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Marine fungal enzymes as potential degraders of the diverse seaweed cell-walls

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ABSTRACT

Marine fungi play a critical yet understudied role in marine ecosystems, contributing to microbial diversity and ecological balance through their interactions with seaweed and other organisms. These interactions are essential for nutrient cycling and maintaining ecosystem health. While the carbohydrate-active enzymes (CAZymes) of terrestrial fungi are well-documented for plant biomass degradation, the enzymatic capabilities of marine fungi, specifically for degrading seaweed biomass, remain less explored. The distinct sugar composition of seaweed has likely shaped the CAZome of marine fungi, specifically in activities targeting seaweed cell wall polysaccharides. This review focuses on the potential of marine fungal CAZymes as biocatalysts for the degradation of seaweed cell wall polysaccharides. We provide a detailed examination of the unique sugar composition of seaweed cell walls, such as alginates, fucoidans, and carrageenans, and analyze the putative CAZy abilities of marine fungi to target these structures. A better understanding of marine fungal enzymatic processes could unlock sustainable strategies for extracting valuable compounds, such as proteins and nutraceuticals, from seaweed biomass, while enabling the comprehensive valorization of all biomass fractions within a biorefinery framework. By summarizing current knowledge and identifying research gaps, this review highlights the untapped potential of marine fungi as key agents in the development of efficient, integrated seaweed biorefineries.

1. Introduction

The exponential increase in the human population, together with the reliance on untenable food production systems has raised several economic, environmental and socio-ecological challenges. A transition towards sustainable resources and processes is urgently needed to tackle the increasing exhaustion of fertile soils, the pollution of aquatic ecosystems as well as reduce our carbon footprint. The utilization of seaweed (marine macroalgae) as a sustainable resource for alternative protein and other valuable compounds is part of this transition and is attracting increasing attention (Ścieszka and Klewicka, 2019) (Fig. 1). Although seaweed have been part of the human diet for centuries, this has been largely limited to traditional Asian cuisines (Yuan, 2007). However, in the last two decades a strong increase in the consumption of seaweed and their derived functional products has been observed in Europe and America (Biris-Dorhoi et al., 2020; Rioux and Turgeon, 2015). Seaweed biorefinery is still in its early stages and significantly lags behind the more established biorefineries based on terrestrial biomass. Key areas that require further development include the creation of dedicated, efficient enzyme cocktails capable of partially degrading the seaweed cell wall. This would facilitate the extraction of valuable components and enable the saccharification of the residual biomass for further valorisation through fermentation (del Río et al., 2019).

1.1. Seaweed biomass valorization and biotechnological applications

The versatile nature of seaweed extends beyond their ecological significance, as their unique biochemical and structural composition positions them as promising feedstocks for sustainable biorefinery approaches. Recent years have witnessed an intensive exploration of seaweed and their derived bioactive compounds, leading to the

Abbreviations: ALYs, Alginate-lyases; CAZymes, Carbohydrate Active Enzymes; CBMs, carbohydrate-binding modules; CE, carbohydrate esterase; FCSPs, fucose-containing sulfated polysaccharides; GH, glycoside hydrolases; Glc*p*A, Glucuronopyranosic acid; GT, glycosyl transferase; Ido*p*A, Iduronopyranosic acid; LPMO, lytic polysaccharide monooxygenase; NCRs, non-catalytic regions; MFS, cellulose microfibrils; PL, polysaccharides lyase; Rha*p*, Rhamnopyranose; Xyl*p*, Xylopyranosyl.

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development of functional products and biomaterials (Fig. 1) (Buschmann et al., 2017; Kadam et al., 2017; Rioux and Turgeon, 2015). This involves a wide spectrum of applications, encompassing biofuel production, including bioethanol (del Río et al., 2019) organic fertilizers, animal feed, pharmaceuticals, cosmetics, and even human food products (Makkar et al., 2016). Notably, the ongoing shift from wild inshore harvesting to inshore or offshore seaweed cultivation in Europe is a response to environmental concerns and increasing regulatory constraints (van Oirschot et al., 2017). While the scale of seaweed production may not yet rival that of terrestrial crops, there has been a significant increase in the cultivation, harvesting, and utilization of seaweed over the last few decades (FAO, 2018).

Seaweed exhibits remarkable variability in their nutritional composition, influenced by factors such as species, harvesting season, and environmental conditions like salinity, light exposure, temperature, and dissolved inorganic nutrient concentrations (Holdt and Kraan, 2011; Mišurcová, 2011). Nevertheless, several distinctive features stand out (Table 1). Their low-fat content, primarily consisting of n-3, n-6, 20:5 n-3, and 22:6 n-3 polyunsaturated fatty acids, has been recognized for its effectiveness in preventing cardiovascular conditions, including coronary heart disease (CHD) (Costa et al., 2022; Givens, 2009; Shannon and Abu-Ghannam, 2019; Sharifuddin et al., 2015). Seaweed is rich sources of phenolic compounds, bioavailable minerals, and vitamins. Notably, they are high in B vitamins (particularly B1 and B12), as well as lipophilic vitamins such as A and E. This makes seaweed an excellent food substitute for vegan diets, which often lack sufficient B12 (Mæhre et al., 2014; Rizzo et al., 2016). The primary minerals found in seaweed are potassium, sodium, magnesium, and calcium, comprising up to 97 % of the total mineral content. Additionally, they contain trace amounts of microminerals like copper, iron, manganese, iodine and zinc, which can reach up to 0.094 % of the dry weight (dw) of the seaweed (Biris-Dorhoi et al., 2020; Rodrigues et al., 2015). Metalloids like arsenic are also present in seaweed where its content varies widely depending on the species and growing environment (Peng et al., 2023).

Pigmented compounds found in many seaweed species, especially red seaweed, have significant potential in applications such as UV protection and food colorants (E407 and E407). The high content of phycobiliproteins and macro-minerals in red seaweed has led to their utilization in various medical applications, including anti-tumor, antioxidant, anti-microbial, prebiotic, immunomodulatory, anti-cancer,

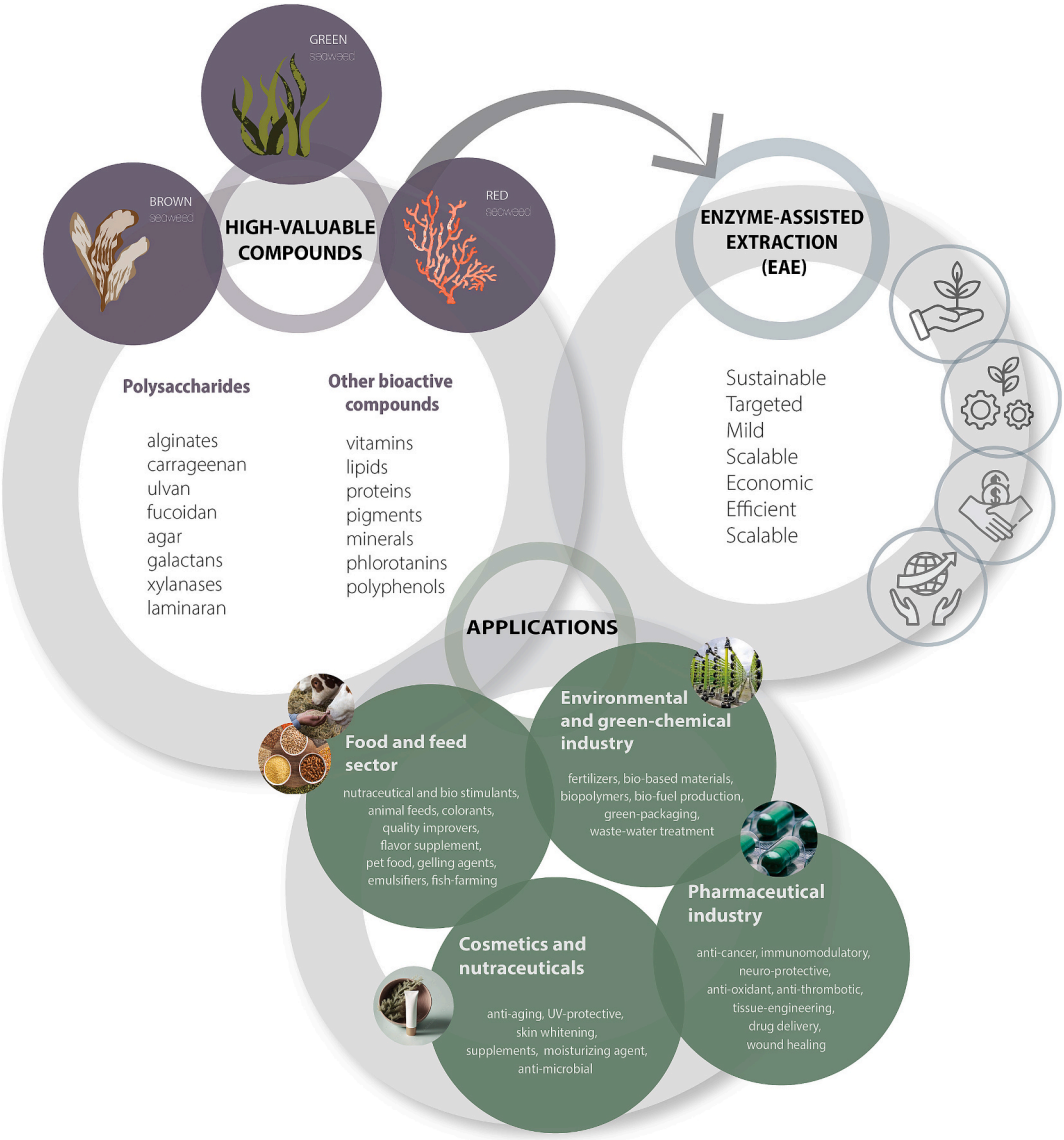

Fig. 1. Application of seaweed based on their bioactive compounds. From the top-left to bottom-right, each circle depicts i) the most valuable compounds of the different groups of seaweed, ii) the most efficient and sustainable extraction methodologies at the moment and iii) the current applications of such compounds on the different biotech sectors.

Table 1
Summary of the most relevant features characterizing the three lineages of seaweed (green, red and brown).

	Green	Red	Brown
Phylum	Chlorophyta	Rhodophyta	Phaeophyceae
Pigmentation	Chlorophyll a and b, carotenoids, xanthophylls	Chlorophylls, carotenoids and phycobilins (phycocyanin and phycoerythrin)	Chlorophyll a and b, carotenoids (fucoxanthin)
Habitat	Fresh and shallow waters (bays and estuaries), also in marine environments	Mostly marine habitats, low tides to 100 m depth and tempered waters	Only marine habitats. Shallow waters and shoreline
Morphology	Multiple levels of complexity. From branching filamentous structures (reticular or bifurcated) to leaf-like branches and green fronds.	Varying thallus size and morphologies: branched (4-8 cm), crusted or laminar with smooth thing/leathery blades (20-40 cm).	Variable complexities: unicellular forms (1 μm) to the largest seaweed (50 m). Generally, small branched bodies or large fronds with ovoid air-bladders
Motility	Sessile and motile with flagella	Sessile	Sessile or free-floating
Reserve polysaccharides	Starch (1.4 %)	Floridean starch and floridoside	Laminarin (35 % dw)
Structural polysaccharides	Cellulose (38-52 %), ulvan (8-29 %)	Carrageenan (75 %), agar (52 %), cellulose, porphyran, xylan, mannan	Alginate (40 %), fucoidan, cellulose
Genus examples	*Chaetomorpha, Cladophora, Codium, Enteromorpha* and *Ulva* (formerly *Enteromorpha*)	*Pyropia, Porphyra, Gracilaria, Chondrus* and *Palmaria*	*Ascophyllum, Laminaria, Macrocystis, Fucus, Nereocystis, Saccharina, Sargassum* and *Undaria*
Other features	8367 species, grouped in 13 classes	7729 species, grouped in 11 classes	2153 species

anti-diabetic, anti-hypertensive, anti-inflammatory, and laxative activities (Aziz et al., 2021; McHugh, 2003) (Fig. 1).

Brown seaweed, in particular, is known for its rich mineral content, including iodine, potassium, and sodium, as well as phlorotannins, a type of phenolic compound. These compounds enhance fiber digestibility in ruminants and promote a balanced human microbiota, making brown seaweed attractive for both feed and nutraceutical industries (Cesário et al., 2018). Laminarin, primarily extracted from brown seaweed, is recognized for its antioxidant, anticancer, anticoagulant, immunomodulatory, and antimicrobial properties, as well as its effectiveness as a drug delivery system (Cesário et al., 2018; Ji and Ji, 2014; Menshova et al., 2014). In addition to their bioactive potential, certain Laminaria and Undaria species (Phaeophyceae) are highly regarded in Asian cuisine for their high glutamic acid content, contributing to the sought-after "umami" taste (Moerdijk-Poortvliet et al., 2022; Yamaguchi and Ninomiya, 2000). The fraction of the brown seaweed cell wall known as fucose-containing sulfated polysaccharides (FCSP) has attracted significant attention due to its various biological and therapeutic activities, including inhibiting inflammation and oxidative processes (Albuquerque et al., 2013; Deniaud-Bouët et al., 2017; Nunes and Coimbra, 2018; Yuan and Macquarrie, 2015). Recent studies have also revealed the positive effects of FCSPs on cell growth and differentiation, making them valuable in the development of drug delivery systems and tissue engineering approaches (Nunes and Coimbra, 2018; Zeng et al., 2019). The rich polysaccharide profile characterizing not only brown seaweed but most algal species, positions them as important sources of bioactive compounds with antimicrobial, antioxidant, and immuno-stimulating qualities (Cesário et al., 2018; Shannon and Abu-Ghannam, 2019).

The protein content of seaweed is equally noteworthy, ranging from 9 % to 31 % of the total dw content, depending on the seaweed species (Espinosa-Ramírez et al., 2023; Holdt and Kraan, 2011; Rioux and Turgeon, 2015). This places them in the same league as other plant protein sources, including legumes, some cereals, and nuts, thus making them attractive candidates for alternative protein production systems (Bleakley and Hayes, 2017; de Souza Celente et al., 2023; Espinosa-Ramírez et al., 2023; Fleurence, 1999).

