreover, soil microorganisms (Gill et al., 2017) degrade glyphosate. The enzyme glyphosate oxidoreductase mineralizes glyphosate, forming aminomethylphosphonic acid (AMPA) and glyoxylate (Viirlaid et al., 2015; Okada et al., 2016). Furthermore, C-P lyase hydrolyses glyphosate to form sarcosine, inorganic phosphate, ammonia, and carbon dioxide (Nguyen, 2018). Glyphosate degrades quicker in sandy soils compared to clayey soils due to the stronger binding ability of clay (De Gerónimo & Aparicio, 2022). However, AMPA is hard to degrade and thus accumulates in soils, while sarcosine degrades quickly and does not accumulate (Viirlaid et al., 2015).

Furthermore, edaphic factors such as temperature, moisture, nutrients and pH levels strongly determine the glyphosate available to the soil microbial community. Of the mentioned factors, temperature and moisture mostly affect biological processes (metabolism and microbial degradation), in turn impacting bioactivity and chemical persistence (Wicke et al., 2019). Glyphosate is steady at temperatures less than 10 °C, increasing soil persistence. At temperatures greater than 10 °C and drought conditions, glyphosate is available to the soil microbial community. According to Miller & Norsworthy (2018), herbicide adsorption is more favourable at 60% soil moisture content than levels below, such as 7.5%. Enzymes produced by soil microorganisms are used to break down glyphosate, and inorganic products are used by these microorganisms for growth, accounting for the increase in soil microbial activity.

Moreover, soil microbial activity is an important bioindicator of glyphosate behaviour in the soil, as it directly correlates to the biodegradation of the herbicide (Gill et al., 2017). Meher et al. (2021) strongly suggested that herbicides serve as a food source for soil microorganisms; hence soil microbial activity increases with an increase in herbicide application. Similarly, Cherni et al. (2015) observed increased soil microbial activity when soil-drenched glyphosate. Increasing glyphosate biodegradation produces aminomethyl phosphonic acid, eventually leading to carbon dioxide, phosphate, and water production, which is essential in plant production (Dennis et al., 2018). This enhancement of soil microbial activity results in microbial community shifts favouring

fungi and actinomycetes over bacteria under low soil pH levels, while it stimulates bacteria levels at high pH levels (Gomes et al., 2014).

At least more than 270 weed species across the globe, with at least 96 countries recorded are herbicide-resistant, with more than 30 species classified as glyphosate-resistant (GR) (Ofosu et al., 2023). Glyphosate resistance was only discovered 20 years after introducing glyphosate into the market (Yanniccari et al., 2016), and ryegrass was the first GR species to be found in Australia around 1996 (Maity et al., 2021). In South Africa, it was not until the early 2000s that GR ryegrass was discovered. Furthermore, six crops have at least five GR weed species competing for natural resources: soya beans (17), maize (14), cotton (12), orchards (10), grapes (8), and wheat (8). The United States of America had the highest number of GR weeds, while South Africa has recently reported at least four crops to date: *Lolium* spp. (annual ryegrass), *Phalaris* spp. (canary grass), *Avena* spp. (wild oats), *Raphanus raphanistrum* L. (wild radish) and *Conyza bonariensis* L. (flax-leaf fleabane) (Matshidze & Ndou 2023; Heap, 2024). To understand the resistance of weeds to glyphosate, it is thus necessary to understand the chemical and physical properties and mechanisms of glyphosate.

Biostimulants

Generally, biostimulants are growth-promoting substances. However, biostimulants were first defined as materials that, in minute quota, stimulate plant growth. The word minute distinguishes biostimulants from soil amendments and nutrients, which play the same role, but in larger quantities (Du Jardin, 2015). Since then, dozens of definitions have surfaced from the research community. However, the concept of biostimulants is not altogether new, as plant growth promoters have been studied in the agricultural field as early as the 1970s regarding their role in food security (Zulfiqar et al., 2019).

On the contrary, plant growth-promoting substances are often mistaken for biofertilisers, which are applied in large quantities. Biofertiliser application, like manure, to agricultural soils is a typical practice among farmers because it enhances physical, chemical and biological soil properties while providing plants with nutrients (Tejada et al., 2014). Beyond that, biofertilisers need time to mineralize when applied to the soil (Hui et al., 2018). Thus, there is a period of little or no activity between the time of application and the plant's uptake. This mineralization time differs and solely depends on the compound composition and the edaphic physicochemical properties, for example, soil dampness and temperature (Tejada et al., 2014). On the other hand, biostimulants do not need time to mineralize as most are directly applied to the plant and absorbed immediately through the leaves.

There are various kinds of biostimulants in the global market. However, no government regulates formal classification, including the European Union and the United States of America. According to various scientists, stakeholders and regulators, the major biostimulant categories are humic substances, seaweed extracts and botanicals, protein hydrolysates and other nitrogen-containing mixtures, chitosan and different biopolymers, beneficial organisms, inorganic mixes and useful microbes (Calvo et al., 2014; Du Jardin, 2015; Halpern et al., 2015).

