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REVIEW

Use of elicitors from macroalgae and microalgae in the management of pests and diseases in agriculture

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Abstract Feeding a growing population is a big challenge for agriculture, being necessary for new and ecological alternatives to reduce chemical fertilizers and pesticides. Scientists have found that micro- and macroalgae are essential reservoirs of chemical compounds with a high potential role as biopesticides. Some of these molecules can act as elicitors, activating systemic and local defensive responses even without biotic stress. Among elicitors from macroalgae, there are ulvans, laminarin, alginate, carrageenan, glucuronan, fucans and tannins, which can activate plant defenses against viruses, bacteria, fungi, oomycetes, nematodes, and insects. The induction of defense mechanisms on crops by microalgae is related to their application as biomass, polysaccharides, exopolysaccharide or other elicitors, such as lactic acid or glucosamine. Unlike macroalgae, the biopesticide effect by microalgae has only been described against bacteria, fungi, and oomycetes, being necessary more studies to elucidate and discover their role as elicitors. In general, both macro- and microalgae are sources of compounds with great potential as biopesticides following the current needs for the development of sustainable agriculture.

Highlights

- Macro and microalgae are new sources of elicitors with agricultural potential.
- These algae elicitors activate plant defenses by different mechanisms.
- Macroalgae elicitors reduce crop losses caused by pathogens and pests.
- Microalgae elicitors reduce crop losses caused by pathogens.
- Algae elicitors can be used in a sustainable agriculture development.

Keywords Biopesticides · Plant defenses · Systemic resistance · Ulvan · Carrageenan

Introduction

The world population continues to overgrow. In 2020 we reached 7.8 billion people, projected to reach 10 billion in 2050 and 11 billion in 2100 (Gu et al.,

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2021). Therefore, world food security is one of the biggest problems to be addressed, which requires an increase in sustainable agricultural production (Boyd et al., 2013). The five main crops worldwide that have the greatest importance in food security are wheat, rice, maize, potato and soybean. There are different biotic agents associated with agricultural losses in these crops, specifically, 137 pathogens and pests have been identified. These biotic stresses cause high global productivity losses: wheat (21.5%), rice (30.0%), maize (22.5%), potato (17.2%) and soybean (21.4%) (Savary et al., 2019). Furthermore, globally, biotic stress causes a loss of between 20 and 40% of global agricultural productivity, of which between 10 and 15% are direct losses caused by pathogens (Mohammad-Razdari et al., 2022). Therefore, plant diseases are widely considered to be one of the most formidable obstacles to achieving global food security in the face of the rising human population in the twenty-first century (Velásquez et al., 2018).

At present, the use of chemical pesticides in agriculture is essential to be able to maintain food production. For example, without the use of chemical pesticides, losses due to pests and diseases in fruit trees would exceed 80% of world production (Tudi et al., 2021). Economically, the use of agrochemical pesticides worldwide represents an expense of > 40 billion USD, with the application of > 3 billion kg (Sharma et al., 2020). However, this strategy causes serious environmental and health problems, accumulating in ecosystems and causing serious diseases, such as cancer to humans (Sharma et al., 2020; Tudi et al., 2021). Therefore, it is necessary to look for new alternatives that respect the environment and health, such as biopesticides or biological control agents (BCAs), including those organisms, chemical compounds or genes derived from them, which are capable of significantly reducing the detrimental effect caused by biotic stresses in crops (Regnault-Roger, 2020). Within these, microorganisms are the main source of BCAs, followed by macro-organisms and natural products. In 2023, the biopesticide market will account for 9.86% of the global agricultural pesticide market, with a constant annual increase, being 6.4% (3.7 billion USD) in 2018 (Regnault-Roger, 2020).

On the other hand, algae constituted a vast source of resources with agricultural applications as in many other areas of interest. Algae are aquatic uni- or multicellular organisms with photosynthetic capacity (Pereira, 2021), which differ from seagrass and macrophytes because they do not have a vascular system (Poveda, 2022), and from cyanobacteria, because they are eukaryotic organisms (Poveda, 2021). In turn, algae are divided into microalgae, not visible to the naked eye, and macroalgae, perfectly visible. Microalgae constitute the phytoplankton, restricted to the euphotic zone of surface waters. Macroalgae or seaweeds are macroscopic marine organisms that can reach 65 m in length (Pereira, 2021).

In recent years, biotechnological research in micro- and macroalgae has accumulated many publications and results of transfer to industry (Garrido-Cardenas et al., 2018). In this sense, national and international laws must be continually renewed to allow all uses and products derived from these organisms to enter the market (Lähteenmäki-Uutela et al., 2021).

The industrial cultivation of microalgae is similar to other microorganisms, although they require specific aspects, such as water, nutrients, oxygen and light. Microalgae are cultivated in open ponds or lakes and closed photo-bioreactors, providing highly controlled environments (Rizwan et al., 2018). Today, microalgae and their products are used in many industries and for very different uses (Rizwan et al., 2018). Highlights, the microalgae are used in different industries as in wastewater as biotreatments (Chai et al., 2021), the production of biogas (Zabed et al., 2020), bioethanol (Simas-Rodrigues et al., 2015) and biodiesel (Chen et al., 2018), or in obtaining high value-added products, such as triacylglycerides, polyunsaturated fatty acids and carotenoids (Liang et al., 2019) for food (Torres-Tiji et al., 2020), cosmeceutical and pharmaceutical use (Mehariya et al., 2021).

In the case of macroalgae, obtaining quantities of industrial biomass is easier than for microalgae. They are mainly obtained from the direct collection in the marine environment, the collection of dead algae on the coast, and their cultivation, mainly in the sea using anchored ropes (Sudhakar et al., 2018). Like microalgae, macroalgae are present in more and more different industries (Leandro et al., 2020). Highlights, their use to obtain biodiesel (Abomohra et al., 2018) and bioethanol (Ramachandra, & Hebbale, 2020), as biomass for livestock feed (Øverland et al., 2019), aquaculture feed (Wan et al., 2019), human food (Afonso et al., 2019), as a source of antimicrobial (Silva et al., 2020) and other bioactive compounds for food (Biris-Dorhoi et al., 2020), cosmetics (Pimentel et al., 2018) or medicine (Biris-Dorhoi et al., 2020).

Macroalgae and microalgae in agriculture

The use of algae as an agricultural resource is established in numerous agricultural systems on the planet, having been widely reviewed by numerous authors, and their use as biofertilizers stands out (Baweja et al., 2019).

In the case of macroalgae, the main way in which they are applied in the field, and found in the market, is through aqueous extracts obtained from biomass, as biostimulants. In the first place, the macroalgal tissues are subjected to cryo-processing or cell rupture with high-pressure treatment to release all the cellular bioactive components. Then these components are separated from the rest of the cellular structures using aqueous (only water-soluble fractions), acidic (with sulfuric acid, extracting phenolic compounds) and/or alkaline (with potassium carbonate solution, extracting small units of polysaccharides) extraction (Sharma et al., 2014). However, macroalgal biomass can be used directly as a biofertilizer (Nabti et al., 2017), and even biomass resulting from other processes, such as obtaining biogas (Akila et al., 2019).

Both in the form of extracts and as solid biomass, macroalgae contribute to crops with different nutrients applied (mainly, tracing, iron, magnesium, potassium and zinc), polysaccharides, amino acids and phytohormones (Nabti et al., 2017). This has numerous benefits for the agricultural system, such as foliar and soil application, promoting plant growth, increasing tolerance to abiotic stresses, acting directly as biopesticides or/and by activating plant defenses or improving plant-bacteria symbiotic relationships (Khan et al., 2009). The promotion of plant growth by macroalgal extracts has been reported in different crops and systems, such as spinach (Fan et al., 2013) and *Comanthera mucugensis* in vitro (Carmo et al., 2020), pepper in greenhouse (Melo, Abreu, et al., 2020), or *Solanaceae* crops in greenhouse and field (Pohl et al., 2019). Under salinity, the extracts of different macroalgae increased the tolerance of rapeseed and wheat plants to abiotic stress due to their content of indole acetic acid, indole butyric acid, gibberellic acid, cytokinins, total carbohydrates and phenolic compounds (Hashem et al., 2019; Zou et al., 2019). Lastly, macroalgae can produce and accumulate a wide spectrum of chemically active metabolites with antimicrobial capacity in their tissues, such as alkaloids, polyketides, cyclic peptides, diterpenoids, phlorotannins, polysaccharides, sterols, quinones, lipids, and glycerols. Consequently, the direct application of extracts in crops has been supposed to significantly reduce harmful organisms through their antibacterial, antifungal, antiviral, nematicidal and insecticidal activity (Hamed et al., 2018; Machado et al., 2019).

Concerning microalgae, a disagreement is about their agricultural use from both points of view, scientific and business. However, some authors include cyanobacteria within microalgae (Gonçalves, 2021), while others do not (Alvarez et al., 2021). In this work, the concept of microalgae has been described and, therefore, cyanobacteria, which are agricultural resources widely reviewed by other authors (Chittora et al., 2020; Poveda, 2021) will not be included. In agriculture, microalgae are used directly as solid biomass or as extracts, highlighting the latter way, as macroalgae (Gonçalves, 2021). Obtaining extracts begins with cell wall elimination, using mechanical/physical (microwaving, sonication, ultra-freezing, etc.), chemical (sodium hydroxide, sulfuric acid, etc.) or enzymatic methods (cellulases, proteases, etc.) (Chiaiese et al., 2018). Subsequently, different bioactive compounds (polysaccharides, lipids, amino acids, pigments, phytohormones, antioxidants or vitamins) are obtained using organic solvents (Behera et al., 2021; Chiaiese et al., 2018).