In summary, seaweed offer various advantages as raw materials, including their functional and bioactive properties, protein quality comparable to other common sources, and the high photosynthetic capacity that enables rapid growth and substantial biomass and protein yields. In some cases, algal biomass yields can even surpass those of terrestrial crops (Bleakley and Hayes, 2017; Jung et al., 2013; van Krimpen et al., 2013). This, combined with their ability to thrive without freshwater supply and arable land, make seaweed a sustainable and efficient resource for food and valuable compound production.

However, despite the high potential, current methods for extracting seaweed-derived products are neither environmentally sustainable nor economically feasible. To harness the full biotechnological potential of seaweed there is a clear need for the development of alternative, efficient and sustainable extraction methods. In the following sections, we will discuss the possibility of enzyme-assisted processing of seaweed biomass, with a specific focus on enzymes produced by marine fungi. For that, we will delve into the diversity in composition of seaweed cell walls and how this might require different enzyme degrading capacities.

2. Diversity of seaweed and their cell wall composition

Seaweed, comprise an extensive group of multicellular, eukaryotic, photosynthetic organisms distributed across many different aquatic habitats, with the marine realm being the predominant one (Bonugli-Santos et al., 2015; Sowell et al., 2008). Currently, 180,853 species have been described in AlgaeBase (accessed at 26.06.25) (Guiry and Guiry, 2022). Seaweed perform core functions in the development of the marine ecosystem and food-web by reducing the CO_2 to organic carbon (meaning food for higher trophic levels) and releasing almost half of the oxygen the planet consumes (Barsanti and Gualtieri, 2024; Brodie et al., 2017; Field et al., 1998). It is broadly believed that seaweed, as we know them to date, originated more than 1.5 billion years ago from a series of reiterated endosymbiotic events that gave rise to such a biologically and phylogenetically diverse group of species (Khan et al., 2020). Seaweed are commonly grouped into three unrelated and taxonomically distant lineages so-called Phaeophyceae (brown seaweed), Rhodophyceae (red seaweed) and Chlorophyceae (green seaweed), based on their pigmentation. Green and brown seaweed mainly live in shallow areas close to the waterline while some red seaweed favor the deep-sea waters where sunlight availability is restricted (Cesário et al., 2018, Caseiro et al., 2022).

Their complex evolutionary history has equipped seaweed with specific traits that can be clearly identified by the distinct carbohydrate profiles present in their cell wall structures. Seaweed cell walls are generally characterized as fibrillar networks embedded in an amorphous matrix. Various specific functions have been attributed to the algal cell wall, depending on the species. They provide protection of the cell against dehydration, physical and ambient perturbations such as water movements or frosting (Percival, 2007). They also regulate other cellular mechanisms such as turgor (through osmotic regulation mechanisms), cell-cell adhesion, reproduction, cell development and differentiation, as well as algal immunity (Brownlee, 2002; Popper et al., 2014; Reed, 1989; Siegel and Siegel, 1973; Synytsya et al., 2015).

2.1. Green seaweed

Green seaweed represent a highly ubiquitous group of organisms that

fostered pivotal evolutionary events not only on the development of the Chlorophyceae lineage but also on the emergence of the first terrestrial plant species (Kenrick and Crane, 1997; Leliaert et al., 2012). Two lineages of green seaweed can be differentiated: Chlorophyta and Streptophyta (Bremer, 1985; Lemieux et al., 2019). While Chlorophyta contains most of the well-known green algal species, the Streptophyta lineage contains the paraphyletic group of Charophyta from which terrestrial plants evolved. Nine different classes are currently described under the green algal phylum, being highly variable in their morphology, size and ecological behavior (Lewis and McCourt, 2004; Rioux and Turgeon, 2015). Green algal cells are characterized by the presence of chloroplasts with double membranes and piled thylakoids, a sheet-like membrane-bound compartment found in chloroplasts and Cyanobacteria and where light-dependent photosynthesis reactions occur. The photosynthetic capacity of green seaweed is due to the presence of chlorophylls (a and b), xanthophylls and carotenes, that are contained in the algal plastid (Table 1) (Tanaka and Tanaka, 2019). These pigments show maximum absorption in the red and blue regions of the light spectrum providing the characteristic green colors of green seaweed (Chronakis and Madsen, 2011). They are found either in freshwater (estuaries, rivers, ponds and lakes) or marine environments, thus forming one of the most heterogeneous groups of photoautotrophic protists inhabiting the planet (Cesário et al., 2018; Naselli-Flores and Barone, 2009).

The most well-known green seaweed include species from the genus *Chaetomorpha, Cladophora, Codium* and *Ulva*, of which the last genus is most commonly consumed and commercially exploited (Cordero, 2003). The Ulvophyceae and Codium groups are mainly found in marine habitats, where they can form large coastal blooms (Leliaert et al., 2012) that, triggered by the invasive nature of some species and/or certain nutrient conditions can lead to an excessed seaweed abundance in certain coastal waters (Not et al., 2004; O'Kelly et al., 2003). *Ulva*, for instance, is a widely distributed blooming seaweed that causes the largest green tide blooms. This phenomenon is described when high eutrophic levels enhance the growth and reproduction of certain seaweed species that thrive when changes in marine nutrient concentrations create favorable conditions for their sporulation. Moreover, the great adaptability of green seaweed has enabled their survival in extreme habitats, including hypersaline (Vinogradova and Darienko, 2008) and highly acidic environments (Zettler et al., 2002) as well as in varying conditions where cold and heat prevail. Other green seaweed have adapted to deep-sea waters where hydrothermal activity is present (Edgcomb et al., 2002; Leliaert et al., 2012). Seaweed have developed different living strategies: while some species survive as free-living organisms, others, like Prototheca (Chlorophyta), establish heterotrophic and obligate parasitic relationships with various living organisms (Huss et al., 1999; Nedelcu, 2014; Sudman, 1974). Likewise, many symbiotic interactions have been identified between green seaweed and organisms like fungi, diverse cnidarians and mollusks including muscles and other aquatic vertebrates (Kerney et al., 2011; Kovačević et al., 2010; Leliaert et al., 2012).

The green algal cell wall is composed of cellulose (up to 52 % of dw) and water-soluble polysaccharides, being ulvan the main representative (8-29 % of dw) of the polysaccharide fraction. This carbohydrate provides green seaweed with the characteristic flexibility and gel-like nature (Cesário et al., 2018; Lahaye and Robic, 2007). Additional polysaccharide structures have been found in certain species of green seaweed, ranging from alkali soluble (1,4)-β-D-glucuronans to sulfated rhamnans (mainly found in Monostroma, Ulva - formerly Enteromorpha, and Ulva species), and sulfated xylomannans and arabinopyranans (in Codium species), showing the diversity of the sugar composition of this lineage (Derksen et al., 2023). Most of these compounds have been intensively studied due to their antitumor and immune-modulating capacities (Jiao et al., 2010) as well as their use as antihyperlipidemic (Qi et al., 2012), antioxidant (Devi et al., 2011; Li et al., 2018) and anticoagulant agents (Wang et al., 2014).

2.2. Red seaweed

It is generally agreed that red seaweed appeared for the first time after the initial endosymbiotic event, together with green seaweed and the Viridiplantae and Glaucophytes groups (Moreira and López-García, 2017). This lineage, called Rhodophyta, contains 5000 to 6000 species divided over seven different classes under two subphyla, Rhodophytina and Cyanidiophytina. Some examples of the most common red seaweed genera are *Pyropia, Porphyra, Gracilaria, Chondrus* and *Palmaria*. Many species of *Porphyra* and *Pyropia* are cultivated at large-scale in Japan, China and South Korea where they are used by the food industry (McHugh, 2003). These species generally grow as soft and thin bodies in the intertidal zones of temperate waters. In contrast, *Palmaria* species develop smooth and leather-like fronts of 30-40 cm of length and prefer to grow in the shores of the North Atlantic waters where they are exposed to tidal currents. Other species, known as coralline red seaweed, have become commercially valuable sources of calcium carbonate which is formed after calcification and deposition of the red algal extract (Makkar et al., 2016).

The striking red coloration of these seaweed is attributed to their high content of pigments, namely phycoerythrin and phycocyanin, which actively participate in photosynthesis and green light absorption (Arad and Yaron, 1992; Chronakis and Madsen, 2011). Carotenoids like β-carotene, zeaxanthin, and antheraxanthin are also prevalent, contributing to their characteristic appearance. Furthermore, red seaweed are rich in phenolic compounds and various vitamins such as pro-vitamin A, vitamin C, and vitamins B2, B9, and B6. Notably, they boast a remarkable amino acid profile, with a protein content ranging from 10 % to 50 % (dw), varying based on species, environmental conditions, and seasonal fluctuations (Gaillard et al., 2018; Makkar et al., 2016). Species within the *Pyropia* and *Porphyra* (Rhodophyta) genera are particularly noteworthy for their high protein ratios, ranging from 18 % to 50 % (dw) (Marsham et al., 2007; Rupérez and Saura-Calixto, 2001; van Groenigen et al., 2022). Although their overall lipid content is relatively low (0.3-3.8 % of dw), approximately 66 % of it consists of nutritionally valuable polyunsaturated fatty acids (PUFAs). Additionally, the presence of phycobiliproteins, macro-minerals, and other trace minerals further enhances the already impressive nutritional and functional profile of red seaweed.

The cell wall of red seaweed is mainly composed of water-soluble and long-chain carbohydrates, with carrageenan reaching up to 75 % (dw) and agar up to 52 % (dw). Cellulose is also present, however to a much lesser extent than in terrestrial plants. Carrageenan and agar have been lately exploited due to their high potential as bioactive compounds, being relevant for many different industrial sectors (Torres et al., 2019).

Amounting to 61 % of the global seaweed production, red seaweed provides the highest economic activities due to the commercial importance of their derived extracts (Álvarez-Viñas et al., 2019; Peñuela et al., 2018). They are mainly used for carrageenan extraction, although the high biomass yields that can be recovered from their cultivation are awakening interests within the biorefinery and biofuel industries (Álvarez-Viñas et al., 2019). An example of a biorefinery has been proposed where seaweed biomass and waste-derived galactose-rich substrates are valorised into tagatose (Baptista et al., 2021).

2.3. Brown seaweed

The phylogenetic description of brown seaweed (Phaeophyceae) has been a major topic of debate for years. While some steps forward are being taken through genomic analysis, an established agreement on the taxonomic relationships of brown seaweed has not been reached yet. Initial classifications have been based on morphologic and/or reproductive traits of the seaweed, identifying the simplest filamentous brown seaweed as the basal forms that later gave place to further structural complexities (Phillips et al., 2008). Currently, this lineage is positioned within the Stramenopiles clade which englobes a wide

variety of eukaryotes including diatoms, oomycetes and other unicellular organisms (Phillips et al., 2008; Torode et al., 2016).

Brown seaweed are characterized by the presence of multicellular structures and cell walls. Although such traits are shared with the other two lineages of seaweed, the evolution of brown seaweed has occurred independently from the green and red lineages for more than a billion years (Coelho and Cock, 2020). The cell wall structure of brown seaweed contains unique polysaccharides that have been attracting significant scientific attention due to their potential as novel biomolecules (Michel et al., 2010). This interest was further fueled by the comprehensive analysis of the first brown algal genome sequence from *Ectocarpus* sp. Ec32 (Birkemeyer et al., 2020; Cock et al., 2010) and subsequent investigations into the biosynthetic pathways responsible for polysaccharide backbone formation (Michel et al., 2010). These collective efforts resulted in the development of the initial model representing the cell wall of the Fucales order (Deniaud-Bouët et al., 2014). Over time, this model went through various refinements and additions, into the current version (Fig. 2), which in this review, serves as a representative example of the diverse structural composition that seaweed cell walls can harbor.

The cell wall of brown seaweed is essentially composed of alginate, FCSPs and cellulose microfibrils (MFs) in a 3:1:1 ratio. To a lesser extent, certain glucans and arabinogalactans establish glycoproteic linkages with the cell wall proteins (Michel et al., 2010). Ions, together with halogenated and sulphated phenols, such as phlorotannins have been additionally identified in some brown seaweed cell walls (Michel et al., 2010; Deniaud-Bouët et al., 2017).

The first speculative model of the cell wall (Drula et al., 2022) already showed the complex interlinkage of the polymeric fraction that provides the particular structural composition of these species of seaweed. However, the extraction and systematic analysis of the individual polymers of close-related species of brown seaweed, provided upgraded versions of the cell wall model (Deniaud-Bouët et al., 2014). Such studies led to conclude that the brown algal cell wall is an ensemble of at least two independents carbohydrate scaffolds: i) a network of cellulose microfibrils crosslinked with FCSPs and proteins. The MFs are assembled in rows of 10-100 subunits, forming a flat ribbon-like structure with a uniform thickness of 2.6 nm and 2,6-30 nm in width ii) a three-dimensional scaffold consisting of alginate and cross-linked polyphenols (Fig. 2). While the first structure contributes to the osmotic response and adaptability, the second one is believed to have an important impact on cell wall stiffness along with calcium ion exchange and polyphenol cross-linkage (Deniaud-Bouët et al., 2014; Michel et al., 2010).

3. Algal polysaccharides and the enzymes acting on them

One of the most sustainable and efficient ways of processing biomass relies on enzyme-assisted methods (Gurpilhares et al., 2019; Hardouin et al., 2016; Sabeena et al., 2020; Wijesinghe and Jeon, 2012). In nature, many microorganisms hold the genetic capacity to encode for different Carbohydrate Active enZymes (CAZymes), rendering them promising tools for marine and terrestrial plant substrate depolymerization (Balabanova et al., 2018a; Jiakang Li et al., 2022a). Based on their amino acid composition and structural homology, these enzymes are classified into protein families under the CAZy classification. A total of 191 glycoside hydrolase (GHs), 44 polysaccharides lyase (PLs), 138 glycosyl transferases (GT), 21 carbohydrate esterases (CE), and 18 auxiliary monooxygenases families (AA) are currently described in the Carbohydrate Active Enzymes database (accessed at 26.06.2025) (http://www.cazy.org; Drula et al., 2022). Accessory depolymerizing enzymes have been described to work in synergy with backbone-degrading enzymes in order to provide a more efficient processing of the polysaccharide structures (Banerjee et al., 2010; Hu et al., 2011). Such process might be regulated at a transcriptional level (Benocci et al., 2017).

