



# Algal polysaccharides as source of plant resistance inducers

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## ABSTRACT

Algal compounds exhibit great potential to enhance plant growth and resistance to abiotic and biotic stresses. This review focuses on aspects concerning the physical-chemical properties, function and biological activity of macroalgae polysaccharides. Updated results of the main poly- and oligosaccharides studied for the control of plant diseases are discussed and summarized. The carrageenans from red algae have a well-established obtaining system, but its high market value discourages its use in plant protection. The fucans found in the cell walls of brown algae are present in several fertilizers and accounted for the benefits of such commercial products on plant physiology. The laminarans, from brown algae mainly *Laminaria digitata*, are currently the main algal polysaccharides on the phytosanitary market. The ulvans, from cell the walls of *Ulva* spp., open new ways to obtain polysaccharides able to induce resistance due to its abundance worldwide. All these algal polysaccharides show ability to activate multiple plant defense mechanisms against a broad spectrum of plant pathogens. Taking into account the promising results reported in the literature and the enormous biochemical diversity of these biopolymers, it is likely that they will provide new types of resistance inducers in a near future.

**Key words:** Carrageenans, fucans, laminarans, ulvans.

## INTRODUCTION

The seaweeds (macroalgae) are a diverse group of organisms that frequently occur in marine environment and usually grow fast and produce high biomass yields. These attributes turn its commercial exploitation attractive for variable purposes such as agriculture (Stadnik & Paulert, 2008).

Almost 70% of the biosphere is covered by marine biomes, with a fantastic taxonomical and biochemical diversity. In this context, macroalgae show a great potential for generation of new agricultural technologies, attested by the success of already commercialized algae derived products (Kulik, 1995; Stadnik & Paulert, 2008; Craige, 2011).

Besides their traditional use as organic fertilizers, algae have expressive biotechnological potential as a source of compounds that can stimulate plant growth and protect them against pathogens. Such applications have made feasible their rational exploitation, because they add market value to the product and use of small quantities per area (Stadnik & Paulert, 2008; Khan et al., 2009).

As well as other marine organisms, macroalgae are source, little explored, of physiological stimulants and resistance elicitors to the cultivated plants. Considering the actual trends of market that looks for efficiency, human health and the environmental friendship, the demand of such products might increase. The algae and their polysaccharides are perfectly inserted in this scenario. Another advantage that favors the use of algae, as raw material to obtain polysaccharides and other bioactive

molecules, is the benefit-cost analysis of investments in research and industrial production, which give high reward because the chemical synthesis of new molecules is not needed (Stadnik & Paulert, 2008; Craige, 2011).

Without the intention of exhausting the topic, this review focuses on different aspects concerning the chemistry, physical-chemical properties and biological function of polysaccharides in the nature. In the sequence, results of the main studied poly- and oligosaccharides for the control of plant diseases are summarized.

### Polysaccharides structure and function

Conceptually, polysaccharides, also known as glycans, are natural macromolecules (biopolymers) of joined monosaccharide units and, as a consequence, with a high molecular mass that is dependent of the number unities that compose it (Nelson & Cox, 2008). Considering that the repeated units in the backbone of polymer are often six-carbon monosaccharides, the general formula can also be represented as  $(C_6H_{10}O_5)_n$  where "n" stands between 20 and 3000. Conventionally, the polysaccharides contain more than 20 monosaccharides units such as glucose, fructose and glyceraldehyde. However, definitions of how large a carbohydrate must be to fall into the categories of polysaccharides or oligosaccharides are subjective. Anyway, these carbohydrates can be hydrolyzed in oligosaccharides, disaccharides or monosaccharides using chemical, physical or biochemical methods (Richter, 1996; Nelson & Cox, 2008).