Table 2. Effects of sepearate BR- and seaweed (extracts and botanicals)-based applied with herbicides and some pesticides on commercial crops		
BR- and seaweed (extracts and botanicals)-based applied with herbicides and some pesticides	Yield and quality parameters improved	Citation
BRASSINAZOLE RESISTANT⁴ (OsBZR4)	The function of OsBZR4, a BR signaling component, in pesticide degradation, is disclosed, along with its possible use in boosting plant resistance to pesticides and speeding up the pesticide degradation process in rice and the environment	Su et al. (2024)
<i>Mastocarpus stellatus</i> and <i>Porphyra dioica</i> spp.	<i>Mastocarpus stellatus</i> and <i>Porphyra dioica</i> flavonoids' phytotoxins contributed to the biosynthesis of organic bioherbicide sources	Chukwuma et al. (2024a)
Organic extracts and fertilizers considered herbicides	The use of organic sources such as seaweed extract, vermiwash, humic acid, panchagavya, and jeevamruth significantly increased the productivity (crop's growth and development and yields) of greengram (<i>Vigna radiata</i> L.)	Rai & Jolly (2024)
Seaweed species (<i>Mastocarpus stellatus</i> and <i>Porphyra dioica</i>)	The existence of phytotoxins in <i>Mastocarpus stellatus</i> and <i>Porphyra dioica</i> on Italian ryegrass may contribute to the creation of new, sustainable, and environmentally friendly bioherbicide sources to supplement synthetic herbicides	Chukwuma et al. (2024b)
Glyphosate herbicide on seaweed growth	The impact of the herbicide glyphosate on the growth traits of the diatoms <i>Thalassiosira weissflogii</i> and <i>Cyclotella caspia</i> showed a significant decrease in the photosynthetic activity of algae and a fall in the quantity of diatom algae, which subsequently resulted in an increase in glyphosate concentration in water	Shoman et al. (2024)
Brassinosteroids and cadmium, and diazinon, imidacloprid, and chlorpyrifos	Through the up-regulation of CYP genes, 24-epibrassinolide reduced the harmful effects of pesticides and Cd by activating both enzymatic and non-enzymatic components that removed ROS. Thus, glutathione and pesticide residue were more easily conjugated, which sped up their passage through the membrane and into the vacuole	Mehrian et al. (2024)
Brassinosteroid and mesotrione	The study confirmed the potential of BRs to counteract the possible negative effects of the mesotrione residue on the morphology, physiology and yield of the three legumes	Mota et al. (2024); Mota (2020)
Brassinosteroids and tribenuron-methyl herbicide	BRs can alter the community structure of soil fungi and bacteria and raise the diversity index. In this study, BR altered a few soils' ecological activities connected to metabolism	Song et al. (2023)
Brassinosteroids and methyl viologen herbicide	In this study, the silico analysis of posttranslational modifications, gene coexpression, and protein-protein interactions verify that BR uses calcium-dependent signaling processes to control the mechanisms of tobacco plant response to methyl viologen, helping to create a balance of reactive oxygen species	Kolesnikov (2023)
Biosimulants and seaweed extracts	The combination of biosimulants and herbicides are an alternative agricultural strategy to lessen damages caused by herbicides, and different factors had different effects on crops, mostly being beneficial to crop productivity	Katsenios et al. (2023)

Table 2 (continued)