The polysaccharide fraction of seaweed is mainly located in the algal cell wall, whereas some storage carbohydrates can be found in the plastid structure (Rioux and Turgeon, 2015). Thus, based on their functionality, two different types of polysaccharides can be identified in

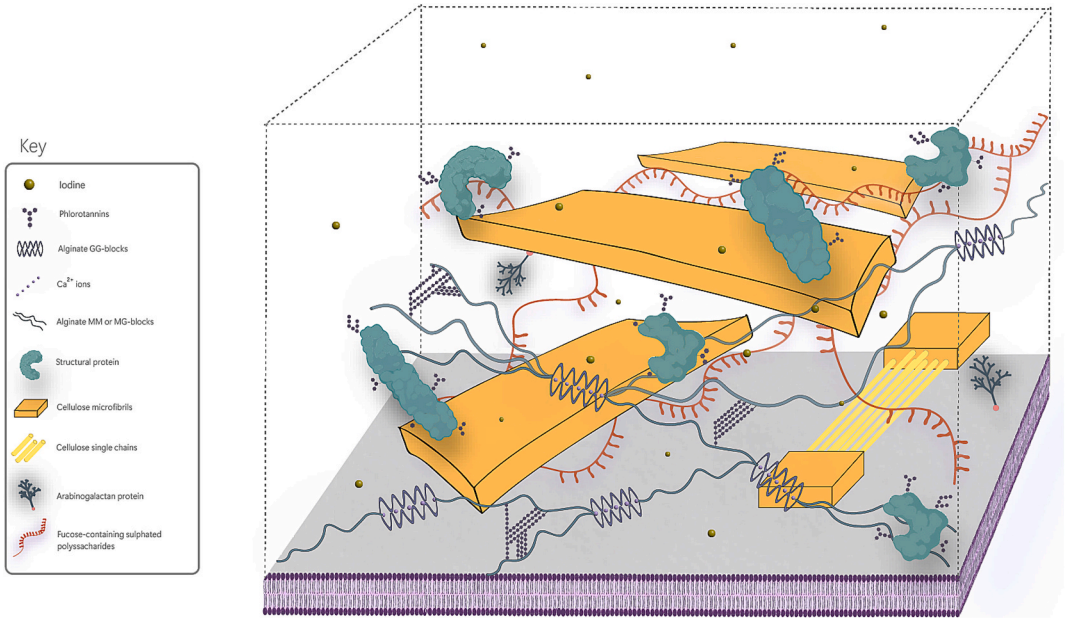

Fig. 2. Brown seaweed primary cell-wall model. The basic composition of the primary cell-wall relies on two independent structural networks: i) alginate network, that is composed by β-(1,4)-D-mannuronic (M) and α-(1,4)-L-glucuronic (G) residues, forming MM, MG or GG assemblies. The latter can be crosslinked by Ca + 2 ions, ii) the cellulose microfibrils (MFs) that are disposed as ribbon-like structures and form a network that is crosslinked with fucose-containing sulphated polysaccharides (FCSPs) and with putative structural proteins. Phlorotannins appear to be crosslinked not only with the alginate network but also with the predicted structural proteins. The structure of the structural proteins and phlorotannins depicted in the model are speculative so far. Halogenated compounds are commonly found in the brown-seaweed cell wall, especially in the case of iodin, found as a free ion. All cell-wall components are shown to scale. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

seaweed: storage polysaccharides such as laminarin and starch; and structural polysaccharides such as agar, carrageenan, ulvan and cellulose (Cesário et al., 2018). With the exception of cellulose and xylan, which are present in both terrestrial and marine biomass, the sugar profile of algal substrates differs drastically from the one present in terrestrial biomass. Specific polysaccharides, such as laminarin, agarose, fucoidan, carrageenan, ulvan, along with their sulfated variants, form a large part the polysaccharide composition of seaweed substrates (Synytsya et al., 2015). Consequently, the enzymatic activities required for the processing of such structures also differ significantly from those known to degrade terrestrial plant polysaccharides (de Vries et al., 2020b).

Next to that, many factors such as the inherent biology of seaweed, as well as the physical and environmental fluctuations to which they are exposed, can cause variations in the structural and proportional distribution of the polysaccharides of the seaweed cell. This variation on the disposition, nature and linkage of the building blocks can ultimately impact the functional properties of the polysaccharide fraction (Bäumgen et al., 2021; Busi et al., 2014; Shanmugam and Mody, 2000; Xu et al., 2017). A close understanding of these variable polysaccharide compositions and structures, together with a comprehensive insight on the specific activity of the enzymes acting on them is therefore crucial for optimal depolymerization and extraction processes.

3.1. Storage polysaccharides of seaweed

3.1.1. Starch

Starch consists of two types of α-D-glucan chains: amylose (20 %) and amylopectin (80 %). While amylose is formed as a linear polymer of α-(1,4) linkages, amylopectin has a branched conformation with an additional 5 % of α-(1,6) linkages in its structure (Møller and Svensson, 2016). Starch serves as the primary reserve carbohydrate in green seaweed constituting up to 4 % of dw. It is stored within chloroplasts, where it forms granular accumulations of varying amounts and sizes (Busi et al., 2014). Starch metabolism plays a pivotal role in cell cycle activities in seaweed, ensuring a consistent supply of carbon and energy, especially when other sources like photosynthesis fall short (Zachleder et al., 2021). Notably, starch can be converted into D-glucose and short gluco-oligosaccharides in industrial processes, finding diverse applications in food and textile manufacturing, paper production, and beer brewing (McHugh, 2003; Mohamad Yazid et al., 2018). In red seaweed a structural variant of starch, floridean starch, is present, which is

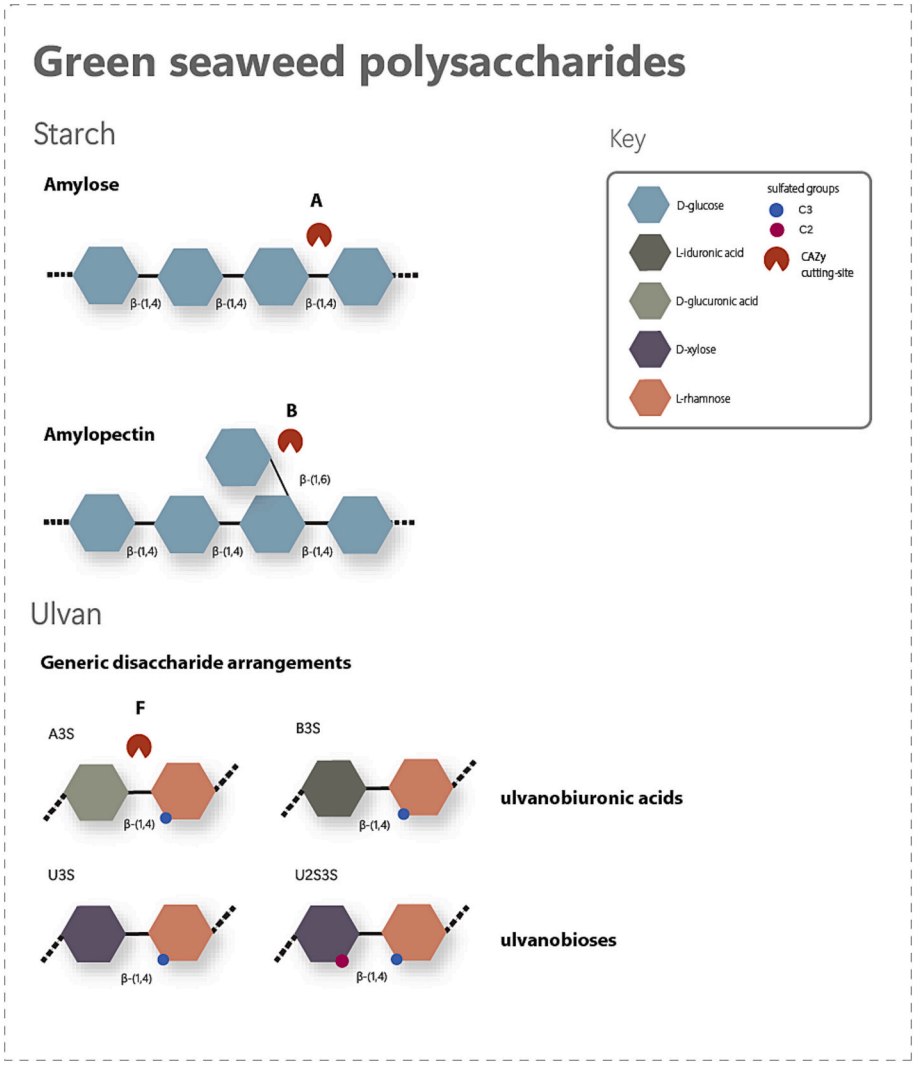

Fig. 3. Main polysaccharides of the green seaweed cell wall. General chemical structures of ulvan and mannan are depicted. The four types of structural conformations established by ulvan are shown and classified under ulvanobiuronic acids or ulvanobioses. Mannan is displayed as its general backbone structure. For simplification, all sugar monomers are depicted as hexagons, followed by the type of linkage established among them. The chemical nature of each monomer is indicated by the color code shown in the key. Sulphated polysaccharides are indicated with round shapes. CAZyme-targeted linkages are indicated with arrows whose letters are linked to their corresponding activities indicated in Table 2.

characterized by its high branching degree and the presence of additional α-(1,3) glucosyl groups in the amylopectin structure (Fig. 3).

3.1.1.1. Starch degrading enzymes. Although starch is a relatively simple polysaccharide mainly formed by α-(1,4)- and α-(1,6)-linked glucose units, several enzymatic activities are required for its degradation (Das and Kayastha, 2023; Steup, 1990). These include various GHs and lytic polysaccharide monooxygenases (LPMOs).

GH families active on starch are GH3, GH13, GH14, GH15, GH31, GH57 and GH119, which include various activities: α-Amylases (EC3.2.1.1) are present in GH13, GH57, GH119 and GH126 and catalyze the breakdown of the α-1,4 linkages present in amylose or amylopectin, but not the α-(1,6) linkages. Two types of exoamylases have been described: glucoamylases (EC 3.2.1.3, GH15 & GH97) that catalyze the cleavage of both α-(1,4) and α-(1,6) glycosidic bonds (Das and Kayastha, 2023); and α-glucosidases (EC 3.2.1.20, GH4, GH13, GH31, GH63,

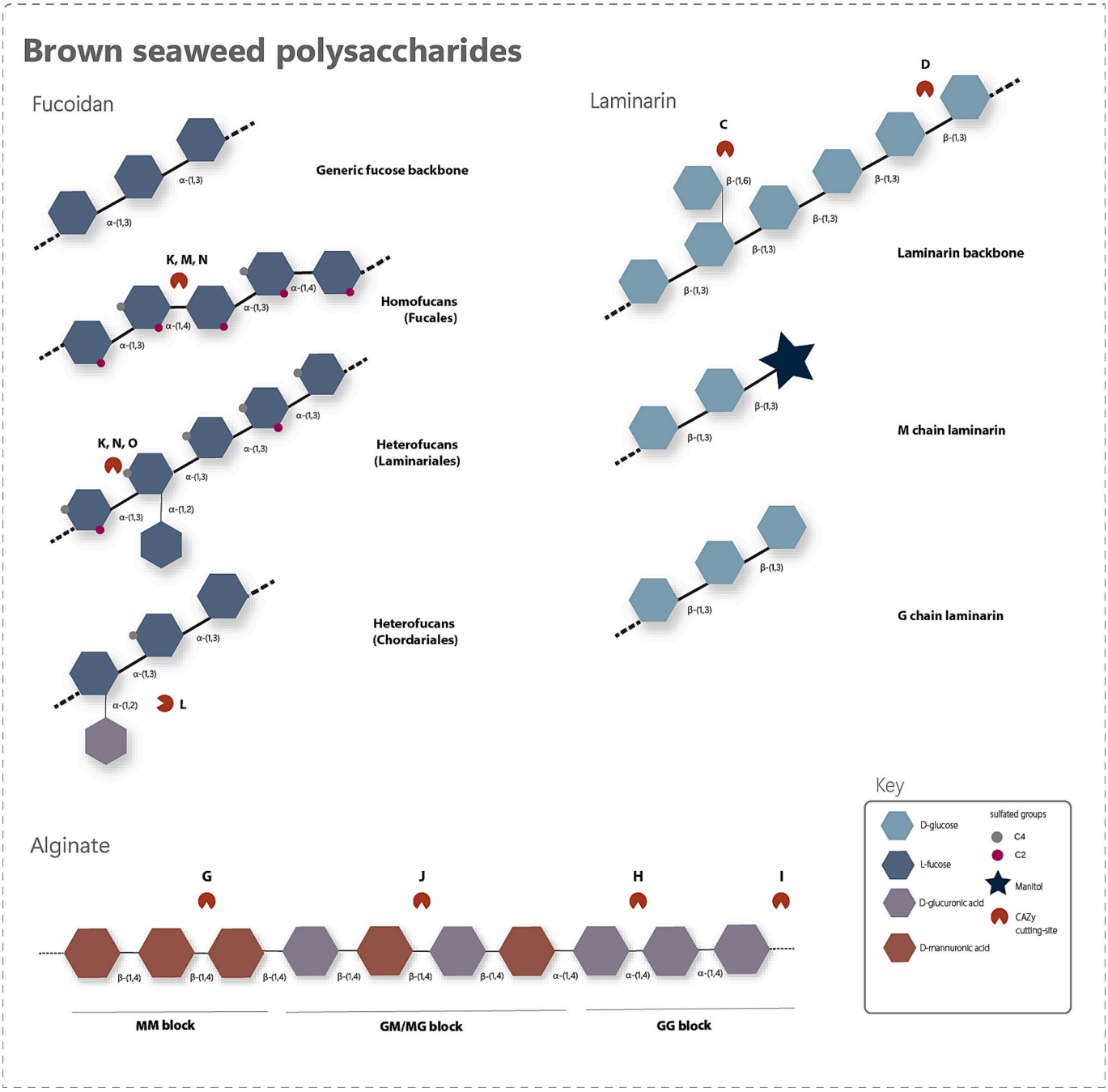

Fig. 4. Main polysaccharides of brown seaweed. Presentation of the basic chemical structures of fucoidan, laminarin and alginate are depicted. In the case of fucoidan. The generic fucose backbone is depicted next to the two most common conformations (homofucan and heterofucan) found in the Fucales, Laminarales and Chordariales order of brown seaweed. The laminarin backbone is depicted next to the mannitol (M) and D-glucose (G) moieties that can form small chains at the reducing ends of the main laminarin backbone structure. The alginate backbone is depicted so that the three types of assemblies formed by D-mannuronic acid (M) and D-glucuronic acid (G) are indicated. For simplification, all sugar monomers are depicted as hexagons, followed by the type of linkage established among them. The chemical nature of each monomer is indicated by the color code shown in the key. Sulphated polysaccharides are indicated with round shapes CAZyme-targeted linkages are indicated with arrows whose letters are linked to their corresponding activities indicated in Table 2. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

GH97 & GH122) that act on short starch-derived oligosaccharides, such as maltose (Lu and Sharkey, 2006), resulting in the release of D-glucose from the non-reducing end (Tagami et al., 2013).