Polysaccharides exhibit a molecular structure that can be linear or highly branched, composed by the same

(homopolysaccharide) or different (heteropolysaccharide) monosaccharide units. Structural differences confer distinct physical-chemical properties. For example, in water, they can be insoluble (such as cellulose) or soluble in gel form (such as pectin and alginate), showing viscoelastic properties. Several polysaccharides are acids due to the presence of carboxylic groups, phosphate groups and/or ester sulfuric in the molecular structure (Nelson & Cox, 2008). In organisms, the polysaccharides are classified according to their biological function in two groups: energy storage and structural polysaccharides. When glucose is not acting in a metabolic pathway, it can be stored as reserve polysaccharide called starch in plants, glycogen in animals and laminaran in brown algae. Polysaccharides can also form organic structures such as cellulose, which is the most important and abundant in the nature, chitin, the main component of the cell walls of fungi and the agar of red algae. In contrast to chitin, chitosan is a water-soluble chitin derivative that acts as an elicitor of plant defense responses (Richter, 1996; Nelson & Cox, 2008).

Besides the energetic reserves and structural functions, several poly and oligosaccharides exhibit different kind of biological activities. Some bacteria and others microorganisms, including fungi and microalgae, developed capsular adaptations by secreting polysaccharides that help their adhesion to surfaces and prevent the desiccation. These capsular polysaccharides, including peptidoglycans, lipopolysaccharides and exopolysaccharides, are water soluble, acids and participate in the host-pathogen interaction. As an example of great structural diversity of polysaccharides is the fact that just the bacterium *Escherichia coli* (Migula) Castellani and Chalmers is able to produce a dozen of complex polysaccharides (Whitfield, 2006).

### Algae polysaccharides

Algae polysaccharides are probably the most abundant organic molecules in the oceans and have a great molecular biodiversity that is far from being understood (Kloareg & Quatrano 1988). In the last decades, studies revealed the enormous potential of these macromolecules as elicitors of plants defense responses (Klarzynski et al., 2000; Mercier et al., 2001; Patier et al., 1995). Aspects and advances related with the use of the most studied macroalgae polysaccharides such as carrageenans, fucans, laminarans and ulvans to protect plants will be discussed.

### Carrageenans

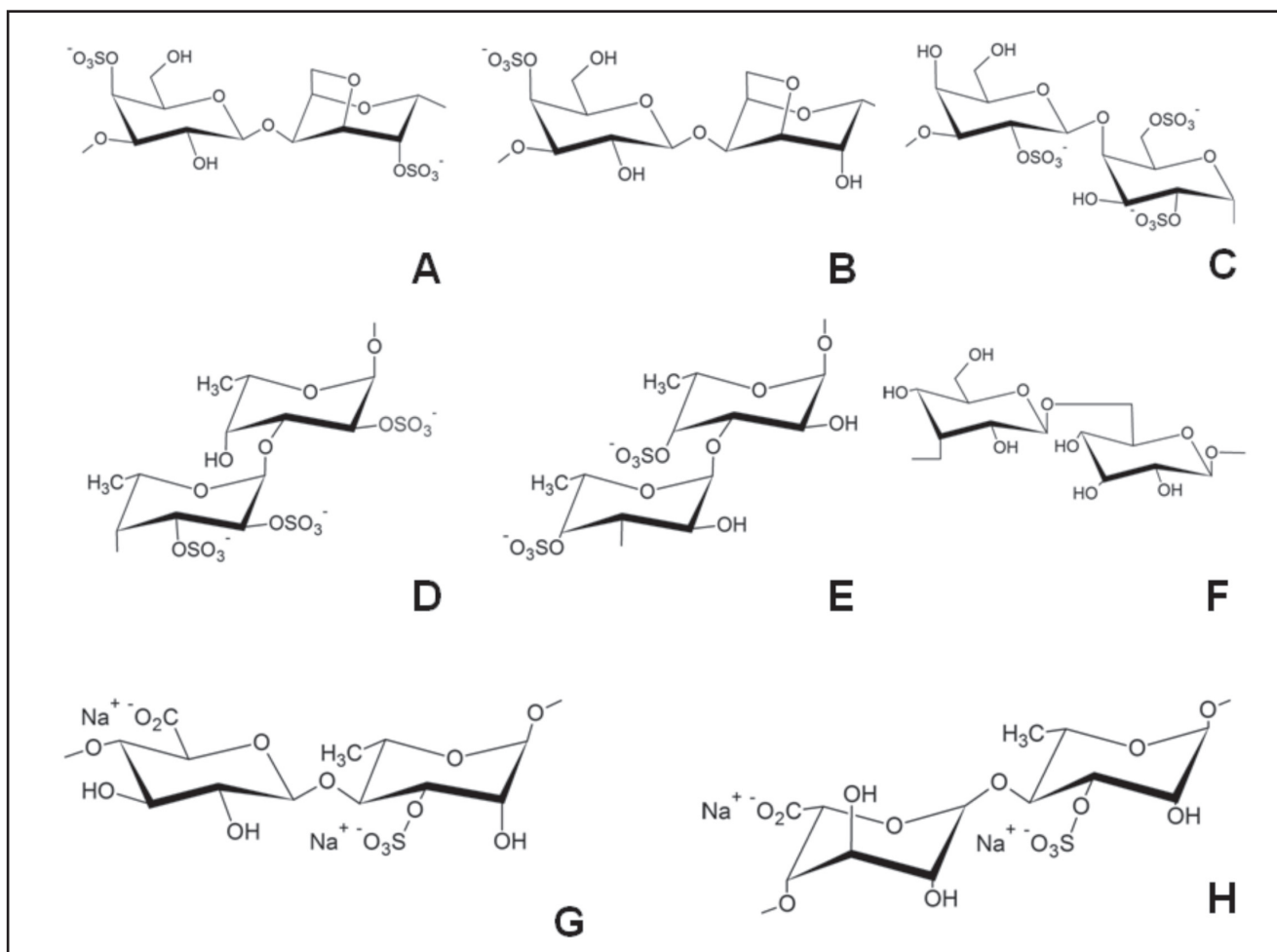
The carrageenans have been used, for hundreds of years, as additives in several industrial processes and food products, mainly as stabilizers, gelling agents, thickeners and clarifiers of beverages. Due to its high value, seaweeds containing carrageenans have been extensively cultivated in sea farming (Bixler, 1996). Carrageenans are extracted from red algae (Rodophyta), mainly from *Kappaphycus alvarezii* (Doty) Doty ex Silva, grown in Philippines. The