Biosimulants and seaweed extracts	The combination of biosimulants and herbicides are an alternative agricultural strategy to lessen damages caused by herbicides, and different factors had different effects on crops, mostly being beneficial to crop productivity	Katsenios et al. (2023)
Herbicide's mixture (Harmony® 50 SX® + Tuarog® + Zetrola®), used in combination with several biosimulant raw materials	The application of humic acids (+7%) and <i>Ascophyllum nodosum</i> (+16%) had a significant effect on yield. Nevertheless, the rise is negated by the herbicides' combined use	Franzoni et al. (2023)
Herbicide (Clodinafop-Propargyl [Topik EC 8% and EC 24%], mesosulfuron + iodosulfuron [Atlantis OD 1.2% and WG 3.6%] and Pinoxaden [Axial EC 5%], and Ino Alg NPK (containing 20% seaweed extract)	In this study, of all the herbicides used, the approved herbicide dosages in conjunction with the I no Alg NPK (NG) adjuvant had the greatest impact on lowering the dry weight of winter wild oats (<i>Avena sterilis</i> Gill et & Magne)	Ghafoori et al. (2023)
Brassinosteroid and pesticides	Because BR lessen the stress pesticides cause on plants, Bakshi et al. (2022) explicitly showed that BRs are crucial in ameliorating pesticidal stress. By promoting the enzymatic and nonenzymatic antioxidative mechanisms that scavenge the produced ROS and activate the pesticidal detoxifying genes, BRs enhance the defense capabilities of the plant	Bakshi et al. (2022)
<i>Asparagopsis armata</i> (Biopesticide) controlling invasive seaweed	In this study, the physiology of the test plants was significantly impacted by <i>Asparagopsis armata</i> . These comparable mechanisms of action to those elicited by conventional chemical pesticides underscore the promise of the <i>A. armata</i> exudate mixture as an environmentally benign biopesticide.	Duarte et al. (2021)
Seaweed extract from the brown algae <i>Durvillaea potatorum</i> and <i>Ascophyllum nodosum</i> under a production system that included herbicides application	In this study, applying seaweed extract to the soil regularly raised wine grape yield by an average of 14.7% throughout several growing years with extreme weather	Arioli et al. (2021)
Herbicide glyphosate by the KELP (<i>Saccharina japonica</i>) female gametophytes	For <i>Saccharina japonica</i> female gametophytes, when glyphosate was the only supply of P and the dosage was less than 20 mg L ⁻¹ , there was an increase in dry cell weight and photosynthesis	Tang et al. (2021)
Brassinosteroid and glyphosate	Application of 24-epibrassinolide did not change the development of the plant, but it did show a modest stimulation of the antioxidant defense and the detoxifying enzyme glutathione S-transferase. Proline and malondialdehyde levels somewhat decreased in response to the hormonal priming. The findings show that 24-epibrassinolide pretreatment partially restored shoot growth and may be able to reduce oxidative damage in plants treated with glyphosate by boosting phenolic chemicals and activating the plant's enzymatic antioxidant defense	Shopova et al. (2021)
Seaweed extract [Kelpak] and MCPA + dicamba, dicamba + trisulfuron, florasulam+2,4-D (herbicides)	In this study, yield and quality of wheat were unaffected by a combination of herbicides and the addition of seaweed extract (Kelpak) and nitrophenols (Asahi); yet the application of the herbicide and biosimulant increased the amount of gluten in grains, a quality trait of the wheat grain crop	Matysiak et al. (2018)

Additionally, due to antioxidant production, biostimulants make crops less sensitive to abiotic/biotic stress conditions; however, it should be noted that these compounds are only a small part of the entire response induced and triggered by biostimulation (Salvi et al., 2016; Hasanuzzaman et al., 2021). Nonetheless, the interest in the effects of biostimulants on herbicide stress may be due to increased plant resistance in various weed species to trusted herbicides, leading to increased herbicide usage on plants, further resulting in enhanced herbicide stress on crops. In recent studies, seaweed extracts and plant botanicals containing BR were used as biostimulants and have become common in studies associated with herbicides and pesticide toxicity; this is detailed in Table 2. For the sole purpose of this study, seaweed extracts and plant botanicals containing BR were used as biostimulants to be discussed further.

Seaweed extracts and botanicals

Various algae species produce seaweed extracts, but brown and red algae are the most used for biostimulant production (Sharma et al., 2014). Of all brown and red algae species identified, *Ascophyllum nodosum* (L.) Le Jolis and *Gracilaria tenuistipitata* (var. *liui*) are presently the most investigated species (Huda et al., 2023). This study focused on the investigation of the brown algae species. Other brown algae species of interest are *Ecklonia maxima*, *Durvillea potatorum*, *Durvillea antarctica*, *Fucus serratus*, *Himanthalia elongate*, *Laminaria digitata*, *L. hyperborea*, *Macrocystis pyrifera*, and *Sargassum* spp. (Sharma et al., 2014).

Furthermore, evidence has shown that seaweed extracts contain various components, such as amino acids, auxins, abscisic acid, cytokinins, gibberellins, macro- and micro-elements, vitamins, sterols, and polyamines. Nonetheless, seaweed extract effects are explained more by the down and up-regulation of hormone biosynthetic genes in plant tissue and less by the hormones contained in them (Stirk et al., 2020). Although seaweeds comprise numerous components, their exact mode of action varies and, at most, is still unknown (Yakhin et al., 2017). Nonetheless, Shukla et al. (2016) demonstrate in Fig. 1 how red seaweed has become a promoter of growth and elicitor of plant defence through carrageenan. In their argument on red seaweed as an elicitor for abiotic stress, authors report that carrageenan deriving from the seaweed acts as an elicitor, which subsequently enhances the growth and development of the plants; this occurs in relation to plant hormones crosstalk (Shukla et al., 2016). If red seaweed shows plant growth regulation activities associated with biostimulation, this calls for future studies to further demonstrate the modes of actions of various types of seaweeds.

Generally, seaweed extracts are either foliar-applied or soil-drenched, affecting soils and plants (Tandathu et al., 2024). They act as fertilisers for plants while enhancing growth, promoting soil bacteria, and suppressing soil pathogens (Du Jardin, 2015). These concentrates stimulate plant development while demonstrating synergistic action. Various authors have agreed that seaweed influences cellular metabolism in treated plants due to its high hormonal content and increased crop growth and yield (Battacharyya et al., 2015). Ocean growth separates are exceptionally bioactive even at low concentrations, for example, 1:1000 (Kelp: water) or more water (Boukhari et al., 2020).