Microalgae can be applied both in soil on the leaves, reporting important benefits for crops, highlighting the promotion of plant growth and increased tolerance to abiotic stresses, but also having direct action as biopesticides and activating plant defenses (Behera et al., 2021; Gonçalves, 2021). The promotion of plant growth has been reported in crops, such as wheat and maize, through root application (Uysal et al., 2015), or petunia, through the foliar application (Plaza et al., 2018). In the case of biotic stresses, microalgae can produce a wide variety of bioactive compounds with antibacterial, antifungal, nematicidal, insecticidal and herbicidal activity, such as phenolic compounds, polyphenols, tocopherols, proteins, oils, carbohydrates, saponins, nitrogen-rich peptides, allelochemicals or sesquiterpenes (Costa et al., 2019). Finally, it is important to note that the microalgae market in agriculture is growing exponentially. A sign of this can be found in the number of registered patents. Between 1982 and 2014, only 10 patents were registered worldwide, however, between 2015 and 2019, a total of 132 current patents were accumulated (Murata et al., 2021).

Elicitors and plant defensive responses in agriculture

Plants are constantly exposed to biotic stresses, which cause structural and metabolic damage, affecting the physiology of the entire plant and reducing its agronomic field. Plants have a sophisticated evolutionary defense strategy to protect themselves from biotic stress. These mechanisms have aroused scientific interest in the search for new compounds for agricultural sustainability (Gimenez et al., 2018). When a plant is attacked by a pest or pathogen, it must recognize chemical components of biotic stress (herbivore-associated molecular patterns [HAMPs] or pathogen-associated molecular patterns [PAMPs]) or the damage they cause to plant (damage-associated molecular patterns [DAMPs]) to activate its defenses in a specific and targeted way (Gimenez et al., 2018; Poveda, 2020). All these chemical structures recognized by plant receptors are called elicitors and lead to plant activation of called pattern-triggered immunity (PTI) (Bigeard et al., 2015). In addition to local plant defense responses against biotic stresses, PTI leads to the activation of a systemic plant defense response in which the hormones salicylic acid (SA), jasmonic acid (JA) and ethylene (ET) are mainly involved. In general, against biotrophic pathogens the so-called systemic acquired resistance (SAR) controlled by SA is activated, while against necrotrophic pathogens and pests the so-called induced systemic resistance (ISR) is activated through JA/ET (Gimenez et al., 2018; Poveda, 2020).

Therefore, elicitors are signal-inducing compounds recognized by the plant that induce and/or prime defensive responses (Wiesel et al., 2014). Elicitors used in agriculture usually have a natural origin, but there are several widely used synthetic products (Bektas & Eulgem, 2015; Wiesel et al., 2014). Among these agrochemicals, the use of SA and JA (and their derivatives and analogs), benzothiadiazole (BTH) and β-amino butyric acid (BABA) stand out, being able to activate the defensive responses of crops against broad-spectrum biotic stresses (Bektas & Eulgem, 2015; Burketova et al., 2015; Poveda, 2020).

Knowing the plant defensive responses derived from PTI, elicitors can be used in a targeted way to pre-activate plant defenses in the absence of pests/pathogens, causing a faster and more effective response when biotic stresses are present, a physiological status called priming (Wiesel et al., 2014). In this sense, there are very diverse bio-based elicitors used in agriculture as priming activators and/or resistance inducers (when biotic stress has attacked) (Boubakri, 2020; Burketova et al., 2015; Wiesel et al., 2014). The main group of elicitors is found in the structural and biochemical components of pathogens. Among bacteria elictiors are found harpins (translocators related to virulence), flagellin (component of flagella), exopolysaccharides (involved in the formation of biofilms), lipopolysaccharides (major cell membrane components) and rhamnolipids (essential for surface motility and biofilm development). In fungi and pests, highlights chitin, the main polysaccharide of the fungal cell walls and arthropod exoskeleton, together with its deacetylated derivative, chitosan. Furthermore, other components of the fungal cell wall are recognized as elicitors of plant defensive responses, including β-1,3-D-glucans, β-1,6-D-glucans and α-1,3-D-glucans. Finally, ergosterol, a component of the plasma membrane of fungi, is another compound (Boubakri, 2020; Burketova et al., 2015; Wiesel et al., 2014). Plant components are also a good source of agricultural elicitors. All cell wall components that can be released by the action of pathogenic enzymes are elicitors within the DAMPs, including cellulose fragments, hemicellulose and other glucans (such as oligogalacturonides), peptides, lignin and lipids. In addition, defense hormones (SA and JA) and their different derivatives are elicitors that are very widespread in agriculture (Wiesel et al., 2014; Boubakri, 2020; Poveda, 2020).

In recent years, the use of elicitors in agriculture is being combined with nanotechnology, improving plant responses directed towards defense and/or the production of secondary metabolites of industrial interest (Rivero-Montejo et al., 2021). In this sense, the use of elicitors in cell cultures and plant tissues to obtain secondary metabolites of interest has been widely developed during the last decades at an industrial level, being an important economic and resource sector for the manufacture of biopesticides, agrochemicals, flavoring agents, essential oils, food additives and, most importantly, for medicine and cosmetics (Alvarado et al., 2019; Bhaskar et al., 2021).

Elicitors from macroalgae

For many years it has been thought that macroalgae defend themselves against their pathogens by constitutive mechanisms. However, in the last two decades, it has been possible to describe the pathogen-induced defense in macroalgae (Weinberger, 2007). The defensive strategies mainly used by macroalgae against biotic stresses include bioactive chemical compounds (Cosse et al., 2007), which can be used, like extracts, directly in agriculture as pesticides (Pan et al., 2019). Furthermore, these extracts and different structural components of macroalgae can be recognized by plant cell receptors and act as powerful elicitors for agricultural use. Table 1 compiles many studies on macroalgae elicitors and their activity in different crops and model plants. Moreover, Fig. 1 summarizes as an infographic the main mechanisms of action involved in the role of macroalgae elicitors in protecting crops against biotic stresses.

Extracts

The discovery of new elicitors from macroalgae for agricultural use begins with the use of different extracts as inducers of plant defenses. In this sense, less systematic effects are reported, but the mechanisms involved in plant defensive strategies are later studied to describe the implicated macroalgae-elicitors has been carried out. For example, the extracts obtained from the chlorophytes *Caulerpa cylindracea* and *Cladophora crispate* reduce incidence and disease severity caused by various viruses in tomato and *Nicotiana benthamiana* by up to 40% when applied to their seeds or leaves, ignoring the plant defense mechanisms involved (Alburquerque et al., 2019; Salim, 2020). Furthermore, different extracts from macroalgae have been used as inducers of plant defenses in the absence of biotic stress, to describe the possible priming effect. In blackberry cell suspension cultures, the addition of *Ascophyllum nodosum*-extracts to the culture medium increased the enzymatic activity β, 1–3 glucanase (GLU) (Patier et al., 1993). In whole tomato and pepper plants, extracts from the same Ochrophyta macroalgae activate the defensive SA- and JA/ET-mediated responses, increasing the activity of various defensive enzymes, such as phenylalanine ammonia-lyase (PAL) or chitinase (CHI) (Ali et al., 2019).

Against bacteria, a reduction in *Xanthomonas campestris* pv. *vesicatoria* disease severity in tomato and sweet pepper by foliar application of *Sargassum vulgare* extracts has been reported, due to local induction of SA- and JA/ET-related genes expression (Ochrophyta) (Ali et al., 2021). Induction of gene expression is also described systemically after applying extracts from *A. nodosum* in *Arabidopsis thaliana* roots and leaves infection by *Pseudomonas syringae* pv. *tomato*, *P. aeruginosa* or *X. campestris* (Cook et al., 2018; Subramanian et al., 2011). These transcriptomic changes increase the activity of defensive enzymes, such as peroxidase (POD) and polyphenol oxidase (PPO), being reported after foliar and seed application of *Cystoseira myriophylloides* (Ochrophyta) extracts against *Agrobacterium tumefaciens* and *P. syringae* pv. *tabaci* (Esserti et al., 2017, 2018). Moreover, plants accumulate defensive secondary metabolites against pathogenic bacteria. Foliar applications with extracts from *Gelidium serrulatum* (Rhodophyta) and *Sargassum* spp., the affectation by *X. campestris* in tomato and cotton is reduced by up to 75%, due to the accumulation of phenolic compounds (Ali et al., 2016; Raghavendra et al., 2007; Ramkissoon et al., 2017).