*K. alvarezii* was recently introduced in Brazil for rational cultivation (Hayashi et al., 2011). Before its introduction, there were attempts to *Hypnea musciformis* (Wulfen) Lamouroux cultivation, a naturally found species in the Brazilian coast, with little success (Hayashi et al, 2007). Besides the advantage of a well-established system for carrageenans production, the great demand to attend current needs, the high market value will possibly be a constraint for its use in agriculture.

Carrageenans, also known as sulfated galactans, are linear polysaccharides and composed by repeating dimmers of  $\alpha$ -1,4-D-galactose, which are linked by alternated bonds of  $\alpha$ -1,3 and  $\beta$ -1,4 and substituted by one ( $\kappa$ -carrageenan), two ( $\iota$ -carrageenan) or three ( $\lambda$ -carrageenan) sulfate ester groups within each repeating unit (Figure 1). In commercial preparations,  $\kappa$ -,  $\iota$ - and  $\lambda$ - carrageenans exhibit high contents of sulfate, *i.e.*, 22%, 32% and 38% (p/p), respectively and different physical-chemical properties (De Ruiter & Rudolf, 1997; Sangha et al., 2010). An interesting fact is that the carrageenans ratio, found in red algae, vary according to the algae species. For example, *K. alvarezii* and *H. musciformis* have more  $\kappa$ -carrageenan, while *Euचेuma denticulatum* (Burman) Collins and Hervey and *Gigartina pistillata* (Gmelin) Stackhouse have more  $\iota$ -carrageenan and  $\lambda$ -carrageenan, respectively (Bixler, 1996; De Ruiter & Rudolph, 1997).

The defense system of plants can be activated by the application of carrageenans and its oligosaccharides. Patier et al. (1995) found that the  $\kappa$ -carrageenan elicited the activity of  $\beta$ -1,3-glucanase in cell cultures of *Rubus fruticosus* L. and that the oligo-  $\kappa$ -carrageenans were more efficient than the original polysaccharide. In tobacco plants, Mercier et al. (2001) observed that the application of carrageenan triggered different defense systems involving ethylene, jasmonic acid and salicylic acid pathways. On the other hand, Sangha et al. (2010) demonstrated that the induction of resistance by  $\lambda$ -carrageenan in *Arabidopsis thaliana* (L.) Heynhold against *Sclerotinia sclerotiorum* (Libert) de Bary was due to an increase in oxalate oxidase activity and is related with the expression of jasmonic acid signaling associated genes, *e.g.*, AOS, PDF1.2 and PR3. In addition,  $\lambda$ -carrageenan was able to induce resistance in a salicylic acid deficient mutant of *A. thaliana* (*ics1*), suggesting that the resistance induction was independent of this pathway.