Additionally, seaweed extracts influence plant growth through root development (Yakhin et al., 2017). The root growth stimulatory effect in the early growth stages of maize and the response matches that of auxin (Ertani et al., 2018). Root growth increases

when seaweed extracts are soil-drenched compared to foliar applications (Xu & Leskovar, 2015). Generally, biostimulants influence root growth by enhancing lateral root formation and increasing root volume (Elansary et al., 2016). Hence, seaweed extracts boost water and nutrient uptake efficiency, increasing plant growth and vigour (Kumar et al., 2020).

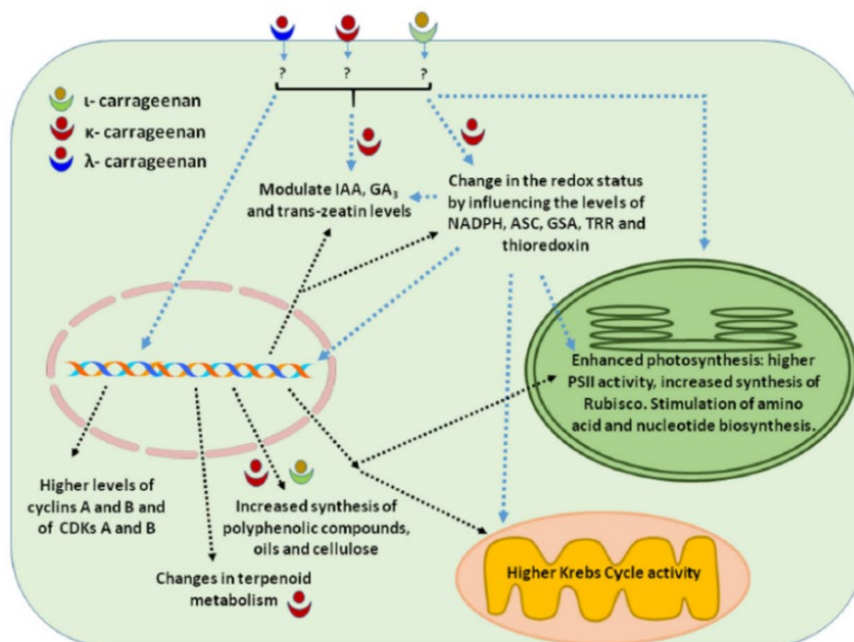


Figure 1. Cellular activities triggered by the application of carrageenans lead to improved plant growth (Shukla et al., 2016).

Moreover, seaweed extracts enhanced chlorophyll levels in tomato plants, where *Ascophyllum nodosum* was either soil-drenched or foliar applied compared to untreated plants (Xu & Leskovar, 2015). According to Castellanos-Barriga et al. (2017), this chlorophyll improvement might be due to decreased chlorophyll degradation, resulting from betaines contained in ocean growth separates. Glycine betaine hinders chlorophyll degradation during obscure storage conditions in chloroplasts, delaying photosynthetic activity in plants (Desoky et al., 2019).

Seaweeds stimulate flowering through robust plant growth initiation. Hence, these concentrates activate early crop flowering and fruit set in different crops (Yakhin et al., 2017). According to Elansary et al. (2016), cytokinins in seaweed extracts increased plant yield. In addition, cytokinins influence vegetative and reproductive plants through nutrient partitioning and nutrient mobilization, respectively (Cortleven et al., 2019).

Nevertheless, the effects of biostimulants on different crops under abiotic and biotic stress conditions (drought, salinity, heat, chilling, heavy metal toxicity nutrient deficiency, pathogen resistance and pesticide application) are studied substantially. Under various crop stressors, seaweed extracts have predominantly enhanced root growth or root-related parameters. These crops include maize and mungbean subjected to drought, lettuce and strawberry under saline conditions, and Swiss chard subjected to water hardiness (Sharma et al., 2014; Araújo et al., 2016).

Brassinosteroid (BR)

The scientific industry has focused mainly on auxins, cytokinins, ethylene, gibberellins and abscisic acid (Khetsha, 2024a; Khetsha et al., 2024b). Brassinosteroids were discovered in the early 1970s in the pollen of rape plants (Peres et al., 2019). Since then, many advances occurred concerning how they influence plants as growth hormone regulators. Moreover, BRs are categorised under the polyhydroxylated steroidal hormone family (Clouse, 2015).

Above all, BR in plants and animals mainly influences plant metabolism and developmental processes like cell and organ elongation, seed germination, plant growth, leaf development and vascular differentiation (Belkhadir & Jaillais, 2015; Peres et al., 2019). According to Waisi et al. (2019), developmental processes influenced by BRs are photo-morphogenesis, reproductive development, leaf senescence, and more. Moreover, soil-drenched and foliar applications of BRs are mainly transported via the root-shoot route compared to the shoot-root route.