As far as fungi are concerned, the application of *A. nodosum* extracts in wheat induces the expression of SA-related genes both locally and systemically, significantly reducing the disease intensity caused by *Fusarium graminearum* or *Zymoseptoria tritici* (Gunupuru et al., 2019; Somai-Jemmali et al., 2020). This leads to an increase in defensive enzymatic activity and accumulation of different fungicidal secondary metabolites. For example, root and foliar applications of extracts from *A. nodosum* reduce the incidence of *Alternaria cucumerinum*, *Didymella applanata*, *Fusarium oxysporum* and *Botrytis cinerea* in cucumber, through an increase in GLU, CHI, POD, PPO, PAL and lipoxygenase (LOX) activity (Jayaraman et al., 2011). Furthermore, the root, foliar and fruit application of *A. nodosum* extracts causes the local accumulation of phenolic and flavonoid compounds, reducing the

Table 1 Plant elicitors from macroalgae

MACROALGAE		ELICITOR	APPLICATION METHOD	PLANT AND EXPERIMENT	PATHOGEN/PEST	MECHANISMS OF ACTION	REFERENCES
PHYLUM	SPECIES						
Chlorophyta	*Caulerpa cylindracea*	Unidentified	Soaked seeds with water extracts	*Nicotiana benthamiana* (in greenhouse)	Virus: Plum pox virus (PPV)	Unidentified	Alburquerque et al., 2019
	Cladophora crispate	Unidentified	Foliar spray of alcoholic extracts	Tomato (in greenhouse)	Virus: Tomato yellow leaf curl virus (TYLCV)	Unidentified	Salim, 2020
	C. glomerata	Unidentified	Root application of extracts	Tomato (in greenhouse)	Nematode: *Meloidogyne javanica*	Increased polyphenol oxidase (PPO) and phenylalanine ammonia lyase (PAL) activity	Ghareeb et al., 2020
	Ulva spp.	Ulvan	Foliar spray	Alfalfa (in growth chamber)	Oomycete: *Phytophthora parasitica* var. *nicotianae*	Increased expression of SA-related genes	Cluzet et al., 2004
			Foliar spray	Alfalfa and *A. thaliana* (in growth chamber)	No biotic stress	Increased expression of JA-related genes	Jaulneau et al., 2010
			Foliar spray	*A. thaliana* (in growth chamber)	Fungi: *Alternaria brassicicola* and *Colletotrichum higginsianum*	Unidentified	de Freitas et al., 2015
			Plant-wound application	Papaya (in fruits)	Fungus: *Colletotrichum gloeosporioides*	Increased superoxide dismutase (SOD), catalase (CAT) and peroxidase (POD) activity	Chiquito-Contreras et al., 2019
	Ulva armoricana	Ulvan	Foliar spray	Cucumber (in greenhouse)	Fungi: *Erysiphe polygoni*, *E. necator* and *Sphaerotheca fuliginea*	Unidentified	Jaulneau et al., 2011
	U. fasciata	Unidentified	Foliar spray of water extracts	Bean (in greenhouse)	Fungus: *Colletotrichum lindemuthianum*	Unidentified	Abreu et al., 2008
		Ulvan	Foliar spray	Bean (in greenhouse)	Fungus: *C. lindemuthianum*	Unidentified	Paulert et al., 2009

Table 1 (continued)

MACROALGAE		ELICITOR	APPLICATION METHOD	PLANT AND EXPERIMENT	PATHOGEN/PEST	MECHANISMS OF ACTION	REFERENCES
PHYLUM	SPECIES						
		Ulvan	Foliar spray	Bean (in growth chamber)	Fungus: *Uromyces appendiculatus*	Increased β-1,3-glucanase (GLU) activity	Borsato et al., 2010
		Ulvan	Foliar spray	Wheat and barley (in growth chamber)	Fungus: *Blumeria graminis*	Increased hydrogen peroxide levels	Paulert et al., 2010
		Ulvan	Foliar spray	Bean (in greenhouse)	Fungus: *C. lindemuthianum*	Increased peroxidase (POD) activity	de Freitas and Stadnik, 2012
		Ulvan	Foliar spray	Apple (in greenhouse)	Fungus: *C. gloeosporioides*	Increased POD activity	Araujo & Stadnik, 2013
		Ulvan	Foliar spray	Bean (in greenhouse)	Fungus: *U. appendiculatus*	Unidentified	Delgado et al., 2013
		Ulvan	Foliar spray	*A. thaliana* (in growth chamber)	Fungus: *Alternaria brassicicola*	Increased NADPH oxidase, ascorbate peroxidase (APX), glutathione reductase (GSR), CAT and SOD activity Increased hydrogen peroxide levels	de Freitas & Stadnik, 2015
		Ulvan	Foliar spray	Bean (in greenhouse)	Fungus: *F. oxysporum* f. sp. *phaseoli*	Unidentified	de Borba et al., 2019
		Unidentified	Foliar spray of ethanolic extracts	Bean (in field)	Fungus: *Pseudocercospora griseola*	Unidentified	Fiallos et al., 2020
		Ulvan	In culture medium	Tobacco, alfalfa and blackberry (cell suspension cultures)	No biotic stress	Induced an NADPH oxidase-dependent oxidative burst	Paulert, Brunel, et al., 2021
	U. intestinalis	Ulvan	Foliar spray	Basil and parsley (in greenhouse)	No biotic stress	Increased SA (parsley) or JA (basil) content	Paulert, Ascrizzi, et al., 2021

Table 1 (continued)

MACROALGAE		ELICITOR	APPLICATION METHOD	PLANT AND EXPERIMENT	PATHOGEN/PEST	MECHANISMS OF ACTION	REFERENCES
PHYLUM	SPECIES						
	U. lactuca	Ulvan Oligoulvan	Internodal injection	Tomato (in growth chamber)	Fungus: *F. oxysporum* f. sp. *lycopersici*	Increased PAL activity Increased phenolic compounds and SA content	El Modafar et al., 2012
		Unidentified	Foliar spray of water extracts	Tomato (in greenhouse)	Fungus: *A. solani*	Increased expression of JA-related genes	Hernández-Herrera et al., 2014
		Ulvan Oligoulvan	Plant tissue injection	Apple (in fruits)	Fungi: *Penicillium expansum* and *Botrytis cinerea*	Increased CAT, SOD, POD, PPO and PAL activity Increased hydrogen peroxide, lignin and phenolic compound content	Abouraïcha et al., 2015
		Unidentified	Foliar spray of water extracts	Potato (in field)	Oomycete: *Phytophthora infestans*	Increased polyphenol content Increased PPO activity	Ahmed et al., 2016
		Glucuronan Oligoglucuronans	Plant-wound application	Apple (in fruits)	Fungi: *P. expansum* and *B. cinerea*	Increased hydrogen peroxide content Increased CAT, SOD, PAL, POD and PPO activity	Abouraïcha et al., 2017
		Unidentified	Foliar spray of alkaline extracts	Tomato (in greenhouse)	Fungus: *Alternaria solani* Bacteria: *Xanthomonas campestris* pv. *vesicatoria*	Increased expression of SA-related genes Increased GLU, chitinase (CHI), PAL, POD and PPO activity Increased phenolic compound content	Ramkissoon et al., 2017
		Ulvan	Twigs application	Olive (in growth chamber)	Fungus: *Verticillium dahliae*	Increased PAL activity Increased polyphenol content	Ben Salah et al., 2018

Table 1 (continued)

MACROALGAE		ELICITOR	APPLICATION METHOD	PLANT AND EXPERIMENT	PATHOGEN/PEST	MECHANISMS OF ACTION	REFERENCES
PHYLUM	SPECIES						
Ochrophyta	*Ascophyllum nodosum*	Unidentified	In culture medium	Blackberry (cell suspension cultures)	No biotic stress	Increased GLU activity	Patier et al., 1993
		Unidentified	Root application	Pepper (in growth chamber)	Fungus: *V. dahliae*	Increased phenolic compound content	Goicoechea et al., 2004
		Unidentified	Foliar spray of extracts	Carrot (in greenhouse)	Fungi: *Alternaria radicina* and *B. cinerea*	Increased expression of SA-related genes Increased POD, PPO, PAL CHI and GLU activity	Jayaraj et al., 2008
		Unidentified	Foliar spray Root application	Cucumber (in greenhouse)	Fungi: *Alternaria cucumerinum*, *Didymella applanata*, *Fusarium oxysporum*, and *B. cinerea*	Increased GLU, CHI, POD, PPO, PAL and lipoxygenase (LOX) activity Increased expression of SA- and JA-related genes	Jayaraman et al., 2011
		Unidentified	Root application	*A. thaliana* (in growth chamber)	Bacteria: *Pseudomonas* *syringae* pv. *tomato* Fungus: *Sclerotinia sclerotiorum*	Increased expression of JA-related genes	Subramanian et al., 2011
		Unidentified	Root application	Broccoli (in growth chamber)	*Plasmodiophora brassicae*	Unidentified	Wite et al., 2015
		Unidentified	Foliar spray Root application	Cucumber (in greenhouse)	Oomycete: *Phytophthora melonis*	Increased GLU, POD and PPO activity Increased phenol content Increased expression of SA- and JA-related genes	Abkhoo and Sabbagh, 2016

Table 1 (continued)

MACROALGAE		ELICITOR	APPLICATION METHOD	PLANT AND EXPERIMENT	PATHOGEN/PEST	MECHANISMS OF ACTION	REFERENCES
PHYLUM	SPECIES						
		Unidentified	Foliar spray of alkaline extracts	Tomato (in greenhouse and in field)	Fungus: *A. solani* Bacteria: *X. campestris* pv. *vesicatoria*	Increased POD, PPO, PAL, CHI and GLU activity Increased phenol content Increased expression of JA/ET-related genes	Ali et al., 2016
		Unidentified	Foliar spray of water extracts	Potato (in field)	Oomycete: *Phytophthora infestans*	Increased PPO activity Increased polyphenol content	Ahmed et al., 2016
		Unidentified	Soaked seedlings with extracts	Tomato (in greenhouse)	Oomycete: *Phytophthora capsici*	Increased expression of SA- and JA-related genes Increased GLU, POD and PPO activity	Panjehkeh & Abkhoo, 2016
		Unidentified	In culture medium	*A. thaliana* (in vitro)	Bacteria: *Pseudomonas syringae*, *P. aeruginosa* and *X. campestris*	Increased expression of SA-related genes	Cook et al., 2018
		Unidentified	Foliar spray	Tomato and pepper (in greenhouse and in field)	No biotic stress	Increased PAL, POD, PPO, CHI y GLU activity Increased expression of SA- and JA/ET-related genes	Ali et al., 2019
		Unidentified	Foliar spray	Strawberry (in greenhouse and in field)	Fungus: *Podosphaera aphanis*	Increased PAL, POD and PPO activity Increased phenolic and flavonoid content	Bajpai et al., 2019
		Unidentified	Soaked seedlings with extracts	Wheat (in greenhouse)	Fungus: *Fusarium graminearum*	Increased expression of SA-related genes	Gunupuru et al., 2019
		Unidentified	Root application of alkaline extracts	*A. thaliana* (growth chamber)	Oomycete: *Phytophthora cinnamomi*	Increased expression of SA-related genes	Islam et al., 2020