Carrageenans and their oligosaccharides can activate defense mechanisms against plant pathogens including bacteria, fungi and virus. Recently, Vera et al. (2012) demonstrated the systemic effect of  $\kappa$ -,  $\iota$ - and  $\lambda$ -oligo-carrageenans against tobacco mosaic virus (TMV), *Botrytis cinerea* Persoon and *Pectobacterium carotovorum* (Jones) Waldee. In this study, higher concentrations and frequent applications of oligo-carrageenans (1-5 mg/mL), mainly  $\lambda$ -oligo-carrageenan resulted in a durable protection of plants against TMV. In addition, the treatment with oligo-carrageenans increased the phenylalanine ammonia-lyase activity (PAL) and pre-infection accumulation of



**FIGURE 1** - Schematic representation of spatial structure of dimers (repeated units) of different polysaccharides. **A.**  $\iota$ -, **B.**  $\kappa$ -, **C.**  $\lambda$ -carrageenans; **D.** Fucans from *Ascophyllum nodosum* and *Fucus* spp.; **E.** Fucan from *Ecklonia* spp.; **F.** Laminaran; **G.** Ulvan type A; **H.** Ulvan type B.

phenolics, suggesting that these compounds were involved in protection.

The efficiency of the eliciting activity depends on the carrageenan type, its degree of sulfation and the pathogen life style. The pre-treatment of *A. thaliana* with a highly sulfated  $\lambda$ -carrageenan induced resistance to *S. sclerotiorum* resulting in less foliar damage while the  $\iota$ -carrageenan, with a lower degree of sulfation, increased disease severity (Sangha et al., 2010). Although different types of oligo-carrageenans protected tobacco plants similarly against *P. carotovorum*, the  $\lambda$ - and  $\iota$ -oligo-carrageenans were more efficient against *B. cinerea* (Vera et al., 2012). In infiltration assays with tobacco leaf,  $\lambda$ -carrageenan, with high sulfate content, was more effective in eliciting defenses reaction than the laminaran and an elicitor polysaccharide extracted from *Phytophthora megasperma* Drechsler. These reactions involved the local production of chitinase and proteinase inhibitors with the effects persisting for a week (Mercier et al., 2001).

Besides the ability to induce systemic resistance, beneficial (biostimulant) effects on plant physiology has

been verified with the application of carrageenans. In this way, Castro et al. (2012) concluded that spraying oligo-carrageenans weekly at the concentration of 1 mg/mL stimulated growth, photosynthesis and the basal metabolism of tobacco plants. Based on these studies with oligo-carrageenans, patents were registered in several countries, including Brazil, and a product has been commercialized in Chile (Karla) as a biostimulant for eucalyptus (SiriusNatura, 2012).

### Fucans

The algal fucans, frequently denominated fucoidans, are linear or not linear polysaccharides, with a structural characteristic defined by the presence of sulfated L-fucose. The fucose is a hexose deoxy sugar naturally found on the surface of animal and plant cells (Bertheau & Mulloy, 2003). The lack of a hydroxyl group on the carbon at the 6-position (C-6) and the L-configuration are characteristics that distinguish fucose from the other hexoses (Richter, 1996; Nelson & Cox, 2008). Sulfated fucans are constituted by L-fucose, joined by  $\alpha(1\rightarrow3)$  glycosidic bond and with

substitutions on positions 2, 3 and/or 4, depending on algae species (Figure 1) (Berteau & Mulloy, 2003).

This structural polysaccharide is found in the cell walls of brown algae species (Phaeophyta) such as *Ascophyllum nodosum* (L.) Le Jolis, *Fucus* spp. and *Ecklonia* spp. (Stadnik & Paulert, 2008). The *A. nodosum* and *Ecklonia* spp. that grow in frozen sea waters in the northern hemisphere and South Africa, respectively, have been used as raw material to produce commercial fertilizers and biostimulants for decades in several countries. An extensive list of commercial extracts obtained with these algae can be found in the literature review of Khan et al. (2009). Despite of many statements of algae extracts as biostimulant and phytoprotector activity properties, the bioactive components are not known yet. Besides the phytohormones, the polysaccharides have been considered the possible responsible for their beneficial effects (Stadnik & Paulert, 2008; Khan et al., 2009).