3.1.2. Laminarin

In brown seaweed, the primary storage polysaccharide is laminarin (a.k.a. laminaran), a water-soluble and low-molecular weight polysaccharide grouped under the β-glucan family (Li et al., 2021). It can reach up to a 62 % of dw, with the highest laminarin content in *Saccharina, Laminarina,* and *Fucus* spp. (Huang et al., 2021). The structure of laminarin differs strongly from other terrestrial glucan storage polysaccharides as it is formed by β-(1,3) glucans rather than by the α-(1,4)-glucans mainly found in terrestrial plants. The backbone structure is formed by β-(1,3)-glucopyranose residues with β-(1,6)-glucose moieties branching from the main chain with a frequency of ≤10 % (Chen et al., 2021; Menshova et al., 2014; Nelson and Lewis, 1974). To a lesser extent, some β-(1,6)-intrachain linkages can also be present (Kadam et al., 2015). Additional moieties like mannitol (M), glucose (G) or and *N*-acetylhexosamine have been occasionally reported forming small chains at the reducing ends of the main backbone structure (Chizhov et al., 1998; Read et al., 1996; Stone, 2009). The presence or absence of M residues on the terminal ends led to establish two different laminarin types: M type, containing a M residue at the reducing end, or G type, where the M unit is replaced by a glucose residue (Ermakova et al., 2013; Menshova et al., 2014) (Fig. 4).

As reviewed by Usoltseva et al. (2020), the ratio of (1,3):(1,6) bonds vary among algal species, resulting in structural and molecular differences. For instance, *Laminaria hyperborea* exhibits very low β-(1,6) content, while *Eisenia bicyclis* shows a higher proportion, up to 1:3 or 2:3 (Schiøtt et al., 2024). Generally, the degree of polymerization in laminarin ranges from 15 to 40 units, with a molecular weight ranging from 3 to 10 KDa (Hentati et al., 2020). Some exceptions within the Laminarales order were observed, reaching MWs of up to 50 KDa (Shevchenko et al., 2007; Zvyagintseva et al., 2003). The content of laminarin varies based on species, harvesting season, stage of development, and environmental conditions (Kadam et al., 2017; Lee et al., 2011; Nelson and Lewis, 1974; Chizhov et al., 1998; Read et al., 1996; Stone, 2009). The highest recovery yields of laminarin are obtained from species belonging the Laminariaceae family (Laminarales order), whereas the lowest appear to be in the *Sargassaceae* family, from the Fucales order (Usoltseva et al., 2020). The harvesting season seems to affect the ratio of (1,3):(1,6) and consequently the type of generated laminarin structure, with the higher MWs identified in the summer harvests. Laminarins with less than 2 % of β-(1,6) glucan residues can only be dissolved in water above 37 °C (Nelson and Lewis, 1974; Usoltseva et al., 2020), while a higher percentage of β-(1,6) moieties result in soluble laminarins (Nelson and Lewis, 1974).

Laminarin was first isolated in 1885 from a seaweed of the *Laminaria* genus (Schmiedeberg, 1885). Today, laminarin is predominantly extracted from the dry thallus of *Laminaria*, *Saccharina*, and *Fucus* species. Laminarin is indigestible in the human intestinal tract, making it a dietary fiber with prebiotic effects. Its ability to tailor the intestinal fatty acid composition, pH, and mucus renders laminarin a highly valued metabolic modulator and bioactive compound (Hussein, 2022).

3.1.2.1. Laminarases as a sort of β-glucanases. The degradation of β-glucan structures has been extensively described in natural environments, where various organisms deploy their CAZyme activities to break down these polysaccharides. β-D-glucanases exhibit two types of activities depending on where they cleave the polysaccharide chain: *endo*-acting enzymes, which hydrolyze internal linkages while maintaining the bond configuration, and *exo*-acting enzymes, which degrade β-(1,3)-D-glucans by sequentially removing monomeric or oligomeric units from the reducing end of the chain (Burtseva et al., 2003). Contrarily, *exo*-acting glucanases are typically produced by fungi to generate energy during the slow degradation of the β-(1,3)-D-glucans. Their activities are deployed over the reducing end of the polysaccharide chain, by sequentially removing its monomeric or sometimes oligomeric units (Kusaykin et al., 2017). These enzymatic activities can result in three types of reactions: i) hydrolysis, producing glucose and oligosaccharides, ii) transglycosylation, yielding glycosides, and iii) glucanosyl transfer, which produces larger, more branched products (Henrissat, 1991a; Usoltseva et al., 2020).

All glucosidases acting as *O*-glycoside hydrolases fall currently under the number EC.3.2.- and are classified as either *exo*-acting glucanases (EC.3.2.1.58); *endo*-β-(1,3)-D-glucanases (EC.3.2.1. 39) or endo- β-(1,3); (1,4)- D-glucanases (EC.3.2.1. 6) (Henrissat, 1991). The optimal activities of reported endo- β-(1,3)-D-glucanases occur at slightly acidic values, ranging from 3.8 to 6 (Martin et al., 2007). Their molecular weights vary widely among the different kingdoms with the largest members belonging to eukaryotic species (Caseiro et al., 2022). Although the most common sizes vary from 30 to 50 kDa, smaller enzymes (12 kDa) are found in species like *Citrus aurantiifolia* (Tracheophyta) and bigger ones of up to 230 kDa in *Aspergillus nidulans* (Fungi, Ascomycota) (Bai et al., 2021; Y. Gueguen et al., 1997; Rotchanapreeda et al., 2020). In fungi and bacteria, the temperature optimum of these enzymes seems to fall within the mesophilic range, from 24 to 40 °C, with some exceptions in archaeal extremophiles like *Pyrococcus furiosus* (Euryarchaeota), which glucanases can reach up to 105 °C of optimal temperature (Alvarez et al., 2015; Martin et al., 2007; Szilágyi et al., 2010).

Laminarases can be classified as a subset of β-glucanases, being able to cleave the laminarin backbone (Bauermeister et al., 2010). Their activities are assigned to various GH families including GH5, GH8, GH16, GH17, GH26, GH30, GH55 and GH157 (Table 2). These enzymes are widely distributed in nature and have been isolated from many microorganisms like bacteria, yeast and fungi, as important assets for biotechnology where they can be used to transform complex substrates into simpler and valuable molecules.

Laminarin utilization has been described to occur at the intra- and extracellular level: two outer membrane *endo*- β-(1,3)-glucanases belonging to the GH16 family together with a periplasmic *exo*-(1,3)-β-glucanase from the GH3 family, were suggested to mediate the degradation of laminarin units into glucose monomers in the marine *Gramella forsetii,* a marine Flavobacteriaceae (Kabisch et al., 2014). Further mobilization of glucose monomers into the cytosolic space take place by a constitutively expressed sugar transporters like the major facilitator superfamily (MFS) permease or ABC-type (ABC) import systems (Kabisch et al., 2014; Hashimoto et al., 2010; Miyake et al., 2004), that ultimately enable glycolysis to take place giving pyruvate as an end product.

3.2. Structural cell wall polysaccharides of seaweed

3.2.1. Ulvan and glucuronan

Ulvan is a complex sulfated biopolymer generally extracted from various Ulvales species such as *Ulva australis* (formely *Ulva pertusa*), *Ulva compressa (*formely *Enteromorpha compressa), Ulva intestinalis* (formerly *Enteromorpha intestinalis*), *Ulva rigida*, and *Ulva arasakii* (Lahaye and Robic, 2007; Ray and Lahaye, 1995). In these species, ulvan can reach up to 30 % of the algal biomass and its structure is based on four different monosaccharide units including rhamnose, glucuronic acid, iduronic acid and xylose (Kidgell et al., 2019). In ulvan, these are mostly found as rhamnopyranosyl (Rha*p*) (16,8-45 % dw), xylopyranosyl (Xyl*p*) (2-12 % dw), glucuronopyranosic acid (Glc*p*A) (0,5-6,4 % dw), iduronopyranosic acid (Ido*p*A) (6,5-19 % dw) (Stiger-Pouvreau et al., 2016). Such groups of rather uncommon sugars assemble in recurring 4-linked disaccharide structures to eventually form the particular ulvan backbone (Brading et al., 1954). The disaccharide sets are characterized as either ulvanobiuronic acids, or ulvanobioses. The two main ulvanobiuronic acids are designated as type A ulvanobiuronic acid 3-sulfate

Table 2
List of CAZyme activities related to the degradation of the various polysaccharides found in the cell wall of brown, green and red algal cell wall. The corresponding families, activities and the specific enzymes are included next to each of the targeted substrates and author(s) characterizing each activity. The activities described in fungi are shown in bold.

CAZyme	Target	Family	Activity	Substrate	Specific enzyme	Reference
Amylases	A	**GH13**, GH57, GH119	EC3.2.1.1	**Starch**	α-Amylases	(Manners, 1963; Schwimmer and Balls, 1949; Vallee et al., 1959)
		GH15, GH97	EC 3.2.1.3		glucoamylases	(Copeland and Miller, 1956; French, 1981; Tsujisaka et al., 1958)
		GH4, **GH13**, GH31, GH63, GH97, GH122	EC 3.2.1.20		α-glucosidases	(Bruni et al., 1970; Flanagan et al., 1978; Sørensen et al., 1982)
	B	GH14	EC 3.2.1.2		β-Amylases	(Kitamoto et al., 1988; Lee et al., 2001; Yamaguchi et al., 1996)
Laminarases	C	GH8, GH3	EC 3.2.1.6	**Laminarin**	endo-β-(1,3)/ (1,4)-glucanase / lichenase-laminarinase	(Reese and Mandels, 1959) (Kabisch et al., 2014)
		GH5, GH16, GH17, GH64, GH157	EC 3.2.1.39		endo-β-(1,3)-glucanase / laminarinase	(Becker et al., 2017; Chesters and Bull, 1963; Reese and Mandels, 1959), (Wang et al., 2021)
		GH55, GH128, GH132, GH131	EC 3.2.1.58		laminarin-degrading enzyme	(Barras and Stone, 1969; Reese and Mandels, 1959)
Mannanases	D	GH30	EC 3.2.1.75		β-(1,6)-glucanase	(Becker and Hehemann, 2018; Reese and Mandels, 1959)
	E	GH5_10, **GH26**	EC 3.2.1.78	**Mannan**	β-mannanase	(Ootsuka et al., 2006), (Reese and Mandels, 1959), (Eriksson et al., 1968)
Ulvan lyases	F	PL24	EC 4.2.2	**Ulvan**	ulvan lyase	(Ulaganathan et al., 2018), (Kopel et al., 2016), (Gao et al., 2019)
		PL25				(Gao et al., 2019)
		PL28				(Nyvall Collén et al., 2011)
		PL37				(Nyvall Collén et al., 2011), (Ulaganathan et al., 2018)
		PL40				(Konasani et al., 2018)
		GH2, GH3, GH39, GH43, GH78, GH88, GH105	EC 3.2.1.-			(Reisky et al., 2019)
Alginate lyases	G	PL5-**PL8**, PL14, PL15, PL17, PL18, PL31, PL32	E.C 4.2.2.3	**Alginate**	alginate lyase/endo-acting polyM lyases	(Reisky et al., 2019)
	H	PL6, **PL7**, PL18	EC 4.2.2.11		poly(α-*L*-guluronate) lyase / endo-acting polyG lyases	(Davidson et al., 1977; Xiao et al., 2006), (Pilgaard et al., 2019)
	I	PL6, **PL7**, PL14, PL15, PL17	EC 4.2.2.26		*exo*-acting oligo-alginate lyases	(Boyd and Turvey, 1977; Davidson et al., 1977), (Pilgaard et al., 2019)
	J	PL6, **PL7**, PL14, PL18, PL24, PL25, PL34, PL39	EC 4.2.2.-		MG-specific alginate lyase	(Boyd and Turvey, 1977; Davidson et al., 1977), (Xu et al., 2018)
Fucoidanases	K	GH29	EC 3.2.1.127	**Fucoidan**	α-(1,6)-L-fucosidase	(Cheng et al., 2020), (Wang et al., 2022), (Gao et al., 2019), (Kopel et al., 2016), (Xu et al., 2018), (Ulaganathan et al., 2018)
			EC 3.2.1.111		α-(1,3)/ (1,4)-*L*-fucosidase	(Yazawa et al., 1986)
	L	GH95	EC 3.2.1.63		α-(1,2)-*L*-fucosidase	(Ogata-Arakawa et al., 1977; Reglero and Cabezas, 1976; Yazawa et al., 1986; Yoshima et al., 1979)
	M	GH107	EC 3.2.1.212		endo-α-(1,4)-*L*-fucosidase	(Bahl, 1970; Ogata-Arakawa et al., 1977; Reglero and Cabezas, 1976)
	N	GH29, GH95, GH141	EC 3.2.1.51		α-*L*-fucosidase	(Berteau and Mulloy, 2003; Kim et al., 2008), (Silchenko et al., 2013, 2014)
	O	GH168	EC 3.2.1.211		endo-α-(1,3)-*L*-fucanase	(Reglero and Cabezas, 1976)
Carrageenases	P	**GH16**	EC 3.2.1.83	**Carrageenan**	κ-carrageenase, α-carrageenase, β-carrageenase	(Bakunina et al., 2002; Berteau and Mulloy, 2003)
	Q	**GH82**	EC 3.2.1.157		I-carrageenase	(Matard-Mann et al., 2017; Weigl and Yaphe, 1966), (Potin et al., 1991, 1993), (Michel et al., 1999, 2001)
	R	GH150	EC 3.2.1.162		λ-carrageenase	(Michel et al., 2001, 2003), (Barbeyron et al., 2000)
Xylanases	S	GH5, GH8, GH10, GH11, GH30,	EC 3.2.1.8	**Xylan**	endo-β-(1,4)-xylanase	(Ohta et al., 2005)
		GH5, GH10, GH11	EC 3.2.1-		arabinoxylan-specific endo-β-(1,4)-xylanase	(Howard et al., 1960; Whistler and Wolfrom, 1962)
		GH10	EC 2.4.2.-		xylan endotransglycosylase	(Reese and Mandels, 1959; Wang et al., 2003)
		GH30	EC 3.2.1.136		glucuronoarabinoxylan endo-β-(1,4)-xylanase	(Petrescu et al., 2000; Wang et al., 2003)
	T	GH8, GH10, GH26	EC 3.2.1.32		endo-(1,3)-β-xylanase	(Nishitani and Nevins, 1988)
	U	GH8, GH10, GH30	EC 3.2.1.156		oligosaccharide reducing-end xylanase	(Araki et al., 1998, 1999), (Okazaki et al., 2005), (Takahiko et al., 1988)
Agarases	V	GH16, GH50, GH86, GH118	EC 3.2.1.81	**Agar**	β-agarase	(Fushinobu et al., 2005; Honda and Kitaoka, 2004)
		PL6, **PL7**, PL18, PL39	EC 4.2.2.11		G-specific alginate lyase	(Ohta et al., 2004), (Allouch et al., 2003), (Jam et al., 2005), (Sugano et al., 1993)
						(Boyd and Turvey, 1977; Davidson et al., 1977)