Table 1 (continued)

MACROALGAE		ELICITOR	APPLICATION METHOD	PLANT AND EXPERIMENT	PATHOGEN/PEST	MECHANISMS OF ACTION	REFERENCES
PHYLUM	SPECIES						
		Unidentified	Foliar spray of extracts	Wheat (in greenhouse)	Fungus: *Zymoseptoria tritici*	Increased of SA-related defenses	Somai-Jemmali et al., 2020
		Unidentified	Fruit immersion	Plum (in fruit)	Fungus: *Monilinia fructicola*	Increased phenolic compounds	Viencz et al., 2020
		Unidentified	Root application of extracts	Tomato and *A. thaliana* (growth chamber)	No biotic stress	Increased expression of SA-related genes	Islam et al., 2021
		Unidentified	Foliar spray of extracts	Soybean (in greenhouse)	Nematode: *M. javanica*	Increased POD, PPO, PAL and GLU activity	Rinaldi et al., 2021
		Unidentified	Root application of alkaline extracts	*A. thaliana* (growth chamber)	Insect: *Myzus persicae*	Increased expression of SA-related genes	Weeraddana et al., 2021
	Bifurcaria bifurcata	Alginate Oligoalginates	Foliar infiltration	Tomato (in growth chamber)	No biotic stress	Increased PAL activity Increased polyphenol content	Aitouguinane et al., 2020
		Oligoalginates: mannuronic and guluronic acid	Root application	Date palm (in greenhouse)	No biotic stress	Increased PAL activity Increased polyphenol content	Bouissil et al., 2020
		Unidentified	Foliar spray of extracts	Pea (in greenhouse)	Fungus: *Erysiphe pisi*	Increased PAL and POD activity Increased hydrogen peroxide content Increased expression of JA/ET-related genes	Patel et al., 2020
	Cystoseira myrica	Unidentified	Soaked seeds with methanolic extracts	Tomato (in greenhouse)	Fungus: *F. oxysporum*	Increased CAT, POD and APX activity	El-Sheekh et al., 2020
	C. myriophylloides	Unidentified	Foliar spray or seed imbibition in water extracts	Tomato (in greenhouse)	Bacteria: *Agrobacterium tumefaciens* Fungus: *V. dahliae*	Increased PPO and POD activity	Esserti et al., 2017

Table 1 (continued)

MACROALGAE		ELICITOR	APPLICATION METHOD	PLANT AND EXPERIMENT	PATHOGEN/PEST	MECHANISMS OF ACTION	REFERENCES
PHYLUM	SPECIES						
		Unidentified	Seed imbibition in water extracts	*Nicotiana benthamiana* (in greenhouse)	Bacteria: *P. syringae* pv. *tabaci*	Increased CAT, APX, POD and guaiacol peroxidase (POX) activity	Esserti et al., 2018
	Dictyota dichotoma	Unidentified	Root application of ethyl acetate extracts	Rice (in greenhouse)	Fungus: *Rhizoctonia solani*	Increased GLU activity	Raj et al., 2019
	Durvillaea potatorum	Unidentified	Root application	Broccoli (in growth chamber)	*Plasmodiophora brassicae*	Unidentified	Wite et al., 2015
		Unidentified	Root application of alkaline extracts	*A. thaliana* (growth chamber)	Oomycete: *Phytophthora cinnamomi*	Increased expression of SA-related genes	Islam et al., 2020
		Unidentified	Root application of extracts	Tomato and *A. thaliana* (growth chamber)	No biotic stress	Increased expression of SA-related genes	Islam et al., 2021
	Ecklonia maxima	Unidentified	Foliar spray of extracts	Tomato (in greenhouse)	Nematode: *Meloidogyne incognita*	Unidentified	Featonby-Smith & Van Staden, 1983
		Eckol	Foliar spray	Cabbage (in greenhouse)	Insect: *Brevicoryne brassicae*	Increased myrosinase activity	Rengasamy et al., 2016
		Unidentified	Foliar spray of extracts	Soybean (in field)	No biotic stress	Increased polyphenol, flavonoid and anthocyanin content	Kocira et al., 2019
		Unidentified	Foliar spray of extracts	Cucumber (in greenhouse)	Fungus: *Podosphaera xanthii*	Increased expression of PR genes	Righini et al., 2020
		Unidentified	Seeds imbibition	Tomato (in greenhouse)	Fugus: *R. solani*	Increased CHI activity	Righini et al., 2021
	Eisenia bicyclis	Laminarin	Cotyledon soaking	Alfalfa (in vitro)	No biotic stress	Increased flavonoid content	Kobayashi et al., 1993
	Fucus spiralis	Unidentified	Foliar spray or seed imbibition in water extracts	Tomato (in greenhouse)	Bacteria: *A. tumefaciens* Fungus: *V. dahliae*	Increased PPO and POD activity	Esserti et al., 2017
		Unidentified	Seed imbibition in water extracts	*N. benthamiana* (in greenhouse)	Bacteria: *P. syringae* pv. *tabaci*	Increased CAT, APX, POD and POX activity	Esserti et al., 2018

Table 1 (continued)

MACROALGAE		ELICITOR	APPLICATION METHOD	PLANT AND EXPERIMENT	PATHOGEN/PEST	MECHANISMS OF ACTION	REFERENCES
PHYLUM	SPECIES						
		Oligoalginates: mannuronic and guluronic acid	Root application	Date palm (in greenhouse)	No biotic stress	Increased PAL activity Increased polyphenol content	Bouissil et al., 2020
	Laminaria digitata	Laminarin	Foliar infiltration	Tobacco (in greenhouse)	Bacteria: *Erwinia carotovora* subsp. *carotovora*	Increased expression of SA-related genes	Klarzynski et al., 2000
			Foliar spray	Grapevine in greenhouse)	Fungus: *B. cinerea* Oomycete: *Plasmopara viticola*	Increased resveratrol and epsilon-viniferin (phytoalexins) content	Aziz et al., 2003
			Foliar infiltration	Tobacco and *A. thaliana* (in growth chamber)	Virus: TMV	Increased scopoletin (phytoalexin) and SA content Increased expression of SA- and JA/ET-related genes	Ménard et al., 2004
			Foliar infiltration	Tobacco and *A. thaliana* (in growth chamber)	Virus: TMV	Increased expression of SA- and JA/ET-related genes	Ménard et al., 2005
			Foliar spray	Grapevine (in greenhouse)	Oomycete: *P. viticola*	Increased expression of JA-related genes Increased callose accumulation	Trouvelot et al., 2008
			Foliar spray	Grapevine in greenhouse)	Oomycete: *P. viticola*	Increased expression of SA-related genes	Gauthier et al., 2014
			Foliar spray	Grapevine in greenhouse)	Oomycete: *P. viticola*	Unidentified	Paris et al., 2016
			Foliar spray	Tea plant (in field)	Insect: *Empoasca onukii*	Increased expression of SA-related genes Increased CHI, PAL, POD, callose and flavonol synthase activity	Xin et al., 2019

Table 1 (continued)

MACROALGAE		ELICITOR	APPLICATION METHOD	PLANT AND EXPERIMENT	PATHOGEN/PEST	MECHANISMS OF ACTION	REFERENCES
PHYLUM	SPECIES						
		Unidentified	Foliar spray or seed imbibition in water extracts	Tomato (in greenhouse)	Bacteria: *Agrobacterium tumefaciens* Fungus: *V. dahliae*	Increased PPO and POD activity	Esserti et al., 2017
		Unidentified	Seed imbibition in water extracts	*N. benthamiana* (in greenhouse)	Bacteria: *P. syringae* pv. *tabaci*	Increased CAT, APX, POD and POX activity	Esserti et al., 2018
	Lessonia trabeculata	Oligoalginates: polyguluronic acid	Foliar spray	Tobacco (in greenhouse)	Virus: Tobacco mosaic virus (TMV)	Increased APX and PAL activity	Laporte et al., 2007
	L. vadosa	Oligoalginates: polymannuronic acid	Plant tissue injection	Wheat (in greenhouse)	No biotic stress	Increased POD and PAL activity	Chandía et al., 2004
		Oligoalginates: polymannuronic acid	Foliar spray	Tobacco (in greenhouse)	Virus: TMV	Increased APX and PAL activity	Laporte et al., 2007
		Fucoidan	Foliar spray	Tobacco (in growth chamber)	No biotic stress	Increased PAL, LOX and glutathione-S-transferase (GST) activity	Chandía & Matsuhiro, 2008
	Pelvetia canaliculata	Oligofucans	Foliar infiltration	Tobacco (in greenhouse)	Virus: TMV	Increased PAL and LOX activity Increased expression of SA-related genes Increased scopoletin (phytoalexin) content	Klarzynski et al., 2003
	Sargassum sp.	Unidentified	Foliar spray of extracts	Tomato (in greenhouse)	Fungus: *F. oxysporum* f. sp. *lycopersici*	Increased GLU, PAL and POD activity	Melo, Collela, et al., 2020
	Sargassum cinereum	Unidentified	Soaked seeds with methanolic extracts	Tomato (in greenhouse)	Fungus: *F. oxysporum*	Increased CAT, POD and APX activity	El-Sheekh et al., 2020
	S. filipendula	Unidentified	Foliar spray of alkaline extracts	Tomato (in greenhouse)	Fungus: *A. solani* Bacteria: *X. campestris* pv. *vesicatoria*	Increased expression of SA-related genes Increased CHI, GLU, PAL, POD and PPO activity Increased phenolic compound content	Ramkissoon et al., 2017