One of the pioneering studies that shows the effect of *A. nodosum* extracts on plant diseases was reported by Lizzi et al. (1998). In this study, the treatment of plants with alga extract controlled *Phytophthora capsici* Leonian and *Plasmopara viticola* (Berkeley and Curtis) Berlese and de Toni in pepper and grapevine, respectively. In association with the control of *P. capsici*, it was observed, in foliar tissues of peeper plant, an increase in peroxidase activity and the synthesis of the phytoalexin capsidiol. For that reason, the authors concluded that the extract of *A. nodosum* acted as a resistance inducer.

Klarzynski et al. (2003) described the eliciting activity of oligosaccharides prepared from enzymatic hydrolysis of sulfated fucan obtained from the brown algae *Pelvetia canaliculata* (L.) Decaisne and Thuret (Phaeophyta). In tobacco cells suspension, these oligosaccharides induced both early (such as alkalization of extracellular media and hydrogen peroxide production) and late defense responses (such as an increase in PAL and lipoxygenase activities).

Although fucans are ingredients of most seaweed-based biostimulants and fertilizers, studies about their eliciting activity are still scarce in comparison with other polysaccharides described in the present review.

### Laminarans

The laminarans, also known as laminarins, are reserve polysaccharide found in brown algae, such as *Laminaria digitata* (Hudson) Lamouroux, that grows in cold waters in the northern hemisphere. It is a linear homopolysaccharide with linkages  $\beta(1\rightarrow3):\beta(1\rightarrow6)$  in a ratio of 3:1 (Figure 1). Another similar polysaccharide is the chrysolaminarin present in phytoplankton and considered one of the most abundant biopolymer in the nature. This water-soluble molecule is composed by glucose units with linkages  $\beta(1\rightarrow3)$  and  $\beta(1\rightarrow6)$  in a ratio of 11:1. Laminaran has an average polymerization degree of 25 glucose units and three simple ramifications of  $\beta$ -glucose at the C-6 position (Read et al., 1996; Ménard et al., 2004).

Laminarans are able to stimulate defense reactions in cells suspensions of tobacco (Klarzynski et al., 2000), grapevine (Aziz et al., 2003) and rice (Inui et al., 1997). Typical defense responses include activation of protein kinase,  $\text{Ca}^{2+}$  influx, oxidative burst and alkalization of extracellular media, increase in chitinase and  $\beta$ -1,3-glucanase activities and phytoalexins production. When sprayed on tobacco and grapevine plants, laminarans induce phytoalexins accumulation and expression of PR-proteins without triggering hypersensitive response (Klarzynski et al., 2000; Aziz et al., 2003). All this happens because the oligosaccharides obtained from laminaran mimics pathogen attack. They are naturally involved in cellular recognizing mechanisms, in plant-pathogen interactions exogenously (produced by degradation of fungi cell walls) or endogenously (fragmented callose) (Klarzynski et al., 2000).

The biological activity of  $\beta$ -glucans is possibly the result of its binding with receptors. In fact, a receptor for  $\beta$ -1,3,  $\beta$ -1,6 heptagluconic (chain of  $\beta$ -1,6 glucose with two  $\beta$ -1,3 glucose ramifications) was cloned on beans (Mithöfer et al., 2000). There are indicatives that plants cells can discriminate glucans close related as example in rice cells that responded to a pentagluconic (chain of  $\beta$ -1,3 glucose with a  $\beta$ -1,6 ramification), obtained from *Pyricularia oryzae* Cavara, but not to hexagluconic (chain of  $\beta$ -1,6 glucose with two  $\beta$ -1,3 ramifications) (Yamaguchi et al., 2000). Nevertheless, tobacco reacts to laminaran, but not to  $\beta$ -1,3,  $\beta$ -1,6 heptagluconic (Klarzynski et al., 2000).