(*continued on next page*)

Table 2 (*continued*)

CAZyme	Target	Family	Activity	Substrate	Specific enzyme	Reference
	W	GH117	EC 3.2.1.159		α-neoagaro-oligosaccharide hydrolase	(Sugano et al., 1993
		GH96	E.C 3.2.1.158		α-agarase	(Ohta et al., 2005; Potin et al., 1993)
Porphyranases	**X**	GH16, GH86	EC 3.2.1.178	**Porphyran**	β-porphyranase	(Correc et al., 2011; Hehemann et al., 2010, 2014; Zhang et al., 2020),

(A3s): (,4)-β-D-Glc*p*A-(1,4)-α-L-Rha*p*3S-(1,); and type B ulvanobiuronic acid 3-sulfate (B3s): (,4)-α-L-Ido*p*A-(1,4)-α-L-Rha*p*3S-(1-); while the structure of ulvanobioses is described as U3S: (,4)-β-D-Xyl*p*-(1,4)-α-L-Rha*p*3S-(1,) (Lahaye et al., 1998; Lahaye and Robic, 2007). Additionally, β-D-Glc*p*A units can be distributed as side chains throughout the main backbone structure, being linked at the C2 of Rha*p*3S. While most of the sulfation events occur in the *O*-3 of Rha*p* (Ray and Lahaye, 1995), sulfation patterns in the *O*-2 of Xyl*p* residues have been also described (Fig. 3) (Kidgell et al., 2024; Lahaye and Ray, 1996).

The molecular weight (MW) of ulvan can vary from 150 to 2000 kDa (Paradossi et al., 2002; Yamamoto, 1980). Different proportions and structural arrangements of the oligosaccharide units can result in the various ulvan conformations that are found among the numerous green algal species (Synytsya et al., 2015) (Fig. 3). Such structural variability strongly influences the bioactivity and functionality of ulvan and its derivates (i.e., high uronic acid levels negatively impact the viscosity of ulvan (Siddhanta et al., 2001). In past decades, ulvan has been widely developed in various industries due to its potential applications in the food, cosmetical, pharmaceutical and biomedical industries (Mo'o et al., 2020). Ulvans amphiphilic and water-soluble nature (Morelli et al., 2019), along with its excellent rheological properties (Shao et al., 2014), make it an asset in colloidal formulations. It acts as an emulsifier and stabilizer, preserving the functionality of compounds in food and cosmetic products. Ulvan, known for its edible properties, has been studied in the formulation of biodegradable films for its application as edible films and smart coatings (Ramu Ganesan et al., 2018).

Ulvan is highly valued in the biomedical industry for its use as a polymer carrier in pharmaceutical formulations. Additionally, its strong antioxidant (Guidara et al., 2019), anti-inflammatory, anticancer, immunomodulatory (de Araújo et al., 2016), and antiviral activities (Chiu et al., 2012), along with its biocompatibility and non-toxicity, make ulvan a promising candidate for various therapies and tissue engineering applications (Popa et al., 2015).

During ulvan extraction, the applied methods and conditions can strongly influence the physiochemical characteristics of ulvan (Alves et al., 2010; Yaich et al., 2013). For instance, the use of acidic extraction conditions triggers the formation of intricate and resistant gel networks able to adopt thixotropic behaviors (Shao et al., 2014). Such capacity has been recently explored within polymer science in order to generate ulvan-based hydrogels intended for biomedical applications like tissue engineering, drug delivery and wound healing (Madany et al., 2021; Muhamad et al., 2019; Sulastri et al., 2021). Next to that, the unusual and modulable nature of the ulvan structure provides this compound with additional bioactivities such as antihyperlipidemic (Pengzhan et al., 2004), and antioxidant (Pengzhan et al., 2004; Qi et al., 2005), which are of great relevance for the food production and healthcare industries (Madany et al., 2021; Tziveleka et al., 2019).

In addition to ulvan, green algae also contain β-(1,4)-glucuronan, a linear polysaccharide composed of *D*-glucuronic acid residues. This glucuronan is co-extracted with ulvan due to its presence in the cell walls of *Ulva* species (Ray, 2006). While glucuronan can pose challenges during the structural analysis of ulvans, efficient methods have been developed to separate and purify this polysaccharide. For instance, extraction using oxalate buffer followed by acid precipitation allows for the isolation of glucuronan with high yield and purity, as demonstrated for *Ulva lactuca* (Elboutachfaiti et al., 2009). Unlike traditional chromatographic techniques, this process eliminates the need for labor-intensive purification steps, making it more viable for industrial applications. β-(1,4)-glucuronan's high uronic acid content and absence of sulfate groups offer unique properties distinct from ulvan, highlighting its potential as a valuable biopolymer for various applications.

3.2.1.1. Ulvan lyases. Ulvan lyases are a group of enzymes that cleave of the glycosidic bond between the 3-sulfated rhamnose (Rha3S) residue and the uronic acids (GlcA or IduA) present in the ulvan backbone. Ulvan lyases were assigned to polysaccharide lyase families PL24 and PL25 in marine bacteria of the Alteromonadales (Gao et al., 2019; Kopel et al., 2016) and PL28, PL37 and PL40 in other species of Flavobacteria (Collén et al., 2014; Konasani et al., 2018; Ulaganathan et al., 2018). Their activities (EC 4.2.2.-) are mainly described as glucuronic and iduronic ulvan lyases. Interestingly, the action of PL40 was described as part of a metabolic marine bacterial cascade in which three sulfatases, seven glycoside hydrolases and an ulvan lyase perform sequential degradation of ulvan (Reisky et al., 2019). The involved GH families (GH2, GH3, GH39, GH43, GH78 and GH88), seem to participate synergistically with some PL families for the use of ulvan and ulvan-derived monosaccharides. They mostly function as β-galactosidases, glycoside hydrolases and α-L-rhamnosidase. Other studies have characterized GH105 as a β-glycuronyl-hydrolase (EC 3.2.1.-) and pinpointed its participation in the removal of unsaturated uronic acid residues in concert with PL28 (Hagestad et al., 2021; Reisky et al., 2019).

3.2.2. Alginate

Alginate is a polysaccharide commonly found in brown seaweed (30-60 % dw). It consists of a soluble linear chain of contiguous disaccharide assemblies of β-(1,4)-D-mannuronic (M) and α-(1,4)-L-guluronic (G) acids. These units assemble homogeneously or heterogeneously to form G, M or GM assemblies. The length and structural distribution of both acids throughout the chain varies among seaweed species. Even though the M/G ratio in brown algal alginate varies between 1.2 and 1.6, several exceptions have been found (Fischl et al., 2016; Kloareg and Quatrano, 1988). For example, in *Laminaria digitata*, M/G ratios vary from 1.4 to 1.6 and from 1.12 to 1.50 in *Macrocystits pyrifera* (Fertah et al., 2017) (Fig. 4). This variation in structural distribution along with changes in acetylation patterns, provide different physiochemical properties to alginate, mostly affecting its viscosity, transition between the inorganic colloidal suspension (sol) and the gelation of the sol in a continuous liquid phase (gel), as well as the water uptake capacities (Khanra et al., 2018; Kloareg and Quatrano, 1988). It is precisely this variable character that makes alginate a valued product in the food and textile industries where it is employed as a stabilizer, smoothing and gelling agent (McHugh, 2003). A higher amount of M units results in increased flexibility of the alginate structure, whereas a higher presence of G units results in better gelling and strengthening capacities (Costa et al., 2021; Hernández-Carmona et al., 2013; Mazéas et al., 2023) (Fig. 4).

3.2.2.1. Alginate lyases. Alginate lyases (ALYs) can cleave the alginate's (1,4) glycosidic bonds using a β-elimination mechanism (Cheng et al., 2020). This results in the release of alginate oligosaccharides, which are highly valued by the food and pharmaceutical industries due to their high bioactive potential as plant bio-stimulants (Salachna et al., 2018),

anticoagulants and anti-tumor agents (Xing et al., 2020). The current classification of Alys divides them over 14 PL families (PL5, PL6, PL7, PL8, PL14, PL15, PL17, PL18, PL24, PL25, PL31, PL32, PL34, and PL39) based on their amino acid sequence. These families contain specific activities depending on the targeted oligosaccharide group: *endo*-acting polyM lyases (EC 4.2.2.3), endo-acting polyG lyases (EC 4.2.2.11), *exo*-acting oligo-alginate lyases (EC 4.2.2.26), and MG lyases (EC 4.2.2.-) (Table 2) (Xu et al., 2018). ALYs can have two different modes of action: *endo*-lyase activity (most common) yields oligosaccharide products of high structural complexity; or *exo*-lyase activity that remove mono- and short oligosaccharides from the end of the polymer or cleave the oligosaccharides produced by the *endo*-acting ALYs. For complete processing of the alginate backbone, the synergistic effect of several ALYs is required. Generally, endo-acting PL7 enzymes initiate the degradation of the alginate backbone, resulting in oligosaccharides. These are subsequently processed by the PL15, PL17 and PL7 enzymes, which result in the removal of unsaturated monosaccharides from their non-reducing end.

ALYs have been isolated from marine and terrestrial organisms like seaweed, mollusks, bacteria, fungi and viruses (Ogura et al., 2009; Zhu and Yin, 2015). This variation in origin is reflected in their diverse biochemical properties, with pH optima between 5 and 10.5 and temperature optima between 20 and 70 °C (Belik et al., 2018). Likewise, the efficiency of the degradation process might be closely linked to the specificity of the ALY towards the alginate substrate, where many factors could influence its activity. For instance, the presence and functionalities of carbohydrate-binding modules (CBMs) and non-catalytic regions (NCRs) can be key factors affecting the action of ALYs, as previously shown (Gao et al., 2018; Yan et al., 2019). These factors can be tweaked towards a more effective reaction in order to streamline the degradation process, which could be ideal so as to fulfill certain industrial application demands (Gao et al., 2018). Protein engineering strategies have been explored in order to improve the inherent biological features involved in the enzyme degradation process (Cheng et al., 2020).

3.2.3. Fucoidan

The second most important structural component in brown seaweed is fucoidan, a sulphated and highly branched polymer whit a heterogenous nature. It is an important component of brown seaweed species, such as those belonging to the Fucales and Laminarales, where the percentage ranges from 5 to 10 % of dw. Its structure is typically described as a backbone of α-(1,3)-L-fucopyranose units or alternating α-(1,3)-, α-(1,4)- and sometimes α-(1,2)-L-fucopyranose units. Side branches of L-fucopyranose residues have also been observed, which can be occasionally substituted by other monosaccharides such as D-xylose, D-galactose, D-mannose, L-rhamnose and D-glucuronic acid (Cesário et al., 2018; Johnston, 1969). Within the fucoidan structure, sulphation of the backbone chain can account for up to 38 % by weight. These sulfated groups are typically located at the C2 of α-(1,3)-linked and/or C4 of α-(1,4)-linked-L-fucopyranose residues (Hreggviðsson et al., 2020; Wang et al., 2020).

Because of the high complexity of the branching and sulphation patterns of fucoidans, many structural variations of this polysaccharide can be found in nature depending on different environmental and physiological factors. Fucoidans can be classified into two main groups: homo- or heterofucans.

Homofucans are the most typical forms found in nature and consist of α-(1,3)- and α-(1,4)-linked L-fucopyranose units with sulphate groups present on C2, C3 or C4. This form is one of the most common ones within the Fucales order: in *Fucus serratus,* the backbone chain is composed of alternating α- (1,3)-and α-(1,4)-linked L-fucopyranose moieties (Berteau and Mulloy, 2003) (Fig. 4). The most common sulfate group substitutions in *Fucus vesiculosus* and *Ascophyllum nodosum* occur in the C2 and C4 of the α-L-fucopyranose backbone structure (Fig. 4) (Ale and Meyer, 2013).

In contrast, heterofucans are distinguished as a different form of sulfated fucoidans in which D-mannose, D-galactose and/or D-glucuronic acid units form a complex branched network around the main α-L-fucopyranose chain (Bilan et al., 2004; Li et al., 2022a). One example is observed in *Chorda filum* (Laminariales) in which the backbone structure is composed of 4-sulfated α-(1,3)-linked α-L-fucopyranose residues, with some additional sulfated groups or 2-*O*-α-L-fucopyranosyl substituents present in C2 and sometimes in C4 (Chizhov et al., 1999). A similar structure has been identified in the fucoidan backbone of *Laminaria saccharina* (Laminariales) being mainly formed by α-(1,3)-linked L-fucopyranose with sulfation groups at C4 and C2 positions and occasionally presenting α-L-fucopyranosyl substituents at C2 (Chizhov et al., 1999; Usov et al., 2022). Other types of heterofucans have been identified in species like *Cladosiphon okamuranus* (Ectocarpales). In this case, the linear α-(1,3) fucopyranose backbone harbors the sulfate substitutions at C4, and some of the residues are *O*-acetylated. The α-glucuronic acid units are located at the C2 positions of the fucopyranose residues (Nagaoka et al., 1999) (Fig. 4).