Table 1 (continued)

MACROALGAE		ELICITOR	APPLICATION METHOD	PLANT AND EXPERIMENT	PATHOGEN/PEST	MECHANISMS OF ACTION	REFERENCES
PHYLUM	SPECIES						
	S. fusiforme	Unidentified	Foliar spray	Tomato (in greenhouse)	Oomycete: *P. infestans* Fungi: *B. cinerea* and *Oidium* spp.	Increased hydrogen peroxide levels	Sbaihat et al., 2015
	S. polycystum	Unidentified	Foliar spray	Rubber tree (in growth chamber)	Oomycete: *Phytophthora palmivora*	Increased CAT, POD and GLU activity Increased scopoletin (phytoalexin) and SA content	Khompatara et al., 2019
	S. tenerrimum	Unidentified	Foliar spray	Tomato (in greenhouse)	Fungus: *Macrophomina phaseolina*	Increased SOD, CAT, APX, POX and glutathione reductase (GR) activity Increased SA content	Khedia et al., 2020
	S. vulgare	Unidentified	Foliar spray of alkaline extracts	Tomato and sweet pepper (in greenhouse and in field)	Fungus: *A. solani* Bacteria: *X. campestris* pv. *vesicatoria*	Increased expression of SA- and JA/ET-related genes	Ali et al., 2021
	S. wightii	Unidentified	Foliar spray of water extracts	Cotton (in greenhouse)	Bacteria: *X. campestris* pv. *malvacearum*	Increased POD activity Increased phenolic compound content	Raghavendra et al., 2007
	Unidentified	Alginate oligosaccharide	Seeds imbibition	Soybean (in growth chamber)	No biotic stress	Increased PAL activity Increased phytoalexin content	An et al., 2009
		Sulfated laminarin	Immerse leaf discs	Grapevine (in vitro)	Oomycete: *P. viticola*	Increased isoprenoid compound content	Adrian et al., 2017
		Alginate oligosaccharide	Foliar spray	Tomato (in greenhouse)	Fungus: *A. solani*	Increased SOD activity	Dey et al., 2019
		Alginate oligosaccharide	Foliar spray	*A. thaliana* (in growth chamber)	Bacteria: *P. syringae* pv. *tomato*	Increased expression of SA-related genes	Zhang et al., 2019

Table 1 (continued)

MACROALGAE		ELICITOR	APPLICATION METHOD	PLANT AND EXPERIMENT	PATHOGEN/PEST	MECHANISMS OF ACTION	REFERENCES
PHYLUM	SPECIES						
Rhodophyta	*Acanthophora spicifera*	Lambda-carrageenan	Foliar spray	Rubber tree (in growth chamber)	Oomycete: *Phytophthora palmivora*	Increased expression of SA- and JA-related genes Increased scopoletin (phytoalexin) content Increased POD activity	Pettongkhao et al., 2019
		Unidentified	Foliar spray of alkaline extracts	Tomato and sweet pepper (in greenhouse and in field)	Fungus: *A. solani* Bacteria: *X. campestris* pv. *vesicatoria*	Increased expression of SA- and JA/ET-related genes	Ali et al., 2021
	Gelidium serrulatum	Unidentified	Foliar spray of alkaline extracts	Tomato (in greenhouse)	Fungus: *A. solani* Bacteria: *X. campestris* pv. *vesicatoria*	Increased expression of SA- and JA-related genes Increased CHI, GLU, PAL, POD and PPO activity Increased phenolic compound content	Ramkissoon et al., 2017
	Gigartina acicularis	Lambda-carrageenan	Foliar infiltration	Tobacco (in growth chamber)	Oomycete: *Phytophthora parasitica* var. *nicotianae*	Increased expression of SA- and JA/ET-related genes	Mercier et al., 2001
	G. pistillata	Lambda-carrageenan	Foliar infiltration	Tobacco (in growth chamber)	Oomycete: *P. parasitica* var. *nicotianae*	Increased expression of SA- and JA/ET-related genes	Mercier et al., 2001
	Hypnea musciformis	Kappa-carrageenan	Foliar infiltration	Tobacco (in greenhouse)	Virus: TMV	Increased expression of SA- and JA/ET-related genes Increased phenolic compound content	Ghannam et al., 2013
	Jania adhaerens	Unidentified	Foliar spray of extracts	Cucumber (in greenhouse)	Fungus: *Podosphaera xanthii*	Increased expression of PR genes	Righini et al., 2020
		Unidentified	Seeds imbibition	Tomato (in greenhouse)	Fugus: *R. solani*	Increased CHI activity	Righini et al., 2021
	Kappaphycus alvarezii	Unidentified	Foliar spray of extracts	Tomato (in greenhouse)	Fungus: *Macrophomina phaseolina*	Increased expression of SA-related genes	Agarwal et al., 2016

Table 1 (continued)

MACROALGAE		ELICITOR	APPLICATION METHOD	PLANT AND EXPERIMENT	PATHOGEN/PEST	MECHANISMS OF ACTION	REFERENCES
PHYLUM	SPECIES						
		Kappa-carrageenan	Foliar spray	Pepper (in greenhouse)	Fungus: *Colletotrichum gloeosporioides*	Increased expression of SA- and JA-related genes Increased POD activity	Mani & Nagarathnam, 2018
		Unidentified	Foliar spray of extracts	Tomato (in greenhouse)	Fungus: *F. oxysporum* f. sp. *lycopersici*	Increased GLU, PAL and POD activity	Melo, Collela, et al., 2020
	Schizymenia binderi	Galactan	Foliar spray	Tobacco (in greenhouse)	Virus: TMV	Increased LOX and PAL activity Increased phenylpropanoid compound content	Laporte et al., 2007
		Oligogalactan	Foliar spray	Tobacco (in growth chamber)	Virus: TMV	Increased APX and PAL activity	Vera et al., 2011a
	Tichocarpus crinitus	Kappa-carrageenan Beta-carrageenan	Foliar spray	Tobacco (in greenhouse)	Virus: TMV	Unidentified	Nagorskaya et al., 2008
		Kappa-carrageenan Beta-carrageenan	Foliar spray	*Datura stramonium* (in greenhouse)	Virus: Potato Virus X (PVX)	Formation of cellular-defense structures	Nagorskaya et al., 2010
	Unidentified	Gamma-carrageenan	Foliar spray	*A. thaliana* (in growth chamber)	Fungus: *S. sclerotiorum*	Increased expression of JA-related genes	Sangha et al., 2010
			Foliar spray	Tomato (in greenhouse)	Viroid: Tomato Chlorotic Dwarf Viroid (TCDVd)	Increased expression of JA-related genes	Sangha et al., 2015
		Iota-carrageenan	Foliar spray	*A. thaliana* (in greenhouse)	Insect: *Trichoplusia ni*	Increased expression of SA- and JA-related genes	Sangha et al., 2011
			Foliar spray	Tobacco (in growth chamber)	Virus: TMV Bacteria: *Pectobacterium carotovorum* Fungus: *B. cinerea*	Increased PAL activity Increased phenylpropanoid compound content	Vera et al., 2012

Table 1 (continued)

MACROALGAE		ELICITOR	APPLICATION METHOD	PLANT AND EXPERIMENT	PATHOGEN/PEST	MECHANISMS OF ACTION	REFERENCES
PHYLUM	SPECIES						
			Foliar spray	*Eucalyptus globulus* (in greenhouse)	No biotic stress	Increased polyphenolic compound content	González et al., 2013
		Kappa-carrageenan	In culture medium	Blackberry (cell suspension cultures)	No biotic stress	Increased GLU activity	Patier et al., 1995
			Foliar spray	*E. globulus* (in greenhouse)	No biotic stress	Increased polyphenolic compound content	González et al., 2013
			Foliar spray	*E. globulus* (in greenhouse)	No biotic stress	Increased terpenoid compound content	González et al., 2014
		Lambda- carrageenan	Foliar spray	Tobacco (in growth chamber)	Virus: TMV Bacteria: *Pectobacterium carotovorum* Fungus: *B. cinerea*	Increased PAL activity Increased phenylpropanoid compound content	Vera et al., 2012
			Foliar spray	*E. globulus* (in greenhouse)	No biotic stress	Increased polyphenolic compound content	González et al., 2013
			Foliar spray	Wheat (in greenhouse)	Fungus: *Z. tritici*	Increased expression of SA- and JA-related genes	Le Mire et al., 2019