Products based on laminaran such as Iodus and Vacciplant have been commercialized in different countries to control powdery mildew in strawberry and cereals, bacterial fire blight in apple tree and the grey mould in grapevine (Elmer & Reglinski, 2006; Renard-Merlier et al., 2007; Goëmar, 2012). The product does not have phytotoxicity risk and the plant energetic costs of induced resistance are apparently low or inexistent. This natural ingredient is easily biodegradable and has a  $\text{LD}_{50}$  higher than 5000  $\text{mg}\cdot\text{kg}^{-1}$  of live weight. The laminaran and its oligomers are potent elicitors of plant defenses of dicots (tomato and green bean) and monocots plants (wheat and rice), constituting a suitable alternative tool for disease control in agricultural crops (Klarzynski, 2000; Aziz et al., 2003). In this sense, its application has been recommended for integrated management associated with other methods of disease control (Goëmar, 2012), considering that the reached control level is generally intermediary. Without the induction of cell death, the treatment of grapevine plants with laminaran reduced the infection of *B. cinerea* and *P. viticola* in 55 and 75%, respectively (Aziz et al., 2003).

The structural analyses of laminarans indicated that a minimal length chain and the presence of sulfate residues are determinant factors of eliciting activity. For example, Ménard et al. (2004) demonstrated that laminaran, with eliciting activity in tobacco and *A. thaliana*, after its sulfation, becomes an inducer of the salicylic acid (SA) pathway.

In tobacco cells suspension, the oxidative burst induced by sulfated laminaran (PS3) was dependent of  $\text{Ca}^{2+}$ , but partially independent of protein kinases. Cells treated with PS3 or laminaran were completely responsive to a second application of laminaran or PS3, respectively, suggesting two different perception systems. While laminaran induced the expression of ethylene dependent protein, PS3 activated the expression of SA-dependent proteins.

### Ulvans

Ulvans are water-soluble sulfated heteropolysaccharides extracted from the cell walls of green marine macroalgae of genus *Ulva*, representing from 8 to 29% of algae dry weight. *Ulva*, popularly known as “sea lettuce”, is widely distributed worldwide and has been used, in small scale, in human food, medicine and agriculture. Otherwise, this genus is frequently involved in ecological problems along the coasts due to its big proliferation in eutrophic environments, called as “green tides”, occurring mainly in hot regions of the planet (Cluzet et al., 2004; Wosnitza & Barrantes, 2005; Lahaye & Robic, 2007; Paulert et al., 2007 e 2009; Henández-Garibay et al., 2011).

Ulvans are composed by rhamnose (16.8-45.0%, p/p), xylose (2.1-12.0%), glucose (0.5-6.4%), uronic acid (6.5-19.0%), iduronic acid (1.1-9.1%) and sulfate (16.0-23.2%). Manose and galactose also have been found in ulvans from some *Ulva* species (Lahaye & Robic, 2007). These sugars are structurally grouped by two main repeating disaccharides, which are: the ulvabiuronic acid type A ( $\beta$ -D-GlcA (1 $\rightarrow$ 4)  $\alpha$ -L-Rha 3S  $\rightarrow$ 1) and type B ( $\alpha$ -L-IdoA (1 $\rightarrow$ 4)  $\alpha$ -L-Rha 3S  $\rightarrow$ 1) (Figure 1) (Paulert et al., 2007; Robic et al., 2009). However, the polysaccharide composition can be more complex and is influenced by taxonomical and/or ecophysiological variations (Lahaye & Robic, 2007).

Bioprospecting studies carried out between 2002 and 2004 evaluated extracts from several macroalgae and macrophytes collected along the Santa Catarina coast in Brazil. As the result, *Ulva fasciata* Delile was identified as a potential source to provide active compounds for the control of foliar diseases, such as powdery mildew (*Erysiphe polygoni* DeCandolle) and anthracnose (*Colletotrichum lindemuthianum* Saccardo and Magnus) on bean (Loffaguen et al., 2004; Abreu, 2005; Abreu et al., 2008). Under greenhouse conditions, spraying of beans with extract of *Ulva* led to a strong reduction (almost 80%) in the number of powdery mildew (*E. polygoni*) colonies on pre-treated leaves (Jaulneau et al. 2011).