Recent studies have comprehensive insights on the compositional variation of the FCSP in more than hundred brown algal species. No direct correlation was observed between the FCSP composition and the taxonomic characterization of the *Phaeophyceae* group (Ponce and Stortz, 2020). Other studies have focused on comparing the seasonal variation of fucoidan in various species of brown seaweed (Fletcher et al., 2017) and others on determining the effect on the structure of the bioactive polysaccharides and biological properties of such substrates (Rioux et al., 2009). This all together suggests that multiple factors such as biotope, water temperature, salinity, waves, currents, depth of immersion, seasonality and climate might drastically influence the compositional profile of seaweed biomass (Bilan et al., 2004; Li et al., 2022b; Mazéas et al., 2023; Miguel et al., 2023; Nielsen et al., 2016).

3.2.3.1. Fucoidanases. Despite fucoidans being an important percentage of the seaweed biomass (up to 30 % of dw), little is known about the activities of the putative enzymes acting upon these substrates. To date, only few enzymes have been described in microbial species to possess fucoidan-degrading activities (Ermakova et al., 2015; Rodríguez-Jasso et al., 2010; Trincone, 2018). Two main GH families, GH107 and GH168, have been widely used for the classification of such activities in the Carbohydrate Active Enzymes database (Drula et al., 2022). The activities described in these two families correspond mostly to *endo*-acting α-(1,4)-L-fucanases (EC 3.2.1.212) and α-(1,3)-L-fucanases (EC 3.2.1.211), respectively (a.k.a. fucoidanases or fucoidan-hydrolases). These promote the cleavage of the α-(1,4) and α-(1,3)-glycosidic bonds present between the sulfated α-L-fucose residues of the fucoidan backbone, a process that yields low molecule weight fucoidan oligosaccharides. Some examples of characterized enzymes belonging to GH107 are: FWf1 and FWf2 that were isolated from *Wenyingzhuangia fucanilytica* (Bacteroidota) CZ1127 (Zueva et al., 2020), MfFcnA and two other members, P5AFcnA and P19DFcnA, inferred from a bacterial species of the genus *Psychromo*nas (Vickers et al., 2018) and FFA1, FFA2 and Fhf1 that were obtained from the marine bacteria *Formosa algae* KM3553 (Silchenko et al., 2018; Silchenko et al., 2013) and *Formosa haliotis* (Vuillemin et al., 2020) respectively. In the GH168 family, the only characterized enzyme so far is FunA, an *endo*-(1,3)-fucanase screened from the marine bacterium *Wenyingzhuangia fucanilytica* (Shen et al., 2020).

Other GH families like GH29, GH95, GH141 have α-L-fucosidase activities targeting the hydrolytic cleavage of the terminal α-L-fucose residues from different fucose-containing glycans and glycoconjugates. The described activities in these families include α-L-fucosidase (EC 3.2.1.51), α-(1,3)-L-fucosidase (EC 3.2.1.111), α-1,2-L-fucosidase (EC 3.2.1.63) and α-(1,6)-L-fucosidase (EC 3.2.1.127) (Silchenko et al., 2022). While the GH29 fucosidase activities target the cleavage of α-(1,2), α-(1,3), α-(1,4), and α-(1,6)-linked L-fucopyranose residues from a variety of glycoconjugates, the enzymes from the GH95 family are

highly specific to α-(1,2)-linked L-fucopyranose residues found in oligosaccharides (Fukaya et al., 2014; Shen et al., 2020).

3.2.4. Carageenan

Carrageenan is a sulfated galactan mainly found in red seaweed. This high-molecular weight polysaccharide consists of a linear structure of repeating 3-linked-β-D-galactopyranose (G unit) or 4-linked-α-(3,6)-anhydro-D-galactopyranose (DA units) and 4-linked-α-D-galactopyranose (D unit). Depending on the amount and distribution of the sulfated groups in the disaccharide units as well as the presence of an anhydro-ring in the α-linked D-galactose, different types of carrageenan can be differentiated: kappa (κ)-, iota (ι), lambda (λ)-, mu (μ)-, nu (ν)-, gamma (γ)-, alpha (α)-, delta (δ), theta (ϴ)-, and beta (β)-carrageenan (Necas and Bartosikova, 2018; Torres et al., 2019). Among them, κ-, ι- and λ carrageenan are the most valued ones in commercial applications. These have one, two, and three sulfate groups, respectively, in every repeating disaccharide unit and they can be also referred as carrageenose 4-sulfate (DA-G4S), carrageenose 2,4-disulfate (DA2S-G4S), and carrageenose 2,6,2-trisulfate (D2S,6S-G2S), respectively (Ghanbarzadeh et al., 2018; Jiao et al., 2011; Knutsen et al., 1994) (Fig. 5).

In the seaweed structure, the various types of carrageenan are present as a hybrid mixture but the proportions can vary among species. For instance, κ-ι-hybrids are mainly found in species of the Phyllophoraceae, while ι-carrageenan is generally extracted from the Cystocloniaceae, and λ-carrageenan is produced in saprobic species like some of the Gigartinaceae. The differences in the molecular structure and composition define the qualities of each type of carrageenan, with κ and ι being especially known for their gelling capacities, while λ-carrageenan is well recognized as a thickening agent (Collén et al., 2014; Pereira et al., 2013). The extraction of carrageenan from red seaweed has been extensively exploited by different industries due to their wide variety of applications, ranging from the food sector to the pharmaceutical industry (Blakemore and Harpell, 2009; Ghanbarzadeh et al., 2018; Rhein-Knudsen et al., 2015).

3.2.4.1. Carrageenases. The cleavage of the alternating α-(1,3) and β-(1,4) linkages present between the D-galactose residues in the carrageenan backbone is performed by enzymes called carrageenases. Based on the substrate specificity and on the primary structure, these can be divided into three enzyme categories: k-, ι-, and λ-carrageenases (Chauhan and Saxena, 2016; Zhu et al., 2018a, 2018b).

κ-Carrageenases (EC 3.2.1.83), and α- and β-carrageenases (EC 3.2.1.-) were identified in several bacterial species isolated from red seaweed and classified in GH16 (Michel et al., 2001; Michel et al., 1999; Potin et al., 1991; Weigl and Yaphe, 1966). ι-Carrageenase (EC 3.2.1.157) is assigned to GH82, where such activities have been generally described from bacterial isolates. In particular, the marine bacterium *Colwellia echini* possess two big gene clusters encoding for enzymes that enable the total degradation of not only κ-carrageenan but also agar (Christiansen et al., 2020; Michel et al., 2003). Marine bacterial species like *Zobellia galactanovorans* and *Alteromonas fortis* as well as various species of *Flavobacterium* also harbor this specific ι-carrageenase activity. In this case, ι-carrageenases work as an endo-type enzyme by hydrolyzing the β-(1,4)-linkages of ι-carrageenan and providing neoι-carratetraose units as the main product (Barbeyron et al., 2000; Li et al., 2017).

λ-Carrageenase (3.2.1.162, GH150) targets the β-(1,4) linkages of the λ-carrageenan backbone resulting in tetra-saccharides. A λ-carrageenase was purified from a culture in which the deep-sea bacteria *Pseudoalteromonas bacterium* CL19 grew in the presence of λ-carrageenan. The gene encoding this enzyme was sequenced enabling its identification as a novel endo-type λ-carrageenase (Ohta and Hatada, 2006).

3.2.5. Agar

Agar is the second most common structural polysaccharide in red seaweed and is structurally related to carrageenan. It is composed of alternating β-D-galactopyranose and (3,6)-anhydro-L-galactopyranose, linked by alternating α-(1,3) and β-(1,4) glycosidic bonds. Agar has two main components: agarose and agaropectin (Pomin, 2010). While agarose is mainly formed by repetition of the two main units above-mentioned, agaropectin contains sulfate groups, pyruvic acid, and D-glucuronic acid in its structure. Such variations differ based on the algal species (Torres et al., 2019) (Fig. 5). Agarose is a neutral linear polysaccharide that can amount to up to 70 % of the composition of agar and that provides the typical gelling properties. Agaropectin has an acidic nature and provides the thickening capabilities that make agar one of the most valued hydrocolloids within the food, chemical, biotechnology and medical industries. The absence of α- and β-agarases in the gastrointestinal human tract impedes the digestion of agar and some of its derivates, rendering them optimal dietary fibers (Mišurcová, 2011). Moreover, the biocompatible character of agarose makes it the optimal biomaterial for tissue engineering and drug delivery systems, among other biomedical applications (Ramana Ramya et al., 2016; Tripathi et al., 2009; Zhang et al., 2012).

Red seaweed are an important source of bioactive compounds of great relevance for many different industrial sectors (Torres et al., 2019). Representing 61 % of the global seaweed production, red seaweed is mainly used in agar and carrageenan extraction, but the high biomass yield that can be recovered from their cultivation is also awakening interest in the biorefinery and biofuel industries (Álvarez-Viñas et al., 2019; Chizhov et al., 1999; Nelson and Lewis, 1974; Read et al., 1996; Stone, 2009).

3.2.5.1. Agarases. Agar degradation is facilitated by a variety of enzymes classified into different families of agarases (Hehemann et al., 2014). Depending on the substrate specificity and mode of action, these enzymes are classified as β- or α-agarases as they respectively target the hydrolysis of the β-(1,4) or α-(1,3) linkages present in the agar structure (Hehemann et al., 2014). β-Agarases (EC 3.2.1.81) are distributed across several glycoside hydrolase (GH) families, including GH16, GH50, GH86, and GH118. Despite significant variability in their amino acid sequences, molecular weights, and catalytic activities, they share similar functional roles in breaking β-linkages (Ohta and Hatada, 2006). In contrast, α-agarases (EC 3.2.1.158) are much less diverse, only being found in GH96 and GH177.

Agarose degradation, a key step in the breakdown of agar, has been extensively studied. It involves three stages: i) *endo*-β-agarases from GH16 (AgaB) and GH86 break agarose into neoagarooligosaccharides with degrees of polymerization (DP) of 4–6 and 6–8, respectively; ii) *exo*-β-agarases from GH50A, GH50D, and possibly GH86 convert these oligosaccharides into neoagarobiose (DP2); and iii) α-agarases from GH117 further degrade neoagarobiose into monomeric sugars (Pluvinage et al., 2013). This multi-step degradation process has been well-documented in the bacterial species *Saccharophagus degradans* (Chi et al., 2012).

The three-dimensional structures of two β-agarases, ZgAgaA and ZgAgaB, have been elucidated from GH16 of the marine bacteria *Zobellia galactanivorans*, allowing to better understand their mode of action on the agar substrate (Allouch et al., 2003). These two β-agarases act as endolytic enzymes enabling the hydrolysis of agar while yielding neoagarotetraose and neoagarohexaose as the main reaction products (Jam et al., 2005; Ohta et al., 2004; Sugano et al., 1993). However, smaller oligosaccharides with smaller polymerization degrees (PD) resist GH16-mediated hydrolysis, serving as intermediates during polymer breakdown. Thus, for the complete hydrolysis of the agar backbone, complementary β- and α-agarolytic activities from other families like GH50 and GH117 are required (Hehemann et al., 2014). It has been proposed that the *exo*-processive capacity of β-agarases from the GH50 family can complement the activity of GH16 β-agarases by continuing the hydrolysis process where the latter enzymes cannot proceed (Kim et al., 2010;

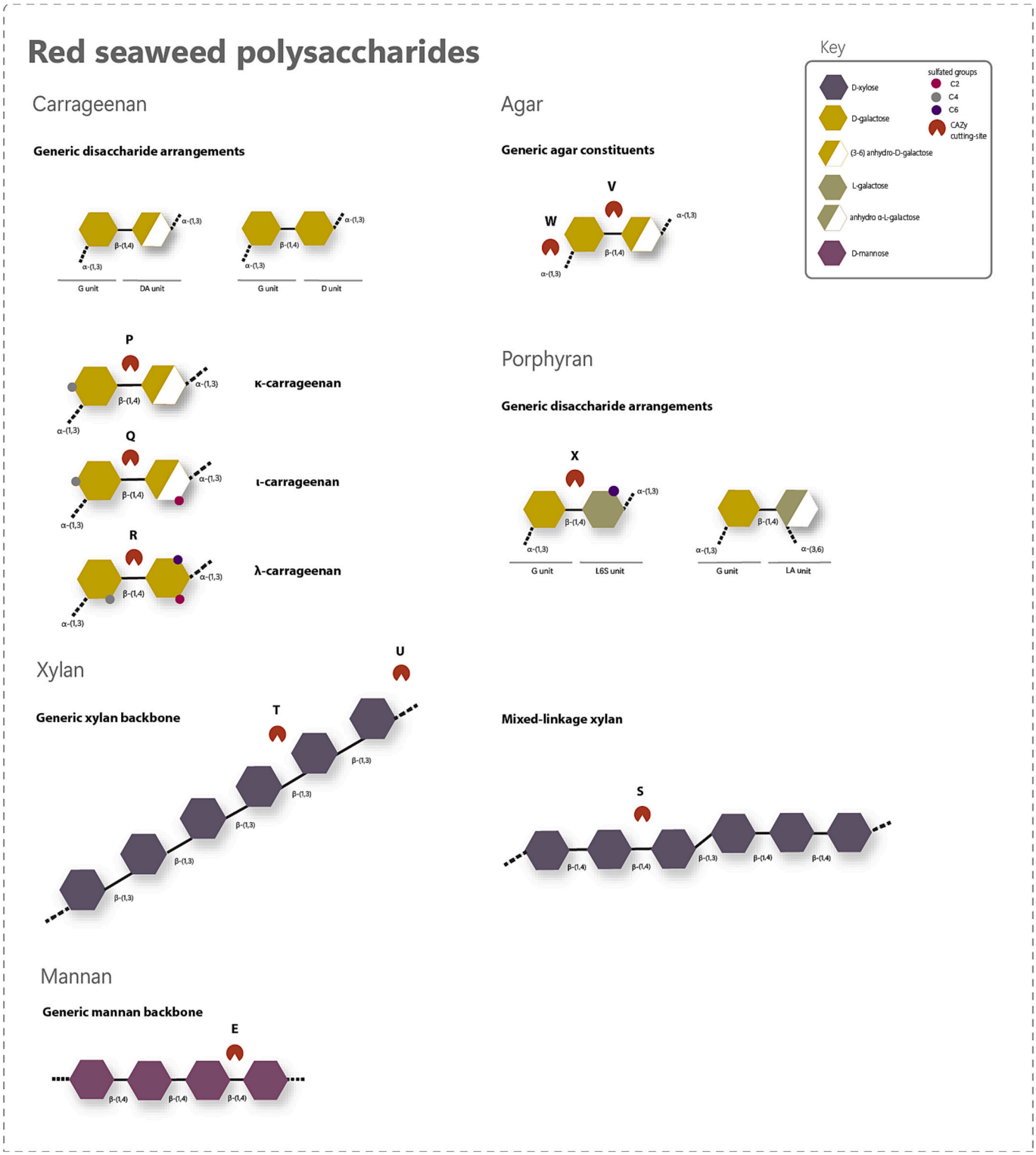

Fig. 5. Main polysaccharides of the red seaweed cell wall. General chemical structures of carrageenan, agar, xylan and porphyran are depicted. The two main carrageenan disaccharide structures are depicted next to three most common types found in nature (κ, α, and ι carrageenans). The basic disaccharide structures of agar and porphyran are shown. Xylan is depicted as its generic backbone and as its mixed-linked structure. The generic structure of mannan is shown. For simplification, all sugar monomers are depicted as hexagons, followed by the type of linkage established among them. The chemical nature of each monomer is indicated by the color code shown in the key. Sulphated polysaccharides are indicated with round, colored shapes. CAZyme-targeted linkages are indicated with arrows whose letters are linked to their corresponding activities indicated in Table 2.