In brief, BR's bioactivity is in pollen, immature seeds and fruit, with lower activity in the leaves (Zheng et al., 2016). Different authors affirmed that BR's bioactivity, such as castasterone and brassinolide, was measured in high levels in plant regenerative organs, such as natural products ($2.2\text{--}3.5\text{ ng g}^{-1}\text{ FW}$) (Sharma et al., 2014). However, low levels of bioactivity in the plant's vegetative tissues ($0.12\text{--}2\text{ ng g}^{-1}\text{ FW}$) and in the root systems ($< 0.05\text{ ng g}^{-1}\text{ FW}$) were observed (Zhu et al., 2015).

Furthermore, BR signalling requires the reciprocity of two proteins: a serine/threonine, a BR-insensitive one (BRI1) protein, and a BRI1-associated receptor kinase (BAK1). BR ties to BRI1, which prompts the separation of an inhibitory protein (BKI1) that hinders the relationship of BAK1 with BRI1 and afterwards advances dimerization with BAK1 and autophosphorylation of BRI1. The phosphorylated complex starts BR flagging. One objective of BR flagging is the protein BZR1 (BRASSINAZOLE RESISTANT 1). BZR1 is a record factor whose area is reliant on its phosphorylation status. In the phosphorylated state, BZR1 is in the cytoplasm, while dephosphorylation permits it to move into the core. The phosphorylation status of BZR1 is influenced by two contending factors: the BR flagging chain and a different protein BIN2 that mediates phosphorylation of BZR1 and hence keeps the protein in the cytoplasm. The BR signal mediates the dephosphorylation of BZR1, which both actuates the recording factor and energizes its relocation into the core. Once in the core, BZR1-P ties to target locales in the advertiser area of the BR-touchy qualities and starts recording. BR flagging may likewise hinder the phosphorylation capacity of BIN2, subsequently further guaranteeing the initiation and atomic limitation of BZR1 (Zhang et al., 2021). Also, the inactivation of BIN2 allows BRI1 EMS SUPPRESSOR 1/Brassinazole-resistant 1 (BES1/BZR1) to translocate to the nucleus, where they regulate the expression of target genes. Additionally, BR signalling pathways interact with other phytohormones (Belkhadir & Jaillais, 2015). A further illustration of the schematic model of BR signal transduction to plant growth and development is illustrated in Fig. 2(A) (Clouse et al., 2015), while BR signalling from the cell surface to the regulation of transduction through BIN2 to specific plant growth and development signalling pathways is shown in Fig. 2(B) (Belkhadir & Jaillais, 2015).