One of the first experiments testing the effect of ulva-extract under field conditions was carried out in 2003 (Loffaguen et al., 2004). In this experiment, monthly sprays of algal extract reduced in 50% the severity of anthracnose on the highly susceptible bean cultivar IPR Uirapuru. This protective effect was similar to the treatment with strubilurin fungicide.

Further studies with a semi-purified polysaccharide demonstrated that the ulvan is the main elicitor ingredient

in extracts of *Ulva* spp. and can reduce the severity of a broad range of diseases on beans, such as rust (*Uromyces appendiculatus* (Persoon) Link) (Borsato et al., 2010; Delgado et al., 2013), anthracnose (*C. lindemuthianum*) (Paulert et al., 2009; Freitas & Stadnik, 2012) and powdery mildew (*E. polygoni*) (Jaulneau et al., 2011). In addition, the polysaccharide has shown promising results against other diseases such as Glomerella leaf spot (*C. gloeosporioides* (Penzig) Penzig and Saccardo) on apple (Araújo et al., 2008; Araújo & Stadnik, 2013) and powdery mildew (*Blumeria graminis* (DeCandolle) Speer) on wheat and barley (Paulert et al., 2010; Jaulneau et al., 2011). The effects of ulvan in different pathosystems are shown on Table 1.

Greenhouse experiments showed that the foliar application of ulvan reduced anthracnose (*C. lindemuthianum*) severity by 50% and protected beans for up to nine days after treatment (Schons et al., 2011). Given the fact that ulvan has a systemic effect, but does not inhibit the mycelial growth and conidial germination of fungus *in vitro* and *in vivo*, the control has been attributed to induction of plant resistance (Paulert et al., 2009; Freitas & Stadnik, 2012). However, ulvan has been found to delay the differentiation and melanization of appressoria of *C. gloeosporioides*, while stimulating elongation of germ tubes (Gonçalves & Stadnik, 2012). Ulvan applied at 1 or 10  $\text{mg.kg}^{-1}$  also conferred an intermediary level of protection against *U. appendiculatus*, reducing the number, diameter and particularly sporulation of rust pustules in susceptible plants. All these effects suggest that mechanisms of resistance operated at latter stages of fungal colonization (Delgado et al., 2013).

Responses to ulvan treatment seem to be multiple and dependent of plant and fungal species involved. According to Cluzet et al. (2004), in alfafa infected with *Colletotrichum trifolii* Bain and Essary, responses included the biosynthesis of phytoalexins and proteins related with the pathogenesis and showed a maximum elicitation two days after spraying of 500  $\mu\text{g/mL}$ . As expected, ulvan did not cause phytotoxicity and any change in the primary plant metabolism. The eliciting defense activated by ulvan has been reported in other pathosystems such as bean-*U. appendiculatus* (Borsato et al., 2010) and bean-*C. lindemuthianum* (Freitas & Stadnik, 2012), where the polysaccharide increased the post-infection activity of glucanase and peroxidase, respectively. Increase in peroxidase activity occurred in apple plants at 72 h after infection with *C. gloeosporioides*, but not earlier and without affecting glucanase (Araujo & Stadnik, 2013).

The eliciting defense responses by ulvan in plants seem to be genotype dependent. Borsato et al. (2010) observed that the ulvan spray increased glucanase activity in the moderately susceptible bean cv. Pérola, but not in ‘Juriti’, a cultivar that is highly susceptible to *U. appendiculatus*. Again, ulvan increased peroxidase activity on a bean genotype resistant to anthracnose, but not in the susceptible one (Freitas & Stadnik, 2012).

The resistance induction is frequently associated to priming where the plant treated with the elicitor becomes

**TABLE 1** - Effects of foliar application of ulvan or extracts from *Ulva* spp. on disease severities in different host-pathogen interactions.