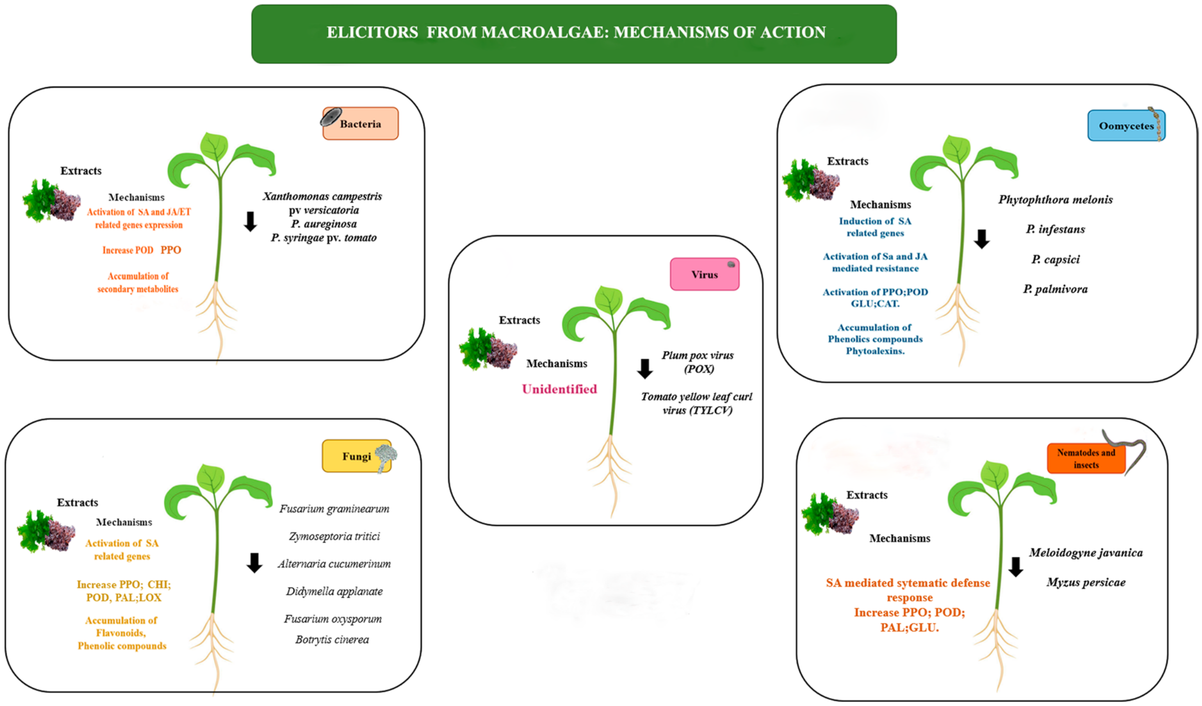

Fig. 1 Summary infographic of macroalgae-elicitors mechanisms of action in plant defenses

incidence of pathogens such as *V. dahliae* in pepper by up to 60% (Goicoechea et al., 2004), *A. solani* in tomato (Ali et al., 2016), *Podosphaera aphanis* in strawberry (Bajpai et al., 2019), or *Monilinia fructicola* in plums (Viencz et al., 2020).

In the case of oomycetes, the activation of local defenses by the root application of *A. nodosum* and *Durvillaea potatorum*-extracts is related to SA-related gene induction, significantly reducing the disease caused by *Phytophthora cinnamomi* in *A. thaliana* (Islam et al., 2020). Similar extracts activate a systemic SA- and JA-mediated resistance against *Phytophthora melonis* in cucumber (Abkhoo and Sabbagh, 2016), *P. infestans* in potato (Ahmed et al., 2016) or *P. capsici* in tomato (Panjehkeh & Abkhoo, 2016), in which the defensive enzymes GLU, POD and PPO, and the accumulation of phenolic compounds are involved. However, activated systemic defensive responses may be macroalgae-extract and plant-dependent. For example, in rubber tree the foliar application of extracts from *Sargassum polycystum* reduces *Phytophthora palmivora* disease by 30%, due to an increase in POD, GLU and catalase (CAT) activity, and the accumulation of phytoalexins, such as scopoletin (Khompatara et al., 2019).

Finally, against nematodes and insects, extracts from *Cladophora glomerata* (C. glomerata) and *A. nodosum* activate the SA-mediated systemic defensive responses. Similar results are reported in tomato and soybean against *Meloidogyne javanica* (Ghareeb et al., 2020; Rinaldi et al., 2021), and *A. thaliana* against *Myzus persicae* (Weeraddana et al., 2021), through an increase in enzymatic activity such as POD, PPO, PAL and GLU.

Ulvan and derivatives

Among the sulfated polysaccharides of seaweeds, the ulvans are present in chlorophytes and especially within the *Ulva* genus, where they account for up to 36% of their biomass (Shukla et al., 2021). They are water-soluble polysaccharides, consisting of a central backbone of disaccharide units formed by an L-rhamnose 3-sulphate linked to uronic acids or xylose (Shukla et al., 2021; Vera et al., 2011b). Normally, using hydrochloric acid and high temperatures (100 ºC), or ultrasound, the depolymerization and/or fragmentation of ulvan and the formation of oligoulvans is achieved (Vera et al., 2011b). In the absence of biotic stresses, the foliar application of ulvans from different *Ulva* species increases systemically and locally plant defenses. In tobacco, alfalfa and blackberry cell suspensions, the addition of ulvan from *U. fasciata* induces an oxidative burst dependent on NADPH oxidase (Paulert et al., 2021a). In this sense, foliar application of ulvans on alfalfa, basil or parsley induces the systemic expression of SA- and JA-related genes (Jaulneau et al., 2010; Paulert et al., 2021b).

In the presence of fungal pathogens, foliar application of ulvan causes a systemic increase in defensive enzyme activity and accumulation of antifungal compounds. An example is described in bean and apple plants, reducing by 40% the disease caused by *Blumeria graminis*, *Colletotricum lindemuthianum* and *C. gloeosporoides*, due to an increase in GLU and POD enzymatic activity (Borsato et al., 2010; de Freitas and Stadnik, 2012; Araujo & Stadnik, 2013). Similarly, applying ulvan to wounds of papaya fruits causes an increase in CAT, POD and superoxide dismutase (SOD) activity, significantly reducing disease incidence and the lesion diameter of anthracnose (*C. gloeosporioides*) (Chiquito-Contreras et al., 2019). Regarding the accumulation of defense chemical compounds, the main plant response reported after foliar application of ulvans is the accumulation of hydrogen peroxide, causing a reduction of up to 90% in the severity of *Alternaria brassicicola* in *A. thaliana* (from Freitas & Stadnik, 2015) and 80% of *B. graminis* in wheat and barley (Paulert et al., 2010). Besides, in twigs application of ulvans from *U. latuca* in olive plants, a systemic increase in the content of polyphenols in the roots was reported, reducing the severity of *V. dahliae* up to 40% (Ben Salah et al., 2018). Regarding oligoulvans, their application by internodal injection in tomato plants reduces the mortality caused by *F. oxysporum* f. sp. *lycopersici*, due to an increase in PAL activity and the accumulation of phenolic compounds in roots (El Modafar et al., 2012). In apple fruits, injection with oligoulvans with a low degree of polymerization causes a significant reduction in the diameter of the lesion formed by the pathogenic fungi *Penicillium expansum* and *Botrytis cinerea*, as a consequence of an increase in the activity of various defensive enzymes and the accumulation of hydrogen peroxide, lignin and phenolic compounds (Abouraïcha et al., 2015).

Laminarin

The main component of some brown seaweeds, such as *Laminaria digitata*, is laminarin, an important reserve polysaccharide and component of the cell wall. In general, laminarin is made up of β-1,3-glucans chains with some 6-*O*-branching (Shukla et al., 2021; Vera et al., 2011b). In absence of biotic stresses, it has been reported how the application of laminarin from *Eisenia bicyclis* (Ochrophyta) to alfalfa cotyledons is capable of inducing systemic plant defenses, causing the accumulation of flavonoid content in tissues (Kobayashi et al., 1993).

All the studies carried out to date with laminarin as a plant elicitor against biotic stresses have used the macroalga *L. digitata* as a source. Against viruses and bacteria, foliar application of laminarin in tobacco and *A. thaliana* causes a reduction in systemic infection by Tobacco Mosaic Virus (TMV) and *Erwinia carotovora* subsp. *carotovora*, as a consequence of an increase in SA- and JA/ET-related genes expression (Klarzynski et al., 2000; Ménard et al., 2004, 2005). In addition to these transcriptomic changes, in grapevine plants infected by the fungus *B. cinerea* and the oomycete *Plasmopara viticola*, a reduction of the disease up to 75% has been reported due to the foliar application of laminarin and sulfated laminarin (PS3), which caused an increase in the tissue content of different phytoalexins (resveratrol and epsilon-viniferin), isoprenoids (Adrian et al., 2017) and callose (Aziz et al., 2003; Gauthier et al., 2014; Trouvelot et al., 2008). In the case of pest insects, foliar application of laminarin in tea plants resulted in a lower performance of the *Empoasca onukii* leafhopper through direct and indirect mechanisms of action. On the one hand, the recognition of laminarin by plant tissues implies an increase in systemic expression of SA-related genes and in the activity of defensive enzymes, such as CHI, PAL, POD, callose and flavonol synthase. On the other hand, laminarin enhanced the attractiveness to the egg parasitoid wasp of *E. onukii*, *Stethynium empoascae* (Xin et al., 2019).

Alginate and derivates

Another polysaccharide present in the cell wall of brown seaweeds is alginate, consisting of a central backbone of (poly)glucuronic and (poly)mannuronic acid. The hydrolysis of these chemical components causes the formation of oligoalginates (Shukla et al., 2021; Vera et al., 2011b). To study the possible priming effect derived from the use of alginates and oligoalginates as plant elicitors, several studies have been carried out in absence of biotic stresses. Using various brown seaweeds as a source, it has been reported how foliar, root and seed application of alginates and oligoalginates (mannuronic and guluronic acids) systemically increases the activity of defensive enzymes (POD and PAL) and the accumulation of polyphenols and phytoalexins in very different crops (Aitouguinane et al., 2020; An et al., 2009; Bouissil et al., 2020; Chandía et al., 2004).