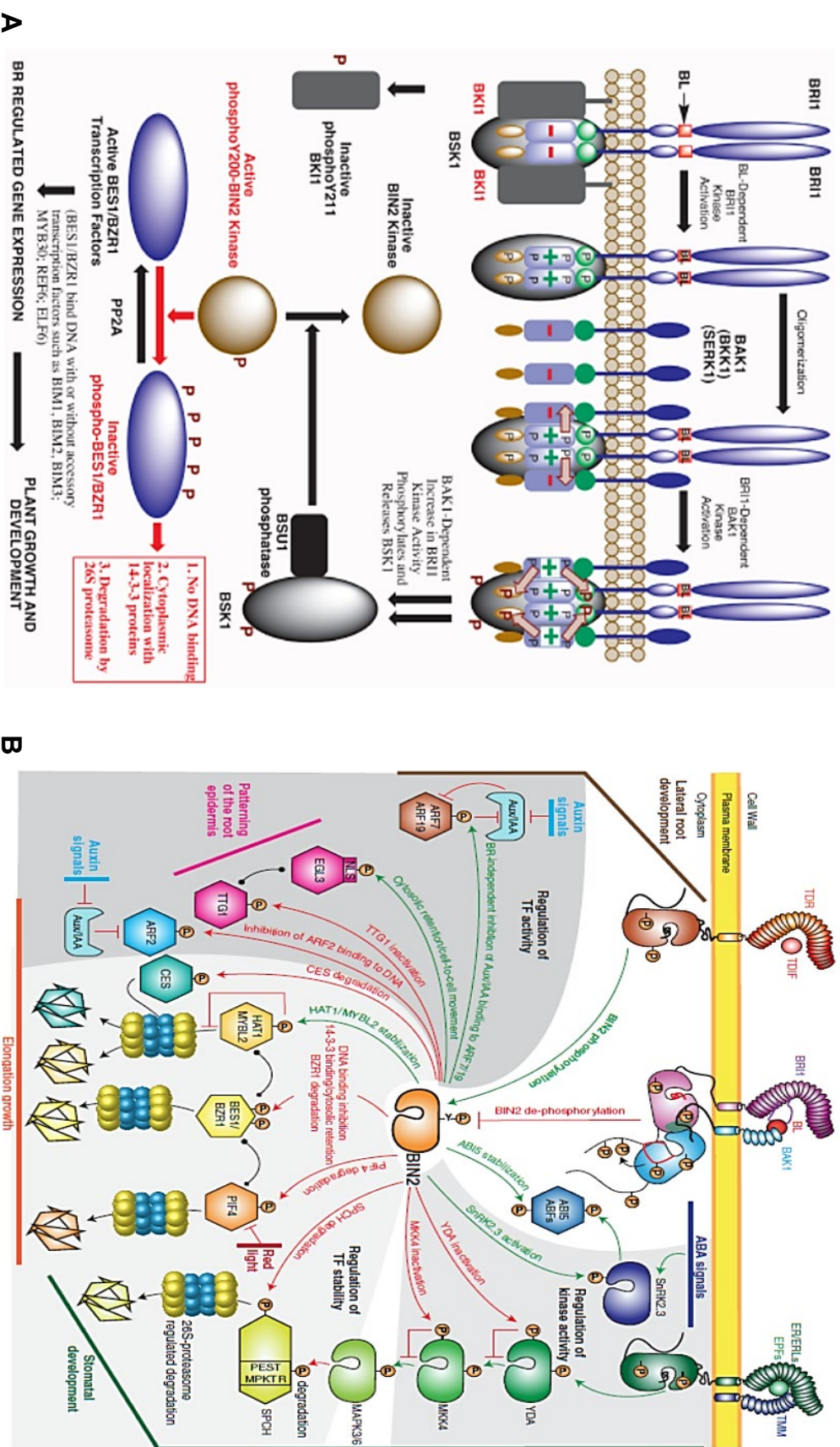


Figure 2. Model of BR signal transduction to plant growth and development (A) (Clouse et al., 2015) and BR signalling from the cell surface to the regulation of transduction through BIN2 to stomatal development, plant elongation, patterning of the root epidermis, lateral root development and abscisic acid signalling pathways (B) (Belkhaoui & Jaillais, 2015).

Nevertheless, BRs alleviate the effects of abiotic and biotic stress on various plants. Under oxidative stress, BRs have been found to enhance the net photosynthetic rate and increase the level of abscisic acid, proline and wheat germ (Belkhadir & Jaillais, 2015; Kumar et al., 2024), while BRs caused an increase in seed germination and seedling growth in maize and cucumber crops under chilling stress (Fang et al., 2019). However, very little research has been done to understand BR's synergistic or antagonistic effect on herbicide applications. Nonetheless, when BRs mixed with various herbicides, fungicides and insecticides were applied in cucumbers, they resulted in an increased carbon dioxide assimilation and net photosynthetic rate treated with insecticides (Sadura & Janeczko, 2018); however, although Rozhon et al. (2019) argued the inhibition of BRs and their biosynthesis and mode of action with other chemicals such as herbicides, the mode of action for BR with herbicides such as glyphosate remains a mystery, and future studies should further unpack this interaction. At least a few recent studies provide promising results on pesticides, i.e. Zhou et al. (2015), Yin et al. (2016) and Qiao et al. (2022).

In the literature, it has been documented GR crops are highly resistant to glyphosate's lethal effects compared to susceptible plants, with a 50-fold resistance ratio (Vieira et al., 2018). Various authors have documented that GR crops are susceptible to pathogens after applying glyphosate (Dalazen et al., 2020). Commercial crops have been reported to show chlorosis symptoms under different environmental conditions, which may be caused by the fast metabolism of glyphosate to its by-product AMPA (Hasanuzzaman et al., 2020). Even though GR crops can withstand glyphosate's mode of action, they cannot withstand AMPA, hence the negative influence on plant growth and development (Viirlaid et al., 2015).

Furthermore, studies on glyphosate susceptible plants have reduced the absorption and translocation of calcium, magnesium, manganese and iron in various crops (Moldes et al., 2017). Moldes et al. (2017) observed changes in calcium distribution and a decline in soya beans' tissue calcium content. The inhibiting effect of glyphosate can explain the negative effect on the development of the rooting system; hence, plants cannot extract nutrients available in the rhizosphere.

Combined application of herbicide and biostimulant on commercial crops

One herbicide application (even if it should give reasonable weed management) is usually inadequate for satisfactory and price-effective weed management. Reliance on one mode of action might hasten the event of resistance; hence, a mixture of two or more herbicides during a tank mixture might reduce application prices, increase the spectrum of weed management and delay the occurrence of resistance to each herbicide applied within the combination (Barbieri et al., 2022). Herbicide mixtures supply many alternative benefits over the use of a single herbicide. The type and the extent of interactions rely totally on the combined herbicides' properties (radical, absorption, translocation, mode of action, pathway metabolism). A tank mixture of herbicides may result in three actions: additive, antagonistic and synergistic effects.