Pluvinage et al., 2013). Additionally, the *exo*-acting capacities of the α-neoagaro-oligosaccharide hydrolase activity (EC 3.2.1.159) from GH117 allow the removal of (3,6)-anhydro-L-galactose from the non-reducing end of the neoagaro-oligosaccharides.

3.2.6. Porphyran

Another example of sulphated galactan is porphyran. As it names suggests, this compound is mainly found in red seaweed that belong to the *Porphyra* genus (i.e., *Pyropia dentata* – formerly *Porphyra dentata*, *Pyropia yezoensis* - formerly *Porphyra yezoensis, Pyropia columbina* - formerly *Porphyra columbina*), of which many species are able to produce (Zhang et al., 2005; Zhang et al., 2004). This water-soluble polysaccharide is chemically related to agarose as it consists of a linear backbone of alternating (1,3)-linked β-D-galactopyranose (G) with (1,4)-linked α-L-galactopyranose-6-sulfate (L6S), that can be substituted in a small extent by (3,6)-anhydro-α-L-galactopyranose (LA) groups. Methylations occur at the C6 and C2 positions of the G and LA residues, respectively (Shen et al., 2020; Zhang et al., 2004). In the case of C6, methylation can happen in up to 64 % of the G residues (Zhou et al., 2012) (Fig. 5). The most common porphyran structures has a 1.2:1 ratio of L6S and LA units, and an average MW of 246 KDa. Although the above-described characterization represents the general porphyran structure, slight variations of it have been described among different species of the genus (Qiu et al., 2021; Rees and Conway, 1962) (Fig. 5). As an example, in *Pyropia yezoensis,* xylose moieties were identified in the porphyran structure at the Cs of one of every 25 β-D-galactopyranose residues (Zhang et al., 2001). Porphyran and its derived oligosaccharides have been intensively studied for their biological and pharmacological activities. Besides being described as good purgative and antilipidemic compounds (Aziz et al., 2021), they provide antioxidants, anti-cancer, anti-allergic hypoglycemic and immunomodulatory activities (He et al., 2019; Hou et al., 2015; Isaka et al., 2015; Qiu et al., 2021) (Fig. 5).

3.2.6.1. Porphyranases. Porphyranases catalyze the cleavage of the (1,4) linkages present between G and L6S residues of the porphyran backbone. This primarily results in the generation of α-L-galactopyranose-6-sulfate-(1,3)-β-D-galactose (L6S-G) disaccharides, although other oligosaccharides of higher length and even residue numbers can also be present (Fig. 5). All porphyranase activities described so far have been classified as *endo*-acting β-porphyranases (EC 3.2.1.178) and are assigned to GH16 and GH86. In *Wenyingzhuangia fucanilytica*, the porphyranase activity was particularly interesting as it seems to accommodate both galactose and methyl-galactose moieties at its subsites, resulting in the first-identified porphyranase able to hydrolyze consecutive methyl-L6S-G (L6S-GMe) residues and therefore bringing new insights into the specificity at the subsite level of porphyranases (Shen et al., 2020).

3.2.7. Xylan

Xylans, being the second most abundant polysaccharides in the cell wall of terrestrial plants, have been intensively studied due to their relevant applications within the food, feed and biotechnology industries. Lesser attention had been paid to the structure of the xylans in macroalgal cell walls. Only some structural studies, mainly related to species of the Rhodophyta group, managed to elucidate the general xylan composition in seaweed, along with the specific traits that differentiate them from terrestrial substrates (Deniaud et al., 2003; Lahaye et al., 2003).

Xylans are found in both the Chlorophyte and Charophyte clades of green seaweed, as well as in the vast majority of the Rhodophyta clade. Structural differences in xylan composition are therefore inferred from such diverse phylogenetic backgrounds. The Charophyte phylum is the closest relative of terrestrial plants which is reflected in the xylan composition of its cell wall. In both terrestrial plants and Charophyta, the xylan backbone consists of (1,4)-linked β-D-xylopyranosyl (β-D-Xyl*p*) residues. Identification of (2,4)- and/or (3,4)-linked Xyl*p* residues suggests the presence of certain variations within the backbone chain (Jensen et al., 2018).

In red seaweed, two different forms of homoxylans have been identified: (1,3)-β-D-xylans and (1,3):(1,4)-β-D-xylans. The first ones form the cell wall microfibrils in species like *Porphyra umbilicales* from the Bangiales order, where the residues are assembled forming triple helix (Frei and Preston, 1964a). The (13;(1,4)-β-D-xylans, generally referred as mixed-linkage xylans, are present in the matrix phase of the cell walls of red seaweed belonging to the Nemaliales and Palmariales. In some species of this last order, 1,4-β-D-xylans have been also identified (Lahaye and Robic, 2007; Mandal et al., 2010; Rennie and Scheller, 2014; Smith et al., 2017). The mixed-linkage xylans are generally characterized as linear structures harboring (1,3) and (1,4) links in a 1:4 ratio. The proportions of both linkages on the cell wall structure vary among the different red algal species, while the (1,3) links seems to follow an irregular distribution pattern (Deniaud et al., 2003; Painter, 1983; Turvey and Williams, 1970) (Fig. 5).

In Chlorophyta phylum, microfibrils of (1,3)-β-D-xylans are present, resulting in triple helices of homoxylan structures (Hsieh and Harris, 2019). In some orders like Bryopsidales, the cell wall microfibrils are typically made up of either (1,3)-β-D-xylan or (1,4)-β-D-mannan, with cellulose being notably absent in most of the studied genera. However, in the *Bryopsis* genus, the cell wall microfibrils include both (1,3)-β-D-xylan and cellulose (Frei and Preston, 1964, 1968; Huizing et al., 1979; Verbruggen et al., 2009). Such variability in the residues forming the backbone structure is not only influenced by phylogenetic factors but also by the stage of development, as compositional changes have been clearly identified between the different phases of the algal life cycle (Hsieh and Harris, 2019; Wutz and Zetsche, 1976).

3.2.7.1. Xylanases. β-xylanases form a set of enzymes able to target the cleavage of the β-linked D-xylose units found in the xylan backbone of many green and some red seaweed cell walls (Hsieh and Harris, 2019). Various xylanase activities have been inferred from marine bacteria, mainly belonging to the *Vibrio, Neiella, Alteromonas*, and *Gilvimarinus* genera (Araki et al., 1999; Araki et al., 1998; Okazaki et al., 2005). In this case, various *endo*-β-(1,3)-xylanase (EC 3.2.1.32) have been identified under the GH10 and GH26 families, while endo-(1,4)-β-xylanase (EC 3.2.1.8) activities were attributed to enzymes of families GH5, GH8, GH10, GH11 and GH30. Other activities like oligosaccharide reducing-end xylanase activity (EC 3.2.1.156) or glucuronoarabinoxylan-specific *endo*-β-(1,4)-xylanase activity (EC 3.2.1.136) were described in families GH8, GH10 and GH30 (Sun et al., 2021; Trivedi et al., 2013).

3.2.8. Mannan

Mannan is an insoluble structural polysaccharide that has been found in most of the generic phases of the life cycle of certain red seaweed. These species belong mainly to the Bangiales order and specifically to the *Porphyra/Pyropia* genus, where mannan can be particularly found in the cuticle of the thallus structure (Frei and Preston, 1964; Usov, 2011). The linear backbone of mannan is generally formed by β-(1,4)-linked mannose units that can eventually result in variable degrees of polymerization, ranging from 20 to 10,000 residues. In some cases, up to 5 % (*w*/w) D-glucose residues have been found in the backbone structure, resulting in the so-called glucomannans (Moreira and Filho, 2008). Low levels of side chains have been detected, providing flexibility to the partially crystalline structure (Jones, 1950), as well as the fibrillar and granular character (Stiger-Pouvreau et al., 2016) (Fig. 5).

In some species of green seaweed, and most particularly in those of the *Codium* genus, mannan is also present at up to a 31 % (*w*/w) of the cell wall. In these species, sulfate groups have been detected in the C2 position of 23 % of the backbone units, while other sulfation patterns have been identified in various species of green seaweed like in *Codium*

and *Capsosiphon* species (Wang et al., 2014). The presence of such sulfation patterns provides higher solubilities when compared to non-sulfated fibrillar mannans (Fernández et al., 2012).

3.2.8.1. Mannanases. Endo-β-1,4-mannases (EC 3.2.1.78) are responsible for the hydrolysis of the β-(1,4)-glycosidic bonds that form the backbone structure of these two polymers (Linton, 2020; Moreira and Filho, 2008), releasing β-(1,4)-manno-oligosaccharides. This *endo*-(1,4)-β-mannosidase activity is assigned to GH26 (Eriksson et al., 1968; Reese and Shibata, 1965; van Zyl et al., 2010), but can also be found in GH5_10 subfamily (Ootsuka et al., 2006).

4. Marine fungi in seaweed cell wall degradation

Marine fungi comprise a highly versatile set of species, playing a crucial role in the decomposition of materials in the ocean (Sridhar, 2012). Degradation of dead and decaying matter occurs by secreting an array of enzymes that promote the deconstruction of the polysaccharide structures present in marine substrates (Bonugli-Santos et al., 2015). Marine fungal strains isolated from various substrates such as seawater, sediments and marine organisms are endowed with specific enzymatic repertoires that have been tailored to the marine realm (Salazar-Alekseyeva et al., 2023). This repertoire includes diverse enzymatic activities including alginate lyase, amylase, cellulase, chitinase, glucosidase and xylanases (Bonugli-Santos et al., 2015), which are all characterized by their carbohydrate-degrading capacities which vary depending on the species, environmental conditions and type of substrate (Balabanova et al., 2018a; Bonugli-Santos et al., 2015; Salazar-Alekseyeva et al., 2023; Wang et al., 2016).

Due to the abundance of seaweed in marine environments and the high carbohydrate composition, it is likely a major substrate for many marine fungi. The ability of marine fungi to use various seaweed and seaweed polysaccharides as a carbon source has been demonstrated (Patyshakuliyeva et al., 2020, mirroring the use of plant biomass as a carbon source by terrestrial fungi. Fungal degradation of seaweed has been mainly inferred from growth studies on brown seaweed species (de Vries et al., 2020), while the full set of enzymatic activities responsible for the degradation remains unclear. A recent study isolated Ascomycete fungi from marine sediments and demonstrated that many of them produced enzyme activities involved in seaweed cell wall degradation (da Silva et al., 2024). They contain sulphate groups or other unique modifications that require specialized enzymatic activities, such as sulphatases, for complete breakdown. Marine fungi will therefore require different sets of enzymes to degrade seaweed than terrestrial fungi use to degrade plant biomass (Balabanova et al., 2018a, 2018b). Our knowledge with respect to fungal degradation of seaweed is poor, especially in comparison to fungal plant biomass degradation or degradation of seaweed by bacteria. This section will provide an overview of the current state-of-the-art of fungal enzymes involved in seaweed polysaccharide degradation and their application potential, as well as an outlook to filling the knowledge gaps.

4.1. CAZy activities characterized from marine fungi

Carbohydrate-active enzymes are crucial for the breakdown of the complex polysaccharides that are found in many natural biotopes. Numerous CAZyme activities have been described that are involved in plant biomass degradation in terrestrial environments (Culleton et al., 2011) and a high diversity has been observed between the putative enzymes sets in different fungal genomes de Vries and Mäkelä (2020). While the CAZy database (www.cazy.org) (Drula et al., 2022) also contains enzyme families related to seaweed polysaccharide degradation, many of these families have only been studied or are even only present in bacteria. However, several GH families containing fungal members have been implicated in the degradation of seaweed. Glycoside hydrolase families GH3, GH5, GH16, GH55, GH64, GH128, GH131 and GH132 have been suggested to be able to cleave β-1,3-linkages in marine polysaccharides, such as laminarin (Table 2) (Balabanova et al., 2018b; Wang et al., 2021). However, fungal laminarases have only been described for GH16 (Kawai et al., 2006b; Nakajima et al., 2012), GH55 (Cohen-Kupiec et al., 1999; Kawai et al., 2006a; Nobe et al., 2003) and GH128 (Santos et al., 2020). In addition, several other CAZy families containing fungal members have been implicated in the degradation of fucoidan (GH29, GH95, GH141), ulvan (GH78, GH105), carrageenan (GH16) and alginate (PL7, PL8, PL15) (Pilgaard et al., 2019; Pilgaard et al., 2021). The identification and purification of marine enzymes has been generally done based on other already described activities of some marine organisms or other terrestrial substrates (Fu and Kim, 2010; Michel and Czjzek, 2013; Thiang Yian Wong et al., 2000). This approach has limited the search to only those communities, conditions and enzymatic activities that are known in these common substrates, neglecting the discovery of novel capacities that other organisms might harbor (Michel and Czjzek, 2013).