In presence of pathogens, oligoalginates have only been used in foliar application as plant elicitors with efficient results in disease reduction. In *A. thaliana*, these elicitors systemically increase the expression of SA-related genes, such as *PR-1*, significantly decreasing disease index and bacteria colonies of *P. syringae* pv. *tomato* (Zhang et al., 2019). Against TMV in tobacco, oligoalginates obtained from *Lessonia trabeculata* and *L. vadosa* reduced the number of necrotic lesions up to 75%, due to an increase in PAL and plant ascorbate peroxidase (APX) activity (Laporte et al., 2007).

Carrageenan and derivates

In the case of red macroalgae, the main components of their cell wall is carrageenans, assuming up to 75% of the algal dry weight. Carrageenans are water-soluble sulphated polysaccharides, made up of a central chain of sulphated D-galactose, linked to anhydrogalactose units. Depending on the carbon where the sulfate group is located, we find different carrageenans: iota(I)-, kappa(K)-, lambda(λ)-, mu(μ)-, nu (Nv)- and theta(Θ)-carrageenans. Oligocarragenans have been obtained by acid hydrolysis of K-, λ—and I-carrageenans (Shukla et al., 2016; Vera et al., 2011b). The priming effect of different carrageenans as plant elicitors has been described under different conditions. In blackberry cell suspensions, the addition of kappa-carrageenan to the culture medium supposes an increase in cellular GLU activity (Patier et al., 1995). In whole plants, foliar application of I-, K- or λ-carrageenan in *Eucalyptus globulus* plants triggers a systemic increase in tissue accumulation of polyphenolic and terpenoid compounds (González et al., 2013, 2014).

Against viruses and viroids, foliar application of K- or γ-carrageenan increases the systemic expression of SA- and JA/ET-related genes, reducing the appearance of the disease caused by TMV in tobacco or Tomato Chlorotic Dwarf Viroid (TCDVd) in tomato up to 75% (Ghannam et al., 2013; Sangha et al., 2015). More specifically, the foliar application of kappa- and beta-carrageenan from *Tichocarpus crinitus* in *Datura stramonium* increases the formation of cellular-defense structures, such as laminar structures, able to bind viral particles and prevent their intracellular translocation and reproduction (Nagorskaya et al., 2010). Diseases caused by different bacteria, fungi and oomycetes are reduced up to 70% after the application of λ-carrageenan. This is due to an increase in the systemic expression of SA- and JA-related genes (Le Mire et al., 2019; Mercier et al., 2001), an increase in PAL and POD activity, and/or a greater accumulation of phytoalexins (scopoletin) and phenylpropanoid compounds in plant-tissues (Pettongkhao et al., 2019; Vera et al., 2012). In the case of kappa- and gamma-carrageenans, the reduction in disease caused by the fungi *C. gloeosporioides* in pepper and *Sclerotinia sclerotiorum* in *A. thaliana* is a consequence of the increase in the expression of defense-related genes, such as *PR-1*, *PR-3*, *PR-5*, *PDF1.2*, *AOS* and *NPR1* (Mani & Nagarathnam, 2018; Sangha et al., 2010). The synthesis and hydrolysis of glucosinolates compounds are triggered under the pathogen's attack with similar mechanisms to those described in *A. thaliana* in response to foliar application of I-carrageenan against the attack of cabbage looper (*Trichoplusia ni*) (Sangha et al., 2011).

Other elicitors

In addition to all the macroalgae-polysaccharides previously described as elicitors of plant defenses, there are many other examples that have caused significant reductions in the disease. Algal glucuronans (β-(1,4)-d-polyglucuronic acids) are present in the cell wall of different green macroalgae (Redouan et al., 2009). In apple fruits, the wound application of glucuronan and oligoglucuronans from *U. lactuca* reduces the severity of blue and gray mold (*P. expansum* and *B. cinerea*), through an increase in CAT, SOD, PAL, POD and PPO tissue activity (Abouraïcha et al., 2017). Fucans (or fucoidans) are polysaccharides present in the cell wall of brown macroalgae and constituted sulfated fucoses (Berteau & Mulloy, 2003). After the extraction of fucans present in *Pelvetia canaliculata*, they were subjected to an enzymatic hydrolysis process that resulted in the formation of mono- and di-sulfated fucose units (oligofucans). In tobacco plants, the foliar application of these oligofulcans provokes a systemic defensive response that reduces the incidence of TMV (Klarzynski et al., 2003).

Other chemical compounds from macroalgae that can act as elicitors are tannins. In brown macroalgae, such as *Ecklonia* species and *Ishige okamurae*, the tannins mainly present are phlorotannins. Specifically, in *Ecklonia* genus the most common phlorotannin is eckol, mainly made up of phloroglucinols (Manandhar et al., 2019). Eckol from *Ecklonia maxima* applied foliarly to cabbage plants eliminates the infestation by cabbage aphid (*Brevicoryne brassicae*), because of a systemic increase in myrosinase activity (an enzyme involved in glucosinolates hydrolysis) (Rengasamy et al., 2016).

Elicitors from microalgae

As macroalgae, microalgae can be infected by different pathogens and need to develop efficient defensive strategies to survive (Lin et al., 2021). Some of these defensive mechanisms include the synthesis of antimicrobial compounds, which can be used directly as agricultural pesticides (Jena & Subudhi, 2019). On the other hand, both chemical compounds and structural components of microalgae can be used as elicitors of plant defenses in agriculture. Table 2 compiles many existing studies on the use of microalgae as plant elicitor resources, whose mechanisms of action are summarized in an infographic in Fig. 2.

As with different beneficial microorganisms, the direct application of microalgae on crops roots involves the systemic activation of plant defenses. This is due to the microalgae-plant interaction are reciprocal. Several studies have reported priming-type responses in different crops, even though the exact microalgae-molecule involved is unknown. In broccoli and guar plants, root inoculation with *Chlorella vulgaris* (Chlorophyta) systemically increased APX, CAT, SOD and glutathione reductase (GR) activity, along with increased tissue accumulation of flavonoid and phenolic compounds (Kusvuran, 2021; Kusvuran & Can, 2020). This elicitation technique with microalgae can be used industrially to produce compounds of industrial interest by plant cells. In this sense, the inoculation of *Capsicum frutescens* calli with *Botryococcus braunii* (Chlorophyta) increased the synthesis and accumulation of vanillylamine and capsaicin (Sharma et al., 2010). These priming-type defensive responses prepare plants for attack by different pathogens. The foliar inoculation of cucumber plants with *Chlorella fusca* (Chlorophyta) reduced the disease caused by *Colletotrichum orbiculare*, through the activation of SAR and the production of various cytological changes, such as accumulation of vesicles, formation of sheath around penetration hyphae, and thickness of cell wells adjoining with intracellular hyphae (Kim et al., 2018).

In all microalgae formulations and extracts used in agriculture, polysaccharides are usually one of the major components, about 50% of dry weight. In general, microalgae-polysaccharides are heteropolymers of galactose, xylose and glucose (Chanda et al., 2019). So far, the activation of plant systemic defensive responses by microalgae-polysaccharides has been described, although the exact molecules involved are still unknown. Polysaccharides from different *Chlorella*, *Dunaliella* (Chlorophyta) and *Porphorydium* (Rhodophyta) species act as powerful plant elicitors in tomato, increasing the activity of various defense-related enzymes (Farid et al., 2019) and the accumulation of defensive compounds, such as polyphenols (Rachidi et al., 2021) or steroidal glycoalkaloids (Rachidi et al., 2020). In addition to structural polysaccharides, microalgae can produce and release exopolysaccharides with eliciting capacity. Different exopolysaccharides produced by *Dunaliella salina* induce CAT, POD and SOD activity, and accumulation of phenolic compounds in tomato leaves (Arroussi et al., 2018). Similarly, exopolysaccharides produced by *Porphyridium sordidum* induce the expression of SA-related genes and PAL activity in *A. thaliana* leaves, reducing diseases caused by *F. oxysporum* (Drira et al., 2021).

Besides polysaccharides, microalgae can produce other molecules and chemical compounds recognized

Table 2 Plant elicitors from microalgae

MICROALGAE		ELICITOR	APPLICATION METHOD	PLANT AND EXPERIMENT	PATHOGEN/PEST	MECHANISMS OF ACTION	REFERENCES
PHYLUM	SPECIES						
Chlorophyta	*Botryococcus braunii*	Unidentified	In culture medium	*Capsicum frutescens* (in vitro: callus)	No biotic stress	Increased vanillylamine and capsaicin content	Sharma et al., 2010
	Chlorella fusca	Unidentified	Foliar spray with microalgae	Cucumber (in growth chamber)	Fungus: *Colletotrichum orbiculare*	Induced SAR and cytological changes	Kim et al., 2018
		D-Lactic acid	Foliar spray	*A. thaliana* (in growth chamber)	Bacteria: *Pseudomonas syringae* pv. *tomato*	Increased expression SA- and JA-related genes	Lee et al., 2020
	C. reinhardtii	Unidentified polysaccharides	Foliar injection	Tomato (in growth chamber)	No biotic stress	Increased ascorbate peroxidase (APX), β-1,3-glucanase (GLU) and peroxidase (POD) activity	Farid et al., 2019
	C. sorokiniana	Unidentified polysaccharides	Foliar injection	Tomato (in growth chamber)	No biotic stress	Increased APX, GLU and POD activity	Farid et al., 2019
	C. vulgaris	Unidentified polysaccharides	Foliar injection	Tomato (in growth chamber)	No biotic stress	Increased APX, GLU and POD activity	Farid et al., 2019
		Unidentified	Root application of microalgae	Guar (in greenhouse)	No biotic stress	Increased flavonoid and phenolic content Increased APX, catalase (CAT), glutathione reductase (GR) and superoxide dismutase (SOD) activity	Kusvuran & Can, 2020
		Unidentified	Root application of microalgae	Broccoli (in greenhouse)	No biotic stress	Increased flavonoid and phenolic content Increased APX, CAT, GR and SOD activity	Kusvuran, 2021
	Dunaliella salina	Exopolysaccharides	Foliar spray	Tomato (in growth chamber)	No biotic stress	Increased phenolic content Increased CAT, POD and SOD activity	Arroussi et al., 2018