The activity of the additive mixture is equivalent to the predicted control of weeds (Gatidou et al., 2015). The additive response provides advantages and, as a result, allows the substitution of another chemical to realize a similar level of weed management. The antagonistic reaction occurs when two or more herbicides are mixed, and their effect is smaller than the anticipated weed control (Merritt et al., 2020). Simultaneously,

synergism occurs when two or more herbicides are mixed and their weed management is more significant than the expected control (Gatidou et al., 2015).

Most importantly, glyphosate combined with adjuvants or surfactants facilitates easy absorption through the plant (Mueller & Steckel, 2019). An example of such an adjuvant, which farmers commonly use, is ammonium sulphate. Adjuvants and surfactants are chemicals added to a tank or spray mixture to facilitate the herbicide performance (Travlos et al., 2017). Surfactants, known as surface-dynamic operators, are a sort of adjuvant intended to help scattering/emulsifying, engrossing, spreading, staying, and gadfly entering the shower blend (Da Cruz et al., 2016). These substances can either enhance or inhibit glyphosate activity.

Ammonium sulphate (AMS) is an inorganic salt used to increase the herbicide effectiveness of salt-based formulations such as glyphosate, 2,4-D, dichlorpropl and MCPA to name a few (Mueller & Steckel, 2019). A few herbicides (Imazethapyr, pyrasulfotole, and glyphosate) require adding AMS during application according to the manufacturer's label (Mueller & Steckel, 2019). AMS has been found to increase or enhance glyphosate effectiveness on stubborn weed species at a recommended application rate of 2% (% v/v). Its mode of action is not yet understood, but a few suggestions have been made: 1) AMS changes the foliar cuticle and cell membrane's permeability, thus facilitating rapid uptake of glyphosate; 2) AMS influences the apoplastic pH, resulting in rapid and significant penetration of a weak acid herbicide into plant cells (Mirzaei et al., 2019).

Generally, the effects of biostimulants on herbicides have been both positive and negative. According to Soltani et al. (2015), plant injury, weed control and yield were statistically non-significant, when a combination of bromoxynil/biostimulant and glyphosate/biostimulant was applied to wheat, oats and maize compared to the application without the biostimulant. In a study by Chaudhary (2016), it was observed that herbicides (Pallas, Atlantis, Affinity, and Sencor) applied alone enhanced plant height, 1,000 grain weight, grain yield and weed control in wheat compared to a control, but, when a biostimulant was applied with the herbicides, plant growth was significantly enhanced compared to herbicide treatments alone. In potatoes, the total sugars were highly significant in plants treated with linuron + chlomazon + Kelp at 2 L ha⁻¹ compared to the control, and plants treated with herbicides alone (Zarzecka & Gugala, 2018). It seems that biostimulants reversed the adverse effects of herbicides; hence, they have an antagonistic effect on each other when applied together. In greater detail, thorough discussions are made in Table 2.

Soil organisms affected by glyphosate

Soil organisms are small entities living in the soil, forming a diverse and complex soil ecosystem (Coleman et al., 2010). These organisms are categorised due to their different sizes, such as microfauna and microflora (< 0.2 mm), mesofauna (between 0.2–2 mm) and macrofauna (> 2 mm). Soil microfauna, especially bacteria, fungi and protozoa, are involved in the decomposition and transformation of soil organic matter (Khatoon et al., 2017). Macrofauna such as earthworms, nematodes and mites help with the initial breakdown and mixing of residues into the soil. In general, soil microorganisms enhance the development of soil profiles. Additionally, soil microorganisms play a vital role in the soil as they regulate pathogens, enable ecosystems to function and influence their physical and biochemical processes (Newman et al., 2016).

Additionally, soil organisms have an immense impact on soil quality, by influencing crop production and other soil functions. Soil quality is the ability of a soil to function in a particular way with regard to water flow and retention, solute transport and retention, physical stability and support, retention and cycling of nutrients, buffering and filtering of potentially toxic materials, and maintenance of biodiversity and habitat (Schloter et al., 2018). The soil ecosystem is divided into chemical, physical and biological components and their respective interactions (Bastida et al., 2015). Over the years, the focus has been mainly on the chemical (pH, nutrients, carbon) and physical (water, temperature, porosity) components of the soil ecosystem, while the biological component is often difficult to quantify (Bastida et al., 2015). Interest in soil biology by researchers only arose after they began to understand the importance thereof in nutrient mineralization and the sensitivity of microorganisms to soil disturbance and perturbation (Bender et al., 2016).

One of the primary roles of soil microorganisms is nutrient cycling, whereby soil microbes break down and transform organic material into easily usable and accessible plant nutrients. Hence, soil microorganisms are known as the 'drivers' of the planet's biogeochemical cycles (Chomel et al., 2016). Biological processes include nutrient and carbon cycling and physical processes, including water movement and temperature gradients (Utobo & Tewari, 2015). The presence of organisms in soils links to sustainability and the soils' resistance to perturbations (Prashar et al., 2014).