Recent research has demonstrated the potential of marine fungi to degrade seaweed biomass. In a study by Patyshakuliyeva et al., 2020, the enzymatic capacities of 22 marine fungi isolated from *Fucus* sp., a brown seaweed, were examined. These species showed significant biomass-degrading capabilities on both plant and seaweed biomass, suggesting they produce specific enzymes capable of degrading seaweed polysaccharides. Much of our understanding of fungal carbohydrate active enzyme abilities is based on terrestrial fungi, the occurrence of several fungal species, such as from *Aspergillus* and *Penicillium*, in both terrestrial and marine environments (Bonugli-Santos et al., 2015; Menezes et al., 2010) suggests that they also possess enzymatic activities to degrade marine-based polysaccharides. However, the limited data available on fungal CAZymes active on marine substrates contrasts sharply with the extensive knowledge of fungal enzymes on terrestrial polysaccharides like cellulose and starch. This gap highlights the importance of further exploring fungal CAZyme diversity, particularly in marine environments, to uncover novel activities that could play a significant role in marine biomass degradation.

4.2. Degradation of polysaccharides present in both seaweed and terrestrial plants

As discussed in section three some polysaccharides are present in both seaweed and terrestrial plants, such as cellulose, starch, mannan and xylan. Degradation of the plant-derived forms of these polysaccharides by fungal enzymes has been studied in detail, while less literature is available on the degradation of the seaweed-derived versions. It is therefore not clear at this time if the seaweed and plant versions are degraded using the same enzyme sets, and therefore the enzymes involved in the plant-derived versions are briefly summarized here.

Degradation of cellulose by fungal enzymes has been studied in detail and many papers demonstrate the enzymatic diversity and functionality involved in this process (Zhang et al., 2024). Most of the commercially available enzyme cocktails are produced using strains from various *Aspergillus* or *Trichoderma reesei*, which are also the best studied fungi related to cellulose degradation (de Vries et al., 2016; Mäkelä et al., 2024). However, most studies relate to cellulose originating from terrestrial plants, while few studies address seaweed-derived cellulose (Barzkar and Sohail, 2020). Similarly, studies on xylan degradation mainly focus on terrestrial xylans, and also this field is dominated by studies on *Aspergillus* and *Trichoderma reesei* (de Vries et al., 2016; Mäkelä et al., 2024). While for both seaweed-derived cellulose and xylan it is currently unclear whether specific enzymes dedicated to the seaweed versions are required for their hydrolysis. There is certainly some cross-reactivity of the enzymes towards terrestrial and marine versions, as evidenced by the use of a commercial β-glucosidase from *Aspergillus niger* to hydrolyze seaweed cellulose (Tan and Lee,

2015a) and the activity of a *Trichoderma harzianum* β-xylosidase on a seaweed-derived xylan (Silveira et al., 1999).

No studies so far have addressed the enzymes required for the hydrolysis of seaweed starch or mannan, despite extensive studies on the fungal enzyme systems related to terrestrial starch and mannan degradation (de Vries et al., 2016). It can be expected that the marine derived versions of these polysaccharides will be sensitive to similar enzymes sets, possibly with different specificities and physical properties.

4.3. Laminarin degrading enzymes

Laminarin is one of many diverse β-glucans that are widely distributed in nature and serve as important structural components in the cell wall of plants (e.g., oat, barley, wheat), mushrooms, bacteria, yeasts as well as in seaweed and microalgae. As reviewed in section 3.1.2, laminarin is the main β-glucan in seaweed and its degradation requires both *endo*- and *exo*-acting enzymes (Chesters and Bull, 1963). In contrast to enzymes involved in the degradation of most other seaweed polysaccharides, fungal laminarases have been more frequently studied, predominantly enzymes assigned to the multi-specific family of GH16 (Mouyna et al., 2002; Liberato et al., 2021). This family includes both *endo*- and *exo*-β-D-1,3-glucanase activities (EC 3.2.1.39), which have been identified in various basidiomycetes, ascomycetes, *Rhizopus* species, and marine yeasts (Chesters and Bull, 1963; Kalomoiri et al., 2019; Reese and Mandels, 2011). In addition to GH16, fungal laminarase activities have been found in several other CAZyme families: GH5 (EC 3.2.1.39/3.2.1.6), GH17 (EC 3.2.1.39), GH30 (EC 3.2.1.75) and GH55 (EC 3.2.1.19/3.2.1.-), although most of them are not marine strains per se (Barras and Stone, 1969a; Barras and Stone, 1969b; Becker et al., 2017; Chesters and Bull, 1963). Several of these enzymes have been shown to hydrolyze laminarin, as well as other glucans, suggesting a relatively broad substrate specificity (Kawai et al., 2006a; Kawai et al., 2006b; Nakajima et al., 2012; O'Connell et al., 2011; Papageorgiou et al., 2017; Peng et al., 2009; Vasur et al., 2009). Interestingly, the gene encoding one of them was specifically induced by the presence of laminarin, suggesting it to be part of a dedicated laminarin-degrading enzyme system (Cohen-Kupiec et al., 1999).

4.4. Carrageenan and agar degrading enzymes

As discussed in section 3.2.4, carrageenan and agar are present in most red seaweed. Marine isolates of fungi like *Phoma* sp., *Aspergillus ochraceus,* and *Aspergillus terreus*, are able to grow on carrageenan as the sole carbon source and were reported to possess carrageenase activities (Solis et al., 2010). These enzymes are part of the multi-specific GH16 family, which, as described above, also includes enzymes involved in the degradation of other marine polysaccharides like laminarin and agarose. Although agarose degradation has been only characterized in bacteria, the high GH16 gene number in fungal genomes (Grigoriev et al., 2014; Zhao et al., 2013), with relatively few of them biochemically characterized, combined with growth of many fungal species on agar itself, may indicate that this family contains these activities in fungi as well.

4.5. Alginate degrading enzymes

Several studies have reported fungal enzymes involved in alginate degradation. An extracellular alginate lyase (ALY) from *Aspergillus oryzae* has been characterized (Singh et al., 2011), while a proteomic analyses of the marine fungus *Paradendryphiella salina* identified three candidate ALYs from PL7 and one from PL8 (Pilgaard et al., 2019). A follow up study revealed that the PL8 enzyme was not active on alginate, but had an *exo*-lyase activity on polymannuronic acid, while all three PL7 enzymes were *endo*-acting alginate lyases (Pilgaard et al., 2021). The three PL7 enzymes possess different physical properties and product profiles and one of them was shown to act synergistically with the PL8 enzyme (Pilgaard et al., 2021). Two recent studies demonstrated activity on alginate of a GH5 and a GH12 endoglucanase from *Trichoderma asperellum* (Zheng et al., 2024; Zhuang et al., 2024). While the authors suggested that this enzyme acted as an alginate lyase, the mechanism of the enzyme on alginate was not demonstrated. The ability of other marine fungi such as *Calcarisporium* sp. and *Scopulariopsis brevicaulis* to use alginate as a carbon source has also been reported, but the enzymes responsible for this were not identified (Balabanova et al., 2018a, 2018b; Wang et al., 2016).

4.6. Fucoidan degrading enzymes

Marine fungal isolates *Paradendryphiella arenariae* (formerly *Dendryphiella arenaria*) TM94 and *Fusarium* sp. LD8, were reported to degrade fucoidan (Wu et al., 2011; Qianqian et al., 2011). This was also observed for 10 terrestrial fungal strains, while DNS-based enzyme activity measurements of them using fucoidan as a substrate revealed high activity for *Aspergillus niger*, while lower activities were observed for *Talaromyces purpureogenus* (formerly *Penicillium purpurogenum*) and *Mucor* sp. (Rodríguez-Jasso et al., 2010). The absence of fucoidanase activity in some of the studied marine fungi associated with seaweed biomass, could be related to the fact that fungal species live as part of microbial communities, in which such activities are covered by bacterial species with enriched algal-polysaccharide degrading abilities (Rodríguez-Jasso et al., 2010; Raghukumar, 2017; Sichert, 2020).

4.7. Ulvan and glucuronan degrading enzymes

So far, few depolymerization activities related to ulvan have been identified in fungi, a *Trichoderma* sp. glucuronan lyase has been isolated that act in an *endo*-fashion releasing a range of glucuronan oligosaccharides (Elboutachfaiti et al., 2009). The enzyme is also active on ulvan (Delattre et al., 2006. A similar enzyme from *Trichoderma reesei* was originally considered to represent a novel PL family (Konno et al., 2009) and has since then been assigned to PL20. A later study in *Trichoderma parareesei* revealed six glucuronan lyases (Pilgaard et al., 2022). Two PL7 and two PL20 enzymes showed *endo*-lyase activity, while a PL8 and a PL38 enzyme showed *exo*-lyase activity. Another study demonstrated a positive effect of exo-1,3(4)-β-glucanase on biomass solubilization of *Ulva lacinulata* (*Ulva armoricana*) (Chlorophyta) (Hardouin et al., 2016), suggesting this activity to be part of the hydrolysis spectrum of *Ulva* polysaccharides.

4.8. Closing the knowledge gap between terrestrial and marine enzyme sets of fungi to facilitate biotechnology

The increasing interest in seaweed as a renewable substrate for biotechnological applications, such as production of biochemicals and biofuels (Li et al., 2016; Tan and Lee, 2015b) or the extraction of valuable components e.g., protein (Liu et al., 2024) or specific carbohydrates (Carvalho et al., 2024), requires a better understanding and availability of the enzyme sets required for seaweed cell wall deconstruction.

The availability of an increasing number of fungal genomes (Grigoriev et al., 2014), enables genome mining for candidate enzymes using either fungal or bacterial enzymes as queries, as was performed recently for glucuronan lyases (Pilgaard et al., 2022). The number of genome sequences for marine fungi is very small (https://mycocosm.jgi.doe.gov/Marine_fungi/Marine_fungi.info.html) but is likely to increase in the near future. These genomes provide a more detailed look into the lifestyle and abilities of these fungi (Hagestad et al., 2021), although detailed comparison to terrestrial relatives is currently lacking. For example, *Emericellopsis atlantica* (TS7) contains CAZy genes, representing 4 % of its total genome (Hagestad et al., 2021). Of these, 149 (38 %) were predicted to encode secreted enzymes, which is crucial for extracellular substrate processing. More extensive genomic studies, combined with post-genomic approaches, such as transcriptomics and proteomics

would expand our knowledge of these fungi. These technologies will facilitate the discovery of novel CAZymes that play key roles in marine biomass degradation. In particular, the identification of novel enzyme candidates from understudied or novel fungal species from the marine biotope are likely to facilitate the design of better enzyme sets for seaweed cell wall depolymerization. It is highly likely that the functionality of marine enzymes has adapted to specific environmental requirements, i.e.: high pH, salinity and ion concentrations, extreme temperatures and high hydrostatic pressures (Gareth Jones et al., 2022), which may be features that are advantageous for their implementation in industrial applications (Bonugli-Santos et al., 2015; Pang et al., 2016; Raghukumar, 2008; Trincone, 2018).

Genomic studies of marine fungi may also provide leads for the production of novel biochemicals, as the seaweed polymers contain monomeric components that are absent or poorly present in terrestrial plants, such as fucose, iduronic acid, mannuronic acid and guluronic acid (Kumar et al., 2021; Jönsson et al., 2020). Currently, no metabolic pathways for these monomers have been described for fungi, but their ability to grow on the seaweed polysaccharides containing them suggests that they can convert these compounds. Identification of the related metabolic enzymes and pathways will expand our metabolic engineering toolkit for fungal cell factories for the production of sustainable biochemicals and platform chemicals.

5. Conclusions and perspectives

In the last few decades, the integration of biotechnology into the biorefinery sector has advanced significantly, particularly in the development of enzymatic approaches for biomass conversion. While terrestrial fungi have long been central to these efforts due to their efficient plant biomass-degrading enzymes (Mäkelä et al., 2014), the enzymatic potential of marine-derived fungi, particularly their carbohydrate-active enzymes (CAZymes), remains vastly underexplored. As the demand for sustainable protein sources intensifies due to global population growth, seaweed have emerged as promising biomass resources (Alcorta et al., 2021; Costa et al., 2021). Their diverse polysaccharide-rich cell walls and potential for protein extraction make them attractive candidates for biotechnological valorization. Seaweed-based food products already resonate with emerging nutritional trends, but the future lies in extracting specific high-value compounds, such as proteins and bioactives, through sustainable bioprocessing approaches. Enzyme-assisted extraction has proven to be the most environmentally friendly and effective method for processing various biomass types (Hardouin et al., 2014; Streimikyte et al., 2022). Enzyme cocktails for terrestrial plant biomass processing are well-established (Lopes et al., 2018), but are poorly suited for seaweed biomass due to their distinct cell wall compositions, especially in the presence of sulfated polysaccharides like fucoidans and ulvans (Hardouin et al., 2014; Lopes et al., 2018). Developing enzyme cocktails tailored to seaweed requires a deeper understanding of how marine organisms, particularly fungi, break down these complex substrates. Marine fungi are uniquely adapted to the ocean's biochemical environment. Their enzymatic potential, shaped by evolution in saline and variable conditions, holds promise for promoting seaweed cell wall deconstruction and enhancing protein recovery. Yet, this potential is largely unexplored.

The biodiversity of fungal communities in marine environments is undeniable, yet their origins and adaptations remain enigmatic (Kumar et al., 2021; Sarma, 2019; Sarma and Jeewon, 2019). Although numerous marine fungal genera have been reported to possess enzymatic activities relevant to seaweed degradation, only a limited subset of these enzymes has been identified, and even fewer have undergone detailed functional or structural characterization. Even among characterized enzymes, such as alginate lyases and agarases, more detailed biochemical and structural studies are needed to fully assess their robustness, substrate specificity, and efficiency under industrial conditions.

Addressing these knowledge gaps is essential to unlock the full potential of marine fungi in seaweed biorefinery applications. To accelerate the application of marine fungal enzymes in biorefinery processes, several aspects should be prioritized. A wider sampling of marine fungal genomics and metagenomics is needed to unravel their enzymatic toolkit for seaweed cell wall depolymerization. This needs to be combined with detailed functional studies of representative enzymes, addressing substrate specificity, product profiles and physical properties. Regulatory studies into the induction of the production of these enzymes in marine fungi suitable for industrial enzyme production and genetic engineering would facilitate the development of marine fungal enzyme factories specifically tailored to seaweed biomass. By addressing these priorities, marine fungi could play a transformative role in next-generation blue biorefineries, supporting sustainable protein production, bioactive compound recovery, and circular bioeconomy goals.

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Raquel Ledo Doval: Conceptualization, Writing – original draft. **Klaas Timmermans:** Funding acquisition, Writing – review & editing. **Ronald P. de Vries:** Conceptualization, Funding acquisition, Supervision, Writing – review & editing.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

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