Table 2 (continued)

MICROALGAE		ELICITOR	APPLICATION METHOD	PLANT AND EXPERIMENT	PATHOGEN/PEST	MECHANISMS OF ACTION	REFERENCES
PHYLUM	SPECIES						
		Unidentified polysaccharides	Root application of microalgae	Tomato (in growth chamber)	No biotic stress	Increased steroidal glycoalkaloid content	Rachidi et al., 2020
		Unidentified polysaccharides	Foliar injection	Tomato (in growth chamber)	No biotic stress	Increased expression SA-related genes Increased phenylalaline ammonia lyase (PAL) and POD activity Increased polyphenols and hydrogen peroxide content	Rachidi et al., 2021
	Haematococcus pluvialis	Unidentified	Water extracts n culture medium	Beet and marigold (in vitro: hairy roots)	No biotic stress	Increased betalaine and thiophene secretion	Rao et al., 2001
	Scenedesmus obliquus	Glucosamine	In culture medium	*Tanacetum parthenium* (in vitro: hairy roots)	No biotic stress	Increased diacetylene compounds secretion	Stojakowska et al., 2008
	S. subspicatus	Unidentified	Root application of microalgae	Onion (in field)	No biotic stress	Increased antioxidant capacity	Gemin et al., 2021
	Ulothrix spp.	Unidentified	Root application of microalgae	Tomato, pepper and eggplant (in greenhouse)	Oomycete: *Pythium* sp.	Unidentified	Alshehrei et al., 2021
Ochrophyta	*Navicula* spp.	Unidentified	Root application of microalgae	Tomato, pepper and eggplant (in greenhouse)	Oomycete: *Pythium* sp.	Unidentified	Alshehrei et al., 2021
Rhodophyta	*Porphorydium* spp.	Unidentified polysaccharides	Root application of microalgae	Tomato (in growth chamber)	No biotic stress	Increased in steroidal glycoalkaloid content	Rachidi et al., 2020

Table 2 (continued)

MICROALGAE		ELICITOR	APPLICATION METHOD	PLANT AND EXPERIMENT	PATHOGEN/PEST	MECHANISMS OF ACTION	REFERENCES
PHYLUM	SPECIES						
		Unidentified polysaccharides	Foliar injection	Tomato (in growth chamber)	No biotic stress	Increased expression SA-related genes Increased phenylalanine ammonia lyase (PAL) and POD activity Increased polyphenols and hydrogen peroxide content	Rachidi et al., 2021
	Porphyridium sordidum	Exopolysaccharides	Foliar spray	*A. thaliana* (in vitro: leaves)	Fungus: *Fusarium oxysporum*	Increased expression SA-related genes Increased PAL activity	Drira et al., 2021

by plants as elicitors. Lactic acid is a chiral organic acid that can be produced by some green microalgae (Augustiniene et al., 2021). The D-lactic acid isoform produced by *C. fusca* is recognized by cellular receptors of *A. thaliana*, inducing the systemic expression of SA- and JA-related genes, and reducing the disease caused by *P. syringae* pv. *tomato* (Lee et al., 2020).

This elicitation of plant defenses can be used at the industrial level to increase the production of secondary metabolites of interest, in systems such as hairy roots. Water extracts obtained from *Haematococcus pluvialis* (Chlorophyta) and applied in a culture medium of beet and marigold hairy roots increase the production and secretion of betalains and thiophene (Rao et al., 2001). More specifically, glucosamine produced by *Scenedesmus obliquus* (Chlorophyta) has been described as the elicitor involved in increasing the synthesis of spiroketal enol ether diacetylenes in *Tanacetum parthenium* hairy roots (Stojakowska et al., 2008).

An aspect recently studied and of great interest for future lines of research is that the activation of plant defenses by microalgae-elicitors can be inherited in future generations. Tomato, pepper and eggplant plants were grown in vermicompost together with the microalgae *Ulothrix* spp. (Chlorophyta) and *Navicula* spp. (Ochrophyta). The harvested seeds were germinated in presence of pathogenic oomycete *Pythium* sp., the results showed a seedling survival increased by 90%, a sign of inherited resistance (Alshehrei et al., 2021).

Conclusions and future perspectives

The scientific evidence of the negative impacts caused by chemical pesticides on human and environmental health has propelled the search for sustainable alternatives to feed an exponentially growing population. Thus, changes in conventional agriculture practices are a big challenge and a necessity. Algae standout as a new and innovative bio-tool to develop agriculture according to the needs of the twenty-first century, being a sustainable way despite the requirements for their cultivation. Additionally, macro- and microalgae are catalogued as biopesticides due to their ability to reduce pest and pathogens diseases. Moreover, it plays an essential role as a preventive tool activating plants' defense mechanisms under no biotic stress.

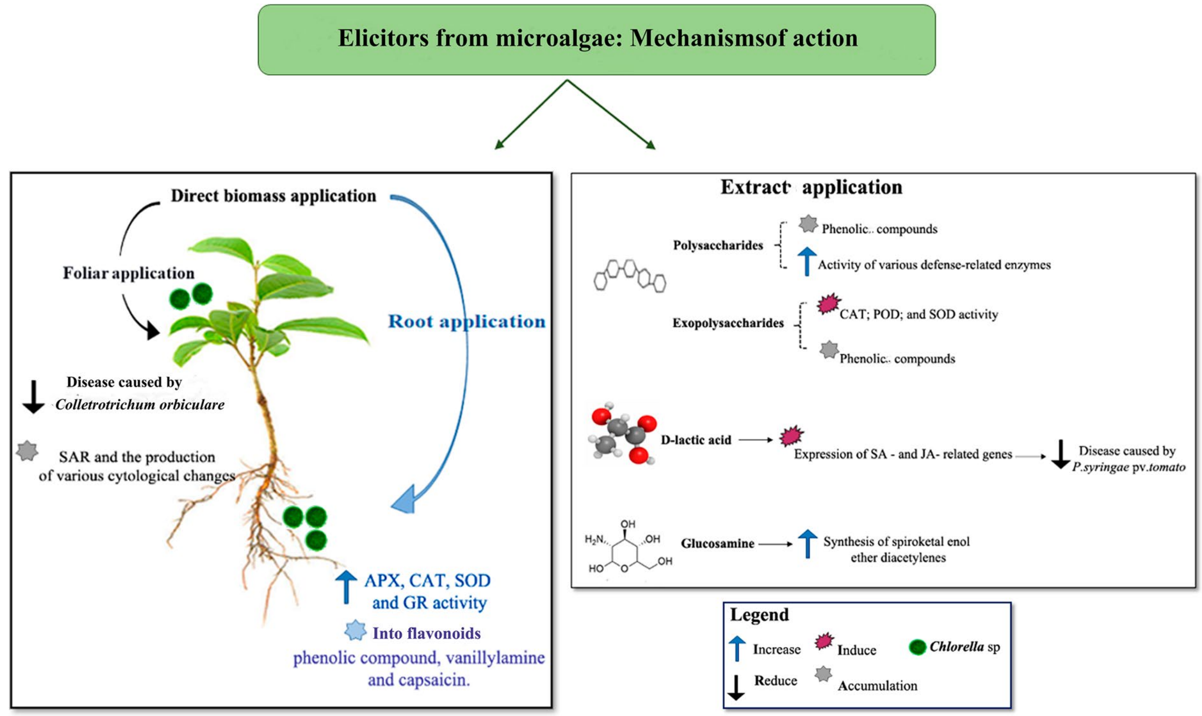

Fig. 2 Summary infographic of microalgae-elicitors mechanisms of action in plant defenses

Thus, it will help reduce diseases caused by pests or pathogens and the economic cost.

Regarding their role as biopesticides, macro and microalgae act as elicitors and can activate the plants' defenses in roots and leaves. In the case of macroalgae, the most common elicitors of plant defenses are ulvan, laminarin, alginate, carrageenan, fucans, glucoran, and tannins with a great range of action against bacteria, fungi, viruses, oomycetes, nematodes and insects. Microalgae biopesticides activity is obtained directly by biomass application or using extracts such as polysaccharides, exopolysaccharides, lactic acid, and glucosamine as elicitors. However, unlike macroalgae, the microalgae-biopesticides role is effective against bacteria, fungi and oomycetes, and the exact molecule involved is unknown. Thus, discovering the target molecules is a challenge for future research. Furthermore, the vast majority of studies carried out with micro- and macroalgae elicitors have been developed in in vitro systems, growth chambers or greenhouses, therefore, there is a need for extensive and rigorous field tests.

Agriculture biotechnology based on ecological alternatives described by macro and micro-algae has different benefits. First, it directly impacts the natural balance of the whole plant health and triggers greater productivity in the present and future campaigns. In addition, their role as biostimulants opens a new path to study and develop compounds that can be used as ecological alternatives to current chemical fertilizers, improving people's health. Thus, algae are postulated as plant growth promoters for their synergic effect between their role as biopesticide and their capacity as biostimulants.

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Declarations

Competing interests The authors declare no competing interests.

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