Host plant	Pathogen	Disease intensities	Reference
Alfafa	<i>Colletotrichum trifolii</i>	reduced	Cluzet et al. (2004)
Apple	<i>Colletotrichum gloeosporioides</i>	reduced	Araújo et al. (2008)
Bean	<i>Colletotrichum lindemuthianum</i>	reduced	Paulert et al. (2009)
	<i>Erysiphe polygoni</i>	reduced	Jaulneau et al. (2011)
Cereals	<i>Uromyces appendiculatus</i>	reduced	Borsato et al. (2010)
	<i>Blumeria graminis</i>	reduced	Paulert et al. (2010)
	<i>Sphaerotheca fuliginea</i> (Schlechtendal) Pollacci	reduced	Jaulneau et al. (2011)
Cucumber	<i>Erysiphe necator</i> Schweinitz	reduced	Jaulneau et al. (2011)
Grapevine	<i>Plasmopara viticola</i>	reduced	Galvão et al. (2006)
		unaffected	Peruch et al. (2007)
	<i>Sphaceloma ampelinum</i> de Bary	reduced	Galvão et al. (2006)
Green onions	<i>Alternaria porri</i> (Ellis) Ciferri	reduced	Araújo et al. (2012)
Onion	<i>Burkholderia cepacia</i> (Palleroni and Holmes)	unaffected	Wordell et al. (2007)
	Yabuuchi <i>Peronospora destructor</i> Caspary	unaffected	Wordell et al. (2007)

primed and activates defense responses faster and more intensely when exposed to pathogen attack compared to untreated plants (Paulert et al. 2010; Conrath, 2011). The ability of ulvan to induce priming was recently demonstrated. Thus, although ulvan itself did not change the production of hydrogen peroxide, in suspension-cultured wheat or rice cells, its previous addition enhanced the chitin-elicited oxidative burst about five to six folds, and that elicited by chitosan about two folds. In rice cells, the production of hydrogen peroxide elicited by chitin or chitosan was strongly primed by pre-treatment, increasing the burst triggered by the elicitors alone, in 150 and 80 times, respectively (Paulert et al., 2010). On the other hand, spraying of ulvan alone can promote a significant increase of peroxidase and glucanase activities in non-inoculated beans plants (Freitas & Stadnik, 2012).

Recent studies demonstrated that the signaling pathway of jasmonic acid is involved in the resistance induction by ulvan application (Jaulneau et al., 2010). Thus, this polysaccharide may be efficient against necrotrophic pathogens, because this pathway is generally involved in defense responses against these pathogens (Glazebrook, 2005; Araújo et al., 2012). However, it was also demonstrated that ulvan can control biotrophic (Borsato et al., 2010; Paulert et al., 2010) and hemibiotrophic fungi (Paulert et al., 2009; Freitas & Stadnik, 2012). The expression of PR-1, a known marker for SA pathway, has been observed after the treatment with ulvan (Cluzet et al., 2004). As consequence, it is possible to argue that the polysaccharide may act in more than one signaling pathway.

Similarly to that reported for other algae species, extracts and/or polysaccharides from *Ulva* spp. also seem to have stimulant effect on plant physiology. As example, in India, Sridhar & Rengasamy (2010) used a liquid fertilizer based on *Ulva lactuca* to improve nutrients absorption, increase the growth, photosynthesis and flowering of marigold (*Tagetes erecta* L.). On beans, it was observed that

the treatment of seeds with ulvan stimulated germination (Paulert et al., 2009).

### Concluding remarks

Although marine seaweeds have been used as biofertilizers since beginning of modern agriculture, only recent studies have focused on the ability of their polysaccharides to enhance plant resistance towards abiotic and biotic stress. In terms of application in agriculture, the algal polysaccharides carrageenans, fucans, laminarans and ulvans have been the most studied ones. The carrageenans are obtained from red algae and have the advantage to have a well-established and sustainable culture system. However, their high market value will probably limit its wide use in plant protection. The fucans, found in the cell walls of brown algae, are constituents of several commercial fertilizers and biostimulants. Studies conducted with fucans have helped to explain some of the beneficial effects of such products on plant physiology. The laminarans are reserve polysaccharides of brown algae, mainly *L. digitata*, which grow in cold waters of the northern hemisphere. These polysaccharides, in a pure form, are currently the most commercially explored to protect plants against a broad spectrum of pathogens. Finally, the ulvans from the cell walls of green seaweeds *Ulva* spp. open new avenues to obtain poly- and oligosaccharides able to induce plant resistance. The *Ulva* species are cosmopolitan and abundant algae that have been weakly exploited. Taking into account the promising results and the enormous biochemical diversity of algal polysaccharides, it is likely that they will provide new resistance inducers to be used in agriculture in a near future.

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