The second leading role of soil microorganisms is carbon cycling, dominated by photosynthesis and respiration (De Graaff et al., 2015). Carbon-fixing organisms are responsible for the transfer of atmospheric carbon dioxide into the soil. These organisms comprise autotrophs, photo- and chemo-autotrophic microbes that synthesize atmospheric carbon dioxide into organic material (Prashar et al., 2014). Photosynthesizing plants release carbon dioxide back into the atmosphere, as do animals that consume plants. Plants and animal death, root exudates and animal excretion combine in the soil to form soil organic matter and feed the diverse soil microbial biomass. When the soil microbial biomass decomposes, carbon dioxide returns to the atmosphere.

Moreover, soil microorganisms affect plants through various mechanisms, including disease suppression, strengthening plant stress tolerance, and phytohormone production (Egamberdieva et al., 2017). Unfortunately, using herbicides in agriculture reduces some vital soil microorganism functions. It leads to risks to the ecosystem through a) modifying soil microorganism biosynthetic mechanism, b) influencing protein synthesis, c) impacting negatively on the cellular membrane, and d) influencing plant growth regulators (Niemeyer et al., 2018).

Glyphosate has been found to affect soil microorganisms directly and indirectly by increasing or decreasing soil microbial activity and disease resistance. Since glyphosate moves via the phloem system, glyphosate accumulates in roots and nodules where it is exuded into the rhizosphere (De Graaff et al., 2015). Root exudates and decaying tissues in the rhizosphere of GR soya beans and glyphosate susceptible maize roots released 15% of the applied glyphosate concentration. This release is a nutrient source to the soil microbial system, stimulating bacterial and fungal populations (Utobo & Tewari, 2015). Hence, an increase in nutrient availability will enhance plant growth due to the mineralization facilitated by the rhizosphere microorganisms.

Occasionally, glyphosate decreases specific microorganism populations by inhibiting certain metabolic pathways, such as the shikimic acid pathway (Chomel et al., 2016). Glyphosate blocks the synthesis of aromatic amino acids in some bacteria and fungi (Gill et al., 2017; Konlan et al., 2019). This inhibition of aromatic amino acids and phytoalexin production results in weak plants, which become susceptible to invading microbial pathogens (Kepler et al., 2020). This can result from the microbe's lack of nutrient cycling due to the blocked shikimic acid pathway.

Additionally, glyphosate's negative influence on soil microorganisms may indirectly change the rhizosphere due to atypical root exudates secreted by plants that may change root growth development (de Brito et al., 2017). As a result, soil microorganisms might sequester the available nutrients, reducing plant growth and yield, and increasing susceptibility to pathogen infection (Bender et al., 2016). According to Huber (2007), glyphosate may reduce the availability, uptake and translocation of manganese in GR crops, leading to a change in the soil/rhizosphere microbiology (Mertens et al., 2018).

According to Wicke et al. (2019), adding amino acids to bacterial cultures showed at least 50% reversal of glyphosate effects. Biostimulants contain many amino acids that can benefit soil microbial activity and increase crop growth and production (Yakhin et al., 2017). Soil microbial activity is stimulated through substrate supply, nutrient addition and augmented nutrient uptake across their cell walls (Drobek et al., 2019). Du Jardin et al. (2015) affirmed that increasing biostimulant concentrations enhanced aerobic bacterial growth. This soil microbial activity increase can be beneficial or detrimental to soil ecology, quality, and plant growth (Halpern et al., 2015). When humic acid is the sole carbon source, it hinders soil microbial activity. Biostimulants were also noted to induce metabolic changes that result in substrate proliferation, which, previously, soil microorganisms could not utilize (Du Jardin, 2015). When biostimulants are applied to plants in excess, they inhibit plant growth by reducing the availability of chelated nutrients (Bhattacharyya et al., 2015).

CONCLUSIONS

The introduction of glyphosate-resistant crops has since revolutionised weed management resulting in non-selective post-emergence herbicides that can be applied more than once in a growing season. Either any substrate applied to plants, soil drenched or foliar administered, will influence soil microbial activity. A dispute has continued over the past few years about whether herbicides used on herbicide-resistant crops harm them. Findings in this review brought the authors to the conclusion that glyphosate and biostimulant interactions increase physiological activities through the carbon content in glyphosate and the amino acids found in biostimulants. However, inhibitions caused by glyphosate are linked to phytotoxic effects caused by glyphosate by-product aminomethylphosphonic acid. To corroborate and assert this hypothesis, future studies should focus on the following to corroborate the findings of this review:

- 1) Examine the influence of herbicides and biostimulants alone and in combination on glyphosate-resistant crops' morphological, physiological and metabolic aspects.
- 2) Determine the glyphosate: biostimulant interaction (additive, antagonistic or synergistic) on a glyphosate resistant crop-biotype.
- 3) Determine the effect of herbicides and biostimulants alone and in combination on the activity of soil microorganisms.

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